



HAL
open science

Early-life events and their consequences for adult performance in populations of large herbivores : evolutionary, ecological and demographic perspectives

Mathieu Douhard

► **To cite this version:**

Mathieu Douhard. Early-life events and their consequences for adult performance in populations of large herbivores : evolutionary, ecological and demographic perspectives. Populations and Evolution [q-bio.PE]. Université Claude Bernard - Lyon I; Norwegian University of Life Sciences, 2014. English. NNT : 2014LYO10204 . tel-01127245

HAL Id: tel-01127245

<https://theses.hal.science/tel-01127245>

Submitted on 7 Mar 2015

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Numéro d'ordre 204-2014

Année 2014

THÈSE DE L'UNIVERSITÉ CLAUDE BERNARD LYON 1

Préparée en cotutelle

avec L' UNIVERSITÉ NORVÉGIENNE DES SCIENCES DE LA VIE, NMBU

pour l'obtention

du DIPLÔME DE DOCTORAT
(arrêté du 7 août 2006)

par

Mathieu DOUHARD

Discipline: Biologie

Spécialité: Ecologie évolutive

Early-life events and their consequences for adult
performance in populations of large herbivores:
evolutionary, ecological and demographic
perspectives

Soutenue le 23 Octobre 2014 à Lyon devant le jury composé de :

Dominique ALLAINÉ	Président du jury
Jean-Dominique LEBRETON	Rapporteur
Neil METCALFE	Rapporteur
Jean-Francois LE GALLIARD	Examineur
Francois KLEIN	Examineur
Oystein HOLLAND	Examineur
Leif Egil LOE	Co-directeur de thèse
Christophe BONENFANT	Co-directeur de thèse

UNIVERSITE CLAUDE BERNARD - LYON 1

Président de l'Université

M. François-Noël GILLY

Vice-président du Conseil d'Administration

M. le Professeur Hamda BEN HADID

Vice-président du Conseil des Etudes et de la Vie Universitaire

M. le Professeur Philippe LALLE

Vice-président du Conseil Scientifique

M. le Professeur Germain GILLET

Directeur Général des Services

M. Alain HELLEU

COMPOSANTES SANTE

Faculté de Médecine Lyon Est – Claude Bernard

Directeur : M. le Professeur J. ETIENNE

Faculté de Médecine et de Maïeutique Lyon Sud – Charles
Mérieux

Directeur : Mme la Professeure C. BURILLON

Faculté d'Odontologie

Directeur : M. le Professeur D. BOURGEOIS

Institut des Sciences Pharmaceutiques et Biologiques

Directeur : Mme la Professeure C. VINCIGUERRA

Institut des Sciences et Techniques de la Réadaptation

Directeur : M. le Professeur Y. MATILLON

Département de formation et Centre de Recherche en Biologie
Humaine

Directeur : Mme. la Professeure A-M. SCHOTT

COMPOSANTES ET DEPARTEMENTS DE SCIENCES ET TECHNOLOGIE

Faculté des Sciences et Technologies

Directeur : M. F. DE MARCHI

Département Biologie

Directeur : M. le Professeur F. FLEURY

Département Chimie Biochimie

Directeur : Mme Caroline FELIX

Département GEP

Directeur : M. Hassan HAMMOURI

Département Informatique

Directeur : M. le Professeur S. AKKOUCHE

Département Mathématiques

Directeur : M. Georges TOMANOV

Département Mécanique

Directeur : M. le Professeur H. BEN HADID

Département Physique

Directeur : M. Jean-Claude PLENET

UFR Sciences et Techniques des Activités Physiques et Sportives

Directeur : M. Y. VANPOULLE

Observatoire des Sciences de l'Univers de Lyon

Directeur : M. B. GUIDERDONI

Polytech Lyon

Directeur : M. P. FOURNIER

Ecole Supérieure de Chimie Physique Electronique

Directeur : M. G. PIGNAULT

Institut Universitaire de Technologie de Lyon 1

Directeur : M. C. VITON

Ecole Supérieure du Professorat et de l'Education

Directeur : M. A. MOUGNIOTTE

Institut de Science Financière et d'Assurances

Directeur : M. N. LEBOISNE

Remerciements

Ces trois années de thèse ont été riches aussi bien en terme d'échanges scientifiques que de rencontres humaines et mes remerciements s'adressent à tous ceux et celles qui ont contribué à la réalisation de ce travail. Je tiens tout d'abord à remercier mes encadrants et l'ensemble des membres du jury:

- Christophe pour m'avoir donné une chance d'intégrer l'équipe, pour la liberté et la confiance que tu m'as accordé durant toutes ces années, pour l'ensemble des connaissances que tu m'as transmises et pour ta bonne humeur au quotidien. De superbes souvenirs, aussi bien personnels que professionnels, me resteront en tête à jamais.

- Jean-Michel pour ton formidable soutien, tes encouragements constants et ton incomparable optimisme qui m'ont permis de passer plus facilement au travers des incontournables moments d'inquiétude et de questionnement qui surgissent inévitablement lors de la réalisation d'un tel projet. Merci pour ces discussions intenses et enrichissantes qui se font néanmoins en toute simplicité et dans la bonne humeur.

- Leif Egil for giving me the opportunity to work in his Lab at Aas. Thanks also for all your helpful advices, your kindness and for being the man you are!

- Dominique Allainé, Jean-Dominique Lebreton, Neil Metcalfe, Jean-Francois Le Galliard, Oystein Holand pour avoir accepté de juger et commenter ce travail.

Je voudrais également remercier l'ensemble des personnes qui ont contribué à l'élaboration de ce travail. Je pense particulièrement au personnel de l'Office National de la Chasse et de la Faune Sauvage et du Centre d'Etudes Biologiques de Chizé, sans qui ce travail n'aurait pu être possible. Merci également, aux membres de mon comité de thèse et de l'équipe (en particulier Jeff, Marlène et Floriane), à Marco Festa-Bianchet, Fanie Pelletier, Nicolas Morellet, Mark Hewison ainsi que l'ensemble des personnes du groupe chevreuil français pour leur critiques, discussions et conseils pertinents et enrichissants.

Enfin, je voudrais remercier l'ensemble des personnes qui m'ont apporté durant ces années amitié et soutien, mes amis du LBBE et autres, ma famille et enfin Fanny pour sa patience, son soutien quotidien et son amour.

Summary

The environment to which individuals are permanently exposed varies greatly over time. The environmental conditions during early life are particularly important in this context because they can have extraordinary long-term consequences on individual performance. The main goal of this PhD thesis was to improve our understanding of the long-term effects of early-life events, including environmental conditions and growth, on life-history traits of large herbivores. In order to meet this objective, we used detailed long-term data from five populations of four species of ungulates. We highlighted that environmental conditions experienced during early life can influence the entire body growth trajectory of an individual. Then, we investigated whether the long-term effects of early environmental conditions on life-history traits represent adaptive responses to differing environments, or are only a consequence of energetic constraints on development. We aimed to address this issue by testing hypotheses issued from human medicine in wild populations. We have shown that harsh early-life conditions impose strong developmental constraints, and individuals born in good conditions generally outperformed those born in poor conditions. Moreover and importantly, the strong viability selection imposed by poor environmental conditions can lead to apparent support for an adaptive hypothesis which seeks to explain the evolution of metabolic disease in human. We have shown, nevertheless, that individuals can mitigate the negative long-term effects of poor early-life conditions by investing more to reproduction in their early adulthood. This response to early environment represents a tactic that makes the best of a bad situation. On the other hand, artificial selection can lead to a paradoxical situation where individuals born under poor conditions can gain a fitness advantage because of their slower growth rates. We have shown that the two undesirable evolutionary consequences of trophy hunting, selection for smaller-horned males and reduced harvests, increased with harvest intensity but can be avoided when offtake was moderate. The selective effects of trophy hunting may be reduced if hunting mimicked natural mortality. We highlighted that the occurrence of the trade-off between horn growth and survivorship did not increase with the intensity of sexual selection and was not restricted to males. In sum, the early-life events characterized by the environmental conditions as well as the growth, play an important role in our understanding of the life-history evolution.

Résumé

La variabilité environnementale à laquelle les individus sont constamment exposés est forte. Dans ce contexte, les conditions environnementales en début de vie sont particulièrement importantes puisqu'elles peuvent avoir des conséquences à long-terme sur la performance des individus. L'objectif de cette thèse est d'améliorer notre compréhension des effets à long-terme des événements vécus tôt dans la vie, incluant aussi bien les conditions environnementales que la croissance, sur les traits d'histoire de vie des grands mammifères herbivores. Afin de répondre à cet objectif, nous avons utilisé les suivis à long-terme de cinq populations appartenant à quatre espèces d'ongulés. Dans une première partie, nous avons montré que les conditions environnementales en début de vie peuvent influencer la trajectoire entière de croissance corporelle d'un individu. Ensuite, nous avons cherché à savoir si les effets des conditions environnementales en début de vie sur les traits d'histoire de vie à l'âge adulte représentaient des réponses adaptatives à différents environnements ou résultaient seulement de contraintes développementales dues à une restriction alimentaire. Nous avons répondu à cette question en testant notamment des hypothèses issues du domaine médical en populations sauvages. Les mauvaises conditions environnementales en début de vie imposent de fortes contraintes développementales, et de fait, les individus qui étaient nés dans des conditions favorables avaient en général une valeur sélective plus élevée que les individus nés dans des conditions difficiles. De plus, une forte sélection de viabilité tôt dans la vie induite par des conditions environnementales difficiles, pouvait conduire à un support apparent pour une hypothèse adaptative qui est souvent avancée pour expliquer l'évolution des maladies métaboliques chez l'homme. Nous avons néanmoins montré, que les individus pouvaient mitiger les effets négatifs des mauvaises conditions environnementales en début de vie en investissant plus dans la reproduction au début de l'âge adulte. Cette réponse à l'environnement précoce représente une tactique de reproduction qui fait, dirons nous, le meilleur du pire. D'un autre côté, la sélection artificielle peut conduire à une situation paradoxale où les individus nés dans des mauvaises conditions soient avantagés à long-terme du fait d'une croissance réduite. Nous avons pu montrer que les conséquences évolutives et indésirables de la chasse aux trophées, c'est-à-dire une sélection pour des animaux avec une croissance des cornes réduite et une diminution du nombre de trophées au cours du temps, augmentaient avec l'intensité de la chasse mais étaient réduites si la pression chasse était relativement faible. Les effets sélectifs de la chasse aux trophées pourraient être réduits si la chasse mimait la mortalité naturelle. Nous avons démontré que l'occurrence d'un compromis entre la lon-

gueur des cornes et la longévité n'augmentait pas avec l'intensité de la sélection sexuelle et n'était pas restreinte aux mâles. En somme, les événements durant la vie précoce, que ce soit les conditions environnementales ou la croissance, ont un rôle prépondérant dans la compréhension de l'évolution des traits d'histoire de vie.

UMR CNRS 5558 - Laboratoire de Biométrie et de Biologie Evolutive
UCB Lyon 1 - Bât. Grégor Mendel
43 bd du 11 novembre 1918
69622 VILLEURBANNE

Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences
NO-1432 As Norway

Contents

List of Figures	8
List of Tables	12
Preface	14
1 General introduction	17
1.1 The key role of environment in the evolution of life history	17
1.1.1 From to interspecific level...	19
1.1.2 ... to the intraspecific level	21
1.2 Age-specific sensitivity to environmental conditions	23
1.3 Early-life environment and body growth	29
1.3.1 Identification of possible pathways	29
1.4 Identifying causal mechanisms	31
1.5 Understanding the nature of the phenotypic changes induced by early-life conditions	34
1.5.1 An adaptationist view in medicine	37
1.5.2 Developmental constraints	39
1.5.3 Make the best of a bad job	41
1.6 When be born in a poor environment becomes advantageous at long-term: the case of selective hunting	45
1.7 Structure of the thesis	46
1.8 A brief overview of the studied species	48

I	Consequences of environmental conditions in early life on body growth trajectories	52
2	Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females	53
2.1	Introduction	55
2.2	Material and methods	58
2.3	Results	63
2.4	Discussion	66
2.5	Supplemental material	72
II	Understanding the nature of the long-term effects of early-life conditions on life history	80
3	Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate	81
3.1	Introduction	83
3.2	Material and methods	86
3.3	Results and Discussion	90
3.4	General Discussion	95
3.5	Supplemental material	99
4	Reproductive tactics are determined during year of birth in a wild mammal	107
4.1	Main article	109
4.2	Supplementary Materials	116
4.2.1	Materials and Methods	116
4.2.2	Supplemental Figures	121
4.2.3	Supplemental Tables	125
III	Evolutionary consequences of growing large secondary sexual characters	126
5	Males and female Pyrenean Chamois pay similar longevity costs when growing long horns	127
5.1	Introduction	129

5.2	Material and methods	131
5.3	Results	135
5.4	Discussion	138
6	Horn development in Stone's sheep under different selective harvesting pressures	142
6.1	Introduction	144
6.2	Material and methods	148
6.3	Results	152
6.4	Discussion	159
6.5	Supplemental material	165
IV	General discussion	171
7	Synthesis and perspectives	172
7.1	Early-life events and their consequences for life-history evolution	173
7.1.1	Predictive adaptive responses or not?	173
7.1.2	Growth trajectories	177
7.1.3	The variance in life-history traits under consideration . . .	180
7.1.4	Exploring the transmission of early life environmental effects across generations	181
7.2	Some applications for wildlife management	182
7.2.1	The concept of indicators of ecological change	183
7.2.2	Environmental variation in demographic models	184
7.2.3	Consequences for conservation	185
7.3	Conclusion	186
	Bibliography	188
	Appendix	214

List of Figures

1.1	An example of genotypic reaction norms illustrating the concept of phenotypic plasticity.	24
1.2	Conditions in early life, characterised by population density in an individual's year of birth, affect female reproductive senescence rate in red deer.	27
1.3	Three examples of the causal mechanisms of how correlations between early conditions, growth and subsequent survival and reproduction can arise.	30
1.4	Effects of food restriction on body growth of rats.	32
1.5	Effects of maternal nutrition on bovine fetal skeletal muscle development.	34
1.6	Catch-up and compensatory growth.	44
1.7	Location of the different study sites for the four species of large herbivores studied here.	49
2.1	Theoretical representation of two possible scenarios to explain long-lasting effects of early environmental conditions (shaded area) on adult body mass.	57
2.2	Path diagram showing how early environmental conditions influence directly and indirectly adult body mass (on a log-scale) of A) female and B) male roe deer at Chizé, France.	64
2.3	Path diagram showing how early environmental conditions influence directly and indirectly adult body mass (on a log-scale) of A) female and B) male roe deer at Trois-Fontaines, France.	65

2.4	Plot showing the direct and indirect effects of environment in early life (interacting effects of population size and temperatures in May at Chizé and effects of April temperatures at Trois-Fontaines) on adult body mass for both sexes at Chizé and Trois-Fontaines, France.	67
2.5	Temporal autocorrelation functions (ACFs) for environmental variables at Chizé.	73
2.6	Temporal autocorrelation functions (ACFs) for environmental variables at Trois-Fontaines.	74
2.7	Conditions in early life influence adult body mass (standardized to females) at Chizé.	76
2.8	Effects of temperatures in (A) April and (B) May in the year of birth on adult body mass in males (open square, dotted line) and females (filled circles, solid line) roe deer at Trois-Fontaines, France.	78
2.9	Plot showing the direct and indirect effects of environment in early life (interacting effects of population size and temperature in May at birth) on adult body mass of (A) 173 females and (B) 146 males at Chizé, France.	79
3.1	Variation in mean fitness as a function of environmental conditions during early life and adulthood under two different scenarios.	85
3.2	Influence of early life and current environmental conditions on annual fitness components and mean annual fitness of adult female roe deer in both sites.	92
3.3	Viability selection during juvenile stage and its consequences on adult survival in the population of Chizé, France.	95
3.4	Relationship between the proportion of adult female roe deer with a body mass > 22 kg and the quality of early life environmental conditions at Chizé, France.	96
3.5	Year-specific body mass (kg \pm 1 SE) of roe deer fawns measured during January-February at A) Trois-Fontaines, B) Chizé, France.	102
3.6	Population projection matrix used for roe deer.	103
3.7	The relationship between average environmental conditions during the adult stage (between 2 and 7 years of age) and early environmental conditions at (a) Trois-Fontaines (TF), (b) Chizé (CH), France.	104

3.8	Annual reproductive success (probability to wean 0, 1 or 2 fawns) of adult female roe deer as a function of early life and current environmental conditions at Trois-Fontaines and Chizé, France. . .	105
3.9	Relationship between survival of yearling female roe deer (between 8-9 and 20-21 months of age) and their body mass at 8-9 months of age (adjusted for date of capture) in relation to the quality of early life environmental conditions at Trois-Fontaines, France. . .	106
4.1	Measures of environmental quality from 1995-2010 in the population of Svalbard reindeer.	111
4.2	Influence of early environmental conditions on skeleton size of female Svalbard reindeer aged three years or older.	111
4.3	Age-specific patterns of reproduction (A and B), survival (C) and fitness (D) in female Svalbard reindeer according the environmental conditions experienced during their birth year.	113
4.4	Environmental conditions in early life influence reproductive effort of female Svalbard reindeer.	114
4.5	Offspring survival and pregnancy rate as a function of mother body mass and the quality of early environment in Svalbard reindeer	122
4.6	Annual estimates of adult body mass as a function of A) rain-on-snow and B) population size in a given year	123
4.7	Variation in A) body mass and B) skeletal size of female Svalbard reindeer as a function of age	124
5.1	Age-specific horn length in male and female Pyrenean chamois. . .	135
5.2	Correlation between horn increment during the first 2 years of age and horn increment in the third, fourth, and fifth year of age of a) male and b) female Pyrenean chamois on a log-scale.	137
5.3	Relationship between late horn growth and longevity in a) male and b) female Pyrenean chamois from a hunting-free population in France.	139
6.1	Study area and distribution of Stone's sheep in British Columbia. .	148
6.2	Yearly variations in number of hunters, divided by the area of Stone's sheep range in two regions of British Columbia.	153
6.3	Relationship between early horn growth during the second and third year of life and age at harvest for Stone's rams.	154

6.4	Relationship between harvest age and A) total horn length, B) horn base circumference of Stone's rams harvested.	154
6.5	Early horn growth of Stone's rams as a function of year of birth in the 'low' and 'high' hunting areas of British Columbia.	157
6.6	Age-specific total horn length of Stone's rams harvested in the 'low' and 'high' hunting areas of British Columbia as a function of year of birth.	158
6.7	Relationship between harvest age and horn length excluding the first annual increment for Stone's rams harvested in two regions of British Columbia.	166
6.8	Age distribution of Stone's rams harvested by resident and non-resident hunters in the A) 'low' and B) 'high' hunting areas of British Columbia.	167
6.9	Allometric relationships between horn length and horn base of males aged 8-13 years during two periods of study in the 'high' hunting area of British Columbia.	170

List of Tables

1.1	Hypotheses and predictions relating early-life environmental conditions and adult performance.	36
1.2	Characteristic for four species of ungulates in five study areas. For Stone’s sheep, data in brackets indicated those for bighorn sheep at Ram Moutain.	51
2.1	Parameter estimates for adult body mass at Chizé obtained from the linear model including the effects of sex, population size (POP) and temperatures in May (T_{May}) during the year of birth and average POP experienced between ages 1 and 4 ($POP_{ages1-4}$)	75
2.2	Parameter estimates for adult body mass at Trois-Fontaines obtained from the linear model including the effects of sex, and temperatures in April (T_{Apr}) and May (T_{May}) during the year of birth.	77
3.1	A detailed description of the study areas at Chizé and Trois-Fontaines, France.	100
3.2	Effects of early life (E_{early}) and current ($E_{current}$) environmental conditions on annual reproductive success and survival of adult female roe deer at Trois-Fontaines and Chizé, France.	101
4.1	Generalized linear mixed models (using a logit link and a binomial error distribution) of offspring survival and pregnancy rates for two age groups in Svalbard reindeer.	125
6.1	Hypotheses and predictions relating selective harvest and changes in horn development of Stone’s sheep in British Columbia.	147

6.2	Effects of time T (i.e. seniority of the cohort) after accounting for effects of climate on cumulative horn growth during the second and third year of life of harvested Stone's sheep males from two regions of British Columbia, Canada.	156
6.3	Effects of time T (seniority of the cohort) after accounting for possible effects of climate on total horn length of Stone's rams harvested in the 'low' hunting area (Skeena) of British Columbia.	168
6.4	Effects of time T (seniority of the cohort) after accounting for possible effects of climate on total horn length of Stone's rams harvested in the 'high' hunting area (Peace) of British Columbia. .	169

Preface

Nowadays, the content and structure of a science thesis are often based on scientific papers. This reflects the current job market where applicants for postdoctoral or permanent positions are mainly evaluated from their publications. This thesis is also based on the presentation of a series of scientific articles (two published, one submitted, and two in preparation). Our general aim is to understand how environmental conditions experienced during early-life can influence adult phenotype and favour different life histories. In order to facilitate the progress of this work and makes it more accessible to every potential reader, I have written general introduction and conclusions sections. A biological context broader than in the introductions of articles is presented in the general introduction. In the general conclusion, the results of the different articles are synthesised and discussed with respect of some publications in appendix.

The papers included in the main manuscript are:

1. **Douhard M**, Gaillard J-M, Delorme D, Capron G, Duncan P, Klein F, Bonenfant C (2013) Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females, *Ecology*, vol. 94 pp.1805-1814.
2. **Douhard M**, Plard F, Gaillard J-M, Capron G, Delorme D, Klein F, Duncan P,

Loe L.E, Bonenfant C (2014) Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate, *Proceedings of the royal society B-Biological sciences*, vol. 281 pp.20140276.

3. **Douhard M**, Loe L.E, Bonenfant C, Stien A, Irvine J, Vebjørn V, Ropstad E, Reproductive tactics are determined during year of birth in a wild mammal. In preparation.

4. **Douhard M**, Gaillard J-M, Lemaître J-F, Loe L.E, Loison A, Crampe J-P, Bonenfant C, Males and female Pyrenean Chamois pay similar longevity costs when growing long horns. In preparation.

3. **Douhard M**, Festa-Bianchet M, Pelletier F, Gaillard, J-M, Bonenfant, C Horn development in Stone's sheep under different selective harvesting pressures. Submitted.

The papers included in appendix are:

Appendix 1. Garratt M, Lemaître J-F, **Douhard M**, Bonenfant C, Capron G, Warnant C, Klein F, Brooks R. C, Gaillard, J-M High juvenile mortality generates sex-specific ageing in wild cohorts of roe deer. In revision.

Appendix 2. Lemaître, J-F, Berger V, Bonenfant C, **Douhard M**, Gamelon, M, Plard F, Gaillard J-M. Disposable soma in wild populations of vertebrates: a theory that does not age. In revision.

Appendix 3. Gaillard J-M, Hewison A J, Klein F, Plard F, **Douhard M**, Davison R, Bonenfant C (2013) How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer, *Ecology letters*, vol. 16 pp.48-57.

Appendix 4. Gamelon M, **Douhard M**, Baubet E, Gimenez O, Brandt S, Gaillard J-M (2013) Fluctuating food resources influence developmental plasticity in wild boar, *Biology Letters*, vol. 9 pp.20130419.

Appendix 5. **Douhard M**, Bonenfant C, Gaillard J-M, Hamann J-L, Garel M, Michallet J, Klein F (2013) Roaring counts are not suitable for the monitoring of red deer *Cervus elaphus* population abundance, *Wildlife Biology*, vol. 19 pp.94-101.

Appendix 6. Hamann J-L, **Douhard M**, Bonenfant C, Mortz P, Michallet J, Garel M, Klein F (2013) De l'utilité des comptages au brame pour la gestion des populations de cerfs, *Faune Sauvage*, vol. 299 pp. 4-8.

Appendix 7. Plard F, Gaillard J-M, Coulson T, Hewison A. J. M, **Douhard M**, Klein F, Delorme D, Warnant C, Bonenfant C The influence of birth date via body mass on individual fitness in a long-lived mammal. In revision.

Chapter 1

General introduction

1.1 The key role of environment in the evolution of life history

Dobzhanski (1973) was surely right to insist that ‘nothing in biology makes sense except in the light of evolution’. Nevertheless, it is equally true that nothing in evolution makes sense except in the light of ecology (the scientific study of interactions among organisms and their environment). Evolution by natural selection requires, (i) between-individual variation in a given trait, (ii) a selective pressure i.e., a relationship between a trait and individual fitness, defined as the success of an individual in passing on copies of its genes to future generations (Fisher 1930), (iii) a heritable basis. The ecology influences thus the evolutionary process by creating selection pressures that cause evolutionary changes. In return, evolution is important to ecology because changes in the traits reveal the ways in which populations respond to changes in environment (Pelletier et al. 2009). It is the field of evolutionary ecology that lies at the intersection of ecology and evolution.

Life-history theory is of central importance in evolutionary ecology since it is the life history that forms the interface between an individual and its fitness (Stearns 1992, Roff 1992). The principal life-history traits include: size at birth, growth patterns, age at maturity, number, size and sex-ratio of offspring, reproductive life span, longevity (Stearns 1992). The life-history theory has a very long history. Darwin (1859) laid the foundations but the first works in life-history evolution appeared in the middle part of the 20th Century, including Fisher (1930), Cole (1954), Cody (1966), Williams (1966), MacArthur and Wilson (1967) and

Pianka (1970). The life-history theory has been popularised in the 1990s with the publication of two major textbooks, summarising the theoretical and empirical state of knowledge of life-history evolution (Stearns 1992, Roff 1992).

Natural selection should tend toward the production of a ‘Darwinian demon’, an organism that reproduces directly after being born, produces infinitely many offspring, and lives indefinitely (Law 1979). However, no such demon exists because the evolution of organisms is bound to certain restrictions. For example, the basic hypothesis underlying most analyses of the evolution of life-history traits is that variation is constrained by trade-offs between traits (Roff 1992). The concept of trade-off is rooted in the principle of energy allocation (Cody 1966, Williams 1966) stating that, for a given amount of energy available, the energy allocated to one fitness component will lead to a decrease in the energy that can be allocated to another fitness components. Classical examples of trade-offs are current survival vs current reproduction, number vs size of offspring, or current reproduction vs future reproduction (Stearns 1992). Thus, the multiple life-history traits do not evolve independently. A life-history strategy refers to the coordinated evolution of the life-history traits together.

Even if natural selection operates at the individual level, variation of life-history strategies can be analysed at different scales. This diversity is often illustrated by comparing different species or taxons. For example, small organisms that multiply quickly such as bacteria contrast with primates that are characterised by relatively late ages at first reproduction, long lives and low fertility (Jones 2011). Life-history strategies vary also across individuals within and between populations (e.g. Reznick et al. 1990; 2002, Descamps et al. 2006). As explained in greater detail below, environmental conditions play a key role in the variation of life histories whatever the level considered. An important point is that environmental conditions, both abiotic such as climate and biotic such as competition, can be characterised by their own values (e.g. a good year vs. a poor year) as well as their variation over time (e.g. between-year variation).

1.1.1 FROM TO INTERSPECIFIC LEVEL...

The theory of the r- and K-selection was one of the first predictive models to explain life-history evolution (Reznick et al. 2002). The original presentation of the theory was proposed by MacArthur and Wilson (1967). They suggested that when an island is first colonised, the density of individuals is low, the resources are abundant and the population size increases with reduced levels of competition. Under such circumstances, selection would favour individuals with a high capacity for increase in population size (the r-selection). When the island becomes fully occupied and resources are limited, individuals would experience density-dependant mortality and would be exposed to intense intraspecific competition (the K-selection). Some years later, Pianka (1970) extended MacArthur and Wilson's theory by making predictions for how life-history traits would evolve in r- and K-environments. In a K-environment, traits that enhance efficiency of individuals, including slow development, delayed reproduction, large body size, iteroparity (i.e., more than one reproductive event per lifetime), high competitive ability, long longevity should be selected. On the other hand, r-environments select for traits that enhance rapid development, early reproduction, small body size, semelparity (i.e., a single reproductive event before death) and a short longevity. The selective pressures vary with environment changes, resulting in a change in life-history strategies along the r-K continuum.

The r-K paradigm has suffered from a large amount of criticism (see Boyce 1984, Stearns 1992, Roff 1992). However, empirical studies have repeatedly reported that life-history strategies vary along a fast-slow gradient analogous to r-K continuum (Gaillard et al. 1989, Rochet et al. 2000, Bielby et al. 2007). For instance, Gaillard et al. (1989) identified two axes when analysing covariation among annual fecundity, age at first reproduction, and adult life expectancy in 80 mammal species and after correction for allometric constraints that accounted for 40% of the variation in life-history strategies. The first axis was interpreted as a fast-slow continuum contrasting, for a given body mass, species with a high

fecundity, a short life expectancy and an early age at first reproduction to long-lived species that reproduced late and had a low fecundity. The position of the species along this fast-slow continuum was intimately correlated to its generation time i.e., the weighted mean age of the mothers at childbirth (Gaillard et al. 2005). For a given body mass and time-scale, the second axis opposed mammals species that were closer to semelparity and those that were closer iteroparity (Gaillard et al. 1989).

The r-K paradigm was challenged because other factors such as age-specific mortality, environmental variability, predation also play an important role in life-history evolution (Reznick et al. 2002). For example, environmental variability and age-specific mortality have had a central role for understanding the evolution of iteroparity/semelparity. In a seminal paper, Cole (1954) came to the following conclusion ‘for an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size’. As the population growth rate measures average individual fitness (see also Fisher 1930), semelparity seemed be advantageous over iteroparity. This expectation, however, was contradicted by the widespread evolution of iteroparity in nature. This problem was known as ‘Cole’s paradox’. The subsequent theoretical developments showed, however, that under temporal variation of the environment, iteroparity can be favoured by natural selection, especially if juvenile survival is more variable than adult survival (Murphy 1968, Shaffer 1974). If adult survival survival is more variable than juvenile survival, then semelparity can be selected.

The direction of future evolutionary changes is contingent upon these past changes (Gould and Lewontin 1979). Natural selection operates indeed under the pressure of current ecological conditions within the boundaries fixed by a species’ evolutionary history. The concept of life-history strategy encapsulates all these interactions between past and present.

1.1.2 ... TO THE INTRASPECIFIC LEVEL

Life-history strategies vary widely within or between populations. Individual differences in life-history strategies are often attributed to the existence of (i) age-specific mortality resulting from environmental conditions, (ii) trade-offs between life-history traits (Williams 1966, Reznick et al. 2002). The following examples on guppy (Reznick et al. 1990) and red squirrel (Descamps et al. 2006) illustrate these two scenarios.

Life-history differences among populations of guppies (*Poecilia reticulata*) were closely associated with the presence of predators that are size-specific in their choice of prey. Populations with a high predation on adults matured at an earlier age, had higher reproductive effort and had more and smaller offspring compared to populations where predation was mainly on juveniles. Such differences in life-history strategies were heritable. Changing predation against adults to predation against juveniles led to life-history evolution in the predicted direction after 11 years, or 30-60 generations, proving that predation caused this pattern and that life-history traits respond quickly to strong selective pressures. In red squirrel (*Tamiasciurus hudsonicus*), the early breeder females gave birth to at least one juvenile for the first time at 1 year. Early breeders had a higher breeding success and achieved a higher lifetime reproductive success than females that delayed their first reproduction (the late breeders). However, early breeders had a lower survival between one and two years of age than late breeders and a lower lifespan. Thus, two strategies co-occurred in this population: one based on early maturity at the cost of a lower survival vs a strategy based on delayed maturity and long lifespan. In this population, the low quality individuals (i.e., the late breeders) did the best of a bad job by delaying their first reproduction.

Despite the importance of trade-offs to life-history theory, they are difficult to detect (Stearns 1992, Roff and Fairbairn 2007). The lack of evidence for trade-offs is often explained by two hypotheses. Firstly, the occurrence of individual heterogeneity in resource acquisition and allocation can make trade-offs (e.g., survival

vs. reproduction) difficult to identify (van Noordwijk and de Jong 1986). If the variation among individuals in energy acquired is large but the variation in fraction allocated to reproduction is small, then the relationship between survival and reproduction is expected to be positive. On the other hand, if individuals vary narrowly in their acquisition of resources but the variation in allocation to reproduction is high, then the relationship will tend to be negative (van Noordwijk and de Jong 1986). Secondly, trade-offs may be expressed only in poor environmental conditions, when resources are scarce (Reznick et al. 2000). In environments with a large amount of resources, individuals acquiring a lot of energy can show both a high performance in growth, reproduction and survival. In poor environments, however, the resources allocated to one function cannot be allocated to other functions. In bighorn sheep (*Ovis canadensis*), for example, trade-off between current and future reproduction occurred mainly in females with low body mass and at high population density (Festa-Bianchet et al. 1998). However, even after controlling for heterogeneity in individual quality and density of population, no survival cost of reproduction was detected in this species (Festa-Bianchet et al. 1998). Related to this, Hamel et al. (2010) proposed an evolutionary model demonstrating that the chance of detecting a cost of reproduction should be lower when the fitness component studied has a low rather than high variance. Variance in survival is smaller and variance in reproduction higher in long-lived vs short-lived species. In support of this model, more studies reported evidence of reproductive costs of reproduction in large herbivores than in rodents, whereas survival costs of reproduction were more frequent in rodents than in large herbivores (Hamel et al. 2010).

Two contrasting, but non-exclusive, evolutionary mechanisms that can explain population responses to environmental conditions are (i) microevolution, (ii) adaptive phenotypic plasticity. Microevolution represents a change in genotypes across generations in response to selection on a trait (i.e., a selection for a fixed optimum). Phenotypic plasticity can be defined as the ability of genotypes to

produce different phenotypes when exposed to different environmental conditions (Pigliucci et al. 2006, Whitman and Agrawal 2009). This definition of plasticity is classically illustrated graphically with a reaction norm describing the change in a genotype's phenotype across an environmental gradient (Fig. 1.1). Until recently, work on plasticity has strongly focused on demonstrating the adaptive nature of reaction norms (Hughes et al. 2003). Many cases of phenotypic plasticity are clearly adaptive such as some immune responses, anti-predator defences, diapause (Whitman and Agrawal 2009). Phenotypic plasticity is notably recognised as being responsible for the majority of adaptive phenotypic changes in response to climate change (Gienapp et al. 2008, Vedder et al. 2013). For example, female great tits (*Parus major*) were able to adjust their laying date to early spring temperature, which predicts the timing of the peak in food availability influencing reproductive success (Charmantier et al. 2008). However, it is important to note that phenotypic plasticity is not necessarily adaptive (Stearns 1989, Pigliucci et al. 2006, Hughes et al. 2003, Nussey et al. 2007b). Some traits are plastic because of unavoidable constraints imposed by the physiology or developmental biology of the organism (Pigliucci et al. 2006). Understanding the nature of plastic responses in wild populations remains an important challenge.

1.2 Age-specific sensitivity to environmental conditions

Within a population of vertebrate, environmental conditions can interact with others structuring factors. For example, in sexually dimorphic large herbivores, the higher energy requirement of males makes they are more vulnerable to environmental harshness (Clutton-Brock et al. 1982). Studies in long-lived iteroparous vertebrates have also revealed that environmental conditions can differently affect individuals according to their age (Coulson et al. 2001, Gaillard and Yoccoz 2003, Pardo et al. 2013). Precisely, survival of juveniles is generally more sensitive to environmental conditions than that of prime-aged individuals. This pattern

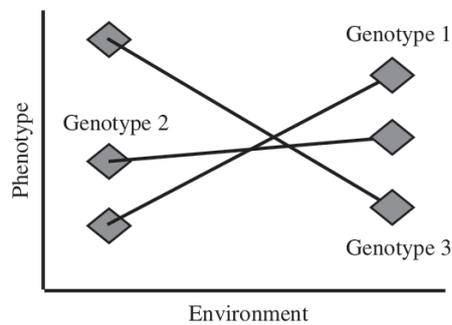


Fig. 1.1. An example of reaction norms illustrating the concept of phenotypic plasticity. In the simple case of two environments, the lines represent the norms of reaction of each genotype, while the slope is a measure of the degree and pattern (positive or negative) of phenotypic plasticity. So, for example, genotypes 1 and 3 are both plastic, but display opposite patterns in response to the same environments; genotype 2, on the other hand, shows little plasticity for this trait in this environmental set. Reproduced from Pigliucci et al. (2006).

has been interpreted as a case of environmental canalisation (Gaillard and Yoccoz 2003) and can be understood in the context of bet-hedging theory (see Seger and Brockmann 1987, for a review).

Bet-hedging theory shows that geometric mean fitness is a better metric than arithmetic mean fitness in a variable environment (Seger and Brockmann 1987). Usually, temporal variability decreases fitness because it reduces the geometric mean of a fitness component even if its arithmetic mean remains unchanged. Consequently, the traits having the highest influence on fitness are expected to be most strongly canalised (i.e., preserved) against environmental variations (Gaillard and Yoccoz 2003). In long-lived species, the elasticity of adult survival on population growth rate is much higher than that of other demographic parameters (Gaillard et al. 1998b), meaning that a small change in adult survival would have a strong effect on population growth rate (i.e., average fitness of individuals, Fisher 1930). In accordance with the process of environmental canalisation, variance in adult survival has been reduced through evolutionary time for these species (Gaillard and Yoccoz 2003 in mammals, Saether and Bakke 2000 in birds). When resource

availability is low, a female allocating a high amount of energy to reproduction should decrease the amount of energy available for maintenance and thereby jeopardise her survival (Cody 1966, Williams 1966). Under such conditions, female in long-lived species usually favour their own survival over that of their offspring. This risk avoidance in adult females lead to reduced allocation in offspring during periods of food shortage, and thereby to high variation of juvenile survival over time (Gaillard and Yoccoz 2003). Hence, the process of environmental canalisation allows to better understand why individuals in long-lived species generally adopt a conservative reproductive tactic to ensure their survival, to the possible detriment of reproductive success. Nevertheless, it is important to recall that many life-history strategies can co-exist within a population. Life-history strategy can depend not only of the environmental conditions but also of internal state (MacNamara and Houston 1996) that varies between individuals, such as differences of body size and morphology, energetic reserves, parasite load, immune functioning, quality of cell-repair mechanisms.

In this context, early-life environmental conditions play a central role in the growth and survival of offspring (e.g., Clutton-Brock et al. 1992, Gaillard et al. 1997, McAdam and Boutin 2003, Loison and Langvatn 1998, Reid et al. 2003, Grande et al. 2008, Le Galliard et al. 2010). For example, in Soay sheep (*Ovis aries*), high population density in winter was associated with reductions in birth weights, which, in turn, were closely correlated with changes in neonatal mortality (Clutton-Brock et al. 1992). Moreover, for newborns surviving early critical period of life, it is now clear that the quality of early environment can have long-term effects on life-history traits (Lindström 1999, Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002, Monaghan 2008). For example, in red deer (*Cervus elaphus*), density experienced during early life can produce delayed effects by influencing senescence rates in reproduction or survival with the steepest ageing of these traits for individuals born in the harshest conditions (see Fig. 1.2). Consequently, at the population level, early-life environmental conditions can

generate both numerical cohort effects and delayed quality cohort effects (see Box 1.1 for definitions). The term ‘early-life’ can be defined as the period from conception to the end of juvenile growth and the start of sexual maturation (Burton and Metcalfe 2014). It is, however, commonly found that the earlier an individual’s development is affected, the stronger the effects (Lindström 1999). Indeed, in most cases, the critical period corresponds to food availability around the time of birth (Lummaa and Clutton-Brock 2002). The long-term effects of early environment are intriguing, but in free-living animals little is known about the mechanisms producing these impacts and their role in evolution of life-history and population dynamics remain largely unexplored (Monaghan 2008, Clutton-Brock and Sheldon 2010). This thesis aims to provide a better understanding of the long-term effects of early events related to environmental conditions, in particular, on life-history traits in large mammalian herbivores.

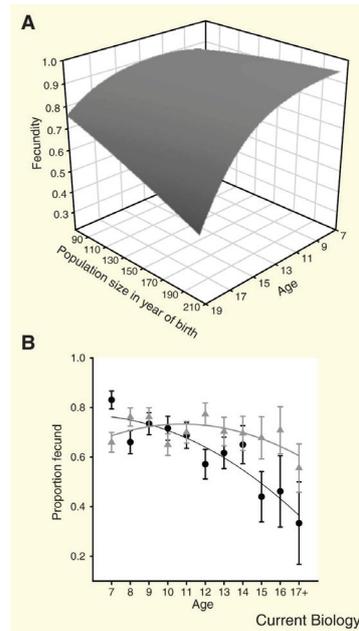


Fig. 1.2. Conditions in early life, characterised by population density in an individual's year of birth, affect female reproductive senescence rate in red deer. A female's probability of producing a calf in a given year declined more rapidly in old age amongst females that experienced harsh early environments. (A) Predicted ageing rates in annual fecundity from the significant age-by-density in birth year interaction. (B) The proportion of fecund females at each age class among females that experienced less than (gray triangles and line), or equal or greater than (black circles and line) the median density in birth year. Reproduced from Nussey et al. (2007a).

Box 1.1. Definition of the terms cohort and cohort effects according to the meaning used in this work

Cohort: All the individuals in a population that were born within a defined time interval and belong to a single age class (Stearns 1992). Births are highly synchronised in many mammal populations in temperate areas, producing one new cohort each spring.

Numerical cohort effects: Between cohorts-differences in recruitment rate (Gaillard et al. 2003c). Recruitment is defined as the establishment of new individuals in the breeding segment of populations. Recruitment is a gradual process. For example, in the Greater Snow Goose (*Chen caerulescens atlantica*), the probability of starting to breed at 2 years is 0.25, at 3 years 0.57 and is completed by 4 years (Reed et al. 2003). In large herbivores, primiparity is generally reached at 2 or 3 years, but in some small- or medium-sized species, females can breed during their first year (Gaillard et al. 2000b).

Delayed cohort quality effects: Between cohorts-differences in phenotypic and/or genetic quality at adulthood (Gaillard et al. 2003c). Quality is defined as the positive co-variation among traits that are related to fitness (Wilson and Nussey 2010). Body mass is considered as a reliable indicator of individual quality in large herbivores (e.g., Hamel et al. 2009b). Early-life environmental conditions can lead to cohort quality effects but such effects can also arise from environmental conditions experienced after sexual maturation.

1.3 Early-life environment and body growth

1.3.1 IDENTIFICATION OF POSSIBLE PATHWAYS

How does the environment in early life influence the adult life-history traits such as body mass, body size, survival, reproduction? Resources availability during early life has been identified as a key factor (Madsen and Shine 2000, Descamps et al. 2008, Rickard et al. 2010). In general, nutrition levels in wild populations are inferred from proxies of food resources such as population density or climate (e.g. Gaillard et al. 1997, Forchhammer et al. 2001, Reid et al. 2003, Nussey et al. 2007a). In temperate ecosystems, the spring and summer seasons, matching with the end of gestation and early lactation for mammals, are regarded as critical periods for income breeders (e.g., Andersen et al. 2000) that rely almost exclusively on available food resources to meet the energetic costs of reproduction (Jönsson 1997). In capital breeders for which body reserves can substantially affect reproductive success (Jönsson 1997), climate and density in the winter preceding birth (when offspring is in utero) play also an important role in the fate of individuals (Clutton-Brock et al. 1992, Forchhammer et al. 2001, Stien et al. 2012). Effects of the environment in early life can act directly on the developing individual. However, in mammals given the mothers' role in provisioning for offspring from conception to weaning, the early environment influences phenotype mostly indirectly through maternal effects.

Although the role of food resources is well recognised, the pathways by which early nutrition influences adult phenotype are poorly known (Lummaa and Clutton-Brock 2002). Even if correlations occur between environmental conditions in early life and fitness components during the adult stage, the causal relationships are largely unknown. Related to this, Lummaa and Clutton-Brock (2002) identified three possible scenarios by stating that between these extremes lies a wide range of possible interactions (Fig. 1.3). In this section, we focus on the various pathways related to body growth but the consequences for fitness components

(survival and reproduction) will be discussed later.

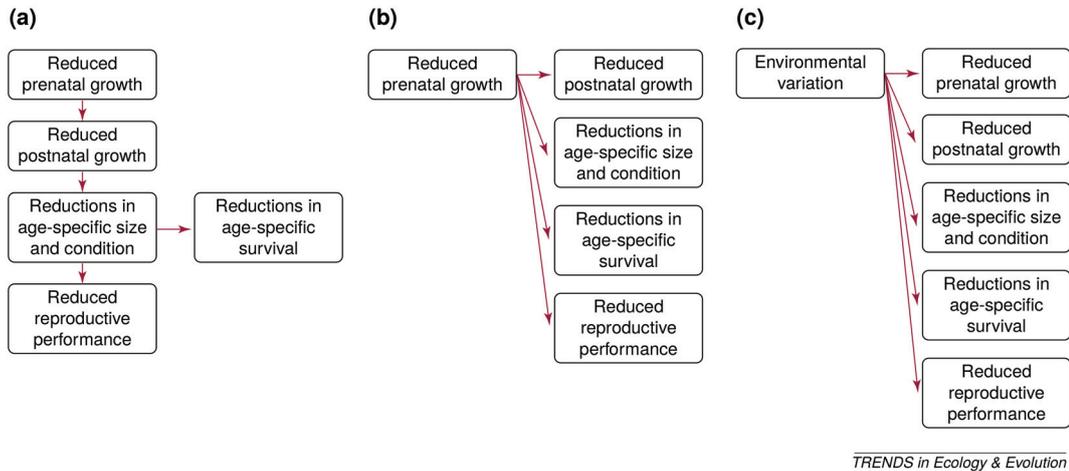


Fig. 1.3. Three examples of the causal mechanisms of how correlations between early conditions, growth and subsequent survival and reproduction can arise. (a) Reduction in early growth rate exerts causal effects on subsequent growth and age-specific size, which, in turn, influence survival and reproductive performance. (b) Variation in prenatal growth exerts independent effects on subsequent growth, survival and reproductive performance. (c) Environmental factors generating variation in prenatal growth rates have independent effects on subsequent growth, survival and breeding success. Reproduced from Lummaa and Clutton-Brock (2002).

In populations of large herbivores, the effects of early environment on adult body mass are commonly interpreted as evidence that early-life conditions influence early growth and thereby juvenile body mass, which in turn determines adult body mass (Fig. 1.3a, see Pettoirelli et al. 2002, Solberg et al. 2004 for examples). Lummaa and Clutton-Brock (2002) offered two different scenarios that might seem at first sight paradoxical (Figs. 1.3b and 1.3c). In both cases, early-life environmental conditions independently influenced adult body mass and early body growth. Under these scenarios, environmental conditions in early life influenced thus entire growth. The concept of ‘programming’, described below, can allow to better understand such effects.

1.4 Identifying causal mechanisms

The sex of most turtles and all species of crocodiles is determined by the temperature they face during early life (Gilbert 2000). One of the best-studied species for the temperature driven sex development is the European pond turtle (*Emys orbicularis*). Each individual starts life with the potential to be either a male or a female. If the eggs are incubated below 28° C, the young turtles develop as males whereas incubating eggs at temperatures above 29.5° C develop all as females (Pieau et al. 1994). The threshold temperature of 28.5° C gives 50% of each sex in experiments. The time window encompassing the last third of embryonic development seems to be the most critical for this temperature-induced sex determination in this species. After this period, sex can not be reversed.

This example illustrates an important fact: a relatively brief stimulus in early life can have long-term, irreversible effects on organism. The stimulus in the example on turtle is temperature but nutrition commonly plays an important role. That nutrition during early development can shape body growth trajectories has been highlighted by the pioneer work of McCance (1962) on rats. In this experiment, rats from large litters received less milk than those from small litters during the 21-days suckling period. Then, both groups were fed normally, but the smallest animals (from large litters) continued to diverge in body mass from the largest animals (Fig. 1.4a). Importantly, the effects of food restriction on body growth trajectories varied according to the age at which they occurred. Fig. 1.4b shows what happened when rats which were growing fast were undernourished from 9 weeks of age till they weighed only as much at 12 weeks as those which have obtained less food during suckling. Food-restricted rats from 9 to 12 weeks reached similar body mass than rats that have never been undernourished.

Lucas (1991) coined the term ‘programming’ to describe a stimulus or insult operating at a critical or sensitive period of development that result in long-standing effects on the structure or function of the organism. Waterland and Garza

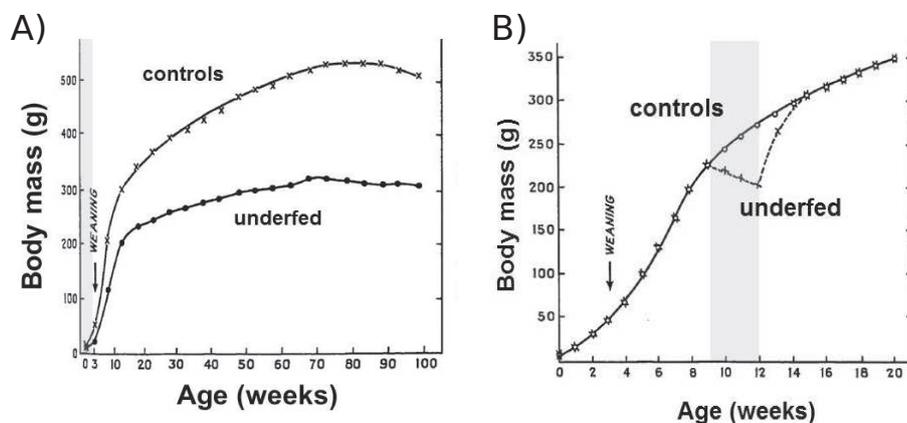


Fig. 1.4. Effects of food restriction on body growth of rats. A) Effects of varying the plane of nutrition during suckling (shaded area) on the whole of the subsequent growth of rats. The animals all has unlimited food after they were 3 weeks old. B) Effect of under-nutrition on rats between the ages of 9 and 12 weeks (shaded area). At this age the delay was rapidly made good. Adapted from McCance (1962).

(1999) proposed to use the term ‘metabolic imprinting’ instead of ‘programming’. The initial use of ‘metabolic imprinting’ was in connection with work of Konrad Lorenz who used imprinting to refer to the life-long setting of some animal behaviours that resulted from their early cognitive experience. Lucas (2000) objected, however, that programming goes beyond resetting metabolism by affecting a range of physiological functions and structure. Personally, I share the Lucas’s point of view and use the term ‘programming’ in this work.

The mechanisms underlying ‘programming’ by early-life environmental conditions include epigenetic changes, variations in organ structure, alterations in cell number (McMillen and Robinson 2005). All these mechanisms are not independent but rather act synergistically (Sookoian et al. 2013). In recent years, there has been particular interest in how environmental conditions can regulate the expression of genetic information. The study of heritable changes in gene expression that occur independent of changes in the primary DNA sequence corresponds to

the field of epigenetic (Feil and Fraga 2012). While the genome defines the potential genetic information, the epigenome defines which genes of this potential repertoire are actually expressed (Booij et al. 2013). The best known and most established epigenetic processes is DNA methylation in the mammalian genome (Booij et al. 2013). Burton and Metcalfe (2014) identified two main reasons to why early-life period is particularly sensitive to environmentally induced epigenetic changes (see also Feil and Fraga 2012). First, epigenetic changes in the early embryo are amplified during development by cell division and thus affect a high proportion of cells at adulthood stage. In contrast, when epigenetic alterations occur in fully differentiated cells they remain restricted to these cells. Second, early life is an especially sensitive period for DNA methylation and such process established during development can be maintained throughout life. Thus, the environmental conditions in early life can have long-term phenotypic effects without apparent associated underlying genetic changes (Feil and Fraga 2012).

Owing to the interest in agricultural productivity, the field of the physiology applied to livestock has provided a lot of knowledge on the effects of early-life conditions on cell number (see Du et al. 2010, for a review). The fetal stage is particularly crucial for skeletal muscle development due to the lack of net increase in the number of muscle fibers after birth. Postnatal muscle growth is mainly due to an increase in muscle fiber size without forming new muscle fibers. Consequently, a decrease in the number of muscle fibers induced by food deprivation permanently reduces muscle mass and animal performance. More specifically, the fetal stage, between 2 months of gestation to the end, is a critical period for bovine development of skeletal muscle (Fig. 1.5). While a lack of nutrients between 2 and 6 months reduces the formation of muscle fibers, nutrient deficiency during mid- to late gestation decreases the number of intra-muscular adipocytes and muscle fiber sizes (Fig. 1.5).

These different mechanisms can have strong implications to explain between-individual variation in life-history but they are difficult to identify in natural popu-

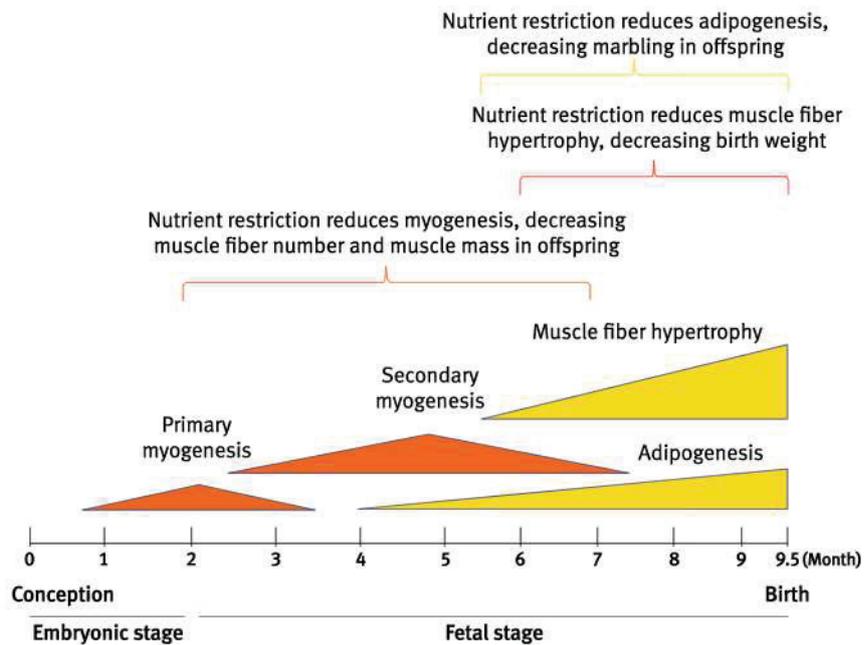


Fig. 1.5. Effects of maternal nutrition on bovine fetal skeletal muscle development. In cattle, gestation normally takes 210 days. Nutrient restriction during mid-gestation reduces muscle fiber numbers, whereas restriction during late gestation reduces both muscle fiber sizes and the formation of intramuscular adipocytes. Reproduced from Du et al. (2010).

lations. Indeed, identification of the proximate mechanisms requires longitudinal field studies with physiological and genetic data. However, data on individual body mass at different ages can be available (e.g., Nussey et al. 2011), allowing to investigate how environmental conditions in early life influence body growth trajectories (see chapter two).

1.5 Understanding the nature of the phenotypic changes induced by early-life conditions

‘Given the pace of global environmental change, understanding the nature and the consequences of these environmentally induced changes, and the extent to which

they are adaptive, is of great importance.'

– Monaghan (2008)

'An increasing number of studies have documented persistent effects of natal conditions on life histories in birds and mammals, including humans. There is now a need to understand [...] whether they represent adaptive responses to differing environments, or are a consequence of energetic constraints on development.'

– Clutton-Brock and Sheldon (2010)

These two quotes represent current opinions on the lack of understanding of the long-term effects of early environment from an evolutionary perspective. The selection pressure on developmental processes should be strong since environmental conditions during early life can have important and long-term consequences on phenotype (Ellison 2010). However, not everything in nature can be explained through the 'adaptationist paradigm' as Gould and Lewontin (1979) wrote in their seminal paper. Below follows a review and discussion of the various hypotheses linking early-life environmental conditions and fitness components (Table. 1.1).

Table 1.1. Hypotheses and predictions relating early-life environmental conditions and adult performance.

Hypothesis	Adaptation	Description	Key reference
Thrifty phenotype	Yes	Individuals born in poor conditions give priority to growth of vital organs but risk of developing chronic diseases	Hales and Barker (2001)
External PAR	Yes	Individuals adjust their metabolism and growth during early development for their anticipated future environment. Fitness is the highest for individuals for whom early-life conditions match conditions during adulthood	Gluckman et al. (2005a)
Internal PAR	Yes	Individuals born in poor conditions anticipate an accelerated reproductive and actuarial senescence and mature early	Nettle et al. (2013)
Compensatory growth	Yes	Individuals born in poor conditions accelerate their growth when environmental conditions improve. This lead to fitness costs often at old ages	Metcalfe and Monaghan (2001)
Silver spoon	No	Poor conditions in early life lead to stunted, poor-performing individuals that have a permanent fitness disadvantage	Monaghan et al. (2008)
Filtering effect	No	High juvenile mortality selectively removes poor-performing individuals from a a given cohort. Poor cohorts have higher adult survival and longevity	Fisher (1930)

1.5.1 AN ADAPTATIONIST VIEW IN MEDICINE

Nutrition during early life can have important long-term health consequences. Using birth weight as a proxy for the quality of the prenatal environment, Barker et al. (1989) showed that people born between 1911 and 1930 in England who had low birth weight were at increased risk of coronary heart disease during adulthood. Since, evidence in humans of links between early-life conditions and chronic disease later in life has been accumulated worldwide (reviewed by Hales and Barker 2001). The risk of developing cardiovascular diseases is exacerbated for individuals born small who subsequently become large (Hales and Ozanne 2003, Metcalfe and Monaghan 2001). Hence, poor fetal growth is increasingly recognised as contributing to cardiovascular diseases in populations experiencing rapid nutritional transitions (Delisle 2002, Kuzawa and Quinn 2009).

On the basis of these findings, Hales and Barker (1992) proposed that the observed relationship between poor fetal growth and adult health outcomes is the result of an adaptation to early environmental conditions (the ‘thrifty phenotype’ hypothesis, see also Hales and Barker 2001). They argued that small babies, experiencing poor environmental conditions in utero, prioritised growth of vital organs such as the brain and heart at the expense of other tissues, such as muscle and the endocrine pancreas. This developmental plasticity was suggested to be adaptive as it allows the offspring a better chance of survival during early-life adversity. In accordance with the concept of ‘programming’ (Lucas 1991), changes in nutrient during crucial periods of rapid cell division can lead to permanent changes of an organism’s physiology. Consequently, low birth-weight individuals who have been adapted to low supplies of resources early in life, have an enhanced predisposition to diabetes and other chronic diseases when nutrition becomes abundant in the postnatal environment. Thus, the ‘thrifty phenotype’ hypothesis proposed that developmental plasticity induced by early-life conditions has immediate adaptive advantage via early survival but to the possible detriment of later-life health.

The ‘thrifty phenotype’ hypothesis involves trade-offs over two time scales

(Monaghan 2008). Firstly, there is a trade-off in the early development; the vital organs are preserved at the expense of 'less essential' organs, individuals making the best of a bad job. Secondly, there is a trade-off over a longer time scale such as phenotypic changes that increase juvenile survival under harsh environmental conditions lead to health costs later in life. In wild populations, observing direct evidence for the first hypothesised trade-off is difficult. Testing the second trade-off seems more realistic by using hemato-biological parameters and components of the immune system. To our knowledge, a test of the 'thrifty phenotype' hypothesis is still lacking in wild populations.

In contrast to the 'thrifty phenotype' hypothesis, it has recently been suggested that the capacity of individuals to adjust their development in response to their early environment has been selected because of the long-term advantages in terms of reproduction and survival (Gluckman and Hanson 2004, Bateson et al. 2004, Gluckman et al. 2005a). According this predictive adaptive response (PAR sensu Gluckman et al. 2005a or external PAR sensu Nettle et al. 2013 for reasons that will become apparent) hypothesis, early-life conditions provide a 'weather forecast' of the future environmental conditions and it is adaptive for individuals to adjust their physiology during early development for this anticipated environment. In poor environmental conditions, for example, small size and slow metabolism may improve survival, whereas larger size and more rapid metabolism may lead to reproductive advantages when resources are plentiful (Bateson et al. 2004). The adaptive value of the external PAR depends, however, on the strength of the correlation between environmental conditions experienced during early-life and those experienced during adulthood, as mismatching may lead to fitness disadvantages (Gluckman and Hanson 2004).

In relation to humans, the external PAR was proposed to account for the developmental origins of chronic disease (Gluckman and Hanson 2006). The predictions made by the external PAR on the health are similar to those on fitness: the greater the degree of mismatch between environment during early-life and adult-

hood, the greater is the risk of disease. However, the external PAR hypothesis is currently much debated mainly because the assumption that early environments generally predicts adult environment conditions seems unrealistic in long-lived species (Wells 2006; 2007, Nettle et al. 2013, Burton and Metcalfe 2014). To date, empirical tests of external PAR are extremely rare in long-lived species, including humans (Hayward et al. 2013). We aimed to fill this gap by performing a test of the external PAR hypothesis in two populations of roe deer (*Capreolus capreolus*) living in contrasting ecological contexts (see chapter three).

1.5.2 DEVELOPMENTAL CONSTRAINTS

An alternative hypothesis, in complete opposition to the external PAR, is the ‘silver spoon’ effect defined as ‘positive correlations between characters in the adult that are positively associated with fitness, brought about by the common underlying cause of favourable or unfavourable events during development’ (Grafen 1988). This definition refers to the idea that early environment can determine individual quality (sensu Wilson and Nussey 2010). Under the ‘silver spoon’ effect, the long-term effects of early environment on life-history traits result from energetic constraints on development rather than of adaptive responses to different environments (Monaghan 2008). Silver spoon or delayed quality cohort effects induced by the early environment (see Box 1.1 for definitions) are thought to be widespread among wild vertebrates; they have been reported in mammals (Albon et al. 1987, Forchhammer et al. 2001, Gaillard et al. 2003c, Descamps et al. 2008, Hamel et al. 2009b), birds (Reid et al. 2003, van de Pol et al. 2006, Wilkin and Sheldon 2009) and snakes (Madsen and Shine 2000). The studies in wild mammals often identified growth and body mass as the main phenotypic link between early environmental conditions and fitness components (see Fig. 1.3a, Lummaa and Clutton-Brock 2002). Indeed, for large herbivores, any factor that influence body mass such as density or climatic conditions can in turn affect individual performance by lowering survival and/or reproduction (reviewed by Gaillard et al.

2000b, Bonenfant et al. 2009a).

A key aspect of the ‘silver spoon’ effect is that individuals born under favourable conditions outperform those born in adverse conditions whatever the subsequent environmental conditions (Monaghan 2008). In contrast, the external PAR hypothesis predicts that fitness should be the highest for individuals for whom early-life conditions match conditions during adulthood (Monaghan 2008). To date, as most studies in wild populations have focused on ‘silver spoon’ effect without testing for interactive effects of early and adult environmental conditions, it is impossible to quantify the relative empirical support of these two hypotheses (external PAR and silver spoon). This probably results from the fact that complementary and similarity between studies in human populations and wild animals have not yet been fully explored (Lummaa and Clutton-Brock 2002).

When harsh early-life conditions impose strong developmental constraints, the ‘silver spoon’ effect is generally predict but there is another, different possibility. The negative consequences of being born in a poor year could be counterbalanced by a strong viability selection (*sensu* Fisher 1930) during the juvenile stage. If the high mortality of juveniles in poor early-life conditions affects mainly individuals with lower phenotypic or genetic quality, this can result in a ‘filtering effect’ leaving a pool of ‘high quality’ individuals at adulthood. For example, cohorts of male red deer which underwent high initial mortality subsequently experienced higher adult survival than cohorts not subjected to high density related selection early in life (Rose et al. 1998). It is important to keep in mind that individuals alive at adulthood after experiencing poor environmental conditions in early life are not a random sample of the initial cohort. Taking into account the effects of past is necessary when investigating the long-term effects of early environment on adult life-history traits (Auer et al. 2012).

1.5.3 MAKE THE BEST OF A BAD JOB

The external PAR and the ‘silver spoon’ can be considered as two extreme hypotheses (Monaghan 2008). Under the external PAR, individuals born under poor condition can perform as well as than individuals born under favourable conditions. Under the ‘silver spoon’ scenario, individuals born under favourable conditions always outperform those born in adverse conditions. Between these two extremes, organisms may also mitigate the effects of poor early conditions through tactics that make the best of a bad situation (Metcalf and Monaghan 2001, Auer 2010). Good examples of such tactics are internal PAR (Nettle et al. 2013) and compensatory growth (Metcalf and Monaghan 2001).

The internal PAR

The internal predictive adaptive response (internal PAR in opposition to external PAR described above, Nettle et al. 2013) hypothesis has been recently developed to describe the different reproductive schedules based on the early environment that occur in humans. Several studies in humans and laboratory animals have indeed shown that adversity in early life is associated with early reproductive maturation (see also Sloboda et al. 2011, for a review). For example, in the female rat, pubertal timing was influenced by the animal’s nutritional status in utero, with maternal caloric restriction resulting in early pubertal onset (Sloboda et al. 2009). Nettle et al. (2013) interpreted this as a strategy in which individuals born under poor conditions anticipate an accelerated decline in reproduction and survival with age (i.e., an accelerated reproductive and actuarial senescence) and mature early to increase the chances of completing at least some reproduction in the lifetime. This model of developmental plasticity can be seen as a PAR hypothesis, however, predictions about the future are not based on the state of the external environment during adulthood but rather on the future somatic state. This more plausible scenario was developed from variation in age at first reproduction but can extend to

allocation in total early reproduction including postnatal maternal care.

The internal PAR hypothesis can be put in the broader context of life-history theory. Early primiparity should be favoured by natural selection because it reduces the period during which animals risk dying before reproducing (Cole 1954) but early reproduction can reduce subsequent growth, survival and reproduction (Stearns 1992). For example, adult bison cows that given birth for the first time at 2 years had smaller body mass after 4 years than cows that first calved at 3 or 4 years (Green and Rothstein 1991). Reproduction is thus expected to begin when the fitness benefits of reproduction outweigh the costs of reproduction on reduced growth, survival, or future reproduction. It is the age-dependent trade-offs that influence the evolution of life-history traits. For example, the disposable soma theory (Kirkwood 1977, Kirkwood and Rose 1991) that has been proposed to explain the senescence process, suggests that because the strength of selection weakens with age, selection favours an individual that allocates more energy into early reproduction vs long-term somatic maintenance. According the internal PAR, many reproductive tactics co-occur within a population and these ones are strongly related to environmental conditions experienced during early life. These tactics could be viewed as a r-K continuum within a population. Individuals born in favourable conditions express the most advantageous tactic by showing a high survival and a prudent reproduction early in life (K strategy), whereas individuals born in poor conditions do the best of a bad job by adopting a riskier reproductive tactic (r strategy).

Tests for internal PAR are currently lacking in wild mammal populations. In large herbivores, a critical body mass above which young females can reproduce is frequently reported (see Bonenfant et al. 2009a, for a review). For example, this threshold body mass is about 19 kg in roe deer (Gaillard et al. 1992), 45 kg in red deer (Bonenfant et al. 2002). However, the relationship between body mass and reproduction may vary according the environmental conditions experienced in early life. Under the internal PAR hypothesis, young females born in poor

conditions should adopt a riskier reproductive tactic, by having, for a given body mass, a higher reproductive rate than those born under favourable conditions. We test this hypothesis in female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) in chapter four.

Costs of compensatory growth

Alternatively, selection can favour processes that mitigate the negative long-term effects of poor early-life conditions through growth (Metcalf and Monaghan 2001). Low food availability during early life is generally linked to a slowing of growth (e.g. McCance 1962, Toïgo et al. 2006) and reduced size or mass at maturity have been associated with decreased fitness in many species (Stearns 1992, Dmitriew 2011). In light of these fitness costs due to reduced growth, many organisms can accelerate their growth when environmental conditions improve after a period of growth restriction, a response called compensatory growth (Bohman 1955, see Box 1.2 for more details).

Compensatory growth is thought to be a tactic that makes the best of a bad situation as it may carry costs, possibly not expressed until later in life (Metcalf and Monaghan 2001). These costs can be greater risks of adult diseases in human (in connection with the ‘thrifty phenotype’ hypothesis, Hales and Ozanne 2003), shortened longevity (Birkhead et al. 1999, Johnsson and Bohlin 2006) or reduced reproduction (Auer et al. 2010, Lee et al. 2012). It is the balance of the fitness costs and benefits (i.e., the net fitness return) that influences how compensatory growth evolves. Intuitively, the benefits of compensatory growth should vary according species and ecological conditions. For species that are predated, elevated foraging activity often necessary for compensatory growth can lead to increased risk of predation in the short-term (Gotthard 2000). In birds, as the probability of an individual being predated increases with its body mass (through flight performance for instance, Witter and Cuthill 1993), selection pressures on compensatory body growth are probably weaker than in large mammal herbivores.

Box 1.2. Definition of the terms compensatory growth and catch up growth to the meaning used in this work

Compensatory growth and catch-up growth have often been used interchangeably. Hector and Nakagawa (2012) clearly distinguished these two terms by defining compensatory growth as a faster than usual growth rate, whereas catch-up growth implies a non-significant difference in size between individuals that grow slowly in early-life and those that grow fast. Therefore, compensatory growth may or may not lead to catch up (Figs. 1.6c and 1.6d). On the other hand, the term ‘catch-up growth’ does not specify how the initial size difference is reduced (Fig. 1.6b). For instance, in female bighorn sheep, growth prolongation, not compensatory growth, led to partial catch-up (Marcil-Ferland et al. 2013).

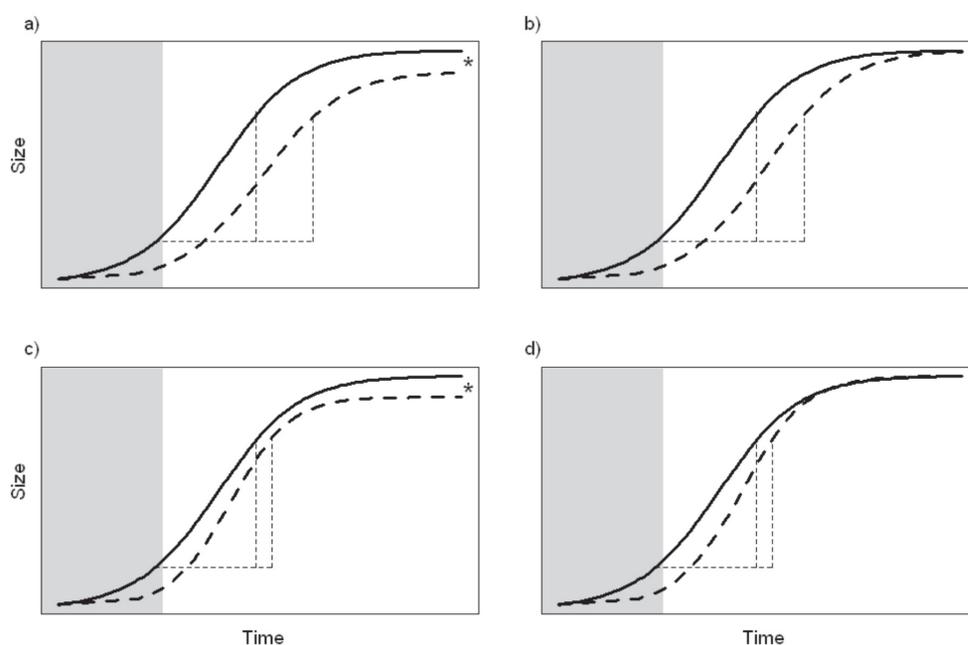


Fig. 1.6. Catch-up and compensatory growth. Theoretical representation of growth patterns following restricted growth: a) no compensation, b) catch-up growth only, c) compensatory growth only and d) both catch-up and compensatory growth. The shaded area indicates the period of growth restriction for the restricted group (dashed line). The control group is the solid line. The asterisk indicates a significantly different final size between the groups, while the dashed lines outline the time taken between 20 % and 80 % of the final size for ease of comparison between growth slopes. Reproduced from Hector and Nakagawa (2012).

Recent meta-analyses conducted on 88 studies including 11 taxonomic classes showed that compensatory growth is a general pattern that results in decreased fitness components (Hector and Nakagawa 2012). However, all studies included in the meta-analyses were based on experiments under controlled environment. Evidence for long-term costs associated with compensatory growth is very scarce in the wild (see Johnsson and Bohlin 2006, for a partially controlled experiment). This gap in knowledge is problematic because it may be difficult to extrapolate results from artificial environments to wild populations (Kawasaki et al. 2008). For instance, compensatory growth requires a substantial increase in the availability of resources during growth, a situation that may be rarely encountered in the wild as unfavourable conditions caused by high density persist generally over several years (Marcil-Ferland et al. 2013). More specifically, compensatory body growth is only one possible compensatory response (Lindström et al. 2005). In large mammal herbivores, reproductive success of males is often linked to the development of antlers, tusks or horns (Andersson 1994). We know, however, relatively little about possible compensatory growth of these weapons and their potential impacts on survival and longevity. We examine this issue in chapter five, using horns of Pyrenean chamois (*Rupicapra pyrenaica*).

1.6 When be born in a poor environment becomes advantageous at long-term: the case of selective hunting

Among the different hypotheses listed above, the external PAR (sensu Nettle et al. 2013) is the only way for individuals born under poor conditions to perform as well as than individuals born under favourable conditions but this hypothesis seems based on some unrealistic assumptions (see chapter two). Until now, we have mainly characterised the environment by climate, population density, predation. However, what happens when life-history traits of animals are affected by artificial selection?

Artificial selection is the selection of advantageous natural variation for human ends (Driscoll et al. 2009). While natural selection often favours larger individuals through increased viability and fertility, selective harvesting usually targets these very same individuals (Coltman 2008). Selective harvesting can thus lead to a paradoxical situation where individuals born under poor conditions having a reduced growth, can be advantaged at long-term. Consequently, it is not difficult to imagine that selective harvesting may lead to evolutionary changes. For example, the collapse of the northern cod fishery was preceded by an evolutionary shift towards earlier maturation and smaller size at maturity probably because faster growing fishes were selectively harvested before reproduction (Olsen et al. 2004). In bighorn sheep, trophy hunters removed males with rapidly growing horns, often at an age before those weapons improved reproductive success (Coltman et al. 2002). The heritability of horn length was substantial, and selective harvest led to a rapid evolution of reduced horn length in males, contrary to sexual selection (Coltman et al. 2003). These examples support the view that humans are clearly ‘the world’s greatest evolutionary force’ (Palumbi 2001). Although the possible evolutionary impacts of human harvests have recently attracted considerable attention both for terrestrial mammals and for fish, no studies have been able to compare the effects of different harvest intensities over decades. This issue is particularly important to identify what harvest rate may limit the potential undesirable effects of artificial selection. We aimed to fill this gap by exploring how hunting pressure affects horn growth of Stone’s sheep (*Ovis dalli stonei*) males in chapter six.

1.7 Structure of the thesis

This PhD thesis seeks to better understand the long-term consequences of early-life events, in particular the environmental conditions, on life-history traits in large herbivore populations. Specifically, this thesis has been divided into four parts:

In the first part, we investigated the pathways by which early environment influenced adult phenotype using adult body mass as the response. We showed that in roe deer, for the same body mass as juveniles, body mass of adult females decreased with adverse conditions in early life. In contrast, we found no evidence for a such effect of early-life conditions on adult body mass of males, suggesting sex-specific long-term responses of body mass to harsh early conditions. Our results on roe deer support the contention that early environmental conditions can influence the adult phenotype through persistent effects over the body development in wild mammal populations.

The second question is whether the long-term environmentally induced changes represent adaptive responses to different environments, or are only a consequence of constraints on development imposed by food resource availability. Firstly, we tested the external PAR (*sensu* Nettle et al. 2013) hypothesis in female roe deer and found no support for this hypothesis. Importantly, the strong viability selection imposed by very harsh environmental conditions led to an apparent support for the external PAR hypothesis. Secondly, we have tested the internal PAR (*sensu* Nettle et al. 2013) in female Svalbard reindeer. The negative effects of poor early-life conditions on body development are such that adult body mass and size were reduced when females were born in a poor environment. Moreover, females born in poor environmental conditions showed faster rates of senescence in both survival and offspring survival. In accordance with the internal PAR hypothesis, female reindeer mitigated the effects of poor early-life conditions by investing more in each episode of early reproduction. This response to early environment is thought to be a tactic that makes the best of a bad situation.

In a third part, we investigated the consequences of early horn growth rather than the early environmental conditions on longevity among two large herbivore species: a hunting-free population of Pyrenean chamois and two populations of Stone's sheep living under contrasting levels of hunting pressures. In Pyrenean chamois, horn growth but no compensatory horn negatively influenced longevity

in males and females. Surprisingly, the costs of growing large horns were similar for both sexes. These results provide important insights into the evolutionary causes of horn growth in females. In Stone's sheep, we showed that the two undesirable evolutionary consequences of trophy hunting, selection for smaller-horned males and reduced harvests, increased with harvest intensity but can be avoided when offtake is moderate.

We conclude by a general discussion where the results of these different studies are synthesised and discussed with respect of some articles in appendix. A special attention is given to the application of these results to wildlife management and potential future directions for research are provided.

1.8 A brief overview of the studied species

The five populations of large herbivores studied here (Fig. 1.7) vary in their position along the slow-fast continuum of life-history strategies. Using generation time as a metric (Gaillard et al. 2005), the pace of life of female Pyrenean chamois was almost twice slower than female roe deer at Trois-Fontaines (Table 1.2).

Females roe deer typically reproduce each year, start from the age of 2 years, and usually give birth to twins. On the other hand, most of the female chamois in the high density of the Causeret area delay primiparity until four years of age and give birth to a single kid annually. With a low productivity, the Chizé forest provides a poor habitat to roe deer (Pettorelli et al. 2006). In contrast, the Trois-Fontaines forest is highly productive. The difference in generation time between the two populations (higher at Chizé than at Trois-Fontaines, Table 1.2) probably results of the lower recruitment in the food-limited population of Chizé (Gaillard et al. 2003a). Although there are no demographic data in Stone's sheep, this species shares many similarities in sexual size dimorphism, mating system and age-specific horn growth with bighorn sheep (Krausman and Bowyer 2003), a species that is intensively studied at Ram Mountain, Alberta (Festa-Bianchet and

Jorgenson 1998, Festa-Bianchet et al. 2000). Hence, female stone's sheep have probably a generation time of about 6 years (Table 1.2). A similar value was reported for female Svalbard reindeer.



Fig. 1.7. Location of the different study sites for the four species of large herbivores studied here.

The level of sexual size dimorphism (approximated as male mass divided by female mass, Loison et al. 1999a) vary a lot between these species (from 1.08 for roe deer or Pyrenean chamois to 1.66 for Svalbard reindeer, Table 1.2). A low sexual size dimorphism should be associated with a low level of sexual selection on male traits (Loison et al. 1999b). Specifically, the potential for competition between males is expected to be higher for highly dimorphic species as Svalbard reindeer or Stone's sheep exhibiting harem defence or tending (because only

males that can defend females from competitors are commonly successful) than for weakly dimorphic species showing a mating tactic based on territoriality such as roe deer (Vanpé et al. 2008).

Finally, these different species are markedly segregated along the income-capital-breeding continuum (Jönsson 1997, Warner et al. 2008). Roe deer are income breeders that rely almost exclusively on available food resources for the high energetic needs of reproduction (Andersen et al. 2000). On the other hand, like many ungulates (Stephens et al. 2009), female Svalbard reindeer and Stone's sheep are capital breeders as body fat reserves can substantially affect their reproductive success.

Table 1.2. Characteristic for four species of ungulates in five study areas. For Stone's sheep, data in brackets indicated those for bighorn sheep at Ram Mountain.

Characteristic	Species				
	Roe deer	Roe deer	Svalbard reindeer	Stone sheep	Pyrenean chamois
Family	Cervidae	Cervidae	Cervidae	Bovidae	Bovidae
Study area	Chizé	Trois-Fontaines	Nordenskiöldland	British Columbia	The Caunterets
Generation time	5.37	4.72	6.21	unknown (6.5)	8.25
Dimorphism	1.09	1.08	1.66	unknown (1.41)	1.08
Predators on adults	no	no	no	bear, coyote, wolf	no
Predators on juveniles	red fox	red fox	arctic fox	golden eagle, bear, coyote, wolf	golden eagle, red fox
Hunting	no	no	no	yes	no
Polygynous mating systems	territorial	territorial	harem defence	tending	unknown
Litter size	1 or 2	1 to 3	1	1	1
Marked animals	yes	yes	yes	no	yes

Part I

Consequences of environmental conditions in early life on body growth trajectories

Chapter 2

Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females

A version of this chapter is published as: Douhard M, Gaillard J-M, Delorme D, Capron G, Duncan P, Klein F, Bonenfant C (2013) Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females, Ecology, vol. 94 pp.1805-1814



Photo credit: Maryline Pellerin

Abstract

There is increasing evidence that environmental conditions experienced early in life can markedly affect an organism's life history, but the pathways by which early environment influences adult phenotype are poorly known. We used long-term data from two roe deer populations (Chizé and Trois-Fontaines, France) to investigate the direct and indirect (operating through fawn body mass) effects of environmental conditions during early life on adult body mass. We found that environmental conditions (population size and spring temperatures) around birth influenced body mass of adult females through both direct and indirect effects in both populations. The occurrence of direct effects means that, for a given fawn body mass, adult female mass decreases with adverse conditions in early life. In contrast, we found no evidence for direct effects of early life conditions on adult body mass of males, suggesting the existence of sex specific long-term responses of body mass to stressful early conditions. Our results provide evidence that early environmental conditions influence the adult phenotype through persistent effects over the body development in wild mammal populations.

2.1 Introduction

Body mass has been intensively studied in a wide range of vertebrates because it shapes the demographic performance of individuals (birds: Haramis et al. 1986, mammals: Gaillard et al. 2000*b*, reptiles: Marquis et al. 2008). In mammals, body mass at weaning is positively associated with subsequent juvenile survival in the Columbian ground squirrel (*Spermophilus columbianus*, Skibieli et al. 2009) and adult body mass is an important component of individual quality among large herbivores (Hamel et al. 2009*b*). This correlation between body mass and survival or reproduction has led to the successful use and incorporation of body mass in demographic studies (Sauer and Slade 1987, Gamelon et al. 2012). For example, temporal changes in the body mass distribution of a population influence its dynamics and growth rate, explaining the phenotypic variation and the selection process occurring on that trait with climate change in several wild populations (Pelletier et al. 2007*a*, Ozgul et al. 2010).

While phenotypic attributes like age and sex account for most observed variation in adult body mass (Stearns 1992), environmental conditions, especially during early life, are now seen as also playing a major role (Larsson and Forslund 1991, Petteorelli et al. 2002). Environmental conditions in early life generate short-term effects on life-history traits such as body mass and juvenile survival (Clutton-Brock et al. 1992) and also induce long-lasting effects on the same traits *i.e.*, between-individual differences still detectable at the adult stage (Lummaa and Clutton-Brock 2002, Monaghan 2008). At the individual level, the long-lasting effects of early-life conditions correspond to the so-called ‘silver spoon effect’ (Grafen 1988), by which individuals born under favorable conditions enjoy fitness benefits for their lifetime compared to individuals born under adverse conditions. At the population level, the ‘silver spoon effect’ translates into delayed cohort effects because individuals born the same year cope with similar environmental conditions during early life (Albon et al. 1987, Gaillard et al. 2003*c*). The

magnitude of delayed cohort effects is tightly linked to the nutrition of individuals during their early life (Madsen and Shine 2000, Descamps et al. 2008). In roe deer (*Capreolus capreolus*) for instance, cohort effects are less pronounced in habitats providing the highest food quality (Pettorelli et al. 2006).

In wild populations, nutrition levels are usually inferred from proxies of food resources such as population density or climatic conditions (Rickard et al. 2010). Accordingly, many studies have provided evidence of delayed cohort effects on adult body mass of large herbivores explained by weather or population density in the year of birth (Mysterud et al. 2002, Pettoelli et al. 2002, Solberg et al. 2004). At least two mechanisms may explain such observed relationships between environmental conditions during early life and adult body mass (Lummaa and Clutton-Brock 2002, Fig. 6.1). As a first and most commonly assumed mechanism (*e.g.*, Pettoelli et al. 2002, Solberg et al. 2004) environmental conditions around the time of birth can influence early growth and thereby the juvenile body mass, which, in turn, determines adult body mass (mechanism 1, Fig. 6.1A). Second, environmental conditions in early life may influence adult body mass throughout the course of development (mechanism 2, Fig. 6.1B). In contrast to the first mechanism, late growth is also influenced by environmental conditions in early life. This second mechanism was first proposed from the early experimental works of McCance (1962) on captive rats involving the manipulation of litter size. Rats from large litters received less milk than those from small litters during the 21-d suckling period. At this point, both groups were fed normally, but the smallest animals (from large litters) continued to diverge in body mass from the largest animals (see also Kapoor and Matthews 2005). Whether such an effect occurs in free-ranging populations of mammals is currently unknown. In comparison to the first mechanism, the difference of adult body mass between individuals born in poor and good environments is expected to be highest with the second mechanism (Fig. 6.1), therefore increasing individual heterogeneity in adult body mass. As such individual heterogeneity is the necessary starting point for natural selection

to operate (Darwin 1859), disentangling these two mechanisms of long-lasting cohort effects is important.

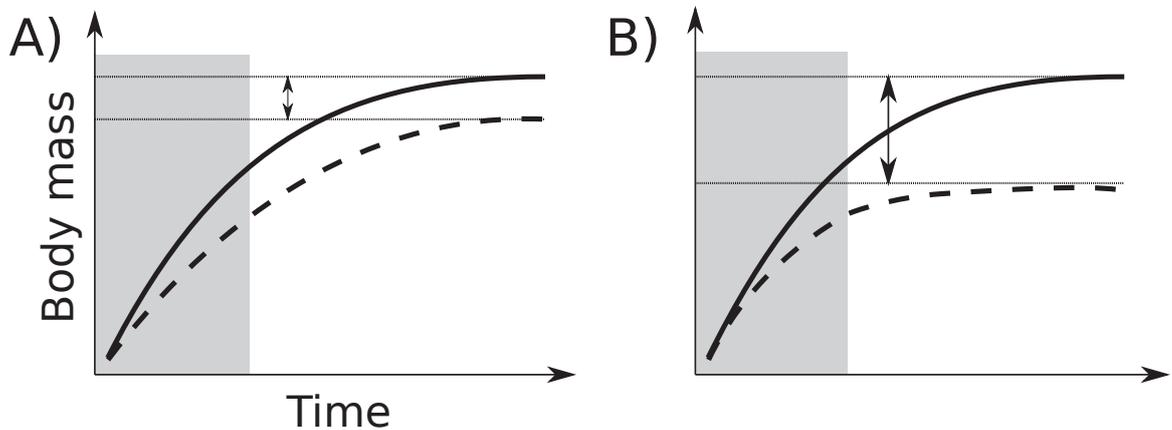


Fig. 2.1. Theoretical representation of two possible scenarios to explain long-lasting effects of early environmental conditions (shaded area) on adult body mass. Growth trajectories for individuals born under good (continuous lines) and poor (broken lines) conditions are displayed. Horizontal dotted lines represent the asymptotic body mass. A) Early environment influences early growth only. B) Early environment influences adult body mass throughout the developmental process.

Taking advantage of marked temporal variation in the environmental conditions recorded in two roe deer populations, we aimed to quantify how much of early-life conditions accounted for adult body mass *via* its effect on fawn body mass only *vs* full growth period. Body growth of roe deer is monomolecular, a pattern in which growth rate decreases continuously from birth onwards (Portier et al. 2000). Individuals reach about 59-70% of their adult body mass within their first 8 months of life (Andersen et al. 1998b). Full body mass is reached at about 4 years of age and remains stable until 10 years of age in both males and females (Nussey et al. 2011). Because roe deer females are income breeders that rely almost exclusively on available food resources to meet the energetic costs of reproduction (Andersen et al. 2000), environmental conditions at birth should thus be a major determinant of fawn (5-8 months of age) and adult (between 4 and 10

years of age) body mass. If environmental conditions during early life affect adult body mass *via* early growth only, they should not influence adult body mass once the effects of fawn body mass are accounted for (mechanism 1, Fig. 6.1A). On the other hand, if environmental conditions during early life shape growth throughout the whole developmental process, it should still influence adult body mass once the effects of fawn body mass are accounted for (mechanism 2, Fig. 6.1B).

2.2 Material and methods

STUDY AREAS AND ROE DEER POPULATIONS

The study was carried out in two fenced forests managed by the Office National des Forêts, the 2,614 ha Réserve Biologique Intégrale of Chizé and the 1,360 ha Territoire d'Étude et d'Expérimentation of Trois-Fontaines. These two study sites differ with respect to climatic conditions. Located in Western France (46°05'N, 0°25'W) Chizé has an oceanic climate under Mediterranean influence, with mild winters (mean \pm SE daily temperature in January is $5.63 \pm 0.36^\circ$ C) and warm, often dry, summers (in July, mean daily temperature is $20.52 \pm 0.28^\circ$ C and total rainfall is 53.39 ± 4.03 mm). On the other hand, Trois-Fontaines in Eastern France (48°43'N, 2°61'W) has a continental climate with relatively colder winters (mean daily temperature in January is $3.07 \pm 0.39^\circ$ C) and warmer but generally wetter summers (in July, mean daily temperature is $19.57 \pm 0.30^\circ$ C and total rainfall is 72.39 ± 6.76 mm).

At Chizé, three habitats with contrasted quality (Pettorelli et al. 2001) have been identified in relation to the type of timber stand and coppice structure (from richest to poorest: oak (*Quercus* sp.) with hornbeam (*Carpinus betulus*), oak with Montpellier maple (*Acer monspessulanum*), and beech (*Fagus sylvatica*) with little coppice). Such a habitat structure was not found at Trois-Fontaines where the forest appears more homogeneous. The primary productivity of the Chizé forest is quite low due to poor soils and frequent summer droughts, while Trois-Fontaines

is a rich and productive forest due to high quality soils and infrequent summer droughts. Long-term average wood production, which measures the potential biomass production, is $5.92 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ at Trois-Fontaines vs $3.77 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ at Chizé (Pettorelli et al. 2006). Accordingly, the demographic performance of roe deer was much higher at Trois-Fontaines than at Chizé (during the 80's, $\lambda = 1.21$ at Trois-Fontaines vs $\lambda = 1.04$ at Chizé, Nilsen et al. 2009), a difference mainly explained by the high pre- and post-weaning juvenile survival observed at Trois-Fontaines (Gaillard et al. 1993a; 1997). Population size in both sites has been controlled by yearly culling in all years (but 2001-2003 at Trois-Fontaines and 2008-2011 at Chizé). Since 2000, roe deer at Chizé have been strongly limited by a combination of harsh climatic events and a relatively high density. No large predators or hunting of roe deer occurred in either site.

ROE DEER DATA

Roe deer have been intensively monitored using Capture-Mark-Recapture (CMR) methods since 1976 at Trois-Fontaines and 1978 at Chizé. Each year, between 8 and 12 capture sessions are carried out from October to March (mainly January and February). For each individual, sex, age, habitat type at Chizé, and body mass were recorded. We also assigned a Julian date to each capture event. Fawns (5-8 months of age) were identified by the presence of a tricuspid third premolar, which provides a reliable way to age deer < 1 year (Hewison et al. 2002). Roe deer belonged to 29 cohorts in both sites, born from 1979 to 2007 at Chizé and from 1977 to 2005 at Trois-Fontaines. We used data from known-aged animals only, weighed using an electronic balance, both as fawn and at least once as adult. Fawn body mass was adjusted for the date of capture to control for body growth that occurs over the capture season (Hewison et al. 2002). As expected, fawns grew by $0.016 \pm 0.004 \text{ kg/day}$ and $0.020 \pm 0.009 \text{ kg/day}$ at Chizé and Trois-Fontaines, respectively. Adult body mass is the median of all measurements between 4 and 10 years of age (Pettorelli et al. 2002). Body mass of adult females

was not influenced by pregnancy status because females were weighed right after the embryonic diapause (that ends in late December, Aitken 1974). Body mass is a composite measure of both body size and body condition (Dobson 1992). However, being income breeders (Andersen et al. 2000) roe deer do not accumulate body reserve for reproduction, so that individual variation in body mass is mostly associated with variation in size. Thus, growth in size and mass are tightly correlated in roe deer, as reported in both populations (Hewison et al. 2011) and respond similarly to changes in environmental conditions while body condition does not (Toïgo et al. 2006).

ENVIRONMENTAL VARIABLES

For each individual, we assessed how population size (POP, *i.e.*, the number of roe deer older than 1 year in March) and weather conditions in the year of birth influenced body mass. Reliable and comparable estimates of POP were available using CMR methods in both populations (Gaillard et al. 2003a) because more than 70% of roe deer older than 1 year are individually marked. At Chizé, population density increased from 13 to 21 animals.km⁻² between 1979 and 1984, then was reduced to around 6 animals.km⁻² in 1994 and increased up to 19 animals.km⁻² in 2006. Population density at Trois-Fontaines varied between 15 and 18 animals.km⁻² from 1978 to 2001, after which the population was allowed to increase up to 25 animals.km⁻² in 2005 due to a reduction of deer removals. We computed weather variables according to both the season and stage of development of roe deer in early life starting from January until August in year of birth. We obtained weather variables from Météo-France stations located < 5 km from the study areas (Beauvoir-sur-Niort and Saint-Dizier for Chizé and Trois-Fontaines, respectively). There was virtually no difference in elevation between Météo-France stations and the study areas. We considered three different seasons, winter (January-March), spring (April-May) and summer (June-August). Because all individuals are *in utero* in winter but born in summer, we computed weather

variables for each season. Weather conditions in winter were assessed using the mean temperature (T) and rainfall (R). In summer, we used the Bagnoul-Gausson drought index calculated as twice the mean temperature in ° C minus the mean precipitations in mm summed over June and August (Gaillard et al. 1997, Hamel et al. 2009b). In spring, following Mysterud and Østbye (2006) and Panzacchi et al. (2009) we tested for the effects of average precipitation and temperature in April that corresponds to the last part of gestation for all females and May when some fawns are still *in utero* while others are born.

STATISTICAL ANALYSES

We used linear models (Rencher 2000) to analyse variation in fawn and adult body mass, and conducted separate analyses for each study area. As a first step, we tested for cohort variation in adult body mass for each sex using year of birth as a factor. At Chizé, we controlled for possible confounding effects of habitat quality (Pettorelli et al. 2002) by including habitat type as a 3-level factor. Then, we investigated the effects of environmental conditions in year of birth on sex-specific body mass of adults. Our models included POP, weather variables, and sex to account for the weak sexual dimorphism in size of roe deer (Andersen et al. 1998b). We explicitly tested the POP by weather interactions (*e.g.*, Portier et al. 1998).

Long-lasting effects of early conditions can be confounded with conditions experienced later in life (Descamps et al. 2008). This problem arises when environmental conditions in early life and in adulthood are correlated. While we did not detect any evidence of temporal auto-correlation for weather variables, population size in both sites did with, respectively, a time lag of 3 and 1 years at Chizé and Trois-Fontaines (Appendix A). Similarly to Nussey et al. (2007a), we controlled for the effect of population size experienced during the end of growth on adult body mass by including the average POP experienced between ages 1 and 4 ($POP_{ages1-4}$) in all models. We used a backward selection procedure, testing

successively the first-order interactions and, if not significant, the main effects of covariates. Statistical significance was assessed by Likelihood Ratio Test (LRT). We set the significance level α at 0.05. We checked for normality of residuals and homogeneity of variance graphically. The proportion of cohort variation in adult body mass explained by a given covariate was assessed by comparing models with the covariate (M_{cov}) to the cohort-dependent (M_{coh}) and constant (M_{cst}) models: $R^2 = (\text{deviance } M_{cst} - \text{deviance } M_{cov}) / (\text{deviance } M_{cst} - \text{deviance } M_{coh})$ (see Skalski et al. 1993).

To quantify the relative importance of the two mechanisms of long-lasting cohort effects, we analysed direct and indirect (*i.e.*, operating through fawn body mass) effects of environmental factors in year of birth on variation in adult body mass using path analyses (Shiple 2009). According to mechanism 1 (Fig. 6.1A), we should observe indirect effects only because environmental conditions in early life only influence early growth. Alternatively, according to mechanism 2 (Fig. 6.1B), both direct and indirect effects should be detected because environmental conditions in early life influence both early and late growth. Separate path analyses were conducted for males and females. Fawn and adult body mass and all environmental covariates retained from the previous analyses were entered into a path diagram. To calculate path coefficients, mass was log-transformed and all variables were standardized (mean = 0, SD = 1). Similarly to Myrsetrud et al. (2008), we tested the significance of path coefficients by examining whether zero was included within confidence interval at 95% of the estimated coefficients. We calculated partial R^2 to measure the effect size of direct and indirect effects. We used R software (R-Development Core team 2011) to perform all analyses.

2.3 Results

COHORT EFFECTS ON ADULT BODY MASS

At Chizé, habitat type did not influence adult body mass of males ($N = 146$, $F_{2,118} = 0.48$, $P = 0.62$) and females ($N = 173$, $F_{2,143} = 1.27$, $P = 0.29$). As expected, strong cohort variation occurred in adult body mass of both males (ranging from 21.0 kg in 2005 to 28.2 kg in 2000: $F_{25,118} = 4.09$, $P < 0.001$) and females (ranging from 19.1 kg in 2006 to 25.0 kg in 1992: $F_{27,143} = 3.67$, $P < 0.001$). T_{May} varied from a minimum of 11.14° C to a maximum of 18.33° C and POP ranged from 165 to 539 individuals older than 1 year (averaging 340 individuals across study years). When using environmental factors in early life to explain variation in adult body mass among cohorts, we found a statistically significant interactive effect between POP and T_{May} (Appendix B). The negative effect of density on adult body mass was greater when roe deer experienced a hot May in their year of birth (Appendix B). Adult body mass decreased with $POP_{ages1-4}$ (Appendix B). POP-by- T_{May} interaction and $POP_{ages1-4}$ accounted for 88% of the observed cohort variation in adult body mass.

At Trois-Fontaines, we detected cohort variation in adult body mass in females only ($N = 161$, $F_{28,132} = 2.21$, $P = 0.001$ for females and $N = 103$, $F_{26,76} = 0.78$, $P = 0.75$ for males) despite the range of adult body mass among cohorts was similar in both sexes (males born in 1979 were on average 5.6 kg heavier than males born in 2001 while females born in 1984 were 6.42 kg heavier than females born in 1995). Average temperatures during the spring of birth (T_{Apr} and T_{May}) had a negative effect on adult body mass (Appendix C) and accounted for 31% of the observed cohort variation in adult body mass.

PATH ANALYSES

For females at Chizé, the path diagram showed that POP-by- T_{May} interaction on adult body mass originated from both fawn body mass (indirect effects) and from

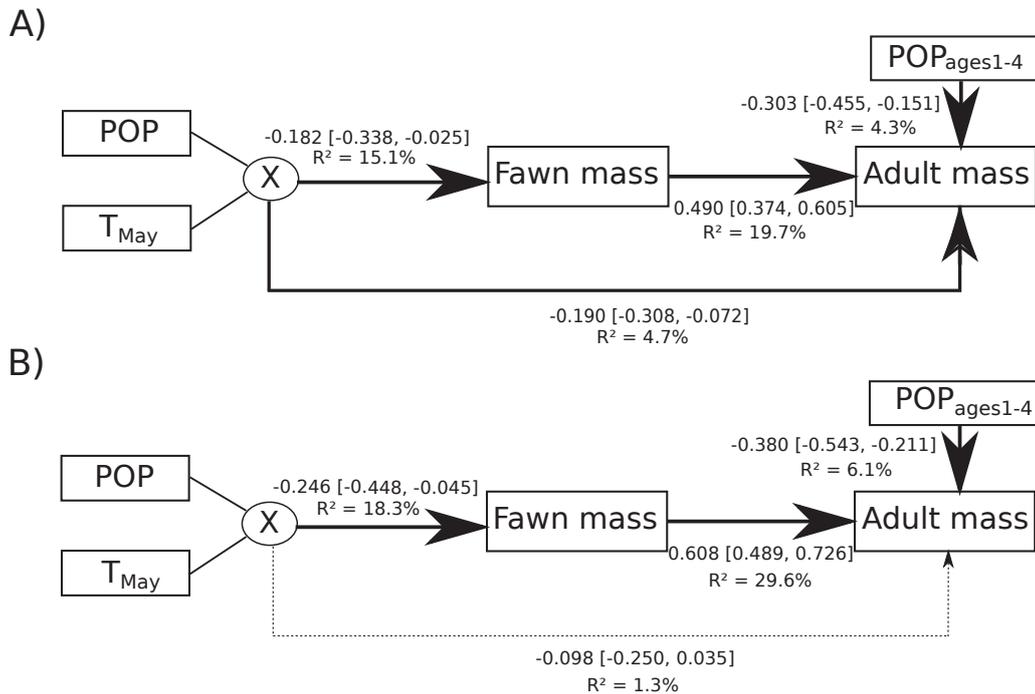


Fig. 2.2. Path diagram showing how early environmental conditions influence directly and indirectly adult body mass (on a log-scale) of A) female and B) male roe deer at Chizé, France. Path coefficients are given with their associated 95 % confidence limits in brackets. Solid lines indicate statistically supported effects (95 % confidence limits exclude 0), and dotted lines indicate non-statistically supported effects (95 % confidence limits include 0). Partial R^2 measures the marginal contribution of a pathway. POP stands for population size, T for average monthly temperatures, POP_{ages1-4} for average population size experienced between ages 1 and 4, and "X" for interactive effects.

direct effects (Fig. 6.2A). When both the direct and indirect effects of POP-by- T_{May} interaction were accounted for, body mass of adult females born in warm springs (*i.e.*, > median temperature in May) decreased by about 1 kg for each increase of 100 roe deer at birth as compared with 0.54 kg when excluding the direct effects (Fig. 6.4A). Direct effects of POP-by- T_{May} interaction accounted for about 5% of the observed variation in adult body mass of females (Fig. 6.2A). In contrast, we found no evidence for a direct effect of POP-by- T_{May} interaction

on body mass of adult males (Fig. 6.2B and Fig. 6.4B for a graphical representation). POP-by- T_{May} interaction influenced body mass of adult males *via* fawn body mass only (indirect effect).

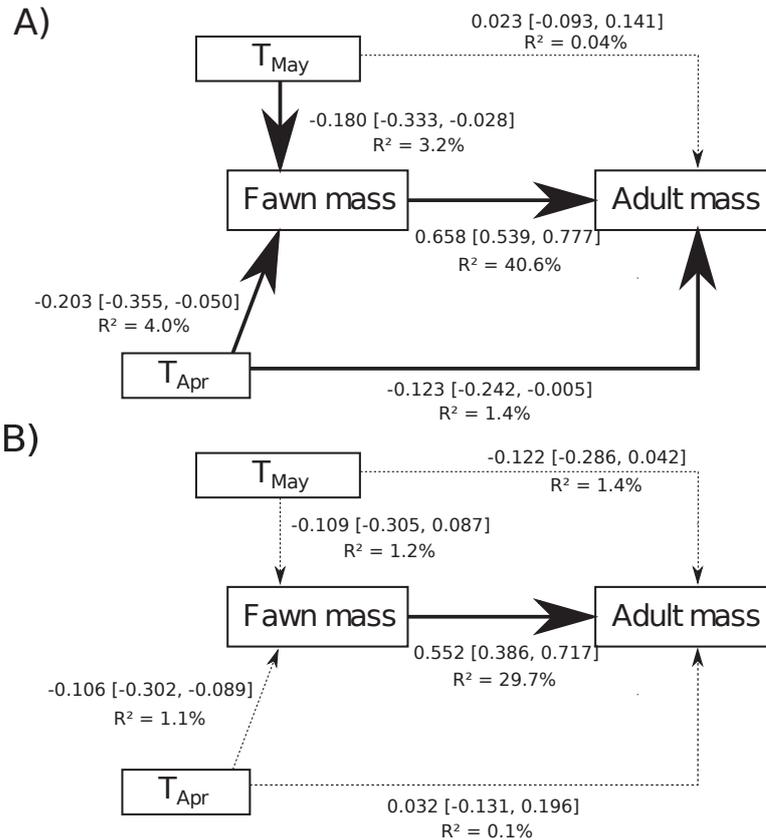


Fig. 2.3. Path diagram showing how early environmental conditions influence directly and indirectly adult body mass (on a log-scale) of A) female and B) male roe deer at Trois-Fontaines, France. Path coefficients are given with their associated 95 % confidence limits in brackets. Solid lines indicate statistically supported effects (95 % confidence limits exclude 0), and dotted lines indicate non-statistically supported effects (95 % confidence limits include 0). Partial R^2 measures the marginal contribution of a pathway. POP stands for population size, T for average monthly temperatures.

For females at Trois-Fontaines, we detected indirect and negative effects of T_{Apr} and T_{May} on adult body mass. Only T_{Apr} showed an additional direct ef-

fect on adult body mass of females (Fig. 6.3A). However this direct effect only accounted for 1.4% of the observed variation in adult body mass of females. After accounting for the indirect and direct effects of T_{Apr} , body mass of adult females decreased by 0.55 kg for a 1° C increase in the average temperature of April as compared with 0.33 kg when excluding the direct effects (Fig. 6.4C). For males, there was evidence neither for direct or indirect effects of T_{Apr} and T_{May} on adult body mass despite indirect effects in the expected direction (Fig. 6.3B and Fig. 6.4D).

2.4 Discussion

Cohort variation in adult body mass of roe deer, which occurred in both sites, was associated with environmental conditions experienced in early life. At Chizé, adult body mass was negatively influenced by the POP-by- T_{May} interaction, while the average temperature in April had a negative influence at Trois-Fontaines. These results support the widespread occurrence of long-lasting effects of early environmental conditions on life history traits (reviewed in Lummaa and Clutton-Brock 2002, Gaillard et al. 2003c, Monaghan 2008) and provide detailed pathways by which early environment generates such long-lasting cohort effects, using adult body mass as the response. In both sexes, environmental conditions early in life influenced adult body mass mainly through their effects on fawn body mass (indirect effects). Furthermore, the POP-by- T_{May} interaction at Chizé and T_{Apr} at Trois-Fontaines also had negative direct effects on adult body mass of females. In contrast, we found no evidence for any direct effects of early life conditions on adult body mass of males. These results mean that in males, early life environmental conditions only affect early growth (as displayed on Fig. 6.1A), whereas in females, early life conditions influence body growth throughout the whole developmental process (as displayed on Fig. 6.1B).

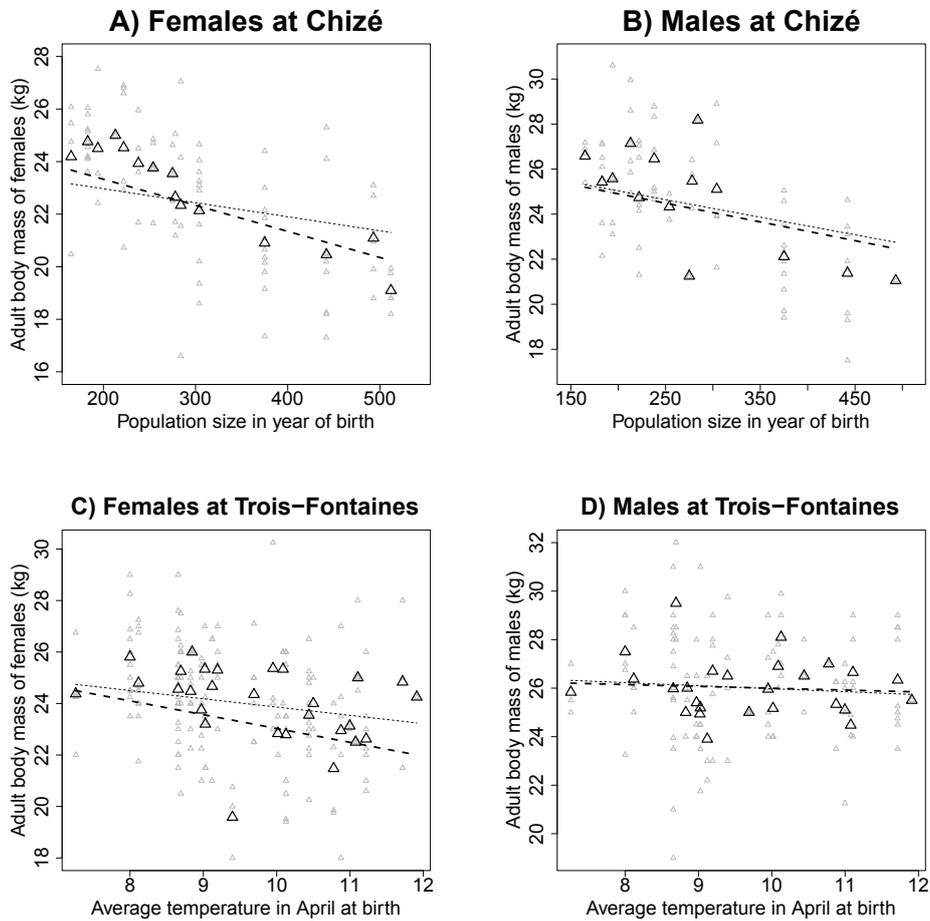


Fig. 2.4. Plot showing the direct and indirect effects of environment in early life (interacting effects of population size and temperatures in May at Chizé and effects of April temperatures at Trois-Fontaines) on adult body mass for both sexes at Chizé and Trois-Fontaines, France. The thick dotted lines represent the predictions of the model with direct and indirect effects, whereas the thin dotted lines represent the predictions of the model with indirect effects only. The small grey triangles represent individual data, the big grey triangles represent mean body mass for a given cohort. At Chizé, roe deer were divided into two groups: those that experienced (1) lower, and (2) equal or greater median temperatures in May at birth. We only represent here individuals that experienced equal or greater median temperatures in May at birth for convenience (but see Appendix D for complete graphs).

COHORT EFFECTS AND SPRING ENVIRONMENTAL CONDITIONS

Variation in quantity and quality of food resources around the time of birth is the major factor explaining the long-lasting effects of early environmental con-

ditions on life history traits (Madsen and Shine 2000, Descamps et al. 2008). In the two studied populations, high spring temperatures around birth had negative short-term and long-term effects on body mass. High temperatures in spring and early summer often correlate negatively with body mass of large herbivores in temperate areas (Albon et al. 1992 on red deer, Gaillard et al. 1996 on roe deer, Solberg et al. 2004 on moose). The positive influence of a cool spring involves delayed lignification of the vegetation and, thereby, prolonged availability of high quality forage (*e.g.*, Solberg et al. 2004). Thus, being born during cool springs may be advantageous for the fawn through a relatively high growth rate. Being income breeders, roe deer females respond immediately to changes in food resources during the last weeks of gestation and early lactation, when reproductive energetic costs peak (Sadleir 1987), by adjusting the amount of energy allocated to their fawn. Besides, population density interacts with weather to shape adult body mass, as previously reported for other life history traits of wild large herbivores (Bonenfant et al. 2009a). At Chizé, for instance, the negative effect of density dependence on body mass was of greater magnitude when average temperatures in May were high.

PATHWAYS GENERATING LONG-LASTING COHORT EFFECTS ON ADULT MASS

In mammalian populations, the effects of environmental conditions around the time of birth on adult body mass are commonly interpreted as evidence that early life conditions influence early growth and thereby juvenile body mass, which, in turn, determines adult body mass (*e.g.*, Pettorelli et al. 2002, Solberg et al. 2004). We found strong empirical support for such a mechanism. However, we also found a direct effect of early life conditions on adult body mass of female roe deer, which was unrelated to their body mass as fawns, showing that early environmental conditions imprint their whole body growth trajectories. Environmental perturbations during early development, which lock individuals within a growth trajectory, directly determine the body mass of female roe deer later in life, in-

dependently of the post-natal environment they meet. That early nutrition can directly shape growth trajectories is known for over 50 years from animal experiments (McCance 1962) but similar effects have been previously reported in the wild for indeterminate growers only, like water pythons (*Liasis fuscus*, Madsen and Shine 2000). Water pythons display a strong ‘silver spoon effect’, whereby high prey abundance in the first year of life positively influences growth during their entire life. Our study indicates that adverse early life conditions negatively influence both early and late growth in determinate growers like female roe deer.

One reason for why body growth is continuously influenced by conditions in early life is that environmental stress during the crucial period of early life can permanently affect the body structure, physiology and metabolism of individuals (Lucas 1991, Lummaa and Clutton-Brock 2002). For instance, the fetal stage is crucial for skeletal muscle development due to the lack of net increase in the number of muscle fibers after birth. A decrease in the number of muscle fibers due to food deprivation permanently reduces muscle mass and animal performance (Du et al. 2010). Animal breeders identified the fetal stages of development as the best time window for nutritional management and manipulation, which can exert long-term effects on the growth performance of individuals (Du et al. 2010). As 75% of fetal growth occurs during the last 2 months of gestation in ruminants (Robinson et al. 1977), maternal stress during this period can have permanent and profound effects on offspring’s body structure. This mechanism can be involved in cohort effects, as we report here, but also in maternal effects (Boonstra and Hochachka 1997, Rossiter 1991) to explain between-individual differences within a given cohort through, for example, the heterogeneity in home range quality among mothers (McLoughlin et al. 2007).

The two roe deer populations we studied live in contrasting environmental conditions. Trois-Fontaines has been a consistently highly productive forest, whereas Chizé has been markedly food-limited in several years. As a result, the average fawn mass in winter, which is a reliable measure of yearly environmental condi-

tions roe deer faced with (Gaillard et al. 1996, Hamel et al. 2009b), was lower and varied twice more at Chizé (mean = 14.92 kg, CV = 0.11) than at Trois-Fontaines (mean = 17.44 kg, CV = 0.06). Moreover, a recent immunological analysis supports the high energetic stress at Chizé (Gilot-Fromont et al. 2012). Consistent with these between-population differences, the effects of environmental conditions in early life on late growth of females were more pronounced at Chizé than at Trois-Fontaines.

SEX-SPECIFIC SENSITIVITY TO EARLY LIFE CONDITIONS

In support of the low level of polygyny in roe deer, there is only a weak sexual size dimorphism and both sexes have similar early life-history traits like birth mass and early growth (Gaillard et al. 1993b) and similar survival up to one year of age (Gaillard et al. 1997). However, despite the weak intensity of sexual selection, there are some marked between-sex differences in roe deer life history. Only males are territorial with a long territory tenure that spans over half the year. Contrary to females, males thus allocate energy to patrol, mark, and defend their territory. Hence, annual adult survival in roe deer is much less in males than in females (Gaillard et al. 1993a). Moreover, recent investigations of sex-specific mass-size allometry in roe deer have reported between-sex differences in ontogeny, structural size, and physiological condition (Hewison et al. 2011). Contrary to females, we found that there was no direct influence of early environmental conditions on adult body mass of males in the two studied populations. While the absence of statistically significant direct effects of early conditions on male adult mass at Trois-Fontaines could be due to a lack of statistical power, similar sample sizes for both sexes at Chizé led to similar between-sex differences involving a lack of direct effects in males. Such between-sex differences could result from sex-specific growth duration and timing of first reproduction. Female roe deer reach their asymptotic body mass more rapidly than males in both populations (Hewison et al. 2011). For instance, males gained an additional 1.5-2.0

kg between 1.5 and 2.5 years of age, whereas females only gained 0.6 kg at Chizé (Hewison et al. 2011). This difference in body growth between sexes is likely due to the earlier occurrence of the trade-off between growth and energy allocation to reproduction for females than for males. At both sites, most females are pregnant for the first time at 2 years of age (Gaillard et al. 2003a) while males become territorial and mate for the first time at 3 years of age (Vanpé et al. 2009). The longer duration of body growth in males confers them a greater flexibility to deviate from their initial growth trajectory compared to females. For instance, individuals may accelerate body growth when environmental conditions improve after a period of food restriction (compensatory growth *sensu* Bohman 1955). In contrast, such an opportunity to deviate from the initial growth trajectory is reduced for roe deer females because of reproductive constraints that shorten the growth period.

In conclusion, environmental conditions in early life has long-lasting effects on body growth in female roe deer. Moreover, the difference in productivity between the two study areas modulate the magnitude of these effects. Sex-specific long-lasting effects of early life conditions on growth are likely related to differences of growth duration between males and females, and thereby to between-sex differences in the timing of first reproduction. While the causal mechanism underlying these effects are not yet known, they are consistent with the idea that environmental stress during the crucial period of early life can permanently affect the body structure, physiology and metabolism of mammals. Further studies are now needed to determine whether direct effects of early conditions on body mass during adulthood result from developmental constraints or correspond to adaptive developmental plasticity.

Acknowledgements

We are grateful to all volunteers who contributed to roe deer captures during all years. We thank Madan Oli, Stephen Dobson, and Sandro Lovari for their insightful comments

on a previous draft. C. Bonenfant and J.-M. Gaillard are supported by research grants from CNRS and ONCFS. M. Douhard was funded by a PhD scholarship from the French Ministry of Higher Education and Research.

2.5 Supplemental material

Appendix A. Estimates of the temporal autocorrelation for weather variables and population size at Chizé and Trois-Fontaines, France.

Appendix B. Parameter estimations and plot representations of variations in adult body mass of roe deer at Chizé, France.

Appendix C. Parameter estimations and plot representations of variations in adult body mass of roe deer at Trois-Fontaines, France.

Appendix D. Graphical representations of direct and indirect effects of environment in early life on adult body mass of roe deer at Chizé, France.

Appendix A. Estimates of the temporal autocorrelation for weather variables and population size at Chizé (Fig. 2.5) and Trois-Fontaines (Fig. 2.6). Temporal autocorrelation functions (ACFs) include confidence intervals (dashed blue lines) based on uncorrelated series. In both sites, temporal autocorrelation was not present for weather variables but occurs for population size.

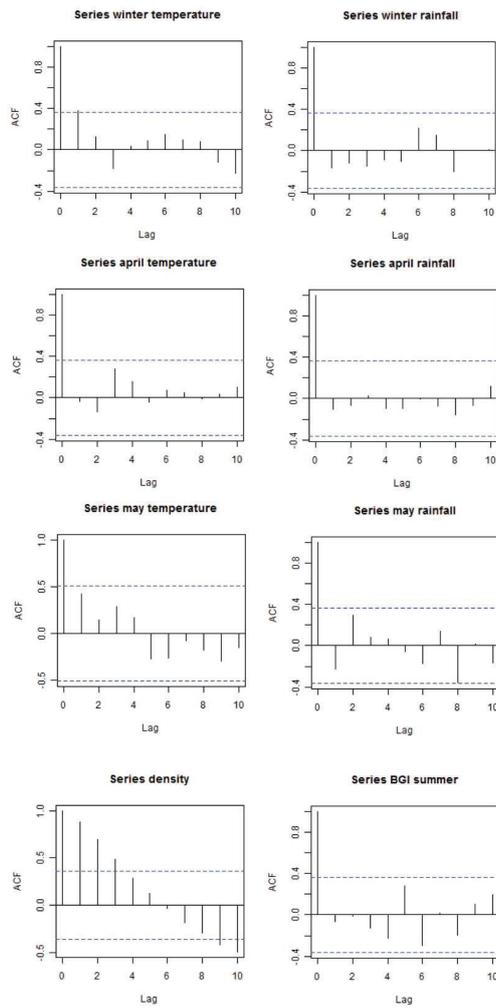


Fig. 2.5. Temporal autocorrelation functions (ACFs) for environmental variables at Chizé.

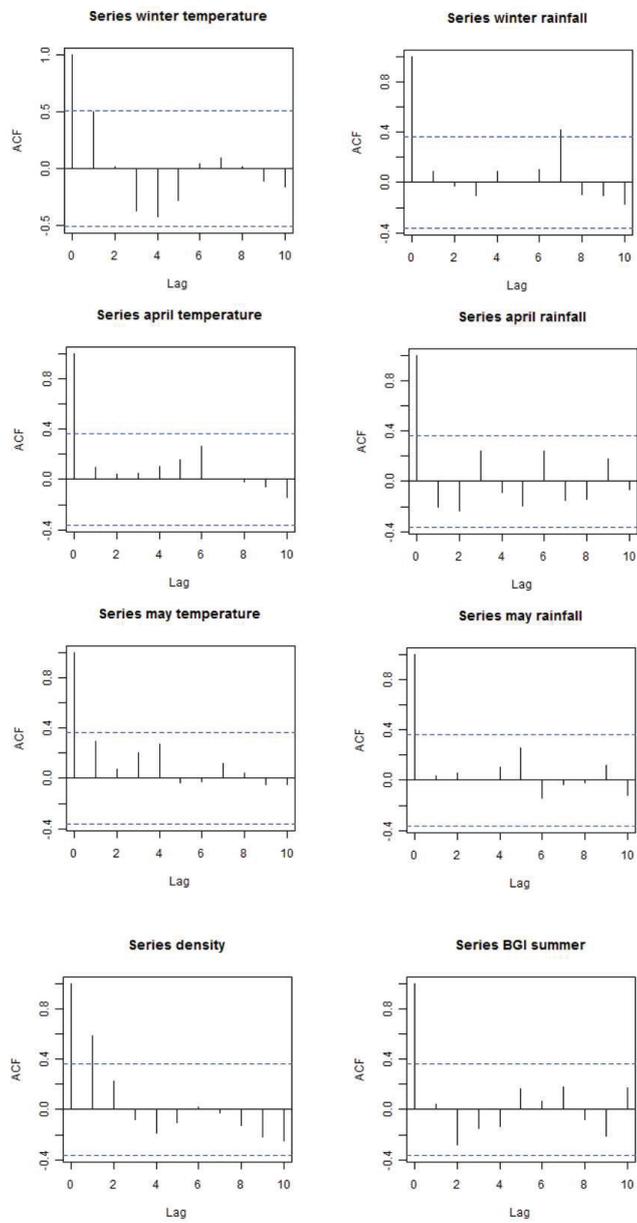


Fig. 2.6. Temporal autocorrelation functions (ACFs) for environmental variables at Trois-Fontaines.

Appendix B. Parameter estimations (Tab. 2.1) and plot representations (Fig. 2.7) of variations in adult body mass of roe deer at Chizé, France.

Table 2.1. Parameter estimates for adult body mass at Chizé obtained from the linear model including the effects of sex, population size (POP) and temperatures in May (T_{May}) during the year of birth and average POP experienced between ages 1 and 4 ($POP_{ages1-4}$) ”:” stand for the interactive effects.

Parameter	Estimate	SE	T value	P value
Intercept	16.26	3.91	4.15	< 0.001
Sex (female)	- 1.76	0.21	- 8.06	< 0.001
$POP_{ages1-4}$	$- 5.05 \times 10^{-3}$	1.45×10^{-3}	- 3.46	< 0.001
POP	0.04	0.01	3.99	< 0.001
T_{May}	0.83	0.25	3.27	0.001
$POP : T_{May}$	$- 3.29 \times 10^{-3}$	7.19×10^{-4}	- 4.58	< 0.001

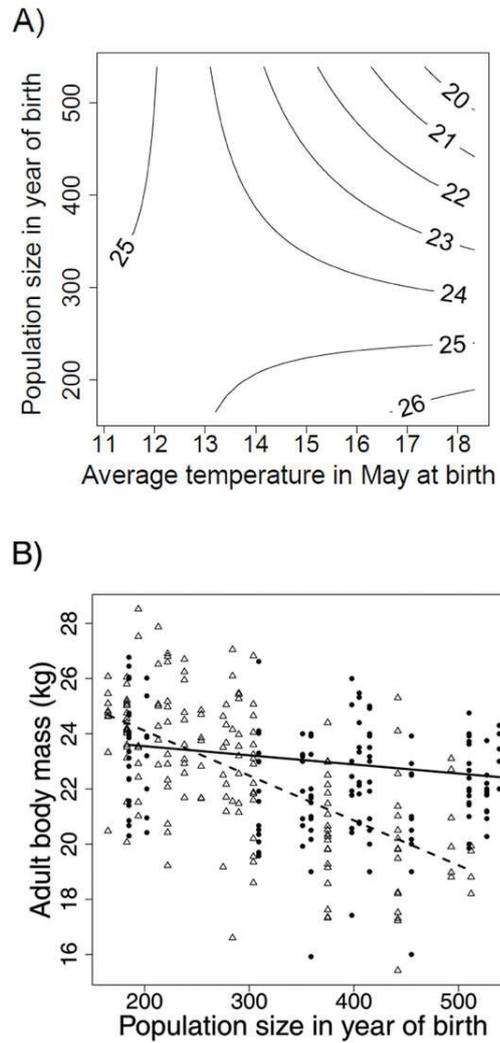


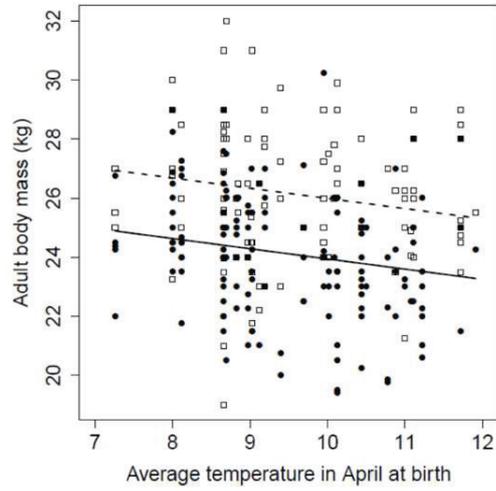
Fig. 2.7. Conditions in early life influence adult body mass (standardized to females) at Chizé. (A) Contour plot showing interaction between population size and temperatures in May during the year of birth influence adult body mass. (B) Relationship between body mass and population size at birth for adults that experienced lower (filled circles, solid line), and equal or greater (open triangles, dotted line) median temperatures in May at birth.

Appendix C. Parameter estimations (Tab. 2.2) and plot representations (Fig. 2.8) of variations in adult body mass of roe deer at Trois-Fontaines, France.

Table 2.2. Parameter estimates for adult body mass at Trois-Fontaines obtained from the linear model including the effects of sex, and temperatures in April (T_{Apr}) and May (T_{May}) during the year of birth.

Parameter	Estimate	SE	T value	P value
Intercept	32.06	1.59	20.15	< 0.001
Sex (female)	- 2.03	0.27	- 7.44	< 0.001
T_{Apr}	- 0.31	0.11	- 2.60	0.009
T_{May}	- 0.21	0.09	- 2.37	0.019

A)



B)

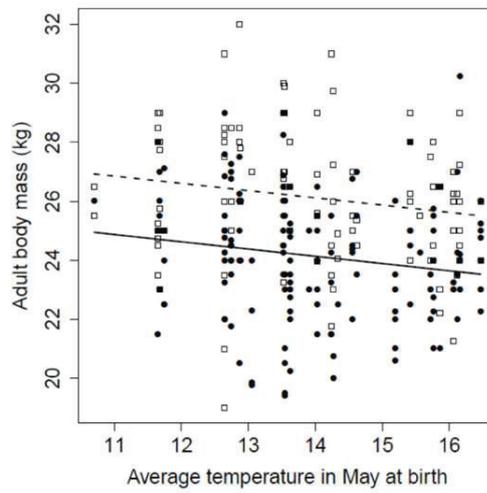


Fig. 2.8. Effects of temperatures in (A) April and (B) May in the year of birth on adult body mass in males (open square, dotted line) and females (filled circles, solid line) roe deer at Trois-Fontaines, France.

Appendix D. Graphical representations of direct and indirect effects of environment in early life on adult body mass of roe deer at Chizé, France (Fig. 2.9).

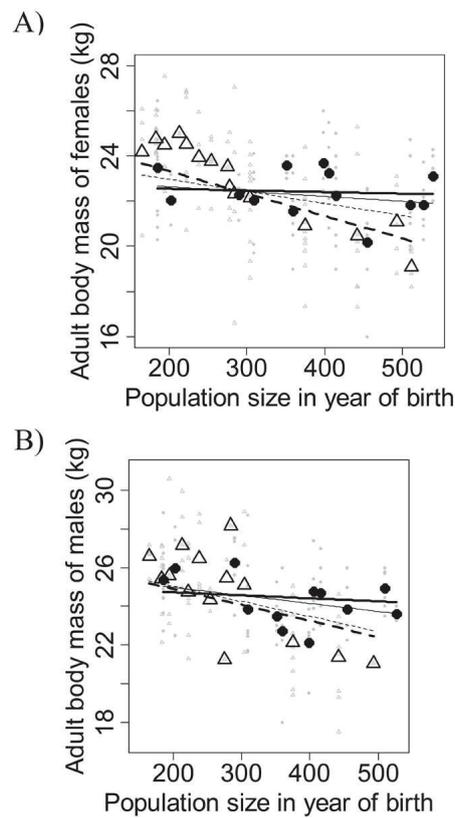


Fig. 2.9. Plot showing the direct and indirect effects of environment in early life (interacting effects of population size and temperature in May at birth) on adult body mass of (A) 173 females and (B) 146 males at Chizé, France. Individuals were divided into two groups for convenience: those that experienced lower (filled circles, solid line), and equal or greater (open triangles, dotted line) median temperatures in May at birth. The thick lines represent the predictions of the model with direct and indirect effects whereas the thin lines represent the predictions of the model with indirect effects only.

Part II

Understanding the nature of the long-term effects of early-life conditions on life history

Chapter 3

Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate

A version of this chapter is published as: Douhard M, Plard F, Gaillard JM, Capron G, Delorme D, Klein F, Duncan P, Loe L E, Bonenfant C (2014) Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate, Proceedings of the royal society B-Biological sciences, vol. 281 pp.20140276-20140276



Photo credit: Maryline Pellerin

Abstract

The Predictive Adaptive Response (PAR) hypothesis proposes that animals adjust their physiology and developmental trajectory during early life in anticipation of their future environments. Accordingly, when environmental conditions in early life match environmental conditions during adulthood, individual fitness should be greater. Here we test this hypothesis in a long-lived mammal, the roe deer, using data from two contrasting populations, intensively monitored for >35 years. In the highly productive site, the fitness of female roe deer increased with the quality of environment during adulthood, and contrary to predictions of PAR, individuals born in good conditions always outperformed those born under poor conditions. In the resource-limited site, the fitness of female roe deer born in poor years was better than those born in good conditions in poor years when the animals were adult, but not in good years. Although consistent with predictions of PAR, we showed that this pattern is likely to be a consequence of increased viability selection during the juvenile stage for animals born in poor years. While PARs are often advanced in evolutionary medicine, our findings suggest that detailed biological processes should be investigated before concluding to the existence of this phenomenon.

3.1 Introduction

Although the role of environment in the development of an individual has been recognized for a long time (Hertwig 1900), understanding the interplay between the developing individual and its environment continues to be a major challenge for evolutionary biologists (Bateson et al. 2004). Previous studies, conducted on a large range of taxa including humans, have shown that environmental conditions early in life (i.e. the period when the architecture of the body is being established, Metcalfe and Monaghan 2001) can have long-term effects on life history traits (Lindström 1999, Lummaa and Clutton-Brock 2002, Beckerman et al. 2002). The question is whether these long-term, environmentally induced changes represent an adaptive response to different environments, or are a consequence of constraints on development imposed by food resource availability (Monaghan 2008, Clutton-Brock and Sheldon 2010).

Building on the concepts of ‘foetal programming’ (Lucas 1991) and of ‘thrifty phenotype’ (Hales and Barker 1992) issued from human medicine, the Predictive Adaptive Response (PAR) posits that a young animal should adjust its physiology during early development in anticipation of its future environment (Gluckman and Hanson 2004, Bateson et al. 2004, Gluckman et al. 2005*a*). Gluckman and colleagues have proposed that the capacity of individuals to adjust their development in response to early environments has evolved via natural selection, in a similar way to adaptive phenotypic plasticity (West-Eberhard 1989, Pigliucci et al. 2006, Nussey et al. 2007*b*). The proximate mechanisms underlying PARs include epigenetic changes in gene regulation, variation in organ structure or alteration in cell number (Gluckman and Hanson 2004, Gluckman et al. 2005*b*). Ultimately, fitness benefits would arise from a slower metabolism increasing survival in food-limited environments, or from a higher metabolism allowing greater reproductive success when food resources are plentiful (Bateson et al. 2004).

PAR is thus a form of developmental plasticity where fitness benefits of the

developmental responses to early life environment are not immediate but postponed to the adult stage (Gluckman et al. 2005a). The adaptive value of the PAR depends, however, on the strength of the correlation between environmental conditions experienced during early life and environmental conditions experienced during adulthood, as mismatching may lead to fitness disadvantages and disease (Gluckman and Hanson 2004). For instance, a mismatch between pre- and post-natal nutrient availability increased the risk for cardiovascular disorder in sheep (*Ovis aries*, Cleal et al. 2007). Hence, a key aspect of the PAR hypothesis is that fitness should be the highest for individuals for whom early life conditions match conditions during adulthood (Fig. 3.1a). The most obvious competing hypothesis is that harsh early life environmental conditions can constrain body development, leading individuals born under favorable conditions to outperform consistently those born in adverse conditions (Fig. 3.1b), also known as the ‘silver spoon’ effect (Grafen 1988).

While long-term consequences of early life conditions have long been recognized in animal populations in the wild (Albon et al. 1987, Madsen and Shine 2000), most studies have focused on testing for ‘silver spoon’ effects without including possible effects of environmental conditions during adulthood. On the other hand, the PAR hypothesis is currently much debated (Wells 2006; 2007, Rickard and Lummaa 2007, Hayward et al. 2013, Hayward and Lummaa 2013). This hypothesis is often advanced in the medical and epidemiological literature for explaining the occurrence of metabolic diseases, but empirical support for PARs remains scarce in long-lived species (Cleal et al. 2007). Moreover, tests of the PAR hypothesis assessing consequences for fitness itself are currently lacking. Comparing the fitness of individuals when early conditions either match environmental conditions during adulthood or do not is a key requirement for testing the PAR hypothesis (Rickard and Lummaa 2007).

Long-term monitoring of a large number of known-age animals in two contrasting roe deer (*Capreolus capreolus*) populations provided us a unique oppor-

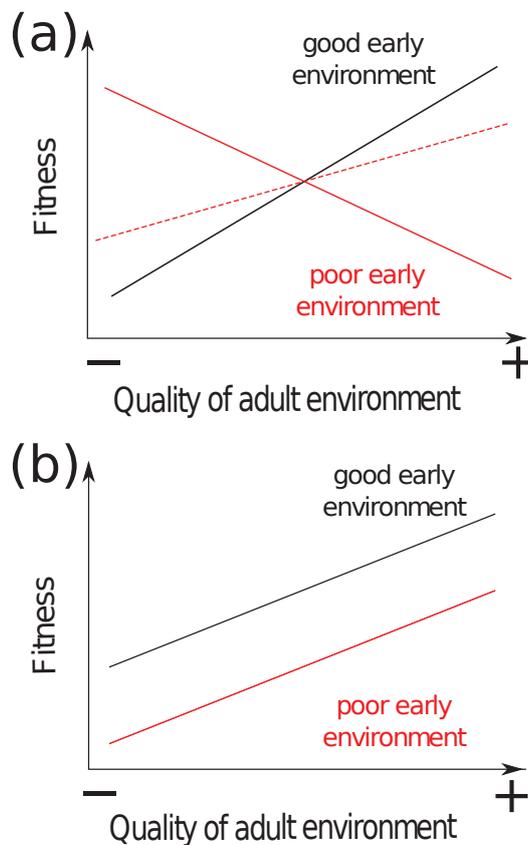


Fig. 3.1. Variation in mean fitness as a function of environmental conditions during early life and adulthood under two different scenarios. (a) Predictive Adaptive Response (PAR). For individuals born in good environmental conditions, mean fitness increases as the adult environment improves. For individuals born in poor environmental conditions, mean fitness may increase weakly (dotted red lines) or decrease (solid red lines) with improvement of the adult environment. In poor environmental conditions during adulthood, however, individuals born in poor conditions perform better than those born in good conditions. In contrast, individuals born under favorable conditions have higher mean fitness than those born under poor conditions when environmental conditions during adulthood are good. (b) 'Silver spoon' effect. Here there is no environmental matching. Mean fitness increases with the quality of adult environment and individuals born in good environmental conditions always have higher mean fitness than those born in poor environmental conditions. Adapted from (Bateson et al. 2004, Monaghan 2008).

tunity to test the PAR hypothesis in a long-lived, wild, mammalian species. After exploring the correlation of environmental conditions during adulthood with those

in early life, we quantified the effects of the conditions in early life and current environmental conditions on annual adult survival, annual adult reproductive success and mean individual fitness of different cohorts. Under the PAR hypothesis, early and current environmental conditions should interact to affect adult performance: individuals should perform better when they experienced similar conditions during early life and adulthood than when they experienced mismatched conditions (Fig. 3.1a).

3.2 Material and methods

ROE DEER AS A BIOLOGICAL MODEL

The European roe deer is a medium-sized, forest-dwelling herbivore (adult body mass ranges between 20 and 30 kg) with weak sexual size dimorphism (Andersen et al. 1998a). Roe deer can live up to 18 years of age in the wild (Loison et al. 1999a) and are weakly polygynous (Vanpé et al. 2009). Females are iteroparous (one reproductive attempt per year) and can give birth to one to three fawns each year in May-June from 2 years of age onwards (triplets are exceedingly rare in our study areas, see below). Weaning occurs in late summer and dispersing individuals generally leave their mothers at 1 year of age. Being income breeders (sensu Jönsson 1997) female roe deer rely almost exclusively on available food resources rather than body reserves to meet the energetic costs of reproduction (Andersen et al. 2000). Hence, growth rates and survival of fawns directly depend on food resources during the spring and summer of birth (Gaillard et al. 1993b; 1997, Toïgo et al. 2006).

STUDY AREAS AND POPULATIONS

The study was carried out in two fenced forests managed by the Office National des Forêts, the 2,614 ha *Réserve Biologique Intégrale* of Chizé (CH) located in

Western France and the 1,360 ha *Territoire d'Étude et d'Expérimentation* of Trois-Fontaines (TF) in Eastern France. Primary production in the CH forest is quite low due to poor soils and frequent summer droughts, while TF is a rich and productive forest due to high-quality soils and infrequent summer droughts (supplementary material, Tab. 3.1). No predator of roe deer occurred in either site and the few roe deer hunted at TF were censored from the data set. Both populations have been intensively monitored by using capture-mark-recapture methods since 1976 at TF and 1978 at CH. About half the roe deer present in a given population were captured every year (between 8 and 12 days of captures, mostly in January-February) using drive nets. At capture, all animals are sexed and weighed to the nearest 100 g. Since 1985, newborn fawns have also been captured and marked around the time of birth, from April 15 to June 15 (Gaillard et al. 1997). In addition to captures, intensive observations took place every year in both study sites during summer and autumn to assess the reproductive success of marked females (see Gaillard et al. 2000a, for details). All procedures for capturing and handling live animals have been performed under the authority of the ONCFS and have been approved by the Director of Food, Agriculture and Forest (Prefectoral order 2009–14 from Paris).

ROE DEER LIFE HISTORY TRAITS

All females included in this study were of known age because they had been marked as newborn fawns during spring, or as fawns in their first winter (8–9 months of age) when age can be reliably established on the basis of the presence of milk teeth (Hewison et al. 2002). We considered reproductive and survival characteristics of prime-aged females (2–8 years) before senescence; these parameters do not vary with age in prime-aged females (Gaillard et al. 1998a; 2004). We divided annual reproductive success into three categories: (i) ‘no offspring weaned’, (ii) ‘one offspring weaned’, and (iii) ‘two or three offspring weaned’ (Hamel et al. 2009a). Triplets were absent at CH and accounted for only 1.8% of

litters at TF.

MEASURES OF ENVIRONMENTAL VARIATION

Previous studies have shown that average body mass of weaned offspring is an integrator of environmental conditions around the time of birth (i.e. in spring-summer) for which weather variables and population size are only proxies (Toïgo et al. 2006, Pettorelli et al. 2006). Thus, we used the average body mass of roe deer fawns in January-February (about 8 months of age) of each year, adjusted for possible confounding effects (see below), as a measure of environmental conditions during the previous year (see Festa-Bianchet et al. 2004, Hamel et al. 2009*b*, for a similar approach). Hence, environmental conditions experienced each year by juveniles and adults were measured by the average body mass of roe deer fawns the next winter. We estimated year-specific body mass of fawns with linear models (one per site), including sex (to account for the weak sexual size dimorphism of roe deer, Andersen et al. 1998*a*), month of capture (to control for fawn growth over the winter catch season, Hewison et al. 2002) and habitat type at CH only (to control for possible confounding effects of habitat quality, see Tab. 3.1 in supplementary material and Pettorelli et al. 2003*a* for further details). No heterogeneity of habitat occurred in TF at the home range scale. The adjusted year-specific body masses of roe deer fawns are shown in Fig. 3.5 (supplementary material).

STATISTICAL ANALYSIS

As a first step, we used linear models to investigate relationships between environmental conditions during early (i.e. year of birth) and adult (i.e. the average environment between 2 and 8 years of age) stages. Then we performed analyses on life history traits with environmental conditions in early life characterized as a two-level factor, dichotomized by a median split (bad conditions: below median value of year-specific fawn body mass, good conditions: above or equal median

value of year-specific fawn body mass). This allowed us to test explicitly the predictions displayed in the Fig. 3.1 (i.e. an interaction for PAR and an additive effect for silver spoon hypothesis; see Hayward and Lummaa 2013 for a similar approach). Interpretation of the results did not change when we considered the quality of early life conditions as a continuous variable (supplementary material, Tab. 3.2).

To test the PAR hypothesis for shaping variation in reproductive success of female roe deer, we used multinomial mixed models (Agresti 2002) of annual reproductive success, such that the cumulative probability that a female weaned 0, 1 and ≥ 2 fawns in a given year is equal to 1. Environmental conditions experienced during year of birth and at a given breeding year plus the interaction between these two variables were entered as fixed effects. Female identity was entered as a random effect, controlling for the non-independence of repeated measures on the same female. Parameters were estimated by maximum likelihood using the package ‘ordinal’ of the software R 2.14 (Christensen 2013). We tested the PAR hypothesis for causing variation in annual adult survival of female roe deer using capture-mark-recapture modelling (Lebreton et al. 1992) with E-SURGE (Choquet et al. 2009). Our models included environmental conditions experienced during year of birth and at a given survival event plus their two-way interactions. Following previous CMR analyses in both populations (Pettorelli et al. 2003b, Choquet et al. 2011), we estimated time-dependent capture probabilities (3 periods at TF, 1976-1999, 2000 and 2001-2010; 13 periods at CH, 1978-1985, 1986-1999, and annual capture probabilities since 2000). In all models, we used a backward selection procedure, testing successively the first-order interactions and, if not statistically significant, the main effects of covariates. Statistical significance was assessed by Likelihood Ratio Test (LRT). Estimates (mean \pm SE) and sample sizes (n) are given in parentheses.

Finally, we quantified the fitness consequences of early and adult conditions of life as a final test of the PAR. At both TF and CH, we built two sets of Leslie

matrix models (Caswell 2001), one for each type of environmental conditions in early life (two groups: bad vs. good). We entered the predicted values of reproduction and survival rates according to their relationship with environmental conditions during adulthood (represented as lines in Figs. 3.2 and 3.8 in supplementary material) in matrix models (supplementary material, Fig. 3.6) to obtain the predicted mean fitness, measured as the asymptotic growth rate (Fisher 1930), of each of these groups facing different adult conditions. We did the same using observed reproduction and survival rates (represented as points in Figs. 3.2 and 3.8 in supplementary material) to get the observed mean fitness of each of these groups facing different adult conditions.

3.3 Results and Discussion

ENVIRONMENTAL VARIABILITY AND PREDICTABILITY

At TF, average body mass of fawns was highly variable among years ($F_{(d.f.=36,1770)} = 12.68$, $p < 0.001$; coefficient of variation = 6.5 %) ranging from 14.80 ± 0.32 kg in 2005 to 20.27 ± 0.28 kg in 1977 (supplementary material, Fig. 3.5a). At CH, average body mass of fawns was also highly variable among years ($F_{(d.f.=34,1757)} = 27.19$, $p < 0.001$; coefficient of variation = 10.0 %) ranging from 12.17 ± 0.36 kg in 2011 to 17.72 ± 0.34 kg in 1995 (supplementary material, Fig. 3.5b). Environmental conditions were extremely harsh between 1983-87 and since 2003 at CH with all average annual body mass < 14.5 kg.

The correlation between the environmental conditions in early and adult stage was high and positive in the highly productive population of TF ($\beta = 0.43 \pm 0.10$, $p < 0.001$, $R^2 = 0.40$, supplementary material, Fig. 3.7a) but non-existent in the food-restricted population of CH ($\beta = 0.17 \pm 0.19$, $p = 0.37$, $R^2 = 0.03$, supplementary material, Fig. 3.7b). Thus, PAR could only occur at TF because without a reliable cue of future environmental conditions, there is no basis for an adaptive scenario in the long run (Kuzawa 2005, Wells 2007, Hayward and

Lummaa 2013, Nettle et al. 2013). However, this prediction must be viewed with caution because the observed environmental variability during the study period does not necessarily represent the long-term and past environment in which PAR could have been favored by natural selection.

TESTING THE PAR HYPOTHESIS

Contrary to expectations from PAR, we found no evidence for an interaction between early life and current environmental conditions on annual reproductive success at TF ($n = 656$, $\chi^2_{(d.f.=1)} = 0.07$, $p = 0.79$) or at CH ($n = 275$, $\chi^2_{(d.f.=1)} = 0.10$, $p = 0.76$). In both populations, the annual reproductive success of adult females increased with the quality of the current environment (TF: $\chi^2_{(d.f.=1)} = 3.48$, $p = 0.06$, $\beta = 0.19 \pm 0.10$; CH: $\chi^2_{(d.f.=1)} = 4.10$, $p = 0.04$, $\beta = 0.18 \pm 0.09$). Being income breeders female roe deer do not accumulate significant body reserves for reproduction (Jönsson 1997, Andersen et al. 2000) so reproductive success strongly depends on changes in food resources during the last weeks of gestation and early lactation, when reproductive energetic costs peak (Sadleir 1987). Overall, females born in favorable conditions had a consistently higher reproductive output than those born in poor conditions (TF: $\chi^2_{(d.f.=1)} = 9.95$, $p = 0.001$, $\beta = 0.62 \pm 0.20$; CH: $\chi^2_{(d.f.=1)} = 5.82$, $p = 0.01$, $\beta = 0.64 \pm 0.26$). For instance, females born in good environmental conditions had 2.15 and 2.29 times higher chances of rearing two fawns to weaning than females born under harsh conditions at TF and CH, respectively (Fig. 3.2a and Fig. 3.2d). This probably resulted from long-term positive consequences of early environmental conditions on body mass (Douhard et al. 2013), which in turn, influenced reproductive performance of females (Gaillard et al. 2000b, Hamel et al. 2009b).

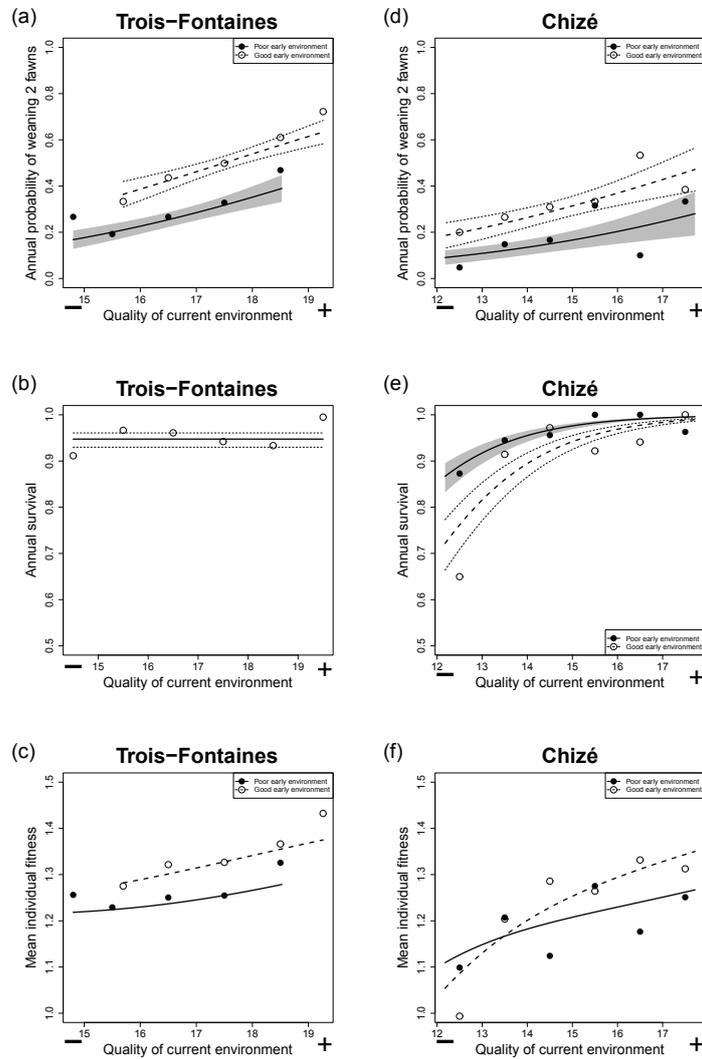


Fig. 3.2. Influence of early life and current environmental conditions on annual fitness components and mean annual fitness of adult female roe deer in both sites. Variation in the annual probability of weaning 2 fawns (a and d), annual survival (b and e) and mean annual fitness (c and f) are shown. The average body mass of roe deer fawns in January-February was used as an annual measure of environmental conditions experienced by female roe deer during the previous year (see Materials and Methods). The lines represent model predictions with their 95% confidence intervals and points indicate the observed means for each class of 1-kg average fawn body mass. See also Fig. 3.8 in supplementary material for effects of early life and current environmental conditions on the annual probability to wean 0 or 1 fawn.

As for reproduction, no interaction between early life and current environmental conditions could be detected for annual adult survival rate (TF: $n = 322$, $\chi^2_{(d.f.=1)} = 0.14$, $p = 0.71$; CH: $n = 331$, $\chi^2_{(d.f.=1)} = 0.15$, $p = 0.70$). Annual survival of adult females was high and quite constant at TF (Fig. 3.2b), irrespective of the environmental conditions experienced early in life ($\chi^2_{(d.f.=1)} = 0.94$, $p = 0.33$) and in the current year ($\chi^2_{(d.f.=1)} = 0.1$, $p = 0.75$). At CH, annual adult survival was positively influenced by the quality of current environment ($\chi^2_{(d.f.=1)} = 31.16$, $p < 0.001$, Fig. 3.2e) but, unexpectedly, females born in favorable conditions consistently showed a lower survival than those born in poor conditions ($\chi^2_{(d.f.=1)} = 11.71$, $p < 0.001$, Fig. 3.2e).

At CH, as female roe deer born in poor conditions have lower reproduction but higher survival rates than females born in good conditions, the overall effect of early conditions on mean fitness depends on the relative effects of the environment on these two demographic rates. We found that under favorable adult conditions, females born in good conditions had a higher mean fitness than those born in poor conditions (Fig. 3.2f). However, when adult conditions became very harsh (as observed in 6 years) at CH, the negative effects of early life conditions on adult survival counteracted their positive influence on reproduction because females born under poor environmental conditions showed a higher mean fitness than those born under good conditions (Fig. 3.2f). At TF, female roe deer born in poor conditions had lower fitness than females born in good conditions independent of the environmental conditions during adulthood.

THE CONFOUNDING EFFECT OF VIABILITY SELECTION ON DETECTION OF PAR

That the mean fitness curves of good and bad cohorts crossed when environmental conditions during adulthood were harsh at CH (Fig. 3.2f) could be interpreted as a support for the PAR (Fig. 3.1a). However, a more parsimonious explanation may involve a difference in viability selection (*sensu* Fisher 1930) during the earli-

est stage of life. Indeed, early body development of roe deer was highly constrained by poor early nutrition in this population (Toïgo et al. 2006, Pettorelli et al. 2006) such that cohorts born under poor conditions may have experienced high condition-dependent mortality. This resulted in a ‘filtering effect’ so that under poor early life environmental conditions only the best roe deer survived to adulthood, leading to a high survival in adulthood for these cohorts. For long-lived species like roe deer, juvenile survival is indeed highly variable and sensitive to environmental conditions (Gaillard et al. 2000*b*). For instance, only 18% of newborns survived until 8-9 months of age during the severe spring-summer drought in 2005 at CH. Conversely, cohorts born under favorable conditions may have experienced a weak viability selection in early life so weaker individuals can be recruited into the population as adults, but have then suffer from increased mortality when meeting harsh environmental conditions during adulthood. In support of this ‘filtering effect’, the strength of viability selection favouring large body mass decreased with the quality of the environment in early life at CH ($\chi^2_{(d.f.=1)} = 4.62$, $p = 0.03$, Fig. 3.3a). In addition, cohorts suffering from high juvenile mortality showed subsequently higher survival in adulthood ($\chi^2_{(d.f.=1)} = 8.15$, $p = 0.004$, Fig. 3.3b). Nevertheless, no effect of viability selection was detectable on reproduction in this population because females surviving harsh early life conditions hardly reached the threshold body mass of 22 kg ($\chi^2_{(d.f.=1)} = 23.01$, $p < 0.001$, Fig. 3.4), above which they raise 2 fawns successfully (Gaillard et al. 1992). Strong viability selection is thus likely to explain the opposite effects of early life conditions on reproduction and survival (Fig. 3.2d and 3.2e) and the resulting interactive effects between environmental conditions during early life and adulthood on mean fitness (Fig. 3.2f) we observed in the food-limited population of CH.

In the highly productive forest of TF, even if the strength of viability selection is higher when early environmental conditions are poor ($\chi^2_{(d.f.=1)} = 3.99$, $p = 0.04$, supplementary material, Fig. 3.9) it was half as strong as the viability selec-

tion that bad cohorts suffered at CH (on a logit scale, $\beta = 0.32 \pm 0.06$ at CH vs. $\beta = 0.17 \pm 0.07$ at TF). Consequently, a low juvenile survival was not associated with higher adult survival at TF ($\chi^2_{(d.f.=1)} = 0.39$, $p = 0.53$), so the low viability selection during juvenile stage had no consequences on mean fitness of good and bad cohorts during adulthood in this population with abundant resources. Hence, not accounting for between-year differences in viability selection during the earliest stages of life can mimic an apparent support for PAR, in particular under harsh environmental conditions.

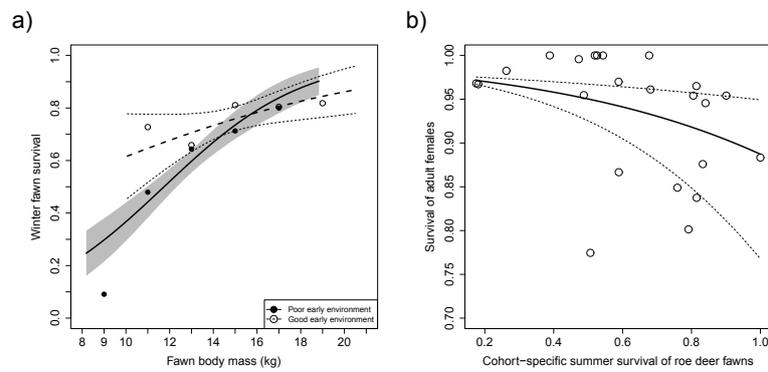


Fig. 3.3. Viability selection during juvenile stage and its consequences on adult survival in the population of Chizé, France. (a) Relationship between winter fawn survival (between 8-9 and 20-21 months of age) of female roe deer and their body mass at 8-9 months of age (adjusted for date of capture) in relation to the quality of early life environmental conditions. (b) Relationship between survival of adult female roe deer and their cohort-specific summer fawn survival (between 0 and 8-9 months of age). The lines represent model predictions with their 95% confidence intervals.

3.4 General Discussion

Female roe deer do not adjust their phenotype during their first year of life in anticipation of their future environments, providing no support for the PAR hypothesis. Much of the empirical evidence in support of the PAR comes from short-lived species (Lee and Zucker 1988, van den Heuvel et al. 2013, Dantzer

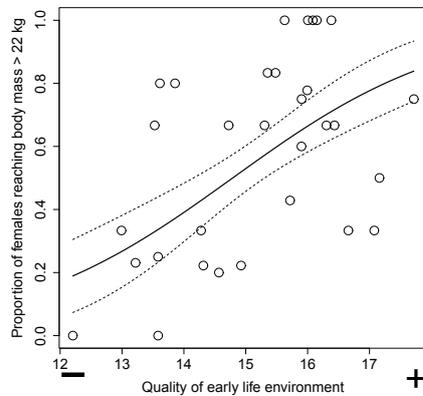


Fig. 3.4. Relationship between the proportion of adult female roe deer with a body mass > 22 kg and the quality of early life environmental conditions at Chizé, France. The average body mass of roe deer fawns in January-February was used as an annual measure of environmental conditions experienced by female roe deer during the previous year (see Materials and Methods). The solid line represents the predicted relationship with 95% confidence intervals (dotted lines).

et al. 2013). For instance, female butterflies experiencing food restriction during larval development change their body allocation via an increased thorax ratio (i.e. thorax mass/body mass) that leads to better flight performances during the adult stage, which, in turn, enhance dispersal into higher quality habitats (van den Heuvel et al. 2013). However, the extrapolation of such results to long-lived species as done by Gluckman and colleagues in humans has often been questioned (Kuzawa 2005, Wells 2006; 2007). The evolution of PAR relies on the assumption that early environmental conditions generally predict adult environmental conditions. Simulations recently performed by Nettle and colleagues showed that environmental autocorrelation has to be very high to allow the occurrence of what they called ‘external PAR’ (Nettle et al. 2013). While in short-lived species matching of the conditions of life at the juvenile and adult stages is likely to occur, the long life and the long time required to achieve reproductive maturity of large mammals make such matching less likely in these species (Wells 2006). Despite the marked difference in the correlation of environmental conditions during adulthood with

those in early life ($R^2 = 0.40$ vs. $R^2 = 0.03$ at TF and CH, respectively), our results rather support the ‘silver spoon’ hypothesis, which predicts that body development is constrained by poor early nutrition in both populations. Although the environmental predictability we recorded over the >35-year study period does not necessarily represent the long-term and past environment in which PAR could have been evolved, past environments of roe deer populations are likely to have been highly variable. Like other polytocous deer species, the roe deer is indeed adapted to the dynamics of early stages of forest succession rather than to stable climax woodland (Bunnell 1987).

Beyond the assumption that the environment in early life provides a reliable clue of the environmental conditions during adulthood, the PAR hypothesis requires that embryos are informed about the quality of environmental conditions during pregnancy. This assumption is questionable for some species. Tactics of energy allocation to reproduction vary along an income-capital continuum (Warner et al. 2008) which may have a central role for the evolution of adaptive responses to environmental variation during early in life. In income breeders such as roe deer (Andersen et al. 2000), the offspring developmental trajectory directly depends on resources available to the mother during the energetically costly periods of late gestation and early lactation. In poor years, embryos receive less energy from mothers and, in turn, should be informed on the environmental conditions. However, this is not the case in capital breeders like humans, which use stored fat reserves to meet the high energy requirements of reproduction (Jönsson 1997). By using energy stored before reproduction, like in humans, capital breeders buffer at least partly offspring dependency from environmental conditions during these critical periods.

Since the initial paper by Williams and Nesse (Williams and Nesse 1991), the field of ‘evolutionary medicine’ or ‘Darwinian medicine’ has progressed substantially and become an important component of public health (see Stearns 2012, for a recent review). In humans, PARs are commonly invoked to account for observed

associations between early life conditions and health (as assessed by occurrence of diabetes or cardiovascular diseases) later in life (Gluckman and Hanson 2006). The connection between PAR and human health is relatively straightforward. If the early life environment matches the environment during adulthood, the risk of diseases in late life is low. In contrast, if a mismatch occurs between environments during early life and adulthood, the risk of diseases increases, especially during the post-reproductive period when diseases become relatively invisible to natural selection (Gluckman and Hanson 2004; 2006). Although fitness and health are distinct concepts (Williams and Nesse 1991), both should peak when early and later life environmental conditions match according to the PAR hypothesis. It is important to note that these predictions from the PAR hypothesis about adult health are exactly similar to those from ‘the thrifty phenotype’ hypothesis (Hales and Barker 1992). In contrast to the PAR hypothesis, the ‘the thrifty phenotype’ hypothesis posits that selection favors developmental responses that improve immediate chances of survival at the expense of risking disease later in life (Hales and Barker 1992). Therefore, understanding the evolutionary processes underlying relationships between early life conditions and adult health is needed to discriminate among the competing hypotheses.

The results of our study, based on two populations of the same species living in contrasting environments, clearly demonstrate that harsh early life conditions impose strong developmental constraints with major fitness consequences and do not support the PAR hypothesis. Similarly, Hayward and colleagues recently provided the first empirical test of PAR in humans and found no support for it because individuals experiencing low crop yields in early life showed lower survival and fertility during the famine than individuals experiencing high early life crop yields in preindustrial Finnish populations (Hayward et al. 2013). Moreover, and importantly, we show here that the strong viability selection imposed by very harsh environmental conditions in early life can lead to apparent support for PAR hypothesis. Confounding effects of viability selection have so far been neglected

when testing the PAR hypothesis. Although the PAR hypothesis requires more empirical tests, its validity in long-lived species is increasingly uncertain.

Acknowledgments

We are grateful the many volunteers who contributed to roe deer captures during all these years. An earlier draft of the manuscript benefited from critical comments by I. Rickard and three anonymous reviewers. M. Douhard and F. Plard were funded by PhD scholarships from the French Ministry of Higher Education and Research. C. Bonenfant and J.-M. Gaillard are supported by research grants from CNRS and ONCFS.

3.5 Supplemental material

Table 3.1. A detailed description of the study areas at Chizé and Trois-Fontaines, France.

Parameter	Chizé	Trois-Fontaines
Size	2619 ha	1360 ha
Climate regime	Oceanic under Mediterranean influence	Continental
Winter climate	Mild (mean \pm SE daily temperature in January is $5.63 \pm 0.36^\circ\text{C}$)	Moderately colder winters (mean daily temperature in January is $3.07 \pm 0.39^\circ\text{C}$)
Summer climate	Warm, often dry (in July, mean daily temperature is $20.52 \pm 0.28^\circ\text{C}$ and total rainfall is $53.39 \pm 4.03\text{ mm}$)	Warm but generally wet (in July, mean daily temperature is $19.57 \pm 0.30^\circ\text{C}$ and total rainfall is $72.39 \pm 6.76\text{ mm}$)
Soils	Shallow, calcareous, and not very fertile	Fertile
Forest productivity (long-term average wood production)	$3.77\text{ m}^3.\text{ha}^{-1}.\text{year}^{-1}$	$5.92\text{ m}^3.\text{ha}^{-1}.\text{year}^{-1}$
Habitat structure	Three broad vegetation associations: (1) an oak <i>Quercus spp.</i> forest with mainly hornbeam <i>Carpinus betulus</i> coppice (1046 ha), (2) a beech <i>Fagus sylvatica</i> forest with virtually no coppice (815 ha), (3) an oak forest in which the coppice is mainly Montpellier maple <i>Acer monspessulanum</i> (758 ha)	Homogeneous at the large scale

Table 3.2. Effects of early life (E_{early}) and current ($E_{current}$) environmental conditions on annual reproductive success and survival of adult female roe deer at Trois-Fontaines and Chizé, France. "x" stand for the interactive effects.

Response variable	Effect tested	χ^2	df	P-value	slope on a logit scale (\pm SE)
Trois-Fontaines population					
Annual reproductive success	$E_{early} \times E_{current}$	0.01	1	0.92	–
	E_{early}	29.15	1	< 0.001	0.79 ± 0.19
	$E_{current}$	0.12	1	0.73	–
Annual survival	$E_{early} \times E_{current}$	0.61	1	0.43	–
	E_{early}	0.009	1	0.92	–
	$E_{current}$	0.10	1	0.75	–
Chizé population					
Annual reproductive success	$E_{early} \times E_{current}$	0.01	1	0.92	–
	E_{early}	4.36	1	0.03	0.25 ± 0.12
	$E_{current}$	3.79	1	0.05	0.18 ± 0.09
Annual survival	$E_{early} \times E_{current}$	0.001	1	0.97	–
	E_{early}	7.77	1	0.005	-0.29 ± 0.10
	$E_{current}$	28.54	1	< 0.001	0.61 ± 0.13

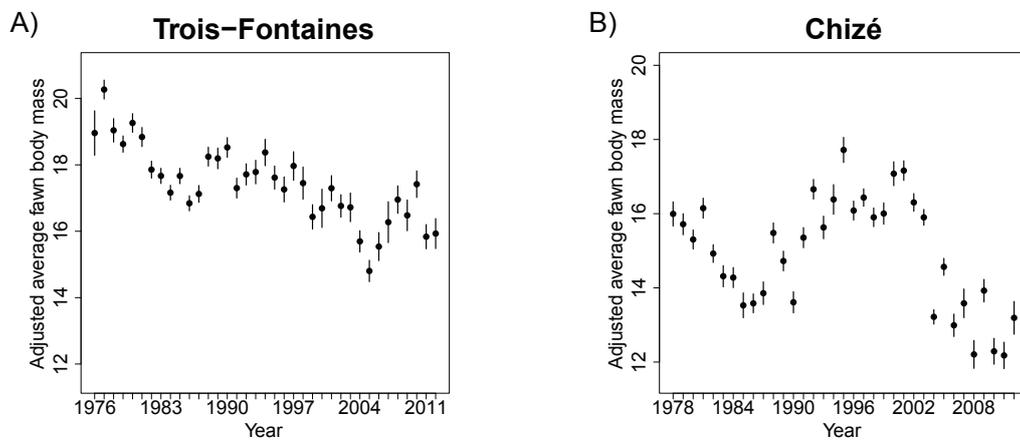


Fig. 3.5. Year-specific body mass (kg \pm 1 SE) of roe deer fawns measured during January-February at A) Trois-Fontaines, B) Chizé, France. Yearly means have been corrected for the influence of the month of capture (standardized to January) and sex (standardized to male) in either population and habitat type at Chizé (standardized to the beech stand).

$$\begin{pmatrix} 0 & R2 & R2 & R2 & R2 & R2 & R2 & R3 \\ \Psi_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \Psi_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \Psi_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \Psi_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \Psi_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \Psi_2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \Psi_2 & \Psi_3 \end{pmatrix}$$

Fig. 3.6. Population projection matrix used for roe deer. R corresponds to recruitment and Ψ to survival. The equality among vital rates is symbolized by the same number. The adult vital rates (R2 and Ψ_2) vary according to the early life and current environmental conditions. The yearling survival (Ψ_1) and vital rates of senescent individuals (R3 and Ψ_3) were fixed at their observed means in each population.

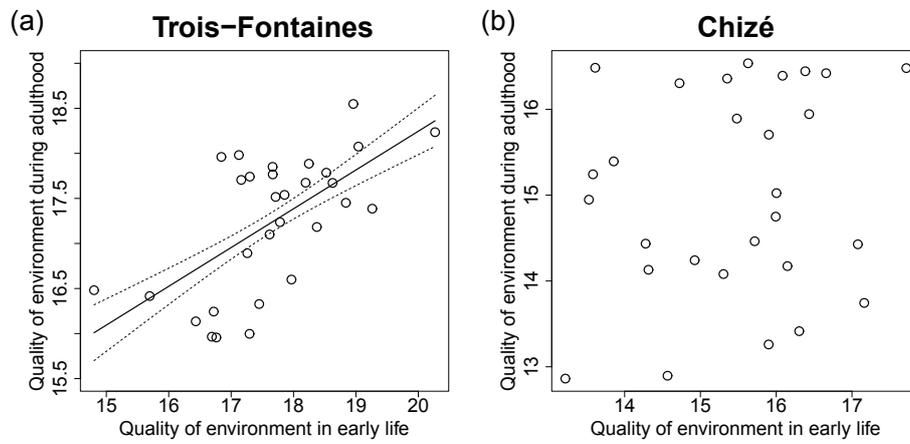


Fig. 3.7. The relationship between average environmental conditions during the adult stage (between 2 and 7 years of age) and early environmental conditions at (a) Trois-Fontaines (TF), (b) Chizé (CH), France. The average body mass of roe deer fawns in January-February was used as an annual measure of environmental conditions experienced by female roe deer during the previous year (see Materials and Methods). The solid line represents predicted relationship with 95% confidence intervals (dotted lines).

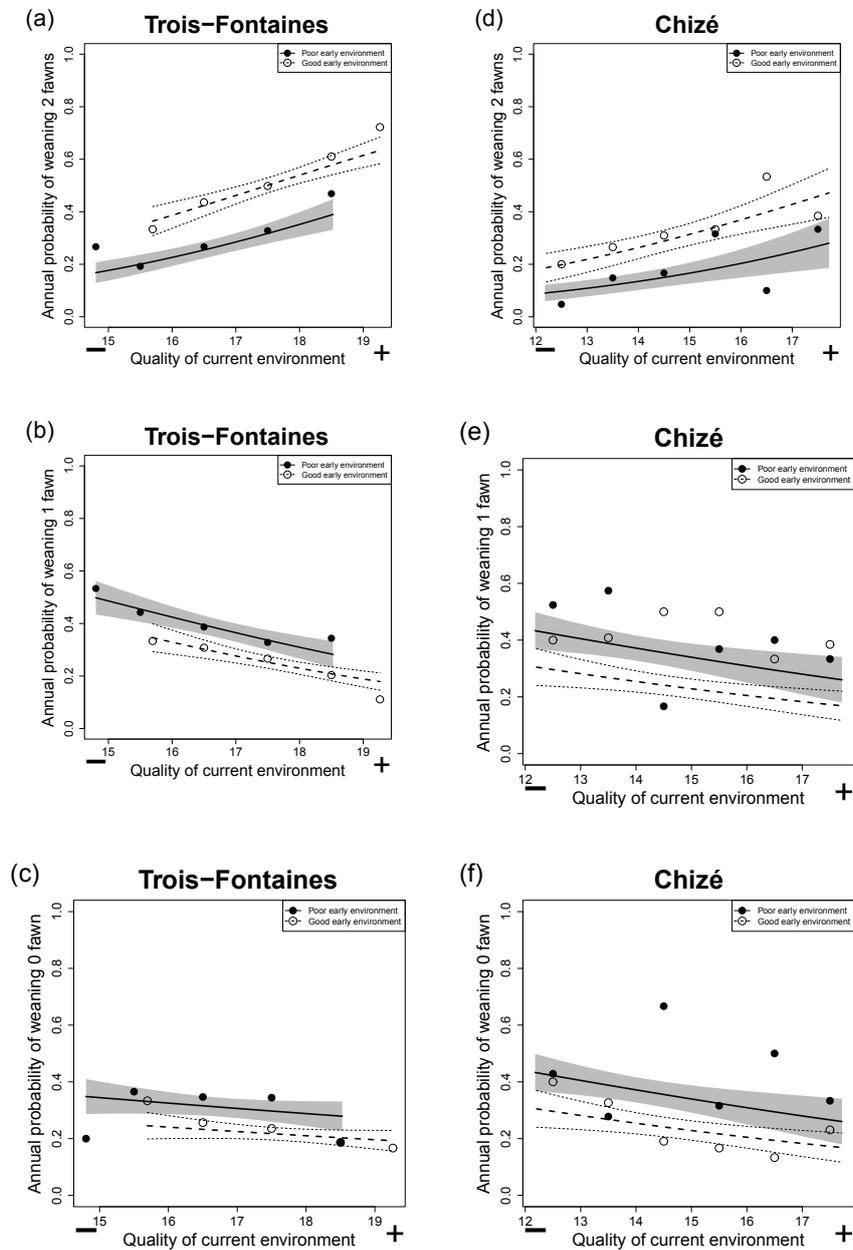


Fig. 3.8. Annual reproductive success (probability to wean 0, 1 or 2 fawns) of adult female roe deer as a function of early life and current environmental conditions at Trois-Fontaines and Chizé, France. Lines represent model predictions with their 95% confidence intervals and points indicate the probabilities of reproduction for each class of 1-kg average fawn body mass (the integrator of current environmental conditions).

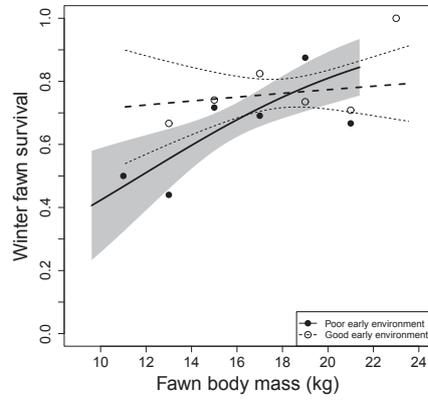


Fig. 3.9. Relationship between survival of yearling female roe deer (between 8-9 and 20-21 months of age) and their body mass at 8-9 months of age (adjusted for date of capture) in relation to the quality of early life environmental conditions at Trois-Fontaines, France. Lines represent model predictions with their 95% confidence intervals and points indicate the observed survival rates for each class of fawn body mass.

Chapter 4

Reproductive tactics are determined during year of birth in a wild mammal

A version of this chapter is: Douhard M, Loe L.E, Bonenfant C, Stien A, Irvine J, Vebjørn V, Ropstad E, Reproductive tactics are determined during year of birth in a wild mammal. In preparation.



Photo credit: Vebjørn Veiberg

Abstract

One of the most fundamental questions in evolutionary ecology is whether long-term effects of early environment arise only because of constraints on development or involve adaptive responses to different environments. To date, empirical studies do not easily separate these possibilities. Using a 20-year population study of the Svalbard reindeer in the high arctic, we show that probabilities of reproducing and surviving declined more rapidly with age amongst females that experienced poor early environments. In response, females born under adversity adopted a reproductive tactic in their early adulthood with increased investment in offspring survival. This developmental plasticity appears to be adaptive, because mothers born in poor conditions, even though they had reduced body size, were able to keep the annual fitness through their first 5 years of life at the same level as females experiencing more favorable early conditions. Developmental plasticity can therefore play an important mitigating role in buffering negative effects of climate change in wild mammal populations.

4.1 Main article

Environmental conditions experienced during the crucial period of early life, can dramatically influence adult phenotypes, from epigenetic changes in gene regulation and metabolism (McMillen and Robinson 2005), to life-history traits such as fecundity and survival (Lindström 1999, Lummaa and Clutton-Brock 2002). The effects of environmental conditions prevailing during early development can also be transmitted across generations (Burton and Metcalfe 2014). However, understanding the nature of these long-term, environmentally induced changes remains an important challenge. Some studies have suggested that the effects of early environment on phenotype only are a consequence of constraints on development imposed by food resource availability (Grafen 1988, Hayward et al. 2013), but other studies argue that these effects have an adaptive basis (Bateson et al. 2004, Gluckman and Hanson 2004).

According to the latter view, poor early-life conditions associated with an accelerated age-related decline in residual reproductive value – defined as the opportunity for future reproduction (Williams 1966) – may create a selective pressure that favors a high energy allocation towards early reproduction (Nettle et al. 2013). Of the few studies to date which have investigated variation in life-history strategies related to early environment, most have been conducted in the laboratory and in human populations (Sloboda et al. 2009, Auer 2010, Nettle et al. 2011). Previous studies in wild vertebrates find evidence for heritability of plasticity (Nussey et al. 2005, Pelletier et al. 2007*b*), suggesting that adaptive phenotypic plasticity can evolve under natural conditions. The evolution of reproductive tactics in response to early environment may have important consequences for population viability and, ultimately, mitigates the negative consequences of climate change. However, the lack of studies of phenotypic plasticity in free-living animals limits our ability to predict the consequences of climate change on these species (Charmantier et al. 2008). Here, we ask how early-life environmental con-

ditions shape life-history responses of females in a wild population of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) in the high Arctic.

Living at high latitudes, the Svalbard reindeer is a large mammal herbivore that experiences almost no predation and human harvesting but must cope with an extreme environment (Solberg et al. 2001). For instance, rain-on-snow events in winter create ice layers in the snow pack that limit access to vegetation which, in turn, increase the risk of starvation (Rennert et al. 2009). The population of reindeer studied here experiences considerable environmental variability, particularly in rain-on-snow events, population density and consequently resource availability. Rain-on-snow events and high population density at adulthood have previously been shown to affect negatively reproductive success of females (Stien et al. 2012). The high environmental variability provides substantial differences between individuals in the environmental quality of their birth year (Fig. 4.1). Furthermore, environmental conditions during early life had profound long-term consequences on body growth in this population. Females born in favorable conditions reached on average a greater skeletal size ($\chi_1^2 = 37.40$, $P < 0.001$, Fig. 4.2) and adult body mass ($\chi_1^2 = 17.33$, $P < 0.001$, slope = 4.21 ± 0.99) than females born under adversity. Adult body condition, calculated as the residuals of the regression of log-transformed body mass on log-transformed skeletal size of each individual, was less affected by the quality of early environment ($\chi_1^2 = 2.71$, $P = 0.10$, slope = 0.029 ± 0.017), suggesting that adult body mass was mainly determined by skeletal growth. To determine whether individuals exhibit adaptive responses that can mitigate the negative effects of poor early environment on development, we: (1) compared age-specific patterns of reproduction (pregnancy rate and offspring survival), survival, and mean individual fitness of different cohorts, and (2) assessed whether individuals born in poor environmental conditions increase their early reproductive effort (Nettle et al. 2013).

Offspring survival from late pregnancy to weaning varied with mother age but in different ways according the environmental conditions experienced early

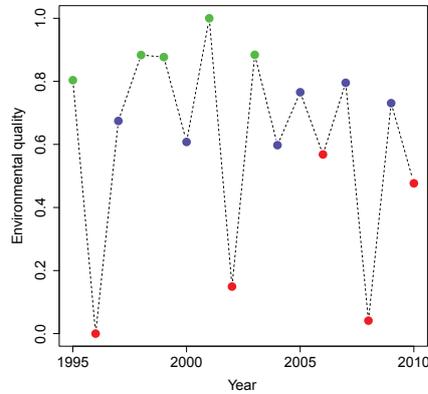


Fig. 4.1. Measures of environmental quality from 1995-2010 in the population of Svalbard reindeer. Environmental quality is estimated as the mean annual body mass of adult females, standardized between 0 and 1 (see material and methods section for a detailed justification). In some analyses, early-life conditions were considered as a three-level factor (red points: poor conditions, blue points: intermediate conditions, green points: favorable conditions).

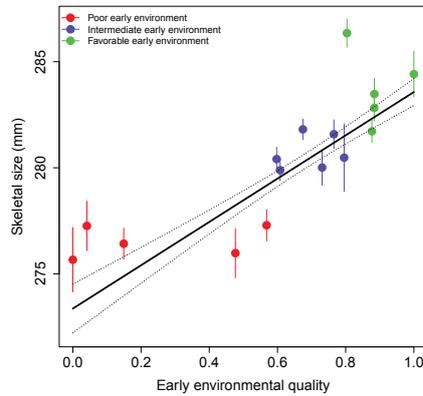


Fig. 4.2. Influence of early environmental conditions on skeleton size of female Svalbard reindeer aged three years or older. The solid line represents the model predictions with SE (dotted lines) and the points are observed mean \pm SE.

in life by mothers (age-by-early life conditions interaction: $\chi^2_1 = 4.15$, $P = 0.04$). Survival of offspring born to mothers that experienced favorable and adverse early

environment was equally high at young maternal age (Fig. 4.3A). However, while offspring survival did not decline with maternal age among mothers born under favorable conditions, females experiencing poor early-life conditions showed a strong age-related decline in this trait (Fig. 4.3A). Survival of offspring born to mothers exposed to intermediate conditions early in life increased initially with mother age, peaking at about 7 years of age, and showed a decline thereafter (Fig. 4.3A). In contrast, there was no effect of environmental conditions in early life on pregnancy rates (age-by-early life conditions interaction: $\chi^2_1 = 0.66$, $P = 0.41$, Fig. 4.3B). Pregnancy rate decreased only at very old ages, supporting the contention that, lactation is more costly than gestation in mammals (Clutton-Brock et al. 1989). Although we did not find evidence for a statistically significant effect of age-by-early life conditions interaction on adult survival ($\chi^2_2 = 3.10$, $P = 0.21$), the trend was similar to results found for offspring survival. Survival was high at young ages, independent of early environmental quality, but tended to decline more rapidly with age amongst females that experienced poor early environments (Fig. 4.3C).

The reproductive responses to environmental conditions experienced during early development found in our study could be a response to natural selection. Since adverse conditions in early life reduce residual reproductive value, a high investment in reproduction at young ages should be selected for in individuals born under poor environmental conditions. On the other hand, a high early reproductive effort may be costly in terms of subsequent growth, survival or reproduction (Williams 1966). Hence, a lower investment in reproduction for individuals born under favorable conditions, that exhibited almost no reproductive senescence, should exceed the lost benefits of intense early reproductive effort. In large mammalian herbivores, body mass is a strong determinant of phenotypic quality (Hamel et al. 2009*b*). Many studies have reported a body mass threshold above which most females reproduce (Albon et al. 1983, Garel et al. 2009*b*). We hypothesized that young females born in poor environmental conditions adopt a high investment re-

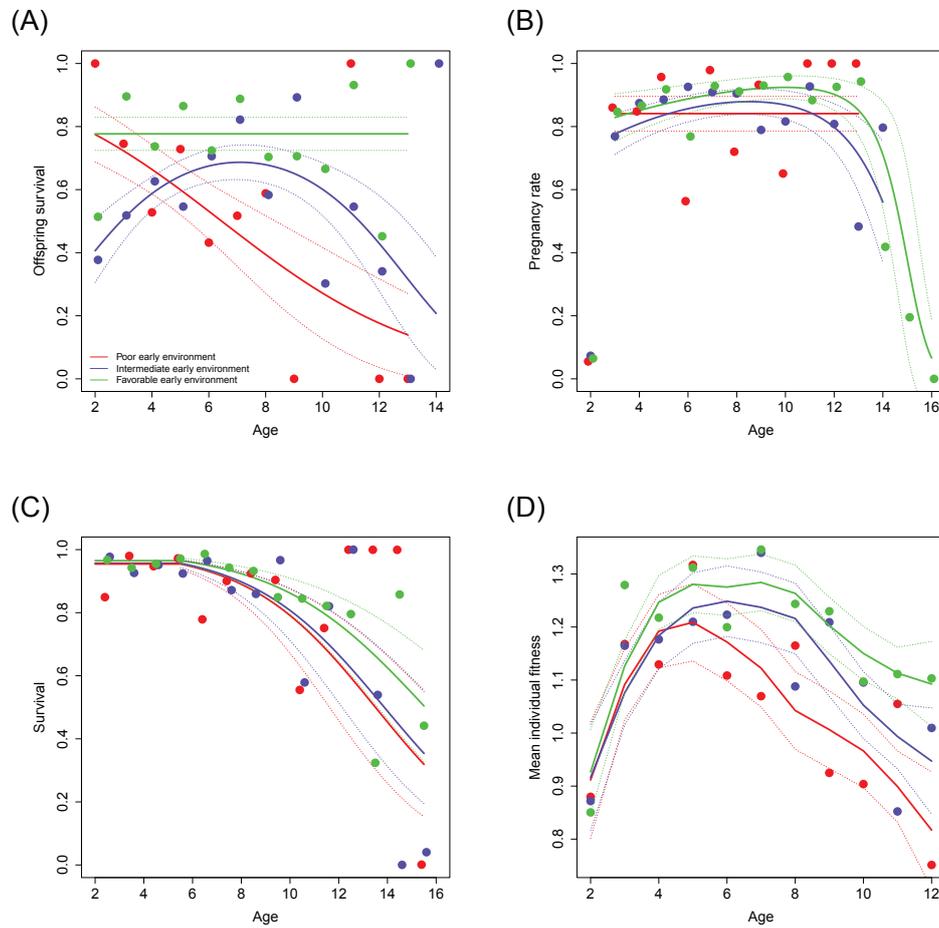


Fig. 4.3. Age-specific patterns of reproduction (A and B), survival (C) and fitness (D) in female Svalbard reindeer according to the environmental conditions experienced during their birth year. The solid lines represent predictions of the models with SE (dotted lines) and the points are observed mean.

productive tactic by having, for a given body mass, a higher reproductive rate than those born in favorable conditions. As predicted, for a given body mass, young females aged 2-5 years old that were born under adversity achieved higher offspring survival (Fig. 4.4 and Tab. 4.1 in supplementary materials) and pregnancy rate (Tab. 4.1 and Fig. 4.5 in supplementary materials). In contrast, although the older

females born under adversity continue to have higher pregnancy rates for a given body mass, their reproductive effort with respect to offspring survival tended to be lower compared to females born under more favorable conditions (Tab. 4.1 and Fig. 4.5 in supplementary materials).

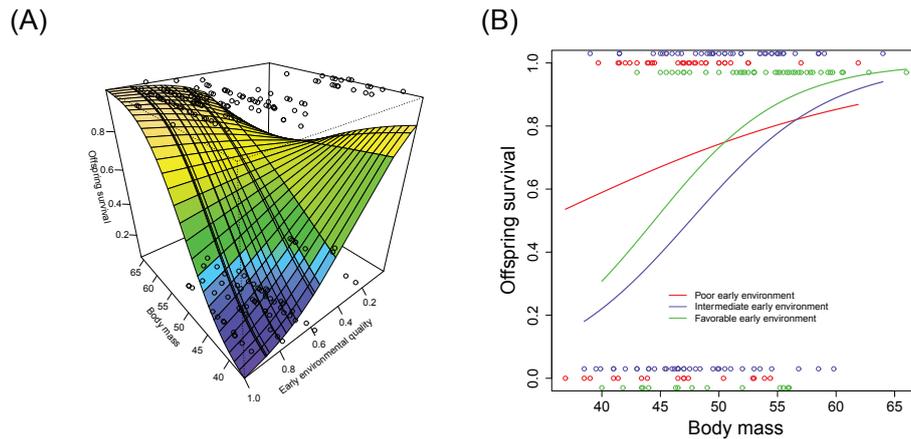


Fig. 4.4. Environmental conditions in early life influence reproductive effort of female Svalbard reindeer. A 3D representation of predicted offspring survival as a function of the interacting effects of maternal body mass and early environmental conditions (see Tab. 4.1 in supplementary materials). (B) Predicted offspring survival as a function of mother body mass in relation with the quality of early environment grouped into three levels (poor, intermediate and good, corresponding to the tertiles of the distribution of environmental quality).

Central to our understanding of the evolution of life histories is the principle that there are trade-offs between the life-history traits of growth, reproduction and longevity (Stearns 1992). In long-lived, iteroparous animals such as large mammalian herbivores, females generally adopt a conservative strategy favoring their own survival over that of their offspring because greater longevity typically increases fitness (Clutton-Brock 1988, Weladji et al. 2006). However, many strategies can co-exist within a population, and the balance between reproduction and survival depends on age-specific mortality resulting from environmental conditions such as predation or quality of food resources (Kirkwood and Rose 1991, Reznick et al. 2002). Selection pressure on developmental processes is

strong since early developmental trajectories shape subsequent morphology and physiology at adulthood which, in turn, can influence survival and breeding performances (McMillen and Robinson 2005, Lummaa and Clutton-Brock 2002). We show here that environmental conditions in early life are related to modifications in the life histories of a wild mammal; individuals born in harsh environmental conditions increased their early reproductive effort compared to individuals that experienced more favorable conditions early in life. Because the fitness of individuals born under contrasting natal environments was comparable up to an age of 5 years (Fig. 4.3D), we think this increase in reproductive effort is an adaptive response of females born under adversity to the greater decline in reproductive value when ageing.

In Biomedical research, early-life conditions were thought to provide a cue of the future environmental conditions during adulthood and the developing organism responds to this cue by producing a phenotype that confers a selective advantage (Bateson et al. 2004, Gluckman and Hanson 2004, Gluckman et al. 2005a). This ‘predictive adaptive response’ model is commonly invoked to account for increased rate of cardiovascular disease and metabolic syndrome among humans experiencing poor conditions early in life but resource-rich adult environments. However, the correlation between early life and adult environments has to be nearly perfect to favor the evolution of predictive adaptive response (Nettle et al. 2013). While matching of the conditions of life at the juvenile and adult stages is likely to occur in short-lived species, the long life and the long time required to achieve reproductive maturity of large mammals make such matching less likely (Wells 2006). On this view, it seems most likely that early-life conditions influence the pattern of reproductive investment of female reindeer through the impact on future state of their own body rather than in anticipation of their adult environment (see Nettle et al. 2013, Burton and Metcalfe 2014 for a related discussion).

Identifying how the early environment influences life-history traits is import-

ant for understanding the potential adaptive value of phenotypic changes in response to different aspects of global change. In one species of tropical bird (*Falco punctatus*), females born in territories affected by anthropogenic changes to the environment invest more in early reproduction at the expense of late life performance (Cartwright et al. 2014). In the high arctic, rain-on-snow events are predicted to become increasingly frequent with climate change (Rennert et al. 2009). These extreme climatic events have large ecosystem implications because they have been shown to synchronize population fluctuations across an entire community of vertebrate herbivores including Svalbard reindeer (Hansen et al. 2013). As rain-on-snow events are highly correlated with our measure of environmental conditions ($R^2 = 0.58$, see Fig. 4.6 in supplementary materials), our results suggest that adjustment of reproduction in response to early environment represents a potential means to mitigate the negative consequences of climate change. More generally, most studies of climate change impacts to date have focused on plasticity in adulthood such as the date of egg laying (Charmantier et al. 2008) or hibernation emergence (Lane et al. 2012). Our results suggests that the role of developmental plasticity in allowing populations to track environmental changes requires further attention.

4.2 Supplementary Materials

4.2.1 MATERIALS AND METHODS

Svalbard reindeer

The Svalbard reindeer is a subspecies of *Rangifer tarandus* endemic to the arctic archipelago of Svalbard and contrasts with the mainland reindeer by being highly sedentary with no migration. This subspecies exhibits a high sexual di-

morphism with respect to several metric traits such body mass, body size or antler size. For instance, adult females are, on average, 33% smaller than adult males (Loe et al. 2006). The maximum longevity appears to be 17 years in females and 12 years in males (Reimers 1983). Mating system is polygynous and the median date of conception is about 24 October (Loe et al. 2006). Females are iteroparous (one reproductive attempt per year) and can give birth to a single calf each year in June from 2 years of age onwards. Weaning occurs approximately 3 months after birth. Despite the fact that reindeers are adapted to extreme winters, through for instance their extraordinary ability of fat deposition, survival and reproductive rates are highly variable between years (Solberg et al. 2001, Albon et al. 2002, Stien et al. 2012). Both density dependent and climatic processes that determine food availability have strong effects on individuals. There are no large terrestrial predators in Svalbard and human harvesting of reindeer occurs at low intensities.

Study area and population

The study was carried out in Nordenskiöldland, Spitsbergen (77°50' - 78°20'N, 15°00' - 17°30'E). The population of Svalbard reindeer has been intensively monitored using capture-mark-recapture (CMR) methods since 1995. Female reindeer were caught every year (mostly in late April/early May) using net from snow-scooters. All females included in this study were of known age, because they have been marked as calf or yearling in their first and second winter respectively when age can be reliably established on the basis of size and on tooth eruption. At capture, body mass and skeletal size (indexed by hind foot length) of all females have been measured and pregnancy status was determined using the progesterone concentration in blood samples and ultrasound diagnosis. In addition to captures, intensive observations took place every year during summer (mostly in August) to assess the reproductive success of marked females (see Albon et al. 2002 for

details). Information on reproductive success was obtained on average on 40% of the individuals captured in a given year. All procedures for capturing and handling animals were performed under license from the animal welfare authorities of Norway and the Governor of Svalbard.

Measures of early environmental conditions

The quality of environmental conditions in early life was defined as the average yearly body mass of adult females (standardized to the interval 0 to 1, see Festa-Bianchet et al. 2004 for a similar approach in bighorn sheep). Hence, the quality of early environment for individuals born in year t was quantified by average body mass of adult females in year t . This method represents a means to obtain an integrator of environmental conditions by avoiding multiple explanatory variables in the analyses (Robinson et al. 2008). The mean annual body mass of adult female Svalbard reindeer is to a large degree determined by the occurrence of rain-on-snow events and population density (Fig. 4.6 in supplementary materials). In years where general environmental conditions are poor, this will be reflected in reduced body mass at the population level. In contrast, years with higher body mass values represent situations where conditions were favorable, in particular that food was relatively abundant and easily available. We estimated year-specific body mass of adult females using linear mixed models (LMMs, package ‘lme4’ in R version 2.15, R Development Core Team 2011a) with year and date of capture fitted as fixed effects. Since body mass increase with age until 4 years of age and then decline after 12 years of age because of senescence (Fig. 4.7 in supplementary materials), we only included females between the ages of 4 and 12 years. In all models, female identity was entered as a random effect controlling for the non-independence of repeated measures on the same female.

Statistical analysis

Early-life conditions and body traits. We used LMMs to determine how the early environment influences body mass, body size and body condition of adult female reindeer. For body mass, we considered females between the ages of 4 and 12 years (see above, $n = 1068$ observations and $n = 293$ females). Since Svalbard reindeer reach asymptotic skeletal size at 3 years of age (Fig. 4.7 in supplementary materials), we included females from the age of 3 years onwards in the analyses on body size ($n = 1564$ observations and $n = 360$ females). Body condition was calculated as the residuals of the regression of log-transformed body mass on log-transformed skeletal size of each individual between 4 and 12 years of age (Schulte-Hostedde et al. 2005, Toïgo et al. 2006). In addition to female identity, year was fitted as a random effect in the analyses on body mass and condition.

Early-life conditions and age-related reproduction. We tested the effects of early environment on age-specific reproductive output by examining two reproductive traits: (1) pregnancy rate measured in April/May ($n = 1326$ observations, $n = 328$ females), (2) offspring survival from birth to weaning ($n = 373$ observations, $n = 171$ females), which was calculated using data on pregnant females observed during the summer with, or without, calf. We used generalized linear mixed models (GLMMs) of annual pregnancy rate and offspring survival with binomial error distributions. The full GLMMs included female's age, its square, the quality of environmental conditions in early-life and their first order interactions as fixed effects. To further investigate a statistically significant interaction, we re-run each model by considering early environmental conditions as a three-level factor, corresponding to the tertiles of the distribution of environmental quality (Reed et al. 2008). Year was added as a random effect to characterize the breeding environment. In models of pregnancy rate, results were examined by excluding

females at the age of 2 years because a quadratic function with age did not manage to capture the very low values of pregnancy at 2 years (see Fig. 4.3B).

Early-life conditions and age-related survival. We used capture-mark-recapture modelling (Lebreton et al. 1992) in E-surge (Choquet et al. 2009) to investigate whether the rate of decline in survival probability with age (hereafter called ‘senescence rate’) differed between each type of environmental conditions in early life ($n = 353$ females). A preliminary capture-mark-recapture analysis of this population showed that adult age-specific survival probability was best described by a declining linear function of age from 5 years. Our baseline model correspond thus to a constant survival between 2 and 4 years followed by a linear-logistic decrease in survival with age beginning at 5 years. The quality of current environment was also included in the baseline model to account for sources of between-year variation in survival. We explored whether the rate of senescence varied with early environment by testing the interaction between age and cohort group on survival rates from 5 years of age. Capture probability was allowed to vary between years.

Early-life conditions and fitness. We calculated an annual contribution to mean fitness (hereafter referred to as ‘annual fitness’) of each group facing different environmental conditions in early life. Annual fitness was defined as the sum of mean annual survival plus one-half of the mean annual reproductive success (Lane et al. 2012). The relationship between annual fitness and age for each cohort group was generated from generalized additive model (GAM). We restricted this analysis to individuals aged 2-12 years because the low sample size beyond 12 years can bias estimates of annual reproduction and survival.

Early-life conditions and reproductive tactic. We explored reproductive tactics

of female reindeer by examining relationship between annual reproductive traits (pregnancy rate and offspring survival) and body mass in two age groups: young adults 2-5 years old, old adults beyond the age of 5 years. In each age group, the full GLMM included annual body mass, the quality of environmental conditions in early-life and their first order interaction as fixed effects. The factor variables year and female identity were included as random effects. To further investigate a statistically significant interaction between early-life conditions and body mass, we re-run each model by considering early environmental conditions as a three-level factor (see above). Body mass was corrected for date of capture.

Modelling approach. In all models, we used a backward selection procedure, testing successively the first-order interactions, and if not statistically significant the main effects of covariates. Statistical significance was assessed by likelihood ratio test.

4.2.2 SUPPLEMENTAL FIGURES

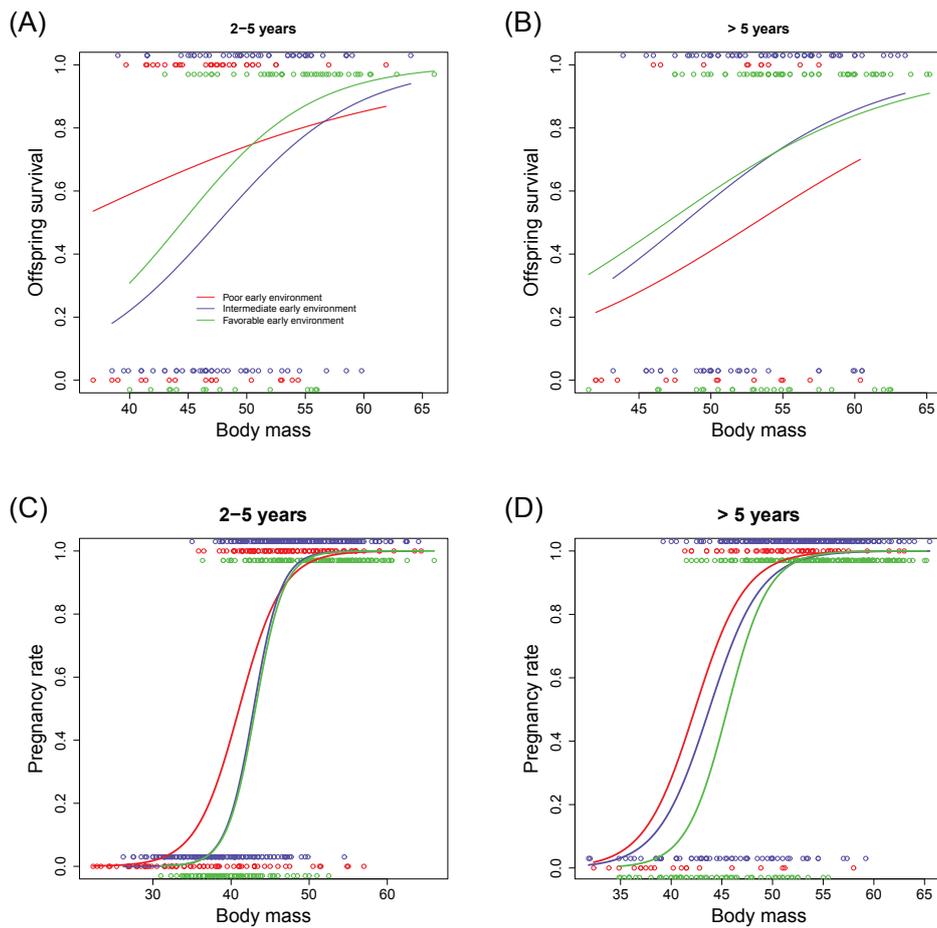


Fig. 4.5. Offspring survival and pregnancy rate as a function of mother body mass and the quality of early environment (three groups corresponding to the tertiles of the distribution of early environmental quality) for two age groups in Svalbard reindeer (A and C: young adults 2-5 years old, B and D: old adults beyond 5 years old.)

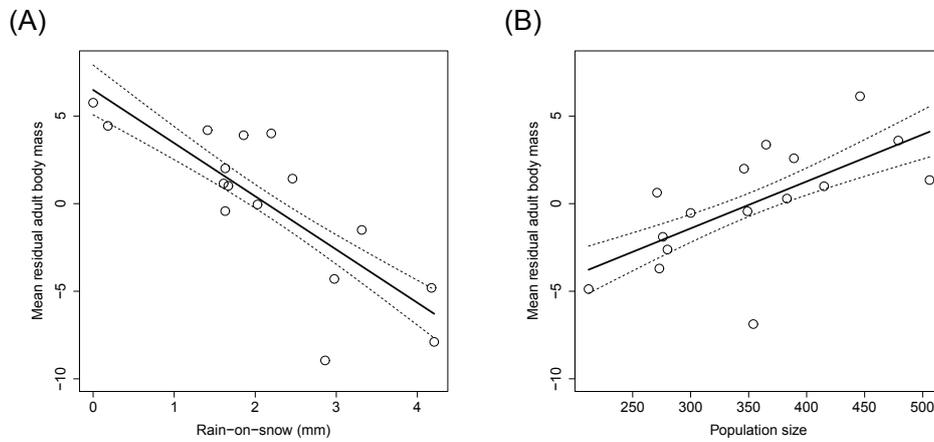


Fig. 4.6. Annual estimates of adult body mass as a function of A) rain-on-snow and B) population size in a given year. The full model included the effects of rain-on-snow (slope = -3.09 ± 0.60 , $R^2 = 0.58$) and population size (slope = 0.027 ± 0.008 , $R^2 = 0.22$). Values are mean residuals of the model after removing the effects of the covariate. Rain-on-snow corresponds to the amount of precipitation that fell at a temperature above one degree C, between 1 November and 30 April. The reindeer population size was the number of animals observed along a transect line going through Colesdalen and Semmeldalen (Stien et al. 2012).

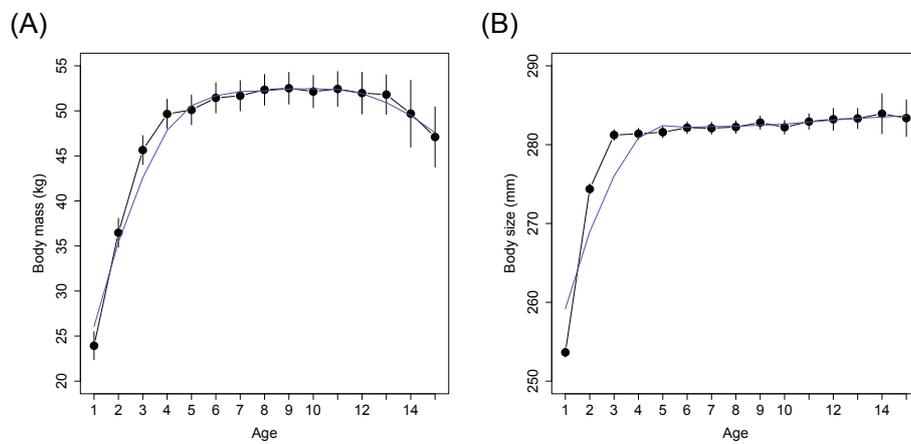


Fig. 4.7. Variation in A) body mass and B) skeletal size of female Svalbard reindeer as a function of age. Points represent the predictions (\pm SE) from linear mixed models including age (factor) as fixed effects and individual identity as random effects. For modeling body mass, date of capture and 'year' were also included as fixed and random effects, respectively. The blue lines represent loess-curves fitted to the values.

4.2.3 SUPPLEMENTAL TABLES

Table 4.1. Generalized linear mixed models (using a logit link and a binomial error distribution) of offspring survival and pregnancy rates for two age groups in Svalbard reindeer. We tested the interaction (symbolized by *) between mother body mass and environmental conditions in early life (ENVbirth), and if not statistically significant the main effects of ENVbirth on reproduction after accounting for the effects of mass. The random effects are ‘year’ and female identity. Df = degree of freedom and SE = standard error.

Age and response variable	Fixed effect	χ^2	Df	P	Slope \pm SE
A) 2-5 yr-old					
Offspring survival	Body mass*ENVbirth	5.14	1	0.02	0.36 \pm 0.16
Pregnancy rate	Body mass*ENVbirth	0.27	1	0.60	0.07 \pm 0.14
	ENVbirth	2.13	1	0.14	-1.06 \pm 0.74
B) > 5 yr-old					
Offspring survival	Body mass*ENVbirth	0.81	1	0.36	-0.15 \pm 0.17
	ENVbirth	2.02	1	0.15	1.17 \pm 0.79
Pregnancy rate	Body mass*ENVbirth	0.33	1	0.57	0.08 \pm 0.15
	ENVbirth	2.97	1	0.08	-1.58 \pm 0.94

Part III

Evolutionary consequences of growing large secondary sexual characters

Chapter 5

Males and female Pyrenean Chamois pay similar longevity costs when growing long horns

A version of this chapter is: Douhard M, Gaillard J-M, Lemaître J-F, Loe L.E, Loison A, Crampe J-P, Bonenfant C, Males and female Pyrenean Chamois pay similar longevity costs when growing long horns. In preparation.



Abstract

In populations limited by food resources, the allocation of energy to growth and reproduction should be costly in terms of survivorship. Growing long horns is thus expected to reduce longevity but empirical evidence of such fitness cost is ambiguous at the best. Previous studies have mainly examined this trade-off in males of sexually dimorphic species under strong sexual selection. However, little is known about the relationship between horn growth and survival or longevity in females, and in both sexes of species with weak sexual selection. We filled the gap by studying the relationship between sex-specific horn growth and longevity in a species of large herbivore subject to weak sexual selection, the Pyrenean chamois (*Rupicapra pyrenaica*). Surprisingly, horn growth negatively influenced longevity and this fitness cost was of similar magnitude in both sexes. These results show that the occurrence of a trade-off between horn growth and survivorship does not depend of the intensity of sexual selection and is not restricted to males. Future studies could investigate the importance of horn growth on female and male reproduction.

5.1 Introduction

In the *Descent of Man*, Darwin (1871) defined the process of sexual selection as the selection that ‘depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction’ (p. 209) and saw in the horns of male bovids one of the most spectacular examples of secondary sexual traits among vertebrates. Darwin proposed that male horns have evolved primarily through male-male competition for access to females, an hypothesis that has been validated later on (Geist 1966a, Andersson 1994). Several studies have shown that males carrying large horns generally have larger reproductive success or higher dominance rank in many species that display high level of polygyny or marked sexual size dimorphism (Coltman et al. 2002 in bighorn sheep *Ovis canadensis*; Singer and Zeingenfuss 2002 in Dall sheep *Ovis dalli*; Preston et al. 2003 and Robinson et al. 2006 in Soay sheep *Ovis aries*), although some notable exceptions to this general rule can be recorded (Mainguy et al. 2009, in mountain goats *Oreamnos americanus*). Developing long horns is expected to be costly because it imposes high metabolic requirements (Picard et al. 1994). In addition, mating is energetically costly in males of large sexually dimorphic and strongly polygynous herbivores (Myserud et al. 2004) and often involves both loss of foraging time (e.g. Bobek et al. 1990, Pelletier 2005) and high risk of injuries (Clutton-Brock et al. 1979). However, whether the energy allocated to grow long horns leads to fitness costs remains poorly understood. Studies of bighorn sheep and Alpine ibex failed to find evidence of cost of growing long horns in terms of survivorship (Bergeron et al. 2008, Bonenfant et al. 2009b, Toïgo et al. 2013), whereas young Soay sheep males (Stevenson and Bancroft 1995, Robinson et al. 2006) and hunted Dall sheep males (Loehr et al. 2006) with large horns have been reported to have shorter lifespan.

Horns are present in males of all bovid species but are absent in females of one-third of these species (Estes 1991). While competition for access to mates

is considered to be the main selective force driving the intensity of horn growth in male bovids (Andersson 1994), the evolution of horns in female bovids is not well understood and several explanations have been put forward to explain it. The presence of horns in females could be a non-adaptive process that is simply maintained by genetic associations between sexes (Lande 1980). In support, an allele conferring large horns in Soay sheep has been recently shown to be associated with male but not female fitness (Johnston et al. 2013). Alternatively, female horns could be an adaptive trait having evolved in response to the selective pressure of either predation (Packer 1983, Bro-Jørgensen 2007) or intrasexual competition for resources (Stankowich and Caro 2009, Robinson and Kruuk 2007). As horns appear to have evolved from different pathways in response to different functions between males and females, we expect marked sex-differences in the relationship between horn growth and survivorship. However, most previous studies have focused on males and very few studies have looked for sex-specific relationships between horn length and survivorship in both sexes (Robinson et al. 2006, Poissant et al. 2008). While increased horn length was negatively associated with breeding success and longevity in Soay sheep (Robinson et al. 2006), there is no relationship between longevity and horn volume in female Bighorn sheep (Poissant et al. 2008). To date, examination of the relationship between sex-specific horn growth and longevity in a species of large herbivore subject to weak sexual selection was still lacking.

The lack of trade-off between horn growth and survivorship in males often reported so far can involve different processes. Trade-offs can be simply masked by large individual variation in resource acquisition (van Noordwijk and de Jong 1986). The handicap principle (Zahavi 1975) argues that secondary sexual traits are reliable indicator of individual differences because only individuals with high resource acquisition are able to grow large traits that are costly in terms of survivorship. However, such individuals have not necessarily an advantage in all environmental conditions. Thus, Reznick et al. (2000) proposed that ‘super phen-

otypes' really are super, but only when resource availability is high. The expression of fitness costs of growing large secondary sexual characters could thus only occur under poor environmental conditions (Robinson et al. 2008).

The entire horn growth trajectory rather than horn length *per se* may carry fitness costs. The growth trajectory can include compensatory growth in periods when horns grow faster than 'normal' following periods of growth depression, which could be caused by food shortage (Wilson and Osbourn 1960, Metcalfe and Monaghan 2001, Hector and Nakagawa 2012). Laboratory studies suggest that compensatory body growth generates fitness costs that are often expressed much later in life. These costs can involve a decline in cognitive performance (Fisher et al. 2006), a reduced reproduction (Auer et al. 2010, Lee et al. 2012) or a reduced longevity (Birkhead et al. 1999, Ozanne and Hales 2004). Although several studies have provided evidence of compensatory horn growth in large herbivores in the wild (Pérez-barbería et al. 1996 in Cantabrian chamois *Rupicapra pyrenaica parva*; Côté et al. 1998 in mountain goats; Toïgo et al. 1999 in female Alpine ibex *Capra ibex*; Rughetti and Festa-Bianchet 2010; 2011 in Alpine chamois *Rupicapra rupicapra*), its impact on survivorship remains virtually unexplored.

To fill the gap, we used a long-term detailed monitoring of a stable hunting-free population of Pyrenean chamois to (1) identify the sex-specific age-related patterns of horn growth and check for possible compensatory in both sexes, (2) determine the sex-specific relationship between total horn length and longevity, (3) assess whether compensatory horn growth led to reduced longevity in either sex.

5.2 Material and methods

STUDY SITE AND POPULATION

Pyrenean chamois have been monitored since 1967 in the Cauterets area, part of the Pyrenees National Park (42°45'-42°55'N, 0°5'-0°15'W) in France. The

Cauterets area stretches over 10,200 ha between 980 and 3,298 m a.s.l. The climate is oceanic-alpine and most winter rainfall falls as snow above 1300 m a.s.l. Three habitats are recognized in the area (Gonzalez and Crampe 2001): (i) the mountain range composed of a forested area below 1,800 m a.s.l, dominated by *Fagus sylvatica* and *Abies alba*; (ii) the sub-alpine range between 1,800 and 2,100 m a.s.l, consisting mainly of *Pinus uncinata* and *Rhododendron ferrugineum* on northern aspects and *Arctostaphylos uva-ursi* and *Juniperus nana* on southern aspects; (iii) the alpine range, above 2,100 m a.s.l, characterized by the absence of trees and dominated by *Festuca eskia* and *Trifolium alpinum*.

Local authorities banned hunting from the Park since 1967 so that no harvest of any species has occurred ever since. The population size of Pyrenean chamois only fluctuates between 700 and 800 individuals since 1984, and the population growth rate is close to 0 (Gonzalez and Crampe 2001, Crampe et al. 2002), leading the population to be stable at quite high density (close to habitat saturation, Crampe et al. 2006). Emigration is rare in both sexes; only 2 of 129 (1.5%) marked females and 6 of 155 (3.8%) marked males were observed outside the study area (Crampe et al. 2006).

DATA COLLECTION

The population was monitored by one person (J-P.C) who searched skulls of dead animals recovered from 1987 to 2010. Most of the skulls (87%) were collected during winter in a core area of 1,400 ha encompassing most of the winter grounds of the population. Each year, this core area was searched once or twice a week along fixed transects, from November to April. Outside winter, when chamois increase a lot their range, dead animals were sought over the entire area in a less systematic way (see Gonzalez and Crampe 2001 for details). The searching effort was similar for all years.

For every skull recovered, the same observer (J-P.C) took several measures. The horn increments of the first five years, sex and longevity were recorded on

273 males and 276 females. In temperate areas, horns stop growing in winter, leading to a pattern of annuli on the horn (Schröder and Elsner-Schak 1985). We combined horn growth during the two first years of life because the two first horn increments cannot be dissociated visually (see Rughetti and Festa-Bianchet 2011 for a similar approach). The measure of annual horn growth increments after the fifth year is not reliable because of the very limited growth beyond this age (see results). We thus defined total horn length as the sum of growth increments between 1 and 5 years of age. Horn morphology allowed distinguishing the sexes. The horn base is thicker and the apical hook more pronounced in males than in females. When dead was recent, the sex was also determined from the genitalia. The age of chamois (measured in years) was accurately determined by counting the horn annuli (Schröder and Elsner-Schak 1985). We only considered in the following analyses individuals that survived at least to five years of age to be sure that horn growth was complete for all individuals.

STATISTICAL ANALYSES

In many studies, compensatory and catch-up growths are used as interchangeable terms. Here, we distinguish these two terms using terminology proposed by Hector and Nakagawa (2012) such as catch-up growth correspond to a non-significant difference in size between individuals that grow slowly early in life and those that grow fast. Therefore, compensatory growth may or may not lead to catch up. On the other hand, compensatory growth is not necessary to achieve catch-up (e.g. Marcil-Ferland et al. 2013). We investigated the possibility of compensatory horn growth in two different ways. First, we log-transformed annual increment length and modelled its variation with age using linear mixed models ('nlme' package, Pinheiro and Bates 2000). Age was entered as a fixed effect and individual identity as a random effect on both intercept and slope. Then, we added a first order autoregressive term specifying the 'corAR1' correlation option with respect to age to test whether the lengths of the successive increments were correlated for a

given individual (e.g. Bergeron et al. 2008, Toigo et al. 2013). Using this parameterization, compensatory horn growth occurred at the population level when the first order autoregressive coefficient (ρ_1) was negative. Second, we used a linear model to test whether early horn growth (i.e. the 2nd increment) was correlated with the sum of growth increments 3, 4 and 5 on a log scale (see Côté et al. 1998, Rughetti and Festa-Bianchet 2010; 2011 for a similar approach). Here, a negative correlation would indicate compensatory horn growth at the population level. To test whether catch-up in horn growth occurred, we investigated the relationship between early horn growth and total horn length on a log scale using linear models (e.g. Toigo et al. 2013). A lack of correlation between the two traits is expected if compensatory horn growth leads to catch-up.

To investigate the relationship between horn growth and longevity, we first tested whether longevity was related to total horn length. We then assessed the effect of compensatory horn growth on longevity by using linear models with longevity as a function of early horn growth, late horn growth and their first order interaction. We defined late horn growth as the residuals from the linear regression of the sum of growth increments 3, 4 and 5 on early horn growth (see Fig. 5.2). Individuals that show a compensatory growth response should have both a low early horn growth and a late horn growth with positive residual values. Therefore, under the hypothesis that compensatory horn growth is costly in terms of longevity, interactive effects between early and late horn growth should influence longevity. More specifically, longevity should decrease with increasing late horn growth only for individuals with reduced early horn growth. Models were re-ran with early horn growth included as a two-level factor (short-horned individuals in early life: 2nd increment < median, long-horned males in early life: 2nd increment > median).

We used likelihood ratio test for model selection. In mixed models, we used restricted maximum likelihood (REML) for the selection of the random effects structure, and maximum likelihood for the selection of fixed effects. Estimates

were provided from the final model fitted with REML (Pinheiro and Bates 2000). All analyses were run in R 2.11 (R Development Core Team, 2011). Estimates are given as mean \pm standard error.

5.3 Results

SEX-SPECIFIC HORN GROWTH PATTERNS

Early horn growth (i.e. the 2nd increment) accounted for 65% and 66% of the total horn length in males and females, respectively. Males had longer horns than females and the sexual dimorphism slightly increased with age (Fig. 5.1). The average difference in horn length between males and females was 2.47 ± 0.14 cm at the age of 1.5 and 4.13 ± 0.13 cm at the age of 4.5.

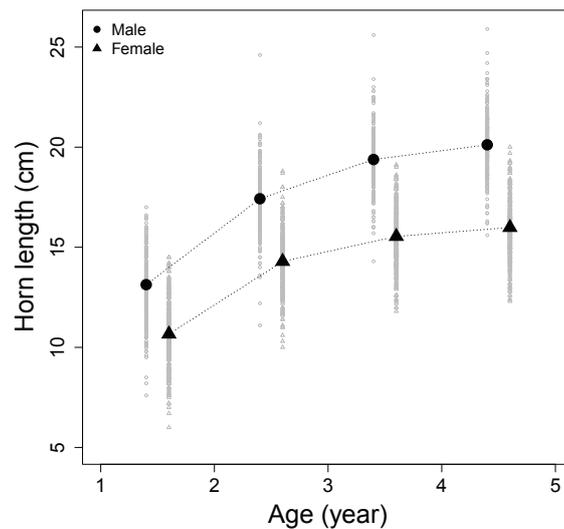


Fig. 5.1. Age-specific horn length in male and female Pyrenean chamois. Large circles in (males) and triangles (females) are the average values of horn length for a given age. Grey circles and triangles correspond to individual.

Annual horn increments decreased with increasing age in both sexes (slope =

-0.97 ± 0.01 , $P < 0.001$ for males, slope = -1.10 ± 0.01 , $P < 0.001$ for females). The random effects on both intercept and slope were highly statistically significant in males ($\sigma_{\mu} = 0.25$, $\chi^2 = 29.99$, $df = 1$, $P < 0.001$; $\sigma_{age} = 0.17$, $\chi^2 = 487.35$, $df = 1$, $P < 0.001$) and females ($\sigma_{\mu} = 0.18$, $\chi^2 = 19.85$, $df = 1$, $P < 0.001$; $\sigma_{age} = 0.15$, $\chi^2 = 179.53$, $df = 1$, $P < 0.001$). For both sexes, a first order auto-regressive term markedly improved the fit of the models ($\chi^2 = 43.46$, $df = 1$, $P < 0.001$ for males; $\chi^2 = 30.32$, $df = 1$, $P < 0.001$ for females). For a given individual, increment length at age i was negatively correlated with increment length at age $i + 1$ ($\rho_1 = -0.27$, 95% CI = $-0.34, -0.19$ for males; $\rho_1 = -0.27$, 95% CI = $-0.35, -0.18$ for females), supporting the hypothesis that compensatory horn growth occurred in Pyrenean chamois. Moreover, a negative relationship between early horn growth and sum of growth increments between 3 and 5 years of age occurred in both males (slope = -0.85 ± 0.08 , $P < 0.001$, Fig. 5.2a) and females (slope = -0.85 ± 0.10 , $P < 0.001$, Fig. 5.2b), confirming the presence of compensatory horn growth at the population level. The level of compensation was similar in both sexes (between-sex difference in slope = 0.0096 ± 0.1301 , $P = 0.94$).

Total horn length was positively correlated to early horn growth for both males (slope = 0.33 ± 0.03 , $P < 0.001$) and females (slope = 0.38 ± 0.03 , $P < 0.001$). Individuals with low early horn growth had thus, on average, shorter horns than individuals with high early horn growth, despite compensatory growth. The difference in horn length between fast and slow horn growers early in life decreased from 23% in males and 27% in females at the age of 1.5 year to 7% and 10%, respectively, at 4.5 years of age.

HORN GROWTH VS. LONGEVITY

On average, males and females lived for 11.07 ± 0.23 and 10.84 ± 0.25 years, respectively. There was no sex difference in longevity ($F_{1,547} = 0.69$, $P = 0.40$). A negative relationship occurred between total horn length and longevity in both males (slope = -0.39 ± 0.15 , $P = 0.01$) and in females (slope = -0.28 ± 0.16 , P

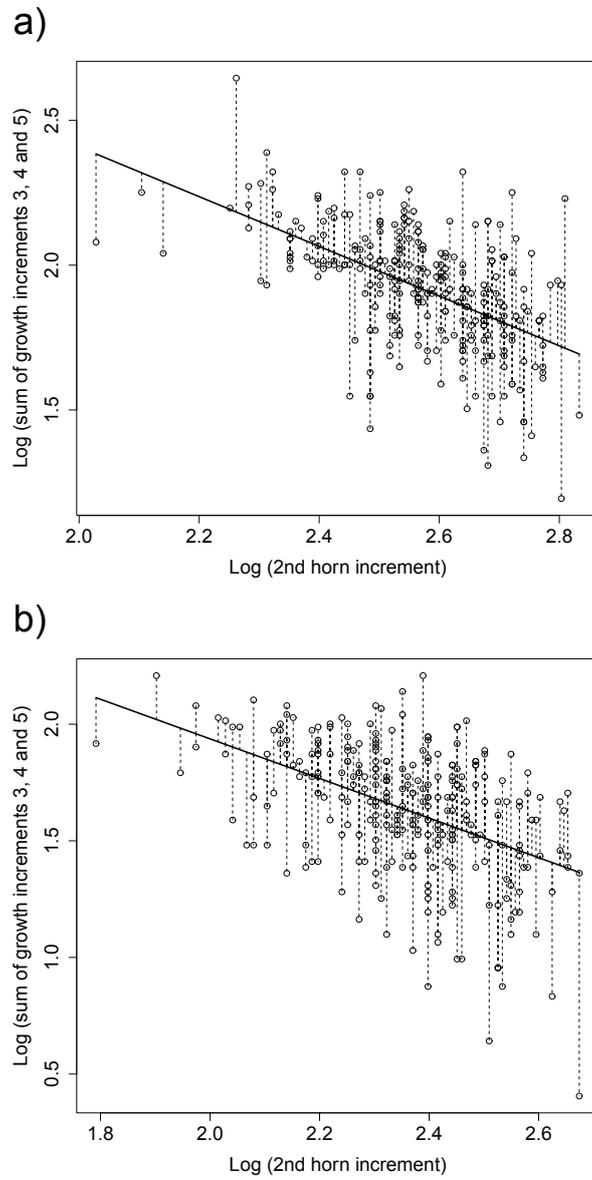


Fig. 5.2. Correlation between horn increment during the first 2 years of age and horn increment in the third, fourth, and fifth year of age of a) male and b) female Pyrenean chamois on a log-scale. Residuals (marked by the dashed lines) correspond to late horn growth.

= 0.07), without any statistical evidence of sex differences in the cost of growing long horns (between-sex difference in slope = -0.11 ± 0.22 , $P = 0.62$).

We found no interactive effects between early horn growth and late horn growth on longevity in either males ($F_{1,269} = 0.69$, $P = 0.41$) or females ($F_{1,272} = 0.73$, $P = 0.39$). This result held for both sexes when we performed analyses with early horn growth included as a two-level factor ($F_{1,269} = 0.87$, $P = 0.35$ for males and $F_{1,272} = 0.003$, $P = 0.95$ for females). Accordingly, compensatory horn growth did not affect longevity. Early horn growth did not influence longevity of either males ($F_{1,270} = 1.53$, $P = 0.21$, slope = -0.17 ± 0.14) or females ($F_{1,273} = 0.30$, $P = 0.58$, slope = -0.09 ± 0.15). However, longevity was negatively related to late growth acceleration for both males ($F_{1,270} = 5.00$, $P = 0.02$, Fig. 5.3a) and females ($F_{1,273} = 3.38$, $P = 0.06$, Fig. 5.3b). Thus, females that grew larger than average horns between 2 and 4.5 years of age died, on average, 1.06 ± 0.25 years earlier than females with lower than average horn growth during the same period. The cost of growing large horns between 2 and 4.5 years was similar in both sexes (between-sex difference in slope = -1.08 ± 1.66 , $P = 0.51$).

5.4 Discussion

In this study, we found that horn length negatively influenced longevity in a wild population of Pyrenean chamois. Growing large horns from 2 years of age onwards was thus costly in terms of survivorship in both sexes. However, contrary to the expectation (Hector and Nakagawa 2012) we did not detect any cost of compensatory growth because all individuals showing longer than average horn growth from 2 years had reduced longevity, irrespective of early horn growth. Our most important finding is that the trade-off between horn growth and longevity was similar in males and females. Although the exact mechanism by which horn growth influences longevity in each sex is unknown, we provide insights into the possible causes that drive this trade-off.

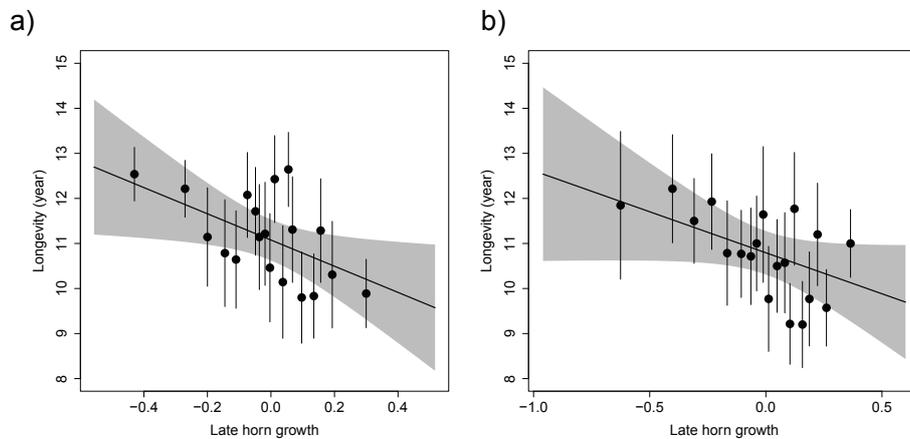


Fig. 5.3. Relationship between late horn growth and longevity in a) male and b) female Pyrenean chamois from a hunting-free population in France. The straight lines correspond to expected longevity according to late horn growth and gray shading to 95% confidence limits of model predictions. Black dots represent average longevity of individuals (\pm 95% confidence limits; horn classes were defined so to have the same number of individuals per class, $n = 273$ males and $n = 276$ females).

Several studies have shown that trade-offs can only be evident in poor environmental conditions (Barbraud and Weimerskirch 2005, Tavecchia et al. 2005, Robinson et al. 2008). The relationship between horn growth and lifetime reproductive success in male Soay sheep was positive under favorable environmental conditions because of increased breeding success but negative under poor environmental conditions as a consequence of reduced survival (Robinson et al. 2008). If individuals allocate a large amount of energy to growth and reproduction when resources are scarce, the allocation to somatic maintenance and repair necessarily decline strongly (Williams 1966). In accordance, the costs of growing large horns detected here occurred in a population of Pyrenean chamois at high density experiencing poor food resources. Compared to another population of Pyrenean chamois (Bazès) at lower density, age at first reproduction was delayed and reproductive success was lower whatever age in this population (Crampe et al. 2006). Generation time which corresponds to the mean weighted age of females that give

birth in a population (Leslie 1966, Gaillard et al. 2005) was almost 2 times higher in this population (8.25 years) than at Bazès (4.97 years) (Crampe et al. 2006).

Strong horn growth between 2 and 5 years, age at which female and male chamois start breeding (Crampe et al. 2006, Garel et al. 2009a), was especially costly in terms of longevity. This contrasts with the lack of association observed between horn volume and longevity in female bighorn sheep (Poissant et al. 2008). Female Pyrenean chamois with longer horns had the highest positions within the social hierarchy (Locati and Lovari 1991). Similarly, female Soay sheep that possessed horns were more likely to initiate and win aggressive interactions than females without (Robinson and Kruuk 2007). The advantage in competition over resources may translate into reproductive benefits. Recently, Rughetti and Festa-Bianchet (2011) showed that female chamois with strong early horn growth attained primiparity early and horn growth was positively correlated with reproduction during senescence stage. Hence, our result may indicate a reproductive cost in females. To clarify this aspect, future studies will need to investigate the relationship between horn growth and reproductive trajectory.

There are no data on reproductive success of male chamois but behavioural observations suggested that males with larger horns usually dominate other males (Lovari and Locati 1991). Nevertheless, the role of horns in reproductive success of male chamois should be relatively weak compared to other bovids (Rughetti and Festa-Bianchet 2010, Corlatti et al. 2013). In male bighorn sheep and Alpine ibex, which fight by clashing horns, there was no evidence of compensatory horn growth (Toïgo et al. 1999, Festa-Bianchet et al. 2004, Bergeron et al. 2008, Toïgo et al. 2013) probably because there is a selective pressure for males that have grown large horn in early life to go on with fast horn growth later in life. In contrast in species with less intense sexual selection in males, such as chamois or mountain goats, compensatory horn growth occurred in males (Côté et al. 1998, Rughetti and Festa-Bianchet 2010, this study) probably because the fighting style of those species, in which horns are used to hook or stab the body of the oppon-

ent, may not favour very long horns (Festa-Bianchet and Côté 2008). Thus, it is surprising to detect a cost of growing large horns in male chamois, because even in males of sexually dimorphic species under strong sexual selection, there is no evidence for a trade-off between horn size and survivorship (e.g. see Bergeron et al. 2008, Bonenfant et al. 2009b, Toïgo et al. 2013). Compared to these species, maybe that male chamois adopt a less conservative survival strategy. A behavioral analysis of horn use in males within this population would be beneficial to better understand the mechanisms underlying horn growth effects on survivorship.

The analyses we report here suffer from one obvious limitation. Horn length may be positively correlated with body mass and act thus as a confounding factor in our analysis. However, Rughetti and Festa-Bianchet (2010) found no correlation between horn length and body mass for male Alpine chamois from the age of 3 years. In addition, the relationship between body mass and longevity in ungulates has consistently been found to be positive rather than negative (Gaillard et al. 2000a).

Sexual selection is central to the understanding of longevity and ageing (Clutton-Brock and Isvaran 2007, Bonduriansky et al. 2008). In polygynous vertebrates, intense intra-sexual competition for breeding opportunities among males, combined with the costs of traits that increase competitive success, reduced their longevity relative to females. In chamois, the intensity of sexual selection in males is quite weak. Accordingly, there are no marked sex-differences in age-specific survival (Loison et al. 1999a, Gonzalez and Crampe 2001, Corlatti et al. 2012) or longevity (this study) and the magnitude of trade-off between horn growth and longevity is similar between males and females. In studies of other bovids in which sexual selection is stronger in magnitude, the trade-off between horn growth and viability has been mainly examined in males (e.g. Loehr et al. 2006, Bergeron et al. 2008, Toïgo et al. 2013). Investigating this potential trade-off in females is needed for testing the hypothesis that sex differences in the relationship between horn growth and longevity should increase with the intensity of sexual selection.

Chapter 6

Horn development in Stone's sheep under different selective harvesting pressures

A version of this chapter is: Douhard M, Festa-Bianchet M, Pelletier F, Gaillard, J-M, Bonenfant, C Horn development in Stone's sheep under different selective harvesting pressures. Submitted.



Abstract

Selective harvest may lead to rapid evolutionary changes. For large herbivores, trophy hunting may favour males with small horns, opposite to sexual selection, with undesirable consequences for management and conservation. There have been no comparisons of long-term changes in trophy size under contrasting harvest pressures. We analysed horn measurements of Stone's rams (*Ovis dalli stonei*) harvested over 37 years in two large regions with strong differences in hunting pressure to identify when selective hunting is strong enough to cause a long-term decrease in horn growth. Under strong selective harvest, horn growth early in life and the number of males harvested declined respectively by 12% and 45% over the study period. Horn shape also changed over time, as horn length became shorter for a given base circumference likely because horn base is not a direct target of hunter selection. In contrast, under low hunting pressure, there were no detectable temporal trends in early horn growth, in the number of males harvested or in horn length relative to base circumference. Trophy hunting is an important recreational activity and can generate revenues for conservation. By favouring males with smaller horns and by reducing the availability of desirable trophies, however, excessive hunting may generate long-term negative ecological and economic consequences that can be avoided by limiting offtake.

6.1 Introduction

Although conservation biologists have only recently begun to pay attention to how humans may affect evolution in wild species (Palumbi 2001, Smith and Bernatchez 2008), there is now convincing evidence that human harvest is a strong selective pressure (Allendorf and Hard 2009, Darimont et al. 2009). Harvesting is usually selective for a certain size, morphology, or behaviour (Allendorf and Hard 2009). Artificial selection is particularly obvious in trophy hunting of large herbivores, where hunters seek males with large horns, antlers, or tusks. These weapons evolved through sexual selection and confer an advantage in male-male competition, female choice or both (Darwin 1871, Andersson 1994). Rapid growth in weapon size is associated with high reproductive success in adults of some species (Coltman et al. 2002, Kruuk et al. 2002). In bighorn sheep (*Ovis canadensis*), however, hunters removed males with rapidly growing horns, often at an age before those weapons improved reproductive success. The heritability of horn length is substantial, and selective harvest led to a rapid evolution of reduced horn length in bighorn males, contrary to sexual selection (Coltman et al. 2003). Recent studies have underlined the potential conservation value of tourist hunting (e.g., Leader-Williams et al. 2005), where much of the revenue generated depends on trophy size of harvested animals (Courchamp et al. 2006). Therefore, the ecological and evolutionary consequences of selective hunting are highly relevant to conservation.

If horn traits are heritable, the evolutionary response to selection through trophy hunting depends on the strength of relationships between trophy size, age, and reproductive success (Festa-Bianchet and Lee 2009), which, in turn, can be influenced by hunting pressure. Evolutionary effects should increase with harvest intensity, particularly if traits that determine trophy quality only confer a fitness advantage at an advanced age. For instance, when hunting pressure is low, some bighorn males with fast-growing horns survive to the age at which large horns

improve reproductive success (Coltman et al. 2002), mitigating the impact of artificial selection. Among African ungulates, the decline in horn length was more pronounced for sable antelope (*Hippotragus niger*) than for impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*), likely because hunting pressure and trophy value were higher for sable than for the other two species (Crosmary et al. 2013). Despite the important ecological, evolutionary and conservation implications of artificial selection (Festa-Bianchet 2003), however, we know little about how horn length may vary in relation to harvest intensity. This issue is particularly important to identify what harvest rate may limit the potential undesirable effects of artificial selection.

Variation in harvest selectivity has been studied in cervids by comparing hunting methods (Martinez et al. 2005) or hunter category (Mysterud et al. 2006, Schmidt et al. 2007, Rivrud et al. 2013). For example, in Alaska guided hunters harvested moose (*Alces alces*) with larger antlers compared to non-guided hunters because guides had a better knowledge of low-density areas producing large-antlered moose (Schmidt et al. 2007). Most guided hunters are non-residents, who pay substantial money to obtain the largest trophies. In British Columbia, however, being a resident vs. non-resident hunter had little effect on horn size of harvested bighorn males (Hengeveld and Festa-Bianchet 2011) and in Alberta guided hunters harvested slightly smaller-horned rams than residents, possibly because the high harvest intensity allowed very few rams to grow large horns (Festa-Bianchet et al. 2014). Although both of these studies reported a decline in horn length over time, neither examined the effects of regional changes in harvest pressure, leaving the possibility that some unknown temporal trend may have contributed to the results.

We explored how hunting pressure affects horn growth of Stone's sheep males in British Columbia, Canada, and compared age and horn length of individuals harvested by residents and by guided non-residents. We used measurements of approximately 10,000 males harvested over 37 years from two areas differing in

hunting pressure to test six hypotheses. The first three concerned hunter selection (Tab. 6.1). First, we expected hunters to prefer males with long horns, so that age at harvest would be higher with lower harvest pressure, particularly for males with rapidly growing horns (H1, Tab. 6.1). Horns grow through life with a decreasing growth rate (Geist 1966*b*, Bonenfant et al. 2009*b*). At the population level, however, horn length could decrease with age at harvest if males with slower horn growth survived to older ages. The selective effect of hunting should increase with harvest pressure, leading to a greater decrease in horn length with harvest age for older males under higher harvest pressure (H2, Tab. 6.1). Unlike residents of British Columbia, non-resident hunters must engage a licensed guide. Guides try to satisfy their clients by providing an opportunity to harvest a large trophy (Schmidt et al. 2007). Therefore, we expected non-residents to harvest older males with larger horns (H3, Tab. 6.1).

We then examined temporal changes in horn size and shape to identify potential evolutionary responses to selective hunting (Coltman et al. 2003). We predicted a greater decrease in horn length over time under high harvest pressure (H4, Tab. 6.1). Unlike horn length, horn base circumference is not a direct target of artificial selection (Pelletier et al. 2012). The allometric relationship between horn length and horn base should thus change over time under high harvest pressure: for a given horn base, we expected horn length to decline in the ‘high’ hunting area (H5, Tab. 6.1). Finally, a decrease in horn growth over time would reduce the availability of trophy males, by lengthening the time when males may die from natural causes before reaching ‘legal’ harvest size. Therefore, we expected a decrease in harvest over time under high harvest pressure (H6, Tab. 6.1).

Table 6.1. Hypotheses and predictions relating selective harvest and changes in horn development of Stone's sheep in British Columbia.

Hypothesis	Rationale	Prediction
<i>Selective harvest</i>		
H1. Trophy hunter selection	Trophy hunting removes males with fast-growing horns but selection intensity varies with hunting pressure	Age at harvest will decrease with early horn growth in both areas, but more markedly in the 'high' hunting area
H2. Filtering effect of hunting	Horn length decreases with harvest age at the population scale if males with slower horn growth survive to older ages	Greater decrease in horn length with harvest age for older males in the 'high' hunting area
H3. The 'hunter origin' effect	Non-resident hunters must engage a guide. Guides deploy substantial effort to find larger trophies	Non-residents take older males with larger horns than residents
<i>Long-term changes in horn development</i>		
H4. Evolutionary consequences of trophy hunting for horn growth	The intense removal of large-horned males can lead to evolution of smaller horns	Horn growth declines over time in the 'high' hunting area only
H5. Evolutionary effects of trophy hunting on horn shape	Trophy hunting removes males with longer horns rather than those with thicker bases	Horn length will shrink over time for a given horn base in the 'high' hunting area only
H6. Intense trophy hunting reduces availability of trophy rams	Rams must have horns describing a complete curl to be harvested. Cohorts with slow-growing horns are thus exposed to a longer period of natural mortality before reaching 'legal' harvest size	Availability of trophy males will decrease over time in the 'high' hunting area only

6.2 Material and methods

STUDY AREAS AND HUNTING PRESSURE

We studied Stone's sheep in the Skeena Region, north-western British Columbia and the Peace Region, north-eastern British Columbia (Fig. 6.1). Ideally, hunting pressure should be estimated by the proportion of a population that is harvested, but no reliable measure of population density was available. Therefore, we used the estimates of hunter numbers each year from 1976 to 2011, provided by the British Columbia Fish, Wildlife and Habitat Management branch. To measure hunting pressure, we divided the average number of hunters by the area of Stone's sheep range in each region.



Fig. 6.1. Study area and distribution of Stone's sheep in British Columbia. We analyzed data from males harvested within the two polygons. We excluded the Omineca Region on the advice of provincial wildlife biologists as very few sheep are harvested.

HARVEST REGULATIONS

Sport harvest of Stone's sheep in British Columbia is restricted to males of either at least 8 years or whose horns describe a complete curl: these are referred to as 'legal' males. Nevertheless, the hunter's decision to shoot likely rests on horn curl in most cases, because it is difficult to count horn growth increments from a distance to determine age. Hunting rules did not vary over time or between areas. Hunting started August 1 and ended October 15. There is no quota on the number of licenses sold to residents of British Columbia, but each hunter may only harvest one 'legal' male. Non-resident hunters had to engage the services of a guide, who received a yearly allocation of about 250 permits.

STONE'S SHEEP DATA

All harvested Stone's sheep must undergo compulsory inspection. We obtained measurements of 12,749 males (3,610 from Skeena and 9,139 from Peace) collected from 1975 to 2012. Measurements usually included horn base circumference, total horn length, length of each annual growth increment and age at death. Data also included the region of harvest and hunter origin (resident or non-resident).

Male horns grow from April to September (Bunnell 1978). Cessation of growth in winter creates a ring, allowing to measure each annual growth increment and to estimate age (Geist 1966*c*). Horns start to grow at about 10 weeks of age (Bowyer and Leslie 1992) and most lambs are born in late May or early June (Bunnell 1980). Hence, the first increment and 20-25% of the second increment develop before a male reaches 1 year of age. Unlike those of bighorn males, the horns of Stone's sheep are rarely 'broomed' or broken at the tips (Krausman and Bowyer 2003, Bunnell 2005). Most males have some wear on the first increment but retain it until death. Because the first annulus is at times difficult to distinguish, however, a common error is to record the sum of growth increments 1 (lamb growth) and 2 (yearling growth) as a single first increment (Hengeveld and

Festa-Bianchet 2011). This error produces an abnormally large first year growth measure, a smaller than average measure for subsequent increments and an erroneous age estimate. We excluded biologically impossible growth increments (increment 1 > 160 mm and sum of increments 1 and 2 > 420 mm, Bunnell 1978, Hik and Carey 2000), eliminating 25% of the dataset. Early horn growth was defined as the sum of increments 2 and 3, grown during the second and third years of life (Hengeveld and Festa-Bianchet 2011). Similarly to Bonenfant et al. (2009b), we used the left horn measurement. Because our data set included few individuals > 13 years (9 in Skeena and 13 in Peace), we pooled all males older than 12.

CLIMATE

High population density and harsh climate reduce antler size or horn growth (Jorgenson et al. 1998, Schmidt et al. 2001, Mysterud et al. 2005). Therefore, it is crucial to determine whether temporal changes in trophy size may be a consequence of changes in environmental conditions (Allendorf and Hard 2009). The Pacific Decadal Oscillation (PDO) in April-May has a positive effect on horn growth of conspecific Dall sheep (*O. d. dalli*) in the Yukon (Loehr et al. 2010), just north of British Columbia (Fig. 6.1). We controlled for possible confounding effects of climate on horn size by using monthly PDO, obtained from <http://jisao.washington.edu/pdo/PDO.latest>, for two seasons that could affect horn growth. April-September (spring-summer) PDO values reflect conditions during horn growth. During winter (November-March) horn growth stops, but climate in winter influences spring and summer plant phenology (Post and Senseth 1999), which in turn, may affect horn growth (Giacometti et al. 2002). We tested the effects of mean PDO between birth and 2 years for each season (winter: PDO_W , spring-summer: PDO_S) on horn size metrics, as growth increment length decreases after 2 years (Bunnell 1978).

STATISTICAL ANALYSES

To test H1, we looked for a relationship between age at death and early horn growth using linear models, including region as a 2-level factor and the interaction between region and early growth. We then compared age-specific total horn length between the two regions (H2) using linear models with horn length as a function of age, either as a linear or a quadratic term, region and their first order interactions. We replicated these analyses using horn base circumference as response variable.

To investigate whether age distribution of harvested males differed between resident and non-resident hunters (H3), we used a χ^2 -test. We used linear models to assess variation in early horn growth, total horn length and horn base circumference as a function of hunter origin (resident or non-resident).

To test our prediction of a greater decrease in horn size in the area with higher harvest pressure (H4), early horn growth and total horn length were regressed against cohort (Garel et al. 2007). Young males born before 1972 may have been shot before 1975, while recent cohorts may not include old males not yet 'legal' by 2012. Given the strong correlations between horn characteristics and age at death (see Results), we included only cohorts from 1972 to 2000 in our analyses. To quantify the amount of temporal variation in horn size accounted for by each covariate, seniority of the cohort (a continuous variable ordering cohorts from the oldest to the most recent), PDO_W and PDO_S , we performed an analysis of deviance (ANODEV, Skalski et al. 1993). The ANODEV compares the deviance of three nested models: a basic model, a basic model including a time-specific covariate and a basic model with cohort as a discrete factor. The R^2 of the ANODEV quantifies how much of the temporal variation in average horn size is accounted for by each covariate. Auto-correlation must be taken into account in time-series analyses to avoid inflated probabilities of type I error (Legendre 1993). To account for temporal autocorrelation in horn size metrics, we used generalized least square models (function 'gls' in R library 'nlme'). We ran each model with a first order auto-regressive structure, specifying the 'corAR1' correlation option with

respect to cohort (Pinheiro and Bates 2000). To test whether horn shape changed over time (H5), we assessed the relationship between horn length and base (on a log-scale to account for the allometric link, Houle et al. 2011) using linear models, including cohort seniority as a 2-level factor (old cohorts: 1972-1986, recent cohorts: 1987-2000) and the interaction between cohort seniority and horn base. Finally, we regressed the number of harvested males from each cohort on the seniority of the cohort in each region (H6). All analyses were run in R 2.11 (R Development Core Team 2011*b*). Estimates are given as mean \pm SE.

6.3 Results

CONTRASTING HUNTING PRESSURES

There were on average 2.3 times more hunters/year in the Peace than in the Skeena region (561 ± 23 vs. 246 ± 7). The range of Stone's sheep was larger in the Skeena (23,360 km²) than in the Peace (19,194 km²). Therefore, hunting pressure was about 2.7 times higher in the Peace than in the Skeena ($\chi^2_1 = 6932$, $P < 0.001$) and this difference increased over time (Fig. 6.2). Overall, 72% of males were harvested in the Peace and only 28% in the Skeena. Henceforth, we refer to the Peace as 'high' and the Skeena as 'low' hunting area.

SELECTIVE PRESSURE OF HARVESTING

A decline in harvest age with increasing early horn growth was more marked in the 'high' than in the 'low' hunting area (interaction of early growth and region, $F_{1,9493} = 10.57$, $P = 0.001$, $R^2 = 0.10$, Fig. 6.3). For an increase in early horn growth of 100 mm, harvest age decreased by 0.64 yr and 0.82 yr in the 'low' and 'high' hunting areas, respectively. Supporting H1, males with rapidly growing horns were consistently harvested at an older age in the 'low' than in the 'high' hunting area (Fig. 6.3). We found interactive effects of age and region on total

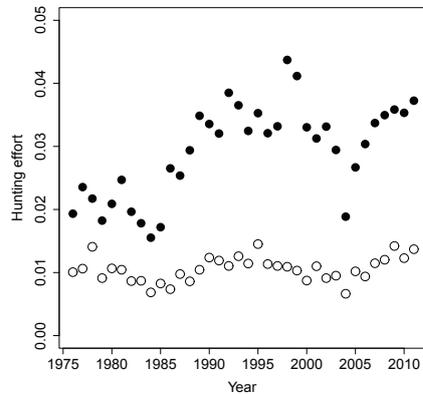


Fig. 6.2. Yearly variations in number of hunters, divided by the area of Stone’s sheep range in two regions of British Columbia (black circles, Peace region or ‘high’ hunting area; white circles, Skeena region or ‘low’ hunting area).

horn length ($F_{1,9370} = 42.47$, $P < 0.0001$, $R^2 = 0.09$). Males harvested between the ages of 5 and 8 in the ‘high’ hunting area had longer horns than in the ‘low’ hunting area, while the reverse was true between the ages of 9 and 13 (Fig. 6.4A). Supporting H2, in the ‘high’ hunting area horn length stopped increasing with harvest age at about 9 years and declined for the oldest males, but increased continuously with age at harvest in the ‘low’ hunting area. These results were similar when excluding the first increment (Appendix A), as expected given that the horns of Stone’s sheep are rarely ‘broomed’. After correcting for age, males harvested in the ‘high’ hunting area had horn bases 2.1% thicker than those in the ‘low’ hunting area ($\beta = 6.64 \pm 0.59$, $P < 0.0001$, Fig. 6.4B). There was no interaction between age and region on base circumference ($F_{1,9340} = 0.36$, $P = 0.55$). Variation in circumference between 5 and 13 years of age was best captured by a quadratic relationship with age that did not differ between regions (age: $\beta = 5.06 \pm 1.28$, age²: $\beta = -0.27 \pm 0.07$, $P = 0.0001$, Fig. 6.4B).

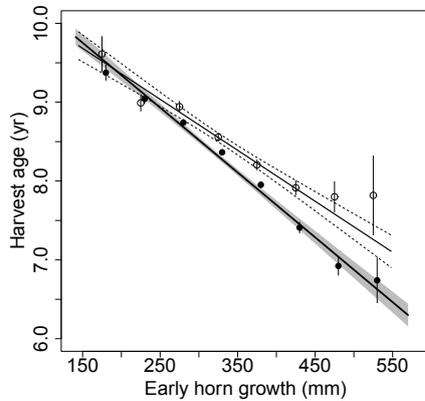


Fig. 6.3. Relationship between early horn growth during the second and third year of life and age at harvest for Stone's rams in the 'low' (white circles, solid line and 95% confidence intervals are shown by dotted lines) and 'high' (black circles, solid line and a shaded area for 95% confidence intervals) hunting areas of British Columbia. Points are average (\pm SE) harvest age for each class of 50-mm horn growth.

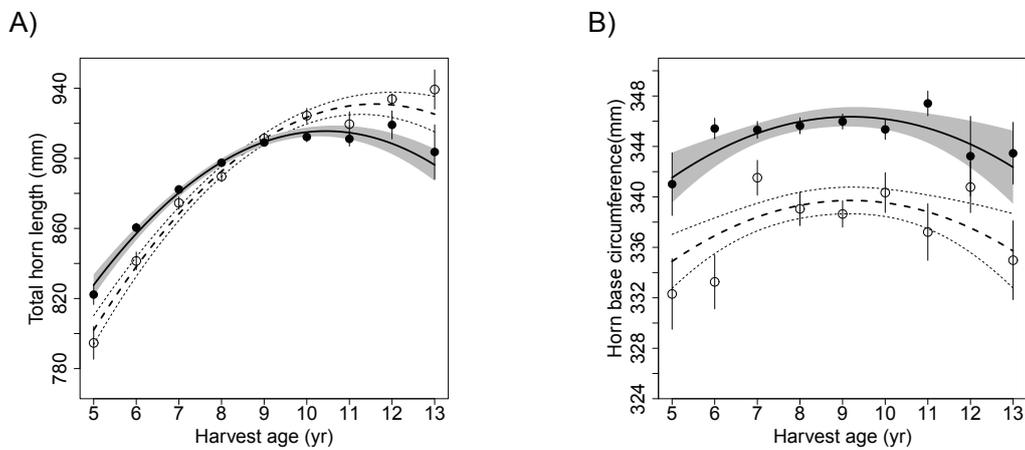


Fig. 6.4. Relationship between harvest age and A) total horn length, B) horn base circumference of Stone's rams harvested in the 'low' (white circles, dashed line and 95% confidence intervals are shown by dotted lines) and 'high' (black circles, solid line and a shaded area for 95% confidence intervals) hunting areas of British Columbia.

HUNTER RESIDENCY AND HORN CHARACTERISTICS

The proportion of males harvested by residents and non-residents differed between regions ($\chi^2_1 = 131.30$, $P < 0.0001$). In the 'low' hunting area, non-resident hunters took 62.6% of males (95% CI = 61.1, 64.2%), while they took 51.6% (95% CI = 50.5, 52.6%) in the 'high' hunting area. The age distribution of males differed between resident and non-residents ('low' hunting area: $\chi^2_8 = 53.50$, $P < 0.0001$, 'high' hunting area: $\chi^2_8 = 212.41$, $P < 0.0001$). Resident hunters shot more males < 8 years of age and fewer older males than non-residents (Appendix B). Early horn growth was influenced by hunter origin in the 'high' hunting area, being 2.1% longer for males taken by residents ($F_{1,5027} = 11.75$, $P = 0.0006$). The relationships between early growth, age at harvest and hunter origin probably accounted for this difference because the effect of hunter origin on early horn growth was not retained when age at harvest was included in the model ($F_{1,5026} = 0.44$, $P = 0.50$). Early horn growth in the 'low' hunting area did not vary with hunter origin ($F_{1,2282} = 0.38$, $P = 0.53$). Non-resident hunters shot males with horns 2.4% and 3.6% longer than resident hunters in the 'low' ($F_{1,2256} = 34.04$, $P < 0.0001$) and 'high' hunting area ($F_{1,4939} = 164.71$, $P < 0.0001$) respectively, independently of male age (interactions between age and hunter origin, $P > 0.40$). Horn base of males harvested by non-residents was slightly thicker than for males taken by residents (1.6% in the 'low' hunting area, $F_{1,2237} = 13.47$, $P = 0.0002$ and 0.7% in the 'high' hunting area, $F_{1,4936} = 11.72$, $P = 0.0006$). These results support H3 that non-resident hunters harvested older males with longer horns than residents of British Columbia.

SPATIO-TEMPORAL TRENDS

There were strong regional differences in temporal trends for early horn growth. Supporting H4, early growth declined by 12% for males born between 1972 and 2000 in the 'high' hunting area, but remained relatively stable in the 'low' hunting

area (Tab. 6.2, Fig. 6.5). The temporal trend accounted for 40% of cohort variation in early horn growth in the ‘high’ hunting area.

Table 6.2. Effects of time T (i.e. seniority of the cohort) after accounting for effects of climate on cumulative horn growth during the second and third year of life of harvested Stone’s sheep males from two regions of British Columbia, Canada. PDO_W and PDO_S are average winter and spring-summer Pacific Decadal Oscillation between birth and 2 years, respectively. In the Peace, the baseline model (base) included hunter origin as a two-level factor (non-residents or residents of British Columbia).

Region	Model	k	Deviance	P-Anodev	R_{dev}^2	Slope (\pm SE)
Skeena (‘low’ hunting area)	Constant	3	25403.17			
	Cohort dependent	31	25282.69			
	Covariate models					
	PDO_W	4	25400.17	0.41	0.02	4.38 ± 2.52
	PDO_S	4	25401.39	0.53	0.01	-3.67 ± 2.74
	T	4	25397.30	0.25	0.05	0.50 ± 0.21
	T + T ²	5	25388.50	0.15	0.12	-319.2 ± 107.5 0.10 ± 0.03
Peace (‘high’ hunting area)	Base	4	56831.26			
	Cohort dependent	32	56589.65			
	Covariate models					
	PDO_W	5	56824.90	0.40	0.03	4.76 ± 1.89
	PDO_S	5	56825.20	0.41	0.03	-5.04 ± 2.05
	T	5	56733.45	< 0.001	0.40	-1.53 ± 0.15
	T + T ²	6	56730.22	0.44	0.41	-141.4 ± 77.8 0.04 ± 0.02

In both regions, seniority of the cohort interacted with harvest age to affect total horn length (all $P < 0.001$). In the ‘low’ hunting area, there was a quadratic increase (5%) in horn length over time for males aged 5-7 years (Appendix C,

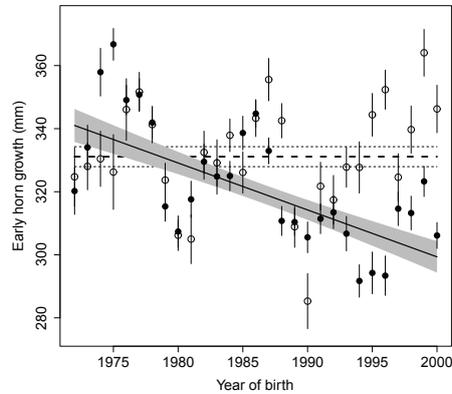


Fig. 6.5. Early horn growth (adjusted for PDO_W and hunter origin, Tab. 6.2) of Stone's rams as a function of year of birth for cohorts born between 1972 and 2000 in the 'low' (white circles, dashed line and 95% confidence intervals are shown by dotted lines) and 'high' (black circles, solid line and a shaded area for 95% confidence intervals) hunting areas of British Columbia.

Fig. 6.6A). Horn length was stable for males aged 8-10 years (Fig. 6.6B) and decreased by 5% in males aged 11-13 years (Fig. 6.6C). In the 'high' hunting area, horn length for males aged 5-7 years varied between cohorts without clear temporal trend (Appendix D, Fig. 6.6D). In contrast, horn length for males aged 8-10 and 11-13 years declined by 3.4% over time (Appendix D, Figs. 6.6E and 6.6F). While PDO_W had a positive influence on horn length in some age groups (Appendix C and D), there were no detectable effects of PDO_S on horn length.

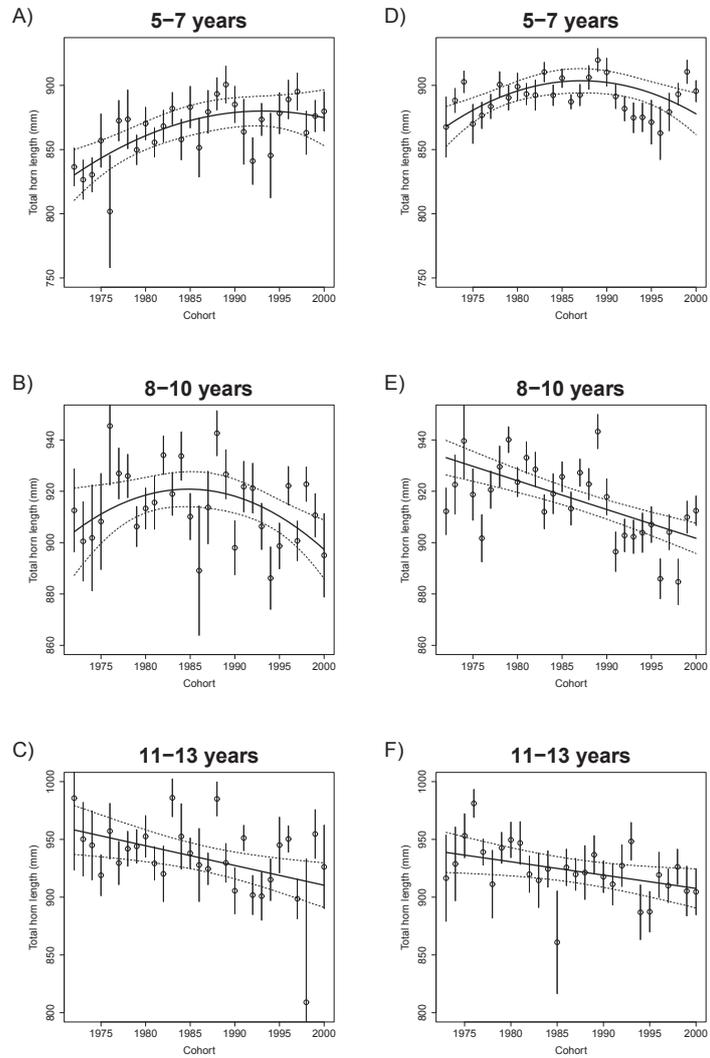


Fig. 6.6. Age-specific total horn length of Stone's rams harvested in the 'low' (A, B and C) and 'high' (D, E, and F) hunting areas of British Columbia as a function of year of birth for cohorts born between 1972 and 2000. Points are average (\pm SE) observed values, solid lines are predicted age-specific temporal trends and dotted lines indicate the 95% confidence intervals.

In the ‘low’ hunting area, the allometric coefficient between horn length and base was similar between the older and more recent cohorts (difference of -0.017 ± 0.053 , $P = 0.75$). For a given horn base, horns were slightly longer for more recent cohorts (difference in intercept of 0.0068 ± 0.0030 , $P = 0.02$). These results did not change when we only considered males older than 7 years (interaction between cohort seniority and horn base = -0.017 ± 0.054 , $P = 0.75$, additive effect of cohort seniority = 0.0057 ± 0.0034 , $P = 0.09$). In the ‘high’ hunting area, there was no interaction between cohort seniority and horn base (difference in allometric coefficient of -0.001 ± 0.036 , $P = 0.97$). In support of H5, however, the intercept was higher for older than for more recent cohorts (difference of -0.0064 ± 0.0020 , $P = 0.001$) especially for males aged 8-13 years (difference of -0.014 ± 0.002 , $P < 0.001$, Appendix E). For the average horn base circumference, horn length of males aged 8-13 years born in 1987-2000 had horns 1.35 cm shorter than males born in 1972-1986.

The number of harvested males from each cohort tended to be positively related to the cohort’s early horn growth in the ‘high’ hunting area ($\beta = 1.12 \pm 0.60$, $P = 0.07$, $R^2 = 0.12$). The number of males harvested from each cohort in the ‘high’ hunting area increased for cohorts born through the 1970’s and then decreased by 45% (from 285 individuals born in 1980 to 156 born in 2000; $\beta = 2015.2 \pm 643.2$, $\beta^2 = -0.5 \pm 0.01$, $P = 0.004$, $R^2 = 0.33$). In contrast, the number of harvested males from each cohort was rather stable in the ‘low’ hunting area ($\beta = 0.03 \pm 0.21$, $P = 0.88$, $R^2 < 1\%$). These results support prediction H6 of a decrease in number of ‘legal’ males over time only in the ‘high’ hunting area.

6.4 Discussion

Horn growth and availability of trophy Stone’s males diminished over time in the ‘high’ hunting area, where selective harvest was strongest. Early horn growth declined by 12% over 37 years, age-specific horn length declined for males aged 8

years and older, horn length became shorter for a given horn base and the number of harvested males declined over time. In contrast in the ‘low’ hunting area, early horn growth, age-specific horn length and horn length for a given base remained stable. These results provide important insights on the conditions under which selective hunting can impact horn length in harvested populations.

REGIONAL DIFFERENCES IN SELECTIVE HARVEST EFFECTS

Over time, harvest pressure became increasingly higher in Peace (‘high’ hunting area) than in Skeena (‘low’ hunting area), likely because of differential access to hunting areas. Road density nearly doubled from 1988 to 1999 in British Columbia but is much greater in the ‘high’ hunting area (Gayton 2007). Roads increase vulnerability of wildlife to hunting (Brody and Pelton 1989). Although all Stone’s sheep populations are now accessible to some degree either by road, all-terrain vehicle, horse, float plane or riverboat (B. Jex and C. Thiessen, personal communication), those closer to roads experience greater hunting pressure than those further away (Paquet and Demarchi 1999). The higher proportion of males harvested by non-residents in the ‘low’ hunting area compared to the ‘high’ hunting area is consistent with greater access in the latter. Non-residents must be accompanied by a licensed guide and guiding services are costly (Stone’s sheep hunts currently cost about \$34,000). Guides deploy substantial efforts to access remote areas and find larger trophies. Hence, non-residents shot older males with greater age-specific horn length than those taken by resident hunters. In addition, guides are rewarded for harvesting old males and penalized for taking young males in their subsequent quota allocation (B. Jex, personal communication), creating an incentive to harvest older males. The difference in horn length of males according to hunter residency underlines that large males remain available to be harvested, likely in more inaccessible sites. In contrast, a recent study in Alberta found no effect of hunter residency on horn size of harvested bighorn males, suggesting that few males survive to grow long horns (Festa-Bianchet et al. 2014).

Likely as a consequence of the difference in harvest pressure between the two regions, males were harvested at a younger age for a given early horn growth in the ‘high’ hunting area than in the ‘low’ hunting area. Heavy harvest of males as soon they became ‘legal’ may explain why males harvested before 8 years had longer horns in the ‘high’ compared to the ‘low’ hunting area, while the reverse was true for older individuals. Strong selection against long horns in young adults increases the proportion of inferior phenotypes at older ages, especially in the region with higher harvest intensity. This age- and phenotypic-specific mortality is particularly important for the possible evolutionary effects of selective hunting, because large horns do not confer a fitness advantage to young males (Coltman et al. 2002). On the other hand, males harvested in the ‘high’ hunting area had thicker horn bases than those in the ‘low’ hunting area. Because the definition of ‘legal’ male is based on age and horn length, base circumference is not a direct target of artificial selection (Pelletier et al. 2012). Thicker bases in the ‘high’ than in the ‘low’ hunting area suggest that overall the ‘high’ hunting area produces larger-horned males, and argues against a possible effect of population density in reducing both the harvest and the horn length of males harvested in the ‘high’ hunting area. Without selective hunting, males in the ‘high’ hunting area should have longer horns at any age than males in the ‘low’ hunting area. Instead, most large-horned males in the ‘high’ hunting area are apparently shot at young ages.

SPATIO-TEMPORAL CHANGES IN HORN CHARACTERISTICS

Although it is often suggested that larger weapons may lower survival, there is little empirical evidence of such costs in large herbivores (Bonenfant et al. 2009b). For instance, Bergeron et al. (2008) and Toigo et al. (2013) found respectively that early horn growth had no impact on longevity and future survival in Alpine ibex (*Capra ibex*). Natural selection co-exists with artificial selection that generates a negative association between early horn growth and survival. The relative strength of these two opposing evolutionary forces shapes horn growth. The decreasing

trend in early horn growth in the ‘high’ hunting area only supports a phenotypic response to selective harvest. Total horn length, however, declined in the ‘high’ hunting area only for males > 7 years. We likely underestimated the decline in horn length in the population because small-horned males cannot be harvested (Pelletier et al. 2012). This bias is particularly important for young males, because only exceptionally well-developed ones become legal. The probability to reach ‘legal’ status increases with age (Festa-Bianchet et al. 2014), therefore the large-size bias of the harvested sample compared to the overall population likely decreased with age. Analyses of Dall sheep in the Yukon show a slight increase in horn growth over time, suggesting a moderate hunting intensity in the territory (Loehr et al. 2010). When hunting pressure remains low, some males with fast-growing horns likely reach the age at which large horns improve reproductive success, mitigating the impact of artificial selection (Festa-Bianchet and Lee 2009). Refugia from hunting such as the Spatsizi wilderness park in the ‘low’ hunting area could also counter artificial selection by providing a source of non-selected immigrants (Tenhumberg et al. 2004, but see Pelletier et al. in press).

A recent study in Hungary reported no long-term negative trend in red deer antler size over more than a century (Rivrud et al. 2013). Unlike horns, however, antlers are regrown each year and are strongly influenced by inter-annual environmental variation (Schmidt et al. 2001, Kruuk et al. 2002). The strength of relationships between trophy size, age, and reproductive success also modulates the response to artificial selection. In chamois (*Rupicapra rupicapra*), for instance, males with rapid early growth do not develop into the largest adults and sexual selection appears relatively weak, likely weakening the potential evolutionary effects of selective removals of large-horned males (Rughetti and Festa-Bianchet 2010). On the other hand, selective hunting induced evolutionary responses in bighorn sheep because males with fast-growing horns were harvested before the age at which large horns influence reproductive success (Coltman et al. 2002; 2003). Although there are no data on the relationships between horn length and

age-specific reproductive success in Stone's sheep, similarities in sexual size dimorphism, mating system and age-specific horn growth among species of mountain sheep in North America (Krausman and Bowyer 2003), suggest that evolutionary responses to selective hunting in Stone's sheep should be similar to those reported for bighorns.

Changes in environmental conditions should be accounted for in analyses of temporal trends in horn or antler size. Development of horns and antlers is affected by factors influencing food quantity or quality, such as population density and climate (Jorgenson et al. 1998, Schmidt et al. 2001, Festa-Bianchet et al. 2004, Mysterud et al. 2005). We controlled for climate but unfortunately no reliable measure of density was available, a problem often encountered in studies examining the effects of trophy hunting at large spatial scales (e.g. Rivrud et al. 2013). Local wildlife managers' opinions and aerial counts conducted every 3 or 4 years between 1987 and 2011, however, suggest that density of Stone's sheep was relatively stable over time in both regions (Demarchi and Hartwig 2004, Kuzyk et al. in press). Finally, it is unlikely that the changes in horn shape suggested by the decrease in length for a given horn base were due to changes in environmental conditions (Garel et al. 2007). Selection on a heritable trait does not always lead to evolutionary change (Kruuk et al. 2002, Ozgul et al. 2009). Thus, we cannot affirm that evolution of smaller horns is responsible for the observed decline in horn growth under high hunting pressure. Our results, however, show that artificial selection is a possible cause of this decline.

MANAGEMENT IMPLICATIONS

We suggest that the decline in male harvest in the 'high' hunting area was partly a consequence of decreasing horn growth. Slow-growing horns require more time to reach 'legal' status, so that more males will die from natural causes before they can be harvested. Monitoring of marked bighorn rams in two populations revealed that 19-27% of 4-year-olds would die of natural causes before reaching

age 6 (Loison et al. 1999a), and age-specific mortality rates of Stone's rams are likely similar. Selection favouring the survival of males with small horns would also reduce the availability of 'legal' males. In the 'low' hunting area, where horn growth was rather constant over time, male harvest from each cohort remained stable.

Trophy hunting is an important economic activity in British Columbia where hunters generated \$48 millions in 2003 (Demarchi and Hartwig 2004) and elsewhere (Leader-Williams et al. 2001, Lewis and Alpert 1997). Trophy hunting can contribute to conservation and management (Lewis and Alpert 1997, Lindsey et al. 2007). For instance, a portion of economic benefits from hunting in British Columbia finances sheep range improvements (Demarchi and Hartwig 2004). Sustainable harvest, however, must consider trade-offs between economic benefits and evolutionary consequences (Garel et al. 2007). By favouring males with smaller trophies and by reducing the availability of desirable phenotypes, excessive hunting may generate long-term negative ecological and economic consequences. Our analyses reveal that low harvest intensity, for instance by limiting the number of permits, is required to limit the undesirable effects of artificial selection.

Acknowledgements

Compulsory inspection data were provided by the British Columbia Ministry of Environment, Wildlife Branch, Victoria. This work was funded by the GDRI program and by a PhD scholarship from the French Ministry of Higher Education and Research. M.F.B. and F.P. are funded by NSERC of Canada. F.P. holds the Canada Research Chair in Evolutionary Demography and Conservation. We are grateful to Gerald Kuzyk, Conrad Thiessen, Bill Jex, Atle Mysterud and Chris Darimont for very constructive comments on earlier drafts.

6.5 Supplemental material

Appendix A. Relationship between harvest age and horn length excluding the first annual increment for Stone's rams.

Appendix B. Age distribution of Stone's rams harvested by resident and non-resident hunters.

Appendix C. Effects of time on total horn length of Stone's rams harvested in the 'low' hunting area.

Appendix D. Effects of time on total horn length of Stone's rams harvested in the 'high' hunting area.

Appendix E. Allometric relationships between horn length and horn base of males aged 8-13 years during two periods of study in the 'high' hunting area.

Appendix A

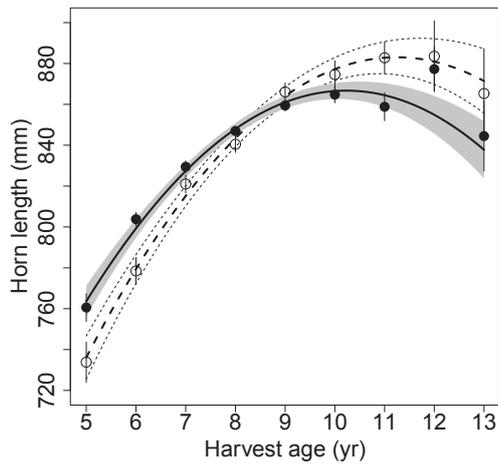


Fig. 6.7. Relationship between harvest age and horn length excluding the first annual increment for Stone's rams harvested in two regions of British Columbia. The solid line represents predicted relationship with 95% confidence intervals (shaded area) in the 'high' hunting area. The dashed line represents predicted relationship with 95% confidence intervals (dotted lines) in the 'low' hunting area.

Appendix B

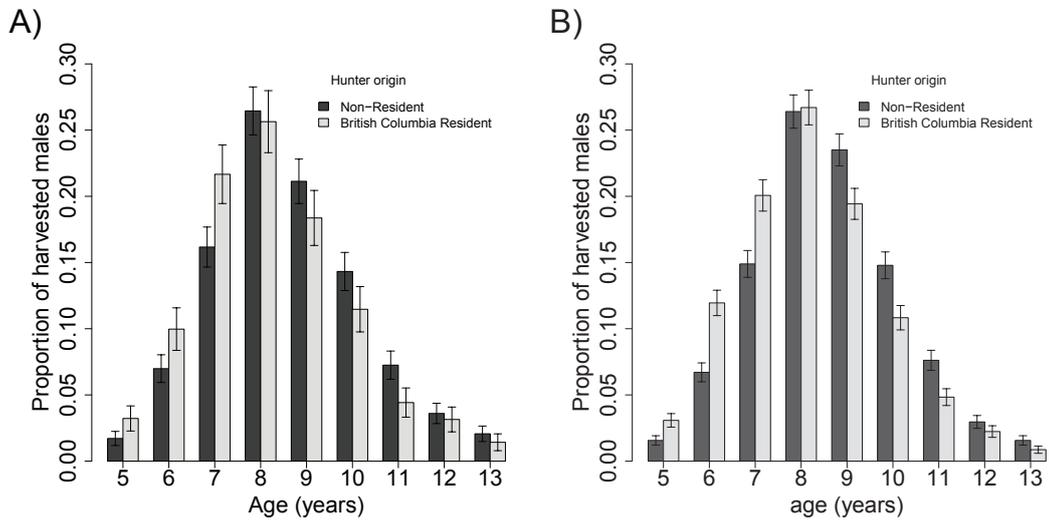


Fig. 6.8. Age distribution of Stone's rams harvested by resident and non-resident hunters in the A) 'low' and B) 'high' hunting areas of British Columbia.

Appendix C

Table 6.3. Effects of time T (seniority of the cohort) after accounting for possible effects of climate on total horn length of Stone’s rams harvested in the ‘low’ hunting area (Skeena) of British Columbia. PDO_W and PDO_S represent average winter and spring-summer Pacific Decadal Oscillations between birth and 2 years, respectively. The baseline model (base) included hunter origin as a two-level factor (non-residents or residents of British Columbia).

Age	Model	k	Deviance	P-Anodev	R_{dev}^2	slope (\pm SE)	
5-7 yr-old	Base	4	6717.3				
	Cohort dependent	32	6680.9				
	Covariate models						
	PDO_W	5	6715.7	0.28	0.04	6.49 ± 5.15	
	PDO_S	5	6714.3	0.13	0.08	10.50 ± 6.06	
	T	5	6704.7	< 0.001	0.34	1.66 ± 0.46	
	T + T ²	6	6700.6	0.03	0.46	444.4 ± 219.1 -0.10 ± 0.06	
8-10 yr-old	Base	4	16179.3				
	Cohort dependent	32	16132.9				
	Covariate models						
	PDO_W	5	16176.2	0.18	0.06	6.26 ± 3.62	
	PDO_S	5	16177.3	0.28	0.04	5.24 ± 3.74	
	T	5	16176.1	0.17	0.07	-0.51 ± 0.29	
	T + T ²	6	16169.4	0.04	0.21	444.4 ± 219.1 -0.10 ± 0.06	
11-13 yr-old	Base	4	3348.7				
	Cohort dependent	32	3288.7				
	Covariate models						
	PDO_W	5	3341.8	0.07	0.11	22.08 ± 8.31	
	PDO_W + PDO_S	6	3340.9	0.52	0.13	29.56 ± 11.70 -11.56 ± 12.64	
	PDO_W + T	6	3334.4	0.05	0.23	21.41 ± 8.02 -1.71 ± 0.62	
	PDO_W + T + T ²	7	3334.3	0.79	0.24	20.04 ± 8.90 141.35 ± 395.60 -0.04 ± 0.10	

Appendix D

Table 6.4. Effects of time T (seniority of the cohort) after accounting for possible effects of climate on total horn length of Stone’s rams harvested in the ‘high’ hunting area (Peace) of British Columbia. PDO_W and PDO_S represent average winter and spring-summer Pacific Decadal Oscillations between birth and 2 years, respectively. The baseline model (base) included hunter origin as a two-level factor (non-residents or residents of British Columbia).

Age	Model	k	Deviance	P-Anodev	R^2_{Dep}	slope (\pm SE)	
5-7 yr-old	Base	4	15877.74				
	Cohort dependent	32	15810.29				
	Covariate models						
	PDO_W	5	15848.21	< 0.001	0.43	17.26 ± 3.11	
	PDO_W	6	15847.96	0.68	0.44	15.15 ± 5.20	
	+ PDO_S					2.97 ± 5.89	
	PDO_W	6	15846.86	0.33	0.45	16.92 ± 3.12	
	+ T					0.32 ± 0.27	
	PDO_W	7	15836.93	0.005	0.60	6.70 ± 4.46	
	+ T					618.7 ± 195.26	
	+ T^2					-0.20 ± 0.05	
	8-10 yr-old	Base	4	35165.33			
Cohort dependent		32	35017.78				
Covariate models							
PDO_W		5	35123.74	0.003	0.28	14.98 ± 2.29	
PDO_W		6	35122.43	0.57	0.29	17.72 ± 3.31	
+ PDO_S						-4.03 ± 3.52	
PDO_W		6	35089.01	0.001	0.51	12.81 ± 2.28	
+ T						-1.12 ± 0.18	
PDO_W		7	35080.99	0.14	0.55	8.50 ± 2.74	
+ T						326.70 ± 115.59	
+ T^2						-0.10 ± 0.03	
11-13 yr-old		Base	4	5728.40			
	Cohort dependent	32	5689.48				
	Covariate models						
	PDO_W	5	5727.86	0.54	0.01	5.07 ± 6.92	
	PDO_S	5	5727.69	0.48	0.01	6.18 ± 7.37	
	T	5	5723.62	0.06	0.12	-1.15 ± 0.52	
	T	6	5722.94	0.47	0.14	243.47 ± 296.95	
	+ T^2					-0.06 ± 0.07	

Appendix E

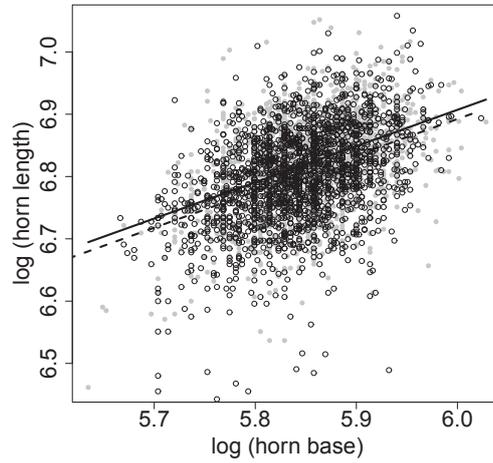


Fig. 6.9. Allometric relationships between horn length and horn base of males aged 8-13 years during two periods of study (old cohorts (1972-1986), grey circles, solid line; recent cohorts (1987-2000), open circles, dashed line) in the 'high' hunting area of British Columbia.

Part IV

General discussion

Chapter 7

Synthesis and perspectives

7.1 Early-life events and their consequences for life-history evolution

7.1.1 PREDICTIVE ADAPTIVE RESPONSES OR NOT?

The heterogeneity of life-history traits within populations can originate from numerous sources, including age (Caughley 1966, Caswell 2001), sex (Clutton-Brock et al. 1982), phenotypic or genetic quality (Pemberton et al. 1988, Gaillard et al. 2000*a*, Nussey et al. 2005) and environmental conditions (Harrison et al. 2011, Auer et al. 2012). In this context, the environmental conditions experienced during early life can be particularly important because they have long-term consequences on life-history traits in addition to the more immediate and obvious effects on early growth and survival (Lindström 1999, Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002). A central question is whether the long-term effects of early environmental conditions on life-history traits represent adaptive responses to differing environments, or are only a consequence of energetic constraints on development (Monaghan 2008, Clutton-Brock and Sheldon 2010). We aimed to address this issue notably by testing hypotheses issued from human medicine in wild populations.

The results presented in chapter three, based on the two contrasting populations of roe deer, clearly show that poor early-life conditions impose strong developmental constraints with major fitness consequences and do not support the external PAR hypothesis (*sensu* Nettle et al. 2013). This hypothesis posits that individuals adjust their physiology and developmental trajectory during early life in anticipation of their future environments (Gluckman and Hanson 2004, Bateson et al. 2004, Gluckman et al. 2005*a*). Accordingly, when environment conditions in early life match environmental conditions during adulthood, individual fitness should be greater (Bateson et al. 2004, Monaghan 2008). In the highly productive site of Trois-Fontaines, the fitness of female roe deer increased with the quality of environment during adulthood and contrary to predictions of external PAR, in-

dividuals born in good conditions always outperformed those born in poor years. This ‘silver spoon’ effect that results from reproductive differences between individuals born under contrasting environmental conditions, provides also a evaluation of the importance of effects of the early-life environment vs. the current environment on life-history traits. Because the effects of environment across life stages have been studied in isolation, their relative influence remain largely unexplored. Consequently, for predicting individual responses to environmental change and their subsequent effect on population dynamics, it remains unclear if we need to account for the entire histories of individuals within a population or if some events are better predictors of individuals performance than others (Auer et al. 2012). At Trois-Fontaines, the influence of annual environmental conditions was slightly weaker than the influence of early environment on reproductive success of females. For instance, the probability of weaning 2 fawns increased by 46% from an unfavourable to a favourable adult environment in a given year (independently of early conditions) and increased by 64% between females born under harsh and good environmental conditions (independently of current environment). In a capital breeder, like mountain goats, the normalised difference vegetation index (NDVI) in year of birth accounted also for 35% of variation in individual quality (Hamel et al. 2009b). Hence, for large herbivores, it seems that effects of past environmental conditions especially during early life, should be integrated in demographic models as well as the effects of current environmental conditions.

In the more resource-limited site of Chizé, the fitness of female roe deer born in poor years was better than those born in good conditions in poor years when the animals were adult, but not in good years. This could be interpreted as a support for external PAR but we showed that difference in viability selection (*sensu* Fisher 1930) during the earliest stage of life was the most parsimonious explanation. Individuals alive at adulthood after experiencing poor environmental conditions in early life are not a random sample of the initial cohorts. Poor cohorts generally experienced a high condition-dependant mortality and this results in a ‘filtering

effect'. In other words, in poor early-life environmental conditions only the more robust females survived to adulthood, leading to a high survival for these poor cohorts (see also Rose et al. 1998). Interestingly, viability selection has opposite effects on adult survival and lifespan of male and female roe deer (see appendix one). Indeed, high juvenile mortality leads to shorter lifespans and reduced adult survival for males surviving early critical period of life. This between-sex difference in a weakly dimorphic species like roe deer is very interestingly because sex differences in the effects of early-life conditions on outcome of individuals are often attributed to sexual size dimorphism and associated different nutritional requirements. For example, in great tit (*Parus major*), both longevity and lifetime reproductive success were influenced by the early environmental conditions for males but not for females (Wilkin and Sheldon 2009) (male great tits are heavier than females). In contrast, in tawny owl (*Strix aluco L.*), female but not male reproductive performance increased with vole density at birth (Millon et al. 2011) (female tawny owls are substantially larger than males). In roe deer, both sexes have similar early life-history traits like birth mass and early growth (Gaillard et al. 1993b) and similar survival up to one year of age (Gaillard et al. 1997). However, high quality roe deer females bias maternal allocation to their daughters over their sons, suggesting that fitness is more strongly condition-dependent in females than males in this species (Hewison et al. 2005). Hence, female roe deer are more susceptible to viability selection during early life than males.

The viability selection can favour the over-representation of high quality individuals in old age classes. This can eventually hide any long-term costs of heavy allocation to early reproduction on survival and reproduction late in life (disposable soma theory Kirkwood 1977, Kirkwood and Rose 1991, see appendix two for a review). We show here that viability selection imposed by very harsh environmental conditions can lead to an apparent support for the external PAR hypothesis. The external PAR hypothesis has frequently been invoked to explain associations between early growth restriction and health outcomes such as diabetes and car-

cardiovascular disease (Gluckman and Hanson 2004; 2006). As an illustration of its importance in medical research, the external PAR hypothesis is already taught in some undergraduate medical courses (Wells 2012). However, understanding the evolutionary processes underlying relationships between early-life conditions and adult health is needed to discriminate among the competing hypotheses such as the 'thrifty phenotype' hypothesis (Hales and Barker 1992; 2001). To date, only two studies have provided a test of external PAR from fitness components in humans and found no support for it (Hayward et al. 2013, Hayward and Lummaa 2013). We suggest that future research on the external PAR hypothesis include the possibility that responses to early-life conditions are adaptive with the constraining effects that environmental conditions appear to impose on growth, survival and reproduction (through viability selection for example). This may lead to other strategies for prevention and treatment of metabolic diseases.

The internal PAR (*sensu* Nettle et al. 2013) is also an adaptive response to early environment. By contrast with the external PAR, the predictions about the future are not based on the state of the environment during adulthood but rather on the future somatic state which seems a most plausible scenario. More specifically, whether poor early-life environmental conditions accelerate either actuarial or reproductive senescence, this may create a selective pressure that favours a high energy allocation towards early reproduction. In accordance with the internal PAR hypothesis, we show in chapter four that young female Svalbard reindeer born in poor environmental conditions had a riskier reproductive tactic by having, for a given body mass, a higher reproductive rate than those born in favourable conditions. The annual fitness of individuals born under very different conditions was comparable up to 5-6 years. Consequently, we suggest that this increase in reproductive effort is an adaptive response of females born under poor conditions to accelerated reproductive and actuarial senescence, these females making the best of a bad job. Alternatively, the causal direction might be the reverse *i.e.*, the trade-off between early and late life reproduction may be more acute for in-

dividuals born in poor environments than in good environments, as predicted by the disposable soma theory (Kirkwood and Rose 1991). To better identify the ‘causal’ relationship, we are currently testing whether the effects of early-life environmental conditions on reproductive ageing rates are independent of the effects of early-life reproduction. Preliminary results show that the relationship between reproductive success and age in relation with the environmental conditions early in life does not change when adding the early-life reproduction as a covariate, supporting the internal PAR. Similarly, the negative effects of high density in year of birth and early-life reproduction on reproductive ageing rates were independent of one another in female red deer (Nussey et al. 2007a).

These results increase our knowledge of nature’s responses to climate and environmental changes. Climate change induced by increased anthropogenic greenhouse gases has emerged as one of the most important environmental issues (Walther et al. 2002, Kerr 2007). If we want to improve our ability to assess impacts of climate change on communities and mitigate its effects, we need to understand the influence of climate on demography over a wide range of species (Boyce et al. 2006). In Svalbard reindeer, the internal PAR can play an important mitigating role in buffering negative effects of ongoing climate change in Arctic (Rennett et al. 2009). The situation is more complicated for roe deer. The absence of external predictive adaptive response and the fact that roe deer can not cope with increasingly early spring (see appendix three) notably because of the lack of response in birth date to climate change (Plard et al. 2014), make this species is now confronting to adverse effects of climate change. The internal PAR remains, nevertheless, to be tested in this species.

7.1.2 GROWTH TRAJECTORIES

Natural selection can also favour processes that mitigate the negative long-term effects of poor early-life conditions through growth (Metcalfe and Monaghan 2001). Many organisms can accelerate their growth when environmental conditions im-

prove after a period of growth restriction (compensatory growth, Bohman 1955, Metcalfe and Monaghan 2001, Hector and Nakagawa 2012). We show in chapter two such an opportunity to deviate from the initial growth trajectory was reduced for female roe deer. Indeed, adverse early-life conditions negatively influenced both their early and late growth. In other words, early environmental conditions imprint whole body growth trajectories of females in this species. These results are consistent with laboratory and human observations suggesting that early nutrition can directly shape growth trajectories (McCance 1962, Lucas 1991, see also Madsen and Shine 2000) and nuance the prevailing view that early-life conditions influence adult body mass only through their effect on early growth (Lummaa and Clutton-Brock 2002, Pettorelli et al. 2002, Solberg et al. 2004). Contrary to females, the effects of early environmental conditions on adult body mass of males were restricted to an influence on early body growth. Such between-sex differences could result from sex-specific growth duration. The longer duration of body growth in males confers them a greater flexibility to deviate from their initial growth trajectory compared to females. Growth patterns vary widely between species (Nussey et al. 2011) suggesting such differences may be perceptible at species level. Our findings point out that the pathways by which early-life environmental conditions affect adult morphological traits in wild mammal populations are more complex than initially thought.

Compensatory body growth is only one possible compensatory response (Lindström et al. 2005). In the chapter five, we show that compensatory horn growth occurred in male and female Pyrenean chamois. Compensatory growth is generally thought to induce fitness costs often expressed later in life (Metcalfe and Monaghan 2001, Hector and Nakagawa 2012). In Pyrenean chamois, we found no evidence of costs of compensatory horn growth on longevity. However, horn length negatively influenced longevity, and this trade-off was of similar magnitude in both sexes. To date, most of studies have tested the trade-off between horn growth and survivorship in males of sexually dimorphic species and there is little

evidence of such costs (see Bonenfant et al. 2009*b*, for a review). For example, in males of the highly sexually dimorphic Alpine ibex, any cost of growing large horn was reported on age-specific survival (Toïgo et al. 2013) or longevity (Bergeron et al. 2008), suggesting a conservative tactic of energy allocation. The chamois is a monomorphic species and the intensity of sexual selection in males is quite weak. Hence, our study points out that the occurrence of the trade-off between secondary sexual traits and survivorship does not increase with the intensity of sexual selection and is not restricted to males. The underlying causes of this trade-off may differ according to sex (cost of mating in males vs reproductive costs in females). We are currently investigating the age-specific costs of growing large horns and the potential confounding effects of body mass to better identify the factors underlying this trade-off between horn growth and longevity.

Understanding the relationship between horn growth and natural mortality is very important for ungulate management. Indeed, the selective effects of trophy hunting that increase the mortality of males with large horns may be reduced if hunting mimicked natural mortality (Bergeron et al. 2008, Festa-Bianchet and Lee 2009). In bighorn sheep, because natural mortality is very different from hunting mortality patterns (Bonenfant et al. 2009*b*), trophy hunting selected for males with smaller body size and shorter horns (Coltman et al. 2003). Our study in chapter six suggests that evolutionary responses to selective hunting in Stone's sheep could be similar to those reported for bighorns. Indeed, the undesirable evolutionary consequences of trophy hunting, such as the production of smaller-horned males and reduced harvests, increased with harvest intensity in this species but can be avoided when offtake by trophy hunters is moderate. Selection on a heritable trait does not always lead to evolutionary change (Kruuk et al. 2002, Ozgul et al. 2009). Hence, a limitation of this study is we cannot affirm that evolution of smaller horns is responsible for the observed decline in horn growth under high hunting pressure. Our results show that artificial selection is only a possible cause of this decline. Studies combining long-term data in horn growth

and pedigree information for several populations with variable level of hunting would be very beneficial to better identify when selective hunting is strong enough to cause evolutionary responses to hunting.

7.1.3 THE VARIANCE IN LIFE-HISTORY TRAITS UNDER CONSIDERATION

Viability selection has a central role to understanding both the apparent support for the external PAR in roe deer as well as the effects of trophy hunting on horn growth in Stone's sheep. In this work, we have focused on the effects of viability selection with respect to average of life-history traits but the variance of these traits is expected to be affected. More specifically, harsh environmental conditions associated with a greater filtering of individuals could lead to lower variance among survivors in cohorts born under unfavourable than under favourable conditions. On the other hand, Lomnicki's model suggests that variance in life-history traits should increase when resources become scarce because unequal partitioning of resources among individuals, either through social effects (dominance and territoriality) or through a higher inter-individual heterogeneity in food acquisition (Lomnicki 1978). Hence, Hamel et al. (2009*b*) suggest that variance in individual quality may peak at intermediate environmental conditions, until conditions deteriorate to a threshold that leads to a reduction of variance among individuals. Although, variance of life-history traits in a population represents the opportunity for selection (Darwin 1859), explicit empirical examination of this model in wild populations is still lacking.

In this thesis, we have also tested several adaptive developmental plasticity hypotheses with respect to average of life-history traits (external PAR, internal PAR). In a variable environment, minimising the variance of a life-history trait among years is also one means of maximising fitness (bet-hedging strategy, Seger and Brockmann 1987). In polytocous and long-lived iteroparous species, mothers can maximise the phenotypic diversity of offspring produced within a year (coin-flipping, Kaplan and Cooper 1984) to minimise among-year variation in re-

productive success. For example, heavy female wild boars (*Sus scrofa scrofa*) produced litters of variable size including a mixture of heavy and light offspring within litters (Gamelon et al. 2013). We show in appendix four that such coin-flipping tactics vary with the food availability with adult female wild boars producing highly diversified offspring phenotypes within a litter in years of abundant food resources. By minimizing sibling rivalry, such a plastic reproductive tactic allows adult wild boar females to maximise the number of littermates for a given breeding event. Overall, the adaptive developmental plasticity hypotheses in link with variance of life-history traits require further attention.

7.1.4 EXPLORING THE TRANSMISSION OF EARLY LIFE ENVIRONMENTAL EFFECTS ACROSS GENERATIONS

This work and other studies (see Lindström 1999, Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002, Monaghan 2008, for a review), clearly show that environmental conditions early in life can have long-term effects on individual life-history traits. However, the influence of early-life conditions may not be limited to the individuals that experienced them but affect the generations to follow (Lummaa and Clutton-Brock 2002, Burton and Metcalfe 2014). For example, female lizard (*Lacerta vivipara*) that experienced high rainfall in utero produced fewer but longer neonates at adulthood (Marquis et al. 2008). In Svalbard reindeer, adverse environmental conditions in utero experienced by the mother were associated with more rapid senescence in offspring survival (see chapter four). To date, studies have focused on the short-term impact of the inter-generational effects induced by the early environment (e.g. the number and the size of offspring in lizard, the offspring survival in Svalbard reindeer). Environmental conditions in which individuals are born may affect their own survival and reproductive success, as well as the adult survival and reproduction of their offspring (Burton and Metcalfe 2014). This possibility remains to be tested in wild mammal populations; this represents nevertheless a challenge because paternity and maternity

assignments are rather rare.

From a population dynamic perspective, the inter-generational effects induced by the early-life environmental conditions are expected to have important consequences by acting as a potential source of delayed density dependence (Beckerman et al. 2002, Plaistow et al. 2006). The time-series analyses have reported evidence of delayed density dependence in populations of large herbivores (see Owen-Smith 2010, for a review). Identifying whether the effects of environmental conditions in early life, through inter-generational effects or not, might account for this phenomenon remains to be explored (Gaillard et al. 2003a).

7.2 Some applications for wildlife management

In this work, it appears that the link between basic and applied research is relatively strong. We have discussed above that understanding the evolutionary processes underlying relationships between early-life conditions and adult health is needed to improve strategies for prevention and management of metabolic disease (see section predictive adaptive responses or not?). In this section, we focus on the application of our results to wildlife management. Large herbivores populations have increased dramatically in size and distribution over recent decades both in Europe and North America (Andersen et al. 1998a, Fuller and Gill 2001). As a result, in many areas, management goals are changing from protection to population control (Milner et al. 2006). Controlling ungulate populations is required to prevent damage to farming and forestry, deer-vehicle collisions or the spread of diseases (Rooney and Waller 2003, Gordon et al. 2004, Seiler 2004). These various types of impacts can be valued in economic terms. For instance, in France, since 1968, compensation for agricultural damage caused by wild boar and cervidae has increased from 2 482 042 euros in 1973 to 21 634 000 euros in 2004/2005 (Maillard et al. 2010).

7.2.1 THE CONCEPT OF INDICATORS OF ECOLOGICAL CHANGE

Historically, two approaches have been used to manage ungulate populations: time series of population counts, which generally consist of yearly estimates of population size, and demographic models based on estimates of fitness components (Gaillard et al. 2003*b*). Counting methods have, however, repeatedly been shown to be neither accurate nor precise (Gaillard et al. 2003*b*). Andersen (1953) showed, for example, that counts in a population of roe deer can lead to a threefold underestimation of the population size. Moreover, the absence of repeated counts within a year prevents the assessment of the precision of population estimates. Lastly, even the best estimate of population size does not provide the required information to set hunting plans because it does not provide information to managers about the state of the plant-herbivore system (Morellet et al. 2007).

In response to this situation, researchers have developed new tools for managing ungulate populations, which are based on the monitoring of a set of indicators of ecological change (IEC Morellet et al. 2007). An IEC is an easily measured parameter, sensitive to changes in the relationship between the population and its habitat. Morellet et al. (2007) proposed to simultaneously monitor three categories of IEC describing (*i*) animal performance (Bonenfant et al. 2002, Zannèse et al. 2006, Garel et al. 2011), (*ii*) habitat quality (Morellet et al. 2001, Chevrier et al. 2012) and (*iii*) animal abundance (Vincent et al. 1991, Loison et al. 2006, Garel et al. 2010). We showed in appendix 5 that roaring counts in red deer cannot be interpreted as a reliable IEC because they do not track abundance of the resident population of red deer (see also appendix 6 for a popularised version). On the other hand, the body mass of juvenile correspond to a reliable ecological indicator of animal performance in roe deer (Gaillard et al. 1996). As juvenile body mass reflects the interaction between habitat quality and population abundance, it provides an objective assessment of the level of density-dependent limitation of a population. The life-history traits display different responses along the colonisation-saturation continuum. For example, in roe deer hind foot length

is less sensitive to density than body mass and decreases with increasing density only when environmental conditions become very harsh (Toïgo et al. 2006). Actually, there is a lack of indicators of ecological change when the population is close to saturation (Gaillard and Bonenfant, pers. com.). In such conditions, the intensity of reproduction at a given mass (used for investigating reproductive tactic in Svalbard reindeer in chapter four) can be viewed as a candidate ecological indicator. Indeed, the relationship between these two traits changes even when environmental conditions become very harsh. A work in progress on roe deer leads to similar conclusions (Bonenfant and Gaillard, unpubl. data). An ICE should be easily measurable (Morellet et al. 2007), this appears to be the case here. Body mass and reproductive status of pregnant females can indeed be collected over large spatio-temporal scales by hunters.

7.2.2 ENVIRONMENTAL VARIATION IN DEMOGRAPHIC MODELS

When managers have accessed to demographic parameters, the simple Leslie matrix model, a deterministic, age-structured, and female-dominated model, is most commonly used to manage ungulate populations (Eberhardt 1991). Leslie matrix models can estimate asymptotic population growth rate (λ) obtained as the greatest positive eigenvalue of the Leslie matrix including age-specific fertility and age-specific survival. When $\lambda > 1$, the population is asymptotically growing; when $\lambda < 1$, the population is asymptotically declining.

The Leslie matrix model can not provide a satisfactory picture of most large herbivore populations because it typically does not account for variation in life-history traits arising from factors other than age (Gaillard et al. 2003*b*). As shown in chapter three, annual growth rates can vary substantially according the environmental conditions experienced during the present and past. In addition, when temporal variation in fitness components is accounted for, often the key parameter affecting changes in population size differs from the one identified by using a deterministic model (Gaillard et al. 2003*b*). Hence, accounting for environmental

variation at different ages should lead to more efficient models of population dynamics. Related to this, the integral projection models (IPMs), which use continuous relations of vital rates (growth, survival and reproductions), provide now a powerful framework to investigate population dynamics (e.g. Coulson et al. 2011).

7.2.3 CONSEQUENCES FOR CONSERVATION

The effects of environmental conditions during early life on life-history traits can also have important consequences for conservation. Translocations and reintroductions of individuals of threatened species are an increasingly common conservation measure (Lindenmayer and Burgman 2005). For example, gray wolf (*Canis lupus*) population declines in many parts of the world have been arrested in part because of reintroduction programs and natural recolonisation (Ripple et al. 2014). Through their long-term effects on demographic traits, the environmental conditions experienced during early life can determined the success of translocation and reintroduction. This is particular true when the conservation measure is based on a little number of individuals.

Recent studies have underlined the potential conservation value of tourist hunting, where much of the revenue generated depends on trophy size of harvested animals (Courchamp et al. 2006). Sustainable harvest, however, must consider trade-offs between economic benefits and evolutionary consequences (Garel et al. 2007). By favouring males with smaller trophies and by reducing the availability of desirable phenotypes, excessive hunting may generate long-term negative ecological and economic consequences (see chapter six). It is therefore surprising that wildlife managers have paid so little attention to the evolutionary consequences of trophy hunting (Festa-Bianchet 2003).

Among the six species of native wild ungulates that currently occur in France, negative effects of selective harvesting on trophy size have only been reported in mouflon (Garel et al. 2007). The strength of relationships between trophy size, age, and reproductive success modulates the response to trophy hunting selection

(Festa-Bianchet and Lee 2009). In chamois, males with rapid early growth do not develop into the largest adults and sexual selection appears relatively weak, likely weakening the potential evolutionary effects of selective removals of large-horned males (Rughetti and Festa-Bianchet 2010). Similarly, in roe deer, the intensity of sexual selection is relatively weak (Vanpé et al. 2008). Moreover, antlers, unlike horns, are regrown each year and are strongly influenced by inter-annual environmental variation (Schmidt et al. 2001, Kruuk et al. 2002, but see Vanpé et al. 2007). In accordance with this view, a recent study in Hungary reported no long-term negative trend in red deer antler size over more than a century (Rivrud et al. 2013). On the other hand, Alpine ibex are highly sexually dimorphic, probably highly polygynous (Toïgo et al. 2007), and show no obvious trade-off between horn growth and adult survival (Toïgo et al. 2013). Intense selective hunting may thus result in directional changes of reduced male horn length over time in this species. This hypothesis remains to be tested.

7.3 Conclusion

In response to questions and issues raised in the introduction (**chapter one**), we have shown that early-life environmental conditions can imprint whole body growth trajectories in accordance with laboratory observations (**chapter two**). We have investigated whether the long-term effects of early-life environmental conditions on life-history traits represent adaptive responses to differing environments, or are only a consequence of energetic constraints on development by testing hypotheses issued from human medicine in wild populations. We have shown that individuals do not develop an appropriate phenotype during early life for their future environment (**chapter three**) but rather on the future somatic state (**chapter four**). This strategy makes the best of a bad situation because early-life environmental conditions impose strong developmental constraint with major fitness consequences (**chapters three and four**). The strong viability selection

imposed by poor environmental conditions can notably lead to apparent support for a hypothesis which seeks to explain the evolution of metabolic disease in human (**chapter three**). While natural selection often favours larger individuals through increased viability and fertility, selective harvesting usually targets these very same individuals. We point out that by favouring males with smaller trophies and by reducing the availability of desirable phenotypes, excessive hunting generates long-term negative ecological and economic consequences (**chapter six**). The selective effects of trophy hunting may be reduced if hunting mimicked natural mortality. We show the trade-off between secondary sexual traits and survivorship does not increase with the intensity of sexual selection and is not restricted to males (**chapter five**). In conclusion, early-life events i.e. the environmental conditions as well as the growth, play an important role in our understanding of the life-history evolution.

Bibliography

- Agresti, A. 2002. Categorical data analysis. Wiley, New-York, USA.
- Aitken, R. J. 1974. Delayed implantation in roe deer (*Capreolus capreolus*). *Journal of Reproduction and Fertility* **39**:225–233.
- Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *Journal of Animal Ecology* **56**:69–81.
- Albon, S. D., T. H. Clutton-Brock, and R. Langvatn, 1992. Cohort variation in reproduction and survival: implications for population demography. Pages 15–21 in R. D. Brown, editor. *The Biology of deer*. Springer-Verlag, New York, USA.
- Albon, S. D., O. Halvorsen, R. J. Irvine, R. Langvatn, E. Ropstad, and A. Stien. 2002. The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society of London B Biological Sciences* **269**:1625–1632.
- Albon, S. D., B. Mitchell, and B. W. Staines. 1983. Fertility and body weight in female red deer: a density-dependent relationship. *Journal of Animal Ecology* **52**:969–980.
- Allendorf, F. W., and J. J. Hard. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceeding of the National Academy of Science, U.S.A.* **106**:9987–9994.
- Andersen, J. 1953. Analysis of a Danish roe-deer population (*Capreolus capreolus* (L.)) based upon the extermination of the total stock. *Danish Review of Game Biology* **2**:127–155.
- Andersen, R., P. Duncan, and J. D. C. Linnell. 1998a. *The European Roe Deer: The biology of Success*. Scandinavian University Press, Oslo, Norway.
- Andersen, R., J.-M. Gaillard, O. Liberg, and C. San José, 1998b. Variation in life-history parameters. Pages 285–307 in R. Andersen, P. Duncan, and J. Linnell, editors. *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, Norway.
- Andersen, R., J.-M. Gaillard, J. D. C. Linnell, and P. Duncan. 2000. Factors affecting maternal care in an income breeder, the European roe deer. *Journal of Animal Ecology* **69**:672–682.

- Andersson, M. B. 1994. Sexual selection. Princeton University Press, Princeton, USA.
- Auer, S. K. 2010. Phenotypic plasticity in adult life-history strategies compensates for a poor start in life in Trinidadian Guppies (*Poecilia reticulata*). *American Naturalist* **176**:818–829.
- Auer, S. K., J. D. Arendt, R. Chandramouli, and D. N. Reznick. 2010. Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (*Poecilia reticulata*). *Ecology Letters* **13**:998–1007.
- Auer, S. K., A. Lopez-Sepulcre, T. Heatherly, T. J. Kohler, R. D. Bassar, S. A. Thomas, and D. N. Reznick. 2012. Life histories have a history: effects of past and present conditions on adult somatic growth rates in wild Trinidadian guppies. *Journal of Animal Ecology* **81**:818–826.
- Barbraud, C., and H. Weimerskirch. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology* **86**:682–692.
- Barker, D. J., P. D. Winter, C. Osmond, B. Margetts, and S. J. Simmonds. 1989. Weight in infancy and death from ischaemic heart disease. *Lancet* **9**:577–580.
- Bateson, P., D. Barker, T. Clutton-Brock, D. Deb, B. D'Udine, R. A. Foley, P. Gluckman, K. Godfrey, T. Kirkwood, M. M. Lahr, J. McNamara, N. B. Metcalfe, P. Monaghan, H. G. Spencer, and S. E. Sultan. 2004. Developmental plasticity and human health. *Nature* **430**:419–421.
- Beckerman, A. P., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. *Trends in Ecology & Evolution* **17**:263–269.
- Bergeron, P., M. Festa-Bianchet, A. von Hardenberg, and B. Bassano. 2008. Heterogeneity in male horn growth and longevity in a highly sexually dimorphic ungulate. *Oikos* **117**:77–82.
- Bielby, J., G. M. Mace, O. R. P. Bininda-Emonds, M. Cardillo, J. L. Gittleman, K. E. Jones, C. D. L. Orme, and A. Purvis. 2007. The fast-slow continuum in mammalian life history: an empirical reevaluation. *American Naturalist* **169**:748–757.
- Birkhead, T. R., F. Fletcher, and E. J. Pellatt. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proceedings of the Royal Society Biological Sciences B* **266**:385–390.
- Bobek, B., K. Perzanowski, and J. Weiner. 1990. Energy expenditure for reproduction in male red deer. *Journal of Mammalogy* **71**:230–232.
- Bohman, V. R. 1955. Compensatory growth of beef cattle: the effect of hay maturity. *Journal of Animal Science* **14**:249–255.
- Bonduriansky, R., A. Maklakov, F. Zajitschek, and R. Brooks. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. *Functional Ecology* **22**:443–453.

- Bonenfant, C., J.-M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, J. Du Toit, and P. Duncan. 2009a. Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research* **41**:313–357.
- Bonenfant, C., J.-M. Gaillard, F. Klein, and A. Loison. 2002. Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. *Ecography* **25**:446–458.
- Bonenfant, C., F. Pelletier, M. Garel, and P. Bergeron. 2009b. Age-dependent relationship between horn growth and survival in wild sheep. *Journal of Animal Ecology* **78**:161–171.
- Booij, L., D. Wang, M. L. Lévesque, R. E. Tremblay, and M. Szyf. 2013. Looking beyond the DNA sequence: the relevance of DNA methylation processes for the stress–diathesis model of depression. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **368**:20120251.
- Boonstra, R., and W. M. Hochachka. 1997. Maternal effects and additive genetic inheritance in the collared lemming *Dicrostonyx groenlandicus*. *Evolutionary Ecology* **11**:169–182.
- Bowyer, R. T., and D. M. Leslie. 1992. *Ovis dalli*. *Mammalian Species* **393**:1–7.
- Boyce, M., C. Haridas, C. Lee, and NCEAS Stochastic Demography. 2006. Demography in an increasingly variable world. *Trends in Ecology & Evolution* **21**:141–148.
- Boyce, M. S. 1984. Restitution of r- and K-selection as a model of density-dependent natural selection. *Annual Review of Ecology and Systematics* **15**:427–447.
- Bro-Jørgensen, J. 2007. The intensity of sexual selection predicts weapon size in male bovids. *Evolution* **61**:1316–1326.
- Brody, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in Western North Carolina. *Wildlife Society Bulletin* **17**:5–10.
- Bunnell, F. 1978. Horn growth and population quality in dall sheep. *Journal of Wildlife Management* **42**:764–775.
- Bunnell, F. L. 1980. Factors controlling lambing period of Dall's sheep. *Canadian Journal of Zoology* **58**:1027–1031.
- Bunnell, F. L., 1987. Reproductive tactics of cervidae and their relationships to habitat. Pages 145–167 in C. M. Wemmer, editor. *Biology and management of the Cervidae*. Smithsonian Institution Press, Washington, USA.
- Bunnell, F. L. 2005. Thinhorn sheep. *Wildlife Afield* **2**:22–30.
- Burton, T., and N. B. Metcalfe. 2014. Can environmental conditions experienced in early life influence future generations? *Proceedings of the Royal Society B: Biological Sciences* **281**:20140311.

- Cartwright, S. J., M. A. Nicoll, C. G. Jones, V. Tatayahn, and K. Norris. 2014. Anthropogenic natal environmental effects on life histories in a wild bird population. *Current Biology* **24**:536–540.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. 2nd edition. Sinauer Associates, Sunderland, USA.
- Caughley, G. 1966. Mortality patterns in mammals. *Ecology* **47**:906–918.
- Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**:800–803.
- Chevrier, T., S. Saïd, O. Widmer, J.-P. Hamard, C. Saint-Andrieux, and J.-M. Gaillard. 2012. The oak browsing index correlates linearly with roe deer density: a new indicator for deer management ? *European Journal of Wildlife Research* **58**:17–22.
- Choquet, R., L. Rouan, and R. Pradel, 2009. Program E-SURGE: a software application for fitting multievent models. Pages 845–865 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. *Modeling demographic processes in marked populations*. Springer, New-York, USA.
- Choquet, R., A. Viallefont, L. Rouan, K. Gaanoun, and J.-M. Gaillard. 2011. A semi-markov model to assess reliably survival patterns from birth to death in free-ranging populations. *Methods in Ecology and Evolution* **2**:383–389.
- Christensen, R. H. B., 2013. *Ordinal: Regression models for ordinal data*. R package version 2012-09-11.
- Cleal, J. K., K. R. Poore, J. P. Boullin, O. Khan, R. Chau, O. Hambidge, C. Torrens, J. P. Newman, L. Poston, D. E. Noakes, M. A. Hanson, and L. R. Green. 2007. Mismatched pre- and postnatal nutrition leads to cardiovascular dysfunction and altered renal function in adulthood. *Proceedings of the National Academy of Sciences of the USA* **104**:9529–9533.
- Clutton-Brock, T. H. 1988. *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago, USA.
- Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guinness. 1979. The logical stag: adaptative aspects of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour* **27**:211–225.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature* **337**:260–2.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *Red deer : behavior and ecology of two sexes*. University of Chicago Press, Chicago, USA.
- Clutton-Brock, T. H., and K. Isvaran. 2007. Sex differences in ageing in natural populations of vertebrates. *Proceeding of the Royal Society of London, B* **274**:3097–3104.

- Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1992. Early development and population fluctuation in Soay Sheep. *Journal of Animal Ecology* **61**:381–396.
- Clutton-Brock, T. H., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* **25**:562–573.
- Cody, M. L. 1966. A general theory of clutch size. *Evolution* **20**:174–184.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* **29**:103–137.
- Coltman, D., P. O'Donoghue, J. Jorgenson, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* **426**:655–658.
- Coltman, D. W. 2008. Evolutionary rebound from selective harvesting. *Trends in Ecology & Evolution* **23**:117–118.
- Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London, Series B* **269**:165–172.
- Corlatti, L., M. Caroli, V. Pietrocini, and S. Lovari. 2013. Rutting behaviour of territorial and nonterritorial male chamois: Is there a home advantage? *Behavioural Processes* **92**:118–124.
- Corlatti, L., K. Lebl, F. Filli, and T. Ruf. 2012. Unbiased sex-specific survival in Alpine chamois. *Mammalian Biology* **77**:135–139.
- Côté, S., M. Festa-Bianchet, and K. G. Smith. 1998. Horn growth in mountain goat (*Oreamnos americanus*). *Journal of Mammalogy* **79**:406–414.
- Coulson, T., D. R. MacNulty, D. R. Stahler, B. vonHoldt, R. K. Wayne, and D. W. Smith. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. *Science* **334**:1275–1278.
- Coulson, T. N., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**:1528–1531.
- Courchamp, F., E. Angulo, P. Rivalan, R. J. Hall, L. Signoret, L. Bull, and Y. Meinard. 2006. Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biology* **4**:e415.
- Crampe, J.-P., J.-M. Gaillard, and A. Loison. 2002. L'enneigement hivernal: un facteur de variation du recrutement chez l'isard (*Rupicapra pyrenaica pyrenaica*). *Canadian Journal of Zoology* **80**:1306–1312.
- Crampe, J.-P., A. Loison, J.-M. Gaillard, E. Florence, P. Caens, and J. Appolinaire. 2006. Monitoring of the reproduction in isard females (*Rupicapra pyrenaica pyrenaica*) in a non-hunted population and demographic consequences. *Canadian Journal of Zoology* **84**:1263–1268.

- Crosmary, W.-G., A. J. Loveridge, H. Ndaimani, S. Lebel, V. Booth, S. D. Côté, and H. Fritz. 2013. Trophy hunting in Africa: long-term trends in antelope horn size. *Animal Conservation* **16**:648–660.
- Dantzer, B., A. E. M. Newman, R. Boonstra, R. Palme, S. Boutin, M. M. Humphries, and A. G. McAdam. 2013. Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. *Science* **340**:1215–1217.
- Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the USA* **106**:952–954.
- Darwin, C. 1859. *On the origin of species by means of natural selection or, the preservation of favoured races in the struggle for life*. John Murray, London, UK.
- Darwin, C. 1871. *The descent of man and selection in relation to sex*. John Murray, London, UK.
- Delisle, H., 2002. Programming of chronic disease by impaired fetal nutrition. Evidence and implications for policy and intervention strategies. Technical report, World Health Organization.
- Demarchi, R. A., and C. L. Hartwig, 2004. Status of Thinhorn Sheep in British Columbia. *Wild-life Bulletin B-119*, British Columbia Ministry of Water, Land and Air Protection Biodiversity Branch Victoria, Victoria, Canada.
- Descamps, S., S. Boutin, D. Berteaux, and J.-M. Gaillard. 2006. Best squirrels trade a long life for an early reproduction. *Proceeding of the Royal Society B* **273**:2369–2374.
- Descamps, S., S. Boutin, D. Berteaux, A. G. McAdam, and J.-M. Gaillard. 2008. Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. *Journal of Animal Ecology* **77**:305–314.
- Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? *Biological Reviews* **86**:97–116.
- Dobson, F. S. 1992. Body mass, structural size, and life-history patterns of the Columbian ground squirrel. *American Naturalist* **140**:109–125.
- Dobzhanski, T. 1973. Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher* **35**:125–129.
- Douhard, M., J.-M. Gaillard, D. Delorme, G. Capron, P. Duncan, F. Klein, and C. Bonenfant. 2013. Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females. *Ecology* **94**:1805–1814.
- Driscoll, C. A., D. W. Macdonald, and S. J. O'Brien. 2009. From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences* **106**:9971–9978.

- Du, M., J. Tong, J. Zhao, K. R. Underwood, M. Zhu, S. P. Ford, and P. W. Nathanielsz. 2010. Fetal programming of skeletal muscle development in ruminant animals. *Journal of Animal Science* **88**:E51–E60.
- Eberhardt, L. L. 1991. Models of ungulates populations dynamics. *Rangifer* **7**:24–29.
- Ellison, P. 2010. Fetal Programming and Fetal Psychology. *Infant and Child Development* **19**:6–20.
- Estes, R. D. 1991. The significance of horns and other male secondary sexual characters in female bovinds. *Applied Animal Behaviour Science* **29**:403–451.
- Feil, R., and M. F. Fraga. 2012. Epigenetics and the environment: emerging patterns and implications. *Nature Reviews Genetics* **13**:97–109.
- Festa-Bianchet, M., 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. Pages 191–207 *in* M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, USA.
- Festa-Bianchet, M., D. Coltman, L. Turelli, and J. T. Jorgenson. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behavioral Ecology* **15**:305–312.
- Festa-Bianchet, M., and S. D. Côté. 2008. *Mountain goats: Ecology, behavior, and conservation of an Alpine ungulate*. Island Press, Washington, USA.
- Festa-Bianchet, M., J.-M. Gaillard, and J. T. Jorgenson. 1998. Mass and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist* **152**:367–379.
- Festa-Bianchet, M., and J. T. Jorgenson. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology and Sociobiology* **9**:144–150.
- Festa-Bianchet, M., J. T. Jorgenson, and D. Réale. 2000. Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology* **11**:633–639.
- Festa-Bianchet, M., and R. Lee, 2009. Guns, sheep and genes; when and why trophy hunting may be a selective pressure. Pages 94–107 *in* B. Dickson, J. Hutton, and B. Adams, editors. *Recreational Hunting, Conservation and Rural Livelihoods: Science and Practice*. Wiley-Blackwell, London, UK.
- Festa-Bianchet, M., F. Pelletier, J. T. Jorgenson, C. Feder, and A. Hubbs. 2014. Decrease in horn size and increase in age of “trophy” sheep in Alberta over 37 years. *Journal of Wildlife Management* **78**:133–141.
- Fisher, M. O., R. G. Nager, and P. Monaghan. 2006. Compensatory growth impairs adult cognitive performance. *PLoS Biology* **4**:e251.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. The Clarendon Press, Oxford, UK.

- Forchhammer, M., T. H. Clutton-Brock, J. Lindström, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* **70**:721–729.
- Fuller, R. J., and R. M. A. Gill. 2001. Ecological impacts of increasing numbers of deer in British woodland. *Forestry* **74**:193–199.
- Gaillard, J.-M., R. Andersen, D. Delorme, and J. D. C. Linnell. 1998a. Family effects on growth and survival of juvenile roe deer. *Ecology* **78**:2878–2889.
- Gaillard, J.-M., J.-M. Boutin, D. Delorme, G. Van Laere, P. Duncan, and J.-D. Lebreton. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112**:502–513.
- Gaillard, J.-M., D. Delorme, J.-M. Boutin, G. Van Laere, and B. Boisaubert. 1996. Body mass of roe deer fawns during winter in 2 contrasting populations. *Journal of Wildlife Management* **60**:29–36.
- Gaillard, J.-M., D. Delorme, J.-M. Boutin, G. Van Laere, B. Boisaubert, and R. Pradel. 1993a. Roe deer survival patterns: a comparative analysis of contrasting population. *Journal of Animal Ecology* **62**:778–791.
- Gaillard, J.-M., D. Delorme, and J.-M. Jullien. 1993b. Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia* **94**:57–61.
- Gaillard, J.-M., P. Duncan, D. Delorme, G. Van Laere, N. Pettorelli, D. Maillard, and G. Renaud. 2003a. Effects of hurricane Lothar on the population dynamics of European roe deer. *Journal of Wildlife Management* **67**:767–773.
- Gaillard, J.-M., M. Festa-Bianchet, D. Delorme, and J. Jorgenson. 2000a. Body mass and individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society of London, Series B* **267**:471–477.
- Gaillard, J.-M., M. Festa-bianchet, and N. G. Yoccoz. 1998b. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* **13**:58–63.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000b. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**:367–393.
- Gaillard, J.-M., A. Loison, and C. Toïgo, 2003b. Variation in life history traits and realistic population models for wildlife: the case of ungulates. Pages 115–132 *in* M. Festa-Bianchet and M. Appolonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, USA.
- Gaillard, J.-M., A. Loison, C. Toïgo, D. Delorme, and G. Van Laere. 2003c. Cohort effects and deer population dynamics. *Ecoscience* **10**:412–420.

- Gaillard, J.-M., D. Pontier, D. Allaine, J.-D. Lebreton, J. Trouvilliez, and J. Clobert. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* **56**:59–76.
- Gaillard, J.-M., A. J. Sempéré, J.-M. Boutin, G. Van Laere, and B. Boisaubert. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Canadian Journal of Zoology* **70**:1541–1545.
- Gaillard, J.-M., A. Viallefont, A. Loison, and M. Festa-Bianchet. 2004. Assessing senescence patterns in populations of large mammals. *Animal Biodiversity and Conservation* **27**:47–58.
- Gaillard, J.-M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* **84**:3294–3306.
- Gaillard, J.-M., N. G. Yoccoz, J.-D. Lebreton, C. Bonenfant, S. Devillard, A. Loison, D. Pontier, and D. Allainé. 2005. Generation time: A reliable metric to measure life-history variation among mammalian populations. *American Naturalist* **166**:119–123.
- Gamelon, M., J.-M. Gaillard, E. Baubet, S. Devillard, L. Say, S. Brandt, and O. Gimenez. 2013. The relationship between phenotypic variation among offspring and mother body mass in wild boar: evidence of coin-flipping? *Journal of Animal Ecology* **82**:937–945.
- Gamelon, M., J.-M. Gaillard, S. Servanty, O. Gimenez, C. Toïgo, E. Baubet, F. Klein, and J.-D. Lebreton. 2012. Making use of harvest information to examine alternative management scenarios: a body weight-structured model for wild boar. *Journal of Applied Ecology* **49**:833–841.
- Garel, M., C. Bonenfant, J.-L. Hamann, F. Klein, and J.-M. Gaillard. 2010. Are abundance indices derived from spotlight counts reliable to monitor red deer *Cervus elaphus* populations? *Wildlife Biology* **16**:77–84.
- Garel, M., J.-M. Cugnasse, D. Maillard, J.-M. Gaillard, A. M. J. Hewison, and D. Dubray. 2007. Selective harvesting and habitat loss produce long-term life-history changes in a mouflon population. *Ecological Applications* **17**:1607–1618.
- Garel, M., J.-M. Gaillard, J.-M. Jullien, D. Dubray, D. Maillard, and A. Loison. 2011. Population abundance and early spring conditions determine variation in body mass of juvenile chamois. *Journal of Mammalogy* **92**:1112–1117.
- Garel, M., A. Loison, J.-M. Jullien, D. Dubray, D. Maillard, and J.-M. Gaillard. 2009a. Sex-specific growth in alpine chamois. *Journal of Mammalogy* **90**:954–960.
- Garel, M., E. J. Solberg, B.-E. Sæther, V. Grotan, J. Tufto, and M. Heim. 2009b. Age, size and spatio-temporal variation in ovulation patterns of a seasonal breeder, the Norwegian moose (*Alces alces*). *American Naturalist* **73**:89–104.
- Gayton, D. 2007. Major impacts to biodiversity in British Columbia (excluding climate change). The biodiversity British Columbia technical subcommittee .

- Geist, V. 1966a. Evolution of horn-like organs. *Behaviour* **27**:175–214.
- Geist, V. 1966b. Evolutionary significance of mountain sheep horns. *Evolution* **20**:558–566.
- Geist, V. 1966c. Validity of horn segment counts in aging bighorn sheep. *Journal of Wildlife Management* **30**:634–646.
- Giacometti, M., R. Willing, and C. Defila. 2002. Ambient temperature in spring affects horn growth in male alpine ibexes. *Journal of Mammalogy* **83**:245–251.
- Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology* **17**:167–178.
- Gilbert, S. F. 2000. *Developmental Biology*. 6th edition. Sinauer Associates, Sunderland, UK.
- Gilot-Fromont, E., M. Jégo, C. Bonenfant, P. Gibert, B. Rannou, F. Klein, and J.-M. Gaillard. 2012. Immune phenotype and body condition in roe deer: Individuals with high body condition have different, no stronger immunity. *Ploce One* **7**:1–6.
- Gluckman, P. D., and M. A. Hanson. 2004. Living with the past: evolution, development, and patterns of disease. *Science* **305**:1733–1736.
- Gluckman, P. D., and M. A. Hanson. 2006. Adult disease echoes of the past. *European Journal of Endocrinology* **155**:S47–S50.
- Gluckman, P. D., M. A. Hanson, and H. Spencer. 2005a. Predictive adaptive responses and human evolution. *Trends in Ecology & Evolution* **20**:527–533.
- Gluckman, P. D., M. A. Hanson, H. Spencer, and P. Bateson. 2005b. Environmental influences during development and their later consequences for health and disease: implications for the interpretation of empirical studies. *Proceedings of the Royal Society B: Biological Sciences* **272**:671–677.
- Gonzalez, G., and J.-P. Crampe. 2001. Mortality patterns in a protected population of isards (*Rupicapra pyrenaica pyrenaica*). *Canadian Journal of Zoology* **79**:2072–2079.
- Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* **41**:1021–1031.
- Gotthard, K. 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. *Journal of Animal Ecology* **69**:896–202.
- Gould, S. J., and R. C. Lewontin. 1979. The spondels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London, Series B* **205**:581–598.

- Grafen, A., 1988. On the uses of data on lifetime reproductive success. Pages 454–471 in T. H. Clutton-Brock, editor. *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago, USA.
- Grande, J. M., D. Serrano, G. Tavecchia, M. Carrete, O. Ceballos, R. Díaz-Delgado, J. L. Tella, and J. A. Donazar. 2008. Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos* **118**:580–590.
- Green, W. C. H., and A. Rothstein. 1991. Trade-offs between growth and reproduction in female bison. *Oecologia* **86**:521–527.
- Hales, C. N., and D. J. P. Barker. 1992. Type 2 (non-insulin dependent) diabetes mellitus: the thrifty phenotype hypothesis. *Diabetologia* **35**:595–601.
- Hales, C. N., and D. J. P. Barker, 2001. The thrifty phenotype hypothesis. Pages 5–21 in D. J. P. Barker, editor. *Type 2 diabetes: The thrifty phenotype*, volume 60. Oxford University Press, Oxford, UK.
- Hales, C. N., and S. E. Ozanne. 2003. The dangerous road of catch-up growth. *Journal of Physiology* **547**:5–10.
- Hamel, S., S. D. Côté, J.-M. Gaillard, and M. Festa-Bianchet. 2009a. Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology* **78**:143–151.
- Hamel, S., J.-M. Gaillard, M. Festa-Bianchet, and S. D. Côté. 2009b. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* **90**:1981–1995.
- Hamel, S., J.-M. Gaillard, N. G. Yoccoz, A. Loison, C. Bonenfant, and S. Descamps. 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecology Letters* **13**:915–935.
- Hansen, B. B., V. Grøtan, R. Aanes, B.-E. Sæther, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz, and A. O. Pedersen. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high arctic. *Science* **339**:313–315.
- Haramis, G. M., J. D. Nichols, K. H. Pollock, and J. E. Hines. 1986. The relationship between body mass and survival of wintering canvasbacks. *The Auk* **103**:506–514.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* **80**:4–18.
- Hayward, A. D., and V. Lummaa. 2013. Testing the evolutionary basis of the predictive adaptive response hypothesis in a preindustrial human population. *Evolution, Medicine and Public Health* **1**:106–117.

- Hayward, A. D., I. Rickard, and V. Lummaa. 2013. Influence of early-life nutrition on mortality and reproductive success during a subsequent famine in a preindustrial population. *Proceedings of the National Academy of Sciences of the USA* **110**:13886–13891.
- Hector, K. L., and S. Nakagawa. 2012. Quantitative analysis of compensatory and catch-up growth in diverse taxa. *Journal of Animal Ecology* **81**:583–593.
- Hengeveld, P. E., and M. Festa-Bianchet. 2011. Harvest regulations and artificial selection on horn size in male bighorn sheep. *Journal of Wildlife Management* **75**:189–197.
- Hertwig, O. 1900. The biological problem of today preformation or epigenesis? The basis of a theory of organic development. The Macmillan, New-York, USA.
- Hewison, A. J. M., J.-M. Gaillard, J. M. Angibault, G. van Laere, and J. P. Vincent. 2002. The influence of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. *Journal of Zoology (London)* **257**:303–309.
- Hewison, A. J. M., J.-M. Gaillard, D. Delorme, G. Van Laere, T. Amblard, and F. Klein. 2011. Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass-size allometry in roe deer. *Oikos* **120**:1217–1226.
- Hewison, A. J. M., J.-M. Gaillard, P. Kjellander, C. Toïgo, O. Liberg, and D. Delorme. 2005. Big mothers invest more in daughters – reversed sex allocation in a weakly polygynous mammal. *Ecology Letters* **8**:430–437.
- Hik, D. S., and J. Carey. 2000. Cohort variation in horn growth of Dall sheep rams in the southwest Yukon, 1969-1999. *Biennial Symposium of Northern Wild Sheep and Goat Council* **12**:88–100.
- Houle, D., C. Pélabon, G. P. Wagner, and T. F. Hansen. 2011. Measurement and meaning in biology. *Quarterly Review of Biology* **86**:3–34.
- Hughes, K. A., M. H. Burlinson, and F. H. Rodd, 2003. Is phenotypic plasticity adaptive? Pages 23–42 *in* J. Rodgers and H.-C. Kohler, editors. *Biodemography of fertility*. Kluwer, Dordrech, Netherlands.
- Johnsson, J. J., and T. Bohlin. 2006. The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proceedings of the Royal Society B: Biological Sciences* **273**:1281–1286.
- Johnston, S. E., J. Gratten, C. Berenos, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and J. Slate. 2013. Life history trade-offs at a single locus maintain sexually selected genetic variation. *Nature* **502**:93–96.
- Jones, J. H. 2011. Primates and the evolution of long, slow life histories. *Current Biology* **21**:R708–R717.
- Jönsson, I. K. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**:57–66.

- Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1998. Effects of population density on horn development in bighorn rams. *Journal of Wildlife Management* **62**:1011–1020.
- Kaplan, R. H., and W. S. Cooper. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the ‘Adaptive Coin-Flipping’ principle. *American Naturalist* **123**:393–410.
- Kapoor, A., and S. G. Matthews. 2005. Short periods of prenatal stress affect growth, behaviour and hypothalamo-pituitary-adrenal axis activity in male guinea pig offspring. *Journal of Physiology* **566**:967–977.
- Kawasaki, N., C. E. Brassil, R. C. Brooks, and R. Bonduriansky. 2008. Environmental effects on the expression of life span and aging: an extreme contrast between wild and captive cohorts of *Telostylinus angusticollis* (Diptera: Neriidae). *American Naturalist* **172**:346–357.
- Kerr, R. A. 2007. Global warming is changing the world. *Science* **316**:188–190.
- Kirkwood, T. B. L. 1977. Evolution of ageing. *Nature* **270**:301–304.
- Kirkwood, T. B. L., and M. R. Rose. 1991. Evolution of senescence: late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **332**:15–24.
- Krausman, P. R., and R. T. Bowyer, 2003. Mountain sheep. Pages 1095–1115. *in* G. Feldhammer and J. Chapman, editors. *Mammals of North America*. The John Hopkins University Press, Baltimore, USA.
- Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherston, F. E. Guinness, and T. H. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. *Evolution* **56**:1683–1695.
- Kuzawa, C. W. 2005. Fetal origins of developmental plasticity: are foetal cues reliable predictors of future nutritional environments? *American Journal of Human Biology* **17**:5–21.
- Kuzawa, C. W., and E. A. Quinn. 2009. Developmental origins of adult function and health: evolutionary hypotheses. *Annual Reviews of Anthropology* **38**:131–147.
- Kuzyk, G. W., P. Dielman, B. Jex, C. Procter, A. Reid, H. Schwantje, I. Teske, and C. Thiessen. in press. Population and harvest trends of mountain sheep and mountain goats in British Columbia. *Biennial Northern Wild Sheep and Goat Council Proceedings* .
- Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**:292–305.
- Lane, J. E., L. E. B. Kruuk, A. Charmantier, J. O. Murie, and F. S. Dobson. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* **489**:554–558.

- Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. *Journal of Evolutionary Biology* **4**:619–636.
- Law, R. 1979. Optimal life histories under age-specific predation. *American Naturalist* **114**:399–417.
- Le Galliard, J.-F., O. Marquis, and M. Massot. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology* **79**:1296–1307.
- Leader-Williams, N., S. Milledge, K. Adcock, M. Brooks, A. Conway, M. Knight, S. Mainka, E. B. Martin, and T. Teferi. 2005. Trophy hunting of black rhino *Diceros bicornis*: proposals to ensure its future sustainability. *Journal of International Wildlife Law and Policy* **8**:1–11.
- Leader-Williams, N., R. J. Smith, and M. J. Walpole. 2001. Elephant Hunting and Conservation. *Science* **293**:2203–2204.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**:67–118.
- Lee, T. M., and I. Zucker. 1988. Vole infant development is influenced perinatally by maternal photoperiodic history. *American Journal of Physiology* **255**:R831–R838.
- Lee, W.-S., P. Monaghan, and N. B. Metcalfe. 2012. The pattern of early growth trajectories affects adult breeding performance. *Ecology* **93**:902–912.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* **74**:1659–1673.
- Leslie, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria aalge* Pont.). *Journal of Animal Ecology* **35**:291–301.
- Lewis, D. M., and P. Alpert. 1997. Trophy hunting and wildlife conservation in Zambia. *Conservation Biology* **11**:59–68.
- Lindenmayer, D., and M. Burgman. 2005. *Practical conservation biology*. CSIRO publishing, Collingwood, Australia.
- Lindsey, P. A., P. A. Roulet, and S. S. Romañach. 2007. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation* **134**:455–469.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* **14**:343–348.
- Lindström, J., N. B. Metcalfe, and N. J. Royle. 2005. How are animals with ornaments predicted to compensate for a bad start in life? A dynamic optimization model approach. *Functional Ecology* **19**:421–428.
- Locati, M., and S. Lovari. 1991. Clues for dominance in female chamois: age, weight or horn size? *Aggressive behavior* **17**:11–15.

- Loe, L., R. Irvine, C. Bonenfant, A. Stien, R. Langvatn, S. Albon, A. Mysterud, and N. Stenseth. 2006. Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of Animal Ecology* **75**:485–496.
- Loehr, J., J. Carey, M. Hoefs, J. Suhonen, and H. Ylönen. 2006. Horn growth rate and longevity: implications for natural and artificial selection in thinhorn sheep (*Ovis dalli*). *Journal of Evolutionary Biology* **20**:818–828.
- Loehr, J., J. Carey, R. B. O’Hara, and D. S. Hik. 2010. The role of phenotypic plasticity in responses of hunted thinhorn sheep ram horn growth to changing climate conditions. *Journal of Evolutionary Biology* **23**:783–790.
- Loison, A., J. Appolinaire, J. J.-M., and D. Dubray. 2006. How reliable are total counts to detect trends in population size of chamois *Rupicapra rupicapra* and *R. pyrenaica*? *Wildlife Biology* **12**:77–88.
- Loison, A., M. Festa-bianchet, J.-M. Gaillard, J. T. Jorgenson, and J.-M. Jullien. 1999a. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* **80**:2539–2554.
- Loison, A., J.-M. Gaillard, C. Pélabon, and N. G. Yoccoz. 1999b. What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research* **1**:611–633.
- Loison, A., and R. Langvatn. 1998. Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia* **116**:489–500.
- Lomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. *Journal of Animal Ecology* **47**:461–475.
- Lovari, S., and M. Locati. 1991. Temporal relationships, transitions and structure of the behavioural repertoire in male Apennine chamois during the rut. *Behaviour* **119**:77–103.
- Lucas, A., 1991. Programming by early nutrition in man. Pages 38–55 in G. R. Bock and J. Whelan, editors. *The Childhood Environment and Adult Disease*. Wiley, Chichester, UK.
- Lucas, A. 2000. Programming not metabolic imprinting. *The American Journal of Clinical Nutrition* **71**:602.
- Lummaa, V., and T. Clutton-Brock. 2002. Early development, survival and reproduction in humans. *Trends in Ecology & Evolution* **17**:141–147.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, USA.
- MacNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. *Nature* **380**:215–221.
- Madsen, T., and R. Shine. 2000. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *Journal of Animal Ecology* **69**:952–958.

- Maillard, D., J.-M. Gaillard, M. Hewison, P. Ballon, P. Duncan, A. Loison, C. Toïgo, E. Baubet, C. Bonenfant, M. Garel, and C. Saint-Andrieux, 2010. Ungulate status and management in France. Pages 441–475 in M. Apollonio, R. Andersen, and R. Putman, editors. *European Ungulates and their Management in the 21st Century*. Cambridge University Press, New York.
- Mainguy, J., S. Côté, M. Festa-Bianchet, and D. Coltman. 2009. Father-offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal. *Proceedings of the Royal Society B: Biological Sciences* **276**:4067–4075.
- Marcil-Ferland, D., M. Festa-Bianchet, A. M. Martin, and F. Pelletier. 2013. Despite catch-up, prolonged growth has detrimental fitness consequences in a long-lived vertebrate. *American Naturalist* **182**:775–785.
- Marquis, O., M. Massot, and J.-F. Le-Galliard. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. *Ecology* **89**:2575–2583.
- Martinez, M., C. Rodriguez-Vigal, O. R. Jones, T. N. Coulson, and A. San Miguel. 2005. Different hunting strategies select for different weights in red deer. *Biology Letters* **1**:353–356.
- McAdam, A. G., and S. Boutin. 2003. Variation in viability selection among cohorts of juvenile red squirrels (*Tamiasciurus Hudsonicus*). *Evolution* **57**:1689–1697.
- McCance, R. A. 1962. Food growth and time. *Lancet* **2**:671–676.
- McLoughlin, P. D., J.-M. Gaillard, M. Boyce, C. Bonenfant, F. Messier, P. Duncan, D. Delorme, B. Van Moorter, S. Saïd, and F. Klein. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology* **88**:3192–3201.
- McMillen, I. C., and J. S. Robinson. 2005. Developmental origins of the metabolic syndrome: prediction, plasticity, and programming. *Physiological Reviews* **85**:571–633.
- Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later. *Trends in Ecology & Evolution* **16**:254–260.
- Millon, A., S. J. Petty, B. Little, and X. Lambin. 2011. Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. *Journal of Animal Ecology* **80**:968–975.
- Milner, J., C. Bonenfant, A. Myrsterud, J. Gaillard, S. Csányi, and N. C. Stenseth. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology* **43**:721–734.
- Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **363**:1635–1645.
- Monaghan, P., A. Charmantier, D. H. Nussey, and R. E. Ricklefs. 2008. The evolutionary ecology of senescence. *Functional Ecology* **22**:371–378.

- Morellet, N., S. Champely, J.-M. Gaillard, P. Ballon, and Y. Boscardin. 2001. The browsing index: new tool uses browsing pressure to monitor deer populations. *Wildlife Society Bulletin* **29**:1243–1252.
- Morellet, N., J.-M. Gaillard, A. J. M. Hewison, P. Ballon, Y. Boscardin, P. Duncan, F. Klein, and D. Maillard. 2007. Indicators of ecological change: new tools for managing populations of large herbivores. *Journal of Applied Ecology* **44**:634–643.
- Murphy, G. I. 1968. Pattern in life history and the environment. *American Naturalist* **102**:391–403.
- Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates. *Journal of Zoology* **264**:209–215.
- Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2002. Large-scale habitat variability, delayed density effects and red deer populations in Norway. *Journal of Animal Ecology* **71**:569–580.
- Mysterud, A., E. Meisingset, R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2005. Climate-dependent allocation of resources to secondary sexual traits in red deer. *Oikos* **111**:245–252.
- Mysterud, A., P. Tryjanowski, and M. Panek. 2006. Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right place. *Biology Letters* **2**:632–635.
- Mysterud, A., N. G. Yoccoz, R. Langvatn, N. Pettorelli, and N. C. Stenseth. 2008. Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **363**:2359–2368.
- Mysterud, A., and E. Østbye. 2006. The effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes: the Lier valley, Norway. *Wildlife Biology* **12**:321–329.
- Nettle, D., D. A. Coall, and T. E. Dickins. 2011. Early-life conditions and age at first pregnancy in British women. *Proceedings of the Royal Society B: Biological Sciences* **278**:1721–1727.
- Nettle, D., W. E. Frankenhuis, and I. J. Rickard. 2013. The evolution of predictive adaptive responses in human life history. *Proceedings of the Royal Society B: Biological Sciences* **280**:20131343.
- Nilsen, E. B., J.-M. Gaillard, R. Andersen, J. Odden, D. Delorme, G. van Laere, and J. D. C. Linnell. 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *Journal of Animal Ecology* **78**:585–594.
- Nussey, D. H., T. Coulson, D. Delorme, T. H. Clutton-Brock, J. M. Pemberton, M. Festa Bianchet, and J.-M. Gaillard. 2011. Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology* **92**:1936–1947.

- Nussey, D. H., L. E. B. Kruuk, A. Morris, and T. H. Clutton-Brock. 2007*a*. Environmental conditions in early life influence ageing rates in a wild population of red deer. *Current Biology* **17**:R1000–R1001.
- Nussey, D. H., E. Postma, P. Gienapp, and M. E. Visser. 2005. Selection on heritable phenotypic plasticity in a wild bird population. *Science* **310**:304–306.
- Nussey, D. H., A. J. Wilson, and J. E. Brommer. 2007*b*. The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology* **20**:831–844.
- Olsen, E., M. Heino, G. Lilly, M. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**:932–935.
- Owen-Smith, N., 2010. The suite of population models. Pages 34–62 *in* N. Owen-Smith, editor. *Dynamics of large herbivore populations in changing environments: towards appropriate models*. Wiley, UK.
- Ozanne, S. E., and C. N. Hales. 2004. Lifespan: catch-up growth and obesity in male mice. *Nature* **427**:411–412.
- Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**:482–485.
- Ozgul, A., S. Tuljapurkar, T. G. Benton, J. M. Pemberton, T. H. Clutton-Brock, and T. Coulson. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science* **325**:464–467.
- Packer, C. 1983. Sexual dimorphism: the horns of African antelopes. *Science* **221**:1191–1193.
- Palumbi, S. 2001. Humans as the world's greatest evolutionary force. *Science* **293**:1786–1790.
- Panzacchi, M., J. D. C. Linnell, M. Odden, J. Odden, and R. Andersen. 2009. Habitat and roe deer fawn vulnerability to red fox predation. *Journal of Animal Ecology* **78**:1124–1133.
- Paquet, M. M., and R. A. Demarchi, 1999. Stone's sheep of the Northern Rockies: the effects of access. Technical report, Foundation for North American wild sheep and Guide-outfitters association of British Columbia.
- Pardo, D., C. Barbraud, M. Authier, and H. Weimerskirch. 2013. Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits. *Ecology* **94**:208–220.
- Pelletier, F. 2005. Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic. *Behavioral Ecology* **16**:280–285.

- Pelletier, F., T. H. Clutton-Brock, J. Pemberton, S. Tuljapurkar, and T. N. Coulson. 2007a. The evolutionary demography of ecological change: linking trait variation and population growth. *Science* **315**:1571–1574.
- Pelletier, F., M. Festa-Bianchet, and J. T. Jorgenson. 2012. Data from selective harvests underestimate temporal trends in quantitative traits. *Biology Letters* **8**:878–881.
- Pelletier, F., M. Festa-Bianchet, J. T. Jorgenson, C. Feder, and A. Hubbs. in press. Harvest refuges do not buffer wild sheep from selective hunting. *Ecology and Evolution* .
- Pelletier, F., D. Garant, and A. P. Hendry. 2009. Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **364**:1483–1489.
- Pelletier, F., D. Réale, D. Garant, D. W. Coltman, and M. Festa-Bianchet. 2007b. Selection on heritable seasonal phenotypic plasticity of body mass. *Evolution* **61**:1969–1979.
- Pemberton, J. M., S. D. Albon, F. E. Guinness, T. H. Clutton-Brock, and R. J. Berry. 1988. Genetic variation and juvenile survival in red deer. *Evolution* **42**:921–934.
- Pettorelli, N., S. Dray, J.-M. Gaillard, D. Chessel, P. Duncan, A. Illius, N. Guillon, F. Klein, and G. Van Laere. 2003a. Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia* **137**:363–369.
- Pettorelli, N., J.-M. Gaillard, P. Duncan, D. Maillard, G. Van Laere, and D. Delorme. 2003b. Age and density modify the effects of habitat quality on survival and movements of roe deer. *Ecology* **84**:3307–3316.
- Pettorelli, N., J.-M. Gaillard, P. Duncan, J.-P. Ouellet, and G. Van Laere. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia* **128**:400–405.
- Pettorelli, N., J.-M. Gaillard, A. Mysterud, P. Duncan, N. C. Stenseth, D. Delorme, G. Van Laere, C. Toïgo, and F. Klein. 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. *Oikos* **112**:565–572.
- Pettorelli, N., J.-M. Gaillard, G. Van Laere, P. Duncan, P. Kjellander, O. Liberg, D. Delorme, and D. Maillard. 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. *Proceedings of the Royal Society of London, Series B* **269**:747–753.
- Pianka, E. R. 1970. On r- and K-selection. *American Naturalist* **104**:592–597.
- Picard, K., D. W. Thomas, M. Festa-Bianchet, and C. Lanthier. 1994. Bovid horns – An important site for heat-loss during winter. *Journal of Mammalogy* **75**:710–713.
- Pieau, C., M. Girondot, N. Richard-Mercier, G. Desvages, M. Dorizzi, and P. Zaborski. 1994. Temperature sensitivity of sexual differentiation of gonads in the European pond turtle: Hormonal involvement. *Journal of Experimental Zoology* **270**:86–94.

- Pigliucci, M., C. J. Murren, and C. D. Schlichting. 2006. Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology* **209**:2362–2367.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effects models in S and S-PLUS*. Statistics and computing, Springer-Verlag, New York, USA.
- Plaistow, S. J., C. T. Lapsley, and T. G. Benton. 2006. Context-dependent intergenerational effects: The interaction between past and present environments and its effect on population dynamics. *American Naturalist* **167**:206–215.
- Plard, F., J.-M. Gaillard, T. Coulson, A. J. Hewison, D. Delorme, C. Warnant, and C. Bonenfant. 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS biology* **12**:e1001828.
- Poissant, J., A. J. Wilson, M. Festa-Bianchet, J. T. Hogg, and D. W. Coltman. 2008. Quantitative genetics and sex-specific selection on sexually dimorphic traits in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences* **275**:623–628.
- Portier, C., P. Duncan, J.-M. Gaillard, N. Guillon, and A. J. Sempéré. 2000. Growth of European roe deer: patterns and rates. *Acta Theriologica* **45**:87–94.
- Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *Journal of Zoology (London)* **245**:271–278.
- Post, R., and N. C. Senseth. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* **80**:1322–1339.
- Preston, B. T., I. R. Stevenson, and K. Wilson. 2003. Soay rams target reproductive activity towards promiscuous females' optimal insemination period. *Proceedings of the Royal Society of London, Series B* **270**:2073–2078.
- Pérez-barbería, F. J., L. Robles, and C. Nores. 1996. Horn growth pattern in Cantabrian chamois *Rupicapra pyrenaica parva*: Influence of sex, location and phaenology. *Acta Theriologica* **41**:83–92.
- R Development Core Team, 2011a. R: A language and environment for statistical computing. URL <http://www.R-project.org>.
- R Development Core Team, 2011b. R: A language and environment for statistical computing. URL <http://www.R-project.org>.
- Reed, E. T., G. Gauthier, R. Pradel, and J.-D. Lebreton. 2003. Age and environmental conditions affect recruitment in greater snow geese. *Ecology* **84**:219–230.
- Reed, T. E., L. E. B. Kruuk, S. Wanless, M. Frederiksen, E. J. A. Cunningham, and M. P. Harris. 2008. Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. *American Naturalist* **171**:89–101.

- Reid, J.-M., E. M. Bignal, S. Bignal, D. I. McCracken, and P. Monaghan. 2003. Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology* **72**:36–46.
- Reimers, E. 1983. Mortality in Svalbard reindeer. *Ecography* **6**:141–149.
- Rencher, A. C. 2000. *Linear models in statistics*. Wiley, New-York, USA.
- Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar Arctic. *Journal of Climate* **22**:2302–2315.
- Reznick, D., M. J. Bryant, and F. Bashey. 2002. r- and K-selection revisited: the role of population regulation in life-history evolution. *Ecology* **83**:1509–1520.
- Reznick, D., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* **346**:357–359.
- Reznick, D., L. Nunney, and A. Tessier. 2000. Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology & Evolution* **15**:421–425.
- Rickard, I. J., J. Holopainen, S. Helama, S. Helle, A. F. Russell, and V. Lummaa. 2010. Food availability at birth limited reproductive success in historical humans. *Ecology* **91**:3515–3525.
- Rickard, I. J., and V. Lummaa. 2007. The predictive adaptive response and metabolic syndrome: challenges for the hypothesis. *Trends in Endocrinology and Metabolism* **18**:94–99.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. *Science* **343**:1241484.
- Rivrud, I. M., K. Sonkoly, R. Lehoczki, S. Csányi, G. O. Storvik, and A. Mysterud. 2013. Hunter selection and long-term trend (1881-2008) of red deer trophy sizes in Hungary. *Journal of Applied Ecology* **50**:168–180.
- Robinson, J. J., I. McDonald, C. Fraser, and R. M. J. Crofts. 1977. Studies on reproduction in prolific ewes. *Journal of Agricultural Science* **88**:539–552.
- Robinson, M. R., and L. E. B. Kruuk. 2007. Function of weaponry in females: the use of horns in intrasexual competition for resources in female Soay sheep. *Biology letters* **3**:651–654.
- Robinson, M. R., J. G. Pilkington, T. H. Clutton-Brock, J. Pemberton, and L. E. Kruuk. 2008. Environmental heterogeneity generates fluctuating selection on a secondary sexual trait. *Current Biology* **18**:751–757.
- Robinson, M. R., J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2006. Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in soay sheep. *Evolution* **60**:2168–2181.

- Rochet, M. J., P. A. Cornillon, R. Sabatier, and D. Pontier. 2000. Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. *Oikos* **91**:255–27.
- Roff, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman and Hall, New York, USA.
- Roff, D. A., and D. J. Fairbairn. 2007. The evolution of trade-offs: where are we? *Journal of Evolutionary Biology* **20**:433–447.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* **181**:165–176.
- Rose, K. E., T. H. Clutton-brock, and F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. *Journal of Animal Ecology* **67**:979–986.
- Rossiter, M. C. 1991. Environmentally based maternal effects: a hidden force in insect population dynamics. *Oecologia* **87**:288–294.
- Rughetti, M., and M. Festa-Bianchet. 2010. Compensatory growth limits opportunities for artificial selection in Alpine chamois. *Journal of Wildlife Management* **74**:1024–1029.
- Rughetti, M., and M. Festa-Bianchet. 2011. Effects of early horn growth on reproduction and hunting mortality in female chamois. *Journal of Animal Ecology* **80**:438–447.
- Sadleir, R. M. F. S., 1987. Reproduction in female cervids. Pages 123–144 in C. M. Wemmer, editor. *Biology and management of the Cervidae*. Smithsonian Institution Press, Washington, USA.
- Saether, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642–653.
- Sauer, J. R., and N. A. Slade. 1987. Size-based demography of vertebrates. *Annual Review of Ecology and Systematics* **18**:71–90.
- Schmidt, J. I., J. M. Ver Hoef, and T. Bowyer. 2007. Antler size of Alaskan moose *Alces alces gigas*: effects of population density, hunter harvest and use of guides. *Wildlife Biology* **13**:53–65.
- Schmidt, K. T., A. Stien, and S. D. Albon. 2001. Antler length of yearling red deer is determined by population density, weather and early life-history. *Oecologia* **127**:191–197.
- Schröder, W., and I. V. Elsner-Schak, 1985. Correct age determination in chamois. Pages 65–70 in S. Lovari, editor. *The biology and management of mountain ungulates*. Croom Helm, London, UK.
- Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology* **86**:155–163.

- Seger, J., and H. J. Brockmann, 1987. What is bed-hedging? Pages 182–211 in P. H. Harvey and L. Partridge, editors. *Oxford Surveys in Evolutionary Biology*. Oxford University Press, New-York, USA.
- Seiler, A. 2004. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildlife Biology* **10**:301–313.
- Shaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. *American Naturalist* **108**:783–790.
- Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* **90**:363–368.
- Singer, F. J., and L. C. Zeingenfuss. 2002. Influence of trophy hunting and horn size on mating behavior and survivorship of mountain sheep. *Journal of Mammalogy* **83**:682–698.
- Skalski, J. R., A. Hoffmann, and S. G. Smith, 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. Pages 9–28 in J.-D. Lebreton and P. M. North, editors. *Marked individuals in the study of bird populations*. Birkhauser Verlag, Basel, Switzerland.
- Skibieli, A. L., F. S. Dobson, and J. O. Murie. 2009. Maternal influences on reproduction in two populations of Columbian ground squirrels. *Ecological Monographs* **79**:325–341.
- Sloboda, D. M., M. Hickey, and R. Hart. 2011. Reproduction in females: the role of the early life environment. *Human reproduction update* **17**:210–227.
- Sloboda, D. M., G. J. Howie, A. Pleasants, P. D. Gluckman, and M. H. Vickers. 2009. Pre- and postnatal nutritional histories influence reproductive maturation and ovarian function in the rat. *PLoS ONE* **4**:e6744.
- Smith, T. B., and L. Bernatchez. 2008. Evolutionary change in human-altered environments. *Molecular Ecology* **17**:1–8.
- Solberg, E. J., P. Jordhoy, O. Strand, R. Aanes, A. Loison, B.-E. Sæther, and J. D. C. Linnell. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography* **24**:441–451.
- Solberg, E. J., A. Loison, J.-M. Gaillard, and M. Heim. 2004. Lasting effects of conditions at birth on moose body mass. *Ecography* **27**:677–687.
- Sookoian, S., T. F. Gianotti, A. L. Burgueño, and C. J. Pirola. 2013. Fetal metabolic programming and epigenetic modifications: a systems biology approach. *Pediatric Research* **73**:531–542.
- Stankowich, T., and T. Caro. 2009. Evolution of weaponry in female bovids. *Proceedings of the Royal Society B: Biological Sciences* **276**:4329–4334.

- Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* **39**:436–445.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, New-York, USA.
- Stearns, S. C. 2012. Evolutionary medicine: its scope, interest and potential. *Proceedings of the Royal Society B: Biological Sciences* **279**:4305–4321.
- Stephens, P. A., I. L. Boyd, J. M. McNamara, and A. I. Houston. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology* **90**:2057–2067.
- Stevenson, I. R., and D. R. Bancroft. 1995. Fluctuating trade-offs favour maturity in male Soay sheep. *Proceedings of the Royal Society of London, Series B* **262**:267–275.
- Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, L. E. Loe, V. Veiberg, and N. G. Yoccoz. 2012. Congruent responses to weather variability in high arctic herbivores. *Biology Letters* **8**:1002–1005.
- Tavecchia, G., T. N. Coulson, B. J. T. Morgan, J. M. Pemberton, J. C. Pilkington, F. M. Gulland, and T. H. Clutton-Brock. 2005. Predictors of reproductive cost in female Soay sheep. *Journal of Animal Ecology* **74**:201–213.
- Tenhumberg, B., A. Tyre, A. Pople, and H. Possingham. 2004. Do harvest refuges buffer kangaroos against evolutionary responses to selective harvesting? *Ecology* **85**:2003–2017.
- Toïgo, C., J.-M. Gaillard, M. Festa-Bianchet, E. Largo, J. Michallet, and D. Maillard. 2007. Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. *Journal of Animal Ecology* **76**:679–686.
- Toïgo, C., J.-M. Gaillard, and A. Loison. 2013. Alpine ibex males grow large horns at no survival cost for most of their lifetime. *Oecologia* **173**:1261–1269.
- Toïgo, C., J.-M. Gaillard, and J. Michallet. 1999. Cohort affects growth of males but not females in Alpine Ibex (*Capra ibex ibex*). *Journal of Mammalogy* **80**:1021–1027.
- Toïgo, C., J.-M. Gaillard, G. Van Laere, A. J. M. Hewison, and N. Morellet. 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography* **29**:301–308.
- van de Pol, M., L. W. Bruinzeel, D. Heg, H. P. van Der Jeugd, and S. Verhulst. 2006. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* **75**:616–626.
- van den Heuvel, J., M. Saastamoinen, P. M. Brakefield, T. B. L. Kirkwood, B. J. Zwaan, and D. P. Shanley. 2013. The predictive adaptive response: modeling the life-history evolution of the butterfly *Bicyclus anynana* in seasonal environments. *American Naturalist* **181**:28–42.

- van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influences on variation in life history tactics. *American Naturalist* **128**:137–142.
- Vanpé, C., J.-M. Gaillard, P. Kjellander, A. Mysterud, P. Magnien, D. Delorme, G. Van Laere, F. Klein, O. Liberg, and A. J. M. Hewison. 2007. Antler size provides an honest signal of male phenotypic quality in roe deer. *American Naturalist* **169**:481–493.
- Vanpé, C., J.-M. Gaillard, N. Morellet, P. Kjellander, O. Liberg, D. Delorme, and A. J. M. Hewison. 2009. Age-specific variation in male breeding success of a territorial ungulate species the European roe deer. *Journal of Mammalogy* **90**:661–665.
- Vanpé, C., P. Kjellander, M. Galan, J.-F. Cosson, S. Aulagnier, O. Liberg, and A. J. M. Hewison. 2008. Mating system, sexual dimorphism and the opportunity for sexual selection in a territorial ungulate. *Behavioral Ecology* **19**:309–316.
- Vedder, O., S. Bouwhuis, and B. C. Sheldon. 2013. Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLOS Biology* **11**:e1001605.
- Vincent, J.-P., J.-M. Gaillard, and E. Bideau. 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta Theriologica* **36**:315–328.
- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**:389–395.
- Warner, D. A., X. Bonnet, K. A. Hobson, and R. Shine. 2008. Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. *Journal of Animal Ecology* **77**:1242–1249.
- Waterland, R. A., and C. Garza. 1999. Potential mechanisms of metabolic imprinting that lead to chronic disease. *The American Journal of Clinical Nutrition* **69**:179–197.
- Weladji, R. B., J.-M. Gaillard, N. G. Yoccoz, Ø. Holand, A. Mysterud, A. Loison, M. Nieminen, and N. C. Stenseth. 2006. Good reindeer mothers live longer and become better in raising offspring. *Proceedings of the Royal Society of London B, Biological Science* **273**:1239–1244.
- Wells, J. C. K. 2006. Is early development in humans a predictive adaptive response anticipating the adult environment? *Trends in Ecology & Evolution* **21**:424–425.
- Wells, J. C. K. 2007. Flaws in the theory of predictive adaptive responses. *Trends in Endocrinology and Metabolism* **18**:331–337.
- Wells, J. C. K. 2012. A critical appraisal of the predictive adaptive response hypothesis. *International Journal of Epidemiology* **41**:229–235.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* **20**:249–278.

- Whitman, D. W., and A. A. Agrawal, 2009. What is phenotypic plasticity and why is it important? Pages 1–63 in D. W. Whitman and T. N. Ananthakrishnan, editors. Phenotypic plasticity of insects: mechanisms and consequences. Science Publishers, USA.
- Wilkin, T. A., and B. C. Sheldon. 2009. Sex differences in the persistence of natal environmental effects on life histories. *Current Biology* **19**:1998–2002.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* **100**:697–690.
- Williams, G. C., and R. M. Nesse. 1991. The dawn of Darwinian medicine. *Quarterly Review of Biology* **66**:1–22.
- Wilson, A. J., and D. H. Nussey. 2010. What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution* **25**:207–214.
- Wilson, P. N., and D. F. Osbourn. 1960. Compensatory growth after undernutrition in mammals and birds. *Biological reviews of the cambridge philosophical society* **35**:324–363.
- Witter, M. S., and I. C. Cuthill. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **340**:73–92.
- Zahavi, A. 1975. Mate selection – Selection for a handicap. *Journal of Theoretical Biology* **53**:205–214.
- Zannèse, A., A. Bâisse, J.-M. Gaillard, A. J. M. Hewison, K. Saint-Hilaire, C. Toïgo, G. Van Laere, and N. Morellet. 2006. Hind foot length : An indicator for monitoring roe deer populations at a landscape scale. *Wildlife Society Bulletin* **34**:351–358.

Appendix

i

Appendix 1

1 **High juvenile mortality generates sex-specific ageing in wild cohorts of roe**
2 **deer**

3
4 **Michael Garratt^{1*}, Jean-François Lemaître², Mathieu Douhard², Christophe**
5 **Bonenfant², Gilles Capron³, Claude Warnant³, François Klein³, Robert C Brooks¹, Jean-**
6 **Michel Gaillard²**

7
8 ¹Evolution & Ecology Research Centre and School of Biological, Earth and Environmental
9 Sciences, The University of New South Wales, Sydney, New South Wales 2052, Australia.

10 ²Université de Lyon, F-69000, Lyon ; Université Lyon 1 ; CNRS, UMR5558, Laboratoire de
11 Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France.

12 ³Office National de la Chasse et de la Faune Sauvage, Centre National d'Etudes et de
13 Recherche Appliquée sur les Cervidés-Sangliers, 85bis Avenue de Wagram, F75008 Paris,
14 France.

15

16 **Contact**

17 *Correspondence to Michael.Garratt@unsw.edu.au

18

19

20

21 **Summary**

22 Male mammals typically have a shorter lifespan than females [1]. Sex differences in ageing
23 may result, in part, from sex-specific optima in investment in reproduction, with higher male
24 mortality rates from sexual competition selecting for a “live-fast die-young” strategy in this
25 sex [2]. In the wild, ageing rates are also influenced by environmental conditions experienced
26 early in life. Poor conditions elevate juvenile mortality, which may selectively remove
27 individuals with a particular phenotype or genotype from a cohort [3], and can alter the
28 subsequent phenotypic condition and fate of those that survive to adulthood [4]. Males and
29 females can respond differently to the same early life environmental experiences [5, 6], but
30 whether such environmental pressures generate sex-differences in ageing has rarely been
31 considered. We show that sex differences in ageing in cohorts of roe deer (*Capreolus*
32 *capreolus*) range from virtually absent in some years to females living 30% longer than males
33 in others. The extent of this sex-difference in adult longevity is strongly linked to the level of
34 mortality each cohort experiences as juveniles, with high juvenile mortality generating a
35 strong sex difference in adult survival and lifespan. In females, high juvenile mortality leads
36 to longer lifespans for those surviving individuals, while in males lifespan is actually
37 reduced. Early environmental conditions and the selective pressures they impose may help to
38 explain variability in sex-specific ageing across animal taxa.

39

40 **Highlights**

- 41 • Sex differences in lifespan range from approximately 0 – 30 % in roe deer.
- 42 • Sex differences in adult lifespan occur after exposure to high juvenile mortality.
- 43 • High juvenile mortality leads to longer lifespans for surviving females.
- 44 • In males, high juvenile mortality is associated with a reduction in adult survival.

45

46

47 **Results and Discussion**

48 Early environmental conditions can have long-lasting effects on the expression of subsequent
49 adult phenotypes, including body mass, age at first reproduction and lifetime reproductive
50 success [5]. When severe, early-life environmental conditions can elevate juvenile mortality
51 [7, 8] and selectively remove particular individuals from a population, changing the
52 frequency of subsequent adult phenotypes [9-11]. There are opposing predictions for how the
53 risk of juvenile mortality, and the environmental conditions that cause juvenile mortality in
54 the wild, could affect the subsequent lifespan of surviving individuals in a particular cohort or
55 population. Harsh environmental conditions experienced early in life – those that generate
56 high juvenile mortality - might have negative effects on survivors, causing them to acquire
57 poor condition and, as a consequence, suffer a shorter lifespan (i.e., the negative corollary of
58 silver spoon effects) [4, 12]. Alternatively, high juvenile mortality may selectively remove
59 stunted, poor-performing individuals from a cohort and thus leave a cohort of predominantly
60 robust individuals with improved survival prospects (viability selection [13]) [3].

61

62 The life history and demography of two enclosed populations (Chizé and Trois Fontaines) of
63 roe deer in France, which face contrasting environmental conditions, have been monitored
64 intensively for over 35 years [14]. This presents a unique opportunity to test how the

65 magnitude of juvenile mortality experienced by each cohort of fawns influences subsequent
66 adult lifespan and survival to old ages. Roe deer also provide a favourable species for
67 examining sex-specific adult responses to early life environments. In this species the intensity
68 of sexual selection is quite weak [15] and, accordingly, no sex differences in phenotypic traits
69 have been detected early in life. Males and females have the same mean birth date [16], size
70 at birth and growth rate throughout the weaning period [17], and juvenile survival ([8] and
71 Figure S1). Thus, both sexes are exposed to equivalent environmental conditions and
72 mortality rates early in life, and evolved sex-differences in lifespan as a consequence of
73 sexual selection are expected to be slight.

74

75 The degree of juvenile mortality experienced by fawns in a given year is not correlated with
76 either the overall (sex-independent) subsequent mean cohort lifespan or percentage of
77 individuals living beyond seven years (Table 1), the age at which actuarial senescence starts
78 in this species [18]. However, this lack of an overall effect is a consequence of the highly
79 divergent responses of the sexes to the level of juvenile mortality (Table 1, Figures 1a and
80 1b). With an increase in juvenile mortality a greater proportion of females in a given cohort
81 survived to senescence (supporting the viability selection scenario; $F_{1,25} = 4.50$, $P = 0.044$),
82 whereas male survival decreased (supporting the silver spoon hypothesis; $F_{1,19} = 6.47$, $P =$
83 0.020). This effect was consistent across both populations and a similar pattern was found
84 when examining average adult lifespan (Figure 1b; Table 1). High juvenile mortality is
85 therefore a strong predictor of the sex differences in ageing in the weakly polygynous roe
86 deer: when juvenile mortality is elevated, females live longer than males and a greater
87 proportion of females than males survive to senescence (relationship between juvenile
88 mortality and sex difference in survival to senescence: estimate \pm s.e. = 0.81 ± 0.24 , $F_{1,22} =$
89 11.53 , $P = 0.003$; Figure 1c).

90

91 To further understand the underlying causes of these sex differences, we explored how
92 juvenile mortality influenced subsequent adult body mass. In mammals such as roe deer,
93 body mass shapes individual performance and correlates with adult survival ([18] and Table
94 S1), thus providing an indication of how juvenile mortality influences adult phenotypic
95 quality. The relationship between juvenile mortality and adult body mass was strongly
96 dependent on sex (and an individual's prior fawn mass; Table 2; Figure 2; Figure S2),
97 suggesting that male and female body condition is indeed differentially impacted in years of
98 high juvenile mortality. The remaining males from cohorts that experienced high juvenile
99 mortality were of a smaller body mass than those males from cohorts where juvenile
100 mortality was less intense (Figure 2). Female body mass, by contrast, did not decline with
101 increased juvenile mortality and instead slightly increased in relation to their original fawn
102 body mass (Table 2; Figure S2).

103

104 Male-specific declines in body mass with elevated juvenile mortality further support the
105 silver spoon hypothesis in this sex. Environmental conditions that negatively impact juvenile
106 survival also lead to impaired adult male body mass, in addition to the lower probability of
107 survival to old age. In highly polygynous species, poor quality environments experienced by
108 offspring and/or their mothers early in life usually generate sex differences in perinatal and
109 early post-natal mortality, with juvenile males showing a dramatic reduction in survival when
110 compared to females, potentially as a consequence of their greater growth requirements [19].
111 However, in weakly polygynous species, like roe deer [15], males and females have similar
112 juvenile survival under all environmental conditions ([19] and Figure S1). Our results
113 indicate that while poor conditions have minimal immediate effects on sex-differences in
114 early life survival, they have long-standing negative effects on male survival in adulthood.

115

116 In females, adult body mass is not negatively impacted by the mean juvenile mortality of
117 their cohort; instead, females that survive from cohorts exposed to high juvenile mortality
118 have a greater probability of reaching old age and a longer lifespan. The most likely cause for
119 increased female adult lifespan in cohorts exposed to high juvenile mortality is that juvenile
120 mortality is condition-dependent and generates a strong viability selection. Juvenile mortality
121 would thus selectively remove poor quality females from a given cohort - individuals in poor
122 condition that would be expected to die at a young age as adults - thus leaving a pool of “high
123 quality” individuals that should be longer lived. Such relationships have recently been
124 documented in nematodes, with condition-dependent mortality generating experimentally
125 evolved populations with longer lifespans [20]. Likewise, guppies from populations exposed
126 to high levels of predation early in life had slower rates of ageing in laboratory conditions
127 than guppies from populations with low predation risk [21]. Our results suggest such viability
128 selection may also operate on a cohort level and are consistent with recent observations in
129 female roe deer at Chizé, where in poor quality years proportionally more fawns of low body
130 mass die over winter, increasing the mean survival of cohorts in adulthood [22].

131

132 An alternative possibility is that roe deer females from cohorts experiencing high juvenile
133 mortality are less able, or less willing, to allocate as much to reproduction, and as a
134 consequence this reduces the damage or the survival costs of reproduction generated from a
135 high investment in this life history trait [23], thereby allowing a longer lifespan. In the Trois
136 Fontaines population, where lifetime reproductive success is known for many females, no
137 detectable relationship was observed between juvenile mortality and either lifetime (Estimate
138 \pm s.e. = -1.55 ± 3.61 , $F_{1,34} = 0.19$, $P = 0.67$; Table S2) or mean annual (Estimate \pm s.e. = -0.47
139 ± 0.47 , $F_{1,63} = 0.97$, $P = 0.33$; Table S3) reproductive success. Thus, increased lifespan of

140 females born in poor cohorts does not appear to be a consequence of reduced reproductive
141 investment.

142

143 Sex-specific responses to early life environments have been largely ignored as potential
144 causes for sex differences in ageing, but our results suggest they may have a surprisingly
145 strong effect. We further predict that the direction and strength of these sex-specific responses
146 may be related to a species mating system, and, particularly, the relationship between
147 condition and fitness within each sex.

148

149 We predict that female roe deer may be more susceptible to viability selection than males
150 because of sex differences in the condition-dependence of fitness. High quality roe deer
151 mothers bias maternal allocation to their daughters over their sons, suggesting that fitness is
152 more strongly condition-dependent in females than males in this species [24]. If adult female
153 fitness (and viability) is more dependent on condition during the juvenile stage than male
154 fitness - and juvenile mortality removes individuals in poor condition - then juvenile
155 mortality is likely to remove from the population a disproportionate number of the low-
156 quality females. These females would have lived shorter lives had they survived to adulthood,
157 leaving only the good quality females who go on to live long adult lives. With weaker male
158 condition-dependent fitness, the relationship between juvenile mortality and adult viability
159 may be less tightly coupled. Instead, the poor conditions experienced early in life by high
160 mortality cohorts might universally depress adult male lifespan.

161

162 Our findings contrast with those predicted in species subject to strong condition-dependent
163 sexual selection on males. In these species, fitness is more variable in males, and mean male
164 quality will be elevated when viability selection eliminates individuals in poor condition.

165 This would lead to the opposite pattern from that which we document here in roe deer. This
166 prediction remains to be tested directly, but separate studies, conducted 10 years apart, on
167 highly polygynous red deer (*Cervus elaphus*), tentatively suggest that this prediction could be
168 realised. Male red deer exposed to high juvenile mortality showed *increased* survival during
169 adulthood [25], whereas in females, juvenile mortality was not detectably related to adult
170 survival and variation in survival was much lower [26]. Greater investigation of the
171 relationship between early life environment and sex differences in ageing across taxa,
172 coupled with controlled manipulations of condition in laboratory studies, may help to reveal
173 the validity of the hypothesis we propose.

174

175 **Experimental Procedures**

176

177 **Study populations**

178 The life history and demography of roe deer in Chizé and Trois Fontaines have been
179 monitored intensively since 1978 and 1976, respectively. Trois Fontaines is an enclosed 1360
180 ha area of highly productive forest in the east of France, composed principally of oak and
181 beech. This area has a continental climate with cold winters and warm, wet summers. Chizé
182 is an enclosed area of poorly productive forest in the west of France (2614 ha) and has an
183 oceanic climate with mild winters and relatively dry, warm summers. Further information on
184 the environment and climatic conditions in these areas has been published recently [14, 27,
185 28].

186

187 **Population monitoring and measurement of body mass and lifespan**

188 Roe deer in both populations have been monitored yearly via capture-mark-recapture
189 methods from October to March, with assessments taking place over 8 to 12 capture sessions

190 in each year. Animals caught are systematically weighed during these capture sessions, and
191 because body mass of adult roe deer is relatively stable within and between years [29], the
192 average value across years from 4 to 10 years of age is used as adult body mass [29] (when
193 only measured at 2 or 3 years of age, body mass has to be adjusted for growth, see [30]). In
194 addition to these trapping sessions, roe deer in both populations are intensively monitored
195 from direct observations each year between March and December. Resighting rates of female
196 roe deer are 0.84 so the last recapture or resighting can be used as a reasonably reliable
197 indicator of age at death [18]. Moreover, a large number of dead roe deer have been
198 recovered. Animals that died from human-related causes (mostly scientific purposes or road
199 traffic accidents) were excluded from the analysis. To define adult lifespan in this study we
200 further followed Gaillard et al. [18], and only examined the lifespan of animals that lived
201 over two years, which corresponds to the age at first reproduction in both sexes.

202

203 **Juvenile Mortality**

204 Newborn roe deer fawns were searched for during fawning time (from April 15 to June 15
205 [16]) each year from 1985 onwards. Newborns were either randomly found using silent
206 drives, or located by repeated observations of marked females. Each fawn captured (by hand)
207 was sexed, aged using the umbilicus features and behaviour at capture [31], weighed, and
208 marked with ear-tags, and then quickly placed in their original location and position. Cohort-
209 specific estimates of juvenile survival from birth to the onset of winter (during winter
210 captures when fawns were about eight months of age) were estimated using capture-mark-
211 recapture methods [8].

212

213 **Statistical analysis**

214 To determine the effects of juvenile mortality on probability of survival from two years of age
215 to over seven years of age (corresponding to the onset of actuarial senescence in roe deer
216 [32]) we first calculated the percentage of individuals in each cohort of adults that survived to
217 over seven years old [18]. In roe deer, once males and females are eight years old, their
218 survival rates decrease, even though there is remarkably little variation in survival rates
219 between animals that range from between two to eight years old [33]. We also determined
220 average lifespan, which is simply the average lifespan of roe deer surviving at least to two
221 years of age in a particular cohort. This analysis was conducted on cohorts born from 1985-
222 2000, and data were included for a sex if there were at least three individual values that could
223 be averaged.

224

225 General Linear Mixed Models (GLMM), fitted in SPSS version 21, were used to assess the
226 relationship between survival to the onset of actuarial senescence (dependent variable) and
227 cohort-specific juvenile mortality (independent variable), while including sex as a fixed
228 effect, year and population as random effects, with year nested within population. We used
229 the auto-correlation structure AR(1) for the random variable year because this accounted for
230 correlations between years and increased the fit of each model when compared to an
231 unstructured covariance random effect structure [34]. We started with a full model containing
232 all factors and interactions and used a backward selection procedure to remove uninformative
233 variables (with P values >0.1). When a statistically significant interaction with sex remained
234 in the final model we reran the model on sex-specific datasets separately to further explore
235 the cause of sex-dependent effects. For adult body mass, individual data were used so that the
236 fawn mass of each individual (measured at eight months of age) could be added to the model
237 as a covariate. GLMM models were again used, with the same random effect covariance

238 structure as described above. This also allowed us to control for non-independence between
239 individuals from the same cohort. Sex and population were included as fixed effects.

240

241 When exploring sex-specific juvenile mortality (Figure S1), we ran generalised linear mixed
242 models using the lme4 package in R. We fitted models with a binomial distribution (either a
243 fawn survived or did not), and with year and population as random effects, then tested for
244 effects of sex and year quality by comparing models with and without the term of interest
245 using a log-likelihood ratio test.

246

247 **References**

248

- 249 1. Clutton-Brock, T.H., and Isvaran, K. (2007). Sex differences in ageing in natural
250 populations of vertebrates. *Proc. R. Soc. B* 274, 3097-3104.
- 251 2. Bonduriansky, R., Maklakov, A., Zajitschek, F., and Brooks, R. (2008). Sexual
252 selection, sexual conflict and the evolution of ageing and life span. *Funct. Ecol.* 22,
253 443-453.
- 254 3. Doblhammer, G., and Vaupel, J.W. (2001). Lifespan depends on month of birth.
255 *Proceedings of the National Academy of Sciences* 98, 2934-2939.
- 256 4. Nussey, D.H., Kruuk, L.E.B., Morris, A., and Clutton-Brock, T.H. (2007).
257 Environmental conditions in early life influence ageing rates in a wild population of
258 red deer. *Current biology : CB* 17, R1000-R1001.
- 259 5. Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends*
260 *Ecol. Evol.* 14, 343-348.
- 261 6. Wilkin, T.A., and Sheldon, B.C. Sex Differences in the Persistence of Natal
262 Environmental Effects on Life Histories. *Curr. Biol.* 19, 1998-2002.
- 263 7. Wilson, A.J., Pemberton, J.M., Pilkington, J.G., Coltman, D.W., Mifsud, D.V.,
264 Clutton-Brock, T.H., and Kruuk, L.E.B. (2006). Environmental Coupling of Selection
265 and Heritability Limits Evolution. *PLoS Biol.* 4, e216.
- 266 8. Gaillard, J.-M., Boutin, J.-M., Delorme, D., Laere, G.V., Duncan, P., and Lebreton, J.-
267 D. (1997). Early Survival in Roe Deer: Causes and Consequences of Cohort Variation
268 in Two Contrasted Populations. *Oecologia* 112, 502-513.
- 269 9. Wilson, A.J., Kruuk, L.E., and Coltman, D.W. (2005). Ontogenetic patterns in
270 heritable variation for body size: using random regression models in a wild ungulate
271 population. *Am. Nat.* 166, 4.
- 272 10. Mojica, J.P., and Kelly, J.K. (2010). Viability selection prior to trait expression is an
273 essential component of natural selection. *Proceedings of the Royal Society B:*
274 *Biological Sciences* 277, 2945-2950.

- 275 11. Lynch, M., and Arnold, S.J. (1988). The Measurement of Selection on Size and
276 Growth. In *Size-Structured Populations*, B. Ebenman and L. Persson, eds. (Springer
277 Berlin Heidelberg), pp. 47-59.
- 278 12. Grafen, A. (1988). On the uses of data on lifetime reproductive success. In
279 *Reproductive success*, T. Clutton-Brock, ed. (Chicago: University of Chicago Press),
280 pp. 454-471.
- 281 13. Fisher, R.A. (1930). *The Genetical theory of natural selection*, (Oxford: Clarendon
282 Press).
- 283 14. Gaillard, J.M., Hewison, A.J.M., Klein, F., Plard, F., Douhard, M., Davison, R., and
284 Bonenfant, C. (2013). How does climate change influence demographic processes of
285 widespread species? Lessons from the comparative analysis of contrasted populations
286 of roe deer. *Ecol. Lett.* *16*, 48-57.
- 287 15. Vanpé, C., Gaillard, J.-M., Kjellander, P., Liberg, O., Delorme, D., and Hewison,
288 A.J.M. (2010). Assessing the intensity of sexual selection on male body mass and
289 antler length in roe deer *Capreolus capreolus*: is bigger better in a weakly dimorphic
290 species? *Oikos* *119*, 1484-1492.
- 291 16. Gaillard, J.M., Delorme, D., Jullien, J.M., and Tatin, D. (1993). Timing and
292 Synchrony of Births in Roe Deer. *J. Mammal.* *74*, 738-744.
- 293 17. Gaillard, J.M., Delorme, D., and Jullien, J.M. (1993). Effects of cohort, sex, and birth
294 date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia* *94*, 57-
295 61.
- 296 18. Gaillard, J.-M., Festa-Bianchet, M., Delorme, D., and Jorgenson, J. (2000). Body
297 mass and individual fitness in female ungulates: bigger is not always better.
298 *Proceedings of the Royal Society of London. Series B: Biological Sciences* *267*, 471-
299 477.
- 300 19. Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. (1985). Parental investment and
301 sex differences in juvenile mortality in birds and mammals. *Nature* *313*, 131-133.
- 302 20. Chen, H.-y., and Maklakov, Alexei A. (2012). Longer Life Span Evolves under High
303 Rates of Condition-Dependent Mortality. *Curr. Biol.* *22*, 2140-2143.
- 304 21. Reznick, D.N., Bryant, M.J., Roff, D., Ghalambor, C.K., and Ghalambor, D.E. (2004).
305 Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* *431*,
306 1095-1099.
- 307 22. Douhard, M., Plard, F., Gaillard, J.-M., Capron, G., Delorme, D., Klein, F., Duncan,
308 P., Loe, L.E., and Bonenfant, C. (2014). Fitness consequences of environmental
309 conditions at different life stages in a long-lived vertebrate. *Proceedings of the Royal*
310 *Society B: Biological Sciences* *281*.
- 311 23. Baudisch, A., and Vaupel, J.W. (2012). Getting to the Root of Aging. *Science* *338*,
312 618-619.
- 313 24. Hewison, A.J.M., Gaillard, J.-M., Kjellander, P., Toïgo, C., Liberg, O., and Delorme,
314 D. (2005). Big mothers invest more in daughters – reversed sex allocation in a weakly
315 polygynous mammal. *Ecol. Lett.* *8*, 430-437.
- 316 25. Rose, K.E., Clutton-Brock, T.H., and Guinness, F.E. (1998). Cohort Variation in Male
317 Survival and Lifetime Breeding Success in Red Deer. *J. Anim. Ecol.* *67*, 979-986.
- 318 26. Albon, S.D., Clutton-Brock, T.H., and Guinness, F.E. (1987). Early Development and
319 Population Dynamics in Red Deer. II. Density-Independent Effects and Cohort
320 Variation. *J. Anim. Ecol.* *56*, 69-81.
- 321 27. Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C.,
322 and Bonenfant, C. (2014). Mismatch Between Birth Date and Vegetation Phenology
323 Slows the Demography of Roe Deer. *PLoS Biol* *12*, e1001828.

- 324 28. Douhard, M., Gaillard, J.-M., Delorme, D., Capron, G., Duncan, P., Klein, F., and
325 Bonenfant, C. (2013). Variation in adult body mass of roe deer: early environmental
326 conditions influence early and late body growth of females. *Ecology* 94, 1805-1814.
- 327 29. Andersen, R., Gaillard, J.-M., Linnell, J.D.C., and Duncan, P. (2000). Factors
328 affecting maternal care in an income breeder, the European roe deer. *J. Anim. Ecol.*
329 69, 672-682.
- 330 30. Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-
331 Bianchet, M., and Gaillard, J.-M. (2011). Patterns of body mass senescence and
332 selective disappearance differ among three species of free-living ungulates. *Ecology*
333 92, 1936-1947.
- 334 31. Jullien, J.M., Delorme, D., and Gaillard, J.M. (1992). Determination de l'âge chez le
335 faon du chevreuil (*Capreolus capreolus*) dans son premier mois de vie. *Mammalia* 56,
336 307-311.
- 337 32. Gaillard, J.M., Delorme, D., Jean-Marie, B., Laere, G.V., Boisaubert, B., and Pradel,
338 R. (1993). Roe Deer Survival Patterns: A Comparative Analysis of Contrasting
339 Populations. *J. Anim. Ecol.* 62, 778-791.
- 340 33. Loison, A., Festa-Bianchet, M., Gaillard, J.M., Jorgenson, J.T., and Jullien, J.M.
341 (1999). Age-specific survival in five populations of ungulates: Evidence of
342 senescence. *Ecology* 80, 2539-2554.
- 343 34. Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., and Smith, G.M. (2009). *Mixed*
344 *Effects Model and Extensions in Ecology with R*, (London, UK: Springer).
- 345
346

347 **Figure Legends**

348
349 **Figure 1.** The level of juvenile mortality in a cohort has sex-dependent effects on lifespan in
350 roe deer at Trois Fontaines (TF) and Chizé (CH). When cohort-specific juvenile mortality is
351 high a strong sex difference is generated in both the percentage of animals reaching the age at
352 onset of actuarial senescence (A) and in average lifespan (B). These effects generate sex
353 differences in ageing when cohort-specific juvenile mortality is high (C).

354
355 **Figure 2.** The level of juvenile mortality in a cohort has sex-specific effects on adult body
356 mass at Trois Fontaines (TF) and Chizé (CH). Average adult body mass for each cohort of
357 males (blue symbols) and females (red symbols); female body mass is not markedly impacted
358 by cohort-specific juvenile mortality, whereas males from cohorts with high juvenile
359 mortality attain a smaller adult body mass.

360 361 362 **Tables**

363 **Table 1.** Final linear mixed effects models examining the effects of sex, cohort-specific
 364 juvenile mortality and population on average survival to the age at onset of actuarial
 365 senescence and adult lifespan in roe deer. Female parameter estimates are provided in relation
 366 to that of males.

Parameter	Estimate	S.E.	DF	F	P Value
Survival to senescence					
Both sexes					
Intercept	0.35	0.47	1,0.6	0.56	0.90
Sex	0.005	0.09	1,33.0	0.003	0.96
Mortality	-0.40	0.18	1,44.5	0.08	0.78
Sex*Mortality	0.72	0.23	1,33.1	9.60	0.004
Males					
Intercept	0.36	0.41	1,0.09	0.80	0.85
Mortality	-0.43	0.17	1,19.0	6.47	0.020
Females					
Intercept	0.50	0.09	1,25	33.0	<0.001
Mortality	0.46	0.22	1,25	4.50	0.044
Average adult lifespan					
Both sexes					
Intercept	5.36	3.16	1,1.0	3.91	0.79
Sex	1.42	0.62	1,22.3	2.67	0.12
Mortality	-1.69	1.27	1,32.7	0.08	0.78
Pop	0.72	1.30	1,9.4	0.04	0.85
Sex*Mortality	3.97	1.50	1,22.7	7.05	0.014
Sex*Pop	-0.96	0.52	1,24.3	3.44	0.076
Male					
Intercept	6.85	0.51	1,28.1	183.9	<0.001
Mortality	-0.45	1.26	1,24.6	0.13	0.73
Female					
Intercept	7.29	2.14	1,0.7	11.61	0.61
Mortality	1.91	1.54	1,20.6	1.55	0.23

367 **Table 2.** Final linear mixed effect models examining the effects of sex, cohort-specific
 368 juvenile mortality, population, and fawn mass on adult body mass of roe deer. Female
 369 parameter estimates are provided in relation to that of males. Because data were normally
 370 distributed adult body mass and fawn mass were not transformed for analysis. However, all
 371 main effects and interactions are similar when these mass values are log transformed.

Parameter	Estimate	S.E.	DF	F	P value
Both sexes					
Intercept	24.89	3.01	1,8.65	63.83	<0.001
Sex	-10.97	3.53	1,220.5	9.70	0.002
Mortality	-22.56	6.40	1,220.0	7.27	0.008
Fawn mass	0.047	0.14	1,220.7	7.86	0.006
Sex*Mortality	21.30	6.40	1,220.3	5.88	0.016
Sex*Fawn mass	0.50	0.21	1,220.8	5.61	0.019
Mortality* Fawn mass	1.26	0.37	1,220.1	7.30	0.007
Sex*Mortality*Fawn mass	-1.05	0.53	1,220.5	4.10	0.044
Males					
Intercept	24.91	57.58	1,01	0.19	0.99
Mortality	-22.17	6.47	1,92.3	11.75	0.001
Fawn mass	0.05	0.14	1,104.9	0.09	0.76
Mortality*Fawn mass	1.23	0.38	1,92.4	10.61	0.002
Females					
Intercept	12.51	1.28	1,117	112.38	<0.001
Pop	0.75	0.32	1,117	5.46	0.021
Mortality	1.61	0.97	1,117	2.73	0.10
Fawn mass	0.64	0.07	1,117	88.44	<0.001

372
 373

374
 375
 376
 377

Figure 1
[Click here to download high resolution image](#)

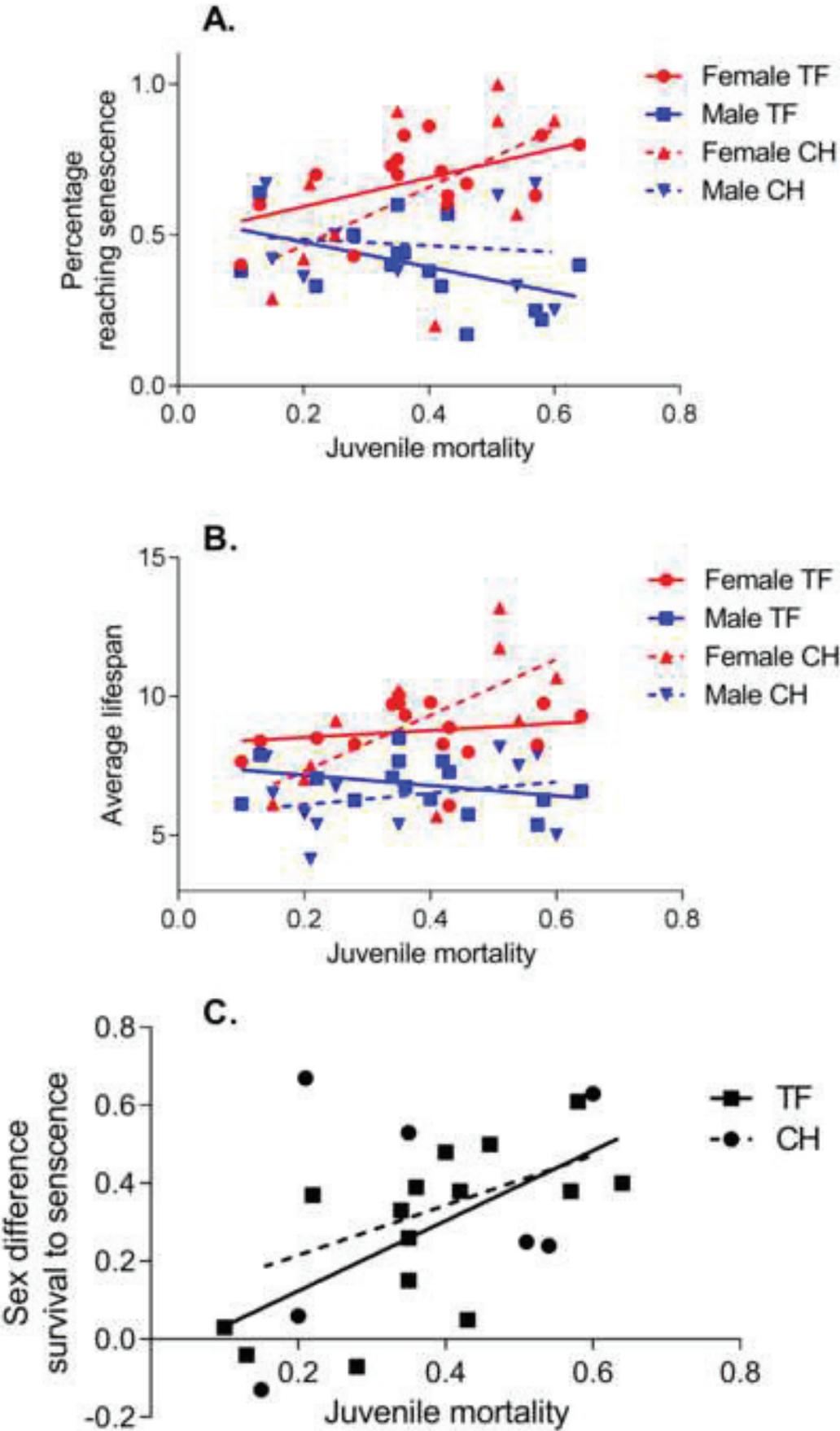
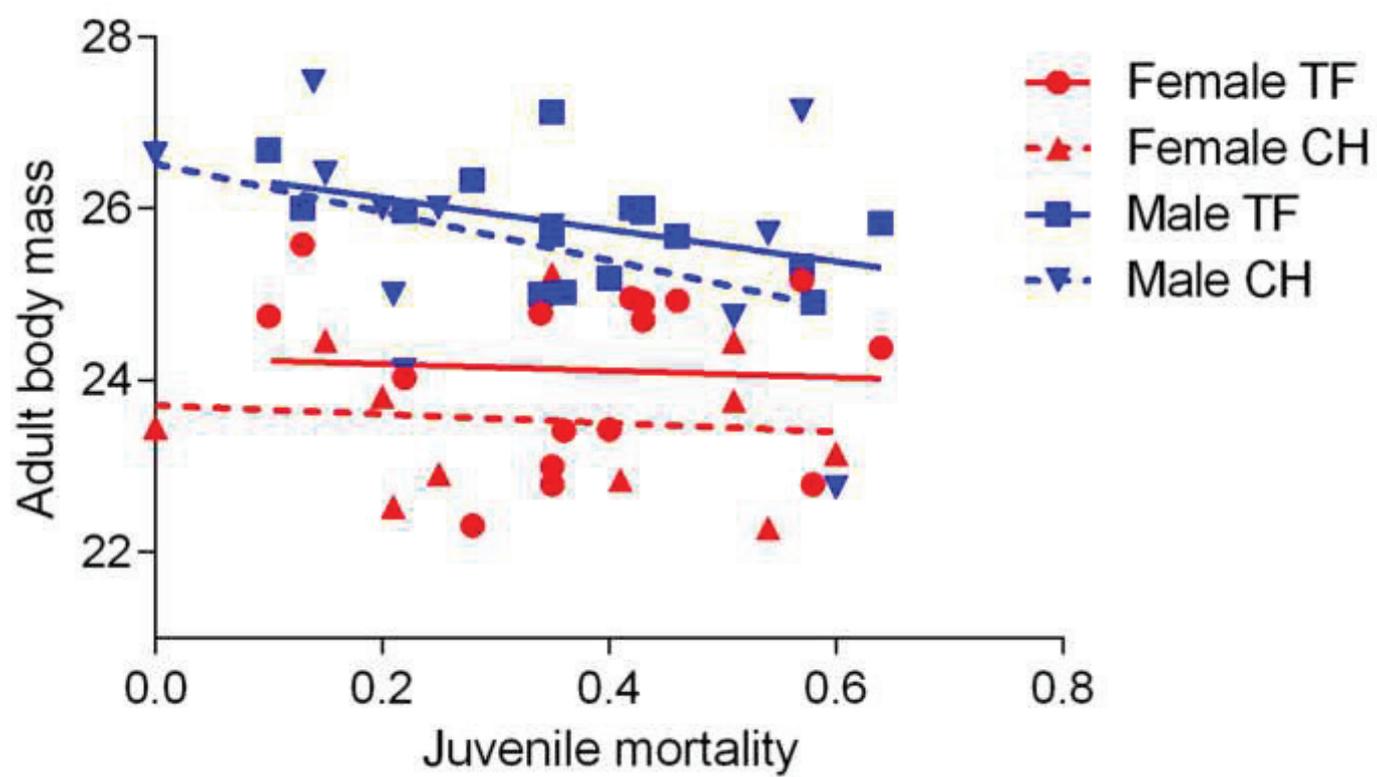


Figure 2
[Click here to download high resolution image](#)



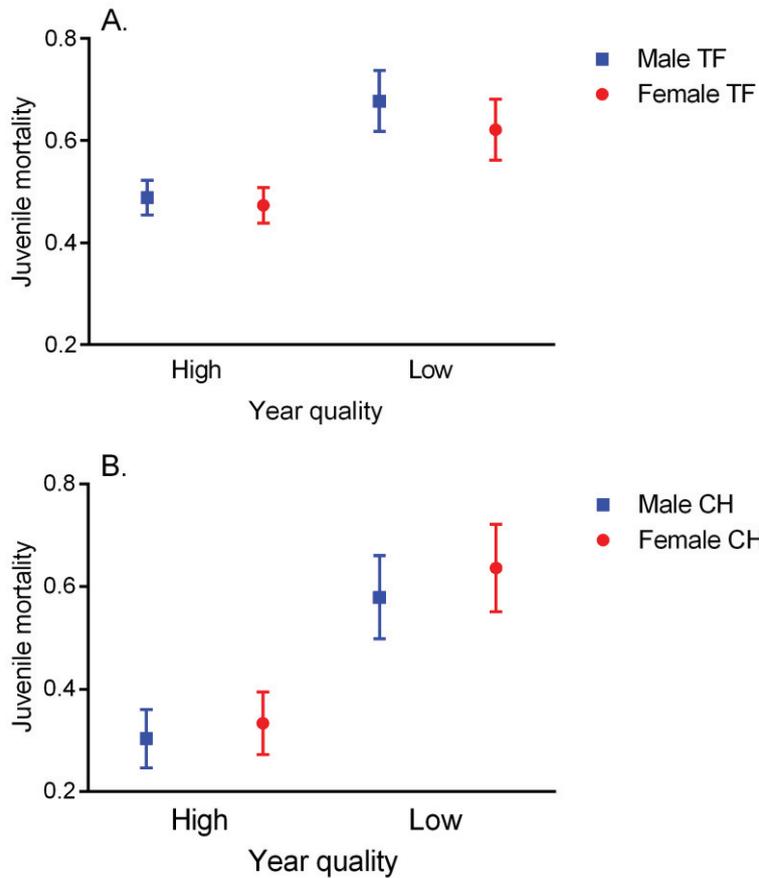


Figure S1. Juvenile mortality of male and female roe deer at (A) Trois Fontaines and (B) Chizé. Data for each population is split according to year quality: low quality years are defined as having over 50% juvenile mortality (irrespective of sex), while high quality years have less than 50% sex-independent mortality. Juvenile mortality is higher in poor quality cohorts (effect of year quality: $\chi^2 = 23.79$, 1 d.f., $P < 0.0001$), and the sexes do not differ in their response to this (interaction between sex and year quality: $\chi^2 < 0.1$, 1 d.f., $P = 0.98$), nor in their overall juvenile mortality levels (effect of sex: $\chi^2 < 0.1$, 1 d.f., $P < 0.93$).

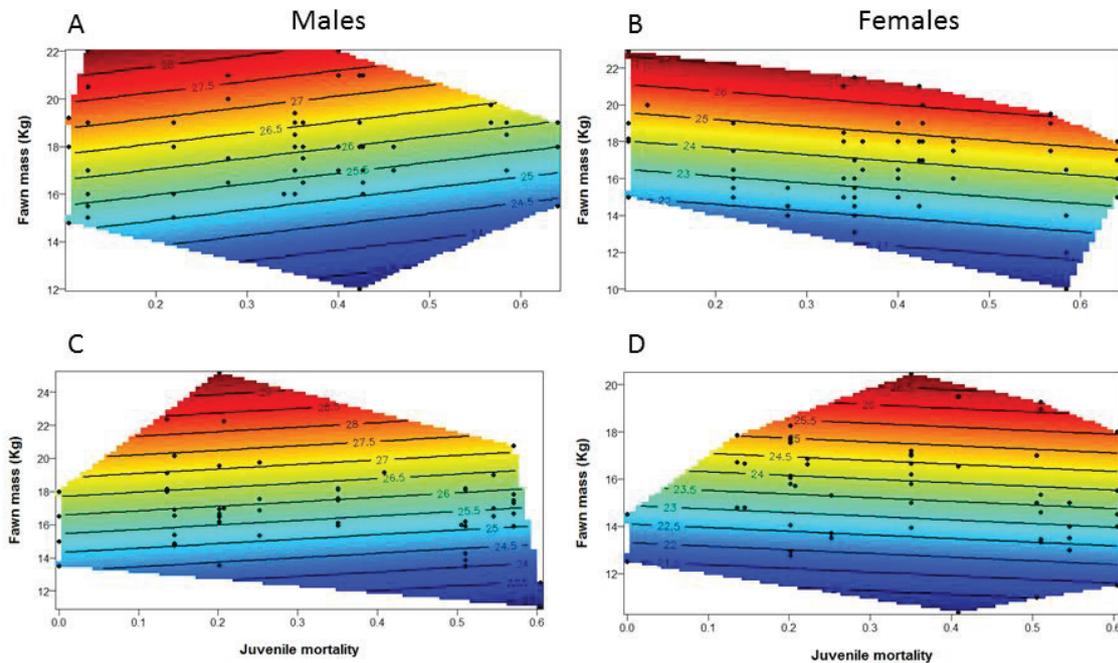


Fig. S2. Influence of cohort-specific juvenile survival and fawn body mass on adult body mass in males (A, C) and females (B, D) in Trois Fontaines (A,B) and Chizé (C,D). In males, body mass decreases with increasing juvenile mortality, which is represented by the lines for adult body mass sloping upwards to the right. In females, the opposite effect tends to occur with the line for adult body mass sloping downwards to the right. The response surface is visualized as non-parametric thin-plate splines projected in two dimensions (fawn mass and juvenile mortality), with colours used to represent the third (adult body mass) dimension. Points represent each individual animal's value.

Table S1. Model examining the effects of body mass and sex on lifespan in roe deer at Chizé and Trois Fontaines. The interaction between sex and adult mass was dropped from the final model. Female parameter estimates are provided in relation to that of males.

Parameter	Estimate	S.E.	DF	F	P
Intercept	4.58	2.15	1,0.9	2.21	0.40
Sex	2.30	0.28	1,474.1	65.64	<0.001
Adult mass	0.18	0.06	1,448.4	8.58	0.004
Sex*Adult mass	-0.026	0.12	1,476.5	0.051	0.82

Table S2. Model examining the relationship between cohort-specific juvenile mortality (mortality), body mass and lifetime reproductive success in females from the Trois Fontaines population. The interaction between adult mass and mortality was dropped from the final model.

Parameter	Estimate	S.E.	DF	F	P
Intercept	-7.08	74.12	1,0.001	0.01	0.99
Mortality	-1.55	3.61	1,19.3	0.19	0.67
Adult mass	0.68	0.23	1,68.8	8.84	0.004
Adult mass*Mortality	-1.98	1.82	1,72	1.18	0.28

Table S3. Model examining the relationship between cohort-specific juvenile mortality (mortality), body mass and annual reproductive success in females from the Trois Fontaines population. The interaction between adult mass and mortality was dropped from the final model.

Parameter	Estimate	S.E.	DF	F	P
Intercept	-0.68	0.65	1,84.2	1.10	0.29
Mortality	0.14	0.44	1,23.0	0.10	0.75
Adult mass	0.069	0.026	1,86.5	7.14	0.009
Adult mass*Mortality	0.027	0.18	1,85.5	0.023	0.88

Appendix 2

1 Disposable soma in wild populations of 2 vertebrates: a theory that does not age

3
4 Jean-François LEMAÎTRE^{1*}, Vérane BERGER^{2*}, Christophe
5 BONENFANT^{3*}, Mathieu DOUHARD^{4*}, Marlène GAMELON^{5*†},
6 Floriane PLARD^{6*} and Jean-Michel GAILLARD^{7*}

7
8
9 *Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR5558, Laboratoire de
10 Biométrie et Biologie Évolutive, F-69622, Villeurbanne, France.

11
12 †Present address: Department of Biology, Centre for Biodiversity Dynamics, Norwegian
13 University of Science and Technology, Trondheim, NO-7491 Norway.

14
15
16
17 ¹Corresponding author: jean-francois.lemaitre@univ-lyon1.fr

18 ² verane.berger@wanadoo.fr

19 ³ christophe.bonenfant@univ-lyon1.fr

20 ⁴ mathieu.douhard@gmail.com

21 ⁵ marlene.gamelon@ntnu.no

22 ⁶ floriane.plard@univ-lyon1.fr

23 ⁷ jean-michel.gaillard@univ-lyon1.fr

24
25 **Running title:** Disposable soma in the wild

26
27
28 **Number of words:** 7243

29 **Number of tables:** 1

30 **Number of figures:** 1

31 **Data supplement:** 1

32

33 **Abstract**

34 The disposable soma theory of ageing, introduced more than 35 years ago, postulates that the
35 limitation of the amount of resources available in the environment should lead to a trade-off
36 between allocation to reproduction early in life and somatic maintenance later on. Individuals
37 with a high reproductive effort during early life should suffer from increased somatic
38 damages, progressively leading to an accelerated senescence and a reduced longevity. Over
39 the last decades, the number of empirical tests of the disposable soma theory in wild
40 populations of vertebrates has rapidly increased. Here, we compiled 27 studies that explicitly
41 or implicitly tested the disposable soma theory in free-ranging populations and found that this
42 theory is well supported. Moreover, our review demonstrates the tight link existing between
43 the disposable soma theory and the principle of energy allocation, which roots the ageing
44 process in the evolution of life history strategies and can potentially open promising avenue of
45 research in evolutionary ecology of ageing. Finally, we outline three new research lines that
46 would be worthy of consideration in future studies focused on the relationship between
47 allocation to reproduction and senescence patterns in wild vertebrates.

48

49

50 **Keywords:** Ageing, Growth, Life history theory, Senescence, Sexual selection, Trade-off

51 **1. Introduction**

52 (a) Evolutionary ecology of ageing and the disposable soma theory

53 Senescence patterns are highly variable at both inter- and intra-specific levels (e.g. [1–3]) and
54 understanding the evolutionary origins of this variation has become a key topic in the study of
55 ageing [4,5]. Medawar was the first to frame the process of senescence in an evolutionary
56 context [6]. In his seminal monograph, he proposed that senescence is the consequence of an
57 accumulation of deleterious alleles in the genome, which starts to be expressed at an age
58 where the reduced forces of natural selection prevent these alleles to be purged. Hamilton
59 formalized Medawar’s ideas by demonstrating that the process of senescence is the
60 consequence of the increasing decline in the forces of natural selection with age [7] starting
61 from age at sexual maturity (but see [8]), and is inevitable for all age-structured populations
62 [7] such as vertebrate populations [9]. Medawar’s work on senescence has been expanded by
63 Williams who proposed the antagonistic pleiotropy theory of ageing stating that an allele with
64 a negative effect on performance in late life could be selected if it has a positive effect on
65 performance during early life [10]. The relationship between early allocation to reproduction
66 and its fitness consequences later in life is also the core of the disposable soma theory of
67 ageing later introduced by Kirkwood [11]. His evolutionary theory of senescence proposes a
68 comprehensive explanation of organisms’ ageing processes starting at the level of molecules.
69 Basically, it posits that accurate gene replication and cell reproduction requires a complex and
70 molecular machinery of error corrections to ensure proper cell functioning in time and across
71 generations [11,12]. Because these error corrections or quality control mechanisms are
72 energetically costly ([11,12] but see also [13] for a thorough discussion of the energetically
73 costs of these mechanisms), individuals are expected to optimize their allocation to the set of
74 mechanisms involved in the maintenance of their soma (e.g. enzyme-based repair mechanism)
75 according to their average lifespan or their risk of environmentally-driven mortality [14].

76 Such relationships are well supported at the inter-specific level where long-lived species have
77 more elaborate repair mechanisms than short-lived species (e.g. [15] and references therein).

78 One fundamental tenet of the disposable soma theory is the limited amount of energy
79 intake that an individual can extract from its environment [14]. This leads individuals to share
80 their finite pool of resources among growth, reproduction, and maintenance [12]. In Kirkwood
81 and Rose's own words: '*an organism is an entity that takes in resources from its environment,*
82 *[...], uses these resources for a variety of metabolic tasks such as growth and maintenance,*
83 *and in due course reproduces to generate an output of progeny. The problem of allocation of*
84 *resources arises because resources used for one purpose are no longer available for other*
85 *purposes'* (see [14], pp 16). Therefore, an individual that uses a large quantity of resources for
86 reproduction will have in return fewer resources available for the protection of its soma [14].
87 Molecular errors will thus accumulate in somatic cells at a fast rate, and biological functions
88 (e.g. body condition, reproduction) and survival will show a stronger decline as individuals
89 age (i.e. a stronger senescence) [12,14].

90

91 (b) Aim of the review

92 Very recently, it has been suggested that among the classical theory of ageing, the disposable
93 soma theory might be the one that best explains this diversity [3], notably since the theory
94 relies on a trade-off where the relative allocation to reproduction or mechanisms preventing
95 from senescence closely depends on environmental conditions [14]. During the first 15 years
96 following the formulation of the disposable soma theory [11], most studies designed to test
97 this theory were conducted in the laboratory. These studies, generally focused on
98 invertebrates (see [16]), provided support for the disposable soma theory. For example, in
99 field crickets (*Teleogryllus commodus*), males with increased allocation to sexual signalling
100 during their whole life suffered from a reduced longevity [17]. The fact that senescence was

101 long thought to be almost absent in wild populations [5] provides the most likely explanation
102 for the long-standing focus on laboratory models. However, thanks to long-term individual
103 monitoring of known-aged animals [18], the number of study cases reporting senescence in a
104 wide range of traits in free-ranging conditions has rapidly increased [5], providing the
105 necessary material for testing evolutionary theories of ageing in the wild. Empirical tests of
106 the disposable soma theory of ageing in the wild are particularly relevant because this theory
107 is based on the assumption of resource limitation [14]. Individuals living under laboratory or
108 captive conditions are usually fed *ad libitum*, which can potentially mask trade-offs between
109 early and late life performance [19]. This clearly stresses the importance of testing theories of
110 ageing in natural environments where both food availability and acquisition are generally
111 limiting [2,5,18].

112 Over the past 10 years, the number of studies looking for a trade-off between
113 allocation to reproduction during early life and fitness components (survival and
114 reproduction) in late life has increased markedly (Table 1). However, whether reported results
115 provide an overall support of the disposable soma theory remained to be assessed. Purposely,
116 we limited the scope of our review to vertebrates because most of these species are strongly
117 age-structured, which fit evolutionary models of senescence and also because longitudinal
118 studies on invertebrates in the wild remain relatively scarce. We first compiled the different
119 studies that looked for such trade-offs and we assessed the overall support for the theory in
120 wild populations of vertebrates. Then, we show how the disposable soma theory is grounded
121 in the life history theory and emphasize the importance of the environment in mediating the
122 early vs. late life trade-off. Finally, we propose new research directions for studies testing the
123 disposable soma theory in the wild, which should improve our understanding of the ageing
124 process in natural conditions.

125

126 2. Tests of the disposable soma theory in the wild

127 To find out all published papers testing explicitly or implicitly the disposable soma
128 theory in wild populations of vertebrates, we have used a strict search protocol (see electronic
129 supplementary material). This protocol allowed identifying 27 studies testing the disposable
130 soma theory in 25 vertebrate species (13 birds, 10 mammals, and 2 reptiles, table 1). Fishes
131 and amphibians were absent from the compiled papers, probably because of the scarcity of
132 long-term individual-based studies of these species in the wild [19].

133 In most of the reviewed studies, authors concluded that the disposable soma theory
134 was supported when at least one of the negative correlations between allocation to
135 reproduction during early life and performance in late life was statistically significant.
136 Following this rule, our literature survey revealed that 74.07 % of the studies provided
137 support for the disposable soma theory (i.e. 20 out of 27 studies, see Table 1). For instance, in
138 free-living jackdaws (*Corvus monedula*), individuals with brood size experimentally
139 increased show a much stronger rate of actuarial senescence [20]. Nevertheless, it is worth
140 noticing that a publication bias can potentially lead to an over-representation of positive
141 results [21].

142 Studies of the disposable soma theory have been performed using a wide array of
143 variables and age at first reproduction was the most commonly used metric of allocation to
144 reproduction early in life (Table 1). However, early reproduction was often associated with
145 high performance later in life (Table 1). For instance in red deer (*Cervus elaphus*), females
146 giving birth at earliest ages showed lowest senescence rates in offspring birth weight [22].
147 This suggests that early reproduction might reflect individual quality (sensu [23]), and prevent
148 the trade-off expected from the disposable soma theory to be revealed (see figure 1). Indeed in
149 red deer, when the fecundity early in life instead of the age at first reproduction is used to
150 measure female reproductive effort, an increased rate of reproductive senescence is observed

151 [22], as predicted by the disposable soma theory. A fundamental assumption of the theory is
152 that allocation to reproduction is costly [14] and testing this theory requires accurate measures
153 of allocation. Therefore, we advocate the use of traits such as litter size, duration of parental
154 care, or number of raised offspring, which provide more reliable information on early life
155 allocation to reproduction than age at first reproduction.

156 For late life, we can distinguish three types of metrics (Table 1), including survival
157 (e.g. longevity, rate of actuarial senescence), reproduction (e.g. rate of senescence in breeding
158 success), or both reproduction and survival (e.g. age at last reproduction, lifetime reproductive
159 success). Several correlations between early and late traits have sometimes been tested within
160 the same study, revealing contrasting results with respect to the disposable soma theory. For
161 example, in female common lizard (*Lacerta vivipara*), a high reproductive effort during early
162 life did not influence senescence in litter size but increased senescence in survival [24]. These
163 results suggest that high reproductive effort can negatively influence only one aspect of the
164 late life performance (e.g. longevity, late reproduction or others, see Table 1) and stress that
165 when testing the disposable soma theory, a wide range of traits needs to be considered.

166 Contrasted patterns can emerge when senescence is investigated jointly in males and
167 females. For instance, in willow tits (*Parus montanus*), while females that did not breed
168 during early life survived better in late life, such a relationship between early reproduction
169 and survival in late life was not found in males [25]. The support of disposable soma theory
170 might thus be sex-specific in some species and this emphasizes the need of testing this theory
171 in both sexes to identify the nature of the reproductive costs influencing performance in late
172 life (see section 4.c for a specific discussion on this topic). However, 63% (17 of the 27) of
173 the studies testing the disposable soma theory focused on females only, likely because it is
174 easier to measure reproductive effort for these latter (e.g. [26]). Moreover, measuring male
175 reproductive senescence (e.g. senescence in sperm quality, secondary sexual traits or

176 reproductive success) based on longitudinal studies is currently extremely difficult in wild
177 populations of vertebrates. However, such studies could potentially bring further support for
178 the disposable soma theory, as suggested by a recent work in captive houbara bustard
179 (*Chlamydotis undulata*) where males that have a higher display rate during early life showed
180 stronger senescence in sperm number and motility [27].

181 At least 7 studies (including 5 on mammals) have failed to support the disposable
182 soma theory (Table 1). There are several possible explanations to this lack of support. First,
183 high reproductive expenditures are not associated with long terms costs and the disposable
184 soma theory does not explain individual variations in senescence patterns or longevity in these
185 species. Second, five of these studies used age at first reproduction to measure early
186 reproduction (e.g. [28,30,31]) and as emphasized above it might not really measure accurately
187 allocation to reproduction. Third, inappropriate methodological tools could be involved.
188 Indeed, tests of the disposable soma theory using longitudinal data requires taking into
189 account both individual heterogeneity and natural selection processes such as the viability
190 selection (see figure 1 for more details). Some of these 7 studies (e.g. [30]) might have failed
191 to detect long-term costs of high allocation to reproduction due to the selective disappearance
192 of poor quality individuals. Such process can favour the over-representation of individuals
193 with high reproductive performance in old age classes and thus mask any long-term costs of
194 heavy allocation to reproduction on survival and reproduction late in life [32].

195

196 3. Disposable soma theory is grounded within the life-history theory

197 The disposable soma theory was initially tackled without an explicit reference to the
198 principle of energy allocation (*sensu* [28]) and was aimed to explain the evolution of ageing at
199 the cellular level, based on the assumption that errors must occur at some stage in somatic
200 macro-molecular synthesis over the organism lifetime, leading to a fatal breakdown of

201 homeostasis, and to death [11]. However, such mechanisms ultimately cause a direct positive
202 link between longevity and the accuracy of synthesis of macromolecules [29]. In long-lived
203 species with delayed reproduction, errors of synthesis should occur sufficiently late to allow
204 most individuals to reproduce, whereas this should not occur in short-lived species. This
205 suggests that the intensity of senescence should decrease with the speed of the life history, as
206 supported by empirical comparative analyses among vertebrate species [8,30,31], and
207 demonstrates that the disposable soma theory is deeply rooted in life history strategies (*sensu*
208 [32]).

209 Even if the disposable soma theory was not initially proposed in a life history context,
210 our review highlights that most published tests of the disposable soma theory in wild
211 populations have been performed using observed variation in life history traits over individual
212 trajectories. Indeed, 45 % (9 of the 20) of studies reporting the existence of a negative co-
213 variation between allocation to reproduction during early life and individual performance in
214 late life were interpreted as an energy trade-off between major biological functions (table S1).

215 The principle of energy allocation, which states that organisms allocate acquired
216 energy either to growth, reproduction, or survival in a competitive way so that trade-offs
217 should occur, is at the core of our current theory of life history evolution [33]. Recently,
218 Baudish and Vaupel [34] proposed that the principle of energy allocation (they called
219 ‘Allocation theory’) could offer a possible framework that would explain currently observed
220 discrepancies between theory and data on ageing (see [3]). For instance, current evolutionary
221 theories of ageing predict that mortality should increase steadily from the age at first
222 reproduction [7], while empirical evidence accumulated so far shows that the age at the onset
223 of senescence is sometimes delayed to much later in adulthood [2]. This might be easily
224 explained if the age at the onset of senescence is determined by the strategy of energy

225 allocation to reproduction vs. maintenance that individuals exhibit during the first part of their
226 life.

227 By providing clear evidence that the ageing process is embedded in the life history
228 strategy and co-varies with other biological processes like growth or reproduction, predictions
229 about life histories response to environmental variability may hence provide a test of the
230 disposable soma theory of ageing. For instance, if the principle of energy allocation underpins
231 the relationships between reproductive effort and ageing process, environmental conditions
232 during early life should alter the optimal allocation between maintenance and reproduction
233 [35]. When individuals have been raised in harsh environmental conditions, the risk of
234 environmentally driven mortality is high and individuals should favour a high allocation to
235 reproduction during their early life to secure offspring production, which ultimately should
236 fasten senescence [14]. Only 4 studies (table 1) assessed the effects of environmental
237 conditions on both early and late life performance [36–39] and revealed that natal
238 environment shapes observed variation in senescence rates. In red deer, females born in years
239 of high population density have faster senescence in both survival and reproduction than
240 females born in years of low population density ([37]; see also [39] on great tits, *Parus*
241 *major*). Interestingly, these studies also provide support for the disposable soma theory by
242 reporting a negative correlation between allocation to reproduction in early life and
243 performance in late life when all females are pooled regardless of their natal conditions (see
244 Table 1). However, whether the effect of early environmental conditions on performance in
245 late life is a consequence of early stress *per se* [40,41] or is due to a change in the energy
246 allocation tactics between reproduction and maintenance remains unknown. Moreover,
247 whether the trade-off between early and late life individual performance is more acute in poor
248 than in good natal environments, as predicted by the disposable soma theory, has not yet been
249 explicitly investigated.

250

251 4. Future directions

252 (a) Energetic costs and somatic damages in the wild

253 Although there is a clear support for the trade-off between allocation to reproduction early in
254 life and intensity of reproductive or actuarial senescence (Table 1), no study of wild animals
255 has actually quantified the exact energetic costs of allocation to reproduction, or the cellular
256 damage caused by this allocation.

257 Experimental manipulations in the wild associated with accurate physiological
258 measures might solve this problem. For instance, in Black-legged kittiwakes, *Rissa tridactyla*
259 [47] or in Columbian ground squirrel *Urocitellus columbianus*, [48] daily energy expenditures
260 are higher in females with experimentally augmented litter size than in control females with
261 reduced litter size [48]. Surprisingly, although they nicely identified a cost in terms of pup
262 quality (i.e. smaller pups with lower survival probabilities during their first winter), Skibieli
263 and colleagues [48] found no effect of enlarged litter size on female survival and breeding
264 probability the following year. However, long-term consequences of enlarged litter size on
265 fitness could potentially be revealed later in life if senescence originates from the progressive
266 accumulation of damage associated [12]. Several techniques (e.g. doubly labelled method [47]
267 or telemetry system [43]) allowing the measurement of various physiological traits (e.g. daily
268 energy expenditures, heart beat rate, body temperature) could allow the assessment of energy
269 expenditures during reproduction, which should refine our current understanding of the
270 disposable soma theory in the wild when associated with information on performance in late
271 life.

272 Similarly, it would be particularly interesting to quantify directly the molecular and
273 cellular damage of wild individuals that massively allocate energy into reproduction early in
274 life. Up to now, studies linked with the oxidative stress theory have often led to contrasted

275 results ([44]). Typically, the oxygen metabolism in the mitochondria produces reactive
276 oxygen species (ROS) such as free radicals (e.g. superoxide anion) that will both damage cell
277 structure (DNA, lipids, proteins) and potentially lead to ageing [44]. To limit the cellular
278 damages caused by the production of ROS, antioxidant mechanisms have evolved within
279 many eukaryotes ([45]). However, individuals that allocate a substantial quantity of energy to
280 reproduction during early life might jeopardize their abilities to allocate into the antioxidant
281 system. ROS production might also be boosted, which could in turn lead to severe damage to
282 cell structure, and ultimately to increased senescence [46]. The role of oxidative stress in
283 mediating early-late life trade-offs has been recently questioned [44,47] and studies
284 combining repeated measures of life-history traits with physiological and/or molecular
285 measures (e.g. [24]) are badly needed. To date, only a few longitudinal studies have tested for
286 an association between reproductive effort and oxidative damage ([48]). For instance,
287 lactating females show stronger oxidative damage in plasmatic proteins than non-lactating
288 females in both red squirrels [49] and eastern chipmunks [50]. Moreover, the development of
289 technical tools for non-model organisms (e.g. transcriptomics, [51]) enabling more complete
290 assessment of the expression of genes involved in the antioxidant system and the cellular
291 reparation machinery [44], should progressively allow fine scale assessment of reproductive
292 costs. Ultimately, studies linking the allocation to reproduction to somatic damage should also
293 test whether the accumulation of molecular damage increases senescence rates ([52]), which,
294 if true, would put the mechanistic explanation proposed by the disposable soma theory as the
295 key factor mediating life history traits in the wild.

296

297 (b) Late life consequences of fast growth

298 The long-term consequences of fast body growth have been mostly neglected so far in studies
299 of wild populations (but see [53]). However, individuals often grow at a suboptimal rate, even

300 when resources are unlimited, suggesting that fitness costs are associated with fast
301 development [54]. So far, most studies linking fast growth and performance in late life come
302 from laboratory studies [55]. For example, in three-spined sticklebacks (*Gasterosteus*
303 *aculeatus*), fast growing individuals showed a reduced longevity suggesting that energy
304 allocation to body development early in life increases actuarial senescence [56]. In
305 vertebrates, this relationship between growth and senescence is likely to be mediated by
306 molecules such as growth hormones (GH) or Insulin-Like Growth Factor-1 (IGF-1), which
307 are known to have long-term effects on fitness [57].

308 Individuals that allocate strongly to reproduction early in life have often experienced
309 fast early growth [55], which might increase cellular damage even more and accelerate
310 thereby senescence. In many vertebrates, individuals grow fast to start reproducing earlier
311 [61] because body size often determines male social rank and success in sexual competition
312 (e.g. [65]) or female ability to reproduce [66]. Studies should thus seek to quantify the relative
313 influence of both growth and reproduction on shaping performance in late life. Quantifying
314 senescence in castrated individuals once they have reached their asymptotic body size might
315 be a first step in this direction.

316

317 (c) Disposable soma and sexual competition in males

318 Current support of the disposable soma theory almost entirely relies on females (table 1).
319 Testing the disposable soma theory in males is required because in most vertebrate species,
320 males strongly allocate to early growth and sexual competition to gain mates [58]. So far, the
321 influence of sexual competition and mating tactic on survival and senescence patterns have
322 been principally tackled at the inter-specific level [59,60]. Although pioneer works on the
323 disposable soma theory did not explicitly mention sexual selection [11,14], energetic costs of
324 sexual competition in males could be high. Unfortunately, long-term consequences of

325 repeated episodes of competition and of breeding activity in males have only been measured
326 in laboratory (reviewed in [16]). Investigating such questions under natural conditions where
327 environmental stochasticity often modulates both direction and intensity of sexual
328 competition [61] could offer a better understanding of between-population variation in
329 senescence rates.

330 Comparing within a given species long-term costs of allocation to reproduction and
331 sexual competition in males and females would also allow understanding sex-differences in
332 senescence patterns [62]. Interestingly, while it is well known that male and female
333 vertebrates differ in longevity (e.g. in mammals, females typically outlive males, whereas the
334 opposite is found in birds; [63]), there is no consensus about a systematic difference in
335 senescence patterns between males and females [64] even if as expected (see [10]), in
336 mammals males tend to suffer from a steeper senescence rate than females [60]. Nowadays,
337 evidence of between-sex differences in the relationship between reproductive effort and
338 cellular damage are accumulating [65], but the consequences in terms of sex-differences in
339 senescence patterns are yet to be discovered.

340

341 5. Concluding remarks

342 The empirical evidence we reviewed largely supports the disposable soma theory in free-
343 ranging populations of vertebrates, demonstrating that high allocation to reproduction during
344 early stages of life is associated with earlier or faster decline in individual performance during
345 the late stages of life. We also emphasize the intimate relationship linking the disposable
346 soma theory and our current understanding of life history evolution. This notably explains
347 why life history traits such as age at first reproduction or litter size often constitute the fuel of
348 these tests. Importantly, this also puts forward the importance of the strategy of energy

349 allocation to explain the diversity of ageing patterns observed in the wild, which opens new
350 paths for future investigations.

351

352 **Acknowledgments:** We are extremely thankful to Jean-Sébastien Bolduc, Rob Brooks,
353 Michael Garratt, Dan Nussey and Benjamin Rey for their insightful comments on a previous
354 version of this article.
355

356 **Funding statement:** JFL was supported by a post-doctoral grant from the Fyssen Foundation,
357 Paris and a Research Grant from the Association for the Study of Animal Behaviour (ASAB).
358 VB, MD and FP are funded by a PhD scholarship from the French Ministry of Higher
359 Education and Research. MG was supported by a grant of the French National Agency for
360 Wildlife (ONCFS).
361

362 **References**

- 363 1. Brommer JE, Wilson AJ, Gustafsson L. 2007 Exploring the genetics of aging in a wild
364 passerine bird. *Am. Nat.* **170**, 643–650.
- 365 2. Lemaître JF, Gaillard JM, Lackey LB, Clauss M, Müller DW. 2013 Comparing free-
366 ranging and captive populations reveals intra-specific variation in aging rates in large
367 herbivores. *Exp. Gerontol.* **48**, 162–167.
- 368 3. Jones OR, Scheuerlein A, Salguero-Gómez R, Camarda CG, Schaible R, Casper BB,
369 Dahlgren JP, Ehrlén J, García MB, Menges ES et al. 2014 Diversity of ageing across the
370 tree of life. *Nature* **505**, 169–173.
- 371 4. Promislow DE, Fedorka KM, Burger JM, 2006 Evolutionary biology of aging: future
372 directions. In *Handbook of the biology of aging, 6th edn.* (Ed: Masoro EJ, Austad SN).
373 Academic Press. San Diego.
- 374 5. Nussey DH, Froy H, Lemaître JF, Gaillard JM, Austad SN. 2013 Senescence in natural
375 populations of animals: widespread evidence and its implications for bio-gerontology.
376 *Ageing Res. Rev.* **12**, 214–225.
- 377 6. Medawar PB. 1952 *An unsolved problem of biology*. London: Lewis.
- 378 7. Hamilton WD. 1966 The moulding of senescence by natural selection. *J. Theor. Biol.* **12**,
379 12–45.
- 380 8. Jones OR. et al. 2008 Senescence rates are determined by ranking on the fast–slow life-
381 history continuum. *Ecol. Lett.* **11**, 664–673.
- 382 9. Tuljapurkar S, Caswell H. 1997 *Structured-Population Models in Marine, Terrestrial,*
383 *and Freshwater Systems*. New York: Chapman & Hall.

- 384 10. Williams GC. 1957 Pleiotropy, natural selection, and the evolution of senescence.
385 *Evolution* **11**, 398–411.
- 386 11. Kirkwood T. 1977 Evolution of ageing. *Nature* **270**, 301–304.
- 387 12. Kirkwood TB, Austad SN. 2000 Why do we age? *Nature* **408**, 233–238.
- 388 13. Speakman JR, Król E. 2010 The heat dissipation limit theory and evolution of life
389 histories in endotherms—time to dispose of the disposable soma theory? *Integr. Comp.*
390 *Biol.* **50**, 793–807.
- 391 14. Kirkwood TB, Rose MR. 1991 Evolution of senescence: late survival sacrificed for
392 reproduction. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **332**, 15–24.
- 393 15. Li Y, de Magalhães JP. 2013 Accelerated protein evolution analysis reveals genes and
394 pathways associated with the evolution of mammalian longevity. *Age* **35**, 301–314.
- 395 16. Bonduriansky R, Maklakov A, Zajitschek F, Brooks R. 2008 Sexual selection, sexual
396 conflict and the evolution of ageing and life span. *Funct. Ecol.* **22**, 443–453.
- 397 17. Hunt J, Brooks R, Jennions MD, Smith MJ, Bentsen CL, Bussiere LF. 2004 High-quality
398 male field crickets invest heavily in sexual display but die young. *Nature* **432**, 1024–
399 1027.
- 400 18. Ricklefs RE, Cadena CD. 2007 Lifespan is unrelated to investment in reproduction in
401 populations of mammals and birds in captivity. *Ecol. Lett.* **10**, 867–872.
- 402 19. Clutton-Brock T, Sheldon BC. 2010 Individuals and populations: the role of long-term,
403 individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol.*
404 *Evol.* **25**, 562–573.
- 405 20. Boonekamp JJ, Salomons M, Bouwhuis S, Dijkstra C, Verhulst S. 2014 Reproductive
406 effort accelerates actuarial senescence in wild birds: an experimental study. *Ecol. Lett.*
407 **17**, 599–605.
- 408 21. Rothstein HR, Sutton AJ, Borenstein M. 2006 *Publication Bias in Meta-analysis:*
409 *Prevention, Assessment and Adjustments*. Hoboken, NJ: Wiley.
- 410 22. Nussey DH, Kruuk LE, Donald A, Fowlie M, Clutton-Brock TH. 2006 The rate of
411 senescence in maternal performance increases with early-life fecundity in red deer. *Ecol.*
412 *Lett.* **9**, 1342–1350.
- 413 23. Wilson AJ, Nussey DH 2010 What is individual quality? An evolutionary perspective.
414 *Trends Ecol. Evol.* **25**, 207–214.
- 415 24. Massot M, Clobert J, Montes-Poloni L, Haussy C, Cubo J, Meylan S. 2011 An
416 integrative study of ageing in a wild population of common lizards. *Funct. Ecol.* **25**,
417 848–858.
- 418 25. Orell M, Belda EJ. 2002 Delayed cost of reproduction and senescence in the willow tit
419 *Parus montanus*. *J. Anim. Ecol.* **71**, 55–64.

- 420 26. Weladji RB, Loison A, Gaillard JM, Holand Ø, Mysterud A, Yoccoz NG, Nieminen M,
421 Stenseth NC. 2008 Heterogeneity in individual quality overrides costs of reproduction in
422 female reindeer. *Oecologia* **156**, 237–247.
- 423 27. Preston BT, Saint-Jalme MS, Hingrat Y, Lacroix F, Sorci G. 2011 Sexually extravagant
424 males age more rapidly. *Ecol. Lett.* **14**, 1017–1024.
- 425 28. Williams GC. 1966 Natural selection, the costs of reproduction, and a refinement of
426 Lack's principle. *Am. Nat.* **100**, 687–690.
- 427 29. Kirkwood T, Holliday R. 1979 The evolution of ageing and longevity. *Proc. R. Soc.*
428 *Lond. B Biol. Sci.* **205**, 531–546.
- 429 30. Ricklefs RE. 2010 Life-history connections to rates of aging in terrestrial vertebrates.
430 *Proc. Natl. Acad. Sci.* **107**, 10314–10319.
- 431 31. Lemaître JF, Gaillard JM. 2013 Polyandry Has No Detectable Mortality Cost in Female
432 Mammals. *PLOS ONE* **8**, e66670.
- 433 32. Stearns SC. 1976 Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**, 3–47.
- 434 33. Stearns SC. 1992 *The Evolution of Life Histories*. Oxford University Press.
- 435 34. Baudisch A, Vaupel JW. 2012 Getting to the Root of Aging. *Science* **338**, 618–619.
- 436 35. Kirkwood TB. 2005 Understanding the odd science of aging. *Cell* **120**, 437–447.
- 437 36. Hammers M, Richardson DS, Burke T, Komdeur J. 2013 The impact of reproductive
438 investment and early-life environmental conditions on senescence: support for the
439 disposable soma hypothesis. *J. Evol. Biol.* **26**, 1999–2007.
- 440 37. Nussey DH, Kruuk LEB, Morris A, Clutton-Brock TH. 2007 Environmental conditions
441 in early life influence ageing rates in a wild population of red deer. *Curr. Biol.* **17**,
442 R1000–R1001.
- 443 38. Reed TE, Kruuk LEB, Wanless S, Frederiksen M, Cunningham EJA, Harris MP. 2008
444 Reproductive senescence in a long-lived seabird: rates of decline in late-life performance
445 are associated with varying costs of early reproduction. *Am. Nat.* **171**, E89–E101.
- 446 39. Bouwhuis S, Charmantier A, Verhulst S, Sheldon BC. 2010 Individual variation in rates
447 of senescence: natal origin effects and disposable soma in a wild bird population. *J.*
448 *Anim. Ecol.* **79**, 1251–1261.
- 449 40. Douhard M, Gaillard JM, Delorme D, Capron G, Duncan P, Klein F, Bonenfant C. 2013
450 Variation in adult body mass of roe deer: early environmental conditions influence early
451 and late body growth of females. *Ecology* **94**, 1805–1814.
- 452 41. Gavrilov LA, Gavrilova NS. 2004 Early-life programming of aging and longevity: the
453 idea of high initial damage load (the HIDL hypothesis). *Ann. N. Y. Acad. Sci.* **1019**, 496–
454 501.

- 455 42. Speakman JR. 1993 How should we calculate CO₂ production in doubly labelled water
456 studies of animals? *Funct. Ecol.* **7**, 746-750.
- 457 43. Turbill C, Ruf T, Mang T, Arnold W. 2011 Regulation of heart rate and rumen
458 temperature in red deer: effects of season and food intake. *J. Exp. Biol.* **214**, 963-970.
- 459 44. Selman C, Blount JD, Nussey DH, Speakman JR. 2012 Oxidative damage, ageing, and
460 life-history evolution: where now? *Trends Ecol. Evol.* **27**, 570-577.
- 461 45. Monaghan P, Metcalfe NB, Torres R. 2009 Oxidative stress as a mediator of life history
462 trade-offs: mechanisms, measurements and interpretation. *Ecol. Lett.* **12**, 75-92.
- 463 46. Metcalfe NB, Alonso-Alvarez C. 2010 Oxidative stress as a life-history constraint: the
464 role of reactive oxygen species in shaping phenotypes from conception to death. *Funct.*
465 *Ecol.* **24**, 984-996.
- 466 47. Speakman JR, Garratt M. 2014 Oxidative stress as a cost of reproduction: Beyond the
467 simplistic trade-off model. *BioEssays* **36**, 93-106.
- 468 48. Nussey DH, Pemberton JM, Pilkington JG, Blount JD. 2009 Life history correlates of
469 oxidative damage in a free-living mammal population. *Funct. Ecol.* **23**, 809-817.
- 470 49. Fletcher QE, Selman C, Boutin S, McAdam AG, Woods SB, Seo AY, Leeuwenburgh C,
471 Speakman JR, Humphries MM. 2013 Oxidative damage increases with reproductive
472 energy expenditure and is reduced by food-supplementation. *Evolution* **67**, 1527-1536.
- 473 50. Bergeron P, Careau V, Humphries MM, Reale D, Speakman JR, Garant D. 2011 The
474 energetic and oxidative costs of reproduction in a free-ranging rodent. *Funct. Ecol.* **25**,
475 1063-1071.
- 476 51. Degletagne C, Keime C, Rey B, De Dinechin M, Forcheron F, Chuchana P, Jouventin P,
477 Gautier C, Duchamp C. 2010 Transcriptome analysis in non-model species: a new
478 method for the analysis of heterologous hybridization on microarrays. *BMC Genomics*
479 **11**, 344.
- 480 52. Gems D, Partridge L. 2013 Genetics of longevity in model organisms: debates and
481 paradigm shifts. *Annu. Rev. Physiol.* **75**, 621-644.
- 482 53. Sparkman AM, Arnold SJ, Bronikowski AM. 2007 An empirical test of evolutionary
483 theories for reproductive senescence and reproductive effort in the garter snake
484 *Thamnophis elegans*. *Proc. R. Soc. B Biol. Sci.* **274**, 943-950.
- 485 54. Metcalfe NB, Monaghan P. 2003 Growth versus lifespan: perspectives from
486 evolutionary ecology. *Exp. Gerontol.* **38**, 935-940.
- 487 55. Dmitriew CM. 2011 The evolution of growth trajectories: what limits growth rate? *Biol.*
488 *Rev.* **86**, 97-116.
- 489 56. Lee WS, Monaghan P, Metcalfe NB. 2013 Experimental demonstration of the growth
490 rate-lifespan trade-off. *Proc. R. Soc. B Biol. Sci.* **280**, 20122370.

- 491 57. Yuan R, Wern-Shirng T, Petkova SB, de Evsikova CM, Xing S, Marion MA, Bogue
492 MA, Mills KD, Peters LL, Bult CJ et al. Aging in inbred strains of mice: study design
493 and interim report on median lifespans and circulating IGF1 levels. *Aging Cell* **8**, 277–
494 287.
- 495 58. Andersson M. 1994 *Sexual selection*. Princeton University Press.
- 496 59. Liker A, Székely T. 2005 Mortality costs of sexual selection and parental care in natural
497 populations of birds. *Evolution* **59**, 890–897.
- 498 60. Lemaître JF, Gaillard JM. 2013 Male survival patterns do not depend on male allocation
499 to sexual competition in large herbivores. *Behav. Ecol.* **24**, 421–428.
- 500 61. Cornwallis CK, Uller, T. 2010 Towards an evolutionary ecology of sexual traits. *Trends*
501 *Ecol. Evol.* **25**, 145–152.
- 502 62. Maklakov AA, Lummaa, V. 2013 Evolution of sex differences in lifespan and aging:
503 causes and constraints. *BioEssays* **35**, 717–724.
- 504 63. Carey J, Judge D. 2002. Longevity records: life spans of mammals, birds, amphibians,
505 reptiles, and fish. Odense University Press. Odense (Denmark).
- 506 64. Austad SN. 2011 Sex differences in longevity and aging. In *Handbook of the biology of*
507 *aging, 7th edn.* (Ed: Masoro EJ, Austad SN). Academic Press. San Diego.
- 508 65. Rubolini D, Colombo G, Ambrosini R, Caprioli M, Clerici M, Colombo R, Dalle-Donne
509 I, Milzani A, Romano A, Romano M, Saino N. 2012 Sex-related effects of reproduction
510 on biomarkers of oxidative damage in free-living barn swallows (*Hirundo rustica*). *PLoS*
511 *One* **7**, e48955.
- 512 66. Krüger, O. 2005 Age at first breeding and fitness in goshawk *Accipiter gentilis*. *J. Anim.*
513 *Ecol.* **74**, 266–273.
- 514 67. Pyle P, Nur N, Sydeman WJ, Emslie SD. 1997 Cost of reproduction and the evolution of
515 deferred breeding in the western gull. *Behav. Ecol.* **8**, 140–147.
- 516 68. Reid JM, Bignal EM, Bignal S, McCracken DI, Monaghan P. 2003 Age-specific
517 reproductive performance in red-billed choughs *Pyrrhonorax pyrrhonorax*: patterns and
518 processes in a natural population. *J. Anim. Ecol.* **72**, 765–776.
- 519 69. Millon A, Petty SJ, Lambin X. 2010 Pulsed resources affect the timing of first breeding
520 and lifetime reproductive success of tawny owls. *J. Anim. Ecol.* **79**, 426–435.
- 521 70. Millon A, Petty SJ, Little B, Lambin X. 2011 Natal conditions alter age-specific
522 reproduction but not survival or senescence in a long-lived bird of prey. *J. Anim. Ecol.*
523 **80**, 968–975.
- 524 71. Kim SY, Velando A, Torres R, Drummond H. 2011 Effects of recruiting age on
525 senescence, lifespan and lifetime reproductive success in a long-lived seabird. *Oecologia*
526 **166**, 615–626.

- 527 72. Charmantier A, Perrins C, McCleery RH, Sheldon BC. 2006 Quantitative genetics of age
528 at reproduction in wild swans: support for antagonistic pleiotropy models of senescence.
529 *Proc. Natl. Acad. Sci.* **103**, 6587–6592.
- 530 73. Gustafsson L, Pärt T. 1990 Acceleration of senescence in the collared flycatcher
531 *Ficedula albicollis* by reproductive costs. *Nature* **347**, 279–281.
- 532 74. Aubry LM, Koons DN, Monnat JY, Cam E. 2009 Consequences of recruitment
533 decisions and heterogeneity on age-specific breeding success in a long-lived seabird.
534 *Ecology* **90**, 2491–2502.
- 535 75. Green WC, Rothstein A. 1991 Trade-offs between growth and reproduction in female
536 bison. *Oecologia* **86**, 521–527.
- 537 76. Hadley GL, Rotella JJ, Garrott RA. 2007 Evaluation of reproductive costs for Weddell
538 seals in Erebus Bay, Antarctica. *J. Anim. Ecol.* **76**, 448–458.
- 539 77. Blomquist GE. 2009 Trade-off between age of first reproduction and survival in a female
540 primate. *Biol. Lett.* **5**, 339–342.
- 541 78. Dugdale HL, Nouvellet P, Pope LC, Burke T, Macdonald DW. 2010 Fitness measures in
542 selection analyses: sensitivity to the overall number of offspring produced in a lifetime.
543 *J. Evol. Biol.* **23**, 282–292.
- 544 79. Berube CH, Festa-Bianchet M, Jorgenson JT. 1999 Individual differences, longevity,
545 and reproductive senescence in bighorn ewes. *Ecology* **80**, 2555–2565.
- 546 80. Ransome RD. 1995 Earlier breeding shortens life in female greater horseshoe bats.
547 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **350**, 153–161.
- 548 81. Neuhaus P, Broussard DR, Murie JO, Dobson FS. 2004 Age of primiparity and
549 implications of early reproduction on life history in female Columbian ground squirrels.
550 *J. Anim. Ecol.* **73**, 36–43.
- 551 82. Descamps S, Boutin S, Berteaux D, Gaillard JM. 2006 Best squirrels trade a long life for
552 an early reproduction. *Proc. R. Soc. B Biol. Sci.* **273**, 2369–2374.
- 553 83. Van de Pol M, Verhulst S. 2006 Age-dependent traits: a new statistical model to separate
554 within-and between-individual effects. *Am. Nat.* **167**, 766–773.
- 555 84. Fisher RA. 1930 *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- 556 85. Nussey D, Coulson T, Festa-Bianchet M, Gaillard JM. 2008 Measuring senescence in
557 wild animal populations: towards a longitudinal approach. *Funct. Ecol.* **22**, 393–406.

558

559 Table 1: Summary of the 27 studies testing the disposable soma theory in vertebrate populations. The species, the measurement of early/late traits, the sex, the support ('-':
 560 negative relationship between early and late trait, '+' : positive relationship between early reproduction and late trait, '0': no relationship between early reproduction and late
 561 trait), the overall conclusion about the support (Yes/No), and the references are provided.

Species	Early trait	Late trait	Sex	Direction of the covariation	DST supported	References
Birds						
Northern Goshawk (<i>Accipiter gentilis</i>)	Age at first reproduction	Lifetime reproductive success	F	-	Yes	[66]
Western gull (<i>Larus occidentalis</i>)	Age at first reproduction	Survival	F	-	Yes	[67]
Willow tit (<i>Parus montanus</i>)	Breeding status	Late survival	M	0	Yes	[25]
Chough (<i>Pyrrhocorax pyrrhocorax</i>)	Clutch size	Female breeding lifespan	F	+	Yes	[68]
	Fledging success	Female breeding lifespan	F	-		
Tawny owl (<i>Strix aluco</i>)	Age at first reproduction	Lifetime reproductive success	M	0	Yes	[69]
	Age at first reproduction	Lifetime reproductive success	F	-		
	Age at first reproduction	Recruitment	M	0	No	[70]
	Age at first reproduction	Recruitment	F	0		
Blue-footed Booby (<i>Sula nebouxii</i>)	Recruit age	Age at last reproduction	M	-		
	Recruit age	Age at last reproduction	F	0	Yes	[71]
	Recruit age	Lifetime reproductive success	F	+		
	Recruit age	Breeding success	M	-		
	Recruit age	Brood size	M	-		
	Recruit age	Laying date	M/F	0		
Common Murre (<i>Uria aalge</i>)	Early life reproductive output	Senescence in breeding success	F	-	Yes	[38]
Mute swan (<i>Cygnus olor</i>)	Age at first reproduction	Lifetime reproductive success	M/F	+	Yes	[72]
	Age at first reproduction	Age at last reproduction	M/F	-		
Collared flycatcher (<i>Ficedulla albicollis</i>)	Age at first reproduction	Lifetime reproductive success	F	-	Yes	[73]
	Age at first reproduction	Clutch size	F	-		

Great tit (<i>Parus major</i>)	Early life fledging	Fledging number	F	-	Yes	[39]
	Early life fledging	Recruit number	F	0		
Black-legged kittiwake (<i>Rissa tridactyle</i>)	Age at first reproduction	Breeding success	M/F	-	Yes	[74]
	Age at first breeding	Onset of actuarial senescence	M/F	-	Yes	[36]
Seychelles warblers (<i>Acrocephalus sechellensis</i>)	Age at first breeding	Rate of actuarial senescence	M/F	0		
	Brood size	Annual survival rate	M/F	-	Yes	[20]
Jackdaws (<i>Corvus monedula</i>)	Brood size	Rate of actuarial senescence	M/F	-		
	Mammals					
Bison (<i>Bison bison</i>)	Age at first reproduction	Offspring number	F	+	No	[75]
	Age at first reproduction	Actuarial senescence	F	+	Yes	[37]
	Early life fecundity	Reproductive senescence	F	-		
Red deer (<i>Cervus elaphus</i>)	Age at first reproduction	Calving date	F	+		
	Age at first reproduction	Offspring birth weight	F	+	Yes	[22]
	Early life fecundity	Calving date	F	-		
	Early life fecundity	Offspring birth weight	F	-		
Weddell seal (<i>Leptonychotes weddellii</i>)	Age at first reproduction	Survival	F	0	No	[76]
	Age at first reproduction	Breeding probability	F	0		
Rhesus macaque ¹ (<i>Macaca mulatta</i>)	Age at first reproduction	Survival	F	0 / -	Yes	[77]
Badger (<i>Meles meles</i>)	Age at first reproduction	Lifespan	M/F	-	Yes	[78]
	Age at first reproduction	Age at last reproduction	M/F	-		
Bighorn sheep ² (<i>Ovis canadensis</i>)	Number of lambs produced	Longevity	F	+ / 0		
	Number of lambs weaned	Longevity	F	+ / 0		
	Number of lambs surviving to 1 year of age	Longevity	F	0	No	[79]
	Number of lambs produced	Number of lambs weaned	F	+		
	Number of lambs weaned	Number of lambs weaned	F	+		
Reindeer (<i>Rangifer tarandus</i>)	Age at first reproduction	Survival	F	+	No	[26]

Greater Horseshoe Bat (<i>Rhinolophus ferrumequinum</i>)	Breeding status	Mean age at death	F	-	Yes	[80]
	Breeding status	Lifetime reproductive success	F	0		
Columbian ground squirrel (<i>Spermophilus columbianus</i>)	Age at first successful rearing	Lifetime reproductive success	F	0	No	[81]
	Age at first reproduction	Longevity	F	-		
Red squirrel (<i>Tamasciurus hudsonicus</i>)	Age first reproduction	Number of juveniles weaned per breeding attempt	F	+	Yes	[82]
	Reproductive effort	Actuarial senescence	F	-		
Common lizard (<i>Lacerta vivipara</i>)	Reproductive effort	Senescence in corpulence	F	+	Yes	[24]
	Reproductive effort	Senescence in litter size	F	0		
	Reproductive effort	Senescence in offspring body size	F	0		
	Reproductive effort	Senescence in litter success	F	+		
Garter snake (<i>Thamnophis elegans</i>)	Body growth tactic (slow vs. fast)	Reproductive effort	F	+	No	[53]

562

563 ¹ The relationship between age at first reproduction is negative and statistically significant only when survival is measured at 16 years of age. The relationship is non-
564 statistically significant when survival is measured at 11, 21 or 26 years of age.

565

566 ² In this study, two populations are considered (Ram Mountain and Sheep River) but the relationships between both the number of lambs produced and the longevity and the
567 number of lambs weaned and the longevity are negative and statistically significant only at Ram Mountain.

568 Figure 1: Guidelines to test the disposable soma theory in free-ranging populations

569

570

How testing the disposable soma theory in wild populations?

571

572

573

574

575

576

577

578

579

580

581

		<u>Type of data</u>	
		With repeated measures per individual (e.g. fecundity, offspring weight, annual reproductive success)	With only one measure per individual (e.g. lifetime reproductive success, age at last reproduction, longevity)
<u>Type of corrections</u>	Heterogeneity in individual quality	Use of mixed model (with individual identity as a random effect)	Add a trait linked to individual quality as covariates (e.g. body mass, social rank)
	Selective appearance and disappearance	Add age at first and last reproduction as covariates	

Appendix 3

IDEA AND PERSPECTIVE

How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer

Jean-Michel Gaillard,^{1*} A. J. Mark Hewison,² François Klein,³ Floriane Plard,¹ Mathieu Douhard,¹ Raziel Davison⁴ and Christophe Bonenfant¹

Abstract

How populations respond to climate change depends on the interplay between life history, resource availability, and the intensity of the change. Roe deer are income breeders, with high levels of allocation to reproduction, and are hence strongly constrained by the availability of high quality resources during spring. We investigated how recent climate change has influenced demographic processes in two populations of this widespread species. Spring began increasingly earlier over the study, allowing us to identify 2 periods with contrasting onset of spring. Both populations grew more slowly when spring was early. As expected for a long-lived and iteroparous species, adult survival had the greatest potential impact on population growth. Using perturbation analyses, we measured the relative contribution of the demographic parameters to observed variation in population growth, both within and between periods and populations. Within periods, the identity of the critical parameter depended on the variance in growth rate, but variation in recruitment was the main driver of observed demographic change between periods of contrasting spring earliness. Our results indicate that roe deer in forest habitats cannot currently cope with increasingly early springs. We hypothesise that they should shift their distribution to richer, more heterogeneous landscapes to offset energetic requirements during the critical rearing stage.

Keywords

Age-structured populations, demographic change, income breeding, perturbation analysis, population growth, Recruitment, Stochastic environment, Survival.

Ecology Letters (2013) 16: 48–57

INTRODUCTION

Variation in population abundance is shaped by the interplay between density-dependence, environmental fluctuations, and demographic stochasticity (Lande *et al.* 2003). The relative importance of these processes has been hotly debated (e.g. Nicholson 1933 vs. Andrewartha & Birch 1954) and, for a while, accounting for density-dependence has been privileged over considering stochastic environments. This is well illustrated by the history of demographic analyses. While Leslie included density-dependence in his deterministic model as early as 1948 (Leslie 1948), we had to wait until the late sixties for the first integration of stochastic variation in population growth rate (Lewontin & Cohen 1969) and the early eighties for a full consideration of the stochastic population growth rate (Tuljapurkar & Orzack 1980).

In recent years, the study of the ecological effects of climate change has become a popular research topic (Both *et al.* 2004; Parmesan 2006; Lebreton 2011 for reviews). Evidence is now accumulating that climate change at a global scale affects the geographical distribution of organisms, while topography interacts with climate to influence local weather. This often involves warmer temperatures and earlier springs (i.e. a change in plant phenology such that the

vegetation flush occurs earlier) in temperate areas (Schwartz *et al.* 2006), which markedly influence the population biology of a large range of organisms (Fig. 1). However, these studies have either focussed on climate niche models (Guisan & Zimmermann 2000; Guisan & Thuiller 2005) to quantify the link between local weather and distribution area for predicting the future spatial distribution of a given taxon (e.g. Huntley *et al.* 2006; for a case study on Dartford warbler *Sylvia undata*) or attempted to assess the magnitude of climate-induced variation in demographic parameters (Grosbois *et al.* 2008) or population growth (Hansen *et al.* 2011).

The interactions between demography and climate have not been investigated (Brook *et al.* 2009), although some studies have recently identified demographic responses to climate change (Ozgul *et al.* 2010; Lane *et al.* 2012). In particular, no study has yet assessed the effects of climate change on the demographic processes involved in shaping population growth rate, despite the fact that Andrewartha & Birch (1954) emphasised more than 50 years ago that population growth rate is a dynamic variable influenced by environmental conditions. Moreover, most studies have been performed on single populations, often declining in size (e.g. Barbraud & Weimerskirch 2001 for a case study on Emperor penguin *Aptenodytes forsteri*). As a result, we have very little information on how climate change is

¹UMR 5558, Biométrie et Biologie Evolutive, Université Claude Bernard Lyon 1, 43 boulevard du 11 novembre 1918, Villeurbanne Cedex, France

²INRA, UR035 Comportement et Ecologie de la Faune Sauvage, Castanet Tolosan, BP 52627, France

³Office National de la Chasse et de la Faune Sauvage, CNERA Cervidés-Sangliers, 1 Place Exelmans, Bar-le-Duc, France

⁴Max Planck Institute for Demographic Research, Rostock, Germany

*Correspondence: E-mail: jean-michel.gaillard@univ-lyon1.fr

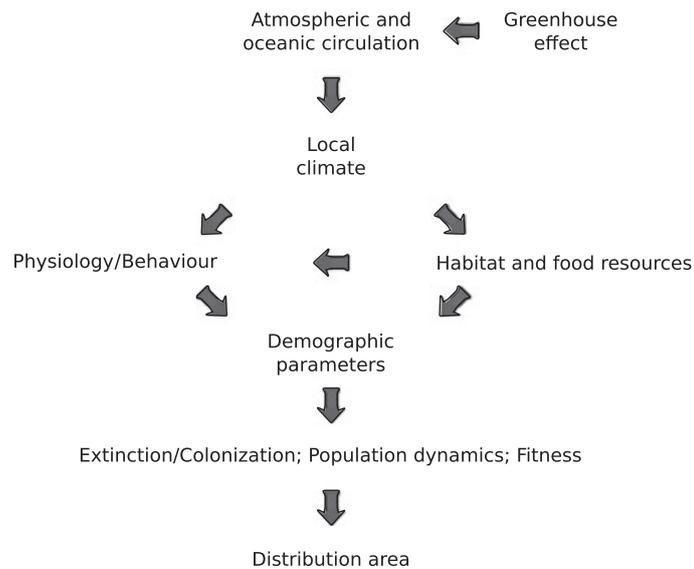


Figure 1 A general framework for linking climate change and ecology. Free-ranging organisms cope with local climatic conditions (shaped by general atmospheric and oceanic conditions) that are influenced by the greenhouse effect. The local climate influences the ecology of organisms through two pathways: direct influences provoking physiological and behavioural responses, and indirect influences through the modification of habitat conditions and the amount and quality of food resources. Both pathways generate effects on demographic parameters by changing the flow of individuals within (through birth and death) and among (through immigration and emigration) populations, thereby influencing individual fitness and population growth. Spatial heterogeneities in the organisms' responses influence the extinction/colonisation processes which determine the species' range.

influencing demographic processes in populations of abundant and widespread species. Previous studies of climate-induced variation in population dynamics of large herbivores have mostly been performed in mountainous or northern areas and have mainly focussed on the effects of winter conditions (Post & Stenseth 1999), using global measures of climate change such as North Atlantic Oscillation (NAO) as a metric (Hallett *et al.* 2004). Moreover, most of these studies have looked for relationships between climatic conditions and population growth, but did not evaluate the effects of climate change (e.g. Garrott *et al.* 2003 on elk *Cervus canadensis*, Grotan *et al.* 2008 on ibex *Capra ibex*). The few studies that have investigated the effects of the timing of spring onset on performance of large herbivores have failed to reveal consistent patterns, either across species or among populations within a given species. Thus, earlier spring was associated with improved individual performance in chamois *Rupicapra rupicapra* (Garel *et al.* 2011) and red deer *Cervus elaphus* (Pettorelli *et al.* 2005), whereas negative effects of earlier springs on recruitment have been reported in bighorn sheep *Ovis canadensis*, mountain goat *Oreamnos americanus* and ibex (Pettorelli *et al.* 2007). Likewise, reindeer were reported to suffer from the increasing mismatch between the availability of high quality food and the timing of births in Greenland (Post & Forchhammer 2008), whereas they appeared to benefit from earlier springs in Finland (Helle & Kojola 2008). The exact demographic mechanisms through which such contrasting effects of climate change arise remain unknown.

We aimed to fill this gap by analysing the demographic responses of roe deer, *Capreolus capreolus*, the most abundant and widespread

medium-sized mammalian species in Western Europe (Andersen *et al.* 1998), to recent climate change using the intensive long-term (> 30 years) monitoring of two contrasted populations. During the last half century, populations of large herbivores have increased substantially over much of the northern hemisphere, both in number and range, due to regulation of hunting and the increased frequency of mild winters (Apollonio *et al.* 2010). The roe deer is the most successful example of this in a European context (Andersen *et al.* 1998). Indeed, due to its marked ecological and behavioural plasticity, roe deer could be expected to cope successfully with climate change. To investigate whether this is so, we looked for three possible types of effect of climate change on demographic processes in roe deer using a comparison of contrasting demographic scenarios in terms of population and climatic conditions.

First, we compared how climate change can potentially modify the role of a given demographic parameter (i.e. age-specific survival and fecundity) on population growth across scenarios. This kind of structural change in demography is observed in response to the occurrence of strong perturbations like hunting (Servanty *et al.* 2011), predation (Nilsen *et al.* 2009) or disease (Jones *et al.* 2008). Second, we identified the critical parameter for determining population growth within each demographic scenario. We expected the contribution of a demographic parameter to increase with both its potential demographic impact and its temporal variation (Coulson *et al.* 2005). Finally, we identified the parameter responsible for driving the observed shift in population growth rate in each demographic scenario.

In temperate areas, climate change involves a co-variation of factors including, for example, earlier spring, higher spring and summer temperatures, a higher peak of plant productivity, a longer vegetative growth season, and an increased frequency of extreme climatic events (IPCC 2007). We focussed on the impact of the timing of the onset of spring on roe deer life history as the effects of climate change are particularly pronounced in this season (Schwartz *et al.* 2006) and because roe deer females are under substantial energetic stress at this time of year due to the high costs of late gestation and early lactation in large herbivores (Mauget *et al.* 1997). Moreover, the roe deer can be considered as an income breeder (*sensu* Jonsson 1997), relying on current resource intake, rather than fat reserves, to offset the costs of reproduction (Andersen *et al.* 2000). Hence, we assumed that the most evident response of roe deer populations to climate change should be revealed by the link between demography and spring conditions. However, we also discussed possible demographic variation induced by summer conditions, as the expected increase in the frequency of summer drought is also likely to influence roe deer demography at the southernmost limit of its range.

MATERIALS AND METHODS

Roe deer as a biological model

The roe deer is a medium-sized forest-dwelling mammal (about 25 kg, Andersen *et al.* 1998). This large herbivore occupied lowland forest as its habitat of origin, but since the early eighties has considerably expanded its distribution range northwards and southwards (Andersen *et al.* 1998), colonising new habitat types including both agricultural landscapes (Kaluzinski 1982) and mountainous areas (Acevedo *et al.* 2005). Roe deer have low sexual size dimorphism,

with males about 10% larger than females (Hewison *et al.* 2011), and a low level of polygyny (typically less than 3 females mated by a given male in a given year, Vanpé *et al.* 2009). Roe deer females are strongly sedentary, spending their whole life within less than 50 ha in forest habitat (Hewison *et al.* 1998). They are long-lived (up to 18 years of age, Loison *et al.* 1999), iteroparous (one reproductive attempt per year, from 2 years of age onwards, Gaillard *et al.* 1998) and allocate high levels of energy to each breeding attempt, most often producing twins that are born heavy (about 1.6 kg each) and grow quickly (about $150 \text{ g}^{-1} \text{ day}$) during the weaning period (Gaillard *et al.* 1993a), compared with other large herbivores (Robbins & Robbins 1979). Births are highly synchronised (> 80% of births within less than 25 days) and the mean birth date (15th of May) is remarkably constant over years (Gaillard *et al.* 1993b).

Study sites

We studied two fenced roe deer populations managed by the Office National de la Chasse et de la Faune Sauvage. These populations inhabit deciduous forests managed by the Office National des Forêts. In both forests, oak (*Quercus* sp.) and beech (*Fagus sylvatica*) are the main tree species. At Trois Fontaines, the understorey is made up of hornbeam (*Carpinus betulus*) and brambles (*Rubus* sp.). At Chizé, three different habitats can be identified in relation to the type of timber stand and coppice structure (from richest to poorest: oak with hornbeam, oak with Montpellier maple (*Acer monspessulanum*), and beech with little coppice, Pettorelli *et al.* 2003). Roe deer have been caught every year since 1975 (at Trois Fontaines) and 1977 (at Chizé) using winter drive-netting (over 10 days per year, mostly in January–February) resulting in the capture of roughly half the roe deer present in the forest each year (Gaillard *et al.* 2003). At capture, all animals are weighed, inspected for marks or newly marked (with both leather numbered collars and ear-tags) and, at Chizé only, the reproductive status of females is assessed using ultrasonography (since 1988). Marked known-aged roe deer are then released back to the forest, while a variable number of animals of unknown age (between 0 and 150) are removed to manipulate population size (Fig. 2). As a result, observed variation in population abundance over time was mainly driven by management strategy and was therefore decoupled from the variation in demographic parameters estimated from the monitoring of known-aged and individually recognisable animals (more than 70% of the population during most years).

The two sites are quite contrasted in terms of environmental conditions. Trois Fontaines is a 1360 ha forest located in Eastern France (48°43' N, 2°61' W), with a continental climate typified by rather cold winters (mean daily temperature in January of 3.1 °C) and warm but often wet summers (mean daily temperature in July of 19.6 °C with an average total rainfall of 72.4 mm). Trois Fontaines lies on rich and fertile soils, leading to high forest productivity (long-term average wood production of $5.9 \text{ m}^3 \text{ ha}^{-1}$ per year, Pettorelli *et al.* 2006). In contrast, the Réserve Biologique Intégrale of Chizé is a 2614 ha forest located in Western France (46°05' N, 0°25' W), with an oceanic climate under some Mediterranean influence, characterised by mild winters (mean daily temperature in January of 5.6 °C) and warm but often dry summers (mean daily temperature in July of 20.5 °C with an average total rainfall of 53.4 mm). Forest productivity at Chizé is quite low (long-term average wood production of $3.8 \text{ m}^3 \text{ ha}^{-1}$ per year, Pettorelli *et al.* 2006). As a direct result of these between-population differences in

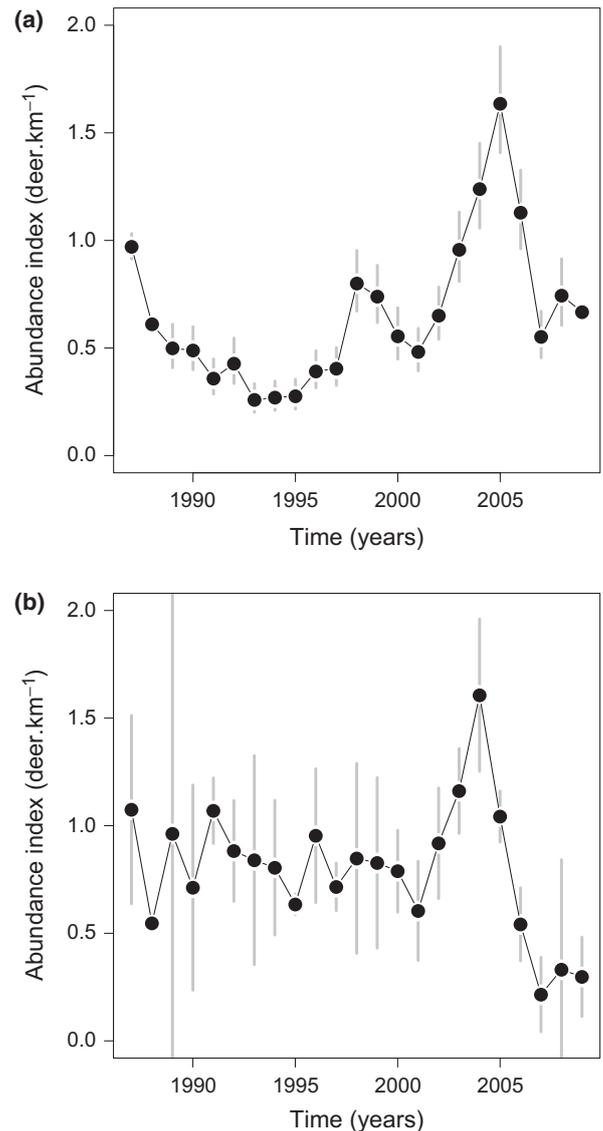


Figure 2 Yearly abundance index of roe deer population size at (a) Chizé and (b) Trois Fontaines. The index corresponds to the average number of roe deer observed per km of standardised transect walked in March–April (see Vincent *et al.* 1991 for further details)

climatic and edaphic conditions, the demographic performance of the roe deer population was substantially higher at Trois Fontaines than at Chizé, especially during the late seventies and early eighties (Nilsen *et al.* 2009), but less so during the period studied here (1988–2009). There are no large predators and no hunting of roe deer on either of the sites, and no epizootic events have been recorded, despite regular epidemiological surveys on the caught roe deer.

We assessed the magnitude of climate change in both study sites using the number of degree-days higher than 7 °C (°D7) from February to April, when early plant growth occurs in both sites. In temperate areas, this metric is indeed directly related to the phenology of vegetation (plant growth), rather than to plant abundance (Wilson & Barnett 1983). That is, the vegetation flush occurs increasingly earlier as the number of degree-days > 7 °C increases. For the period 1976–2011, annual mean daily temperature and total

rainfall were obtained from Météo-France weather stations located within 5 km of the study areas (Beauvoir-sur-Niort for Chizé and Saint-Dizier for Trois Fontaines). To detect evidence of climate change over the study period, we then regressed the number of degree-days $> 7^\circ\text{C}$ against time (in years).

Assessing demographic processes

The intensive Capture-Mark-Recapture monitoring of roe deer in both study sites allowed us to obtain a complete time series of reliable annual estimates of all demographic parameters from 1988 to 2009 (Gaillard *et al.* 2003; Nilsen *et al.* 2009). To investigate a possible regime shift of demography in response to climate change, we divided the population-specific time series into two periods of equal duration (i.e. 11 year periods). We expected the spring vegetation flush to occur later on average during the first period (1988–1998) than during the second period (1999–2009). We thus built four demographic scenarios using population- and period-specific parameters. To account for possible confounding effects of density-dependence, we tested for density-dependent responses of all demographic parameters in both populations (see Appendix S1 for further details). As density-dependent responses occurred in most parameters during the study period at Chizé, we replicated the demographic analysis for this site by standardising the yearly estimates to the median density (Appendix S1). We modelled each scenario using a pre-census Leslie matrix model (Caswell 2001). The life cycle graph (Fig. 3) included four age classes and four demographic parameters. Female recruitment in a given age class was defined as the product between the proportion of females that give birth, the number of female offspring produced by those females, and offspring survival between birth and 1 year of age. We obtained yearly estimates of these parameters by updating previous analyses (e.g. Gaillard *et al.* 2003). As roe deer females reproduce for the first time at 2 years of age (but see Van Laere *et al.* 1997 for an exceptional case of successful reproduction at 1-year old), recruitment at 1 year old was set to 0. Although female fertility decreases from 12 years of age onwards in roe deer (Gaillard *et al.* 1998), we assumed a constant recruitment rate with age because we were unable to generate reliable year-specific estimates of recruitment for old females due to the scarcity of data. Following previous analyses (Gaillard *et al.* 2003), we considered three age classes for survival: a prime-age stage, from 1 to 7 years of age, an old-age stage, from 7 to 12 years of age, and a senescent stage, from 12 years onwards.

For each population- and period-specific matrix, we estimated the deterministic population growth rate (λ) and the elasticity of each demographic parameter (i.e. the proportional change in λ obtained

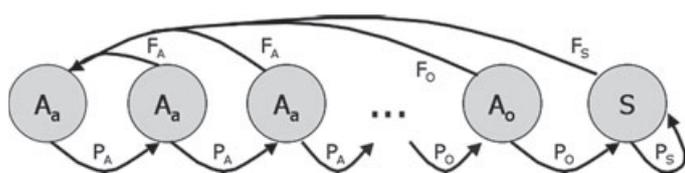


Figure 3 Life cycle graph of roe deer. A_a : females in the prime-age stage (from 1 to 7 years of age), A_o : females in the old-age stage (from 7 to 12 years of age), S : females in the senescent stage (from 12 years of age onwards), P : annual survival probability, F : recruitment (measured as the number of female offspring at 1 year of age produced by a female of 2-years old or older).

when changing a given parameter by 1%) using standard matrix calculations (Caswell 2001). To assess the potential impact of a given demographic parameter on λ , we performed a prospective analysis (sensu Caswell 2000) by comparing the ranking and the relative values of elasticities among demographic scenarios. We then measured the contribution of a given demographic parameter to the observed variance in λ by performing a retrospective analysis (sensu Caswell 2000). Using the approximation of variance in λ proposed by Horvitz *et al.* (1996), we measured the absolute contribution of a given parameter as the product of its squared elasticity and its squared coefficient of variation (CV). The sum of the contributions of all demographic parameters provided a measure of variance in λ . The relative contribution of a given demographic parameter to the observed variance in λ was then obtained as the ratio between the absolute contribution of that parameter and the variance in λ . As co-variations can be important, we also measured the contribution of the two-way interactions between demographic parameters to the observed variance in λ . However, we did not account for possible serial autocorrelations in demographic parameters. Lastly, we performed a Life Table Response Experiment (LTRE, Caswell 2001) to measure the contribution of a given demographic parameter to the observed difference in λ between scenarios. We excluded senescent

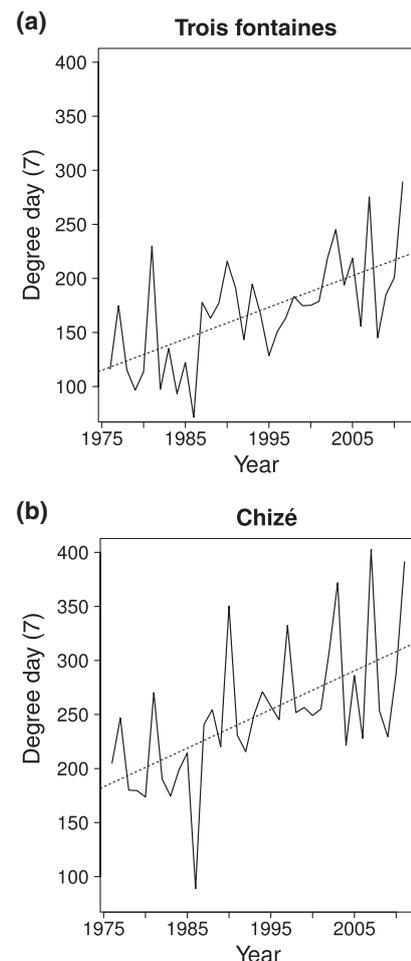


Figure 4 Yearly changes in the number of degree-days $> 7^\circ\text{C}$ (February to April) between 1976 and 2011 at (a) Trois Fontaines and (b) Chizé. The dotted line corresponds to the best-fit linear increase over time.

Table 1 Potential impact of a proportional change in a given demographic parameter on λ (measured by the elasticity) for the four contrasting scenarios describing roe deer demography for two periods (normal (1988–1998) and early (1999–2009) springs) and two populations (Chizé and Trois Fontaines)

Demographic scenario	Recruitment	Prime-age stage survival	Old-age stage survival	Senescent stage survival
Chizé (Normal springs)	0.230	0.703	0.065	0.002
Chizé (Early springs)	0.215	0.704	0.076	0.005
Trois Fontaines (Normal springs)	0.246	0.705	0.048	0.001
Trois Fontaines (Early springs)	0.217	0.715	0.065	0.003

stage survival from these analyses because of its negligible contribution (i.e. an order of magnitude lower than the smallest contribution of other parameters) to variation in population growth rate.

RESULTS

A strong signal of climate change

In both study sites, the number of degree-days $> 7^{\circ}\text{C}$ increased markedly over time (yearly increase of $2.91^{\circ}\text{D7} \pm 0.65$, $P < 0.001$ and $3.58^{\circ}\text{D7} \pm 0.84$, $P < 0.001$ at Trois Fontaines and Chizé, respectively, Fig. 4), demonstrating that spring occurred increasingly earlier over years at both locations. From these models, we obtained a clear difference in the timing of the onset of spring between the two 11-year periods (model estimates of 167.49 and 247.46°D7 for 1988–1998, hereafter denoted ‘normal spring period’, vs. 199.55 and 286.79°D7 for 1999–2009, hereafter denoted ‘early spring period’, for Trois Fontaines and Chizé respectively).

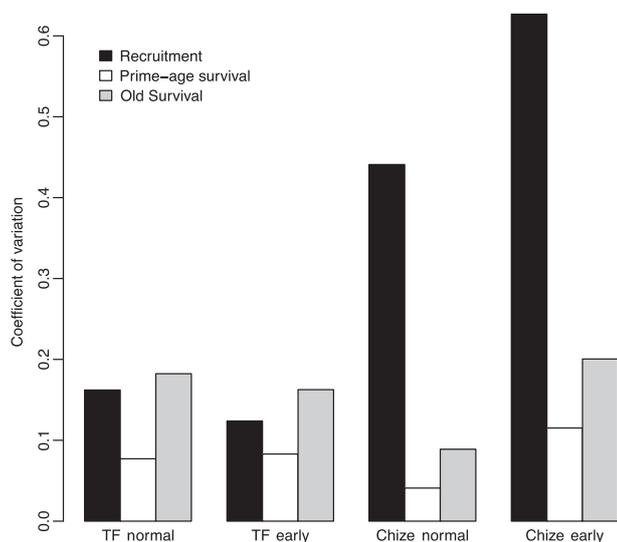


Figure 5 Coefficients of variation for temporal variation in each demographic parameter for the four demographic scenarios. TF Normal: Trois Fontaines population monitored during years with normal springs (1988–1998); TF Early: Trois Fontaines population monitored during years with early springs (1999–2009); Chizé Normal: Chizé population monitored during years with normal springs (1988–1998); Chizé Early: Chizé population monitored during years with early springs (1999–2009).

Prospective demographic analysis

The potential impact of a proportional change in a given demographic parameter on λ was remarkably constant across demographic scenarios (Table 1). A given proportional change in prime-age stage survival consistently had the largest impact on growth rate, provoking a modification in λ that was about three times greater than an equivalent change in recruitment and about 10 times greater than an equivalent change in old-age stage survival. In contrast, the impact of an equivalent change in senescent stage survival on λ was negligible (Table 1). Clearly, therefore, the relative potential impact of the different demographic parameters on λ was insensitive to both the difference in the earliness of spring between periods and to the differences in environmental conditions between populations. Accounting for density-dependence (Chizé only) did not influence this general pattern (Table S2).

Retrospective demographic analysis

In all four demographic scenarios, prime-age stage survival was less variable among years than recruitment rate and old-age stage survival (with a CV of around 0.10 or less, Fig. 5). However, marked between-population differences occurred in both the magnitude of temporal variation in demographic parameters and the sensitivity of this variation to changes in the earliness of spring. At Trois Fontaines, the overall variation in all demographic parameters was quite low (all CVs less than 0.20, Fig. 5) and was not influenced by the between-period difference in the earliness of the onset of spring. In contrast, there was marked temporal variation in recruitment at Chizé, with a CV of more than 0.40 (Fig. 5) [or more than 0.30 (Fig. S1) when accounting for density-dependence] and the observed between-year variation in all parameters was higher during

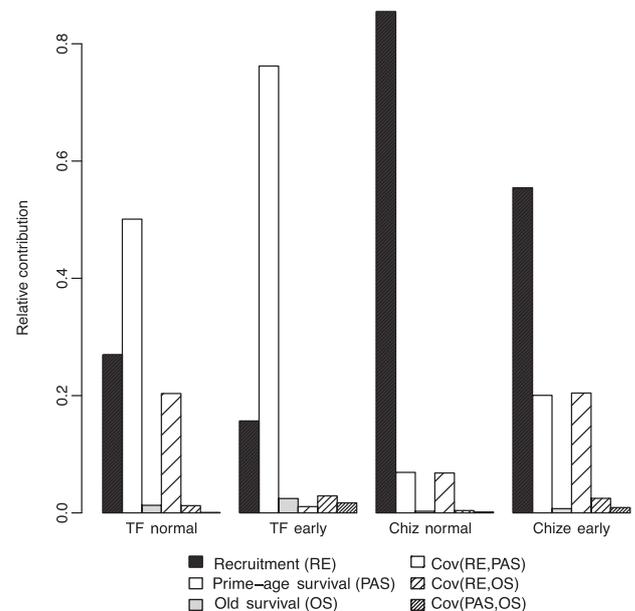


Figure 6 Relative contribution of the demographic parameters to observed variation in population growth rate in the four demographic scenarios. TF Normal: Trois Fontaines during normal springs (1988–1998); TF Early: Trois Fontaines during early springs (1999–2009); Chizé Normal: Chizé during normal springs (1988–1998); Chizé Early: Chizé during early springs (1999–2009).

the early spring period compared with the normal spring period [0.40 vs. 0.6 (Fig. 5), or 0.30 vs. 0.36 (Fig. S1) when accounting for density-dependence]. These clear differences in the variation of demographic parameters between populations, periods and parameters (Fig. 5) are in marked contrast with the virtually constant patterns of parameter elasticity across demographic scenarios (Table 1). As a consequence, it remains clear that among-scenario differences in demography were driven by differences in the relative amount of temporal variation among demographic parameters. As a result of the above, the variance in λ was one order of magnitude larger at Chizé than at Trois Fontaines, and was largest during the period of early spring in both populations (variance of 0.0328 vs. 0.0119 and of 0.0044 vs. 0.0033 in the period of early spring vs. normal spring at Chizé and Trois Fontaines respectively). This pattern was consistent even when correcting for density-dependence at Chizé (variance of 0.0130 vs. 0.0074).

The marked variation in recruitment rate over years observed at Chizé meant that the observed variation in λ was mostly accounted for by changes in this demographic parameter (Fig. 6). However, although temporal variation in recruitment rate was higher during the early spring period compared with the normal spring period at Chizé, the relative contribution of recruitment rate to variance in λ was lower during the early spring period (Fig. 6 and Fig. S2) because temporal variation in adult survival (when either not accounting for density-dependence or doing so respectively) was also higher during this period (Fig. 5 and Fig. S1). As a result, temporal variation in prime-age stage survival (respectively old stage survival) accounted for about one-fifth (respectively one tenth) of the observed variation in λ in this scenario [compared to about one tenth (respectively one per cent) in normal years, Fig. 6 (respectively Fig. S2)]. At Trois Fontaines, the observed variance in λ was mostly

driven by variation in prime-age stage survival (Fig. 6), despite the fact that temporal variation in both recruitment rate and old-age stage survival was clearly more marked (Fig. 5). This pattern was due to the low absolute variation in all four demographic parameters during both the normal spring and early spring periods (Fig. 5) which limited the degree of variance in λ . As a result, the relative contribution of the three demographic parameters to variance in λ was predominantly shaped by their elasticity values. The co-variation among parameters contributed relatively little to variance in λ (from 5.7 to 23.8%) compared to their main effects (Fig. 6 and Fig. S2). The co-variation between recruitment rate and prime-age stage survival was the most important of the co-variations, but there was no obvious pattern concerning the contribution of this co-variation among scenarios, that is, in relation to the earliness of the onset of spring or between populations (Fig. 6 and Fig. S2).

Life table response analyses (LTRE)

We performed four LTREs to assess the relative contributions of the three demographic parameters to observed differences in population growth rate among scenarios, both between populations for a given period of spring earliness and between periods for a given population (Fig. 7). The between-period difference in λ within a given population was much larger than the between-population difference within a given period. The slightly higher λ at Chizé (1.298) than at Trois Fontaines (1.284) during the normal spring period was due to higher survival at Chizé for both prime-age (0.958 vs. 0.911 at Trois Fontaines) and old-age (0.921 vs. 0.819 at Trois Fontaines) stages, which almost exactly compensated for the lower recruitment rate observed at Chizé (0.48 vs. 0.55 at Trois Fontaines). As a result, recruitment rate and survival had an approximately equivalent influence on the between-population difference in λ . In contrast, during the early spring period, λ was higher at Trois Fontaines than at Chizé, and this was almost entirely due to the between-population difference in prime-age stage survival (0.955 at Trois Fontaines vs. 0.895 at Chizé). When accounting for density-dependence (Chizé only), the between-period difference in λ was weak (1.278 vs. 1.264).

The lower values of λ during the early spring period compared with the normal spring period were mostly driven by a fall in recruitment rate in both populations between periods (from 0.48 to 0.36 at Chizé and from 0.55 to 0.34 at Trois Fontaines). This result held when accounting for density-dependence at Chizé (Fig. S3). However, despite this more marked susceptibility of recruitment rate to earlier springs at Trois Fontaines, the observed λ was slightly higher in this population (1.187) compared with Chizé (1.147) during the early spring period. This was due to an increase in prime-age stage survival at Trois Fontaines during the early spring period (0.955 vs. 0.911 during the normal spring period), which dampened the decrease of λ between periods. Hence, at Trois Fontaines, the lower value λ observed during the early spring period compared to the normal spring period was essentially due to a lower recruitment rate. In contrast, at Chizé, a lower level of prime-age stage survival (respectively old-age stage survival when accounting for density-dependence) during the early spring period [0.895 (respectively 0.874) compared with 0.958 (respectively 0.914) observed during normal springs] acted in concert with the lower level of recruitment to generate the lower value of λ in this demographic scenario.

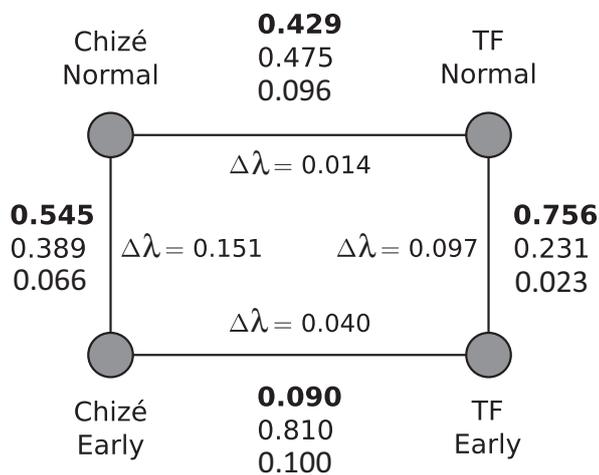


Figure 7 Results of the Life Table Response Experiment analyses performed for four scenarios comprising two populations and two periods of contrasting spring earliness. We report the relative contributions of recruitment rate (in bold), prime-age stage survival (in standard typeface) and old-age stage survival (in italics) to observed differences in λ ($\Delta\lambda$) among scenarios: between populations within a given period (horizontal comparisons) and between periods within a given population (vertical comparisons). TF Normal: Trois Fontaines during normal springs (1988–1998); TF Early: Trois Fontaines during early springs (1999–2009); Chizé Normal: Chizé during normal springs (1988–1998); Chizé Early: Chizé during early springs (1999–2009).

DISCUSSION

Two main outcomes can be identified from our comparative analyses of contrasted populations of roe deer. First, there is a clear evidence for a strong signature of climate change involving increasingly earlier springs over time in both study sites. This is in line with previous studies that have identified similar trends across the whole Northern hemisphere (e.g. Schwartz *et al.* 2006). However, it is noteworthy that the signature of climate change was almost identical in both study sites (with a linear increase of about 3 degree-days $> 7^{\circ}\text{C}$ per year) despite the fact that they are 600 km apart. Interestingly, a remarkably similar signature of climate change was observed in a third site (Aurignac in South France, $43^{\circ}13' \text{N}$, $0^{\circ}52' \text{E}$) where the roe deer population has been intensively monitored for about 12 years (Hewison *et al.* 2009). In this site, composed of forest patches interspersed within a matrix of agricultural land and subject to an Aquitanian climatic type (a warmer and drier variant of an oceanic climate), the number of degree-days $> 7^{\circ}\text{C}$ also increased by about 3 units per year (slope of 3.396 ± 0.786). This suggests the existence of a rather constant speed of change in the earliness of spring across the lowlands of Western Europe.

Second, the population growth rate for roe deer at both study sites was lower during the more recent period with early springs compared to the preceding period with normal springs (Fig. 7). This demographic shift involved several demographic processes which differed in relation to the environmental conditions of the focal population. The relative potential role of the different demographic parameters did not vary, either in response to earlier springs or between populations experiencing contrasting environmental conditions. This indicates, irrespective of whether density-dependence occurred, that the continuous and regular increase in the earliness of spring did not markedly affect the functional dependence of population growth rates on given demographic parameters. This contrasts with the demographic response to sudden and strong perturbations generated by disease (Jones *et al.* 2008), heavy hunting (Proaktor *et al.* 2007; Servanty *et al.* 2011) or strong predation pressure (Wittmer *et al.* 2005; Festa-Bianchet *et al.* 2006). This has practical consequences, as it means that the demographic signature of climate change is potentially much harder to detect than that of other types of perturbation and requires long-term and detailed monitoring to be assessed. Indeed, obtaining accurate estimates of demographic parameters across climatic gradients is an important priority for future data collection (Brook *et al.* 2009). Likewise, the critical demographic parameter that contributed most strongly to the observed variance in growth rate among years of a given population did not differ between the period with normal springs and the period with early springs, but this critical parameter did differ between populations. At Chizé, recruitment rate had the highest contribution to observed variance in population growth rate in both periods, whereas prime-age stage survival was the critical parameter for both periods at Trois Fontaines. This supports the view that the identity of the critical demographic parameter is context-dependent (Coulson *et al.* 2005). We tentatively propose that the amount of variation observed in population growth rate could determine which parameter is critical. When this variance is low, we expect demographic parameters with the highest potential demographic impact to drive variation in population growth, whereas when it is high, demographic parameters with the highest temporal variation should contribute the most.

In contrast, in both populations, the lower growth observed during the early spring period was mainly due to a marked decline in recruitment. This reinforces our inference that spring is the critical period for roe deer, with early fawn mortality in relation to maternal condition and climatic conditions during late gestation and early lactation driving roe deer recruitment (Gaillard *et al.* 1997). This also provides some of the first evidence that the demographic parameters that are responsible for most of the variation in population growth rate among years may not necessarily be the same as those that drive changes in mean growth rate between periods of contrasting environmental conditions. It is also noteworthy that at Chizé, where roe deer suffered most from early springs, adult survival also decreased in the period of early springs and partly accounted for the observed decline in population growth rate. The marked increase in adult prime-age survival between periods when accounting for density-dependence (from 0.895 to 0.934) indicates that both high density and climate change must occur simultaneously to influence prime-age adult survival markedly. As adult survival is generally buffered against environmental variation in long-lived mammals (Gaillard & Yoccoz 2003), the low values of this parameter that we observed in recent years at Chizé during high density might indicate severe energetic stress in this population. This was supported recently by biochemical and immunological analyses (Gilot-Fromont *et al.* 2012). This observation suggests that, in addition to spring earliness, summer climatic conditions might also limit population growth in water-stressed environments. Severe summer droughts such as that in 2003 at Chizé have indeed been linked to increased female mortality in roe deer (Bonenfant *et al.* unpublished data).

The identification of recruitment as the key parameter in the observed decline of population growth rate in response to increasingly earlier springs in both populations suggests the existence of a general explanation related to the life history of the focal species. In temperate regions, we can consider three possible ways for organisms of a given species to cope with climate change involving increasingly earlier springs. The simplest way involves resisting this change, maintaining invariant timing of life history events and constant demographic performance. To be efficient, this (absence of) response requires some degree of decoupling between vegetation phenology and the resource acquisition process needed for meeting the energy requirements of reproduction. Previously accumulated body reserves (i.e. capital breeding tactic, Jonsson 1997) or a diet based on food items which are not directly dependent on the vegetation might provide potential pathways to acquire resources independently of the timing of the vegetation flush. These pathways are clearly not available to a medium-sized herbivore feeding on plants which are available in forest coppice and displaying an income breeder tactic such as the roe deer. As a result, the roe deer is unable to resist the energetic constraints imposed by increasingly early springs and the increasing frequency of summer droughts, likely because of its strong dependence on high quality vegetation (Latham *et al.* 1999). This resulted in a marked decline in demographic performance in both our study populations.

A second way to deal successfully with increasingly early springs involves adapting the timing of life history events to track changes in the phenology of vegetation. This has been reported to occur in several vertebrate species (Visser 2008; Carey 2009), including large herbivores (Moyes *et al.* 2011 on red deer). The lower population growth that we observed in both populations during the period of

early springs indicates that roe deer are unable to adjust the timing of their reproductive cycle to maintain constant demographic performance. In particular, contrary to other large mammalian herbivores such as red deer (Coulson *et al.* 2003) or wild boar (Gamelon *et al.* 2011), roe deer females have inflexible birth dates (Plard *et al.* unpublished data), leading to an increasingly marked mismatch between the earlier vegetation flush and the birth peak which has remained constant over years. For an income breeder which allocates substantially to reproduction, a decrease in resource availability during late gestation-early lactation, when energy expenditure peaks in large herbivores (Oftedal 1985), is likely to lead to increased early mortality of offspring. In both populations, a decrease in recruitment was responsible for most of the observed decline in population growth, involving a marked decrease in early survival of fawns when shifting from normal to early springs (from 0.75 to 0.64 and from 0.60 to 0.42 at Chizé and Trois Fontaines respectively). The ability, or lack of it, to match the phenology of reproductive events to earlier springs might thus be the critical factor determining which organisms can and cannot adapt to climate change in seasonal environments (Coppack & Both 2002). For instance, Salido *et al.* (2012) recently showed that increased flexibility of laying date positively correlated with population growth rate among UK passerine bird species. Likewise, Pau *et al.* (2011) predicted that the phenology of plant species of temperate areas should shift in time in response to earlier springs. Although data from a larger range of populations would be required, our findings strongly suggest that the inflexibility of birth date in roe deer leads to the observed decline of population growth in early spring years through increased early offspring mortality because roe deer females are unable to track temporal changes in the phenology of the vegetation flush.

The last way to cope with changing spring conditions involves escaping this change by moving. For instance, seasonal migration has been observed in a large range of organisms and has been interpreted as a tactic for tracking spatio-temporal variation in resources (Swingland & Greenwood 1983; Fryxell & Sinclair 1988). Shifting spatial distribution is also predicted to be the response of tropical plant species to climate change (Pau *et al.* 2011). However, in a context of global change, moving through space is unlikely to enable populations or species to directly escape increasingly early springs, as this is a general phenomenon across temperate areas. However, individuals may successfully cope with earlier springs by moving into secondary habitats that provide alternative food resources during the critical mismatch period. Agricultural landscapes, which include forest patches disseminated within open habitats of differing nature and containing a variety of food resources, might provide such a suitable habitat for roe deer. Interestingly, roe deer began to colonise agricultural landscapes in the late seventies and now occupy most of this habitat type throughout Western Europe. Moreover, roe deer appear to perform better in these open agroecosystems than in forest blocks. Indeed, by obtaining access to higher quality diets, especially in terms of nitrogen and phosphorous content, roe deer in open areas are able to attain larger body mass than in strict forest habitat (Hewison *et al.* 2009). As fast early body development is positively associated with increased early survival (Da Silva *et al.* 2009), we might expect roe deer in agricultural landscapes to cope with ongoing climate change, and in particular increasingly earlier springs, without adjusting the timing of their reproductive cycle.

Our demographic analysis suggests that the roe deer, following a very rapid increase in abundance over the eighties-nineties through-

out Western Europe, could be now confronting the adverse effects of increasingly early springs. This seems to be a general pattern throughout its geographical range. Indeed, hunting statistics show that the previously marked increase in the number of roe deer shot annually has reached a ceiling, or may even be decreasing, in most European countries since the early part of this century (Apollonio *et al.* 2010). We suggest that these are the first signs that the 'success story' of forest roe deer that began in the second half of the last century (Andersen *et al.* 1998) might be nearing its end due to climate change. Indeed, given the current level of hunting pressure that is exerted on this economically important game species, roe deer populations in strict forest habitat may soon decline markedly as spring becomes increasingly early. In contrast, because the breeding phenology of sympatric large herbivores such as red deer and wild boar appears more flexible (Gamelon *et al.* 2011; Moyes *et al.* 2011), these species may cope more efficiently with ongoing climate change. This predicted interspecific asynchrony in the effects climate change among sympatric large herbivores (but see Mysterud *et al.* 2007) is likely to impact on interspecific relationships within multi-herbivore communities. We suggest that the only way roe deer can escape the adverse effects of climate change is by increasingly shifting their distribution to open landscapes which offer richer food resources during spring, enabling females to successfully offset their energetic requirements during the critical rearing stage. This testable prediction is a promising avenue for future investigation.

ACKNOWLEDGEMENTS

We warmly thank the organisers of the conference on 'Ecological Effects of Environmental Change' held on June 22nd 2012 in the CNRS auditorium at Paris for the invitation to present this study. We are grateful to all participants at this conference for stimulating discussion. We also thank three anonymous referees for constructive comments on a previous draft of this article.

REFERENCES

- Acevedo, P., Delibes-Mateos, M., Escudero, M.A., Vicente, J., Marco, J. & Gortazar, C. (2005). Environmental constraints in the colonization sequence of roe deer (*Capreolus capreolus* Linnaeus, 1758) across the Iberian Mountains, Spain. *J. Biogeogr.*, 32, 1671–1680.
- Andersen, R., Duncan, P. & Linnell, J.D.C. (1998). *The European Roe Deer: the Biology of Success*. Scandinavian University Press, Oslo, Norway.
- Andersen, R., Gaillard, J.-M., Linnell, J.D.C. & Duncan, P. (2000). Factors affecting maternal care in an income breeder, the European roe deer. *J. Anim. Ecol.*, 69, 672–682.
- Andrewartha, H.G. & Birch, L.C. (1954). *The Distribution and Abundance of Animals*. Chicago University Press, Chicago, Illinois, USA.
- Apollonio, M., Andersen, R. & Putman, R. (2010). *European Ungulates and their Management in the 21st Century*. Cambridge University Press, Cambridge, UK.
- Barbraud, C. & Weimerskirch, H. (2001). Emperor penguins and climate change. *Nature*, 411, 183–186.
- Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T. *et al.* (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc. R. Soc. Lond. B*, 271, 1657–1662.
- Brook, B.W., Akçakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G. & Araujo, M.B. (2009). Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biol. Lett.*, 5, 723–725.
- Carey, C. (2009). The impacts of climate change on the annual cycles of birds. *Phil. Trans. R. Soc. B*, 364, 3321–3330.

- Caswell, H. (2000). Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, 81, 619–627.
- Caswell, H. (2001). *Matrix Population Models: construction, Analysis and Interpretation*, 2nd edn. Sinauer Associates, Sunderland, Massachusetts, USA.
- Coppack, T. & Both, C. (2002). Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea*, 90, 369–378.
- Coulson, T., Kruuk, L.E.B., Tavecchia, G., Pemberton, J.M. & Clutton-Brock, T.H. (2003). Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution*, 57, 2879–2892.
- Coulson, T., Gaillard, J.-M. & Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *J. Anim. Ecol.*, 74, 789–801.
- Da Silva, A., Gaillard, J.-M., Yoccoz, N.G., Hewison, A.J.M., Galan, M., Coulson, T. *et al.* (2009). Heterozygosity–fitness correlations revealed by neutral and candidate gene markers in roe deer from a long-term study. *Evolution*, 63, 403–417.
- Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T. & Pelletier, F. (2006). Stochastic predation events and population persistence in bighorn sheep. *Proc. R. Soc. B.*, 273, 1537–1543.
- Fryxell, J.M. & Sinclair, A.R.E. (1988). Causes and consequences of migration by large herbivores. *Trends Ecol. Evol.*, 3, 237–241.
- Gaillard, J.-M. & Yoccoz, N.G. (2003). Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, 84, 3294–3306.
- Gaillard, J.-M., Delorme, D. & Jullien, J.-M. (1993a). Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia*, 94, 57–61.
- Gaillard, J.-M., Delorme, D., Jullien, J.-M. & Tatin, D. (1993b). Timing and synchrony of births in roe deer. *J. Mamm.*, 74, 738–744.
- Gaillard, J.-M., Boutin, J.M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J.D. (1997). Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, 112, 502–513.
- Gaillard, J.-M., Liberg, O., Andersen, R., Hewison, A.J.M. & Cederlund, G. (1998). Population dynamics of roe deer. In *The European Roe Deer: the Biology of Success*. (eds Andersen, R., Duncan, P. & Linnell, J.D.C.). Scandinavian University Press, Oslo, Norway, pp. 309–335.
- Gaillard, J.-M., Duncan, P., Delorme, D., Van Laere, G., Pettorelli, N., Maillard, D. *et al.* (2003). Effects of hurricane Lothar on the population dynamics of European roe deer. *J. Wildl. Manage.*, 67, 767–773.
- Gamelon, M., Besnard, A., Gaillard, J.-M., Servanty, S., Baubet, E., Brandt, S. *et al.* (2011). High hunting pressure selects for earlier birth date: wild boar as a case study. *Evolution*, 65, 3100–3112.
- Garel, M., Gaillard, J.-M., Jullien, J.M., Dubray, D., Maillard, D. & Loison, A. (2011). Population abundance and early spring conditions determine variation in body mass of juvenile chamois. *J. Mamm.*, 92, 1112–1117.
- Garrott, R.A., Eberhardt, L.L., White, P.J. & Rotella, J. (2003). Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology*, 81, 33–45.
- Gilot-Fromont, E., Jégo, M., Bonenfant, C., Gibert, P., Rannou, B., Klein, F. *et al.* (2012). Immune phenotype and body condition in roe deer: individuals with high body condition have different, not stronger immunity. *PLoS ONE*, 7, e45576.
- Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J. *et al.* (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.*, 83, 357–399.
- Grotan, V., Saether, B.E., Filli, F. & Engen, S. (2008). Effects of climate on population fluctuations of ibex. *Global Change Biol.*, 14, 218–228.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.*, 8, 993–1009.
- Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecol. Model.*, 135, 147–186.
- Hallett, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Grenfell, B.T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, 430, 71–75.
- Hansen, B.B., Aanes, R., Herfindal, I., Kohler, J. & Saether, B.E. (2011). Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology*, 92, 1917–1923.
- Helle, T. & Kojola, I. (2008). Demographics in an alpine reindeer herd: effects of density and winter weather. *Ecography*, 31, 221–230.
- Hewison, A.J.M., Vincent, J.-P. & Reby, D. (1998). Social organisation of European roe deer. In: *The European Roe Deer: the Biology of Success* (ed. Andersen, R., Duncan, P. & Linnell, J.D.C.). Scandinavian University Press, Oslo, Norway, pp. 189–219.
- Hewison, A.J.M., Morellet, N., Verheyden, H., Daufresne, T., Angibault, J.M., Cargnelutti, B. *et al.* (2009). Landscape fragmentation influences winter body mass of roe deer. *Ecography*, 32, 1062–1070.
- Hewison, A.J.M., Gaillard, J.M., Delorme, D., Van Laere, G., Amblard, T. & Klein, F. (2011). Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass-size allometry in roe deer. *Oikos*, 120, 1217–1226.
- Horvitz, C., Schemske, D.W. & Caswell, H. (1996). The relative “importance” of life-history stages to population growth: prospective and retrospective analyses. In: *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems* (ed. Tuljapurkar, S. & Caswell, H.). Chapman & Hall, New York, New York, USA, pp. 247–271.
- Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. & Willis, S.G. (2006). Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, 148, 8–28.
- IPCC (2007). *Intergovernmental Panel on Climate Change: fourth Assessment Report*. (<http://www.ipcc.ch>).
- Jones, M.E., Cockburn, A., Hamede, R., Hawkins, C., Hesterman, H., Lachish, S. *et al.* (2008). Life-history change in disease-ravaged Tasmanian devil populations. *PNAS*, 105, 10023–10027.
- Jonsson, K.I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78, 57–66.
- Kaluzinski, J. (1982). Dynamics and structure of a field roe deer population. *Acta Theriol.*, 27, 385–408.
- Lande, R., Engen, S. & Sæther, B.-E. (2003). *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford, UK.
- Lane, J.E., Kruuk, L.E.B., Charmantier, A., Murie, J.O. & Dobson, F.S. (2012). Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature*, 489, 554–557.
- Latham, J., Staines, B.W. & Gorman, M.L. (1999). Comparative feeding ecology of red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Scottish plantation forests. *J. Zool.*, 247, 409–418.
- Lebreton, J.-D. (2011). The impact of global change on terrestrial vertebrates. *Comptes Rendus Biologies*, 334, 360–369.
- Leslie, P.H. (1948). Some further notes on the use of matrices in population mathematics. *Biometrika*, 35, 213–245.
- Lewontin, R.C. & Cohen, D. (1969). On population growth in a randomly varying environment. *PNAS*, 62, 1056–1060.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T. & Jullien, J.M. (1999). Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, 80, 2539–2554.
- Mauget, C., Mauget, R. & Sempéré, A. (1997). Metabolic rate in female European roe deer (*Capreolus capreolus*): incidence of reproduction. *Can. J. Zool.*, 75, 731–739.
- Moyes, K., Nussey, D.H., Clements, M.N., Guinness, F.E., Morris, A., Morris, S. *et al.* (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biol.*, 17, 2455–2469.
- Mysterud, A., Tryjanowski, P., Panek, M., Pettorelli, N. & Stenseth, N.C. (2007). Inter-specific synchrony of two contrasting ungulates: wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*). *Oecologia*, 151, 232–239.
- Nicholson, A.J. (1933). The balance of animal populations. *J. Anim. Ecol.*, 2, 132–178.
- Nilsen, E.B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., Van Laere, G. *et al.* (2009). A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *J. Anim. Ecol.*, 78, 585–594.
- Oftedal, O.T. (1985). Pregnancy and lactation. In: *Bioenergetics of Wild Herbivores* (ed. Hudson, R.J. & White, R.G.). CRC Press, Florida, USA, pp. 215–238.
- Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T. & Olson, L.E. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, 466, 482–485.
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Evol. Syst.*, 37, 637–669.

- Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J.B., Bolmgren, K. *et al.* (2011). Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biol.*, 17, 3633–3643.
- Pettorelli, N., Dray, S., Gaillard, J.-M., Chessel, D., Duncan, P., Illius, A. *et al.* (2003). Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia*, 137, 363–369.
- Pettorelli, N., Mysterud, A., Yoccoz, N.G., Langvatn, R. & Stenseth, N.C. (2005). Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc. R. Soc. B*, 272, 2357–2364.
- Pettorelli, N., Gaillard, J.-M., Mysterud, A., Duncan, P., Stenseth, N.C., Delorme, D. *et al.* (2006). Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. *Oikos*, 112, 565–572.
- Pettorelli, N., Pelletier, F., von Hardenberg, A., Festa-Bianchet, M. & Côté, S.D. (2007). Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. *Ecology*, 88, 381–390.
- Post, E. & Forchhammer, M.C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Phil. Trans. R. Soc. B*, 363, 2369–2375.
- Post, E. & Stenseth, N.C. (1999). Climatic variability, plant phenology, and northern ungulates. *Ecology*, 80, 1322–1339.
- Proaktor, G., Coulson, T. & Milner-Gulland, E.J. (2007). Evolutionary responses to harvesting in ungulates. *J. Anim. Ecol.*, 76, 669–678.
- Robbins, C.T. & Robbins, B.L. (1979). Fetal and neonatal growth- Patterns and maternal reproductive effort in ungulates and sub-ungulates. *Am. Nat.*, 114, 101–116.
- Salido, L., Purse, B.V., Marrs, R., Chamberlain, D.E. & Shultz, S. (2012). Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. *Ecography*, 35, 604–613.
- Schwartz, M.D., Ahas, R. & Aasa, A. (2006). Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biol.*, 12, 343–351.
- Servanty, S., Gaillard, J.-M., Ronchi, F., Focardi, S., Baubet, E. & Gimenez, O. (2011). Influence of harvesting pressure on demographic tactics: implications for wildlife management. *J. Appl. Ecol.*, 48, 835–843.
- Swingland, I.R. & Greenwood, P.J. (1983). *The Ecology of Animal Movements*. Oxford University Press, Oxford, UK.
- Tuljapurkar, S. & Orzack, S.H. (1980). Population dynamics in variable environments. 1. Long-run growth rates and extinction. *Theor. Pop. Biol.*, 18, 314–342.
- Van Laere, G., Renaud, G. & Gaillard, J.-M. (1997). Observation d'un cas de reproduction réussie chez un chevreuil (*Capreolus capreolus*) de moins de 12 mois. *Mammalia*, 61, 267–270.
- Vanpé, C., Gaillard, J.-M., Morellet, N., Kjellander, P., Liberg, O., Delorme, D. *et al.* (2009). Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. *J. Mamm.*, 90, 661–665.
- Vincent, J.-P., Gaillard, J.-M. & Bideau, E. (1991). Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta Theriol.*, 36, 315–328.
- Visser, M.E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. Lond. B*, 275, 649–659.
- Wilson, L.T. & Barnett, W.W. (1983). Degree days: an aid in crops and pest management. *Calif. Agric.*, 37, 4–7.
- Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S. *et al.* (2005). Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia. *Canada. Can. J. Zool.*, 83, 407–418.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Editor, Hector Arita

Manuscript received 6 September 2012

First decision made 9 October 2012

Second decision made 21 November 2012

Manuscript accepted 29 November 2012

Appendix 4



Research

Cite this article: Gamelon M, Douhard M, Baubet E, Gimenez O, Brandt S, Gaillard J-M. 2013 Fluctuating food resources influence developmental plasticity in wild boar. *Biol Lett* 9: 20130419.
<http://dx.doi.org/10.1098/rsbl.2013.0419>

Received: 4 May 2013
Accepted: 11 July 2013

Subject Areas:
ecology

Keywords:
coin-flipping, fetus mass, food resources, mast production, variable environment

Author for correspondence:
Marlène Gamelon
e-mail: marlene.gamelon@univ-lyon1.fr

Population ecology

Fluctuating food resources influence developmental plasticity in wild boar

Marlène Gamelon^{1,2,3}, Mathieu Douhard¹, Eric Baubet², Olivier Gimenez³, Serge Brandt² and Jean-Michel Gaillard¹

¹UMR 5558, Laboratoire de Biométrie et Biologie Evolutive, Université de Lyon, 69000 Lyon; Université Lyon 1, 69622 Villeurbanne, France

²Office National de la Chasse et de la Faune Sauvage, 2 Bis Rue des Religieuses, BP 19, 52120 Châteauvillain, France

³UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive, Campus CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France

To maximize long-term average reproductive success, individuals can diversify the phenotypes of offspring produced within a reproductive event by displaying the 'coin-flipping' tactic. Wild boar (*Sus scrofa scrofa*) females have been reported to adopt this tactic. However, whether the magnitude of developmental plasticity within a litter depends on stochasticity in food resources has not been yet investigated. From long-term monitoring, we found that juvenile females produced similar-sized fetuses within a litter independent of food availability. By contrast, adult females adjusted their relative allocation to littermates to the amount of food resources, by providing a similar allocation to all littermates in years of poor food resources but producing highly diversified offspring phenotypes within a litter in years of abundant food resources. By minimizing sibling rivalry, such a plastic reproductive tactic allows adult wild boar females to maximize the number of littermates for a given breeding event.

1. Introduction

In unpredictable and variable environments, optimal reproductive tactics of iteroparous organisms should minimize variance in reproductive success among years to maximize long-term average reproductive success [1,2]. To minimize among-year variation in reproductive success, individuals can minimize the variance in the number of offspring produced at each reproductive event (bet-hedging *sensu* [3]). Bet-hedging includes two non-exclusive mechanisms, risk-spreading and risk-minimizing. Producing the same limited number of offspring each year corresponds to risk-spreading. To minimize variance in reproductive success, individuals can also diversify the phenotypic quality of offspring produced at a given reproductive event (coin-flipping *sensu* [4]). Such developmental plasticity is widespread in invertebrates, fishes, amphibians and reptiles but not common in homeotherms [5].

Evidence of coin-flipping within a given reproductive event in warm-blooded species has been reported only in wild boar (*Sus scrofa scrofa*) [5]. Large wild boar females produce offspring with highly diversified phenotypes within a litter, whereas small females display the individual optimization tactic [6,7] by increasing litter size with mass and keeping fetus mass constant [5]. Coin-flipping in wild boar is thus a tactic which depends on female size. By feeding on forest mast, the abundance of which fluctuates greatly among years, wild boar face highly variable and unpredictable environments [8,9]. Therefore, we expect that fluctuating food availability should influence the magnitude of offspring phenotypic variance within a litter. Such a prediction has never been investigated for any species reported to display coin-flipping.

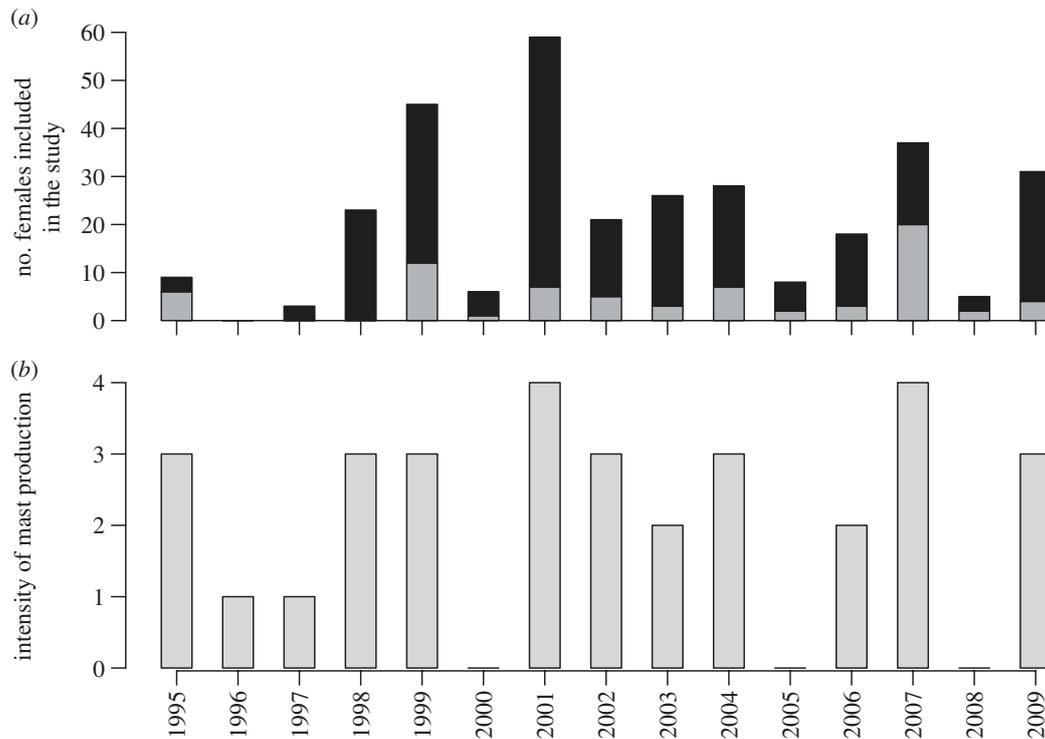


Figure 1. (a) Number of females shot in the population of Châteauvillain-Arc-en-Barrois, France, for which both litter size and fetus mass were measured in a given hunting season and at a given age (72 juvenile females and 247 adult females including 143 between 1 and 2 years of age and 104 older than 2 years of age). (b) Intensity of mast production (beechnuts + acorns) (from 0 corresponding to years without mast production to 4 corresponding to years with a very high mast production). Black shaded area represents females greater than 1 year of age and grey shaded area represents those less than 1 year of age.

Taking advantage of a long-term detailed monitoring programme for a heavily hunted population, we aim to fill the gap by testing whether female wild boar produce littermates with increasingly variable phenotypes when there is increased masting.

2. Material and methods

(a) Study site and data collection

This study was conducted on a wild boar population in north-eastern France in the 11 000 ha forest of Châteauvillain-Arc-en-Barrois. This forest is mainly composed of oak (*Quercus petraea*), beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*). Population size of wild boar fluctuated between 1200 and 1500 individuals over the course of the study [10]. Wild boar have no natural predators but are heavily hunted each year between October and February (see [11] for estimates of mortality owing to hunting). The hunting pressure was mainly oriented towards juveniles [10]. Between 1995 and 2009, we recorded the age class of each female shot (juvenile (less than 1 year of age) versus adult (older than 1 year of age)) based on tooth eruption pattern [12]. We examined uteri for the presence of fetuses. Changes in resource availability did not influence the fetal sex ratio [9]. Litter size was recorded and each fetus was weighed, measured (crown–rump length, in millimetres) and sexed. Measurements of 1743 fetuses from 319 females were collected during 15 hunting seasons (figure 1a).

(b) Mast production

Each year, food availability was measured indirectly through diet composition, using the analysis of stomach contents during the hunting period [13]. We recognized five categories depending on the quantity of beechnuts and acorns found in the stomachs (see [14] for further details, figure 1b).

(c) Statistical analyses

Not all litters were at the same gestation stage when shot, because mating of wild boar occurs throughout the year [10]. To correct fetus mass among litters by gestation stage, we standardized all fetuses at 110 days of gestation [5].

To assess whether females produced fetuses which were more diverse in terms of mass with increasing mast production, we first provided a measure of within-litter variation in mass by calculating the coefficient of variation (CV) of fetus mass corrected for gestation stage for each litter. We then fitted a generalized least squares (GLS) framework linking the CV of corrected fetus mass as a response variable to the fixed effects of age (categorical variable with two classes), mast production (treated as a continuous variable to describe the continuum of food resources availability) and their interaction.

We checked the expectation that fetuses are not heavier when food resources are abundant. We used linear mixed models with individual fetus mass corrected for gestation stage as the response variable, and mother identity as a random effect to account for the non-independence of fetuses within a litter. We then tested the fixed effects of age and mast production, and their interaction. We assessed whether larger litters are produced in years with abundant food. We fitted a linear regression including litter size as the response variable and mast production, age and their interaction as explanatory variables.

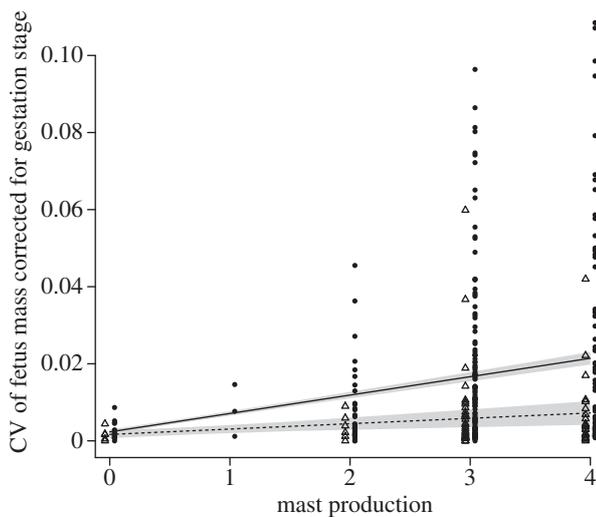
When necessary, we applied a correction for heteroscedasticity by using the ‘varIdent’ variance function [15] to account for different standard deviations among mast productions (performed with R v. 2.12.2 [16]). Data deposited in the Dryad repository: doi:10.5061/dryad.8hf1c.

3. Results

The CV of fetus mass was affected by a positive interaction between mast production and age (slope = 0.003 (s.e.: 0.0009);

Table 1. Effects of mast production and female age on (a) fetus mass (using linear mixed models) and (b) litter size (using linear regression).

response	effect	slope \pm s.e.	<i>p</i> -value
(a)			
fetus mass	mast production \times age	0.080 \pm 3.146	0.980
fetus mass	mast production	-0.697 \pm 1.340	0.603
fetus mass	age	1.357 \pm 3.509	0.699
(b)			
litter size	mast production \times age	-0.151 \pm 0.219	0.491
litter size	mast production	0.169 \pm 0.094	0.072
litter size	age	1.701 \pm 0.225	<0.01

**Figure 2.** Relationships between the CV of fetus mass and mast production for juvenile (triangles) and adult (circles) females collected in the wild boar population of Châteauvillain-Arc-en-Barrois, France. The lines correspond to the predicted values from the GLS linking the CV of fetus mass to mast production, age and their interaction (dotted line for juvenile females and solid line for adult females).

p -value \ll 0.01). In juvenile females, the CV of fetus mass increased with mast production (p -value \ll 0.01; figure 2), but the slope was weak (0.001 (s.e.: 0.0004)). A much stronger positive relationship between within-litter variation in fetus mass and mast production occurred in adult females (slope: 0.005 (s.e.: 0.0005), p -value \ll 0.01; figure 2).

We did not find any influence of mast production and age on fetus mass (table 1). A weak positive effect of mast production occurred on litter size for both juvenile and adult females (table 1). Both female categories increased their litter size only slightly in years of abundant food compared with non-masting years (from 3.65 to 4.32 in juveniles and from 5.35 to 6.02 in adults).

4. Discussion

Nutrition often shapes observed variation in growth of warm-blooded species [17]. Using a direct measure of nutrition for wild boar, we found that fetus mass and litter size are not markedly dependent on mast production. Such a noteworthy lack of effect of food resources on offspring mass and litter size does not mean, however, that wild boar

reproductive tactics are independent of food. Mast production strongly influenced the within-litter variation in fetus mass in adult females (figure 2).

By contrast, juvenile females produced fetuses of similar mass independent of food availability. Juveniles usually do not reproduce in wild boar and did here in response to the high hunting pressure [14,18]. Having reached only 33–41% of their full body mass [14], juvenile females have to allocate a large amount of energy to both growth and reproduction. This constraint might explain why juvenile females did not adjust the phenotype of their offspring to available resources.

Adult females diversified the phenotype of their offspring in masting years. Competition between siblings might be involved in this diversification of offspring phenotype. Sibling rivalry is common among species where young share the same litter [19]. In wild boar, variation in milk availability at different teats (teat order effect [20]) leads littermates to compete for the most productive teats [20,21]. Large offspring have an advantage over small ones in this competition [22]. By producing highly diversified offspring phenotypes, adult females match the mass variation of their offspring with variation in productivity among teats, leading to decreased sibling rivalry and thereby increasing the chance of rearing many offspring at a given breeding event. Adult females displayed a coin-flipping tactic involving the diversification of phenotypes within a litter only in masting years, while maintaining a constant mean fetus mass independent of resource availability. In masting years, females thus produce large fetuses requiring more energy allocation and also small ones requiring less allocation but likely to survive under good food conditions. On the contrary, in non-masting years, small fetuses are no longer viable [21], thus leading adult females to equi-allocate to offspring by producing fetuses of similar mass.

This study provides further support that wild boar females exhibit a unique life-history strategy among ungulates [23] by displaying different reproductive tactics to maximize the number of viable offspring in variable environments.

Acknowledgements. We are grateful to all those who helped collecting harvested wild boars, particularly P. Van den Bulck and G. Corbeau. We are grateful to the Office National des Forêts and to F. Jehlé, who allowed us to work on the study area. We thank two anonymous referees for constructive comments on a previous draft.

Funding statement. M.D. is supported by a PhD scholarship from the French Ministry of Higher Education and Research. M.G. is supported by a grant of the French National Agency for Wildlife (ONCFS).

- Philippi T, Seger J. 1989 Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **4**, 41–44. (doi:10.1016/0169-5347(89)90138-9)
- Starrfelt J, Kokko H. 2012 Bet-hedging: a triple trade-off between means, variances and correlations. *Biol. Rev.* **87**, 742–755. (doi:10.1111/j.1469-185X.2012.00225.x)
- Slatkin M. 1974 Hedging one's evolutionary bets. *Nature* **250**, 704–705. (doi:10.1038/250704b0)
- Kaplan RH, Cooper WS. 1984 The evolution of developmental plasticity in reproductive characteristics: an application of the 'adaptive coin-flipping' principle. *Am. Nat.* **123**, 393–410. (doi:10.1086/284211)
- Gamelon M, Gaillard J-M, Baubet E, Devillard S, Say L, Brandt S, Gimenez O. 2013 The relationship between phenotypic variation among offspring and mother body mass in wild boar: evidence of coin-flipping? *J. Anim. Ecol.* **82** (doi:10.1111/1365-2656.12073)
- Smith CC, Fretwell SD. 1974 Optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506. (doi:10.1086/282929)
- Lloyd DG. 1987 Selection of offspring size at independence and other size-versus-number strategies. *Am. Nat.* **129**, 800–817. (doi:10.1086/284676)
- Bieber C, Ruf T. 2005 Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *J. Anim. Ecol.* **42**, 1203–1213. (doi:10.1111/j.1365-2664.2005.01094.x)
- Servanty S, Gaillard J-M, Allainé D, Brandt S, Baubet E. 2007 Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. *Behav. Ecol.* **18**, 427–432. (doi:10.1093/beheco/arl099)
- Gamelon M, Besnard A, Gaillard J-M, Servanty S, Baubet E, Brandt S, Gimenez O. 2011 High hunting pressure selects for earlier birth date: wild boar as a case study. *Evolution* **65**, 3100–3112. (doi:10.1111/j.1558-5646.2011.01366.x)
- Toïgo C, Servanty S, Gaillard J-M, Brandt S, Baubet E. 2008 Disentangling natural from hunting mortality in an intensively hunted wild boar population. *J. Wildl. Manage.* **72**, 1532–1539. (doi:10.2193/2007-378)
- Baubet E, Brandt S, Jullien J-M, Vassant J. 2004 Valeur de l'examen de la denture pour la détermination de l'âge chez le sanglier (*Sus scrofa*). *Gibier Faune Sauvage* **11**, 119–132.
- Brandt S, Baubet E, Vassant J, Servanty S. 2006 Régime alimentaire du sanglier (*Sus scrofa* L.) en milieu forestier de plaine agricole. *Faune Sauvage* **273**, 20–27.
- Servanty S, Gaillard J-M, Toïgo C, Brandt S, Baubet E. 2009 Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *J. Anim. Ecol.* **78**, 1278–1290. (doi:10.1111/j.1365-2656.2009.01579.x)
- Pinheiro JC, Bates DM. 2000 *Mixed-effects models in S and S-PLUS*. New York, NY: Springer.
- R Development Core Team. 2011 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Clutton-Brock TH. 1991 *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- Servanty S, Gaillard J-M, Ronchi F, Focardi S, Baubet E, Gimenez O. 2011 Influence of harvesting pressure on demographic tactics: implications for wildlife management. *J. Appl. Ecol.* **48**, 835–843. (doi:10.1111/j.1365-2664.2011.02017.x)
- Mock DW, Parker GA. 1997 *The evolution of sibling rivalry*. Oxford, UK: Oxford University Press.
- Fraser D, Thompson BK. 1991 Armed sibling rivalry among suckling piglets. *Behav. Ecol. Sociobiol.* **29**, 9–15. (doi:10.1007/BF00164289)
- Drake A, Fraser D, Weary DM. 2008 Parent–offspring resource allocation in domestic pigs. *Behav. Ecol. Sociobiol.* **62**, 309–319. (doi:10.1007/s00265-007-0418-y)
- Stockley P, Parker GA. 2002 Life history consequences of mammal sibling rivalry. *Proc. Natl Acad. Sci. USA* **99**, 12 932–12 937. (doi:10.1073/pnas.192125999)
- Focardi S, Gaillard J-M, Ronchi F, Rossi S. 2008 Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. *J. Mamm.* **89**, 1113–1123. (doi:10.1644/07-MAMM-A-164.1)

Appendix 5

Roaring counts are not suitable for the monitoring of red deer *Cervus elaphus* population abundance

Mathieu Douhard, Christophe Bonenfant, Jean-Michel Gaillard, Jean-Luc Hamann, Mathieu Garel, Jacques Michallet & François Klein

The successful management of large herbivores requires the monitoring of a set of indicators of ecological change (IEC) describing animal performance, herbivore impact on habitat and relative animal abundance. Roaring counts during the rut have often been used to assess the abundance of red deer *Cervus elaphus* populations, but a formal evaluation of this method is still lacking. In this paper, we examined the usefulness of the number of red deer recorded during roaring counts for managing red deer populations. Using standardised spotlight counts applied for the monitoring of red deer at La Petite Pierre, France, as a reference method, we found that roaring counts did not correlate with spotlight counts. Moreover, we did not find any evidence that roaring counts decreased with increasing number of male and female red deer harvested in the reserve during the previous hunting season. We thus conclude that managers should not rely on roaring counts for managing red deer populations.

Key words: abundance index, *Cervus elaphus*, count data, indicator of ecological change, red deer, roaring

Mathieu Douhard, Christophe Bonenfant & Jean-Michel Gaillard, Université de Lyon, Université Lyon 1, CNRS, UMR5558, Laboratoire de Biométrie et Biologie Évolutive, Bâtiment G. Mendel, 43 boulevard du 11 novembre 1918, F-69622, Villeurbanne, France - e-mail addresses: mathieu.douhard@etu.univ-lyon1.fr (Mathieu Douhard); christophe.bonenfant@univ-lyon1.fr (Christophe Bonenfant); jean-michel.gaillard@univ-lyon1.fr (Jean-Michel Gaillard)

Jean-Luc Hamann, Jacques Michallet & François Klein, Office National de la Chasse et de la Faune Sauvage, Centre National d'Étude et de Recherche Appliquée Cervidés Sanglier, 1 place Exelmans, F-55000 Bar le Duc, France - e-mail addresses: jean-luc.hamann@oncfs.gouv.fr (Jean-Luc Hamann); jacques.michallet@oncfs.gouv.fr (Jacques Michallet); francois.klein@oncfs.gouv.fr (François Klein)

Mathieu Garel, Office National de la Chasse et de la Faune Sauvage, Centre National d'Étude et de Recherche Appliquée Faune de Montagne, 5 allée de Bethléem, Z.I. Mayencin F-38610, Gières, France - e-mail: mathieu.garel@oncfs.gouv.fr

Corresponding author: Christophe Bonenfant

Received 5 April 2012, accepted 17 August 2012

Associate Editor: Klaus Hackländer

Deer populations have increased dramatically in size and distribution over recent decades both in Europe and North America (Andersen et al. 1998, Fuller & Gill 2001). As a result, in many areas, management goals are changing from protection to population control (Milner et al. 2006). Controlling deer populations is required to prevent damage to farming and forestry, deer-vehicle collisions or the spread of diseases (Rooney & Waller 2003, Côté et al. 2004, Gordon et al. 2004, Seiler 2004). In areas where large predators have been eliminated, deer populations are usually controlled through hunting (Langvatn &

Loison 1999, Festa-Bianchet 2003, Milner et al. 2006). To define the hunting quotas, managers typically use estimates of population size obtained from counting methods (e.g. Williams et al. 2002).

Counting methods have repeatedly been shown to be neither accurate nor precise (CV > 30%; Andersen 1953, Gaillard et al. 2003) except when a high proportion of individuals are marked (Strandgaard 1967, Vincent et al. 1991). Andersen (1953) showed, for example, that counts in a population of roe deer *Capreolus capreolus* can lead to a threefold underestimation of the population size. Moreover,

the absence of repeated counts within a year prevents the assessment of the precision of population estimates. Lastly, even the best estimate of population size does not provide the required information to set hunting plans because it does not provide information to managers about the state of the plant-herbivore system (Morellet et al. 2007).

In this context, researchers have developed new tools for managing ungulate populations, which are based on the monitoring of a set of indicators of ecological change (IEC; Cederlund et al. 1998, Morellet et al. 2007). An IEC is an easily measured parameter, sensitive to changes in the relationship between the population and its habitat (Cederlund et al. 1998). IEC are based on the concept of density-dependence (Bonenfant et al. 2009), from which wildlife managers should be able to monitor deer populations without population size estimates. Morellet et al. (2007) proposed to simultaneously monitor three categories of IEC describing 1) animal performance (Bonenfant et al. 2002, Zannèse et al. 2006, Garel et al. 2011), 2) habitat quality (Morellet et al. 2001, Chevrier et al. 2012) and 3) animal abundance (Vincent et al. 1991, Loison et al. 2006, Garel et al. 2010). It is important to note that only the complementarity of different IEC monitored over several years allows for the measurement of population-habitat relationships.

Among indices of red deer *Cervus elaphus* abundance, spotlight counts are commonly used by managers (e.g. Gunson 1979, McCullough 1982, Fafarman & DeYoung 1986). Recently, Garel et al. (2010) showed that, after controlling for observation conditions, spotlight counts can provide a reliable IEC of relative abundance for the monitoring and management of red deer populations living in forested areas. Spotlight counts are inexpensive and allow for rapid cover of large areas (McCullough 1982). However, this method is restricted to areas with good network of roads and tracks. An alternative option could be to carry out roaring counts from fixed spots (Albaret et al. 1989).

Counting red deer during the period of reproduction (rut) in autumn is often used in addition to spotlight counts, or when spotlight counts are difficult to apply (Bobek et al. 1986, Albaret et al. 1989), to assess trends in population abundance. Mature red deer males, like many other ungulates, commonly spend most of the year in areas separated from those occupied by the females except in the breeding season (Clutton-Brock & Albon 1979, Clutton-Brock et al. 1982). At this particular time

of the year, stags use vocalisations (roars) to monopolise a number of hinds. With their highly conspicuous behaviour, red deer are easily detected during the rut based on acoustic and visual clues. Hence, roaring counts have two components: first, counting the number of roaring stags, and second, counting hinds and stags seen in rutting areas, both being used for the calculation of the abundance index. However, Ciucci et al. (2009) have suggested that roaring counts are poor indicators of red deer abundance because the timing of the survey is not consistently synchronous with the roaring peak. Overall, the roaring counts method has never been formally validated.

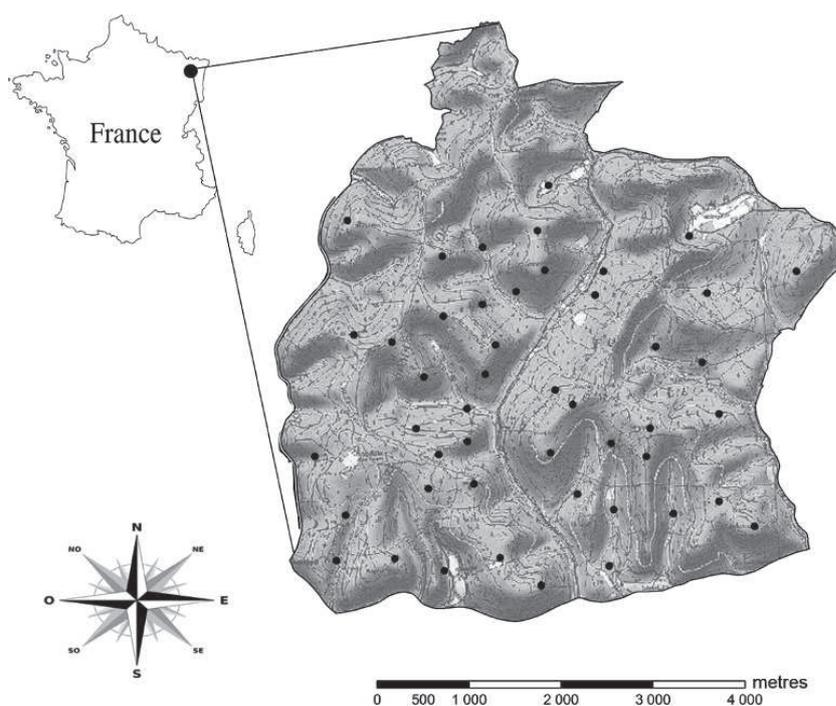
In our study conducted at La Petite Pierre, France, we examined the usefulness of roaring counts for the management of red deer populations. Managers of our study site have monitored red deer using both spotlight and roaring counts for 31 years. Providing that roaring counts allow for reliable assessment of the abundance of red deer resident populations, we expected a positive correlation between roaring and spotlight counts because spotlight counts provide a suitable measure of annual variation in abundance of the resident population (Garel et al. 2010). Second, as variation in hunting pressure accounted for most annual changes in population size in the studied population (Bonenfant et al. 2002, Richard et al. 2010; see also section Material and methods), the number of counted red deer during rut should decrease with the number of deer harvested during the previous hunting season (Garel et al. 2005b).

Material and methods

Study site and population

La Petite Pierre National Reserve (PPNR) is a 2,674 ha unfenced forest located in the Vosges mountain range, northeastern France (48.82°N, 7.34°E; Fig. 1). The PPNR is characterised by a succession of small hills and steep-sided valleys ranging between 200 and 400 m a.s.l. in elevation (see Fig. 1). The climate is continental with oceanic influences, leading to cold winters and cool summers (average January and July temperatures are 0.6 and 18.4°C, respectively). The PPNR consists of a balanced mix of broadleaved, mainly European beech *Fagus sylvatica*, and coniferous trees such as silver fir *Abies alba*, Norway spruce *Picea abies* and Douglas fir *Pseudotsuga douglasii*. The sandstone substrate produces acidic and poor soils, resulting in a vegetation of low

Figure 1. Location of the Petite Pierre National Reserve in northeastern France. The focused area details the landscape topography and the observation spots (●) during roaring counts.



nutritive quality for herbivores. Roe deer and wild boar *Sus scrofa* are also present within the reserve. All three ungulates are managed through hunting, either with quotas (deer) or without quotas (wild boar). Since 1978, the red deer population has been hunted on an annual basis between 1 August and 1 February by both professional and sport hunters (more details on hunting practice in France can be found in Maillard et al. 2010). A temporal variation in hunting pressure controlled by the Office National de la Chasse et de la Faune Sauvage and the Office National des Forêts occurred throughout the study period (see Results), leading to marked variation in population size over the past 30 years (Richard et al. 2010). This management context provided us with a quasi-experimental manipulation of red deer density to assess the relevance of roaring counts as a management tool of red deer (Sinclair 1989). Every deer shot was sexed and aged. Our study area was free of predators that could have any influence on deer behaviour or habitat use.

Roaring counts

We analysed roaring counts of red deer performed during 31 consecutive years from 1978 to 2008. Each year, four surveys have been conducted ($N = 124$) at the time of the rut from mid-September to mid-October (Loe et al. 2005; mean date of counts was 25 September). Red deer were counted at 47 observation spots within the PPNR (see Fig. 1), with one or two observers at each spot. Counts were performed at

dusk and the next morning at dawn, twice a year and required approximately three hours to be completed. Observations included both red deer seen and heard. The animals seen during counts were classified into three age-sex classes (calves, stags and hinds) according to antler and body size characteristics. For seen red deer, observers recorded the exact location, the direction and time of arrival and departure, the activity (roaring or silent) and the shape of antlers for males. For heard red deer, the approximate location, the start time and end of roar were recorded. Similarly to Ciucci et al. (2009), we used triangulation to locate red deer males more accurately using bearings taken by different observers. All this information was simultaneously analysed (by J-L. Hamann) to correct as far as possible for double counting and distinguish sighted stags from roaring stags. Hence, roaring males corresponded to stags that were not seen.

For each survey, we calculated an abundance index as the total number of red deer observed (AI-R). Poisson regression is often used to model count variables (Agresti 2002). However, overdispersion often occurs when a Poisson regression is used, resulting in an underestimated variance of the regression model parameters (Poortema 1999). Here, the overdispersion parameter Φ , calculated as a ratio of the deviance to degrees of freedom, was $\gg 1$ for AI-R ($\Phi = 4.35$), providing evidence for overdispersion. Thus, similarly to Garel et al. (2010), we used generalised linear models (GLM) with a log-link

and negative binomial distribution to obtain annual estimates of AI-R. The model included year as a factor (31 modalities) and both daily rainfall and daily mean temperature, which are likely to influence roaring counts (Ciucci et al. 2009). We coded the rainfall variable as a two-level factor (i.e. presence/absence of rainfall). Climate data were obtained from a Météo-France weather station at Danne-et-Quatre-Vents (48.7°N, 7.29°E) located < 5 km from our study area. To obtain corrected values of annual AI-R, we used back-transformed year-specific coefficients of the fitted model.

AI-R included both acoustic and visual components, which did not necessarily have the same detection probabilities, and these ones may be influenced by different factors. Consequently, we derived two other abundance indices following the procedure used for AI-R; one based on acoustic detection of stags (AI-Ra) and the other based on visually detected individuals (AI-Rv).

Estimates of population size and spotlight counts

Spotlight counts of red deer were conducted from February to April each year from 1979 to 2009 (N = 495). The method consisted of driving three independent routes (median length of 33 km) within the PPNR twice a month and counting every deer seen with a powerful spotlight. We used a generalised linear model with a log-link and negative binomial distribution to obtain the total number of red deer observed during annual spotlight counts (AI-I). The model included year as a factor (31 modalities), the route length (log-transformed) as an offset covariate and a two-level factor describing the conditions of observation ('good' (i.e. clear sky) vs 'bad' (i.e. occurrence of rainfall, snowfall and/or fog); see Garel et al. 2010 for details). As hunting occurred between roaring counts and spotlight counts five months later, we added the number of deer killed in the PPNR between the two counts as a variable. Indeed, the number of deer killed during the hunting season varied strongly among years and affected the number of red deer counted during spotlight counts negatively ($\beta = -0.028 \pm 0.010$, $P = 0.005$), supporting that hunting pressure accounted for most annual changes in population size (Bonenfant et al. 2002, Richard et al. 2010). More details about spotlight counts and its relationship with population size can be found in Garel et al. (2010). Here, we only used spotlight counts as a reference because spotlight counts were available for 31 years, whereas Capture-Mark-Re-

capture (CMR) estimates were available for only 16 years (Garel et al. 2010).

Testing roaring counts as an index of abundance

We first examined the relationship between AI-R estimated from the generalised model (see section Roaring counts) and AI-I, using a standard linear model. Then, we tested for the negative relationship between AI-R and the number of red deer shot within the PPNR during the previous hunting season using a standard linear model. We log-transformed all these variables to satisfy the homoscedasticity hypothesis of linear models (see also Loison et al. 2006, Garel et al. 2010). We tested the statistical significance of correlation coefficients (r) by examining whether zero was included within coefficient confidence interval at 95%.

Results

Roaring counts (inter-annual CV = 22%) led to an average of 69.0 ± 1.9 animals during the study period. Visual and acoustic detections accounted for 70% and 30% of the total number of observed red deer, respectively. Temperature ranged from 7.3 to 20.6°C (averaging 13.3°C across study years) and was negatively correlated with AI-R ($\beta = -0.024 \pm 0.010$, $P = 0.016$). AI-R tended to decrease with the occurrence of rainfall ($\beta = -0.083 \pm 0.049$, $P = 0.095$). Once the conditions of observation were accounted for, AI-R was highly variable from year to year ($\chi^2 = 121.8$, $df = 30$, $P < 0.001$) ranging from 46.0 ± 5.6 animals in 1991 to 108.4 ± 12.1 animals in 1997 (Fig. 2). Since the value of deviance divided by the number of degrees of freedom was close to 1 ($\Phi = 1.41$), the model fitted the data satisfactorily.

In contradiction with our first prediction, the log-transformed AI-R was not correlated to log-transformed AI-I ($r = -0.01$, $CI = -0.36 - 0.34$, $N = 31$ years; Fig. 3). We also assessed the relationship between the two components of AI-R (AI-Ra and AI-Rv) and AI-I, but our results remained unchanged with or without distinguishing between visual and acoustic detection of deer (see Appendix I).

On average, 43 red deer were shot each year between 1978 and 2007 in the PPNR, but the hunting effort varied considerably among years, with 78 deer shot during the 1979 hunting season and 24 during the 1996 hunting season. Contrary to our second prediction, log-transformed AI-R was not influenced by the log number of male and female red deer killed

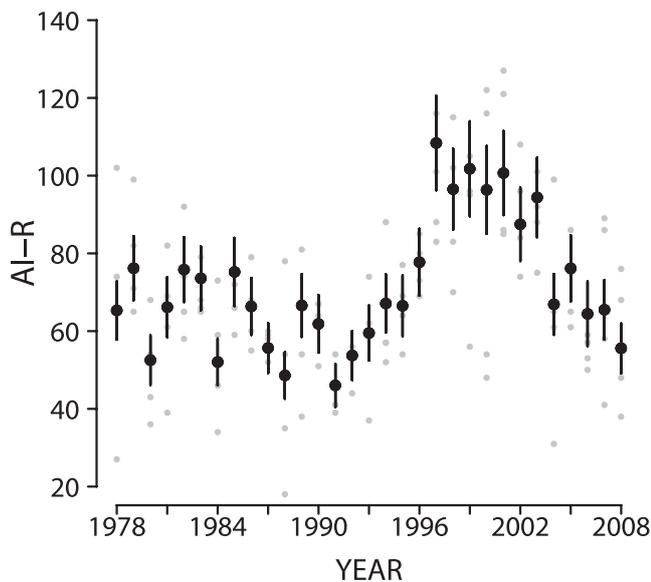


Figure 2. Yearly variations in the total number of red deer observed during roaring counts (AI-R) from 1978 to 2008 in the red deer population of the La Petite Pierre, France. Estimates (\pm SE) account for climatic conditions and were obtained from a negative binomial model (see Material and methods), and the grey points correspond to raw data.

during the previous hunting season ($r = -0.27$, CI = $-0.58 - 0.09$, $N = 30$ years).

Discussion

Roaring counts are commonly used in addition to spotlight counts by managers in European countries to monitor red deer populations (Ciucci et al. 2009). For instance, the method has been systematically used since the 1970s to monitor the endangered Corsican red deer *C. e. corsicanus* in Sardinia (Lovari et al. 2007). Indeed, at the time of the mating season, red deer gather and are easily detected, particularly roaring stags, due to movements and sounds. Although roaring counts might be a useful alternative to counting methods such as spotlight counts in mountainous areas (Bobek et al. 1986, Albaret et al. 1989), a formal evaluation of its reliability has been lacking. In our study, we found no relationship between the total number of red deer observed during roaring counts (AI-R) and spotlight counts, suggesting that roaring counts do not capture the variation of abundance of the resident deer population.

Bias can occur in analysis of counts when data contain sources of variation other than the changes in the size of the population. Potential sources of variation include weather, habitat or differences between observers in their ability to detect animals

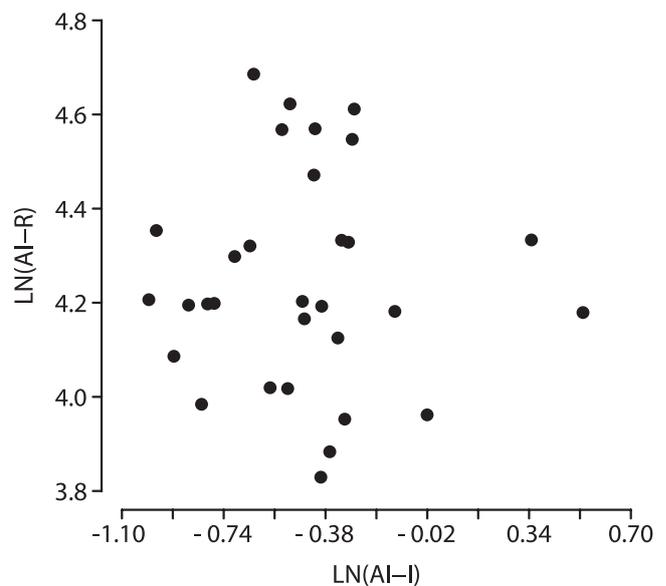


Figure 3. Relationship between roaring count index (AI-R) and the spotlight counts (AI-I) on a log scale ($r = -0.01$, $P = 0.96$) in the red deer population of the La Petite Pierre, France.

(Garel et al. 2005a). These effects should be taken into account to get reliable measures of population change (for an example in red deer, see Garel et al. 2010). Here, we reported a negative relationship between temperature and AI-R, which can be explained by a reduction of animal activity when temperature increases. Garel et al. (2005b) found similar results on ground and aerial counts during summer in mouflon *Ovis gmelini musimon*. Roars can usually be heard from a long distance in good weather conditions, and therefore, sampling points in the field are generally separated by several hundred metres. Heavy rainfall decreases the vocal activity of stags (Pépin et al. 2001). However, the negative effect of rainfall on AI-R we reported here reflected the difficulty for observers to see animals under rainy conditions rather than a difficulty to hear roars (see Appendix I).

In addition to weather conditions, the proportion of roaring stags in a population depends on several factors such as condition of the stags, age structure, population density, quality and spatial distribution of the resources (Clutton-Brock & Albon 1979, Carranza 1995, Pépin et al. 2001, Yoccoz et al. 2002). Moreover, differential visibility of the various age and sex classes introduces additional sources of uncertainty in the population abundance estimates (Ciucci et al. 2009). Deer activity during the rut is fundamentally different between sexes, with stags roaring and moving a lot, whereas females remain rather elusive during this period. The detection

probability is thus higher and less variable in males than in females which explains that 62% of the red deer recorded during the rut in the PPNR were males.

In mountainous areas, the altitudinal movements of red deer from a low-elevation winter range to a high-elevation summer range is a common pattern of migration (Mysterud et al. 2001). In the PPNR, due to a very low range in elevation (see section Material and methods), such an altitudinal migration to benefit from high quality food did not occur. However, a marked sex-specific seasonal migration occurred in relation to mating opportunities. While females tend to occupy the same particular area during the whole year, in autumn, males move to rutting areas that are up to 30 km from the area occupied during the rest of the year (Bonenfant 2004:226). This form of partial migration (*sensu* Dingle & Drake 2007) has also been reported in a red deer population in Sweden where an average distance of 14 km and a maximum distance of 47 km were recorded between rut and summer/winter observations (Jarnemo 2008). Consequently, a high proportion of the stags that are observed during roaring counts are not resident of PPNR. On the contrary, red deer counted and monitored during spotlight counts that occurred from February to April were resident deer of PPNR. A combination of seasonal migration and unreliability of roaring counts are likely to explain the lack of a positive relationship between AI-R and spotlight counts found in our study. Although we can not prove that roaring counts were unreliable because the population size in autumn was unknown, the observed effects of hunting provided further support to our interpretation. Indeed, we found an absence of a relationship between AI-R and the number of red deer harvested in the reserve during the previous hunting season, whereas hunting quotas led to a decrease in the number of red deer counted during spotlight counts.

Successful management of large herbivores requires the monitoring of IEC describing animal performance, herbivore impact on habitat and animal abundance (Morellet et al. 2007). Monitoring temporal changes in these indicators provides a basis for setting hunting quotas to achieve specific management objectives. In this sense, spotlight counts provide a reliable index of the abundance of resident populations in a given area for red deer (Garel et al. 2010). On the other hand, roaring counts cannot be interpreted as a reliable IEC because they do not track abundance of the resident population of red deer despite a much larger sampling effort compared

to spotlight counts (average annual number of 184 observers for roaring counts vs 72 for spotlight counts). Based on a least-cost approach for achieving management objectives, roaring counts should not be used for managing resident red deer populations.

Acknowledgements - we are grateful to the Office National des Forêts and to all volunteers for their participation during roaring counts. We would also like to thank Météo-France for the climatic data and Aurélie Barboiron for Figure 1. We also thank Stefano Focardi and an anonymous reviewer for insightful comments on a previous draft of the manuscript.

References

- Agresti, A. 2002: Categorical Data Analysis. 2nd edition. - John Wiley & Sons, New York, New York, USA, 710 pp.
- Albaret, M., Lartiges, A. & Peroux, R. 1989: Recensements des cerfs au brame. Essais réalisés sur la Pinatelle d'Allanche (Cantal). - Bulletin Mensuel de l'Office National de la Chasse 132: 21-26. (In French).
- Andersen, J. 1953: Analysis of a Danish roe-deer population (*Capreolus capreolus* (L)) based upon the extermination of the total stock. - Danish Review of Game Biology 2: 127-155.
- Andersen, R., Duncan, P. & Linnell, J.D.C. 1998: The European Roe Deer: The biology of Success. - Scandinavian University Press, Oslo, Norway, 376 pp.
- Bobek, B.K., Perzanowski, K. & Zielinski, J. 1986: Red deer population census in mountains: testing of an alternative method. - Acta Theriologica 31: 423-431.
- Bonenfant, C. 2004: Rôle des contraintes évolutives dépendantes du sexe en biologie des populations: l'exemple du Cerf Élaphe (*Cervus elaphus*). - PhD thesis, University Claude Bernard Lyon 1, Lyon, France, 344 pp.
- Bonenfant, C., Gaillard, J-M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Loe, L.E., Blanchard, P., Pettorelli, N., Owen-Smith, N., Du Toit, J. & Duncan, P. 2009: Empirical evidence of density-dependence in populations of large herbivores. - Advances in Ecological Research 41: 313-357.
- Bonenfant, C., Gaillard, J-M., Klein, F. & Loison, A. 2002: Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. - Ecography 25: 446-458.
- Carranza, J. 1995: Female attraction by males versus sites in territorial rutting red deer. - Animal Behaviour 50: 445-453.
- Cederlund, G., Bergqvist, J., Kjellander, P., Gill, R., Gaillard, J-M., Boiseaubert, B., Ballon, P. & Duncan, P. 1998: Managing roe deer and their impact on the environment: maximising the net benefits to society. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); The European roe deer: the biology of success, Scandinavian University Press, Oslo, Norway, pp. 337-372.
- Chevrier, T., Saïd, S., Widmer, O., Hamard, J.P., Saint-

- Andrieux, C. & Gaillard, J-M. 2012: The oak browsing index correlates linearly with roe deer density: a new indicator for deer management? - *European Journal of Wildlife Research* 58: 17-22.
- Ciucci, P., Catullo, G. & Boitani, L. 2009: Pitfalls in using counts of roaring stags to index red deer (*Cervus elaphus*) population size. - *Wildlife Research* 36: 126-133.
- Clutton-Brock, T.H. & Albon, S.D. 1979: The roaring of red deer and the evolution of honest advertisement. - *Behaviour* 69: 145-170.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982: Red deer: behavior and ecology of two sexes. - University of Chicago Press, Chicago, Illinois, USA, 400 pp.
- Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C. & Waller, D.M. 2004: Ecological impacts of deer overabundance. - *Annual Review of Ecology and Systematics* 35: 113-147.
- Dingle, H. & Drake, V.A. 2007: What is migration? - *Bioscience* 57: 113-121.
- Fafarman, K.R. & DeYoung, C.A. 1986: Evaluation of spotlight counts of deer in South Texas. - *Wildlife Society Bulletin* 14: 180-185.
- Festa-Bianchet, M. 2003: Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. - In: Festa-Bianchet, M. & Apollonio, M. (Eds.); *Animal behavior and wildlife conservation*, Island Press, Washington D.C., USA, pp. 191-207.
- Fuller, R.J. & Gill, R.M.A. 2001: Ecological impacts of increasing numbers of deer in British woodland. - *Forestry* 74: 193-199.
- Gaillard, J-M., Loison, A. & Toïgo, C. 2003: Variation in life history traits and realistic population models for wildlife: the case of ungulates. - In: Festa-Bianchet, M. & Apollonio, M. (Eds.); *Animal behavior and wildlife conservation*, Island Press, Washington D.C., USA, pp. 115-132.
- Garel, M., Bonenfant, C., Hamann, J-L., Klein, F. & Gaillard, J-M. 2010: Are abundance indices derived from spotlight counts reliable to monitor red deer *Cervus elaphus* populations? - *Wildlife Biology* 16(1): 77-84.
- Garel, M., Cugnasse, J-M., Gaillard, J-M., Loison, A., Santosa, Y. & Maublanc, M-L. 2005a: Effect of observer experience on the monitoring of a mouflon population. - *Acta Theriologica* 50: 109-114.
- Garel, M., Cugnasse, J-M., Loison, A., Gaillard, J-M., Vuiton, C. & Maillard, D. 2005b: Monitoring the abundance of mouflon in South France. - *European Journal of Wildlife Research* 51: 69-76.
- Garel, M., Gaillard, J-M., Jullien, J-M., Dubray, D., Maillard, D. & Loison, A. 2011: Population abundance and early spring conditions determine variation in body mass of juvenile chamois. - *Journal of Mammalogy* 92: 1112-1117.
- Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. 2004: The management of wild large herbivores to meet economic, conservation and environmental objectives. - *Journal of Applied Ecology* 41: 1021-1031.
- Gunson, J.R. 1979: Use of night-lighted census in management of deer in Alberta and Saskatchewan. - *Wildlife Society Bulletin* 7: 259-267.
- Jarnemo, A. 2008: Seasonal migration of male red deer (*Cervus elaphus*) in southern Sweden and consequences for management. - *European Journal of Wildlife Research* 54: 327-333.
- Langvatn, R. & Loison, A. 1999: Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in Central Norway. - *Wildlife Biology* 5(4): 213-223.
- Loe, L.E., Bonenfant, C., Mysterud, A., Gaillard, J-M., Langvatn, R., Klein, F., Calenge, C., Ergon, T., Pettorelli, N. & Stenseth, N.C. 2005: Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. - *Journal of Animal Ecology* 74: 579-588.
- Loison, A., Appolinaire, J., Jullien, J-M. & Dubray, D. 2006: How reliable are total counts to detect trends in population size of chamois *Rupicapra rupicapra* and *R. pyrenaica*? - *Wildlife Biology* 12(1): 77-88.
- Lovari, S., Cuccus, P., Murgia, A., Murgia, C., Soi, F. & Plantamura, G. 2007: Space use, habitat selection and browsing effects of red deer in Sardinia. - *The Italian Journal of Zoology* 74: 179-189.
- Maillard, D., Gaillard, J-M., Hewison, M., Ballon, P., Duncan, P., Loison, A., Toïgo, C., Baubet, E., Bonenfant, C., Garel, M. & Saint-Andrieux, C. 2010: Ungulate status and management in France. - In: Apollonio, M., Andersen, R. & Putman, R. (Eds.); *European Ungulates and their Management in the 21st Century*, Cambridge University Press, New York, New York, USA, pp. 441-475.
- McCullough, D.R. 1982: Evaluation of night spotlighting as a deer study technique. - *Journal of Wildlife Management* 46: 963-973.
- Milner, J., Bonenfant, C., Mysterud, A., Gaillard, J-M., Csányi, S. & Stenseth, N.C. 2006: Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. - *Journal of Applied Ecology* 43: 721-734.
- Morellet, N., Champely, S., Gaillard, J-M., Ballon, P. & Boscardin, Y. 2001: The browsing index: new tool uses browsing pressure to monitor deer populations. - *Wildlife Society Bulletin* 29: 1243-1252.
- Morellet, N., Gaillard, J-M., Hewison, A.J.M., Ballon, P., Boscardin, Y., Duncan, P., Klein, F. & Maillard, D. 2007: Indicators of ecological change: new tools for managing populations of large herbivores. - *Journal of Applied Ecology* 44: 634-643.
- Mysterud, A., Langvatn, R., Yoccoz, N.G. & Stenseth, N.C. 2001: Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. - *Journal of Animal Ecology* 70: 915-923.
- Pépin, D., Cargnelutti, B., Gonzales, G., Joachim, J. & Reby, D. 2001: Diurnal and seasonal variations of roaring ac-

- tivity of farmed red deer stags. - *Applied Animal Behaviour Science* 74: 233-239.
- Poortema, K. 1999: On modelling overdispersion of counts. - *Statistica Neerlandica* 53: 5-20.
- Richard, E., Gaillard, J-M., Saïd, S., Hamann, J-L. & Klein, F. 2010: High red deer density depresses body mass of roe deer fawns. - *Oecologia* 163: 91-97.
- Rooney, T.P. & Waller, D.M. 2003: Direct and indirect effects of white-tailed deer in forest ecosystems. - *Forest Ecology and Management* 181: 165-176.
- Seiler, A. 2004: Trends and spatial patterns in ungulate-vehicle collisions in Sweden. - *Wildlife Biology* 10(4): 301-313.
- Sinclair, A.R.E. 1989: Population regulation in animals. - In: Cherrett, J.M. & Bradshaw, A.D. (Eds.); *Ecological concepts: the contribution of ecology to an understanding of the natural world*. Blackwell Scientific Publications, Oxford, UK, pp. 197-241.
- Strandgaard, H. 1967: Reliability of the Petersen method tested on a roe deer population. - *Journal of Wildlife Management* 31: 643-651.
- Vincent, J-P., Gaillard, J-M. & Bideau, E. 1991: Kilometric index as biological indicator for monitoring forest roe deer populations. - *Acta Theriologica* 36: 315-328.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. 2002: *Analysis and management of animal populations: modeling, estimation, and decision making*. - Academic Press, New York, New York, USA, 817 pp.
- Yoccoz, N.G., Mysterud, A., Langvatn, R. & Stenseth, N.C. 2002: Age- and density-dependent reproductive effort in male red deer. - *Proceedings of the Royal Society, Series B* 269: 1523-1528.
- Zannèse, A., Baïsse, A., Gaillard, J-M., Hewison, A.J.M., Saint-Hilaire, K., Toïgo, C., Van Laere, G. & Morellet, N. 2006: Hind foot length: An indicator for monitoring roe deer populations at a landscape scale. - *Wildlife Society Bulletin* 34: 351-358.

Appendix I. Relationship between spotlight counts (AI-I) and the acoustic (AI-Ra) and visual (AI-Rv) components of roaring counts

Methods

We used generalised linear models (GLM) with a log-link and negative binomial distribution to obtain annual standardised estimates of AI-Ra and AI-Rv. The models included year as a factor (31 modalities), and the daily rainfall and daily mean temperature which were likely to influence the results of roaring counts. We coded the rainfall variable as a two-level factor (i.e. presence/absence of rainfall). We examined the relationship between AI-Ra and AI-Rv estimated from the generalised model and AI-I, using a standard linear model. We tested the significance of correlation coefficients (r) by examining whether zero

was included within coefficient confidence interval at 95%.

Results

We found no evidence of any influence of climate on AI-Ra (all P -values > 0.40) while AI-Rv decreased with increasing temperature ($\beta = -0.030 \pm 0.013$, $P = 0.02$) and rainfall ($\beta = -0.130 \pm 0.060$, $P = 0.04$). Neither the log-transformed AI-Ra nor the log-transformed AI-Rv was correlated with the log-transformed AI-I (LN AI-Ra: $r = -0.35$, $CI = -0.69 - 0.11$, $N = 31$ years; LN AI-Rv: $r = 0.14$, $CI = -0.33 - 0.55$, $N = 31$ years).

Appendix 6



De l'utilité des comptages au brame pour la gestion des populations de cerfs



© J.-L. Hamann / ONCFS

JEAN-LUC HAMANN¹,
MATHIEU DOUHARD²,
CHRISTOPHE BONENFANT²,
PHILIPPE MORTZ³,
JACQUES MICHALLET¹,
MATHIEU GAREL⁴,
FRANÇOIS KLEIN¹

¹ ONCFS, CNERA Cervidés – sanglier.
jean-luc.hamann@oncfs.gouv.fr
francois.klein@oncfs.gouv.fr

² UMR CNRS 5558 –

Université Claude Bernard Lyon 1.
mathieu.douhard@gmail.com
christophe.bonenfant@univ-lyon1.fr

³ ONF, Maison forestière Zellerhof –
67330 Dossenheim-sur-Zinsel.

philippe.mortz@onffr

⁴ ONCFS, CNERA Faune de montagne.
mathieu.garel@oncfs.gouv.fr

Les comptages au brame sont une institution dans le monde cynégétique. Mais au-delà de l'émotion et de la convivialité qu'ils suscitent, sont-ils réellement utiles et pertinents pour la gestion des grands cervidés vivant en milieu forestier ? Pour le savoir, cette pratique, qui est conduite depuis trente ans dans la RNCFS de La Petite-Pierre (67), a été comparée à la méthode de l'indice nocturne. Les résultats montrent que ces comptages au brame ne sont pas fiables... Explications.

Des ICE pour suivre la dynamique des populations

La recherche de méthodes de suivi permettant d'apprécier la dynamique des populations de grands herbivores dans un contexte de gestion est l'objet de nombreux travaux menés par l'ONCFS. Faisant aujourd'hui référence dans le domaine, le suivi à long terme d'indicateurs de changements écologiques ou ICE (Morellet, 2008), qui se déclinent en différentes familles complémentaires (indicateurs d'abondance, de performance et d'impact sur le milieu), apporte un diagnostic objectif et fiable sur la relation entre une population et son environnement. Les ICE permettent alors aux gestionnaires de savoir si la population est contrôlée, en croissance ou en décroissance.

Récemment, l'indice nocturne a été validé pour le cerf sur la Réserve nationale de chasse et de faune sauvage (RNCFS) de La Petite-Pierre, comme un indicateur capable de suivre les variations réelles d'abondance de la population présente (Hamann *et al.*, 2011). Nous avons également observé que cet indice diminue avec l'augmentation du nombre d'individus chassés au cours de la saison de chasse précédant les comptages. De même, à mesure que l'indice nocturne augmente, les indicateurs de performance que sont le taux de gestation des bichettes et le poids des faons diminuent (Bonenfant *et al.*, 2002). Comme attendu pour un ICE, l'indice nocturne offre donc aux gestionnaires un moyen d'apprécier la dynamique des populations de cerfs.

Les comptages au brame, quelle valeur indiciaire ?

Dans la présente étude, nous avons cherché à savoir si les comptages au brame, largement utilisés pour suivre les populations de cerfs, avaient les mêmes propriétés que l'indice nocturne et pouvaient constituer un nouvel ICE (Douhard *et al.*, 2013). À cette fin, nous avons comparé les variations temporelles de l'indice brame (nombre moyen d'animaux dénombrés par sortie) avec celles de l'indice nocturne et des prélèvements. Notre hypothèse de travail était la suivante : si l'indice brame est représentatif de la dynamique des populations, on devrait observer une relation positive avec l'indice nocturne.

Le suivi du brame, un moment unique

Chaque année à la même période, une émulation fiévreuse agite le site d'étude de La Petite-Pierre, comme pour de nombreux autres massifs en France : de mi-septembre à mi-octobre, le cerf brame.

Pour l'occasion, quatre sorties ont été organisées tous les ans, de l'automne 1978 à l'automne 2008. Sur les 2 800 hectares de la RNCFS, de 30 à 47 postes d'observation ont été placés, avec un ou deux observateurs par poste (figure 1). Les sorties vont par paire, la première étant faite un soir, la seconde le lendemain matin au crépuscule. Par comparaison, l'indice phare mobilise seulement douze personnes, avec deux sorties par mois pendant trois mois.

Chaque sortie dure approximativement trois heures, au cours desquelles les observateurs notent soigneusement le nombre et la localisation des animaux vus, ainsi que celle des cerfs bramant entendus. Chaque contact, visuel ou auditif, est reporté sur une carte. Pour les animaux vus, le sexe, la classe d'âge et les heures d'arrivée et de départ de la zone visible sont reportés sur une fiche de terrain. Sont également décrits par un dessin la ramure des cerfs ainsi que leur comportement (bramant ou pas). Pour les cerfs uniquement entendus, les heures de début et de fin du brame sont notées. L'ensemble de ces informations est ensuite dépouillé et analysé, afin de corriger au mieux les doubles comptages.

L'indice brame est défini comme étant le nombre total d'individus différents comptabilisés par sortie, toutes classes d'âge et de sexe confondues. En moyenne, dans notre étude, cet indice vaut 69 individus par sortie, parmi lesquels 70 % ont été vus et

30 % entendus – ces derniers étant constitués uniquement de mâles. Sur la durée de l'étude, l'indice brame a fortement varié d'une année à l'autre, passant de moins de 50 individus en 1991 à près de 110 en 1998, avant

de revenir à des valeurs moyennes pour les dernières années (figure 2). Du fait de la plus forte probabilité de détection des mâles par rapport aux femelles, l'indice brame est composé à 62 % de mâles.

Figure 1 Situation géographique de la RNCFS de La Petite-Pierre (2 800 hectares) et répartition des 48 postes d'observation (points gris foncé) utilisés lors des trente ans de comptages au brame.

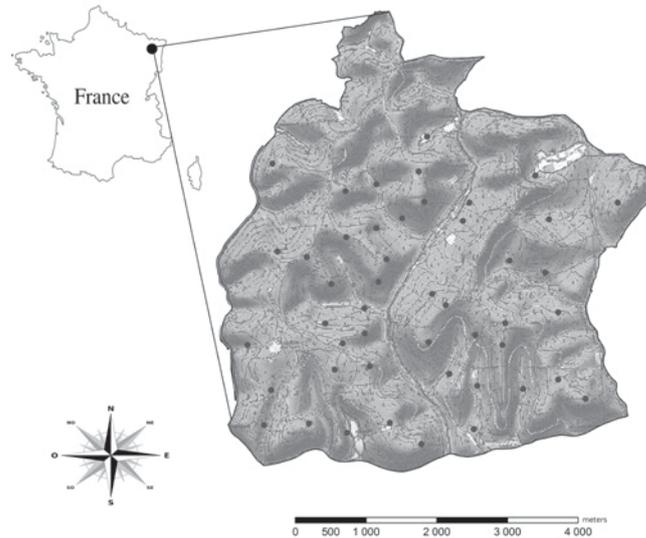
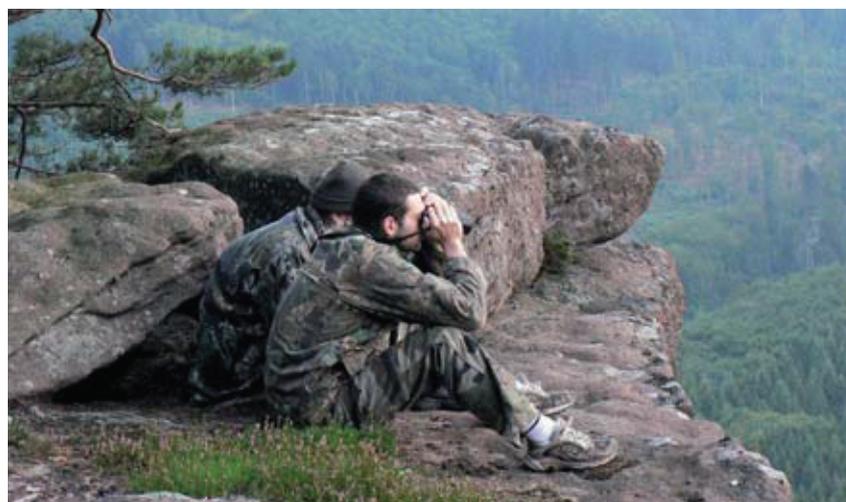
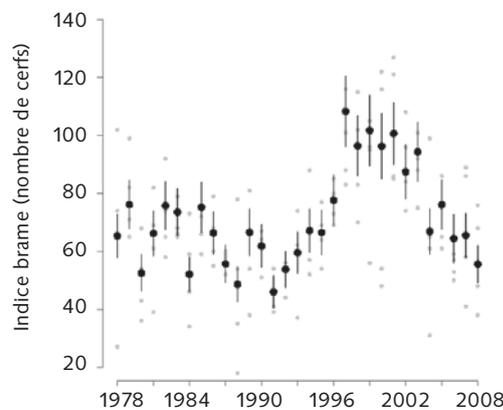


Figure 2 Variation interannuelle du nombre moyen d'animaux vus et entendus sur la RNCFS de La Petite-Pierre.

Les points gris représentent les répétitions des comptages, les points noirs correspondent à la moyenne du nombre d'animaux observés par sortie et les barres, aux intervalles de confiance à 95 % autour de la moyenne.



© J.-L. Hamann/ONCFS

Le suivi du brame est toujours un moment attendu qui mobilise les énergies.

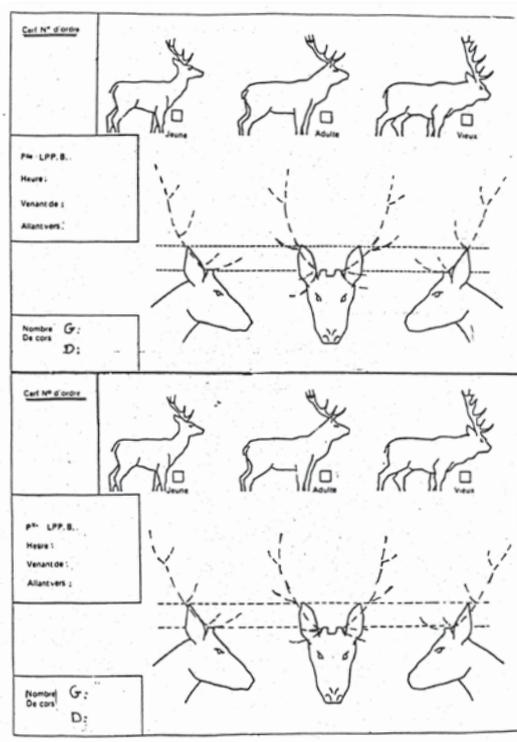
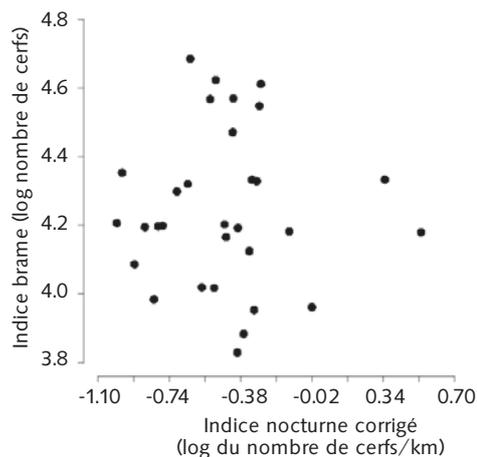
Un indice qui s'avère peu informatif

Comme pour la plupart des indices d'abondance étudiés jusqu'ici, l'indice brame s'est lui aussi montré sensible aux conditions d'observation. Ainsi, par exemple, nous avons trouvé que la pluie faisait diminuer le nombre d'animaux vus et entendus : quand les comptages avaient lieu sous la pluie, 12 % d'animaux en moins étaient vus par rapport à des conditions sans précipitations. À l'inverse, l'indice brame a augmenté fortement après la tempête Lothar de 1999, qui a créé subitement 15 % de zones ouvertes en plus... Nous avons donc pris en compte ces effets environnementaux pour rendre les différentes séries de comptages au brame comparables, tant au cours de la saison que d'une année sur l'autre.

Nous avons ensuite comparé les variations annuelles de la moyenne des comptages au brame avec l'indice nocturne d'abondance réalisé l'hiver suivant (Hamann *et al.*, 2011) et avec le plan de chasse réalisé dans la RNCFS de La Petite-Pierre. Malgré la forte densité d'observateurs sur le terrain (1,7 aux 100 hectares), nous n'avons trouvé aucune relation ($r = -0,01$) entre l'indice nocturne et les comptages au brame réalisés sur le même site, à cinq mois d'intervalle (*figure 3*). De même, les prélèvements cynégétiques réalisés la saison précédente n'expliquent pas de manière significative les variations interannuelles observées pendant les comptages au brame ($r = -0,27$).

De cette étude de près de trente ans, il ressort très clairement que les comptages au brame ne reflètent pas la dynamique des populations de cerfs. Plus étonnant encore, les prélèvements par la chasse, qui expliquent une large part des variations interannuelles de l'effectif de la population à La Petite-Pierre, n'influencent pas non plus le nombre d'animaux vus et entendus en période de brame. De cette absence de relation, il découle que les comptages au brame ne peuvent pas être considérés comme un ICE d'abondance.

Figure 3 Relation observée entre l'indice nocturne et les comptages au brame sur la RNCFS de La Petite-Pierre.



Exemple de fiche de relevés de terrain.

La présence de plusieurs cerfs bramant dans un même périmètre complique singulièrement leur dénombrement.



En conséquence, nous déconseillons fortement aux gestionnaires de la faune sauvage d'établir les plans de chasse, ou de suivre l'abondance de leurs populations de cerfs, sur la base de données issues des comptages au brame.

Des observations délicates

A priori, le brame constitue une période propice pour réaliser des observations et en déduire un indice d'abondance. En effet, les animaux sont très actifs durant cette période et donc plus faciles à détecter. Les mâles sont mobiles et passablement bruyants. Quant aux femelles, elles sont également plus visibles que durant le reste de l'année à cause des nombreuses sollicitations des mâles. Mais ce qui pourrait passer pour un avantage se révèle rapidement problématique pour la mise en œuvre d'un indice d'abondance fiable.

Au cours de toutes ces années d'observation, de nombreux problèmes nous sont apparus qui peuvent influencer les résultats de l'indice brame. Tout d'abord, la détermination auditive du nombre de cerfs différents est très difficile quand plusieurs individus sont présents au même endroit. Ensuite, un même cerf peut se déplacer en seulement quelques minutes sur des distances de plusieurs centaines de mètres, en effectuant de nombreux allers-retours. Ainsi, les mouvements des cerfs et des biches engendrent des risques importants de doubles comptages sur les nombreux postes d'observation. De plus, l'évaluation des distances entre observateurs et cerfs bramant est très incertaine. Au final, malgré le dépouillement attentif des données pour éliminer les doubles comptages, il existe une forte incertitude sur le nombre de cerfs différents comptabilisés et donc sur la valeur de l'indice brame.

Qu'est-ce qu'une population de cerfs ?

Les raisons pour lesquelles les comptages au brame sont très peu liés à la dynamique des populations trouvent probablement aussi leur origine dans la biologie particulière du cerf. L'une, cruciale pour l'indice brame, concerne l'utilisation de l'espace.

Les cerfs et les biches de la RNCFS de La Petite-Pierre ont fait l'objet de suivis de leurs déplacements à l'aide de colliers émetteurs (VHF) ou géo-localisés (GPS). Une caractéristique de cette espèce est la différence marquée dans l'utilisation de l'espace entre les mâles et les femelles. Quand les biches montrent une forte philopatrie et un domaine vital centré sur une zone (Hamann *et al.*, 1997), les mâles dont les domaines vitaux sont structurés en plusieurs zones (Klein & Hamann, 1999) font notamment

d'importants mouvements saisonniers entre leur zone de refait et leur zone de rut, utilisée de début septembre à fin octobre (figure 4). Au cours de ces migrations saisonnières, ils peuvent parcourir jusqu'à 30 km pour se reproduire. De plus, certains changent de zone de rut en cours de saison, contrairement à la très grande majorité des femelles qui restent fidèles à leur domaine vital.

La conséquence de ces mouvements saisonniers est que de nombreux individus, et tout particulièrement les mâles adultes qui sont les plus visibles et audibles pendant le rut, sont comptés au brame alors qu'ils n'appartiennent pas à la population de cerfs résidant dans la RNCFS de La Petite-Pierre ou dans sa périphérie immédiate. À l'inverse, les animaux comptabilisés au cours des comptages nocturnes réalisés de février à

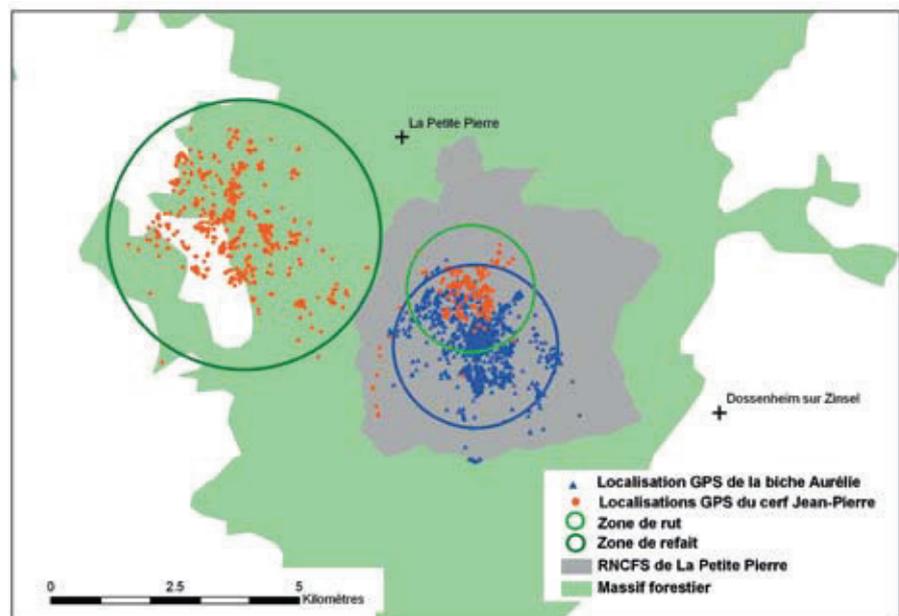


© B. Hamann

L'utilisation du collier émetteur (ici sur une biche) a permis de mettre en évidence que, si les biches sont fidèles à un domaine vital, les cerfs peuvent parcourir de grandes distances durant le rut. Certains peuvent donc être dénombrés alors qu'en fait, ils n'appartiennent pas à la population locale ; ce qui a des conséquences sur la gestion.

Figure 4 Migration saisonnière d'un mâle de cerf adulte suivi sur le secteur de La Petite-Pierre.

La figure met en évidence la distance qui peut exister entre la zone de refait (cercle vert foncé), où l'animal vit dix mois de l'année, et la zone de rut (cercle vert clair), où il se rend pour la reproduction de septembre à octobre. Les localisations annuelles d'une biche résidente de la RNCFS de La Petite-Pierre sont également représentées à titre de comparaison (cercle bleu).



avril résident une grande partie de l'année dans la RCNFS, y compris les mâles.

De plus, l'indice brame peut varier indépendamment de l'abondance des mâles dans la population, mais en fonction de leurs classes d'âge selon les années. Par exemple, pour un même effectif, le brame sera moins marqué si la population se compose essentiellement de jeunes mâles plutôt que d'adultes. Ceci parce que ces derniers sont plus actifs et peuvent provoquer l'émulation générale. Un dérangement excessif (lors de comptages, par des photographes, par du public venant écouter le brame...) peut également rendre les cerfs plus discrets. Autant de situations qui compliquent l'utilisation et l'interprétation de l'indice brame.

Conclusions

Chez les cervidés, les femelles représentent le moteur de la dynamique des populations. Chez le cerf, la reproduction annuelle des biches, leur mortalité et celle de leurs faons déterminent très largement les variations annuelles d'abondance. Les mâles étant très fortement polygynes (un mâle peut féconder de nombreuses femelles), qu'ils soient sous-représentés ou au contraire surreprésentés dans la population, la reproduction des femelles – et donc la dynamique de population – s'en trouvera peu affectée. En d'autres termes, la variation d'abondance des mâles n'est pas nécessairement représentative de la dynamique des populations.

L'indice brame montre une absence de fiabilité et ne reflète aucune variation de

l'abondance d'une population ; il ne peut donc pas être considéré comme un ICE pertinent et fiable. Toutefois, il peut potentiellement refléter l'expansion géographique d'une population (mais alors elle sera visible avec d'autres indices). Les comptages au brame peuvent par ailleurs revêtir un caractère convivial ou relationnel parfois recherché (fédérer différents gestionnaires). Des alternatives existent pour comprendre comment fonctionne une population de cerfs comme l'indice nocturne qui, associé à la mesure du poids des faons et du taux de gestation des bichettes, permet d'obtenir un résultat bien plus pertinent et avec un effort logistique bien moindre.

Remerciements

Les comptages au brame ont mobilisé de très nombreux participants, professionnels de l'ONCFS (DER, SD, BMI, DIR) et de l'Office national des forêts (ONF), ainsi que des bénévoles dont certains sont fidèles depuis le début des suivis. À ces quelques centaines de bonnes volontés nous voulons témoigner notre gratitude. Merci à Aurélie Barboiron (ONCFS) pour la réalisation de la carte des domaines vitaux. Merci à Gilles Delacour (ONC) qui, en 1976, a initié les premiers comptages au brame malgré certaines oppositions. ■

Bibliographie

- Bonenfant, C., Gaillard, J.-M., Klein, F. & Loison A. 2002. Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. *Ecography* 25: 446-458.
- Douhard, M., Bonenfant, C., Gaillard, J.-M., Hamann, J.-L., Garel, M., Michallet, J. & Klein F. 2013. Roaring counts are not suitable for the monitoring of red deer *Cervus elaphus* population abundance. *Wildlife Biology* 19: 94-101.
- Hamann, J.-L., Klein, F. & Saint-Andrieux, C. 1997. Domaine vital diurne et déplacements de biches (*Cervus elaphus*) sur le secteur de la Petite-Pierre (Bas-Rhin). *Gibier Faune Sauvage* 14 : 1-17.
- Hamann, J.-L., Bonenfant, C., Michallet, J., Holveck, H., Klein, F. & Garel, M. 2011. L'indice nocturne : un indicateur des variations d'abondance des populations de Cerfs. *Faune sauvage* 292 : 17-22.
- Klein, F. & Hamann, J.-L. 1999. Domaines vitaux diurnes et déplacements de cerfs mâles (*Cervus elaphus*) sur le secteur de la Petite-Pierre (Bas-Rhin). *Gibier Faune Sauvage* 16 : 251-271.
- Morellet, N. 2008. La gestion des grands herbivores par les indicateurs de changements écologiques. *Faune sauvage* 282 : 9-18.



© B. Hamann

L'indice brame s'avère être inadapté au suivi de l'évolution d'une population de cerfs. À cette fin, mieux vaut utiliser l'indice nocturne, couplé à la mesure du poids des faons et au taux de gestation des jeunes biches.

Appendix 7

1 The influence of birth date via body mass on individual
2 fitness in a long-lived mammal

FLORIANE PLARD^{1,*}, JEAN-MICHEL GAILLARD¹, TIM COULSON²,
A.J. MARK HEWISON³, MATHIEU DOUHARD¹, FRANÇOIS KLEIN⁴, DANIEL
DELORME⁴, CLAUDE WARNANT⁴, AND CHRISTOPHE BONENFANT¹

3 ¹*Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR5558, Laboratoire de
Biométrie et Biologie Évolutive, F-69622, Villeurbanne, France.*

²*Department of Zoology, University of Oxford, The Tinbergen Building, South Parks Road,
Oxford, OX1 3PS, United Kingdom*

³*INRA, UR035 CEFS, B.P. 52627, 31326 Castanet-Tolosan cedex, France*

⁴*Centre National d'Études et de Recherches Appliquées sur les Cervidés et Sanglier, Office
National de la Chasse et de la Faune Sauvage, 85bis avenue de Wagram, 75017 Paris, France*

4

* Email: floriane.plard@ens-lyon.fr

1 *Abstract.* The timing of birth has marked impacts on early life and early
2 development of newborns in many species. Early-born offspring often survive and
3 grow better than late-born offspring, but despite the long-lasting effects of early
4 conditions on life history traits, the influence of birth date on fitness has rarely been
5 investigated for long-lived species. In this study, we analyzed both the short- and
6 long-term effects of birth date on individual life history traits and explored its
7 subsequent impact on individual fitness in a population of roe deer. We considered
8 both the direct effects, as well as the indirect effects of birth date mediated through
9 the effects of body mass, on demographic parameters. We found that in addition to
10 short-term effects on early body growth and survival, birth date generates “silver
11 spoon” effects on adult life history traits of female roe deer. Birth date had
12 long-lasting effects on female adult body mass such that early-born females were,
13 on average, 3 kg heavier as adults than late-born females, although female adult
14 survival was similar between these categories. Based on the observed relationships
15 between birth date, body mass and demographic parameters, we built an integral
16 projection model describing the simultaneous distributions of birth date and body
17 mass to quantify the fitness consequences of birth date. We found that the fitness of
18 early-born females was higher than that of late-born females. These long-lasting
19 effects of birth date on fitness were mostly mediated through the influence of birth
20 date on recruitment and adult body mass. By determining development of newborns
21 during the early stages of life, birth date has a critical influence on each step of an
22 individual’s subsequent life history trajectory.

23 *Key words:* silver spoon effect, life history traits, IPM, roe deer, body mass

INTRODUCTION

The timing of reproduction is critical in most species because it determines reproductive success of individuals (Price et al. 1988) and thus influences annual population growth. The timing of reproduction has been particularly well studied in the context of climate change (Dickey et al. 2008, Moyes et al. 2011) because a mismatch between birth timing and peak resource availability decreases annual recruitment (Post and Forchhammer 2008). At the population level, a high degree of birth synchrony may be the result of selection pressure on individuals to minimize this mismatch (Rutberg 1987) or, alternatively, be linked to a predator-swamping tactic (Estes 1976, Ims 1990). Indeed, in temperate areas, births are generally characterized by a high degree of seasonality and synchrony each year (Bronson 1989). However, within population variation in individual birth date has the potential to influence greatly early survival and body growth. Because body growth affects adult life history traits, birth date is expected to generate long-term effects on fitness (Lindström 1999, Cam and Aubry 2011). To date, most studies have focused on the short-term consequences of variation in individual birth date on the early stages of life, while evidence for long-term effects of birth date on adult life history stages and on fitness are lacking for long-lived species (Green and Rothstein 1993, Lindström 1999, Cam and Aubry 2011). In this paper, we thus investigated the long-term effects of individual birth date on adult life history traits and individual fitness. Yearly variation in weather conditions influences both the quality and the quantity of available resources during the period around birth. In temperate and northern areas, early-born young benefit from a longer growth period and attain a higher body mass before the onset of the harsh season than neonates born after the peak of vegetation production (moose *Alces alces*, Solberg et al. 2007, bighorn sheep, *Ovis canadensis* Feder et al. 2008). For example, in bighorn sheep, for each day of delayed birth, male and female lambs were respectively 210g and 196g lighter in mid-September (Feder et al. 2008). For a given individual, being born early in the season also

1 has positive effects on early survival in many species (red deer, *Cervus elaphus*, Guinness et al.
2 1978, western gulls, *Larus occidentalis*, Spear and Nur 1994, mosquitofishes, *Gambusia affinis*,
3 Reznick et al. 2006). For instance, the probability of surviving until the end of the first winter
4 for red deer calves born very early was more than double that of calves born very late in the
5 season (Guinness et al. 1978). In some cases, young born very early in the season may
6 encounter harsh environmental conditions (Wilson et al. 2005) or suffer from higher predation
7 (Estes 1976) than young born during the peak of births. However, as a general rule, late-born
8 young have a lower early survival than individuals born early or during the birth peak in most
9 large herbivores and passerine birds.

10 Because it affects the early body development of young which, in turn, often determine
11 performance during adulthood (Douhard et al. 2013), the date of birth has the potential to
12 generate long-term effects on adult phenotypic traits, but this question has seldom been
13 investigated in long-lived species so far. Indeed, a link between reproductive timing and fitness
14 components has been demonstrated for short-lived species (hatching date in lizard (Sinervo and
15 Doughty 1996), birth date in fish (Schultz 1993, Reznick et al. 2006) hatching date and fledging
16 date in birds (Visser and Verboven 1999, Sheldon et al. 2003, Saino et al. 2012) and birth date in
17 small mammals (Réale et al. 2003, Rödel et al. 2009)). However, the long-term effects of
18 environmental conditions in early life on adult life history traits are not universal (e.g., Wauters
19 and Dhondt 1995 on European squirrels, Dobson et al. 1999 on Columbian ground squirrels)
20 because some individuals born in poor conditions can compensate for a bad start (Auer 2010 on
21 guppies). Nevertheless, poor early conditions may also permanently constrain body growth and
22 generate positive covariation among adult life history traits (the “silver spoon effect”, Grafen
23 1988) in long-lived species. For instance, environmental conditions at birth influence both early
24 survival and growth (Gaillard et al. 2003, Landete-Castillejos et al. 2001, Beauplet et al. 2005),
25 but also adult life history traits such as body mass (roe deer, *Capreolus capreolus*, Pettorelli
26 et al. 2002), and lifetime reproductive success (red deer, Kruuk et al. 1999, oystercatchers,

1 *Haematopus ostralegus*, Van de Pol et al. 2006).

2 As a consequence of the long-term effects of early life conditions on life histories, females born
3 early should have high early survival and, when adult, could themselves give birth early in the
4 season. Because birth date and laying date have been found to be heritable (Réale et al. 2003,
5 Sheldon et al. 2003), the young of these early-born females should therefore also have high
6 early survival so that, early-born females should achieve higher fitness than late-born females.
7 Moreover, in species for which adult body mass is positively correlated with juvenile body
8 mass, females born early in the birth season should also be heavier and so produce larger
9 average litter size, than late-born females. While such relationships are often assumed in studies
10 using laying (or birth) date as a proxy of female quality (Sydeman and Eddy 1995, Catry et al.
11 1999, Blums et al. 2005), very few studies have explicitly investigated the relationship between
12 reproductive timing and individual fitness. In the present study, we defined individual fitness
13 after Fisher (1930) as the reproductive value of an individual. In contrast to more commonly
14 used measures like lifetime reproductive success, individual reproductive value accounts for
15 how fast a given phenotype will spread in the population. Thus, in long-lived species, two
16 individuals that successfully raise the same number of offspring during their lifetime, but at
17 different ages, will have identical lifetime reproductive success, but different reproductive
18 values.

19 In this study, we investigated both the short-term and the long-term effects of birth date on
20 individual life history traits and on fitness in an intensively monitored population of a long-lived
21 mammal, the roe deer. We tested the following hypotheses: (i) as predicted from the match
22 between early growth and resource availability (Rutberg 1987), early-born fawns should survive
23 better and show higher early body growth than late-born fawns because the former benefit from
24 high quality resources (Plard et al. 2014a), (ii) early-born individuals should be heavier when
25 adults, gain higher annual reproductive success, and live longer than late-born individuals
26 because early conditions have the potential to generate “silver spoon” effects (Grafen 1988).

1 Finally, using the observed relationships between birth date, body mass and demographic
2 parameters, we built an integral projection model (Easterling et al. 2000) to analyse the link
3 between birth date and fitness. We used an IPM (instead of a classical analysis on lifetime
4 reproductive success) for the following reasons: the IPM allowed us to estimate a reproductive
5 value for each birth date and to identify the exact pathways (i.e. survival, reproduction, growth,
6 or inheritance) by which birth date influences fitness. Moreover, by building an IPM based on
7 the distribution of two continuous traits, we could investigate both the direct influence of birth
8 date on fitness through its effect on annual reproductive success and survival, as well as the
9 indirect influence of birth date on fitness through its effect on body mass. (iii) As long-lasting
10 effects of early life often occur through permanent developmental constraints (Lummaa and
11 Clutton-Brock 2002), early-born individuals should achieve higher fitness than late-born
12 individuals, mainly because of the positive association between early birth and fast body growth
13 (e.g., Feder et al. 2008).

14 MATERIALS AND METHODS

15 *Study population*

16 The roe deer population located at Trois Fontaines inhabits an enclosed 1,360ha forest in
17 north-eastern France (48°43'N, 2°61'W). The climate is continental, with relatively cold winters
18 and warm summers. This roe deer population has been intensively monitored since 1976 using
19 a Capture-Mark-Recapture (CMR) sampling design. Captured animals are individually marked
20 using collars (numbered or with VHF or GPS devices) and ear tags. The roe deer population at
21 Trois Fontaines is highly productive, mostly because of the rich habitats and soils which
22 promote high forest productivity (Pettorelli et al. 2006). Roe deer mate between mid-July and
23 mid-August. After copulation, embryos cease their development so that their implantation is
24 delayed by a five month diapause. Embryo development starts again in late December-early

1 January (Aitken 1974). Births in roe deer are highly seasonal, synchronous and occur from
2 mid-April to mid-June, with 80% of births taking place between the 5th and 27th of May at Trois
3 Fontaines (Gaillard et al. 1993). Birth dates are normally distributed, with a median birth date
4 of May 16th. Females are monoestrous and give birth to one, two, or occasionally three fawns
5 (triplets accounted for only about 2% of the litters), once per year, from 2 years of age onwards.

6 *Date of birth*

7 From the beginning of the birth season (mid-April), a systematic search for fawns was
8 conducted every year from 1985 to 2012 by the Office National de la Chasse et de la Faune
9 Sauvage (Delorme et al. 1988). Between 21 and 63 newborn fawns were found each year
10 through either intensive searches performed by a line of people, or by directed searches targeted
11 towards the fawns of radio-collared females. Fawns were ear-tagged, weighed, sexed and aged
12 using umbilicus characteristics and behavior at marking (Jullien et al. 1992). Error when
13 estimating capture age is less than 2 days (Gaillard et al. 1993). Birth date was therefore
14 back-calculated based on the fawn's estimated age at the date it was found. Body mass at
15 capture did not allow us to estimate body mass at birth because early growth rates vary among
16 fawns. Roe deer fawns display a "hider" tactic (Lent 1974), only coming into close contact with
17 the mother for suckling. However, the mother stays in close proximity to its fawns, remaining
18 spatially isolated from other females. We relied on this behaviour to identify the fawn's mother
19 through direct observation of lactation behavior or by identification of an escaping female in the
20 vicinity of the fawn.

21 *Life history traits*

22 Winter captures of roe deer took place each year between January and mid-March. At each
23 capture, animals were weighed to the nearest 100g. Yearling and adult body masses
24 corresponded respectively to the body mass of a given female at 8 months old (i.e. at first winter

1 capture) and to its median mass as an adult between 4 and 10 years old (Pettorelli et al. 2002).
2 We assumed that the body mass of a given fawn at first capture measured between early January
3 and early March provides a reliable estimate of its body mass at 8 months of age because body
4 mass remains almost constant over the winter in roe deer (Hewison et al. 2002). The annual
5 reproductive success of each female was assessed by the capture of its marked fawns at 8
6 months old. As we did not have access to father-fawn filiations, and thus to male reproductive
7 success, we only included females for the analysis of the effect of birth date on adult stage
8 traits. The age of all reproducing females analyzed here was known exactly because they were
9 first captured either as newborns or at 8 months of age during their first winter (identified using
10 the tooth eruption sequence, Flerov (1952)).

11 *Statistical analysis*

12 To investigate the short- and long-term influences of birth date on female life history traits and
13 fitness, we considered both the direct effect of birth date on demographic parameters (survival,
14 reproduction) and the indirect effect of birth date on demographic parameters mediated through
15 its effect on body mass (see Fig. 1). Thus, we tested for both an effect of individual birth date
16 and of body mass (as a yearling or as an adult) on female adult body mass and annual survival.
17 For early life stage traits, we investigated the short-term influence of individual birth date on
18 early (survival from birth to 8 month old) and yearling survival, and yearling body mass. In
19 addition, as heavy mothers give birth earlier than light mothers in roe deer (Plard et al. 2014b),
20 we considered the relationship between maternal body mass and early life history traits of her
21 offspring to control for possible maternal effects. Because these relationships included
22 information on both mother and newborn fawns, we included both male and females newborns
23 and corrected for sex when necessary to increase our sample size. There is no cost of being born
24 very early in the season in roe deer because the earliest born fawns will have the highest early
25 survival (Plard et al. 2014a) and the highest yearling body mass which is highly positively

1 correlated to yearling survival in ungulates (Gaillard et al. 2000b). We thus tested for the linear
2 effect of birth date on yearling and adult body masses, and on adult survival. Moreover, we have
3 previously shown that early survival is linked to birth date through a threshold relationship
4 (Plard et al. 2014a). As we expected a directional effect of body mass on life history traits, we
5 only tested for linear effects of body mass.

6 **Birth date and early life stage traits:** The influence of birth date and maternal body mass on
7 individual early survival (proportion of fawns of each litter that survived up to 8 months of age)
8 was investigated using a generalized linear mixed model with a logit link and a binomial
9 distribution. Because there is no difference between the sexes in individual early survival in roe
10 deer (mean survival difference: 0.13, SE: 0.25, p-value: 0.61, see also Gaillard et al. (1997)),
11 we pooled fawns of both sexes in this analysis. We modeled a threshold regression for birth date
12 (with constant survival until the 12th of May, then decreasing from this birth date onwards) and
13 a linear regression for maternal body mass on individual early survival. The influence of birth
14 date and maternal body mass on yearling body mass was modeled using linear mixed models.
15 As males are heavier than females at 8 months of age in roe deer (Gaillard et al. 1996), we
16 included an effect of sex. In models describing individual early survival and yearling body
17 mass, we included cohort as a random effect on the intercept to control for among-year
18 variation in environmental conditions and maternal identity as a random effect to control for the
19 fact that among-female heterogeneity in reproductive performance is partly unrelated to body
20 mass and birth date. The influence of a female's birth date and yearling body mass on its
21 yearling survival (i.e. from 8 to 20 months old) was investigated using a generalized linear
22 mixed model, including cohort as a random effect.

23 **Birth date and adult stage traits:** To investigate whether individual birth date has a direct
24 effect on female adult body mass (over and above its indirect effect on adult body mass
25 mediated through its effect on individual yearling body mass), we performed a path analysis
26 (Shiple 2009). In all models, we included an influence of individual birth date on yearling

1 body mass and tested for direct effects of both individual birth date and yearling body mass on
2 individual adult body mass using a linear model, including only females. The influence of a
3 female's birth date and adult body mass on its adult survival was tested using a
4 capture-mark-recapture (CMR) framework. Models were fitted using capture histories of 110
5 females in the software ESURGE (Choquet et al. 2009). Based on previous studies in this
6 population (e.g., Choquet et al. 2011), recapture probability was modeled for 3 discrete time
7 periods (1986-1999, 2000, 2001-2012).

8 For each life history trait except adult body mass, the best model was selected using the Akaike
9 information criterion (AIC, Burnham and Anderson 2002). We selected the model with the
10 lowest AIC and highest AIC weight (w_i , calculated as a measure of the likelihood that a given
11 candidate model is the best among the set of fitted models). For modeling adult body mass, we
12 used a path analysis in a Bayesian framework (Gelman and Hill 2007) with OpenBUGS and
13 tested for both the influence of yearling body mass and for the direct effect of individual birth
14 date on adult body mass using the Deviance Information Criterion (DIC, following Gelman and
15 Hill 2007, see also Spiegelhalter et al. 2002). We conducted 20000 simulations and used the
16 first 5000 as burn-in. We checked that the parameters estimated from the models we fitted were
17 not influenced by multi-colinearity problems (especially between birth date and body mass). We
18 compared the values of body mass and birth date estimated from models with and without body
19 mass and birth date included. Estimates were similar in all models. Diagnostic plots displaying
20 the residuals of each selected model are presented in the supplementary material (Fig. S6 and
21 S7).

22 **Birth date and individual fitness.** To investigate the influence of birth date on fitness
23 (measured using reproductive value), we used an integral projection model (IPM) to analyse the
24 dynamics of the distributions of two continuous traits over time (Easterling et al. 2000, Ellner
25 and Rees 2006, Coulson 2012): body mass (bm) and birth date (bd), for female roe deer in the
26 population of Trois Fontaines. The contemporaneous distributions of body mass and birth date

$\mathbf{n}(a + 1, t + 1, bm, bd)$ at year $t + 1$ according to their age $a + 1$ depend on their distributions at year t and on five functions: (1) the *inheritance function for birth date* ($\mathbf{I}_{bd}(a, t, bm, bd'|bd)$) links the offspring's birth date to the birth date and body mass of the mother. (2) The *recruitment function* ($\mathbf{R}(a, t, bm, bd')$) describes the number of offspring a mother successfully raised as a function of their birth date and the mother's body mass. (3) The *inheritance function for body mass* ($\mathbf{I}_{bm}(a, t, bm'|bm, bd')$) links an offspring's body mass at 8 months of age (yearling body mass) to its birth date and maternal body mass. (4) The *growth function* ($\mathbf{G}(a, t, bm'|bm, bd)$) describes the individual-level relationship between body mass as a yearling and body mass as an adult, given that individual's birth date, while (5) the *survival function* ($\mathbf{S}(a, t, bm, bd)$) describes the probability that an individual survives in relation to its birth date and body mass. Then:

$$\mathbf{n}(1, t + 1, bm', bd') = \sum_a \int \int \mathbf{I}_{bm}(a, t, bm'|bm, bd') \mathbf{R}(a, t, bm, bd') \mathbf{I}_{bd}(a, t, bm, bd'|bd) \mathbf{n}(a, t, bm, bd) dbm dbd$$

$$\mathbf{n}(a + 1, t + 1, bm', bd) = \int \int \mathbf{G}(a, t, bm'|bm, bd) \mathbf{S}(a, t, bm, bd) \mathbf{n}(a, t, bm, bd) dbm dbd, \quad a \geq 1$$

The continuous IPM can be approximated as a high dimensional discrete matrix (Easterling et al. 2000, see also supplementary material, Fig. S3). To minimize the size of the matrix, we used a two age-class structure: yearling (1 year old) and adult females (Nilsen et al. 2009). All functions required to build the IPM were investigated in the previous analyses (i.e. on birth date and early life stage traits and on birth date and adult stage traits) except the inheritance function for birth date. We thus used the parameters (intercepts and slopes) previously estimated from the selected models of early and adult life history traits (Table S3, Fig. 1) for the survival, growth, inheritance for body mass and recruitment functions and investigated the effects of maternal birth date and body mass on the inheritance function for birth date to build the IPM. For the inheritance function for birth date, we modeled the link between offspring birth date and maternal birth date and body mass using a linear mixed model, including year and maternal identity as random effects on the intercept. Sex was not included as there is no difference in average birth date between male and female roe deer (Gaillard et al. 1993).

1 As almost all roe deer females give birth to two fawns in the studied population (Gaillard et al.
2 1998), we considered litter size at birth as a fixed parameter and modeled the *recruitment*
3 *function* based solely on estimates of early survival from birth to the onset of winter (at 8
4 months of age). As the sex ratio at birth of roe deer is close to 0.5 (Hewison et al. 1999), litter
5 size at birth was set to one as only females were considered in the IPM. We modeled both the
6 *inheritance* and the *growth functions* using a normal probability density. The mean of each of
7 these functions provides the link between the offspring trait and the maternal trait (including the
8 effect of the individual's birth date for the inheritance function for body mass) for the
9 inheritance functions and between an individual's adult body mass and its yearling body mass
10 and its birth date for the growth function. The variances of these functions were estimated from
11 the squared residuals of the mean relationships and were kept constant. As adult body mass of
12 an individual female varies little among years in roe deer (e.g. Andersen et al. 2000, Plard et al.
13 2014b), we assumed that an individual's body mass was constant from 2 years old to death and
14 equal to its median adult body mass (between 4 and 10 years old), so limiting the size of the
15 matrix to two age classes. While this assumption may lead to a slight over-estimate of body
16 mass for 2 and 3 year old individuals and for females older than 10 years old, this is unlikely to
17 overly influence our analyses. Roe deer females indeed reach 93% of their adult body mass at 2
18 years of age and body mass of senescent females is 96% of their adult body mass (a decrease of
19 1 kg on average, Hewison et al. 2011). We generated 60 birth date class intervals of 1 day
20 between the 15th of April and the 14th of June and 60 body mass classes of 0.5kg between 5 and
21 35 kg. The stable distributions of body mass and birth date were estimated from the right
22 eigenvector of the projection matrix.

23 We quantified the influence of birth date on fitness by estimating the reproductive value of
24 yearling roe deer at 8 months of age in relation to their birth date. To estimate the confidence
25 interval of the difference of fitness between early- (May, 1st) and late- (May, 31st) born
26 individuals, we performed a bootstrap analysis with 2000 simulations of the datasets used to

1 estimate the different functions of the IPM (except for adult survival that remained constant
2 among body mass and birth date, see results). Second, to investigate the relative influence of
3 each function on the difference in fitness between early- and late- born individuals, we
4 performed a perturbation analysis. We estimated the percentage change in the difference in
5 fitness between early- and late-born females after a 1% change of one of the slopes linking birth
6 date and body mass to the vital rates. Finally, we simulated 60 groups of 1000 yearling females
7 which differed in terms of their birth date and that were monitored until the death of all
8 individuals in the group. For each group, we recorded mean adult body mass, annual
9 reproductive success, and both mean female offspring body mass and life expectancy at 8
10 months of age as predicted by the IPM. All statistical analyses were performed with the R
11 software from codes (available in the supplementary material, Text S1) that we wrote based on
12 Easterling et al. (2000) and Coulson (2012).

13 RESULTS

14 *Birth date and early life stage traits*

15 Early survival of individual fawns was best described by a model that included additive effects
16 of individual birth date and maternal body mass (Table 1A, $w_i = 0.67$, N=256 including 120
17 different mothers with 2.1 repetitions per mother on average). Fawns born before the 12th May
18 had a probability of 0.52 [0.42;0.61], on average, of surviving to 8 months old. Early survival
19 probability decreased from this date onwards such that fawns born late in the season (May, 31st,
20 Fig. 2A) had a probability of only 0.32 [0.20;0.48], on average, of surviving to the same age
21 (Table S1A and Fig. 2A). Maternal body mass influenced early survival positively (Table S1A)
22 such that fawns born to mothers weighing 20 kg had on average a 0.25 [0.14;0.40] probability
23 of surviving, while those born to mothers weighing 28 kg had, on average, a 0.71 [0.54;0.83]
24 probability of surviving (for fawns born at the peak of the birth season). This model accounted

1 for 6% (of which, 1% was due to the effect of birth date) of the observed variation in early
2 survival (note that the proportion of variation explained for a binomial response variable is
3 always much lower than that for a Gaussian variable).

4 Individual yearling body mass was best described by a model that included additive effects of
5 maternal body mass and individual birth date (Table 1B, $w_i = 0.94$, N=112 including 68
6 different mothers with 1.6 repetitions per mother on average) and which explained 19% (of
7 which, 6% was due to the effect of birth date) of the observed variation in yearling body mass.

8 Early-born fawns (1st May) were 2.5 kg (16.5%) [0.4;4.7 kg] heavier, on average, at 8 months of
9 age than late-born fawns (31st May) (Table S1B and Fig. 2B). Moreover, for a given birth date,
10 heavy mothers (28 kg) produced offspring that were, on average, 3.4 kg (24%) [0.5;6.4 kg]
11 heavier at 8 months of age than light (20 kg) mothers.

12 The best model describing individual yearling survival from 1 to 2 years of age included an
13 effect of individual yearling body mass (Table 1C, $w_i = 0.44$, N=113). Heavier yearlings had a
14 higher probability of surviving to 2 years of age than lighter yearlings (0.89 vs. 0.99 for
15 yearlings of 12 kg and 20 kg, respectively, Fig. S1)

16 *Birth date and adult stage traits*

17 The best model describing individual adult body mass included additive effects of birth date
18 together with the indirect effect of birth date on adult body mass mediated through yearling
19 body mass (Table 1D, N=67). The retained model accounted for 50% of the observed variation
20 in adult body mass, of which 6% was explained by the direct effect of individual birth date
21 (Table S1D). Whether or not we included the two individuals with adult body mass of 18 kg that
22 appear as outliers in Fig. 3 had no influence on model selection or parameter estimates. When
23 considering only the direct effect of birth date on adult body mass, early-born individuals (1st
24 May) reached a body mass that was 6.5% higher than late-born individuals (31st May) (24.0 kg
25 vs. 22.5 kg, Fig. 3). However, individual birth date influenced adult body mass mainly through

1 its effect on yearling body mass which was a better predictor of adult body mass than birth date
2 (Fig. 2, $\Delta DIC = 40.6$ if we removed the effect of yearling body mass from the best model vs.
3 $\Delta DIC = 1.4$ if we removed the effect of birth date from the best model, Table 1D). A yearling
4 weighing 12 kg reached an adult body mass of, on average, 20.8 kg, whereas a yearling
5 weighing 20 kg weighed, on average, 25.8 kg as an adult.
6 As no effects of female birth date or body mass on individual adult survival were detected
7 (Table 1E, Table S1E, N=110), we used all monitored females to estimate an overall adult
8 survival probability (N=418). The annual survival rate of adult females was 0.824 [0.796;0.850]
9 (Fig. S1).

10 *Birth date and fitness*

11 We built an IPM from the parameter estimates that we generated above for each function (Table
12 S3). For the inheritance function for birth date, offspring birth date was positively related to
13 maternal birth date (Table S2, $w_i = 0.35$, N=89 including 33 different mothers with 2.7
14 repetitions per mother on average) such that females born early in the season (1st May) gave
15 birth, on average, 5 [-2;13] days earlier than females born late in (31st May) in the season (Fig.
16 S2). Five per cent of the observed variation in offspring birth date was explained by this model.
17 We evaluated the stable distribution of body mass from the IPM which revealed two peaks
18 corresponding to a mean body mass of 16 kg and 23 kg for yearling and adult female roe deer,
19 respectively (Fig. S5A). The stable distribution of yearling birth dates was also in agreement
20 with field observations, with a mean birth date of 135.5 (15th May vs. 16th May for the observed
21 mean birth date of newborns in this population) and a normal distribution of birth dates (Fig.
22 S5B).
23 Using this IPM allowed us to estimate the reproductive value, and thereby the fitness, of females
24 in relation to their birth date (Fig. S4). We estimated that the fitness of early-born females (1st
25 May) was 1.34 (95% confidence interval: [1.01 3.47]) higher than that of late-born females (31st

1 May). The perturbation analysis showed that the long-term effect of birth date on fitness was
2 influenced by both the direct effect of birth date on early survival (recruitment) and on the
3 inheritance function for birth date and by the indirect effect of birth date through body mass
4 (Fig. 4). Indeed, the difference in fitness between early- and late- born individuals was closely
5 related to the slopes linking birth date to early survival (when we decreased the slope of the
6 birth date of the recruitment function by 1%, the difference in fitness between early- and late-
7 born females increased by 0.71%) and linking maternal birth date to offspring birth date (a 1%
8 change in the slope of the inheritance function for birth date led to a 0.45% change in the
9 difference in fitness). This difference was also closely related to the indirect effect of birth date
10 on fitness mediated through body mass. Indeed, a 1% change in the slope of birth date in the
11 growth function and in the inheritance function for body mass led to a 0.42% and to a 0.21%
12 change in the difference in fitness between early- and late-born females, respectively.
13 Simulating 60 groups of yearlings born on different days indicated that early-born females (1st
14 May) weighed 3 kg (14%) more as adults than late-born females (31st May). Moreover a 1%
15 change in the slopes linking body mass and the vital rates led to a change in the difference in
16 fitness between early- and late- born females of 0.59% for recruitment, 0.47% for growth and
17 0.09% for the inheritance function for body mass. Only the survival function contributed
18 relatively little to the difference in fitness between early- and late-born females (Fig. 4).
19 Because birth date had no statistically significant direct effects on survival but was weakly
20 related to yearling survival through its effect on yearling body mass, life expectancy at 8 months
21 of age was slightly higher for early-born individuals than for late-born individuals (6.57 +/- 4.91
22 vs. 6.42 +/-4.93).

23

DISCUSSION

24 Using the relationships between birth date, body mass and early and late life history traits, we
25 built an IPM that allowed us to estimate the difference in fitness between early- and late-born

1 individuals. The fitness of early-born individuals was 1.3 higher than that of late-born
2 individuals. While the importance of variation in birth timing for life histories has been
3 acknowledged for a long time (Bronson 1989, Lindström 1999), the few studies demonstrating
4 long-lasting effects of birth date in mammals are recent and confined to short-lived species (e.g.
5 European rabbit *Oryctolagus cuniculus*, Rödel et al. 2009). Indeed, Wilson et al. (2005) found
6 no evidence for direct effects of birth timing on fitness in the Soay sheep (*Ovis aries*), the only
7 moderately long-lived mammal studied so far. Our results in a wild population of roe deer
8 suggest that the timing of birth can have a strong long-term influence on life histories, even in
9 long-lived species.

10 Building an IPM based on the distribution of two contemporaneous traits allowed us to identify
11 the relative contribution of each function (i.e. survival, recruitment, growth, and inheritance) to
12 the difference in fitness observed between early- and late-born individuals. We found that the
13 silver spoon effect of birth date in roe deer is generated by both the direct effect of birth date on
14 recruitment and by the indirect effect of birth date on the different vital rates through body
15 mass. The indirect effect of birth date on fitness through body mass is a crucial pathway,
16 because the higher body mass that early-born fawns attained when adult mostly accounts for
17 their higher fitness. Body mass has a strong influence on reproduction in large herbivores and is
18 often directly linked to individual quality (Gaillard et al. 2000a, Hamel et al. 2009). As a
19 consequence, compared to body mass, birth date per se only has a minor impact on the
20 demography of the studied roe deer population. An IPM based on body mass only (i.e. without
21 including birth date) would provide a reliable picture of the dynamics of this population but
22 could not provide a mechanistic understanding of the influence of birth date on fitness. The IPM
23 including both birth date and mass highlighted two key findings: (1) birth date plays a
24 determinant role in shaping individual fitness, with early-born females enjoying higher fitness
25 than late-born ones, and (2) the influence of birth date is mostly indirect, with the main pathway
26 involving changes in body mass.

1 Birth date commonly affects early life history traits in many species (Guinness et al. 1978,
2 Reznick et al. 2006, Feder et al. 2008, Solberg et al. 2007), including roe deer. Indeed, we
3 found that birth date had a marked influence on early survival, with early-born fawns surviving
4 much better than late-born individuals. Early-born fawns also reach a higher body mass as
5 yearlings than late-born individuals. These short-term effects of birth date probably result from
6 the high food quality available in early spring. The nutritional value of plants is high at the
7 beginning of the growing season and decreases as they mature (Klein 1965, Albon and
8 Langvatn 1992). Thus, early-born fawns access high quality milk, and in large quantities, from
9 their mothers who have access to plentiful, highly digestible food resources. As a consequence,
10 they reach a higher body mass as yearlings than late-born individuals.

11 Long-lasting impacts of environmental conditions at birth have often been supposed to be
12 mediated through early development (Lindström 1999, Kruuk et al. 1999). For instance,
13 environmental conditions at birth affect both early and late body growth in female roe deer
14 (Douhard et al. 2013). Similarly, birth date influences fitness of female roe deer through
15 long-lasting effects on both juvenile and adult body masses in the same population. The indirect
16 effect of birth date on adult body mass through yearling body mass is clearly related to the
17 match between birth timing and food resource availability. Fawns of temperate areas that are
18 born early grow for a longer time during the plant growing season and so survive better. The
19 biological interpretation of the direct influence of birth date on adult body mass is more
20 challenging, but, the establishment of permanent physiological and metabolic functions during
21 gestation and very early life could explain the direct effect of early conditions on adult life
22 history traits (Lummaa and Clutton-Brock 2002). In particular, the development of muscle
23 tissues up until the adult stage is linked to fetal and very early life conditions because the
24 number of muscle fibers is fixed at birth and strongly influenced by maternal nutrition (Du et al.
25 2010). Moreover, although natal dispersal is quite frequent in roe deer of both sexes (Gaillard
26 et al. 2008, Debeffe et al. 2012), many fawns remain philopatric and settle on a home range that

1 is contiguous or overlapping with their maternal home range (Strandgaard 1972). An alternative
2 explanation for the direct effect could be the correlation between individual and habitat
3 conditions could thus at least partly explain the direct influence of early life on adult body mass.
4 Our results contrast with those on Soay sheep where no direct influence of birth date on fitness
5 was detected and the long-lasting effect of birth date was simply linked to birth mass (Wilson
6 et al. 2005). The markedly fluctuating environmental conditions faced by the Soay sheep
7 population (Coulson 2001) have a strong influence on annual body mass and could mask any
8 direct long-term effect of birth date on fitness.

9 The influence of birth timing on adult life history traits has been intensively studied in birds. In
10 the intensively studied barn swallow, a short-lived species (< 6 years in this study), hatching
11 date was negatively associated with lifetime reproductive success (Saino et al. 2012). However,
12 the biological link between reproductive timing and fitness differs between barn swallows and
13 roe deer. In barn swallows, early hatched individuals are longer-lived than late hatched birds
14 and thereby obtain higher lifetime reproductive success through a greater number of
15 reproductive attempts. In contrast, in roe deer, we have shown that birth date has no effect on
16 adult survival which, as a general rule, varies little among years in large mammals (Gaillard
17 et al. 2000b, Gaillard and Yoccoz 2003). In roe deer, birth timing-related fitness differences
18 among individuals arise because of variation in annual reproductive success rather than in
19 reproductive lifespan. This difference in reproductive performance is likely linked to the 3 kg
20 higher adult body mass of early-born females as compared to late-born females. Thus,
21 early-born females are more successful in raising their offspring (Andersen et al. 2000).
22 Females which are born the earliest, which are also the heaviest and attain the highest fitness,
23 can be considered as the highest quality individuals (Hamel et al. 2009). Indeed, while a variety
24 of mechanisms may link birth or hatching date to fitness, birth date can be considered as an
25 important component of the multi-dimensional complex that describes individual quality (sensu
26 Wilson and Nussey 2010). In roe deer, we have shown that birth date influences the whole life

1 history trajectory of an individual. Nonetheless, one cannot predict an individual's trajectory
2 from its birth date alone. Individual life history trajectories are shaped by both early
3 environmental conditions (including birth date) and current environmental conditions
4 (Tuljapurkar et al. 2009). The relative role of traits that are fixed at birth, such as maternal home
5 range or environmental conditions at birth, versus traits that vary across an individual's lifetime
6 in response to dynamic environmental variations remains to be quantified (Tuljapurkar et al.
7 2009, but see Helle et al. 2012 on the bank vole). In our models including both early and late life
8 history traits, birth date explained a maximum of 6% of the observed variation in the life history
9 traits that we studied. The large amount of unexplained variation in these life history traits can
10 be assumed to be linked to either annual environmental conditions or stochastic variation.
11 Yearly variation in environmental conditions affects annual body condition (McNamara and
12 Houston 1996) and the environmental cues used by different species to time their reproduction
13 (Reed et al. 2010). In a species like roe deer that displays little among-year variation in body
14 mass, body condition (Andersen et al. 2000) or timing of birth (Plard et al. 2013), we expect
15 that birth date and early life conditions would markedly influence individual life history
16 trajectories. On the contrary, in a species that shows large among-year variation in annual body
17 condition (bighorn sheep, Festa-Bianchet 1998) or in species with marked phenotypic plasticity
18 (such as the great tit, *Parus major*, Nussey et al. 2005), the relative influence of current annual
19 environmental conditions on life history trajectories should be higher than in roe deer.
20 Consequently, the magnitude of the long-lasting effects of early conditions for shaping
21 individual life history trajectories and population dynamics is likely to vary as a function of the
22 life history strategy of the species.

23

ACKNOWLEDGEMENTS

24 We are grateful to the Office National de la Chasse et de la Faune Sauvage and to the many volunteers
25 and colleagues who participated in the roe deer captures in winter and who gave their time to catching

1 and monitoring fawns on the study site of Trois Fontaines. Tim Coulson was funded by an ERC
2 advanced grant. We thank Steve Dobson and two anonymous reviewers for constructive comments on a
3 previous version of the manuscript.

1

2

LITERATURE CITED

- 3 Aitken, R. J., 1974. Delayed implantation in roe deer (*Capreolus capreolus*). *Journal of Reproduction*
4 and Fertility 39:225–233.
- 5 Albon, S. D. and R. Langvatn, 1992. Plant phenology and the benefits of migration in a temperate
6 ungulate. *Oikos* 65:502–513.
- 7 Andersen, R., J.-M. Gaillard, J. D. C. Linnell, and P. Duncan, 2000. Factors affecting maternal care in an
8 income breeder, the European roe deer. *Journal of Animal Ecology* 69:672–682.
- 9 Auer, S. K., 2010. Phenotypic plasticity in adult life-history strategies compensates for a poor start in life
10 in trinidadian guppies (*Poecilia reticulata*). *The American Naturalist* 176:818–829.
- 11 Beauplet, G., C. Barbraud, M. Chambellant, and C. Guinet, 2005. Interannual variation in the
12 post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and
13 oceanographic conditions. *Journal of Animal Ecology* 74:1160–1172.
- 14 Blums, P., J. D. Nichols, J. E. Hines, M. S. Lindberg, and A. Mednis, 2005. Individual quality, survival
15 variation and patterns of phenotypic selection on body condition and timing of nesting in birds.
16 *Oecologia* 143:365–376.
- 17 Bronson, F. H., 1989. *Mammalian reproductive biology*. University of Chicago Press, Chicago.
- 18 Burnham, K. P. and D. R. Anderson, 2002. *Model selection and multimodel inference – A practical*
19 *information-theoretic approach*. 2nd, Springer-Verlag, New York, USA.
- 20 Cam, E. and L. Aubry, 2011. Early development, recruitment and life history trajectory in long-lived
21 birds. *Journal of Ornithology* 152:S187–S201.
- 22 Catry, P., G. D. Ruxton, N. Ratcliffe, K. C. Hamer, and R. W. Furness, 1999. Short-lived repeatabilities
23 in long-lived great skuas: implications for the study of individual quality. *Oikos* 84:473–479.

- 1 Choquet, R., L. Rouan, and R. Pradel, 2009. Modeling Demographic Processes in Marked Populations,
2 Volume 3 of Springer Series: Environmental and Ecological Statistics, chapter Program E-SURGE: a
3 software application for fitting Multievent models, pages 845–865. Springer, dunedin edition.
- 4 Choquet, R., A. Viallefont, L. Rouan, K. Gaanoun, and J.-M. Gaillard, 2011. A semi-Markov model to
5 assess reliably survival patterns from birth to death in free-ranging populations. *Methods in Ecology*
6 *and Evolution* 2:383–389.
- 7 Coulson, T., 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*
8 292:1528–1531.
- 9 Coulson, T., 2012. Integral projections models, their construction and use in posing hypotheses in
10 ecology. *Oikos* 121:1337–1350.
- 11 Debeffe, L., N. Morellet, B. Cargnelutti, B. Lourtet, R. Bon, J.-M. Gaillard, and A. J. M. Hewison, 2012.
12 Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to
13 disperse and travel further. *Journal of Animal Ecology* 81:1327–1337.
- 14 Delorme, D., J.-M. Gaillard, and J.-M. Jullien, 1988. Intérêt de l'étude de la période juvénile pour le suivi
15 de l'évolution d'une population de chevreuils (*Capreolus capreolus*). *Gibier Faune Sauvage* 5:15–26.
- 16 Dickey, M.-H., G. Gauthier, and M.-C. Cadieux, 2008. Climatic effects on the breeding phenology and
17 reproductive success of an arctic-nesting goose species. *Global Change Biology* 14:1973–1985.
- 18 Dobson, F. S., T. S. Risch, and J. O. Murie, 1999. Increasing returns in the life history of Columbian
19 ground squirrels. *Journal of Animal Ecology* 68:73–86.
- 20 Douhard, M., J.-M. Gaillard, D. Delorme, G. Capron, P. Duncan, F. Klein, and C. Bonenfant, 2013.
21 Variation in adult body mass of roe deer: early environmental conditions influence early and late body
22 growth of females. *Ecology* 94:1805–1814.
- 23 Du, M., J. Tong, J. Zhao, K. R. Underwood, M. Zhu, S. P. Ford, and P. W. Nathanielsz, 2010. Fetal

- 1 programming of skeletal muscle development in ruminant animals. *Journal of Animal Science*
2 88:E51–E60.
- 3 Easterling, M. R., S. P. Ellner, and P. M. Dixon, 2000. Size-specific sensitivity: applying a new
4 structured population model. *Ecology* 81:694–708.
- 5 Ellner, S. P. and M. Rees, 2006. Integral projection models for species with complex demography. *The*
6 *American Naturalist* 167:410–428.
- 7 Estes, R. D., 1976. The significance of breeding synchrony in the wildebeest. *African Journal of Ecology*
8 14:135–152.
- 9 Feder, C., J. G. A. Martin, M. Festa-Bianchet, C. Bérubé, and J. Jorgenson, 2008. Never too late?
10 Consequences of late birthdate for mass and survival of bighorn lambs. *Oecologia* 156:773–781.
- 11 Festa-Bianchet, M., 1998. Condition-dependent reproductive success in bighorn ewes. *Ecology Letters*
12 1:91–94.
- 13 Fisher, R. A., 1930. *The genetical theory of natural selection*. The Clarendon Press, Oxford, England. by
14 R. A. Fisher. Plate II accompanied by leaf with descriptive letterpress. Includes index. "Works cited":
15 p. [266]-268.
- 16 Flerov, K., 1952. *Fauna of USSR: Mammals*. vol. 1 no. 2. Musk deer and deer. Academy of sciences of
17 the USSR, Leningrad .
- 18 Gaillard, J.-M., R. Andersen, D. Delorme, and J. D. C. Linnell, 1998. Family effects on growth and
19 survival of juvenile roe deer. *Ecology* 79:2878–2889.
- 20 Gaillard, J.-M., J.-M. Boutin, D. Delorme, G. Van Laere, P. Duncan, and J.-D. Lebreton, 1997. Early
21 survival in roe deer: causes and consequences of cohort variation in two contrasted populations.
22 *Oecologia* 112:502–513.
- 23 Gaillard, J.-M., D. Delorme, J.-M. Boutin, G. van Laere, and B. Boisaubert, 1996. Body mass of roe deer
24 fawns during winter in 2 contrasting populations. *the Journal of Wildlife Management* 60:29–39.

- 1 Gaillard, J.-M., D. Delorme, J.-M. Jullien, and D. Tatin, 1993. Timing and synchrony of births in roe
2 deer. *Journal of Mammalogy* 74:738–744.
- 3 Gaillard, J.-M., M. Festa-Bianchet, D. Delorme, and J. Jorgenson, 2000a. Body mass and individual
4 fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society B:
5 Biological Sciences* 267:471–477.
- 6 Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo, 2000b. Temporal variation in
7 fitness components and population dynamics of large herbivores. *Annual Review of Ecology and
8 Systematics* 31:367–393.
- 9 Gaillard, J.-M., A. J. M. Hewison, P. Kjellander, N. Pettorelli, C. Bonenfant, B. V. Moorter, O. Liberg,
10 H. Andren, G. V. Laere, F. Klein, et al., 2008. Population density and sex do not influence fine-scale
11 natal dispersal in roe deer. *Proceedings of the Royal Society B: Biological Sciences* 275:2025–2030.
- 12 Gaillard, J. M., A. Loison, C. Toïgo, D. Delorme, and G. Van Laere, 2003. Cohort effects and deer
13 population dynamics. *Écoscience* 10:312–320.
- 14 Gaillard, J.-M. and N. G. Yoccoz, 2003. Temporal variation in survival of mammals: a case of
15 environmental canalization? *Ecology* 84:3294–3306.
- 16 Gelman, A. and J. Hill, 2007. *Data analysis using regression and multilevel/hierarchical models*.
17 Cambridge University Press, New York.
- 18 Grafen, A., 1988. On the uses of data on lifetime reproductive success. In T. H. Clutton-Brock, editor,
19 *Reproductive success : studies of individual variation in contrasting breeding systems*, pages
20 454–471. University of Chicago Press, Chicago.
- 21 Green, W. C. H. and A. Rothstein, 1993. Persistent influences of birth date on dominance, growth and
22 reproductive success in bison. *Journal of Zoology* 230:177–186.
- 23 Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon, 1978. Factors affecting calf mortality in red deer
24 (*Cervus elaphus*). *Journal of Animal Ecology* 47:817–832.

- 1 Hamel, S., J.-M. Gaillard, M. Festa-Bianchet, and S. D. Côté, 2009. Individual quality, early-life
2 conditions, and reproductive success in contrasted populations of large herbivores. *Ecology*
3 90:1981–1995.
- 4 Helle, H., E. Koskela, and T. Mappes, 2012. Life in varying environments: experimental evidence for
5 delayed effects of juvenile environment on adult life history. *Journal of Animal Ecology* 81:573–582.
- 6 Hewison, A. J. M., R. Andersen, J.-M. Gaillard, J. D. C. Linnell, and D. Delorme, 1999. Contradictory
7 findings in studies of sex ratio variation in roe deer (*Capreolus capreolus*). *Behavioral Ecology and*
8 *Sociobiology* 45:339–348.
- 9 Hewison, A. J. M., J.-M. Gaillard, J.-M. Angibault, G. Van Laere, and J. P. Vincent, 2002. The influence
10 of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. *Journal of Zoology*
11 257:303–309.
- 12 Hewison, A. J. M., J.-M. Gaillard, D. Delorme, G. Van Laere, T. Amblard, and F. Klein, 2011.
13 Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass-size
14 allometry in roe deer. *Oikos* 120:1217–1226.
- 15 Ims, R. A., 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *The*
16 *American Naturalist* 136:485–498.
- 17 Jullien, J.-M., D. Delorme, and J.-M. Gaillard, 1992. Détermination de l'âge chez le faon de chevreuil
18 (*Capreolus capreolus*) dans son premier mois de vie. *Mammalia* 56:307–311.
- 19 Klein, D. R., 1965. Ecology of deer range in Alaska. *Ecological Monographs* 35:259–284.
- 20 Kruuk, L. E. B., T. H. Clutton-Brock, K. E. Rose, and F. E. Guinness, 1999. Early determinants of
21 lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society B:*
22 *Biological Sciences* 266:1655–1661.
- 23 Landete-Castillejos, T., A. Garcia, and L. Gallego, 2001. Calf growth in captive Iberian red deer (*Cervus*

- 1 *elaphus hispanicus*): effects of birth date and hind milk production and composition. Journal of
2 Animal Science 79:1085–1092.
- 3 Lent, P. C., 1974. Mother-infant relationships in ungulates. In V. Geist and F. R. Walther, editors, *The*
4 *behaviour of ungulates and its relation to management*, pages 14–55. IUCN New Series, Morges,
5 Switzerland.
- 6 Lindström, J., 1999. Early development and fitness in birds and mammals. Trends in Ecology &
7 Evolution 14:343–348.
- 8 Lummaa, V. and T. H. Clutton-Brock, 2002. Early development, survival and reproduction in humans.
9 Trends in Ecology & Evolution 17:141–147.
- 10 McNamara, J. M. and A. I. Houston, 1996. State-dependent life histories. Nature 380:215–221.
- 11 Moyes, K., D. H. Nussey, M. N. Clements, F. E. Guinness, A. Morris, S. Morris, J. M. Pemberton,
12 L. E. B. Kruuk, and T. H. Clutton-Brock, 2011. Advancing breeding phenology in response to
13 environmental change in a wild red deer population. Global Change Biology 17:2455–2469.
- 14 Nilsen, E. B., J.-M. Gaillard, R. Andersen, J. Odden, D. Delorme, G. Van Laere, and J. D. C. Linnell,
15 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer
16 populations. Journal of Animal Ecology 78:585–594.
- 17 Nussey, D. H., E. Postma, P. Gienapp, and M. E. Visser, 2005. Selection on heritable phenotypic
18 plasticity in a wild bird population. Science 310:304–306.
- 19 Pettorelli, N., J.-M. Gaillard, A. Mysterud, P. Duncan, N. C. Stenseth, D. Delorme, G. Van Laere,
20 C. Toïgo, and F. Klein, 2006. Using a proxy of plant productivity (NDVI) to find key periods for
21 animal performance: the case of roe deer. Oikos 112:565–572.
- 22 Pettorelli, N., J.-M. Gaillard, G. Van Laere, P. Duncan, P. Kjellander, O. Liberg, D. Delorme, and
23 D. Maillard, 2002. Variations in adult body mass in roe deer: the effects of population density at birth
24 and of habitat quality. Proceedings of the Royal Society B: Biological Sciences 269:747–753.

- 1 Plard, F., J.-M. Gaillard, C. Bonenfant, A. J. M. Hewison, D. Delorme, B. Cargnelutti, P. Kjellander,
2 E. B. Nilsen, and T. Coulson, 2013. Parturition date for a given female is highly repeatable within five
3 roe deer populations. *Biology letters* 9:20120841.
- 4 Plard, F., J.-M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, and C. Bonenfant, 2014a. Mismatch
5 between birth date and vegetation phenology slows the demography of roe deer. *Plos Biology*
6 12:e1001828.
- 7 Plard, F., J.-M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, E. B. Nilsen, and C. Bonenfant,
8 2014b. Long-lived and heavier females give birth earlier in roe deer. *Ecography* 37:241–249.
- 9 Post, E. and M. C. Forchhammer, 2008. Climate change reduces reproductive success of an Arctic
10 herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society of London B*
11 *Biological Sciences* 363:2367–2373.
- 12 Price, T., M. Kirkpatrick, and S. J. Arnold, 1988. Directional selection and the evolution of breeding date
13 in birds. *Science* 240:798–799.
- 14 Réale, D., D. Berteaux, A. G. McAdam, and S. Boutin, 2003. Lifetime selection on heritable life-history
15 traits in a natural population of red squirrels. *Evolution* 57:2416–2423.
- 16 Reed, T. E., R. S. Waples, D. E. Schindler, J. J. Hard, and M. T. Kinnison, 2010. Phenotypic plasticity
17 and population viability: the importance of environmental predictability. *Proceedings of the Royal*
18 *Society B: Biological Sciences* 277:3391–3400.
- 19 Reznick, D., E. Schultz, S. Morey, and D. Roff, 2006. On the virtue of being the first born: the influence
20 of date of birth on fitness in the mosquitofish, *Gambusia affinis*. *Oikos* 114:135–147.
- 21 Rödel, H. G., D. von Holst, and C. Kraus, 2009. Family legacies: short- and long-term fitness
22 consequences of early-life conditions in female European rabbits. *Journal of Animal Ecology*
23 78:789–797.

- 1 Rutberg, A. T., 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. The
2 American Naturalist 130:692–710.
- 3 Saino, N., M. Romano, R. Ambrosini, D. Rubolini, G. Boncoraglio, M. Caprioli, and A. Romano, 2012.
4 Longevity and lifetime reproductive success of barn swallow offspring are predicted by their hatching
5 date and phenotypic quality. Journal of Animal Ecology 81:1004–1012.
- 6 Schultz, E., 1993. The effect of birth date on fitness of female dwarf perch, *Micrometus minimetus*
7 (Perciformes: Embiotocidae). Evolution 47:520–539.
- 8 Sheldon, B. C., L. E. B. Kruuk, and J. Merilä, 2003. Natural selection and inheritance of breeding time
9 and clutch size in the collared flycatcher. Evolution 57:406–420.
- 10 Shipley, B., 2009. Confirmatory path analysis in a generalized multilevel contextsinervo. Ecology
11 90:363–368.
- 12 Sinervo, B. and P. Doughty, 1996. Interactive effects of offspring size and timing of reproduction on
13 offspring reproduction: experimental, maternal, and quantitative genetic aspects. Evolution
14 50:1314–1327.
- 15 Solberg, E. J., M. Heim, V. Grøtan, B.-E. Sæther, and M. Garel, 2007. Annual variation in maternal age
16 and calving date generate cohort effects in moose (*Alces alces*) body mass. Oecologia 154:259–271.
- 17 Spear, L. and N. Nur, 1994. Brood size, hatching order and hatching date: effects on four life-history
18 stages from hatching to recruitment in western gulls. Journal of Animal Ecology 63:283–298.
- 19 Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde, 2002. Bayesian measures of model
20 complexity and fit. Journal of the Royal Statistical Society. Series B (Statistical Methodology)
21 64:583–639.
- 22 Strandgaard, H., 1972. An investigation of corpora lutea, embryonic development, and time of birth of
23 roe deer (*Capreolus capreolus*) in Denmark. Vildtbiologisk Station.

- 1 Sydeман, W. J. and J. O. Eddy, 1995. Repeatability in laying date and its relationship to individual
2 quality for common murre. *The Condor* 97:1048–1052.
- 3 Tuljapurkar, S., U. K. Steiner, and S. H. Orzack, 2009. Dynamics heterogeneity in life histories. *Ecology*
4 *letters* 12:93–106.
- 5 Van de Pol, M., L. Bruinzeel, D. Heg, H. Van der Jeugd, and S. Verhulst, 2006. A silver spoon for a
6 golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus*
7 *ostralegus*). *Journal of Animal Ecology* 75:616–626.
- 8 Visser, M. E. and N. Verboven, 1999. Long-term fitness effects of fledging date in great tits. *Oikos*
9 85:445–450.
- 10 Wauters, L. A. and A. A. Dhondt, 1995. Lifetime reproductive success and its correlates in female
11 eurasian squirrels. *Oikos* 72:402–410.
- 12 Wilson, A. J. and D. H. Nussey, 2010. What is individual quality? An evolutionary perspective. *Trends*
13 *in Ecology & Evolution* 25:207–214.
- 14 Wilson, A. J., J. G. Pilkington, J. M. Pemberton, D. W. Coltman, A. D. J. Overall, K. A. Byrne, and
15 L. E. B. Kruuk, 2005. Selection on mothers and offspring: whose phenotype is it and does it matter?
16 *Evolution* 59:451–463.

1 **Table 1.** Model selection for the early life stage and adult stage traits. **A. Early survival**
2 **(Recruitment function of the IPM).** Influence of maternal body mass (BM_M) and individual
3 birth date (BD , with a threshold date on May 12th) on individual early survival (to 8 months of
4 age). **B. Yearling body mass (Inheritance function for body mass).** Influence of individual
5 birth date (BD) and of maternal body mass (BM_M) on individual yearling body mass. An
6 effect of sex was included in the models because yearling males are heavier than yearling
7 females. **C. Yearling survival.** Influence of individual birth date (BD) and yearling body mass
8 (BM_Y) on individual yearling survival (Y). **D. Adult body mass (Growth).** Influence of
9 individual birth date (BD) and yearling body mass (BM_Y) on female adult body mass. An
10 indirect effect of birth date on adult body mass through its effect on yearling body mass was
11 also included in all models using a path analysis. **E. Adult survival.** Influence of individual
12 birth date (BD) and adult body mass (BM_{Ad}) on female adult survival (Ad). k indicates the
13 number of estimated parameters, LL is the maximum log likelihood, Dev is the deviance of the
14 model, ΔAIC indicates the difference in the AIC between two competing models, and w_i
15 corresponds to Akaike weights. Pd is the estimated number of parameters, \hat{D} is the deviance of
16 the model and ΔDIC indicates the difference in the DIC between two competing models. The
17 selected models are indicated in bold. 1 represents the constant model (i.e. intercept only).

TABLE 1.
Early life stage traits

Early life stage traits				
A. early survival				
$BM_M + BD$	<i>k</i>	LL	ΔAIC	<i>wi</i>
$BM_M + BD$	5	-181.347	0	0.673
<i>BD</i>	4	-185.941	7.187	0.018
BM_M	4	-183.140	1.585	0.304
1	3	-188.334	9.975	0.005
B. yearling body mass				
$sex + BM_M + BD$	<i>k</i>	LL	ΔAIC	<i>wi</i>
$sex + BM_M + BD$	7	-257.068	0	0.935
$sex + BD$	6	-257.038	5.870	0.050
$sex + BM_M$	6	-258.077	7.948	0.018
<i>sex</i>	5	-262.589	14.972	0.001
C. yearling survival				
$BM_Y + BD$	<i>k</i>	LL	ΔAIC	<i>wi</i>
$BM_Y + BD$	4	-20.757	0.488	0.345
BM_Y	3	-21.513	0	0.441
<i>BD</i>	3	-22.875	2.724	0.113
1	2	-23.980	2.934	0.102
Adult stage traits				
D. adult body mass				
$BM_Y + BD$	<i>Pd</i>	\hat{D}	ΔDIC	
$BM_Y + BD$	7	537.400	0	
BM_Y	6	540.900	1.400	
<i>BD</i>	6	580.300	40.600	
1	5	585.300	43.500	
E. adult survival				
$BM_{Ad} + BD$	<i>k</i>	Dev	ΔAIC	<i>wi</i>
$BM_{Ad} + BD$	7	1462.309	3.733	0.080
BM_{Ad}	6	1462.531	2.055	0.185
<i>BD</i>	6	1462.323	1.746	0.216
1	5	1462.576	0	0.518

FIGURE CAPTION

1

2 **Figure 1.** Conceptual model of the relationships among life history traits used to build the five
3 functions of the IPM: the inheritance function for birth date, the inheritance function for body
4 mass, the recruitment, the growth and the survival functions. Dotted arrows indicate potential
5 effects that were not supported by the selected model.

6 **Figure 2.** Influence of individual birth date on individual early survival (A.) and yearling body
7 mass (B.) for roe deer at Trois Fontaines, France. (A.) Data used to fit the model are represented
8 by filled circles whose size is proportional to the number of observed births within 25 classes of
9 birth date (of 2 days from April 17th to June 5th). Males and females were pooled in this
10 analysis (B.) Males and females are presented in black and grey, respectively, with one point
11 representing one individual. The predictions of the model with their 95% confidence intervals
12 are presented with a grey shade and black dotted lines for female and male offspring,
13 respectively.

14 **Figure 3.** Long-term direct and indirect (i.e. mediated through body mass) influence of
15 individual birth date on individual adult body mass for female roe deer at Trois Fontaines,
16 France. The dotted line gives the predictions of the direct effect of birth date, only.

17 **Figure 4.** Percentage change of the difference in fitness between early- and late-born
18 individuals generated by a 1% change in the slopes of each vital rate (Rec: Recruitment,
19 Inh_bd: Inheritance for birth date, Inh_bm: Inheritance for body mass, Gro: Growth and
20 Sur:survival). Perturbations of slopes linking birth date and body mass to the early and adult life
21 history traits are presented in black and white, respectively.

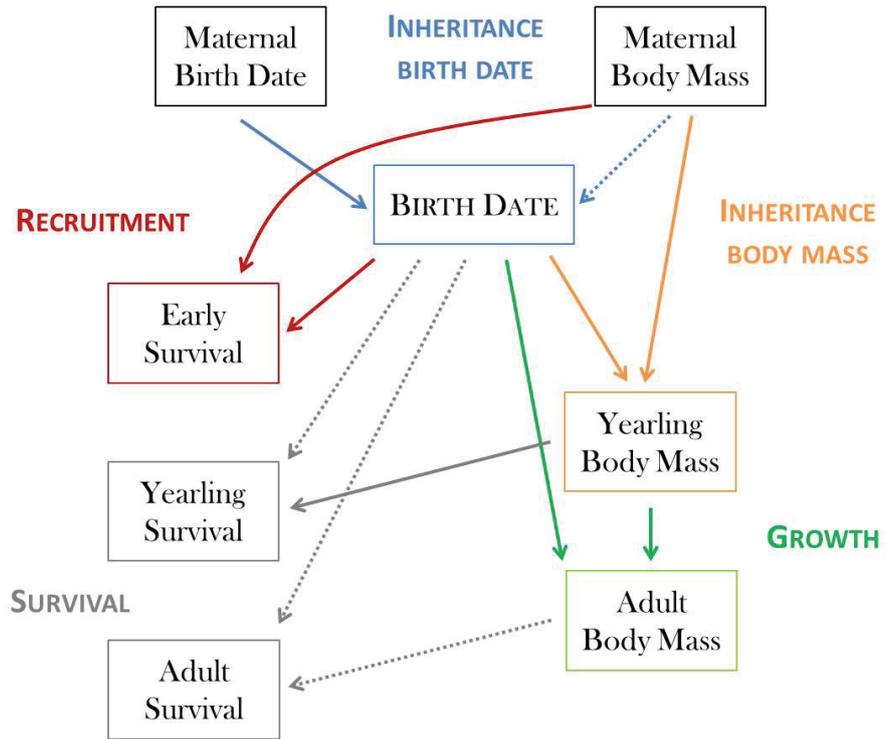
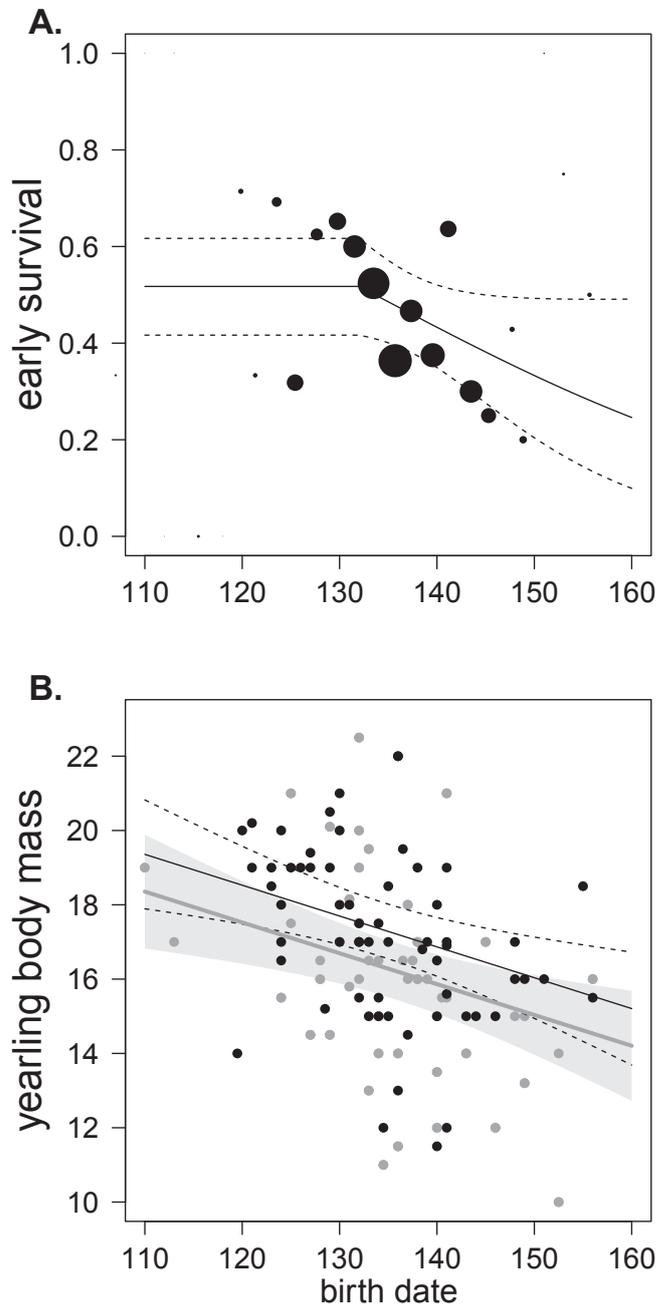


Fig. 1

1

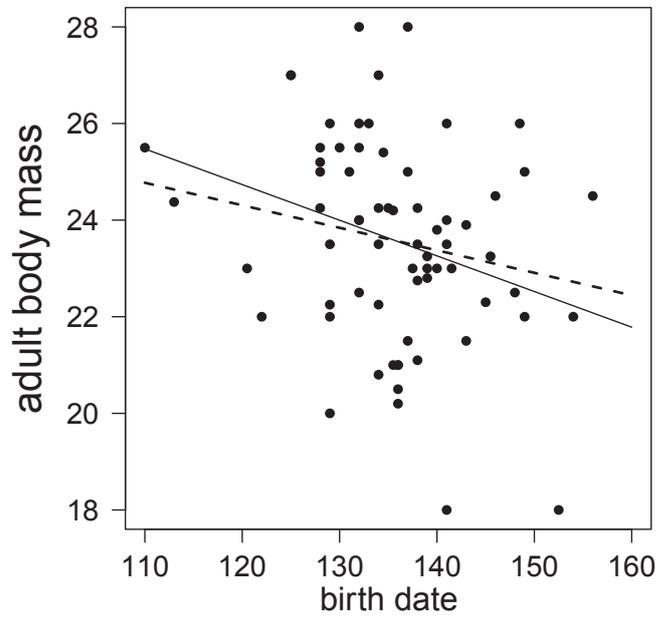
2



1

2

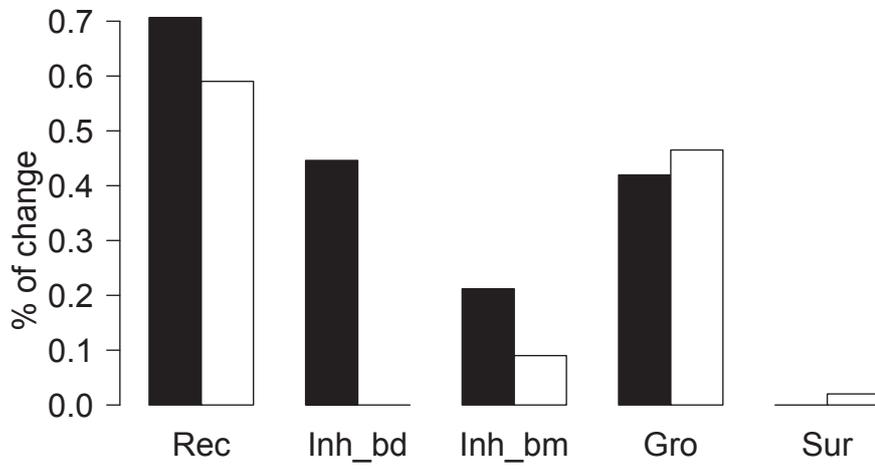
Fig. 2



1

2

Fig. 3



1

2

Fig. 4

SUPPLEMENTARY MATERIAL

Table S1. Parameter estimates and their standard errors for the selected models describing the early life stage and adult stage traits. s_{id} and s_{year} give the standard deviations of the random effects on maternal identity and year, respectively, when included in the model. **A. Early survival (Recruitment function of the IPM).** Influence of maternal body mass (BM_M) and individual birth date (BD , with a threshold date on May 12th) on individual early survival (to 8 months of age). **B. Yearling body mass (Inheritance function for body mass).** Influence of individual birth date (BD), of maternal body mass (BM_M) and of sex on individual yearling body mass. **C. Yearling survival.** Influence of individual yearling body mass (BM_Y) on individual yearling survival. **D. Adult body mass (Growth).** Influence of individual birth date (BD) and yearling body mass (BM_Y) on individual adult body mass. **E. Adult survival** was independent of both adult body mass and birth date. Early survival and yearling survival were modeled using generalized linear mixed models with a logit link and a binomial error. Adult survival was estimated using a capture-mark-recapture model. Other life history traits were modeled using linear mixed models.

Early life stage traits

A. early survival	value	SE
<i>Intercept</i>	-0.24	3.64
<i>BD</i>	-0.04	0.02
<i>BM_M</i>	0.25	0.08
<i>s_{id}</i>	0.91	
<i>s_{year}</i>	0.24	

B. yearling body mass	value	SE
<i>Intercept</i>	17.97	5.33
<i>BD</i>	-0.08	0.03
<i>BM_M</i>	0.43	0.15
<i>sex</i>	-1.00	0.40
<i>s_{id}</i>	2.07	
<i>s_{year}</i>	0.48	
<i>var(residuals)</i>	1.43	

C. yearling survival	value	SE
<i>intercept</i>	-4.24	3.88
<i>BM_Y</i>	0.53	0.26
<i>s_{year}</i>	2.19	

Adult stage traits

D. adult body mass	value	SE
<i>Intercept</i>	19.49	3.53
<i>BD</i>	-0.05	0.02
<i>BM_Y</i>	0.63	0.09
<i>var(residuals)</i>	2.32	0.35

E. adult survival	value	SE
	0.82	0.01

Table S2. Model selection (**A.**) and parameter estimates (**B.**) for the inheritance function for birth date. Influence of maternal birth date (BD_M) and body mass (BM_M) on offspring birth date. k indicates the number of estimated parameters, LL is the maximum log Likelihood, ΔAIC indicates the difference in the AIC between two competing models, and w_i corresponds to Akaike weights. The selected models are indicated in bold. 1 represents the constant model (i.e. intercept only). The inheritance function for body mass was modeled with a linear mixed model. s_{id} and s_{year} give the standard deviations of random effects on maternal identity and year, respectively.

A. Models	k	LL	ΔAIC	w_i
$BM_M + BD_M$	6	-304.071	1.330	0.179
BD_M	5	-304.406	0	0.347
BM_M	5	-305.128	1.443	0.169
1	4	-305.533	0.254	0.306

B. Estimates	value	SE
<i>Intercept</i>	112.90	15.38
BD_M	0.17	0.11
s_{id}	4.33	
s_{year}	4.02	
$var(residuals)$	21.61	

Table S3. Models of the five functions used to build the IPM describing the contemporaneous distributions of birth date (BD) and body mass (BM). M : Maternal, Y : Yearling, Ad : Adult.

recruitment (early survival)	$R(BM_M, BD) = \frac{1}{1+e^{-(-0.24+0.25*BM_M-0.04*BD)}}$
growth	$G(BM_{Ad} BM_Y, BD) = \frac{1}{\sqrt{2\pi*1.52}} e^{-\frac{(BM_{Ad}-(19.49+0.63*BM_Y-0.05*BD))^2}{2*1.52^2}}$
inheritance BD	$I_{BD}(BD BD_M) = \frac{1}{\sqrt{2\pi*4.65}} e^{-\frac{(BD-(112.9+0.17*BD_M))^2}{2*4.65^2}}$
inheritance BM	$I_{BM}(BM_Y BM_M, BD) = \frac{1}{\sqrt{2\pi*1.20}} e^{-\frac{(BM_Y-(17.97+0.43*BM_M-0.08*BD))^2}{2*1.20^2}}$
survival	$S_Y(BM_Y) = \frac{1}{1+e^{-(-4.24+0.53*BM_Y)}}$ $S_{Ad} = 0.82$

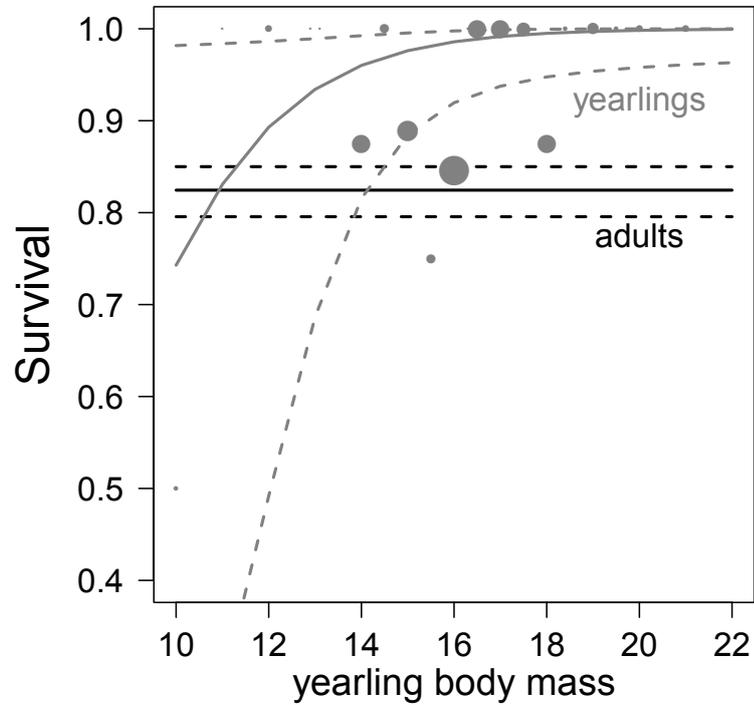


Figure S1. Influence of yearling body mass on yearling and adult survival for female roe deer at Trois Fontaines, France. Observed mean yearling survival for a given yearling body mass are represented by filled circles whose size is proportional to the number of yearlings of a given body mass. Data used to estimate adult survival are capture-mark-recapture data and are thus not presented in the figure.

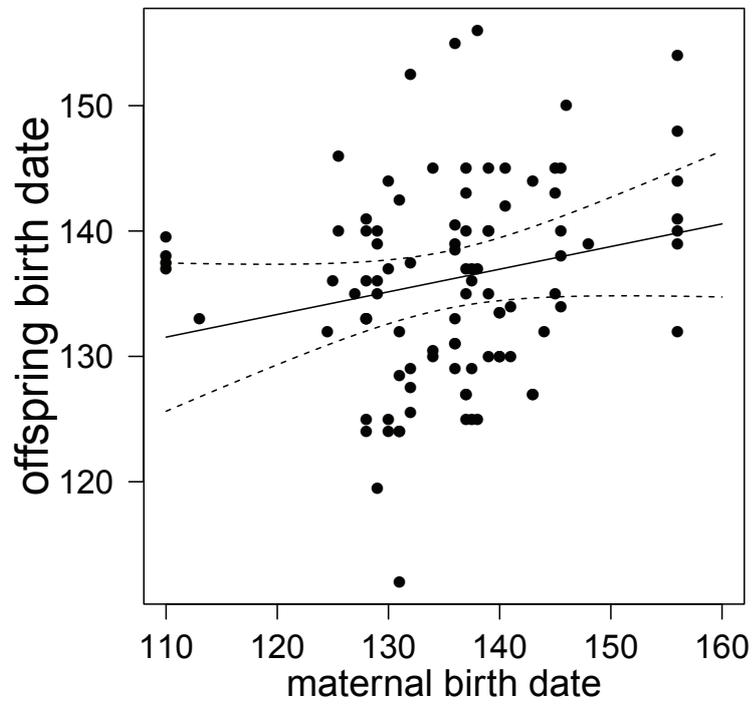


Figure S2. Influence of maternal birth date on offspring birth date for female roe deer at Trois Fontaines, France.

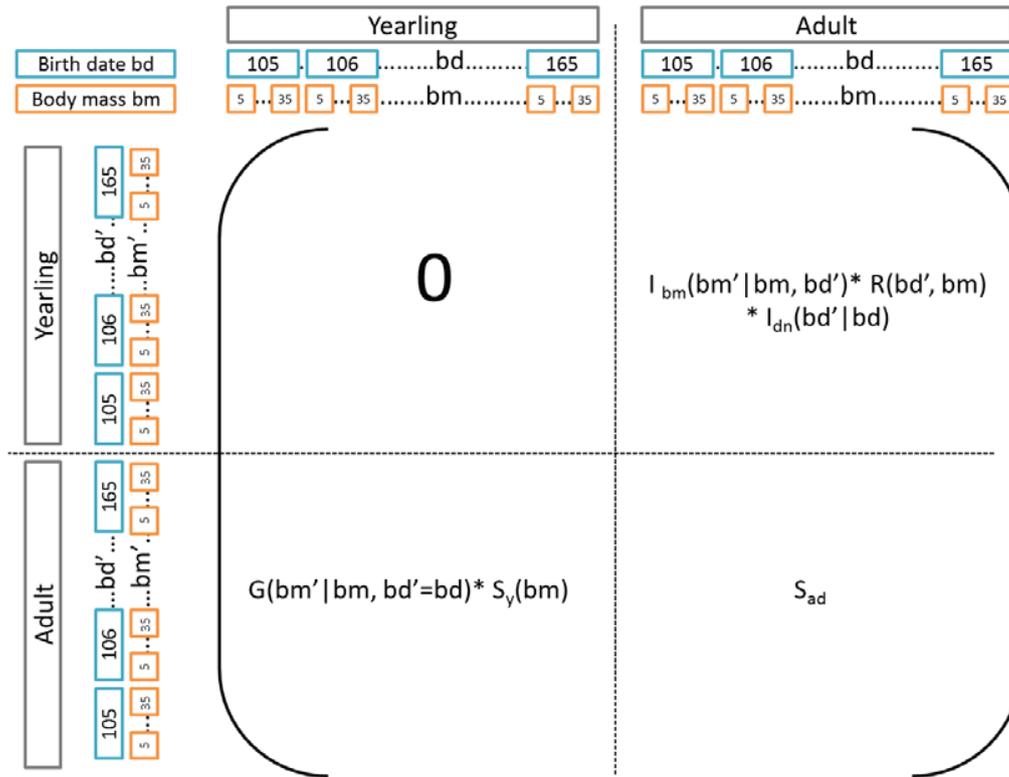


Figure S3. Representation of the matrix used to build the IPM.

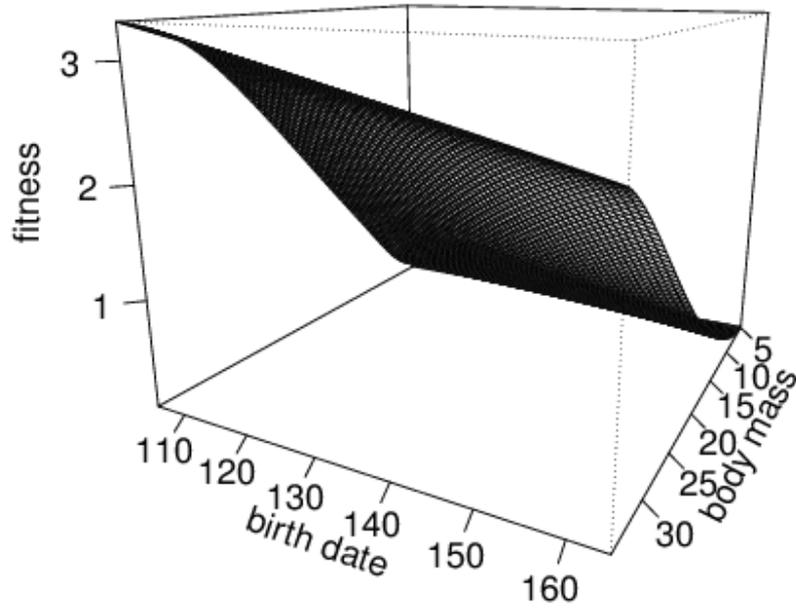


Figure S4. Fitness (as estimated by reproductive value) of 8 month old roe deer in relation to their birth date and body mass estimated from the IPM.

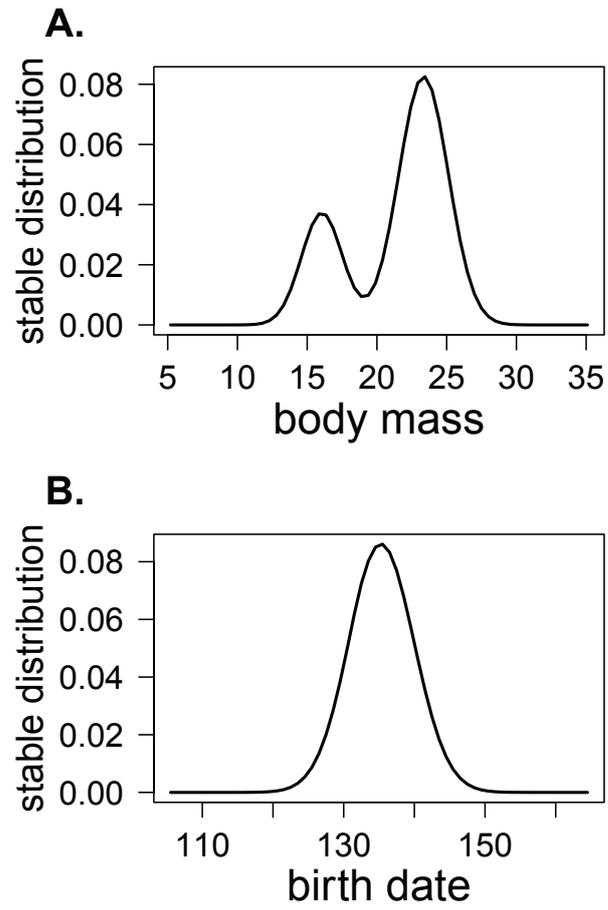


Figure S5. Stable distributions of body mass in the population (A.) and of birth date among yearling individuals (B.).

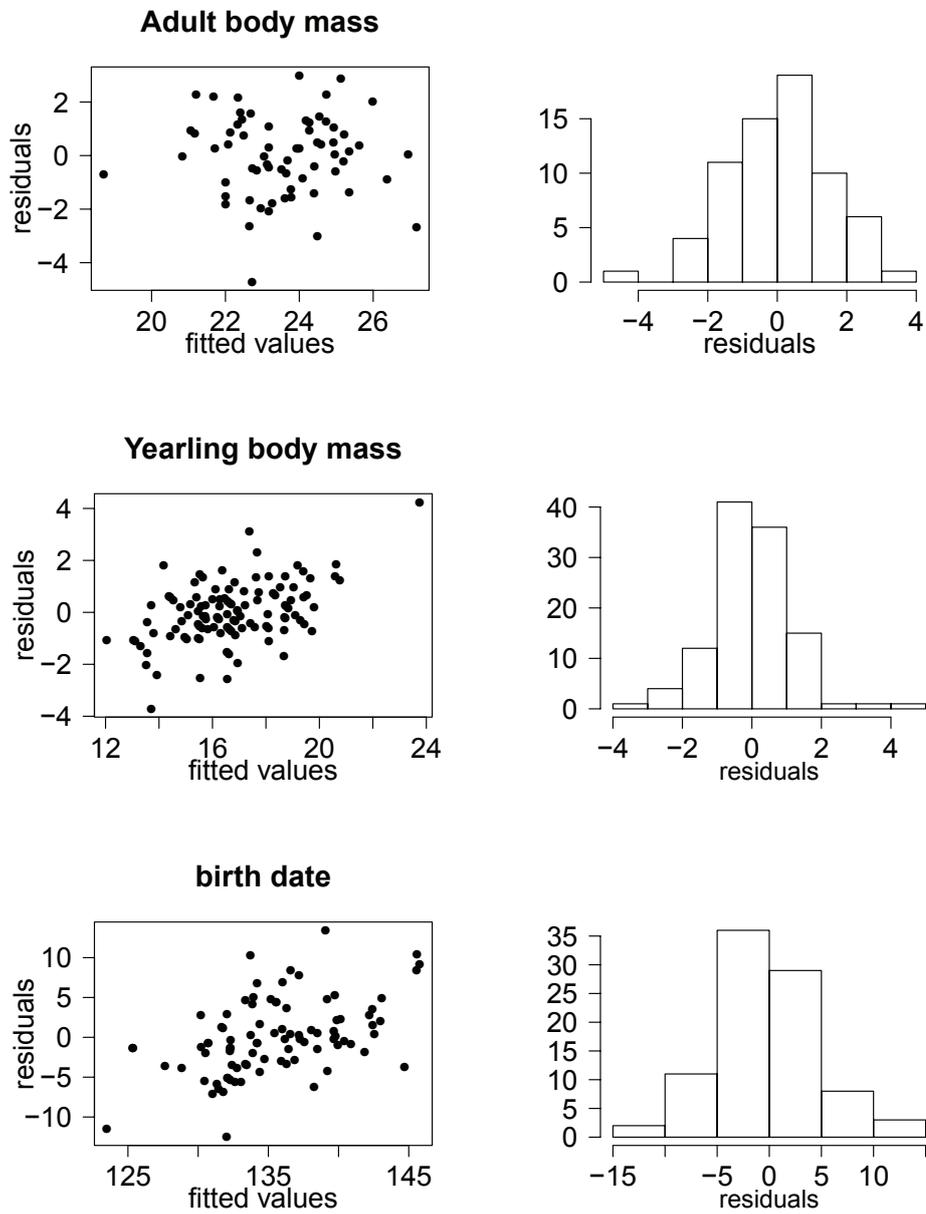


Figure S6. Diagnostic plots of the models describing the early and adult life history traits with a Gaussian distribution. For each vital rates, we present a plot of the residuals against the fitted values (right panels) and the distribution of the residuals (left panels).

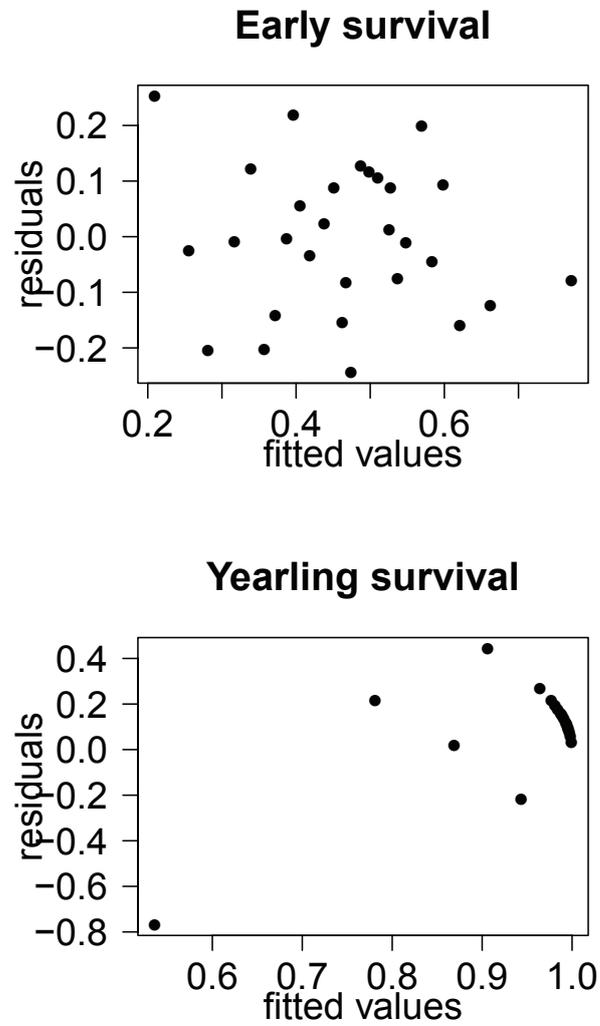


Figure S7. Diagnostic plots of the models describing the early and adult life history traits with a binomial distribution. For early and yearling survival, we present a plot of the binned residuals against the fitted values.