



HAL
open science

Caractérisation des interactions entre la structure de population et l'histoire de vie

Marianne Mugabo

► **To cite this version:**

Marianne Mugabo. Caractérisation des interactions entre la structure de population et l'histoire de vie. Ecologie, Environnement. Ecole Normale Supérieure de Paris - ENS Paris, 2011. Français. NNT : . tel-00585658v1

HAL Id: tel-00585658

<https://theses.hal.science/tel-00585658v1>

Submitted on 13 Apr 2011 (v1), last revised 5 Jun 2011 (v2)

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.

ECOLE NORMALE SUPERIEURE DE PARIS
Ecole Doctorale Interdisciplinaire 474 FRONTIERES DU VIVANT
Laboratoire Ecologie & Evolution – UMR 7625

THESE DE DOCTORAT

Spécialité : Ecologie

Présentée par Marianne Mugabo

Pour obtenir le grade de Docteur de l’Ecole Normale Supérieure de Paris

**Caractérisation des interactions entre
la structure de population et l’histoire de vie**

Thèse dirigée par :

Régis Ferrière et Jean-François Le Galliard

Soutenue le 11 Avril 2011 devant le jury composé de :

Dr. Jean-Michel Gaillard	Rapporteur
Dr. Christophe Barbraud	Rapporteur
Pr. Tim Benton	Examinateur
Dr. Anne Charmantier	Examinatrice
Pr. François Sarrazin	Examinateur
Pr. Michel Morange	Examinateur
Dr. Jean-François Le Galliard	Directeur de thèse

ECOLE NORMALE SUPERIEURE DE PARIS
Ecole Doctorale Interdisciplinaire 474 FRONTIERES DU VIVANT
Laboratoire Ecologie & Evolution – UMR 7625

PhD thesis

Major: Ecology

Presented by Marianne Mugabo

To become a doctor from the Ecole Normale Supérieure de Paris

Characterisation of the interactions between
population structure and life history

PhD advisors:

Régis Ferrière and Jean-François Le Galliard

Defended on the 11th of April 2011

Jury:

Dr. Jean-Michel Gaillard	Reviewer
Dr. Christophe Barbraud	Reviewer
Pr. Tim Benton	Examiner
Dr. Anne Charmantier	Examiner
Pr. François Sarrazin	Examiner
Pr. Michel Morange	Examiner
Dr. Jean-François Le Galliard	Advisor

*Les chiffres sont aux analystes ce que les lampadaires sont aux ivrognes :
ils fournissent bien plus un appui qu’un éclairage.*

Jean DION. Extrait du journal québécois Le Devoir 4 juin 1997

REMERCIEMENTS

Je voudrais tout d’abord remercier Jean-François. Que dire sinon que je te suis infiniment reconnaissante pour ton encadrement et ton soutien pendant ces quatre dernières années mais aussi pour ta grande disponibilité et ta passion de l’écologie. Mes remerciements vont également à Régis Ferrière ainsi qu’aux membres de mon jury : Jean-Michel Gaillard, Christophe Barbraud, Tim Benton, Anne Charmantier, Michel Morange et François Sarrazin, qui vont allouer un peu de leur temps précieux pour juger mon travail de recherche.

Je souhaiterais également remercier les membres de mon comité de thèse : Pierre-Yves Henry, Claire Doutrelant, David Claessen et Manuel Massot pour nos discussions scientifiques et les bons conseils qu’ils m’ont donnés !

Mes remerciements vont aussi au réseau R2DS de la Région Île-de-France, à l’école doctorale 474 Frontières Du Vivant, à l’Ecole Normale Supérieure, à l’Agence Nationale de la Recherche, au CNRS, au CEREEP UMS 3194 et au Laboratoire Ecologie et Evolution UMR 7625 qui ont financé mes recherches et rendu possible la réalisation de mes expériences.

Un grand merci à toutes les personnes avec qui j’ai collaboré au cours de cette thèse : Olivier Marquis, Manuela Gonzalez-Suarez, Bieke Vanhooydonck, Kathleen Huyghe, Sandrine Meylan et Stéphane Legendre, qui m’a initiée aux joies de la modélisation sous Ulm 3 mois avant la fin de ma thèse ! Ces personnes ont grandement contribué à rendre cette thèse si enrichissante. Je tiens également à associer ces remerciements aux personnes qui ont collaboré à mes projets : Murielle Richard, Pierre Federici et Claudy Haussy; et sans qui j’aurais eu bien du mal à effectuer les analyses génétiques et les dosages hormonaux.

Merci aux membres du CEREEP UMS 3194 : Isabelle, Sophie, Cécilia et Jean-Jacques pour leur accueil chaleureux ! Je tiens en particulier à remercier Béatriz Decencièrre pour son aide et son soutien depuis le début de ma thèse. Je suis également très reconnaissante envers Samuel Perret et Matthieu Paquet qui m’ont sauvée du naufrage pendant ma première saison de terrain et ont été un soutien constant par la suite. De même, je remercie tous les membres du laboratoire Ecologie et Evolution et en particulier Sandrine, Manuel, Clotilde,

Paulina, Thomas, Adrien, Julien, Pierre, Murielle, Nicolas et Thibaud pour nos discussions diverses et variées qui ont égayées mes journées !

Je voudrais également remercier tous les étudiants pour leur aide précieuse sur le terrain et au laboratoire : Karine Longatte, Magalie Evanno, Matthieu Cisel, Fanny Boutard, Lucas Legendre, Franck Bailly, Bastien Morisseau, Mathilde Huet, Jérémy Aubry et Cristina Acuso. J’en profite également pour remercier Laura de Senneville qui a travaillé au CEREEP quelques mois en 2010 m’a beaucoup aidé.

Je continuerais en remerciant tous mes amis qui m’ont supporté (dans les deux sens du terme ...) pendant ces dernières années. Bien entendu la fine équipe des Palois expatriés : Cléa, Lucie, Claire, Nils alias Dr Poupou, et Emilie avec qui j’ai partagé les bancs des amphis de bio de la Grandissime Université de Pau et des Pays de l’Adour ! Merci à tous les anciens Rennais et en particulier à Gaëlle, mon fournisseur officiel de supers bouquins. Merci aux « Parisiens » (anciens et actuels) Gaby, Willou, Michael, Cléa (la Paloise devenue Malakoffiote !), Benoit, Juliette et les inconditionnels du pot de labo : Lisa, Simon, Joséfa, Robin, Blandine, Rodolphe et les dernières arrivées : Mélissa, Anaïs et Claudia, avec qui j’ai partagé de grands moments et sans qui cette thèse aurait été bien triste ! Un grand merci au Toulousain, le seul, l’unique : Julien, qui fait mon éducation musicale depuis plus de 10 ans. Que serais-je devenue sans les Queens of The Stone Age, Rodrigo y Gabriela et autres Ginzu pour me donner la pêche pendant toutes ces longues heures de saisie, mise en forme et analyses de données ??? Et puis encore merci à Samuel et Matthieu pour tous les bons moments passés en dehors des murs du CEREEP et de Jussieu !

Et pour finir, merci à mes parents pour leur soutien sans faille pendant ces quatre longues années de labeur.

Thèse préparée au

Laboratoire Ecologie et Evolution, UMR 7625

Université Pierre et Marie Curie

7 Quai Saint Bernard

Bâtiment A 7^{ème} étage

75005 Paris, France

TABLE DES MATIERES

Résumé	8
Introduction générale	10
Contexte de l’étude	19
Influences de la structure de population sur l’histoire de vie du lézard vivipare	24
Influences de la structure de population sur le système d’appariement et l’intensité de la sélection sexuelle chez le lézard vivipare	39
Conséquences pour la dynamique des populations de lézards vivipares.....	41
Conclusion	46
Références	48
Annexes	62
Chapitre 1 – Effets cohortes dans des populations structurées et conséquences démographiques	72
Chapitre 2 – Effets de l’environnement nutritif précoce sur l’histoire de vie dans des populations structurées en cohortes	98
Chapitre 3 – Effets de l’environnement nutritif tardif sur l’histoire de vie dans des populations structurées en cohortes	129
Chapitre 4 – Densité de population et interactions trophiques proies-prédateurs	156
Chapitre 5 – Densité dépendance de l’histoire de vie et risque d’extinction	182

RÉSUMÉ

La structure des populations influence de manière importante le taux de croissance des populations et donc leurs capacités à faire face à des changements environnementaux. En effet, elle détermine la part d’individus qui contribuent au renouvellement des générations ainsi que l’intensité des interactions sociales compétitives et coopératives. Utilisant le lézard vivipare (*Zootoca vivipara*, Jacquin 1787) comme modèle d’étude, mon travail de thèse consiste à caractériser la relation entre la structure de population (en termes de cohortes, densité et classes d’âge et de sexe), l’histoire de vie et la dynamique de petites populations isolées. Pour cela, nous combinons des approches expérimentales en conditions semi-naturelles à des approches théoriques utilisant des modèles populationnels à un et deux sexes structurés en classes d’âge. Une analyse critique de la littérature montre que la variabilité environnementale peut générer des différences d’histoire de vie entre cohortes de naissance, ou effets cohortes, à travers son influence sur la qualité des individus et sur l’intensité de la compétition intraspécifique au sein d’une cohorte et entre cohortes. Un premier travail empirique démontre que ces trois mécanismes induisent de la variation d’histoire de vie entre cohortes, mais met également en évidence que les effets directs de la variabilité environnementale sur la qualité des individus interagissent de manière complexe avec des effets indirects sur l’intensité de la compétition entre individus. Au cours d’une deuxième étude empirique, nous analysons les processus et conséquences démographiques de ces interactions compétitives. Une élévation de la densité augmente la compétition trophique et pourrait également induire des réponses hormonales au stress social, ce qui ralentit la croissance corporelle et la reproduction. Un modèle stochastique démontre que cette densité dépendance de l’histoire de vie interagit avec les fluctuations stochastiques du sexe ratio pour façonner la dynamique d’extinction des petites populations de lézards. Ces prédictions seront affinées par l’analyse d’une troisième étude empirique impliquant une manipulation conjointe de la densité et du sexe ratio de la population. Nos résultats, intégrés dans le contexte général de l’écologie des populations, soulignent l’importance de prendre en compte la structure de la population et l’hétérogénéité de l’histoire de vie pour établir des prédictions fiables sur le devenir des petites populations et mettre en place des mesures de gestion efficaces.

Mots-clés : effets cohortes, densité dépendance, structure d’âge, sexe ratio adulte, histoire de vie, système d’appariement, sélection sexuelle

ABSTRACT

Population structure influences importantly population growth rate and their ability to cope with environmental variations. Indeed, it determines the proportion of individuals who contribute to produce new generations as well as the intensity of competitive and cooperative social interactions. Using the common lizard (*Zootoca vivipara*, Jacquin 1787) as a model species, my work consists in the characterization of the relationship between population structure (in terms of cohorts, density and age and sex classes), life history and the dynamics of small isolated populations. To this aim, we combine experimental approaches in semi-natural conditions with modeling approaches using one-sex and two-sex age-structured population models. A critical review of the literature reveals that environmental variation can give rise to life-history differences among birth cohorts, or cohort effects, through its effects on individual quality and the intensity of intraspecific competition within and between cohorts. A first empirical study demonstrates that these three mechanisms generate life-history variation among cohorts, but also highlight the fact that direct effects of environmental variation on individual quality interact in a complex manner with indirect effects on the intensity of competition among individuals. During a second empirical study, we analyze the demographic processes and consequences of these competitive interactions. An elevation of density increases trophic competition and could induce hormonal responses to social stress, which reduce body growth and reproduction. A stochastic model demonstrates that this density dependence of life history interacts with the stochastic fluctuations of sex ratio to shape extinction dynamics of small populations of lizards. These predictions will be completed by the analysis of a third empirical study involving a joint manipulation of population density and sex ratio. Our results, integrated in the broad context of population ecology, highlight the importance of taking into account population structure and life-history heterogeneities in order to draw accurate predictions of the fate of small populations and to develop efficient management policies.

Keywords: cohort effects, density dependence, age-structure, adult sex ratio, life history, mating system, sexual selection.

Caractérisation des interactions entre
la structure de population et l’histoire de vie



INTRODUCTION GÉNÉRALE

Des populations structurées

Les taux démographiques des individus déterminent le taux de croissance des populations (Caswell, 2001). Or, les individus au sein d’une population peuvent différer dans leurs performances en fonction de traits tels que l’âge et le sexe (Caswell, 2001). Ces hétérogénéités entre groupes d’individus définissent la structure d’une population. Une autre caractéristique importante d’une population est sa densité ou sa taille. En effet, la densité dépendance est l’un des principaux mécanismes de régulation des populations animales et végétales (Sibly et al., 2005, Henle et al., 2004).

La structure des populations évolue dans le temps et dans l’espace sous l’influence des réponses individuelles au sein des classes d’âge et de sexe aux variations de l’environnement abiotique (ex : climat, Coulson et al., 2001), trophique (ex : densité de proies et de prédateurs, de Roos et al., 2003), et social (ex : nombre de compétiteurs et de partenaires sexuels, Begon et al., 2006, Gascoigne et al., 2009). Ainsi, il existe un lien de rétroaction fort entre la structure des populations et l’histoire de vie, la structure des populations influençant les performances des individus à travers les interactions sociales et les performances des individus déterminant la structure de population. Ici, nous nous concentrerons sur le lien existant entre la structure de population, l’histoire de vie et la dynamique de petites populations isolées. Nous ne discuterons donc pas de la structuration spatiale des populations.

Structure de population et histoire de vie

Structure d’âge et effets cohortes

Dans les populations structurées en cohortes de naissance, c’est-à-dire en groupes d’individus nés pendant un même épisode de reproduction, des effets cohortes émergent lorsque la variation environnementale génère de la variation d’histoire de vie entre cohortes (Albon et al., 1987, Gaillard et al., 2003, Lindström, 1999). Deux types d’effets cohortes ont été décrits par les écologistes des populations : les effets cohortes numériques directs et les effets cohortes qualitatifs décalés. La variation environnementale produit des effets cohortes

numériques directs lorsqu’elle influence la survie et les trajectoires de croissance des individus avant la maturité sexuelle et donc provoque de la variation dans le taux de recrutement (ex : chez les ongulés, Gaillard et al., 2003). Les effets cohortes qualitatifs décalés sont quant à eux la conséquence des effets à long terme des conditions environnementales sur les performances et la qualité intrinsèque des individus et peuvent être transmis entre générations via des effets parentaux (ex : Marquis et al., 2008, Plaistow et al., 2006). Les effets à long terme de l’environnement peuvent ainsi générer des effets « cuillère en argent » (ou « silver spoon effects », Grafen, 1988), lorsque des conditions favorables confèrent un avantage durable de valeur sélective aux individus par rapport à des individus ayant expérimenté des conditions défavorables. De tels effets de l’environnement créent de l’autocorrélation individuelle positive des traits d’histoire de vie (ex : taux de croissance corporelle plus élevé tout au long de la vie chez des espèces à croissance indéterminée, Madsen & Shine, 2000) et peuvent générer des covariations positives entre traits d’histoire de vie (ex : entre la survie et la reproduction, van de Pol et al., 2006). Cependant, des phénomènes de compensation de type croissance compensatoire, lorsque les conditions environnementales s’améliorent, peuvent également produire des covariations négatives entre les traits, ces phénomènes étant souvent associés à des coûts physiologiques et/ou écologiques (ex : augmentation du taux métabolique et du risque de prédation, Metcalfe & Monaghan, 2001).

Les conditions climatiques, la densité de population, la disponibilité en nourriture et la qualité de l’habitat sont les principaux facteurs environnementaux à l’origine d’effets cohortes (ex : Albon et al., 1987, Forchhammer et al., 2001, Reid et al., 2003, Roach, 2003). Les conditions environnementales pendant le développement précoce sont souvent prédites comme étant à l’origine des effets cohortes (Lindström, 1999, Metcalfe & Monaghan, 2001). Cependant, les conditions expérimentées plus tard dans la vie peuvent également générer de la variation cohorte, notamment par l’intermédiaire d’effets intergénérationnels des conditions expérimentées par la mère pendant la saison de reproduction (ex : Marquis et al., 2008, Plaistow et al., 2006). Les différentes routes d’influence de l’environnement sur l’histoire de vie pouvant générer des effets cohortes numériques et qualitatifs sont discutées en détail **Chapitre 1** et illustrées à l’aide d’exemples trouvés dans la littérature. Elles comprennent (i) les effets directs de l’environnement sur la qualité des individus au sein des cohortes tels que présentés précédemment, c’est-à-dire des effets densité-indépendants, (ii) ainsi que ses effets indirects via l’intensité de la compétition intraspécifique intra- et inter-cohortes, c’est-à-dire

des effets densité-dépendants. Deux types de compétitions intraspécifiques peuvent être distingués. Les effets cohortes densité-dépendants peuvent impliquer des interactions sociales de types symétriques, c’est-à-dire entre individus d’aptitudes compétitrices équivalentes, au sein d’une même cohorte (compétition intra-cohortes) ou entre cohortes (compétition inter-cohortes Beckerman et al., 2003, Lindström & Kokko, 2002). Cependant, la compétitivité des individus étant fortement influencée par leur taille (ou masse) corporelle (Bystrom & Andersson, 2005, Kooijman, 2000, Persson et al., 1998), les effets cohortes densité-dépendants impliquent généralement des interactions sociales asymétriques entre individus appartenant à différentes cohortes, de types compétition par exploitation asymétrique des ressources et cannibalisme (ex : Claessen et al., 2000, Claessen et al., 2002, Persson et al., 1998). Dans ce dernier cas nous verrons que la structure d’âge de la population peut avoir des effets importants sur les trajectoires d’histoire de vie des cohortes en compétition (voir Chapitre 1 et Claessen et al., 2000, Claessen et al., 2002, Persson et al., 1998).

Densité de population

La densité (ou la taille) de population peut affecter les performances des individus de manière négative (ex : Forrester et al., 2011, Massot et al., 1992, Bonenfant et al., 2009) ou positive (ex : Angulo et al., 2007, Bercé et al., 2001, Courchamp et al., 2000). La densité dépendance négative est le résultat de la compétition intraspécifique pour l’accès à des ressources limitées telles que la nourriture ou l’espace (Begon et al., 2006). Elle peut être due à des interactions indirectes entre compétiteurs via l’exploitation et la déplétion des ressources, c’est-à-dire de la compétition par exploitation, ou à des interactions directes entre individus via des phénomènes d’interférence, c’est-à-dire de la compétition par interférence, où les meilleurs compétiteurs monopolisent les ressources (Begon et al., 2006). A l’opposé, la densité dépendance positive, aussi appelée effet Allee (Allee et al., 1949), est due à la réduction du nombre d’interactions sociales coopératives à faibles densités telles que la rencontre de partenaires sexuels potentiels, la facilitation de la reproduction, la reproduction coopérative ou encore la dilution de la prédation (voir Chapitre 2 dans Courchamp et al., 2008). Deux types d’effets Allee peuvent être distingués : les effets Allee élémentaires ou « component Allee effects » et les effets Allee démographiques ou « demographic Allee effects » (Stephens et al., 1999). Les effets Allee élémentaires correspondent à de la densité dépendance positive sur une des composantes de la valeur sélective des individus, par exemple sur la survie, tandis que les effets Allee démographiques correspondent à de la densité dépendance positive sur la

valeur sélective globale des individus, qui dépend à la fois de paramètres de survie et de paramètres de reproduction (Courchamp et al., 2008). Ainsi, un effet Allee élémentaire ne se traduit pas nécessairement par une réduction de la valeur sélective des individus à faibles densités et donc par un effet Allee démographique s’il existe par exemple des compromis entre les différentes composantes de la valeur sélective tels qu’une compensation des coûts de survie à faible densité par une fécondité plus élevée (Stephens et al., 1999, Courchamp et al., 2008, Gascoigne et al., 2009).

La détection et la caractérisation de la forme de la densité dépendance de l’histoire de vie est souvent rendue difficile par le manque de données empiriques de bonne qualité et couvrant une large gamme de densités de population, ce qui est particulièrement vrai pour les populations en déclin (Morris & Doak, 2002, Courchamp et al., 2008, Beissinger & McCullough, 2002, Ferrière et al., 2004). Cependant, une relation négative entre la densité de population et la survie, la reproduction, la croissance, et des traits physiologiques tels que l’immuno-compétence a été décrite chez un grand nombre de taxa (ex : chez les poissons, Edeline et al., 2010, Forrester et al., 2011, les mammifères, Bonenfant et al., 2009, Koskela et al., 1999, les oiseaux, Both, 1998, les arthropodes, , les reptiles, Massot et al., 1992, Svensson et al., 2001, et les plantes Turkington et al., 2005). Des effets Allee élémentaires ont également été décrits chez un grand nombre d’espèces (voir revue par Courchamp et al. (2008) chez des mammifères, oiseaux, insectes, reptiles, amphibiens, poissons et autres organismes marins). En revanche, il n’existe que peu d’exemples empiriques d’effets Allee démographiques (voir revue par Gregory et al., 2010). Ainsi, alors que des effets Allee élémentaires provoqués par un manque de partenaires sexuels ont été rapportés chez une grande variété d’espèces marines et terrestres, des évidences empiriques d’effets Allee démographiques n’ont été décrites que chez deux espèces de papillons, une espèce de crustacée et une espèce de plante (Gascoigne et al., 2009). Une approche alternative pour lier la densité à un effet Allee démographique, lorsqu’un effet Allee élémentaire a été détecté, est de combiner des données empiriques d’histoire de vie avec des modèles populationnels à deux sexes incluant des fluctuations du sexe ratio et une fonction d’appariement décrivant la formation des couples reproducteurs (ex : Bessa-Gomez et al., 2004, Engen et al., 2003, Legendre et al., 1999).

Structure de sexe

La structure de sexe d’une population peut affecter de manière importante la valeur sélective des mâles et des femelles. En effet, elle détermine le taux de fertilisation des femelles reproductrices (Rankin & Kokko, 2007) et influence fortement l’accès à la reproduction des mâles (ex : Mysterud et al., 2003, Fitze et al., 2008). La théorie sur l’évolution du sexe ratio prédit que les individus du sexe le plus rare ont une valeur sélective plus élevée que les individus du sexe le plus abondant (ex : Fisher, 1930). Le sexe ratio adulte devrait donc être fortement régulé par la compétition intersexuelle et varier faiblement dans le temps et dans l’espace. Cependant, la variation des conditions environnementales peut générer des fluctuations dans la structure de sexe si les mâles et les femelles ne répondent pas de la même manière à l’environnement (ex : Coulson et al., 2001, Tschirren et al., 2003, Metcalfe & Monaghan, 2001, Le Galliard et al., 2005d). C’est particulièrement le cas chez les espèces présentant un dimorphisme sexuel de taille corporelle, où le sexe le plus grand fait face à des demandes énergétiques plus élevées (Lindström, 1999, Coulson et al., 2001, Clutton-Brock et al., 1985). Ainsi, la théorie sur l’allocation optimale au sexe (« optimal sex allocation theory », Charnov, 1982) prédit que les variations du sexe ratio générées par l’environnement devraient être compensées par une augmentation de l’investissement maternel dans le sexe rare. Cependant, chez des espèces où la détermination du sexe est génétique (chez les plupart des vertébrés) et les soins parentaux sont limités ou inexistant, les capacités des femelles à ajuster leur investissement en fonction du sexe de leurs descendants peuvent être réduites (Cockburn et al., 2002). Par exemple, chez une espèce polygyne où les comportements sexuels des mâles sont délétères pour la survie et la fécondité des femelles, une incapacité des femelles à ajuster le sexe ratio primaire en réponse à un sexe ratio adulte mâle-biaisé peut conduire à une augmentation du biais de sexe ratio vers les mâles, réduisant d’autant plus la valeur sélective des femelles (ex : Le Galliard et al., 2005c, Le Galliard et al., 2005d).

Interactions entre la densité de population et les structures d’âge et de sexe

La densité de population, la structure d’âge et la structure de sexe peuvent également interagir pour façonner les trajectoires d’histoire de vie. Par exemple, dans le cas de populations structurées en cohortes, la densité de population et la structure d’âge déterminent l’intensité de la compétition asymétrique entre cohortes et les conséquences pour l’histoire de vie des cohortes en compétition (voir **Chapitre 1**). De même, la densité de population et le sexe ratio

adulte peuvent agir en interaction lorsque les performances des individus sont sensibles au nombre absolu plutôt qu’au nombre relatif d’individus d’un sexe (Kvarnemo & Ahnesjö, 2002). C’est par exemple le cas chez le poisson zèbre où les comportements territoriaux et les comportements de cour des mâles sont affectés par une interaction entre le sexe ratio adulte et la densité de population (Spence & Smith, 2005). Dans cette étude, la production d’œufs moyenne par femelle n’a pas été affectée par une interaction entre la densité et le sexe ratio. Cependant la modification des comportements sexuels des mâles résultant de l’interaction entre ces deux paramètres démographiques pourraient avoir des conséquences importantes pour le degré de fertilisation des œufs et donc le succès reproducteur des femelles et des mâles (Spence & Smith, 2005).

Hétérogénéités des réponses individuelles

Le lien entre structure de population et histoire de vie peut être compliqué par l’existence d’hétérogénéités des réponses en fonction de caractéristiques individuelles (Benton et al., 2006, Clutton-Brock & Coulson, 2002, Coulson et al., 2001). Ainsi, au sein d’une classe d’âge, les mâles et les femelles peuvent répondre différemment à la structure de population, générant ainsi de la variation dans la structure de sexe. De même, au sein d’un sexe, les individus d’âges différents peuvent varier dans leur réponse à la densité de population ou à la structure de sexe, générant ainsi de la variation dans la structure d’âge (ex : Coulson et al., 2001, Le Galliard et al., 2005d). Une autre source importante de variabilité interindividuelle dans la réponse à l’environnement, et dans le cas présent, à l’environnement social vient des effets maternels d’origine génétique ou environnementale (Räsänen & Kruuk, 2007). Or des effets maternels sur les performances démographiques des descendants peuvent également modifier la structure d’âge des populations de manière importante (ex : Benton et al., 2008).

Structure de population, système d’appariement et sélection sexuelle

La sélection sexuelle résulte de la compétition entre individus pour l’accès aux partenaires sexuels potentiels (Andersson, 1994). Le sexe ratio opérationnel, qui correspond au sexe ratio parmi les individus sexuellement réceptifs, a été identifié de longue date comme le déterminant majeur de l’intensité de la compétition pour l’accès à la reproduction et donc de la direction et de l’intensité de la sélection sexuelle (Emlen & Oring, 1977). Plus récemment, il a été proposé que la densité de population pouvait également influencer le système

d’appariement et la sélection sexuelle (voir revue par Kokko et Rankin, 2006). En effet, de la même manière que la densité de population détermine l’intensité de la compétition intraspécifique pour l’accès à la nourriture ou à l’espace, elle peut aussi influencer l’intensité de la compétition pour l’accès à un ou plusieurs partenaires sexuels (Emlen & Oring, 1977).

Deux théories s’opposent quant à l’influence du sexe ratio opérationnel et de la densité sur le système d’appariement et l’intensité de la sélection sexuelle. La théorie classique de la sélection sexuelle prédit que l’intensité de la sélection sexuelle devrait être la plus forte dans le sexe le plus abondant sous l’action de la compétition intra- et intersexuelle (Emlen & Oring, 1977). Cependant, en raison de l’accumulation de contre-exemples, une nouvelle théorie a été proposée par Kokko et al. (Kokko & Johnstone, 2002, Kokko & Monaghan, 2001, Kokko & Rankin, 2006), qui prédit que l’influence du sexe ratio opérationnel et de la densité sur la direction et l’intensité de la sélection sexuelle est déterminée par les caractéristiques du système d’appariement telles que les coûts de mortalité et les coûts de reproduction.

Conséquences démographiques de la structure de population

Conséquences démographiques des effets cohortes

Les effets cohortes peuvent être un facteur important de variation temporelle de la structure d’âge (Gaillard et al., 2003). En effet, les effets cohortes numériques directs se traduisent par une variation de la taille des nouvelles cohortes recrutées tandis que les effets cohortes qualitatifs décalés déterminent le succès reproducteur moyen au sein des cohortes d’individus matures. Malgré le fait que des effets cohortes numériques et qualitatifs aient été décrits chez un grand nombre d’espèces (voir **Chapitre 1**), leurs mécanismes proximaux restent souvent inexplorés et seules quelques études ont tenté de quantifier les conséquences démographiques des effets cohortes densité-indépendants et densité-dépendants pour la dynamique des populations.

Les conséquences démographiques des effets cohortes densité-indépendants sont déterminés par la variation cohorte, l’autocorrélation et la covariation des traits d’histoire de vie provoquées par la variation des conditions environnementales qui diminuent le taux de croissance stochastique des populations (Haridas & Tuljapurkar, 2005, Pfister & Stevens, 2003, Doak et al., 2005, Tuljapurkar et al., 2009). Ainsi, il a été montré chez trois espèces que

le taux de croissance des populations est généralement plus affecté par des effets cohortes densité-indépendants numériques que par des effets cohortes qualitatifs (Gaillard et al., 2003, Le Galliard et al., 2010, Wittmer et al., 2007). Les effets cohortes densité-dépendants impliquant des interactions sociales symétriques affecteraient, quant à eux, la dynamique des populations via une modification de la forme de la densité dépendance négative des taux démographiques résultant en la stabilisation ou la déstabilisation de la dynamique en fonction de son état initial (Beckerman et al., 2003, Lindström & Kokko, 2002). Finalement, il a été prédit que la compétition asymétrique inter-cohortes par exploitation et déplétion des ressources aurait des effets déstabilisateurs sur la dynamique des populations, alors que du cannibalisme taille-dépendant aurait des effets dynamiques stabilisateurs (Claessen et al., 2000, Claessen et al., 2002, Persson et al., 1998). Une revue détaillée des effets dynamiques de la variation cohorte mis en évidence par ces différentes études est présentée **Chapitre 1**.

Conséquences démographiques de la densité de population et des structures d’âge et de sexe

La densité, la structure d’âge et la structure de sexe d’une population peuvent fortement affecter sa dynamique (ex : Edeline et al., 2010, Coulson et al., 2001). Dans les domaines de la biologie de la conservation et de la gestion des populations, les analyses de viabilité des populations ont démontré l’importance de la structure des populations pour la probabilité d’extinction de populations soumises à de la stochasticité démographique et environnementale (Henle et al., 2004, Lande et al., 2003, Morris & Doak, 2002, Ferrière et al., 2004). Ainsi, la densité dépendance négative peut stabiliser les populations à des densités où le risque d’extinction est élevé sous l’action de la stochasticité démographique (Lande et al., 2003, Morris & Doak, 2002), tandis que les effets Allee démographiques impliquent l’existence d’un équilibre instable, appelé seuil d’effet Allee, en-dessous duquel les populations s’éteignent de manière déterministe (Courchamp et al., 2008). Il a de plus été montré que les conséquences de la densité sur la probabilité d’extinction d’une population étaient déterminées par la forme et la force de la densité dépendance négative et positive de l’histoire de vie (Henle et al., 2004, Pascual et al., 1997, Runge & Johnson, 2002). Malgré cela, la densité dépendance négative est souvent ignorée dans les analyses de viabilité des petites populations en déclin, qui sont considérées comme étant très en-dessous de la capacité de charge de l’environnement et donc non régulées par densité dépendance négative (Morris & Doak, 2002, Grant & Benton, 2000). Or, même dans une petite population, la densité peut

être localement élevée et affecter négativement les performances des individus (Grant & Benton, 2000, Schoener et al., 2003).

De même, un grand nombre de modèles populationnels ne prennent en compte que la portion femelle des populations (Caswell, 2001), émettant ainsi l’hypothèse que les sexes ne diffèrent pas dans leur taux démographiques et que les performances d’un sexe n’affectent pas les performances de l’autre sexe. Cependant, nous venons de voir que la structure de sexe peut être un déterminant majeur des performances des individus et donc de la dynamique des populations. L’utilisation de modèles à deux sexes a ainsi permis de démontrer que les fluctuations stochastiques du sexe ratio et de la formation des couples provoquées par la stochasticité démographique et environnementale pouvaient conduire à des effets Allee démographiques liés à des déficits de partenaires sexuels et ainsi précipiter les populations vers l’extinction (ex : Bessa-Gomez et al., 2004, Engen et al., 2003, Legendre et al., 1999). De plus, le système d’appariement peut être important pour la persistance des populations, les espèces polygames étant généralement moins susceptibles aux effets Allee que les espèces monogames (ex : Legendre et al., 1999, Bessa-Gomez et al., 2004). De même, l’intensité de la sélection sexuelle pourrait mettre en péril la persistance des populations (voir revue par Kokko et Rankin, 2006 et références citées).

Finalement, en comparant des modèles populationnels incluant ou non une structure d’âge, Coulson et al. (2001) et Schoener et al. (2003) ont démontré l’importance de prendre en compte les caractéristiques du cycle de vie pour établir des prédictions fiables sur la dynamique et la persistance de populations structurées en classe d’âge.

CONTEXTE DE L’ÉTUDE

Structure de population et histoire de vie chez le lézard vivipare

Au cours de cette thèse, nous nous sommes intéressés à l’influence de la structure de population sur l’histoire de vie au sens large et sur le système d’appariement et à ses conséquences pour le fonctionnement des populations chez un organisme modèle : le lézard vivipare (*Zootoca vivipara*). Pour cela, nous avons effectué trois expériences en conditions semi-naturelles au Centre de Recherche en Ecologie Expérimentale et Prédictive (CEREEP à Saint-Pierre-lès-Nemours en Seine-et-Marne, France ; Figure 1). Les protocoles expérimentaux ont consisté en la manipulation de la structure de populations expérimentales

maintenues dans des enclos extérieurs et en la description des réponses (i) des traits d’histoire de vie au sens strict, c’est-à-dire la croissance en taille, la survie et la reproduction, (ii) de différents traits phénotypiques connus pour affecter la valeur sélective des individus : des traits physiologiques (immunocompétence, taux hormonaux et taux de consommation de nourriture), des traits de performances (performances locomotrices) et (iii) des stratégies d’appariements. Nous avons ensuite étudié comment les réponses individuelles à la structure de population affectent la dynamique de population.

Une première expérience a porté sur l’influence de la disponibilité en nourriture passée et de l’environnement social sur l’histoire de vie dans des populations structurées en cohortes (**Chapitres 2 et 3**). En parallèle, nous avons réalisé une revue de la littérature sur les mécanismes des effets cohortes et leurs conséquences pour la dynamique des populations (**Chapitre 1**). Lors d’une deuxième expérience, nous avons décrit la densité dépendance de l’histoire de vie (**Chapitre 4 et 5**) et ses conséquences pour la persistance de petites populations isolées de lézards à l’aide d’un modèle matriciel de populations structurées en classes d’âge (**Chapitre 5**). Dans un troisième temps, nous avons manipulé conjointement ces deux traits démographiques (Expérience 3). Au cours de l’Expérience 2, nous avons également caractérisé la réponse physiologique à l’environnement social en mesurant les niveaux d’hormones de stress (taux de corticostérone plasmatique). Afin d’avoir une vision plus globale de la réponse au stress chez cette espèce, nous avons réalisé une expérience complémentaire en conditions contrôlées en laboratoire (Expérience 4) nous permettant de caractériser la réponse à court terme (à l’échelle de quelques jours) à un stress ponctuel (stress de manipulation) et à un stress social (conditionnement en binôme pendant plusieurs jours).

Après une présentation du modèle d’étude, nous décrirons dans un premier temps les effets observés de la structure de population sur l’histoire de vie au sens large. Cette question sera traitée en détail dans les **Chapitres 2, 3, 4 et 5**. Dans un second temps, nous nous intéresserons à l’influence de la structure de population sur le système d’appariement et l’intensité de la sélection sexuelle. Les données issues de cette étude n’ont pas encore été analysées. Les résultats attendus seront donc présentés dans l’introduction générale. Nous conclurons sur les conséquences des réponses individuelles à la structure de population sur la dynamique des populations de lézards. Cette dernière question sera traitée en détail dans les **Chapitres 2 et 5**. Les protocoles expérimentaux qui ne seront pas présentés dans les chapitres feront l’objet d’annexes (**Annexes 1 à 3**).

Il est à noter que les appels aux Chapitres et Annexes seront toujours présentés en gras et vert.

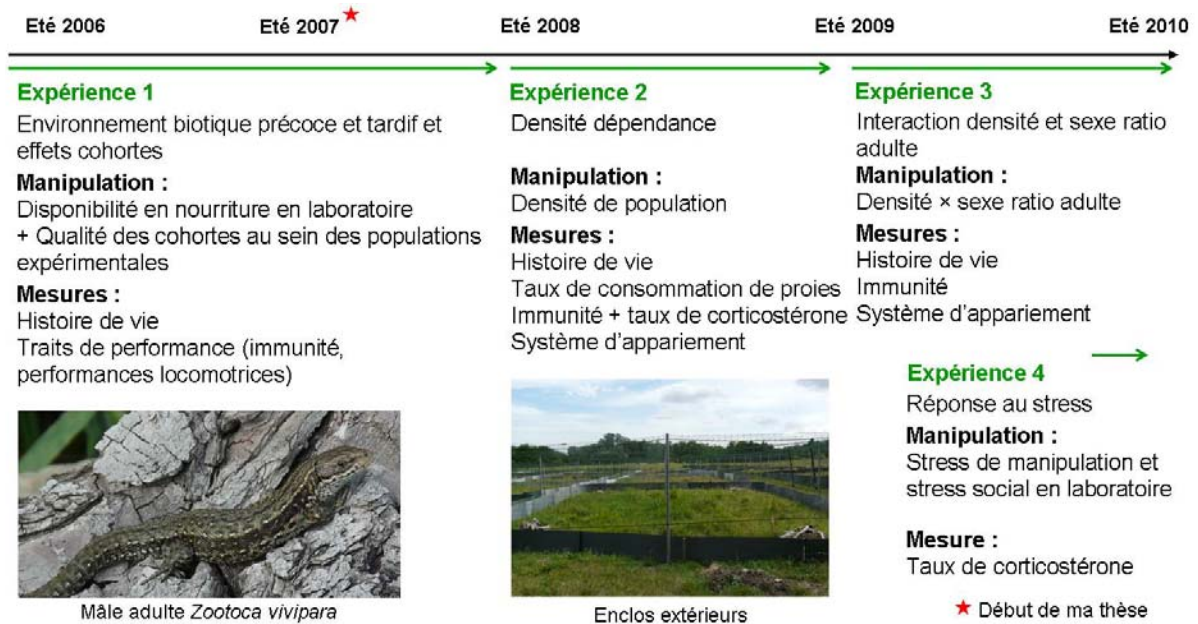


Figure 1. Présentation chronologique des expériences réalisées au cours de cette thèse. Pour chaque expérience, sont précisés les facteurs environnementaux ou démographiques manipulés, ainsi que les traits individuels mesurés.

Le lézard vivipare comme organisme modèle

Histoire de vie

Le lézard vivipare (*Zootoca vivipara*, Jacquin 1787, ex *Lacerta vivipara*) est un petit Larcertidé inféodé aux milieux froids et humides du continent eurasiatique. Il s’agit de l’un des vertébrés terrestres présentant la plus grande aire de répartition puisqu’il est présent de l’Europe de l’ouest jusqu’au Japon et du cercle polaire jusqu’à la Mer Méditerranée et la Mer Adriatique. En conséquence, l’espèce est caractérisée par une histoire de vie très plastique particulièrement sensible aux conditions climatiques (température et humidité), à la disponibilité en nourriture (ex : Le Galliard et al., 2005b, 2010, Marquis et al., 2008, Lorenzon et al., 2001) ainsi qu’à la structure de population (Le Galliard et al., 2005b, 2005d, Massot et al., 1992). Le lézard vivipare présente un cycle de vie annuel et une durée de vie courte de 3-4 ans en moyenne, pouvant aller jusqu’à 7 ans chez les mâles et 10 ans chez les femelles (Massot et al., 2011). Dans notre site d’étude, les animaux entrent en hibernation au mois d’octobre. Les mâles adultes sont les premiers à sortir d’hibernation à la fin de l’hiver, entre fin février et début mars, et sont suivis par les juvéniles. Les femelles adultes émergent

autour de début avril. La spermatogénèse et la vitellogenèse ont lieu dans les semaines qui suivent la sortie d’hibernation et les accouplements débutent dès l’émergence des femelles adultes (Bauwens et al., 1989, Bauwens & Verheyen, 1985). Le lézard vivipare possède un système d’appariement polygynandre et un mode de reproduction ovovivipare. Les femelles produisent une portée par an de 1 à 12 œufs non-calcifiés (5 œufs en moyenne) avec un à six mâles, tandis que les mâles peuvent se reproduire avec jusqu’à 14 femelles (Fitze et al., 2005). Les stratégies d’appariements seraient âge-dépendantes chez les deux sexes. Chez les jeunes femelles et les femelles âgées la stratégie polyandre est favorisée (Richard et al., 2005), tandis que les femelles d’âge intermédiaire sont plutôt monoandres. Chez les mâles, le degré de polygynie (c’est-à-dire le nombre de partenaires sexuels) augmente avec l’âge (Dreiss et al., 2010). Pendant la saison des accouplements, des combats peuvent avoir lieu entre mâles pour l’accès aux femelles et les mâles peuvent harasser et forcer les femelles à s’accoupler (Heulin, 1988). En effet, lors de l’accouplement les mâles maintiennent fermement les femelles en les mordant à l’abdomen (Fitze et al., 2005).

Durant la gestation, qui dure environ deux mois, des échanges d’eau (mais pas de nutriments) se produisent entre la mère et ses œufs (Meylan & Clobert, 2004 et références citées), et les conditions environnementales expérimentées par la mère ainsi que sa condition influencent les performances de ses descendants (ex : Le Galliard et al., 2010, Marquis et al., 2008, Meylan et al., 2010). Les juvéniles viables sortent de l’œuf quelques minutes à quelques heures après la ponte et sont immédiatement indépendants. Dans notre site d’étude, les pontes s’échelonnent entre mi-juin et fin juillet-début août. Comme chez beaucoup de reptiles, la croissance structurale est continue mais la majorité de la croissance a lieu pendant les 2 premières années de la vie (Fitze & Le Galliard, 2008). L’espèce est sexuellement dimorphique. Notamment, les femelles sont plus grandes que les mâles, généralement dès la naissance, tandis que les mâles ont une condition corporelle plus élevée (masse corporelle corrigée par le LMA, Kratochvil et al., 2003, Le Galliard et al., 2005b). Dans notre site d’étude, les mâles et les femelles peuvent accéder à la reproduction dès l’âge d’un an.

Le lézard vivipare possède des capacités de dispersion limitées de l’ordre de quelques dizaines de mètres (Clobert et al., 1994, Massot & Clobert, 1995). La dispersion a lieu principalement pendant les 10 premiers jours de la vie et est influencée par la structure de la métapopulation et les conditions environnementales (ex : Massot et al., 1992, Clobert et al., 1994, Massot & Clobert, 1995, Massot et al., 2002, Le Galliard et al., 2005a). Dans le cadre de cette thèse, nous n’étudions que le cas de petites populations isolées ou l’immigration et l’émigration sont nulles. Le lézard vivipare est un prédateur opportuniste qui consomme une

large gamme d’arthropodes incluant des Araignées, des Homoptères, des Hétéroptères et des Orthoptères (Avery, 1966, Pilorge, 1982, Le Galliard et al., 2005a). Le régime alimentaire et la taille des proies consommées se chevauchent entre les classes d’âge, conduisant à de la compétition asymétrique inter-cohortes pour l’accès à la nourriture (Lecomte et al., 1994, Massot et al., 1992).

Structure de population

Les populations naturelles de lézards vivipares sont constituées de 3 classes d’âge : les juvéniles ou jeunes de l’année, d’une longueur museau-anus (LMA) de 15 à 25 mm à la naissance, les sub-adultes (entre 1 et 2 ans) et les adultes (\geq à 2 ans), d’une taille de 50 à 75 mm. Dans les populations du Mont Lozère (Massif Central, France, 44°27’N, 3°44’E) desquelles les animaux utilisés pour nos expériences sont originaires, la structure de population fluctue dans l’espace et dans le temps (Bauwens et al., 1986, Le Galliard et al., 2005d). La densité de population varie entre 200 à 2000 adultes et sub-adultes par hectare (Massot et al., 1992). De manière générale le sexe ratio adulte des populations est femelle-biaisée (proportion de mâles adultes moyenne = 0.18 ± 0.18 SD) mais peut varier de 0 à 0.80 (Le Galliard et al., 2005d). La structure d’âge pré-reproduction (proportion d’adultes parmi les adultes et sub-adultes) est en moyenne de 0.47 ± 0.09 SD et s’échelonne de 0.35 à 0.65 (Massot et al., 1992, Meylan et al., 2007).

Intérêts du modèle d’étude

La variation naturelle de l’histoire de vie et de la structure des populations fait de cette espèce un modèle idéal pour étudier l’influence de la structure de population à l’échelle individuelle et populationnelle. A l’instar de certaines espèces de passereaux (mésanges bleue et charbonnière), d’ongulés (chevreuil, mouton), ou de poissons (Salmonidés, Percidés), il existe une importante littérature sur la variation d’histoire de vie du lézard vivipare, ses déterminants environnementaux et démographiques et ses conséquences pour la dynamique des populations (ex : Le Galliard et al., 2005d, Le Galliard et al., 2010, Massot et al., 1992, Massot et al., 2008). Dans le cadre de cette thèse, nous verrons que les réponses individuelles à la structure de population chez un ectotherme à courte durée de vie tel que le lézard vivipare sont en accord avec les réponses observées chez des espèces de reptiles longévifs (ex : Madsen & Shine, 2000) et chez des espèces de mammifères, d’oiseaux et de poissons (ex : Coulson et

M. Mugabo – Caractérisation des interactions entre la structure de population et l’histoire de vie al., 2001 , Bonenfant et al., 2009, Reid et al., 2003 , Edeline et al., 2010, Forrester et al., 2011, Cureton et al., 2010). Les implications de nos travaux ne se limitent donc pas simplement au cas du fonctionnement des populations de lézards mais s’inscrivent dans le cadre plus général de l’écologie des populations structurées. De plus, la possibilité de manipuler des populations en conditions semi-naturelles procure une occasion unique de lier de manière réaliste la structure de population, l’histoire de vie, la dynamique de population et le risque d’extinction (ex : Cote et al., 2007, Le Galliard et al., 2005d, Lecomte et al., 2004).

INFLUENCES DE LA STRUCTURE DE POPULATION SUR L’HISTOIRE DE VIE DU LÉZARD VIVIPARE

Structuration en cohortes, environnement biotique et interactions sociales

Nous nous intéressons ici à l’influence de la structuration des populations en cohortes de naissance sur l’histoire de vie. Plus particulièrement, nous avons étudié si la disponibilité en nourriture expérimentée pendant le développement précoce ou plus tard dans la vie pouvait générer de la variation à long terme de l’histoire de vie dans des populations structurées en cohortes. La disponibilité en ressources alimentaires est l’un des principaux facteurs environnementaux à l’origine de la variation de l’histoire de vie (ex : Madsen & Shine, 2000, Metcalfe & Monaghan, 2001, Lummaa & Clutton-Brock, 2002, Koskela et al., 1998) et peut agir par l’intermédiaire de ses effets directs sur la qualité intrinsèque des individus et de ses effets indirects sur l’intensité de la compétition intra- et inter-cohortes. La variation temporelle de la disponibilité en nourriture peut générer des effets cohortes intra- et intergénérationnels via ces trois mécanismes (voir **Chapitre 1**). Pendant la saison de reproduction, elle peut également avoir d’importantes répercussions sur les performances des individus reproducteurs, indépendamment de leur cohorte de naissance (ex : sur la fécondité, l’immunité, la survie, et la reproduction future, Koskela et al., 1998, Martin et al., 2007, Saino et al., 1999, Brommer et al., 2004). De même, la disponibilité en nourriture hors saison de reproduction peut influencer les performances futures des individus chez des espèces allouant à la reproduction de l’énergie stockée sur le long-terme (c’est-à-dire une stratégie « capital breeding » ou de reproduction par capitalisation Drent & Daan, 1980).

Les effets directs, immédiats ou à long terme de la disponibilité en nourriture ont été décrits chez de nombreuses espèces (ex : Descamps et al., 2008, Koskela et al., 1998,

Metcalfe & Monaghan, 2001, Taborsky, 2006, Brommer et al., 2004). A l’inverse, les effets de l’environnement biotique passé sur l’intensité de la compétition intraspécifique restent très largement inexplorés (mais voir Beckerman et al., 2003). Afin de caractériser les effets directs et indirects de l’environnement trophique sur l’histoire de vie, nous avons manipulé la quantité de nourriture en laboratoire et l’environnement social en conditions semi-naturelles chez une cohorte de nouveaux-nés d’une part et chez des cohortes de sub-adultes et adultes d’autre part (Figure 2). Les juvéniles bien nourris (ou mal nourris) ont ensuite été lâchés dans des enclos extérieurs avec des juvéniles du même traitement de nourriture et avec des sub-adultes et adultes bien nourris ou mal nourris, créant ainsi 4 types de populations expérimentales. Ces populations ont ensuite été suivies pendant deux ans afin de caractériser les réponses d’histoire de vie. L’ensemble du protocole expérimental est détaillé **Chapitres 2 et 3**.

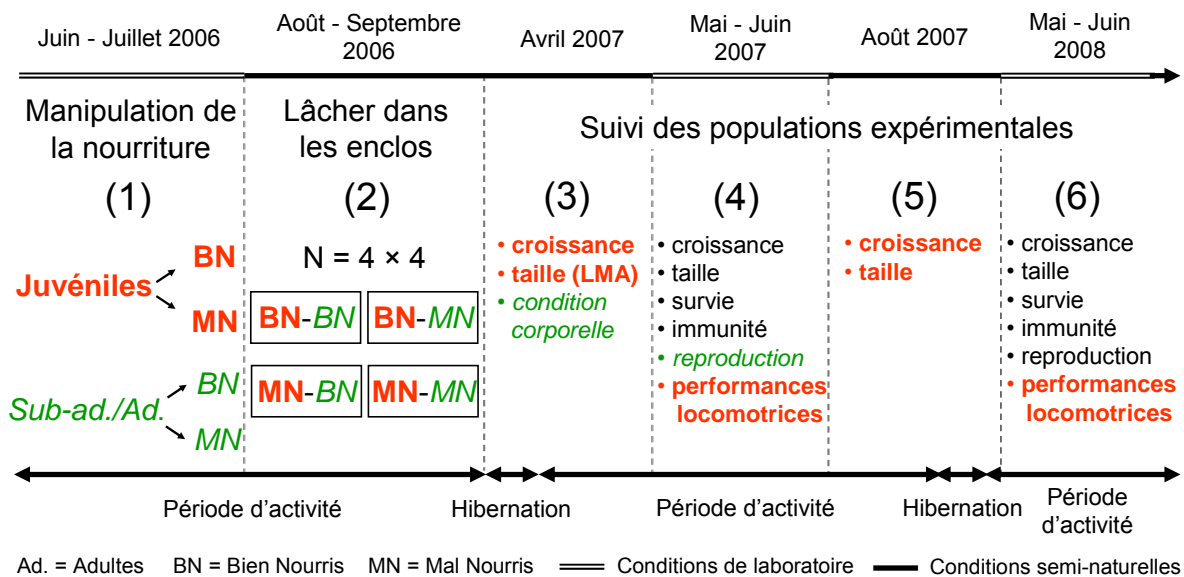


Figure 2. Représentation schématique du dispositif expérimental mis en place pour caractériser les effets de l’environnement biotique et social sur les performances des individus. (1) Nous avons simulé une privation de nourriture en laboratoire chez une cohorte de juvéniles et chez des cohortes de sub-adultes et d’adultes. (2) Après 50 jours de manipulation, les individus ont été lâchés dans des enclos extérieurs en fonction d’un design expérimental croisé. Les performances des individus ont ensuite été mesurées au cours de quatre sessions réalisées (3) à la sortie de l’hivernation, (4) pendant la 1^{ère} saison de reproduction après le début de l’expérience, (5) à la fin de l’été et (6) pendant la 2^{ème} saison de reproduction. Les traits notés en orange et gras ont été mesurés uniquement chez les juvéniles ; les traits notés en vert et italique ont été mesurés uniquement chez les sub-adultes et adultes ; les traits notés en noir ont été mesurés chez tous les individus.

Cette expérience nous a permis de mettre en évidence quatre résultats clés. Premièrement, la disponibilité en nourriture précoce et tardive a affecté de manière directe et immédiate la croissance en taille et en masse. Ceci est classiquement expliqué par les effets négatifs d'une privation de nourriture sur les réserves lipidiques, la masse musculaire et la croissance structurale (Kooijman, 2000). Deuxièmement, la disponibilité en nourriture précoce et tardive a eu des effets directs et à long terme sur l'immunocompétence des individus. Des résultats équivalents ont été démontrés chez des oiseaux en réponse à la disponibilité en nourriture à la naissance et pendant la reproduction (ex : Birkhead et al., 1999, Tschirren et al., 2009, Saino et al., 1999). Troisièmement, une privation de nourriture à la fin de la période de reproduction n'a pas affecté les performances reproductrices futures des femelles. Or, à la sortie de l'hibernation, les femelles mal nourries pendant l'été présentaient toujours une condition corporelle inférieure à celle des femelles bien nourries. Ce résultat suggère que non seulement les femelles ont été capables de compenser pour de faibles réserves énergétiques au début de la saison de reproduction, mais également qu'elles ont utilisé de l'énergie acquise pendant la vitellogenèse, c'est-à-dire récemment acquise, pour produire leurs œufs. Ces résultats sont en accord avec une étude réalisée par Avery (1975), qui a montré que les femelles lézards vivipares utilisaient en stratégie d'allocation de la reproduction mixte, basée sur des ressources récemment acquises (« income breeding ») et sur des réserves accumulées sur le long terme (« capital breeding », Drent & Daan, 1980). Une telle stratégie mixte de l'allocation de l'énergie à la reproduction a été décrite chez d'autres espèces de reptiles à durée de vie courte ou longue (ex : Lourdais et al., 2003, Warner et al., 2008). Quatrièmement, les conditions nutritives passées ont affecté de manière indirecte et à long terme la croissance en taille, la reproduction, la survie et les performances tôt dans la vie des descendants produits au cours de l'expérience. Ces effets indirects sont le produit d'une interaction entre les effets directs des conditions nutritives passées sur la qualité intrinsèque des individus et ses effets indirects sur l'intensité de la compétition inter-cohortes. Par exemple, dans les populations où juvéniles et sub-adultes et adultes ont connu des conditions nutritives passées favorables, une forte compétition inter-cohortes a eu des effets négatifs sur la survie des juvéniles et des mâles adultes et sub-adultes, probablement en raison d'un chevauchement de niche élevé conduisant à une déplétion de la ressource à la sortie de l'hibernation. A l'opposé, dans les populations où à la fois les juvéniles et les sub-adultes et adultes ont subi une privation de nourriture, un faible niveau de compétition inter-cohortes a été propice à de la croissance compensatoire (**Chapitres 2 et 3**). Ces résultats démontrent que les effets directs de l'environnement et ses effets indirects sur les interactions sociales peuvent

interagir pour façonner les trajectoires d’histoire de vie dans les populations structurées en taille ou en classes d’âge.

Densité dépendance de l’histoire de vie

Nous nous intéressons ici au lien entre la densité de population et les performances des individus. Notre but était non seulement de déterminer les traits individuels sensibles à la densité mais également de caractériser la forme de la densité dépendance et d’identifier les mécanismes proximaux. Pour cela, nous avons manipulé la densité initiale de 24 petites populations expérimentales de lézards de manière à créer un gradient de densité allant de densités faibles à des densités élevées. Nous avons ensuite suivi ces 24 populations pendant un cycle d’une année afin de mesurer les réponses d’histoire de vie. Les détails du protocole expérimental sont fournis dans les **Chapitres 4 et 5**.

Interactions trophiques

Dans un premier temps, nous nous sommes intéressés à l’influence de la densité de lézards sur leur consommation de proies et la densité de proies (**Chapitre 4**). La capacité des individus à acquérir de la nourriture a de nombreuses implications à l’échelle individuelle, populationnelle et des communautés. En effet, elle détermine la quantité de ressources qu’un individu peut allouer à sa croissance structurale, sa maintenance et sa reproduction et donc influence fortement sa valeur sélective (Amundsen et al., 2007). Elle peut également affecter l’intensité de la compétition intra- et interspécifique pour l’accès aux ressources trophiques ainsi que les relations proies-prédateurs (ex : Arditi & Akcakaya, 1990, Gilg et al., 2003). Le taux d’alimentation dépend de caractéristiques individuelles, la plus importante étant la taille (taille corporelle ou masse corporelle Bystrom & Andersson, 2005, Claessen et al., 2000, Persson et al., 1998), de la densité de proies et de prédateurs, de la structure de l’habitat et des conditions climatiques, en particulier chez les ectothermes (ex : Avery, 1971, Miller et al., 2006, Pitt & Ritchie, 2002). Classiquement, la variation du taux de consommation de nourriture est étudiée à l’aide de modèles de réponses fonctionnelles qui font le lien entre le taux d’alimentation et la densité de proies et de prédateurs (Hassell & Varley, 1969, Holling, 1959) ; ou à l’aide de fonctions allométriques qui incluent les effets de la taille du prédateur et/ou de la proie sur le taux d’alimentation (Kooijman, 2000). La première méthode ignore la

variation inter-individuelle des capacités à acquérir la nourriture tandis que la seconde ne prend pas en compte les régulations densité-dépendantes qui régissent les interactions proies-prédateurs et les facteurs environnementaux pouvant affecter l’efficacité de fourragement.

Ainsi, nous avons comparé la capacité à expliquer la variation du taux de consommation de proies en conditions semi-naturelles de modèles allométriques simples et de modèles de réponses fonctionnelles simples (incluant la densité de proies et de prédateurs) ou complexes (incluant également des effets individuels et environnementaux, **Chapitre 4**). Pour cela nous avons estimé le taux d’alimentation des lézards et la biomasse en invertébrés dans les enclos extérieurs contenant des populations de lézards plus ou moins denses (protocoles décrits **Chapitre 4**). Grâce à cette étude, nous avons pu montrer que des modèles allométriques simples de taux d’alimentation, incluant la masse et le sexe des individus, étaient plus parcimonieux que les meilleurs modèles de réponses fonctionnelles, incluant des effets populationnels (densités de prédateurs et densités de proies), environnementaux (climat) et individuels (masse et sexe). Ces résultats suggèrent que, dans notre système expérimental, le taux de consommation de proies est faiblement limité par la densité de proies. Malgré cela, la densité de lézards a eu un effet négatif sur la biomasse de leurs proies préférées et en particulier sur la biomasse des araignées (**Chapitre 4, Figure 3**). Ainsi, les populations de lézards influencent la biomasse de la communauté d’invertébrés et pourraient également affecter sa composition via ses effets directs sur les populations de proies et ses effets indirects sur le reste de la chaîne trophique, les araignées étant elles-mêmes des prédateurs (Spiller & Schoener, 1998). Cependant, à l’échelle de notre expérience, qui a duré une année, nous n’avons pas démontré d’effets significatifs de la densité de lézards sur la composition des communautés d’invertébrés.

Dans un second temps, nous avons décrit la nature de la relation entre la densité et l’histoire de vie des individus (**Chapitre 5**). A l’échelle intraspécifique, la densité dépendance négative de l’histoire de vie peut être provoquée par (1) les interactions trophiques de types interférence et compétition par exploitation de la ressource et (2) les interactions sociales entre congénères (Edeline et al., 2010 et références citées). Ces dernières peuvent générer des modifications hormonales ponctuelles et chroniques avec la production de glucocorticoïdes, ou hormones de stress, par la glande surrénale (Harvey et al., 1984). La production de glucocorticoïdes permet de rapidement mobiliser l’énergie allouée à des fonctions non-essentiels vers des activités permettant de faire face à la menace (Wingfield & Ramenofsky, 1999), et est donc souvent associée à des modifications comportementales (ex : augmentation

de l'agressivité, réduction des comportements sexuels, Creel, 2005, Cloutier & Newberry, 2000, Moore & Mason, 2001). Cependant, une production chronique de glucocorticoïdes en réponse à des conditions stressantes prolongées est connue pour inhiber l'activité de la glande thyroïdienne (Kuhn et al., 1998, Walpita et al., 2007), conduisant à une réduction de l'allocation d'énergie à la croissance structurale, l'immunité et la reproduction (ex : Comendant et al., 2003, Edeline et al., 2010, Moore & Jessop, 2003, Wingfield & Ramenofsky, 1999). Chez le lézard vivipare, nous venons de démontrer que les interactions trophiques intraspécifiques pouvaient affecter le taux d'alimentation et donc les performances des individus (**Chapitre 4**). Il a par ailleurs été montré qu'une augmentation expérimentale chronique du taux de corticostérone plasmatique, principale hormone impliquée dans la réponse au stress chez les oiseaux et les reptiles (Wingfield & Ramenofsky, 1999), augmente l'activité journalière et le métabolisme au repos et affecte positivement la survie des mâles et négativement les performances reproductrices des femelles (ex : Cote et al., 2006, Meylan et al., 2010).

Ici, le taux de croissance en taille, la taille corporelle, l'accès à la reproduction chez les juvéniles, la date de parturition, la taille de portée, la condition corporelle post-parturition et l'immunocompétence ont été affectés négativement par la densité (**Chapitre 5**). La croissance en taille et la taille corporelle ont diminué de manière linéaire ou faiblement non-linéaire (décroissance quadratique) avec la densité en fonction de la période étudiée et des caractéristiques individuelles (pas d'effets chez les adultes mâles). Une diminution de la densité dépendance de la croissance avec la densité (voir **Chapitre 5, Figure 1**) a été décrite à plusieurs reprises chez les Salmonidés (ex : Grant & Imre, 2005, Amundsen et al., 2007, Jenkins et al., 1999) et serait liée à la relation asymptotique entre le taux d'alimentation et la densité de proies (Amundsen et al., 2007, Chapitre 4). D'autre part, nous avons montré que les effets négatifs de la densité sur la proportion de juvéniles reproducteurs et sur la taille de portée étaient en grande partie expliqués par des effets taille : la densité a influencé négativement la taille corporelle des femelles qui elle-même a influencé positivement leurs performances reproductrices. De plus, nous avons montré lors de notre précédente étude qu'une diminution de la quantité de ressources disponibles pouvait provoquer une diminution de l'immunocompétence (**Chapitre 3**). Ainsi, en accord avec notre étude du taux de consommation de proies, nos données indiquent que la densité dépendance de l'histoire de vie pourrait en partie avoir été provoquée par des interactions trophiques.

Stress social

Nous avons ensuite cherché à savoir si des réponses hormonales chroniques à la densité de population pouvaient être impliquées dans la densité dépendance de l'histoire de vie et de l'immunocompétence. Pour cela, nous avons mesuré les niveaux de corticostérone avant l'introduction dans les enclos et à trois reprises après l'introduction (**Annexe 1**). La session 2, réalisée quelques jours après le lâcher a permis de mesurer la réponse physiologique à court terme à la densité. Les sessions 3 et 4, effectuées respectivement quelques semaines avant et quelques semaines après l'hibernation, correspondent à des périodes où la compétition intraspécifique pour la nourriture peut être forte et donc provoquer un stress chronique (**Chapitres 2 et 3**). Les protocoles expérimentaux de prélèvements sanguins et de dosages de la corticostérone plasmatique sont présentés dans l'**Annexe 1**.

Aucun effet de la densité n'a été détecté sur les niveaux de corticostérone plasmatique pendant les sessions 2 et 4, c'est-à-dire quelques jours après l'introduction dans les enclos ($F_{1,22} = 1.74$, $P = 0.20$) et à la sortie d'hibernation ($F_{1,20} = 0.18$, $P = 0.68$). En revanche, un effet significatif de la densité en interaction avec le sexe (densité \times sexe : $F_{1,70} = 4.48$, $P = 0.04$) a été détecté dans les échantillons récoltés pendant la session 3, c'est-à-dire quelques semaines avant l'entrée en hibernation. Le niveau de corticostérone plasmatique a augmenté avec la densité chez les mâles (test *post-hoc* : $F_{1,16} = 4.86$, $P = 0.04$) mais pas chez les femelles ($F_{1,19} = 0.24$, $P = 0.63$, Figure 3, page 34). Dans l'ensemble, nos résultats suggèrent que la densité de population n'affecte que faiblement le taux de corticostérone plasmatique et ce de manière saisonnière. Cependant, cela ne signifie par pour autant que des niveaux élevés de compétition intraspécifique n'ont pas affecté la production d'hormones impliquées dans la croissance ou la reproduction (Summers, 2002). En effet, chez le brochet (*Esox lucius*), une augmentation de la densité n'a eu aucun effet significatif sur les niveaux de cortisol plasmatique (principal glucocorticoïde sécrété lors de la réponse au stress chez les poissons, Edeline et al., 2010). Cependant l'augmentation de la densité a provoqué une diminution de l'activité thyroïdienne, de la masse du foie et de la croissance structurale. Ces effets, qui n'étaient pas expliqués par des interactions trophiques (Edeline et al., 2010), sont classiques de l'activation de l'axe hypothalamo-hypophysio-surrénalien, qui contrôle la libération de glucocorticoïdes dans le sang (Walpita et al., 2007, Wingfield & Ramenofsky, 1999). Ainsi, l'étude d'un trait physiologique tel que la concentration plasmatique en glucocorticoïdes ne semble pas suffisante pour détecter des effets non trophiques de la densité sur l'histoire de vie et devrait être complétée par d'autres mesures physiologiques et comportementales (ex :

mesures de l’activité de la glande thyroïdienne, de la production d’autres corticoïdes impliqués dans la réponse au stress, de l’agressivité, des relations de dominance, Dauphin-Villemant & Xavier, 1987, Edeline et al., 2010, Hawley et al., 2006, Summers, 2002).

Effets d’histoire de vie de l’interaction entre la densité de population et le sexe ratio adulte

Ici, nous nous intéressons aux effets de l’interaction entre la densité de population et le sexe ratio adulte sur l’histoire de vie. Nous avons donc manipulé conjointement la densité et le sexe ratio adulte des populations. Nous avons croisé trois niveaux de densité (faible, intermédiaire et élevée) avec deux niveaux de sexe ratio adulte (femelle-biaisé et mâle biaisé) chez 24 populations expérimentales de lézards que nous avons suivies pendant un cycle d’une année. Les détails du protocole sont présentés dans l’**Annexe 2**. Les données démographiques issues de cette expérience ont été récoltées pendant l’été 2010 et n’ont pas encore été analysées. Nous pouvons néanmoins émettre plusieurs hypothèses quant à l’influence de la manipulation sur les performances des individus en se basant sur nos connaissances des effets de la densité d’une part (**Chapitre 5**) et des effets du sexe ratio adulte d’autre part (Le Galliard et al., 2005d, 2008, Fitze et al., 2008, Fitze et al., 2005).

Lors de leur manipulation de sexe ratio adulte dans des populations expérimentales de lézards vivipares, Le Galliard et al. (2005d, 2008) ont montré que :

- la survie des mâles n’est pas affectée par le sexe ratio adulte,
- la survie des femelles adultes et sub-adultes mais pas des femelles juvéniles est nettement inférieure dans les populations mâle-biaisées que dans les populations femelles-biaisées. Cet effet a été observé pour la survie post-hibernation, c’est-à-dire pendant la saison des accouplements, mais pas pour la survie pré-hibernation,
- l’accès à la reproduction des femelles n’est pas sensible au sexe ratio adulte,
- la taille de ponte des femelles est fortement diminuée par un sexe ratio adulte mâle-biaisé,
- la date de parturition est négativement affectée par le sexe ratio adulte chez les femelles adultes,

- la qualité des juvéniles produits en terme de taille et de condition corporelle à la naissance, de survie jusqu’à l’âge adulte et de succès reproducteur mâle et femelle sont indépendants du sexe ratio adulte,
- la croissance en taille et la condition corporelle pré-hibernation n’est pas affectée par le sexe ratio adulte.

Ces résultats démontrent qu’un excès de mâles dans la population affecte négativement la survie et la reproduction des femelles, cet effet étant vraisemblablement dû aux agressions des mâles pendant les accouplements plutôt qu’à une compétition intersexuelle pour l’accès à la nourriture (effets négatifs sur la survie post-hibernation mais pas d’effets sur la morphologie des femelles Le Galliard et al., 2005d, 2008).

Ainsi, nous nous attendons à ce que la survie et la croissance en taille des mâles et la taille à la naissance des juvéniles soient indépendantes de la densité et du sexe ratio adulte. La croissance en taille devrait diminuer avec la densité chez les juvéniles et sub-adultes mâles et femelles et chez les femelles adultes mais ne devrait pas être affectée par le sexe ratio adulte. De même, l’accès à la reproduction devrait être négativement affecté par la densité chez les juvéniles mais pas chez les adultes et sub-adultes et devrait être insensible au sexe ratio adulte. Nous nous attendons également à ce que le sexe ratio adulte affecte négativement la survie des femelles adultes et sub-adultes. Dans l’hypothèse où le nombre total de mâles rencontrés dans la population plutôt que le nombre relatif de mâles serait le déterminant majeur des effets des mâles sur les performances des femelles (Kvarnemo & Ahnesjö, 2002), la survie des femelles adultes et sub-adultes dans les populations mâle-biaisées devrait également diminuer avec la densité de population. Pour la taille de portée et la date de parturition qui sont affectées par la densité et par le sexe ratio adulte, deux cas de figure sont possibles. Premièrement, les effets des deux paramètres s’additionnent. Deuxièmement, les deux paramètres interagissent. Dans les deux cas, la fécondité devrait être particulièrement faible et la date de parturition très tardive dans les populations denses mâle-biaisées. Finalement, la condition post-parturition devrait diminuer avec la densité et potentiellement avec le sexe ratio adulte si le harcèlement sexuel est coûteux en énergie ou provoque un stress (Le Galliard et al., 2005d). Là encore les effets des deux paramètres pourront être additifs ou multiplicatifs.

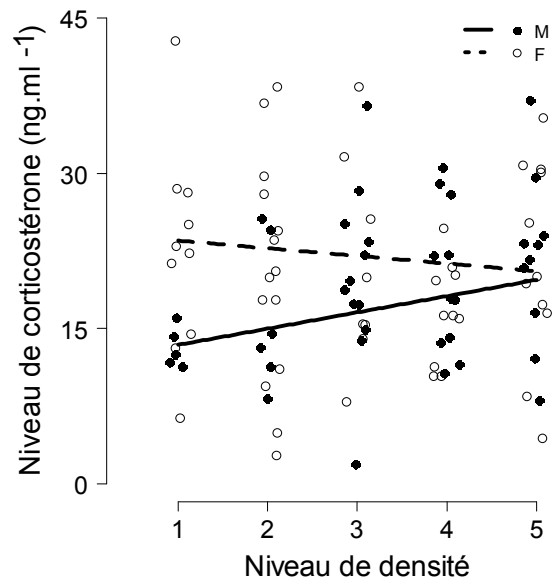
L’importance du sexe, de l’âge et de la famille dans les réponses individuelles à la structure de population

Au cours de cette thèse, nous avons mis en évidence l’existence d’une importante hétérogénéité des réponses des individus aux conditions environnementales et à la structure de population en fonction de leur sexe, de leur âge et même de leur famille. Plusieurs mécanismes semblent être responsables de ces hétérogénéités parmi lesquels des différences d’acquisition ou d’allocation de la ressource entre sexes, classes d’âge et familles et des différences comportementales et de régulations hormonales.

Des réponses sexe-spécifiques

Nous avons mis en évidence des différences de réponses à l’environnement biotique et social entre les sexes pour la croissance corporelle, la survie et les niveaux de corticostérone plasmatique. Concernant la croissance corporelle, nous avons observé que les femelles étaient plus sensibles que les mâles à la compétition inter-cohortes et à la densité de populations (**Chapitres 3 et 5**). Ces différences peuvent apparaître dès le stade juvénile, comme cela a été le cas en réponse à la densité de population (**Chapitre 5, Figure 1**). Ces sensibilités sexe-spécifiques à l’environnement pourraient refléter l’existence de différences de demandes énergétiques entre les mâles et les femelles. En effet, chez les espèces présentant un dimorphisme sexuel de taille corporelle, le sexe le plus grand est généralement plus affecté par des conditions environnementales défavorables (ex : chez les oiseaux, les mammifères et les reptiles, Lindström, 1999, Toigo et al., 1999, Madsen & Shine, 2000). En accord avec cette hypothèse, nous avons montré que les femelles lézards vivipares ont un taux de consommation alimentaire supérieur aux mâles, ce qui suggère des demandes énergétiques plus élevées chez les femelles (**Chapitre 4**). Cependant, ces différences peuvent également être dues à des stratégies sexe-spécifiques d’investissement dans la croissance structurale. Par exemple, les femelles juvéniles investissent plus dans la croissance en taille tandis que les juvéniles mâles investissent plus dans la condition corporelle (Le Galliard et al., 2005b). Elles pourraient également être le résultat de différences dans les aptitudes compétitrices à acquérir des ressources limitées, les mâles adultes lézards vivipares étant socialement dominants sur les femelles adultes, les sub-adultes et les juvéniles (Lecomte et al., 1994, Massot et al., 1992).

Figure 3. Densité dépendance du taux de corticostérone plasmatique à la fin de l’été chez les mâles ($n = 44$) et les femelles ($n = 53$) sub-adultes et adultes. Les estimations des droites de régressions sont issues du meilleur modèle sélectionné (mâles : pente = 1.57 ± 1.09 ; femelles : pente = -0.74 ± 0.85). M = mâles, F = femelles.



A l’opposé, le taux de corticostérone plasmatique a augmenté avec la densité chez les mâles adultes et sub-adultes mais pas chez les femelles (Figure 3). Des différences mâles-femelles dans la réponse au stress social ont été montrées chez plusieurs espèces de mammifères dont l’homme (ex : Trainor et al., 2010, Weiser & Handa, 2009, Dixon et al., 2004). Selon les espèces, soit les mâles (ex : Dixon et al., 2004) soit les femelles (ex : Trainor et al., 2010, Weiser & Handa, 2009) répondent de manière plus importante à un stress social. Les causes de ces différences entre espèces dans les réponses physiologiques des mâles et des femelles au stress social restent encore inconnues (Trainor et al., 2010). Une augmentation du taux de glucocorticoïdes plasmatiques en réponse à un stress social est souvent associée à une augmentation des comportements agressifs et à la mise en place de relations de dominance entre individus (Summers, 2002, Creel, 2005). Ainsi, des régulations sexe-spécifiques de l’axe hypothalamo-hypophyso-surrénalien pourraient expliquer l’existence de différences comportementales dans la réponse à un stress social telles que celles observées chez le lézard vivipare chez qui une augmentation de la densité conduit à une augmentation de l’agressivité chez les mâles adultes mais pas chez les femelles (Lecomte et al., 1994). De plus, la photopériode est connue pour affecter la réponse des individus à un stress social. En effet, une augmentation de l’agressivité avec la diminution de la durée du jour a été décrite chez plusieurs espèces de rongeurs (ex : Nelson et al., 1990, Silva et al., 2010). En accord avec ces études, nous avons mis en évidence un effet de la densité sur le taux de corticostérone plasmatique des mâles uniquement à la fin de l’été, soit quelques semaines avant l’entrée en hibernation. Cet effet de la photopériode serait lié à une diminution de la disponibilité en

nourriture et de la température avec la durée du jour, conduisant à une augmentation de la compétition intraspécifique à une période où les animaux font leur stock de réserves énergétiques pour passer l’hiver (Nelson et al., 1990).

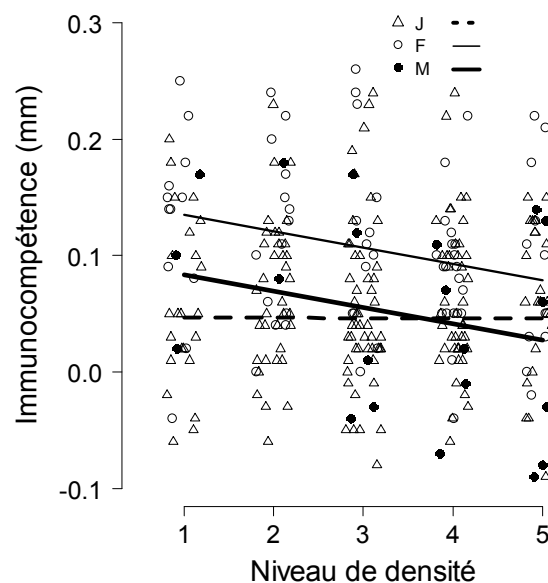
Par ailleurs, dans le cadre de notre première expérience, nous avons observé des différences de survie entre mâles et femelles adultes et sub-adultes en réponse à l’environnement biotique et social (**Chapitre 3, Figure 3A**). Des patterns similaires de survie ont été observés chez les mâles et chez les juvéniles, tandis que la survie des femelles n’a pas été affectée. Ces différences mâles-femelles pourraient être liées à des différences de phénologie. En effet, chez cette espèce, les mâles et les juvéniles sortent d’hibernation à la fin de l’hiver ou au début du printemps, soit plusieurs semaines avant les femelles (Bauwens et al., 1989, Bauwens & Verheyen, 1985). La sortie précoce des mâles est nécessaire à la complétion de la spermatogénèse (Bauwens et al., 1989) et augmente la saison d’activité chez les juvéniles et donc les opportunités de croissance. Cependant, ils s’exposent à des conditions environnementales sub-optimales où les risques de famine peuvent être élevés. Ainsi, des conditions environnementales défavorables entre la sortie d’hibernation des mâles et des juvéniles et celle des femelles, couplée à une forte compétition intraspécifique pour l’accès à la nourriture, pourraient expliquer la faible survie des mâles et des juvéniles dans les populations où toutes les cohortes ont subi des conditions nutritives passées favorables (**Chapitre 2, Figure 4A et Chapitre 3, Figure 3A**).

Des réponses âge-spécifiques

La différence de réponse à l’environnement trophique et social entre classes d’âge la plus remarquable vient de l’immunocompétence. L’environnement nutritif passé a eu des effets opposés sur l’immunocompétence des juvéniles et des adultes et sub-adultes. En effet, une privation de nourriture pendant le développement précoce a eu un effet positif à long terme (jusqu’à l’âge adulte) sur l’immunocompétence des juvéniles, tandis qu’une privation de nourriture à l’âge d’un an ou plus a eu des effets négatifs et à plus court terme (sur une durée d’un an) sur l’immunocompétence des adultes et sub-adultes. (**Chapitres 2 et 3**). De plus, la densité de population n’a pas affecté l’immunocompétence des juvéniles mais a eu des effets négatifs chez les adultes et sub-adultes (**Chapitre 5** et Figure 4). Des effets similaires de conditions défavorables pendant le développement précoce sur l’immunocompétence ont été mis en évidence chez le diamant mandarin (*Taeniopygia guttata*, Birkhead et al., 1999,

Tschirren et al., 2009). Des conditions défavorables pendant le développement précoce (qualité de la nourriture, Birkhead et al., 1999, et taille de la nichée, Tschirren et al., 2009) ont eu un effet immédiat négatif sur l’immunocompétence des poussins (Birkhead et al., 1999). Cependant, à l’âge adulte, les individus ayant subi des conditions délétères pendant le développement ne présentaient plus de différence d’immunocompétence avec les individus ayant expérimenté des conditions favorables et présentaient même, dans certains cas, une immunocompétence plus forte (Birkhead et al., 1999, Tschirren et al., 2009). Ces résultats suggèrent l’occurrence d’une compensation ou surcompensation de l’immunocompétence en réponse aux effets immunosuppresseurs immédiats de conditions défavorables tôt dans la vie (Birkhead et al., 1999). Ainsi, de mauvaises conditions environnementales pendant le développement précoce pourraient être à l’origine d’une modification des patterns d’allocation d’énergie au système immunitaire, afin de maximiser les chances de survie si les conditions ne s’améliorent pas (exemple de plasticité développementale, Tschirren et al., 2009, Bateson et al., 2004). A l’opposé, chez des individus matures, des conditions environnementales défavorables ou un investissement élevé dans la reproduction sont connus pour avoir des effets immunosuppresseurs (ex : Martin et al., 2007, French et al., 2007, Fedorka et al., 2004). Cependant, quelle que soit l’origine de ces différences entre classes d’âge, la réponse de l’immunocompétence à l’environnement biotique et social ne semble pas avoir influencé positivement ou négativement les performances démographiques des individus puisque la survie, la croissance et la charge parasitaire des juvéniles n’étaient pas corrélées à leur immunocompétence (**Chapitre 2**); et la densité de population n’a pas influencé la survie des juvéniles, sub-adultes et adultes (**Chapitre 5**).

Figure 4. Effets de la densité de population sur l’immunocompétence chez les sub-adultes et adultes mâles et femelles ($n = 100$) et chez les juvéniles ($n = 194$). Les estimations des droites de régressions sont issues du meilleur modèle d’immunocompétence sélectionné chez les adultes et sub-adultes et chez les juvéniles (**Chapitre 5**). Les valeurs négatives sont dues aux erreurs de mesures. J = juvéniles, F = femelles, M = mâles.

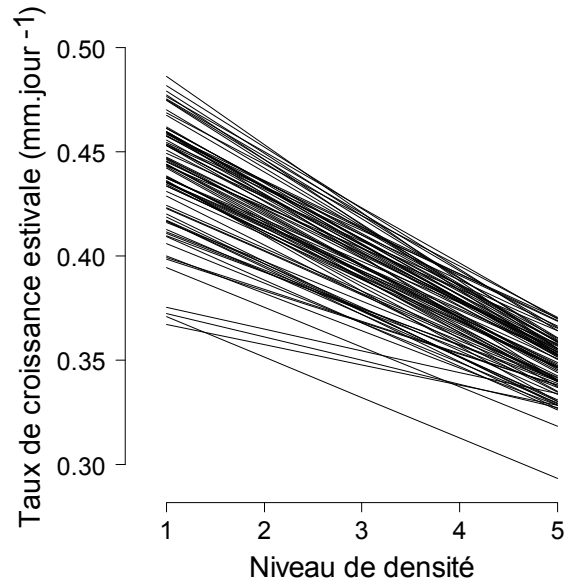


Par ailleurs, nous avons observé une différence de réponse de l’accès à la reproduction à la densité de population entre juvéniles et adultes femelles. La proportion d’individus reproducteurs était densité-dépendante chez les juvéniles et densité-indépendante chez les adultes et sub-adultes (**Chapitre 5**). Chez les juvéniles, l’accès à la reproduction est fortement dépendant de la taille corporelle pendant la saison de reproduction (**Chapitre 5**). Récemment, Massot et al. (2011) ont ainsi démontré l’existence d’un seuil de LMA de 56 mm en dessous duquel 95.6 % des jeunes femelles sont non reproductrices dans les populations du Mont Lozère. Ces résultats signifient que l’accès à la reproduction chez les femelles lézards vivipares est déterminé par des phénomènes de maturation. Une fois la maturité sexuelle atteinte, l’accès à la reproduction ne semble pas être affecté par la structure de population, contrairement à la taille de portée (Chapitre 5 et Le Galliard et al., 2005d).

Des réponses famille- spécifiques

Au cours des Expériences 2 et 3, nous nous sommes intéressés à la plasticité phénotypique familiale du taux de croissance en réponse à la disponibilité en nourriture tôt dans la vie et à la densité de population. Pour cela, nous avons étudié les normes de réaction familiales à l’environnement (voir **Chapitres 2 et 5** pour une présentation détaillée des designs expérimentaux). Dans les deux cas, nous avons mis en évidence l’existence d’une variation interfamiliale de la sensibilité du taux de croissance à l’environnement. La réponse du taux de croissance annuel à la disponibilité en nourriture tôt dans la vie a fortement varié entre familles. En effet, un grand nombre de familles a été affecté négativement par une diminution de la disponibilité en nourriture et ce de manière plus ou moins importante. Cependant, certaines familles n’ont pas été sensibles à une augmentation de la quantité de ressources tandis que d’autres familles ont même répondu négativement (**Chapitre 2, Figure 2B**). A l’opposé, le taux de croissance estivale a diminué avec la densité chez toutes les familles. Cependant, celles qui présentaient un taux de croissance élevé à faible densité ont été plus affectées par la densité que les familles à croissance limitée (Figure 5). Dans les deux cas, ces résultats suggèrent l’existence d’un polymorphisme de l’acquisition ou de l’allocation de l’énergie à la croissance structurale d’origine génétique (Gebhardt-Henrich & van Noordwijk, 1994, Hoffmann & Merilä, 1999) ou parentale (maternelle ou paternelle, Mousseau & Fox, 1998, Galloway, 2001), et sont en accord avec une étude des normes de réactions familiales de la croissance en réponse à l’humidité de l’habitat chez cette espèce (Lorenzon et al., 2001).

Figure. 5 Normes de réaction familiales pour la croissance en taille pendant le stade juvénile précoce, c.à.d. pendant le premier été ($n = 83$ familles). Les données correspondent au taux de croissance moyen par famille et ont été obtenues à partir du meilleur modèle de croissance sélectionné incluant une variation aléatoire entre familles dans l’intercept et la pente de la densité dépendance (**Chapitre 5, Table 2**). Les estimations par famille d’intercepts et de pentes ont été obtenues à l’aide de la fonction *ranef* de la procédure *lme* dans R (Pinheiro & Bates, 2000).



Dans le cas de la réponse à la disponibilité en nourriture, nous avons testé si des effets maternels et paternels pouvaient expliquer cette variation familiale de la plasticité phénotypique. Aucun des traits maternels testés (date de parturition, sexe ratio de la ponte et taille moyenne des juvéniles à la naissance) n’a expliqué les réponses familiales du taux de croissance et nous n’avons pas trouvé de variation de la plasticité entre lignées paternelles (seulement 21 lignées pour 460 jeunes, **Chapitre 2**). De plus, des normes de réaction familiale non parallèles pourraient indiquer l’existence d’interactions génotype-environnement (Hoffmann & Merilä, 1999, Postma & van Noordwijk, 2005, Räsänen & Kruuk, 2007). Deux types d’interactions génotype-environnement peuvent être distingués : (i) l’héritabilité du trait varie avec l’environnement conduisant à une expression contexte-dépendante de variance génétique et donc de la plasticité phénotypique ; (ii) la corrélation génétique entre environnements est inférieure à 1, conduisant à un croisement des normes de réaction (Hoffmann & Merilä, 1999, Postma & van Noordwijk, 2005). Ici, la variation interfamiliale de la plasticité du taux de croissance en réponse à la disponibilité en nourriture suggère l’existence de faibles corrélations génétiques entre environnements (changement du rang des familles entre environnements, **Chapitre 2, Figure 2B**) tandis que la variation interfamiliale de la réponse plastique à la densité suggère l’existence d’une expression contexte-dépendante de la plasticité phénotypique (Figure 5). Ce dernier résultat va dans le sens d’une expression plus importante de la variance génétique en conditions environnementales favorables qu’en conditions défavorables (ex : Charmantier et al., 2004, Charmantier & Garant, 2005, Hoffmann & Merilä, 1999). De telles interactions génotype-environnement peuvent avoir des conséquences évolutives importantes. Par exemple, la

variation de l’expression de la variance génétique entre environnements implique une variation du potentiel évolutif des populations et donc de leur capacité d’adaptation à un environnement variable (Hoffmann & Merilä, 1999, Charmantier & Garant, 2005, Postma & van Noordwijk, 2005).

INFLUENCES DE LA STRUCTURE DE POPULATION SUR LE SYSTÈME D’APPARIEMENT ET L’INTENSITÉ DE LA SÉLECTION SEXUELLE CHEZ LE LÉZARD VIVIPARE

Nous avons montré qu’à faibles densités, la date de parturition a été affectée positivement par la densité, révélant ainsi l’existence d’un effet Allee (**Chapitre 5, Figure 2B**). Le lézard vivipare n’étant pas une espèce coopérative (pas de fourragement ou de reproduction coopérative), on peut supposer qu’un manque de mâles reproducteurs dans les populations de faibles densités a pu décaler le début de la reproduction chez les femelles. Ce résultat laisse à penser que la densité de population a affecté le système d’appariement, c’est-à-dire la proportion et le degré de polygynie et de polyandrie et potentiellement l’intensité de la sélection sexuelle (voir revue par Kokko et Rankin, 2006). Afin de vérifier cette hypothèse, nous avons réalisé des analyses de paternités nous permettant de déterminer le succès reproducteur des mâles, de caractériser le système d’appariement et d’estimer l’intensité de la sélection sexuelle chez les mâles et chez les femelles. Pour cela, tous les animaux participant à l’expérience ont été génotypés pour 5 marqueurs microsatellites. Les méthodes utilisées pour le génotypage et les assignements de paternités sont présentées dans l’**Annexe 3**. Nous venons de terminer les attributions de paternités (voir **Annexe 3**). Malheureusement, ces données n’ont pas encore été analysées. Cependant, sur la base de nos connaissances du système d’appariement du lézard vivipare, nous pouvons émettre plusieurs hypothèses quant à l’effet de la densité sur les stratégies d’appariements mâles et femelles et sur l’intensité de la sélection sexuelle.

Le harcèlement sexuel a des effets délétères sur la survie et la fécondité des femelles, ce qui démontre l’existence d’un conflit sexuel (Fitze & Le Galliard, 2008, Fitze et al., 2005, Le Galliard et al., 2008, Le Galliard et al., 2005d). En effet, chez les mâles, le succès reproducteur augmente avec le nombre de femelles fécondées et la proportion ainsi que le degré de polygynie augmentent avec le nombre relatif de femelles présentes dans la

population (Fitze et al., 2005, Dreiss et al., 2010). De même, les femelles polyandres produisent en moyenne plus de jeunes que les femelles monoandres (ex : Fitze et al., 2005, Eizaguirre et al., 2007). Cependant, la proportion de polyandrie semble être contrôlée par les femelles tandis que le degré de polyandrie (c’est-à-dire le degré de paternité multiple chez les femelles polyandres) est déterminé par le harcèlement sexuel des mâles sur les femelles (Fitze et al., 2005, Dreiss et al., 2010, Richard et al., 2005). De plus, en accord avec de récents travaux théoriques sur le sujet (voir revue par Kokko et Rankin, 2006), il a été montré que l’intensité de la sélection sexuelle directionnelle positive sur la taille des mâles est plus faible dans les populations où les coûts des appariements chez les femelles sont les plus forts et les coûts de reproduction les plus faibles, c’est-à-dire dans les populations où le nombre de mâles est élevé (populations mâle-biaisées, Fitze et al., 2008, Le Galliard et al., 2008). Ce résultat suggère que la sélection intersexuelle est un déterminant majeur du succès reproducteur des mâles (Fitze et al., 2008). A l’inverse, l’intensité de la compétition mâle-mâle, qui devrait augmenter avec le nombre de mâles (Emlen & Oring, 1977), n’influencerait que faiblement la valeur sélective des mâles (Fitze et al., 2008, Fitze & Le Galliard, 2008). L’augmentation de l’intensité de la sélection sexuelle chez un sexe pouvant conduire à la réduction de l’intensité de la sélection chez l’autre sexe (Kokko & Johnstone, 2002, Kokko & Monaghan, 2001), l’intensité de la sélection sexuelle sur la taille des femelles est plus faible dans les populations femelle-biaisées (Fitze et al., 2008).

Contrairement aux variations du sexe ratio adulte, les variations de la densité de population affectent le nombre de partenaires sexuels potentiels pour les deux sexes, même si les sexes répondent différemment à la densité (Kokko & Rankin, 2006). Ainsi, nous nous attendons à ce que (i) la proportion et le degré de polygynie augmente avec le nombre de femelles et donc avec la densité; (ii) le harcèlement des mâles sur les femelles et donc le degré de polyandrie augmente avec la densité; (iii) la sélection sexuelle sur la taille des mâles soit plus faible à forte densité ; et à ce que (iv) la sélection sexuelle directionnelle sur la taille des femelles soit plus forte dans les populations denses.

Récemment, Dreiss et al. (2010) se sont intéressés à l’influence de la densité de population sur le système d’appariement et l’intensité de la sélection sexuelle chez le lézard vivipare. Malheureusement, aucun effet de la densité n’a été détecté sur le système d’appariement. Ces résultats suggèrent que les stratégies d’appariements et l’intensité de la sélection sexuelle seraient plus sensibles au nombre relatif de mâles présents dans la

population (c’est-à-dire au sexe ratio adulte, Fitze et al., 2008, Le Galliard et al., 2005d) qu’à leur nombre absolu (c’est-à-dire nombre total de mâles). Cependant, dans cette expérience, seulement deux niveaux de densité ont été comparés : une densité intermédiaire et une densité élevée (17 ± 5 versus 29 ± 6 adultes et sub-adultes). Ainsi, la gamme de densités étudiée n’était peut être pas suffisante pour détecter des effets densité-dépendants sur le système d’appariement et l’intensité de la sélection sexuelle. Nos données expérimentales vont donc nous permettre de confirmer ou d’infirmer les résultats de cette étude.

Dans l’hypothèse où la densité de population influence le système d’appariement et l’intensité de la sélection sexuelle en plus du sexe ratio adulte chez le lézard vivipare, nous nous attendons à ce que la proportion et le degré de polygynie soient les plus élevés dans les populations femelles-biaisées de forte densité et le degré de polyandrie soit le plus fort dans les populations denses mâle-biaisées, sous l’action du harcèlement sexuel. De même, l’intensité de la sélection sexuelle sur la taille des mâles devrait être la plus faible dans les populations denses mâle-biaisées tandis que l’intensité de la sélection sexuelle sur la taille des femelles devrait elle être la plus élevée dans ces populations.

CONSÉQUENCES POUR LA DYNAMIQUE DES POPULATIONS DE LÉZARDS VIVIPARES

Après avoir caractérisé les réponses individuelles à la structure de population, nous nous sommes intéressés à leurs conséquences pour la dynamique de petites populations de lézards vivipares. Pour cela, nous avons adopté deux approches. Premièrement, nous avons identifié les paramètres démographiques influençant la dynamique déterministe des populations (taux de croissance asymptotique et densité à l’équilibre, **Chapitres 2 et 5**). Deuxièmement, nous avons effectué une analyse de viabilité de petites populations isolées régulées par densité dépendance (**Chapitre 5**). Dans les deux cas, nous avons utilisé des modèles matriciels de populations structurés en classes d’âge et paramétrés avec nos données expérimentales. Ces modèles incluaient 3 classes d’âge (juvéniles, sub-adultes et adultes) et supposaient un recensement post-reproduction et un épisode de reproduction par cycle annuel (Caswell, 2001).

Pour l’étude des conséquences démographiques de l’interaction entre l’environnement nutritif précoce et l’environnement social, nous avons calculé le taux de croissance asymptotique λ comme la valeur propre dominante de la matrice de transition et estimé les intervalles de confiance à 95% du λ pour chaque groupe expérimental. La survie annuelle et la reproduction ayant été affectées par la manipulation uniquement chez la cohorte de juvéniles, nous avons paramétré le modèle avec les taux démographiques estimés chez cette cohorte aux stades juvénile, sub-adulte et adulte.

Pour l’étude de l’influence de la densité dépendance de l’histoire de vie sur la dynamique déterministe des populations, nous avons réalisé des analyses d’élasticités du taux de croissance λ des populations (modèle déterministe densité-indépendant) et de la densité à l’équilibre N_{eq} (modèle déterministe densité-dépendant). Les élasticités du λ et de N_{eq} prédisent respectivement le changement proportionnel du λ ou de N_{eq} en réponse à un changement proportionnel de faible ampleur dans un paramètre démographique du modèle (Caswell, 2001).

Pour l’analyse de viabilité des populations régulées par densité dépendance, nous avons construit des modèles stochastiques incluant de la stochasticité démographique sur tous les paramètres démographiques. Nous avons combiné des modèles à un sexe et à deux sexes afin de pouvoir distinguer les effets principaux de la densité dépendance sur le risque d’extinction de ses effets combinés aux fluctuations du sexe ratio et de la formation des couples reproducteurs. Les modèles à un sexe incluaient uniquement la portion femelle des populations tandis que les modèles à deux sexes incluaient la portion mâle et la portion femelle et supposaient un système d’appariement de type polygyne avec une taille de harem de 4. Cela signifie qu’un mâle reproducteur peut féconder 4 femelles reproductrices, ce qui correspond à une estimation conservative du degré de polygynie moyen chez cette espèce (Fitze et al., 2005). La fécondité dans chaque classe d’âge était le produit de la proportion de femelles reproductrices (densité-dépendante chez les juvéniles), de la taille de portée (densité-dépendante chez toutes les classes d’âge) du succès de la portée et du sexe ratio primaire (tous deux densité-indépendants). Le taux de survie annuel, densité-indépendant à toutes les classes d’âge, était inférieur chez les mâles à celui des femelles pour les sub-adultes et adultes (voir **Chapitre 5, Table A1**).

Une description complète des modèles est présentée **Chapitre 2** pour l’influence de la structuration de populations en cohortes et **Chapitre 5** pour l’influence de la densité de population sur la dynamique des populations de lézards.

Conséquences pour la dynamique déterministe des populations

Lors d’une étude sur la variation cohorte en réponse aux conditions climatiques et de son influence sur la dynamique d’une population naturelle de lézards vivipares, Le Galliard et al. (2010) ont montré que les différences d’histoire de vie inter-cohortes provoquées par la variation inter-annuelle du climat influençaient le taux de croissance asymptotique de la population principalement via la variation du taux de survie juvénile, c’est-à-dire via des effets cohortes directs numériques (voir **Chapitre 1, Figure 2**). En accord avec ces résultats, nous avons montré que l’environnement nutritif précoce en interaction avec l’environnement social pouvait affecter la contribution d’une cohorte au taux de croissance de la population à travers ses effets sur la survie juvénile (voir **Chapitre 3, Figure S1**).

De même, les analyses d’élasticités des modèles déterministes densité-indépendants et densité-dépendants ont montré que le taux de croissance asymptotique et de la densité à l’équilibre étaient le plus affectés par la variation du taux de survie des juvéniles puis par la variation du taux de survie des sub-adultes. Cependant, les analyses d’élasticités ont également démontré l’importance de la fécondité des sub-adultes et des juvéniles et de la force de la densité dépendance sur l’accès à la reproduction des juvéniles sur la densité à l’équilibre (**Chapitre 5, Table 3**).

Ces résultats sont en accord avec les patterns d’élasticité attendus pour une espèce itéropare à courte durée de vie, c’est-à-dire des élasticités plus élevées pour la survie juvénile et la fécondité que pour la survie adulte (Yoccoz et al., 1998, Gaillard & Yoccoz, 2003, Wittmer et al., 2007). Ils démontrent également l’importance d’estimer les élasticités de la taille ou de la densité à l’équilibre pour les populations régulées par densité dépendance afin de déterminer les stades du cycle de vie et les traits démographiques influençant le plus la dynamique des populations (Yearsley et al., 2003, Grant & Benton, 2000, Grant & Benton, 2003).

Conséquences pour le risque d’extinction des populations

Les modèles stochastiques densité-indépendants et densité-dépendants à un sexe et à deux sexes ont mis en évidence trois résultats majeurs sur l’influence de la densité dépendance négative de la reproduction sur la persistance des populations (**Chapitre 5, Figure 3**). Premièrement, la densité dépendance négative tamponne les effets de la densité initiale sur la probabilité d’extinction. Deuxièmement, elle diminue la probabilité d’extinction des populations de faible densité initiale. Troisièmement, elle interagit avec les fluctuations du sexe ratio et de la formation des couples reproducteurs pour façonner la dynamique des populations initialement denses. Les deux premiers résultats correspondent à des effets de la densité dépendance négative classiquement décrits dans les analyses de viabilité des populations. En effet, l’influence de la stochasticité démographique sur le temps d’extinction d’une population régulée par densité dépendance dépend de la densité initiale des populations mais également (i) de la capacité de charge de l’environnement, qui détermine la limite supérieure de la densité de population, (ii) du taux de croissance à long terme et (iii) de la forme de la densité dépendance (Lande, 1993, Lande et al., 2003). Une relation linéaire entre la densité de population et la croissance structurale, la maturation et le nombre de jeunes produits telle que décrite dans notre expérience signifie que la fécondité augmente quand la densité de population diminue. Ainsi, dans les populations de faible densité initiale, la densité dépendance négative agissant sur la fécondité permet aux populations de s’échapper plus rapidement de densités où le risque d’extinction est élevé à cause de la stochasticité démographique, que des populations densité-indépendantes (Morris & Doak, 2002, Henle et al., 2004).

En revanche, le troisième résultat met en lumière un effet inattendu de la densité dépendance de l’histoire de vie dans les petites populations. Les fluctuations du sexe ratio et de la formation des couples reproducteurs, associées à des biais de mortalité mâles-femelles, sont connues pour augmenter le risque d’extinction des populations via des déficits de partenaires sexuels potentiels et donc des effets Allee (ex : Bessa-Gomez et al., 2004, Legendre et al., 1999, Engen et al., 2003). En accord avec ces études, nos modèles densité-dépendants et densité-indépendants à deux sexes ont prédit des probabilités d’extinction plus élevées que nos modèles à un sexe. Cependant, dans les populations initialement denses, cette augmentation a été nettement plus marquée pour les populations régulées par densité dépendance que pour les populations densité-indépendantes. A l’opposé, à faibles densités

initiales, les effets positifs de la densité dépendance négative de la fécondité sur le taux d'extinction ont été maintenus en présence de fluctuations du sexe ratio et de la formation des couples.

Afin de déterminer les mécanismes à l'origine de cette interaction entre la densité dépendance de la fécondité et les fluctuations du sexe ratio et de la formation des couples, nous avons réalisé des simulations de notre modèle stochastique à deux sexes (i) avec une taille de harem non limitée, c'est-à-dire qu'un seul mâle reproducteur suffit à inséminer toutes les femelles d'une population quelle que soit sa densité, ou (ii) sans biais de mortalité entre les femelles et les mâles adultes et sub-adultes. Ces simulations ont montré que le degré de polygynie, et donc le système d'appariement, n'affectait que faiblement les patterns d'extinction des populations densité-indépendantes et densité-dépendantes. A l'inverse, les modèles à deux sexes sans biais de mortalité entre mâles et femelles adultes et sub-adultes ont produit des patterns d'extinction similaires aux modèles à un sexe (voir **Chapitre 5, Figures 3 et D1**). Ainsi, dans les petites populations initialement denses, la densité dépendance négative de la fécondité augmente le risque d'extinction des populations en les maintenant à une densité proche de l'équilibre, où le risque qu'aucun mâle reproducteur ne survive sous l'action de la stochasticité démographique est élevé (6 mâles adultes et sub-adultes pour 14 femelles à l'équilibre déterministe, **Chapitre 5**).

Notre expérience combinée à l'analyse de viabilité des populations démontre l'importance de la densité dépendance négative dans les petites populations (Schoener et al., 2003). En effet, dans une population en déclin, la densité peut être localement élevée particulièrement chez les espèces à capacités de dispersion limitées ou si la fragmentation de l'habitat limite les possibilités d'émigration (Grant & Benton, 2000). Ainsi, les analyses de viabilité de populations n'intégrant pas de régulations densité-dépendantes pour des petites populations en déclin peuvent conduire à des mesures de conservation inefficaces. Par exemple, nos modèles démontrent que chez une espèce où la survie est densité-indépendante et la fécondité décroît linéairement avec la densité, augmenter la densité locale en introduisant un grand nombre d'individus ne devrait avoir qu'un effet limité sur la probabilité d'extinction puisque la densité dépendance négative de la fécondité tamponne les effets de la densité sur la probabilité d'extinction.

D'autre part, notre étude montre que la densité dépendance négative peut interagir avec les fluctuations du sexe ratio adulte pour modeler les dynamiques d'extinction des petites populations. Ainsi, dans les populations où le sexe ratio est fortement femelle-biaisé en

raison d’un biais de mortalité entre mâles et femelles, tel que décrit ici, un manque de mâles reproducteurs peut précipiter les petites populations vers l’extinction. A l’opposé, Le Galliard et al. (2005d, 2005c) ont démontré que dans les populations mâle-biaisées, le harcèlement sexuel et les agressions des mâles sur les femelles mettent en péril la survie et la fécondité des femelles et que ces dernières n’ajustent pas le sexe ratio de leur ponte en réponse au sexe ratio adulte. Ces réponses ont pour conséquences d’exacerber le biais de sexe ratio adulte et d’amplifier fortement le risque d’extinction des populations (Le Galliard et al., 2005d). Par ailleurs, le degré de polygynie n’ayant que peu d’influence sur la probabilité d’extinction de petites populations de lézards régulées par densité dépendance (Chapitre 5 et Le Galliard et al., 2005d), on peut imaginer que les stratégies d’appariements ont une influence réduite sur la persistance des populations chez cette espèce, même elles varient avec la densité et le sexe ratio. A partir des données issues de l’Expérience 3, nous pourrions déterminer plus précisément de quelle manière l’interaction entre la densité de population et le sexe ratio adulte modèle les dynamiques d’extinction de petites populations isolées.

CONCLUSION

L’ensemble de nos études ont démontré l’existence d’un lien étroit entre la structure de population, l’histoire de vie et la dynamique de populations de lézards. En particulier, les réponses plastiques de l’histoire de vie à l’environnement biotique et social influencent en retour la structure de population ce qui contribue aux réponses observées à l’échelle populationnelle. Ainsi, nous avons vu que la variation de la qualité des cohortes au sein d’une population en réponse à la disponibilité en nourriture passée avait le potentiel d’influencer le fonctionnement des populations et l’évolution de l’histoire de vie à travers les trois mécanismes d’action décrits dans la littérature, c’est à dire (i) les effets directs de l’environnement sur la qualité intrinsèque des individus au sein des cohortes, (ii) les effets indirects de l’environnement passé sur l’intensité de la compétition intraspécifique intra- et inter-cohortes de type symétrique, et (iii) ses effets indirects sur l’intensité de la compétition intraspécifique inter-cohorte de type asymétrique (**Chapitre 1**). De plus, à notre connaissance, il s’agit de la première démonstration empirique que les mécanismes d’action densité-indépendants et densité-dépendants des effets cohortes peuvent agir en interaction pour façonner les trajectoires d’histoire de vie. Ainsi, chez les espèces régulées par de la compétition par exploitation asymétrique et de la mortalité taille-dépendante (ex : chez une

espèce de poisson prédatrice, Claessen et al., 2000, Claessen et al., 2002), de la stochasticité environnementale dans la densité de proies devrait introduire de la variation temporelle dans la distribution de taille des cohortes en compétition et dans la taille des cohortes. Cela devrait fortement influencer l’intensité de la compétition intra- et inter-cohorte et donc les trajectoires d’histoire de vie et la dynamique des populations (**Chapitre 1**). Cependant, nos travaux ne permettent pas de tester cette hypothèse. Pour cela, il aurait fallu manipuler conjointement la qualité et la taille des différentes cohortes au sein des populations expérimentales.

De plus, en accord avec littérature existante sur la densité dépendance de l’histoire de vie (ex : Bonenfant et al., 2009, Both, 1998, Edeline et al., 2010, Forchhammer et al., 2001, Svensson et al., 2001), nous avons montré que la densité de population affectait la plupart des aspects de l’histoire de vie du lézard vivipare, à l’exception de la survie et de la qualité des jeunes à la naissance. Notre approche de modélisation de la dynamique de petites populations isolées soumises à de la stochasticité démographique nous a permis de mettre en évidence l’importance de la densité dépendance négative dans la persistance de petites populations, paramètre trop souvent ignoré dans les analyses de viabilité des populations menacées d’extinction (Grant & Benton, 2000, Morris & Doak, 2002). Plus particulièrement, elle nous a montré que la densité dépendance négative de l’histoire de vie pouvait interagir avec les fluctuations du sexe ratio pour déterminer le risque d’extinction des populations. Nous pourrions vérifier ce résultat théorique à l’aide de nos données expérimentales dans un futur proche.

Ces travaux ont avancé notre compréhension de la variation d’histoire de vie et du fonctionnement des populations de lézards vivipares et plus généralement d’espèces itéropares à reproduction sexuée et présentant des populations structurées en âge ou en taille ainsi qu’une histoire de vie plastique. Cependant, des questions sans réponses demeurent. Premièrement, quels sont les mécanismes proximaux de la réponse d’histoire de vie à la structure de population ? Nous avons tenté de répondre à cette question en combinant l’étude de l’histoire de la vie au sens strict à des mesures de performances individuelles supposées liées à la valeur sélective, telles que le taux de consommation de proies, l’immunocompétence et les performances locomotrices (ex : Amundsen et al., 2007, Sinclair & Lochmiller, 2000, Le Galliard et al., 2004). Malheureusement les réponses observées ne nous ont permis d’expliquer qu’une partie des patterns d’histoire de vie décrits en réponse à l’environnement social (voir **Chapitres 1, 2, 4 et 5**). Cela indique qu’une étude plus intégrative de la réponse à l’environnement, incluant par exemple des mesures du métabolisme, des mesures comportementales et des mesures complémentaires du système immunitaire et hormonal (ex :

Ketterson & Nolan, 1992, Massot et al., 2011, Meylan et al., 2010, Edeline et al., 2010), est requise. Deuxièmement, quelle est l’origine de la variation familiale de la plasticité phénotypique du taux de croissance structurale à l’environnement et en quoi contribue-telle à la réponse des populations à une modification de l’environnement ? Pour cela, l’utilisation de données de pedigree (disponibles dans notre système expérimental) nous permettrait d’estimer la part de variance génétique et environnementale dans la réponse des traits à l’environnement (ex : Sheldon et al., 2003).

RÉFÉRENCES

- Albon, S. D., Cluttonbrock, T. H. & Guinness, F. E. 1987. Early development and population-dynamics in Red deer. 2. Density-independent effects and cohort variation. *Journal of Animal Ecology* **56**: 69-81.
- Allee, W. C., Emerson, A., Park, O., Park, T. & Schmidt, K. 1949. *Principles of Animal Ecology*. WB Saunders Company, Philadelphia, USA.
- Amundsen, P. A., Knudsen, R. & Klemetsen, A. 2007. Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *Journal of Animal Ecology* **76**: 149-158.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton.
- Angulo, E., Roemer, G. W., Berec, L., Gascoigne, J. & Courchamp, F. 2007. Double Allee effects and extinction in the island fox. *Conservation Biology* **21**: 1082-1091.
- Arditi, R. & Akcakaya, H. R. 1990. Underestimation of mutual interference of predators. *Oecologia* **83**: 358-361.
- Avery, R. A. 1966. Food and feeding habits of common lizard (*Lacerta vivipara*) in West of England. *Journal of Zoology* **149**: 115-121.
- Avery, R. A. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology* **40**: 351-365.
- Avery, R. A. 1975. Clutch size and reproductive effort in the lizard *Lacerta vivipara* Jacquin. *Oecologia* **19**: 165-170.
- Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D’Udine, B., Foley, R. A., Gluckman, P., Godfrey, K., Kirkwood, T., Lahr, M. M., McNamara, J., Metcalfe, N. B., Monaghan, P., Spencer, H. G. & Sultan, S. E. 2004. Developmental plasticity and human health. *Nature* **430**: 419-421.

- Bauwens, D., Heulin, B. & Pilorge, T. (1986) Variation spatio-temporelle des caractéristiques démographiques dans et entre populations du lézard *Lacerta vivipara*. In: *Biologie des populations*, (Legay, J.-M., ed.). pp. 531-536. CNRS, Université Claude Bernard Lyon I.
- Bauwens, D., van Damme, R. & Verheyen, R. F. 1989. Synchronization of spring molting with the onset of mating behavior in male lizards, *Lacerta vivipara*. *Journal of Herpetology* **23**: 89-91.
- Bauwens, D. & Verheyen, R. F. 1985. The timing of reproduction in the lizards *Lacerta vivipara*: differences between individual females. *Journal of Herpetology* **19**: 353-364.
- Beckerman, A., Benton, T. G., Lapsley, C. T. & Koesters, N. 2003. Talkin' 'bout my generation: environmental variability and cohort effects. *American Naturalist* **162**: 754-767.
- Begon, M., Townsend, C. R. & Harper, J. L. (2006) Intraspecific competition. In: *Ecology: from individuals to ecosystems*. pp. 132-162. Blackwell publishing.
- Beissinger, S. R. & McCullough, D. R. 2002. *Population viability analysis*. The University of Chicago Press, Chicago.
- Benton, T. G., Plaistow, S. J. & Coulson, T. N. 2006. Complex population dynamics and complex causation: devils, details and demography. *Proceedings of the Royal Society B-Biological Sciences* **273**: 1173-1181.
- Benton, T. G., St Clair, J. J. H. & Plaistow, S. J. 2008. Maternal effects mediated by maternal age: from life histories to population dynamics. *Journal of Animal Ecology* **77**: 1038-1046.
- Berec, L., Boukal, D. S. & Berec, M. 2001. Linking the allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. *American Naturalist* **157**: 217-230.
- Bessa-Gomez, C., Legendre, S. & Clobert, J. 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecology Letters* **7**: 802-812.
- Birkhead, T. R., Fletcher, F. & Pellatt, E. J. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proceedings of the Royal Society B-Biological Sciences* **266**: 385-390.
- 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. In:

- Advances in Ecological Research, Vol 41*, Vol. 41. pp. 313-357 *Advances in Ecological Research*.
- Both, C. 1998. Experimental evidence for density dependence of reproduction in great tits. *Journal of Animal Ecology* **67**: 667-674.
- Brommer, J. E., Karell, P. & Pietiainen, H. 2004. Supplementary fed Ural owls increase their reproductive output with a one year time lag. *Oecologia* **139**: 354-358.
- Bystrom, P. & Andersson, J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (*Arctic char*). *Oikos* **110**: 523-536.
- Caswell, H. 2001. *Matrix population models*, 2 ed. Sinauer Associates, Sunderland.
- Charmantier, A. & Garant, D. 2005. Environmental quality and evolutionary potential: lessons from wild populations. *Proceedings of the Royal Society B-Biological Sciences* **272**: 1415-1425.
- Charmantier, A., Kruuk, L. E. B. & Lambrechts, M. M. 2004. Parasitism reduces the potential for evolution in a wild bird population. *Evolution* **58**: 203-206.
- Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton University Press, Princeton.
- Claessen, D., de Roos, A. M. & Persson, L. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. *American Naturalist* **155**: 219-237.
- Claessen, D., Van Oss, C., de Roos, A. M. & Persson, L. 2002. The impact of size-dependent predation on population dynamics and individual life history. *Ecology* **83**: 1660-1675.
- Clobert, J., Massot, M., Lecomte, J., Sorci, G., de Fraipont, M. & Barbault, R. (1994) Determinants of dispersal behavior: the common lizard as a case study. In: *Historical and Experimental Perspectives*, (Vitt, L. J. & Pianka, E. R., eds.). pp. 183-206. Princeton University Press, Princeton, USA.
- Cloutier, S. & Newberry, R. C. 2000. Recent social experience, body weight and initial patterns of attack predict the social status attained by unfamiliar hens in a new group. *Behaviour* **137**: 705-726.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**: 131-133.
- Clutton-Brock, T. H. & Coulson, T. 2002. Comparative ungulate dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **357**: 1285-1298.
- Cockburn, A., Legge, S. & Double, M. C. (2002) Sex ratios in birds and mammals: can the hypotheses be disentangled? In: *Sex Ratios: Concepts and Research Methods*, (Hardy, I. C. W., ed.). pp. 266-286. Cambridge University Press, Cambridge.

- Comendant, T., Sinervo, B., Svensson, E. I. & Wingfield, J. 2003. Social competition, corticosterone and survival in female lizard morphs. *Journal of Evolutionary Biology* **16**: 948-955.
- Cote, J., Clobert, J. & Fitze, P. S. 2007. Mother - offspring competition promotes colonization success. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 9703-9708.
- Cote, J., Clobert, J., Meylan, S. & Fitze, P. S. 2006. Experimental enhancement of corticosterone levels positively affects subsequent male survival. *Hormones and Behavior* **49**: 320-327.
- Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. & Grenfell, B. T. 2001. Age, sex, density, winter weather, and population crashes in soap sheep. *Science* **292**: 1528-1531.
- Courchamp, F., Berec, L. & Gascoigne, J. 2008. *Allee effects in ecology and conservation*. Oxford University Press, Oxford.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. 2000. Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*. *Animal Conservation* **3**: 277-285.
- Creel, S. F. 2005. Dominance, aggression, and glucocorticoid levels in social carnivores. *Journal of Mammalogy* **86**: 255-264.
- Cureton, J. C., Martin, R. E. & Deaton, R. 2010. Short term changes in sex ratio and density alter coercive male mating tactics. *Behaviour* **147**: 1431-1442.
- Dauphin-Villemant, C. & Xavier, F. 1987. Nychthemeral variations of plasma corticosteroids in captive female *Lacerta vivipara* Jacquin: influence of stress and reproductive state. *General and Comparative Endocrinology* **67**: 292-302.
- de Roos, A. M., Persson, L. & McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* **6**: 473-487.
- Descamps, S., Boutin, S., Berteaux, D., McAdam, A. G. & Gaillard, J. M. 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.
- Dixon, K. E., Thorn, B. E. & Ward, L. C. 2004. An evaluation of sex differences in psychological and physiological responses to experimentally-induced pain: a path analytic description. *Pain* **112**: 188-196.

- Doak, D. F., Morris, W. F., Pfister, C., Kendall, B. E. & Bruna, E. M. 2005. Correctly estimating how environmental stochasticity influences fitness and population growth. *American Naturalist* **166**: E14-E21.
- Dreiss, A. N., Cote, J., Richard, M., Federici, P. & Clobert, J. 2010. Age- and sex-specific response to population density and sex ratio. *Behavioral Ecology* **21**: 356-364.
- Drent, R. H. & Daan, S. 1980. The prudent parent - energetic adjustments in avian breeding. *Ardea* **68**: 225-252.
- Edeline, E., Haugen, T. O., Weltzien, F. A., Claessen, D., Winfield, I. J., Stenseth, N. C. & Vollestad, L. A. 2010. Body downsizing caused by non-consumptive social stress severely depresses population growth rate. *Proceedings of the Royal Society B-Biological Sciences* **277**: 843-851.
- Eizaguirre, C., Laloï, D., Massot, M., Richard, M., Federici, P. & Clobert, J. 2007. Condition dependence of reproductive strategy and the benefits of polyandry in a viviparous lizard. *Proceedings of the Royal Society B-Biological Sciences* **274**: 425-430.
- Emlen, D. J. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215-223.
- Engen, S., Lande, R. & Saether, B.-E. 2003. Demographic stochasticity and Allee effects in populations with two sexes. *Ecology* **84**: 2378-2386.
- Fedoraka, K. M., Zuk, M. & Mousseau, T. A. 2004. Immune suppression and the cost of reproduction in the ground cricket, *Allonemobius socius*. *Evolution* **58**: 2478-2485.
- Ferrière, R., Dieckmann, U. & Couvet, D. 2004. *Evolutionary Conservation Biology*. Cambridge University Press, Cambridge.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Oxford University Press, Oxford.
- Fitze, P. S., Cote, J., Martinez-Rica, J. P. & Clobert, J. 2008. Determinants of male fitness: disentangling intra- and inter-sexual selection. *Journal of Evolutionary Biology* **21**: 246-255.
- Fitze, P. S. & Le Galliard, J.-F. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. *Ecology Letters* **11**: 432-439.
- Fitze, P. S., Le Galliard, J.-F., Federici, P., Richard, M. & Clobert, J. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. *Evolution* **59**: 2451-2459.

- Forchhammer, M. C., Clutton-Brock, T. H., Lindström, J. & Albon, S. D. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* **70**: 721-729.
- Forrester, G., Harmon, L., Helyer, J., Holden, W. & Karis, R. 2011. Experimental evidence for density-dependent reproductive output in a coral reef fish. *Population Ecology* **53**: 155-163.
- French, S. S., DeNardo, D. F. & Moore, M. C. 2007. Trade-offs between the reproductive and immune systems: facultative responses to resources or obligate responses to reproduction? *American Naturalist* **170**: 79-89.
- Gaillard, J. M., Loison, A., Toigo, C., Delorme, D. & Van Laere, G. 2003. Cohort effects and deer population dynamics. *Ecoscience* **10**: 412-420.
- Gaillard, J. M. & Yoccoz, N. G. 2003. Temporal variation in survival of mammals: A case of environmental canalization? *Ecology* **84**: 3294-3306.
- Galloway, L. F. 2001. The effect of maternal and paternal environments on seed characters in the herbaceous plant *Campanula americana* (Campanulaceae). *American Journal of Botany* **88**: 832-840.
- Gascoigne, J., Berec, L., Gregory, S. & Courchamp, F. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology* **51**: 355-372.
- Gebhardt-Henrich, S. G. & van Noordwijk, A. J. 1994. The genetic ecology of nestling in the great tit: environmental influences on the expression of genetic variances during growth. *Functional Ecology* **8**: 469-476.
- Gilg, O., Hanski, I. & Sittler, B. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. *Science* **302**: 866-868.
- Grafen, A. (1988) On the uses of data on lifetime reproductive success. In: *Reproductive Success*, (Clutton-Brock, T. H., ed.). pp. 454-471. University of Chicago Press, Chicago.
- Grant, A. & Benton, T. G. 2000. Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* **81**: 680-693.
- Grant, A. & Benton, T. G. 2003. Density-dependent populations require density-dependent elasticity analysis: an illustration using the LPA model of *Tribolium*. *Journal of Animal Ecology* **72**: 94-105.
- Grant, J. W. A. & Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *Journal of Fish Biology* **67**: 100-110.

- Gregory, S. D., Bradshaw, C. J. A., Brook, B. W. & Courchamp, F. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. *Ecology* **91**: 2151-2161.
- Haridas, C. V. & Tuljapurkar, S. 2005. Elasticities in variable environments: Properties and implications. *American Naturalist* **166**: 481-495.
- Harvey, S., Phillips, J. G., Rees, A. & Hall, T. R. 1984. Stress and adrenal-function. *Journal of Experimental Zoology* **232**: 633-645.
- Hassell, M. P. & Varley, G. C. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* **223**: 1133-&.
- Hawley, D. M., Lindstrom, K. & Wikelski, M. 2006. Experimentally increased social competition compromises humoral immune responses in house finches. *Hormones and Behavior* **49**: 417-424.
- Henle, K., Sarre, S. & Wiegand, K. 2004. The role of density regulation in extinction processes and population viability analysis. *Biodiversity and Conservation* **13**: 9-52.
- Heulin, B. 1988. Observations sur l'organisation de la reproduction et sur les comportements sexuels et agonistiques chez *Lacerta vivipara*. *Vie et Milieu* **38**: 177-187.
- Hoffmann, A. A. & Merilä, J. 1999. Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology & Evolution* **14**: 96-101.
- Holling, C. S. 1959. Some characteristics of simple type of predation and parasitism. *The Canadian Entomologist* **91**: 385-398.
- Jenkins, T. M., Diehl, S., Kratz, K. W. & Cooper, S. D. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology* **80**: 941-956.
- Ketterson, E. D. & Nolan, V. 1992. Hormones and life histories: an integrative approach. *American Naturalist* **140**: S33-S62.
- Kokko, H. & Johnstone, R. A. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **357**: 319-330.
- Kokko, H. & Monaghan, P. 2001. Predicting the direction of sexual selection. *Ecology Letters* **4**: 159-165.
- Kokko, H. & Rankin, D. J. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B-Biological Sciences* **361**: 319-334.

- Kooijman, S. A. L. M. 2000. *Dynamic energy and mass budgets in biological systems*. Cambridge University Press, Cambridge.
- Koskela, E., Jonsson, P., Hartikainen, T. & Mappes, T. 1998. Limitation of reproductive success by food availability and litter size in the bank vole, *Clethrionomys glareolus*. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**: 1129-1134.
- Koskela, E., Mappes, T. & Ylonen, H. 1999. Experimental manipulation of breeding density and litter size: effects on reproductive success in the bank vole. *Journal of Animal Ecology* **68**: 513-521.
- Kratochvil, L., Fokt, M., Rehak, I. & Frynta, D. 2003. Misinterpretation of character scaling: a tale of sexual dimorphism in body shape of common lizards. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **81**: 1112-1117.
- Kuhn, E. R., Geris, K. L., van der Geyten, S., Mol, K. A. & Darras, V. M. 1998. Inhibition and activation of the thyroïdal axis by the adrenal axis in vertebrates. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **120**: 169-174.
- Kvarnemo, C. & Ahnesjö, I. (2002) Operational sex ratios and mating competition. In: *Sex Ratios: Concepts and Research Methods*, (Hardy, I. C. W., ed.) pp. 366-382. Cambridge University Press, Cambridge.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**: 911-927.
- Lande, R., Engen, S. & Saether, B. E. 2003. *Stochastic population dynamics in ecology and conservation*. Oxford University Press, Oxford.
- Le Galliard, J.-F., Clobert, J. & Ferrière, R. 2004. Physical performance and darwinian fitness in lizards. *Nature* **432**: 502-505.
- Le Galliard, J.-F., Cote, J. & Fitze, P. S. 2008. Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. *Ecology* **89**: 56-64.
- Le Galliard, J.-F., Ferrière, R. & Clobert, J. 2005a. Effect of patch occupancy on immigration in the common lizard. *Journal of Animal Ecology* **74**: 241-249.
- Le Galliard, J.-F., Ferrière, R. & Clobert, J. 2005b. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* **111**: 368-376.
- Le Galliard, J.-F., Fitze, P. S., Cote, J., Massot, M. & Clobert, J. 2005c. Female common lizards (*Lacerta vivipara*) do not adjust their sex-biased investment in relation to the adult sex ratio. *Journal of Evolutionary Biology* **18**: 1455-1463.

- Le Galliard, J.-F., Fitze, P. S., Ferrière, R. & Clobert, J. 2005d. Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 18231-18236.
- Le Galliard, J.-F., Marquis, O. & Massot, M. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology* **79**: 1296-1307.
- Lecomte, J., Boudjemadi, K., Sarrazin, F., Cally, K. & Clobert, J. 2004. Connectivity and homogenisation of population sizes: an experimental approach in *Lacerta vivipara*. *Journal of Animal Ecology* **73**: 179-189.
- Lecomte, J., Clobert, J., Massot, M. & Barbault, R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. *Ecoscience* **1**: 300-310.
- Legendre, S., Clobert, J., Moller, A. P. & Sorci, G. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *American Naturalist* **153**: 449-463.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* **14**: 342-348.
- Lindström, J. & Kokko, H. 2002. Cohort effects and population dynamics. *Ecology Letters* **5**: 338-344.
- Lorenzon, P., Clobert, J. & Massot, M. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. *Evolution*: 392-404.
- Lourdais, O., Bonnet, X., Shine, R. & Taylor, E. N. 2003. When does a reproducing female viper (*Vipera aspis*) 'decide' on her litter size? *Journal of Zoology* **259**: 123-129.
- Lummaa, V. & Clutton-Brock, T. 2002. Early development, survival and reproduction in humans. *Trends in Ecology & Evolution* **17**: 141-147.
- Madsen, T. & Shine, R. 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.
- Marquis, O., Massot, M. & Le Galliard, J.-F. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. *Ecology* **89**: 2575-2583.
- Martin, L. B., Navara, K. J., Weil, Z. M. & Nelson, R. J. 2007. Immunological memory is compromised by food restriction in deer mice *Peromyscus maniculatus*. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology* **292**: R316-R320.

- Massot, M. & Clobert, J. 1995. Influence of maternal food availability on offspring dispersal. *Behavioral Ecology and Sociobiology* **37**: 413-418.
- Massot, M., Clobert, J. & Ferriere, R. 2008. Climate warming, dispersal inhibition and extinction risk. *Global Change Biology* **14**: 461-469.
- Massot, M., Clobert, J., Lorenzon, P. & Rossi, J. M. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology* **71**: 253-261.
- Massot, M., Clobert, J., Montes-Polini, L., Haussy, C., Cubo, G. & Meylan, S. 2011. An integrative study of ageing in a wild population of common lizards (*Lacerta vivipara*). *Functional Ecology* **In press**.
- Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**: 1742-1756.
- Metcalf, N. B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution* **16**: 254-260.
- Meylan, S. & Clobert, J. 2004. Maternal effects on offspring locomotion: Influence of density and corticosterone elevation in the lizard *Lacerta vivipara*. *Physiological and Biochemical Zoology* **77**: 450-458.
- Meylan, S., Clobert, J. & Sinervo, B. 2007. Adaptive significance of maternal induction of density-dependent phenotypes. *Oikos* **116**: 650-661.
- Meylan, S., Haussy, C. & Voituron, Y. 2010. Physiological actions of corticosterone and its modulation by an immune challenge in reptiles. *General and Comparative Endocrinology* **169**: 158-166.
- Miller, D. A., Grand, J. B., Fondell, T. E. & Anthony, M. 2006. Predator functional response and prey survival: direct and indirect interactions affecting a marked prey population. *Journal of Animal Ecology* **75**: 101-110.
- Moore, I. T. & Jessop, T. S. 2003. Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. *Hormones and Behavior* **43**: 39-47.
- Moore, I. T. & Mason, R. T. 2001. Behavioral and hormonal responses to corticosterone in the male red-sided garter snake, *Thamnophis sirtalis parietalis*. *Physiology & Behavior* **72**: 669-674.
- Morris, D. L. & Doak, D. F. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates Inc., Sunderland.

- Mousseau, T. A. & Fox, C. W. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution* **13**: 403-407.
- Mysterud, A., Holand, O., Roed, K. H., Gjostein, H., Kumpula, J. & Nieminen, M. 2003. Effects of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). *Journal of Zoology* **261**: 341-344.
- Nelson, R. J., Badura, L. L. & Goldman, B. D. 1990. Mechanisms of seasonal cycles of behavior. *Annual Review of Psychology* **41**: 81-108.
- Pascual, M. A., Kareiva, P. & Hilborn, R. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* **11**: 966-976.
- Persson, L., Leonardsson, K., de Roos, A. M., Gyllenberg, M. & Christensen, B. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology* **54**: 270-293.
- Pfister, C. A. & Stevens, F. R. 2003. Individual variation and environmental stochasticity: implications for matrix model predictions. *Ecology* **84**: 496-510.
- Pilorge, T. 1982. Ration alimentaire et bilan énergétique individuel dans une population de montagne de *Lacerta vivipara*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **60**: 1945-1950.
- Pinheiro, J. C. & Bates, D. M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer Verlag, New York.
- Pitt, W. C. & Ritchie, M. E. 2002. Influence of prey distribution on the functional response of lizards. *Oikos* **96**: 157-163.
- Plaistow, S. J., Lapsley, C. T. & Benton, T. G. 2006. Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. *American Naturalist* **167**: 206-215.
- Postma, E. & van Noordwijk, A. J. 2005. Genetic variation for clutch size in natural populations of birds from a reaction norm perspective. *Ecology* **86**: 2344-2357.
- Rankin, D. J. & Kokko, H. 2007. Do males matter? The role of males in population dynamics. *Oikos* **116**: 335-348.
- Räsänen, K. & Kruuk, L. E. B. 2007. Maternal effects and evolution at ecological time-scales. *Functional Ecology* **21**: 408-421.
- Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. & Monaghan, P. 2003. Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology* **72**: 36-46.

- Richard, M., Lecomte, J., de Fraipont, M. & Clobert, J. 2005. Age-specific mating strategies and reproductive senescence. *Molecular Ecology* **14**: 3147-3155.
- Roach, D. A. 2003. Age-specific demography in plantago: Variation among cohorts in a natural plant population. *Ecology* **84**: 749-756.
- Runge, M. C. & Johnson, F. A. 2002. The importance of functional form in optimal control solutions of problems in population dynamics. *Ecology* **83**: 1357-1371.
- Saino, N., Calza, S., Ninni, P. & Moller, A. P. 1999. Barn swallows trade survival against offspring condition and immunocompetence. *Journal of Animal Ecology* **68**: 999-1009.
- Schoener, T. W., Clobert, J., Legendre, S. & Spiller, D. A. 2003. Life-history models of extinction: A test with island spiders. *American Naturalist* **162**: 558-573.
- Sheldon, B. C., Kruuk, L. E. B. & Merila, J. 2003. Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* **57**: 406-420.
- Sibly, R. M., Barker, D., Denham, M. C., Hone, J. & Pagel, M. 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science* **309**: 607-610.
- Silva, A. L., Fry, W. H. D., Sweeney, C. & Trainor, B. C. 2010. Effects of photoperiod and experience on aggressive behavior in female California mice. *Behavioural Brain Research* **208**: 528-534.
- Sinclair, J. A. & Lochmiller, R. L. 2000. The winter immunoenhancement hypothesis: associations among immunity, density, and survival in prairie vole (*Microtus ochrogaster*) populations. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **78**: 254-264.
- Spence, R. & Smith, C. 2005. Male territoriality mediates density and sex ratio effects on oviposition in the zebrafish, *Danio rerio*. *Animal Behaviour* **69**: 1317-1323.
- Spiller, D. A. & Schoener, T. W. 1998. Lizards reduce spider species richness by excluding rare species. *Ecology* **79**: 503-516.
- Stephens, P. A., Sutherland, W. J. & Freckleton, R. P. 1999. What is the Allee effect? *Oikos* **87**: 185-190.
- Summers, C. H. 2002. Social interaction over time, implications for stress responsiveness. *Integrative and comparative biology* **42**: 591-599.
- Svensson, E., Sinervo, B. & Comendant, T. 2001. Density-dependent competition and selection on immune function in genetic lizard morphs. *Proceedings of the National Academy of Sciences of the United States of America* **98**: 12561-12565.

- Taborsky, B. 2006. The influence of juvenile and adult environments on life-history trajectories. *Proceedings of the Royal Society B-Biological Sciences* **273**: 741-750.
- Toigo, C., Gaillard, J. M. & Michallet, J. 1999. Cohort affects growth of males but not females in alpine ibex (*Capra ibex ibex*). *Journal of Mammalogy* **80**: 1021-1027.
- Trainor, B. C., Takahashi, E. Y., Silva, A. L., Crean, K. K. & Hostetler, C. 2010. Sex differences in hormonal responses to social conflict in the monogamous California mouse. *Hormones and Behavior* **58**: 506-512.
- Tschirren, B., Fitze, P. S. & Richner, H. 2003. Sexual dimorphism in susceptibility to parasites and cell-mediated immunity in great tit nestlings. *Journal of Animal Ecology* **72**: 839-845.
- Tschirren, B., Rutstein, A. N., Postma, E., Mariette, M. & Griffith, S. C. 2009. Short- and long-term consequences of early developmental conditions: a case study on wild and domesticated zebra finches. *Journal of Evolutionary Biology* **22**: 387-395.
- Tuljapurkar, S., Gaillard, J. M. & Coulson, T. 2009. From stochastic environments to life histories and back. *Philosophical Transactions of the Royal Society B-Biological Sciences* **364**: 1499-1509.
- Turkington, R., Goldberg, D. E., Olsvig-Whittaker, L. & Dyer, A. R. 2005. Effects of density on timing of emergence and its consequences for survival and growth in two communities of annual plants. *Journal of Arid Environments* **61**: 377-396.
- van de Pol, M., Bruinzeel, L. W., Heg, D., van Der Jeugd, H. P. & Verhulst, S. 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.
- Walpita, C. N., Grommen, S. V. H., Darras, V. M. & Van der Geyten, S. 2007. The influence of stress on thyroid hormone production and peripheral deiodination in the Nile tilapia (*Oreochromis niloticus*). *General and Comparative Endocrinology* **150**: 18-25.
- Warner, D. A., Bonnet, X., Hobson, K. A. & Shine, R. 2008. Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. *Journal of Animal Ecology* **77**: 1242-1249.
- Weiser, M. J. & Handa, R. J. 2009. Estrogen impairs glucocorticoid dependent negative feedback on the hypothalamic-pituitary-adrenal axis via estrogen receptor alpha within the hypothalamus *Neuroscience* **159**: 883-895.
- Wingfield, J. C. & Ramenofsky, M. (1999) Hormones and the behavioral ecology of stress. In: *Stress physiology in animals*, (Balm, P. H. M., ed.). pp. 1-51. Sheffield Academic Press, Sheffield.

- Wittmer, H. U., Powell, R. A. & King, C. M. 2007. Understanding contributions of cohort effects to growth rates of fluctuating populations. *Journal of Animal Ecology* **76**: 946-956.
- Yearsley, J. M., Fletcher, D. & Hunter, C. 2003. Sensitivity analysis of equilibrium population Size in a density-dependent model for Short-tailed Shearwaters. *Ecological Modelling* **163**: 119-129.
- Yoccoz, N. G., Nakata, K., Stenseth, N. C. & Saitoh, T. 1998. The demography of *Clethrionomys rufocanus*: from mathematical and statistical models to further field studies. *Researches on Population Ecology* **40**: 107-121.

ANNEXES



Annexe 1 – Caractérisation de la réponse au stress

Etude réalisée par Marianne Mugabo, Sandrine Meylan, Claudy Haussy, Samuel Perret & Jean-François Le Galliard.

Réponse au stress social en conditions semi-naturelles

Dans le cadre de notre étude de la densité dépendance de l’histoire de vie, nous avons caractérisé la réponse physiologique des individus à la densité de population. Pour cela, nous avons estimé le taux de corticostérone plasmatique à plusieurs reprises au cours de l’expérience chez des sub-adultes et adultes mâles et femelles. Les sessions de prélèvements ont été effectuées : 2 jours avant le lâcher dans les enclos (session 1), environ une semaine après le lâcher (session 2), quelques semaines avant l’entrée en hibernation (session 3) et quelques semaines après la sortie d’hibernation (session 4, Table E1).

Table A1. Présentation des conditions de prélèvements et des effectifs participant à l’étude de la réponse physiologique à la densité de population. Les effectifs ont été répartis équitablement entre les 5 niveaux de densité. Le temps moyen depuis le lâcher est donné \pm l’écart type.

	Session 1	Session 2	Session 3	Session 4
Période	Juin 2008	Juin-juillet 2008	Septembre 2008	Avril 2009
Conditions	Laboratoire	Semi-naturelles	Semi-naturelles	Semi-naturelles
Temps depuis le lâcher		11.4 \pm 2.9	84.4 \pm 12.8	148.3 \pm 13.3
Effectifs				
Mâles adultes	54	21	10	9
Femelles adultes	0	0	21	13
Mâles sub-adultes	94	51	34	14
Femelles sub-adultes	75	25	32	28

La session 1, effectuée en conditions contrôlées en laboratoire, sert de référence et les niveaux de corticostérone ne différaient pas entre les niveaux de densité avant l’introduction dans les enclos (test des effets simples du traitement de densité et en interaction avec l’âge et le sexe : tests F, tous les $P > 0.45$). Les individus de moins de 2 grammes et les femelles gestantes ont été exclus de l’étude afin de ne pas affecter leur survie et la gestation respectivement.

Réponse à un stress ponctuel de manipulation et à un stress social chronique en conditions de laboratoire

Afin de compléter notre caractérisation de la réponse au stress chez le lézard vivipare, nous avons également étudié en conditions contrôlées en laboratoire l’influence d’un stress ponctuel (Expérience 5.1) et d’un stress chronique d’origine sociale (Expérience 5.2) sur les niveaux de corticostérone plasmatique sur une durée de quelques jours. Ces deux expériences ont été réalisées pendant l’été 2010 (du 20 au 27 juin 2010 pour l’expérience 1 et du 24 juin au 14 juillet pour l’expérience 2).

Sur les 30 lézards adultes mâles qui ont participé à l’expérience 1, 15 individus ont subi un stress ponctuel de manipulation (groupe « stress ») et 15 individus ont servi de contrôle. Le stress de manipulation a consisté à effrayer à l’aide d’un pinceau un individu placé dans un terrarium pendant une durée de 10 minutes. Après un stress ponctuel, du type prise prélèvement sanguin et contention, le retour au niveau basal de corticostérone plasmatique peut prendre plusieurs heures à quelques jours (Moore et al., 1991). Le taux basal de corticostérone a donc été mesuré dans les deux groupes 5 jours avant le début de l’expérience afin de s’assurer du retour au taux basal au moment de la manipulation et la réponse au stress de manipulation a été mesurée immédiatement et un jour après la manipulation. Les animaux du groupe contrôle ont été prélevés en même temps que les animaux du groupe stress.

Sur les 32 lézards adultes mâles qui ont participé à l’expérience 2, 16 lézards ont subi un stress social chronique (groupe « stress ») et 16 lézards ont servi de contrôle (groupe « contrôle »). Les individus du groupe stress ont été maintenus par 2 dans le même terrarium pendant une période de 10 jours. Pour éviter l’établissement de relations de dominance entre les individus maintenus par 2, nous avons créé des paires d’individus de taille et de même masse corporelles similaires. Dans le même temps, les animaux du groupe contrôle ont été maintenus en terrarium individuel. Le taux basal de corticostérone a été mesuré chez les animaux des deux groupes 5 jours avant le début de l’expérience. 3 prélèvements ont été réalisés pendant la durée de l’expérience chez les animaux des deux groupes : 1 jour, 5 jours et 10 jours après le début de l’expérience. Après 10 jours de maintien en binôme, les animaux du groupe stress ont été replacés en terrarium individuel. Un dernier prélèvement a été effectué 5 jours après le retour en terrarium individuel.

Pendant toute la durée de l’expérimentation, les animaux ont été nourris *ad libitum* et maintenus dans des conditions de température et d’humidité optimales pour l’espèce (voir Le Galliard et collaborateurs, 2003 pour une présentation détaillée des conditions d’élevage en

laboratoire). Les animaux n’ont subi aucune manipulation en dehors des prélèvements sanguins et du stress ponctuel ou social.

Prélèvements sanguins et dosage de la corticostérone plasmatique

Les échantillons de sang (40-70 μ l par prélèvement) ont été collectés au niveau du sinus-post-orbital à l’aide de tubes micro-capillaires non héparinés de 50 μ l (Meylan et al., 2003). Les prélèvements ont été réalisés en moins de 3 minutes à partir de la capture de l’animal afin d’éviter une augmentation du taux de corticostérone plasmatique lié à la manipulation (Dauphin-Villemant & Xavier, 1987). Les échantillons de sang ont été centrifugés immédiatement après le prélèvement et le plasma récolté a été conservé à -20 °C jusqu’au dosage. Les niveaux de corticostérone ont été quantifiés à l’aide d’une méthode de compétition enzymatique utilisant un anticorps poly-clonal de corticostérone (Kits Corticosterone EIA pour « enzymeimmunoassay », produits IDS, France).

Analyses statistiques

Les données issues de l’expérience densité ont été analysées par sessions de prélèvements à l’aide de modèles linéaires mixtes (Pinheiro & Bates, 2000). Ces modèles incluait un effet aléatoire de l’enclos ainsi que les effets fixes du traitement de densité en interaction simple avec le sexe et la classe d’âge et les effets additifs de l’heure et de la date de prélèvement ainsi que du temps écoulé depuis le lâcher dans les enclos. Toutes les analyses statistiques ont été effectuées dans R 2.10.1 (<http://cran.r-project.org/>) en suivant les mêmes méthodes d’analyses et de sélection de modèles que dans le **Chapitre 5**.

Les données issues des expériences 5.1 et 5.2 n’ont pas été analysées.

Références

- Dauphin-Villemant, C. & Xavier, F. 1987. Nychthemeral variations of plasma corticosteroids in captive female *Lacerta vivipara* Jacquin: influence of stress and reproductive state. *General and Comparative Endocrinology* **67**: 292-302.
- Le Galliard, J.-F., Le Bris, M. & Clobert, J. 2003. Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. *Functional Ecology* **17**: 877-885.
- Meylan, S., Dufty, A. M. & Clobert, J. 2003. The effect of transdermal corticosterone application on plasma corticosterone levels in pregnant *Lacerta vivipara*. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **134**: 497-503.

M. Mugabo – Caractérisation des interactions entre la structure de population et l’histoire de vie

Moore, M. C., Thompson, C. W. & Marler, C. A. 1991. Reciprocal changes in corticosterone and testosterone levels following acute and chronic handling stress in the tree lizard, *Urosaurus ornatus*. *General and Comparative Endocrinology* **81**: 217-226.

Pinheiro, J. C. & Bates, D. M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer Verlag, New York.

Annexe 2 – Expérience Densité de population × sexe ratio adulte

Etude réalisée par Marianne Mugabo & Jean-François Le Galliard.

Design expérimental

Pendant l’été 2009, nous avons manipulé la densité de population et le sexe ratio de 24 populations expérimentales maintenues dans des enclos extérieurs de 100 m² situés dans une prairie naturelle au Centre de Recherche en Ecologie Expérimentale et Prédictive (CEREEP à Saint-Pierre-lès-Nemours en Seine-et-Marne, France, 48°17’N, 2°41’E). Nous avons établi les populations après la reproduction selon 3 niveaux de densité croisés avec 2 niveaux de sexe ratio (Table 1). Les populations de densité D1, D2 et D3 comprenaient respectivement 10, 20 et 30 adultes et sub-adultes, le niveau de densité D2 correspondant à la densité à l’équilibre dans notre système expérimental (**Chapitre 5**). Pour le sexe ratio (proportion de mâles), nous avons manipulé à la fois le sexe ratio adulte (SRA) et le sexe ratio sub-adulte (SRS) en prévision de la saison de reproduction 2010 pour laquelle les sub-adultes seront devenus adultes. Nous avons ainsi créé des populations femelle-biaisées (FB = 25 % de mâles adultes) et des populations mâle-biaisées (MB = 75 % de mâles adultes, Table 1). Ces niveaux de sexe ratio se situent dans la gamme de variation observée en populations naturelles (gamme = 0-0.8, ASR moyen = 0.18 ± 0.18 SD Le Galliard et al., 2005). Le nombre de répliquas par traitement a été ajusté de manière à maintenir des effectifs similaires entre traitements (traitement 1 : N = 5, traitement 2 : N = 7, traitement 3 : N = 3, traitement 4 : N = 4, traitement 5 : N = 2, traitement 6 : N = 3). Les enclos ont été attribués aléatoirement à un traitement.

Les sub-adultes et adultes ont été capturés dans les enclos du CEREEP en Mai 2009 et tous les juvéniles ont été produits par les femelles gestantes capturées. Les individus ont été sexés, mesurés pour la LMA (au mm près) et pesés (au mg près). Les adultes ($n = 164$), et sub-adultes ($n = 246$) ont été assignés aléatoirement aux traitements expérimentaux. Comme pour l’Expérience 2, les juvéniles ($n = 492$) issus d’une même portée ont été répartis de manière équitable entre les 6 traitements expérimentaux afin d’étudier les normes de réaction familiales. Au début de l’expérience, les groupes expérimentaux ne différaient pas en termes de LMA et de condition corporelle (estimée par une analyse de covariance de la masse contrôlée pour la LMA, ANPOVA, tous les $P > 0.10$). Les mâles et les femelles sub-adultes et adultes ont été lâchés dans les enclos les 8 et 9 juillet tandis que les juvéniles ont été lâchés le

jour de la mise bas (du 16 juin au 3 juillet). Le jour du lâcher, un échantillon de tissus a été prélevé sur tous les animaux pour l’analyse du succès reproducteur des mâles et des stratégies d’appariements mâles et femelles (**Annexe 3**). Les populations expérimentales ont été suivies pendant un an.

Table 1. Densité et structure de sexe et d’âge initiales des populations expérimentales. D correspond au niveau de densité, FB à un sexe ratio femelle-biaisé et MB à un sexe ratio mâle-biaisé. Le sexe ratio juvénile était équilibré. ♀ = femelles, ♂ = mâles, sub-ad. = sub-adultes, N_0 = densité initiale, SRA = sexe ratio adulte et SRAS = sexe ratio adulte et sub-adulte.

Traitement	♀ adultes	♂ adultes	♀ sub-ad.	♂ sub-ad.	Juvéniles	N_0	SRA	SRAS
1 : D1-FB	3	1	3	3	12	22	0.25	0.4
2 : D1-MB	1	3	2	4	12	22	0.75	0.7
3 : D2-FB	6	2	6	6	24	44	0.25	0.4
4 : D2-MB	2	6	4	8	24	44	0.75	0.7
5 : D3-FB	9	3	9	9	36	66	0.25	0.4
6 : D3-MB	3	9	6	12	36	66	0.75	0.7

Mesure de l’histoire de vie et de l’immunocompétence

Les données individuelles ont été collectées au cours de 2 sessions de captures réalisées à la fin de l’été 2009 (du 20 au 26 Août, $n = 649$) et à la fin du printemps 2010 (du 5 Mai au 16 Juin, $n = 511$). La croissance corporelle, la survie, les performances reproductrices et l’immunocompétence ont été estimées de la même manière que pour l’Expérience 2 (voir **Chapitre 5**). Nous avons également prélevé des échantillons de tissus sur tous les œufs produits afin d’effectuer les analyses de paternités (**Annexe 3**).

Les données d’histoire de vie et d’immunité n’ont pas encore été analysées. Les analyses génétiques nécessaires aux attributions de paternité et à l’analyse du système d’appariement sont en cours (collaboration avec C. Acuso, P. Federici et M. Richard).

Références

Le Galliard, J.-F., Fitze, P. S., Ferrière, R. & Clobert, J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences of the United States of America* 102: 18231-18236.

Annexe 3 – Analyses de paternités

Etude réalisée par Marianne Mugabo, Jean-François Le Galliard, Murielle Richard & Pierre Federici.

Dans le cadre de l’Expérience 2 sur la densité dépendance de l’histoire de vie et de l’Expérience 3 sur l’interaction entre densité de population et le sexe ratio adulte, nous avons effectué des analyses génétiques afin de déterminer le succès reproducteur des mâles et d’étudier le système d’appariement. Pour toutes nos expériences, une session de capture est organisée à la fin de la saison des appariements (en mai-juin). Tous les animaux présents dans les enclos sont capturés et placés en laboratoire. Les femelles gestantes sont maintenues en laboratoire jusqu’à la mise bas ce qui nous permet d’avoir directement accès au succès reproducteur des femelles et de connaître la mère de chaque œuf produit (œufs jaunes, œufs avortés et juvéniles viables et non viables).

Génotypage

Nous avons collecté un morceau de queue sur tous les animaux participant à nos expériences avant leur introduction dans les enclos en début d’expérience et immédiatement à la naissance pour les œufs produits au cours de l’expérience. Les échantillons ainsi récoltés ont été conservés dans de l’alcool à 70°. Nous avons ensuite extrait l’ADN de tous les échantillons à l’aide d’un kit « Perfect gDNA Blood Mini Isolation kit » (Eppendorf, Hamburg, Allemagne). Tous les échantillons ont été génotypés pour 5 marqueurs microsatellites hautement polymorphes (Lv-3-19, Lv-4-72, Lv-4-alpha, Lv-4X et Lv-4-115, Boudjemadi et al., 1999). Lorsque deux mâles étaient identifiés comme père équiprobables, nous avons utilisé 3 marqueurs supplémentaires (Lv-5-19, Lv2-145 et Lv-5-145, Richard et al. Manuscrit non publié). Pour cela des PCR (réactions en chaîne par polymérase) ont été réalisées puis les échantillons ont été séquencés pour les 5 marqueurs à l’aide d’un séquenceur automatisé AB1 310 (Applied Biosystems, Life Technologies Corporation, Carlsbad, USA). Les protocoles d’extractions, de PCR et de lecture des génotypes ont été décrits en détail par Laloï et al. (2004).

Assignements de paternité

Les attributions de paternité ont été réalisées à l’aide du logiciel Cervus 3.0 (<http://www.fieldgenetics.com>). Dans le cadre de l’Expérience 2, 700 œufs ont été produits dont 579 juvéniles viables, 40 juvéniles non viables, 30 œufs avortés et 50 œufs jaunes. Nous avons attribué un père à 668 des œufs produits, les 32 œufs non attribués étant des œufs jaunes non fertilisés à l’exception d’1 juvénile non viable et de 3 œufs avortés. Nous venons de terminer les analyses de paternités pour cette expérience mais les analyses du succès reproducteur des mâles et du système d’appariement restent à faire. Dans le cadre de l’expérience 4, 718 œufs ont été produits dont 555 juvéniles viables, 54 juvéniles non viables, 51 œufs avortés et 58 œufs jaunes. Le génotypage des œufs est en cours.

Références

- Boudjemadi, K., Martin, O., Simon, J. C. & Estoup, A. 1999. Development and cross-species comparison of microsatellite markers in two lizard species, *Lacerta vivipara* and *Podarcis muralis*. *Molecular Ecology* **8**: 518-520.
- Laloi, D., Richard, M., Lecomte, J., Massot, M. & Clobert, J. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellite markers. *Molecular Ecology* **13**: 719-723.

CHAPITRES



CHAPITRE 1 – Effets cohortes dans des populations structurées et conséquences démographiques

Mécanismes des effets cohortes et leurs conséquences pour la dynamique de populations

Marianne Mugabo,¹ & Jean-François Le Galliard,^{1,2}

¹ CNRS UPMC ENS, UMR 7625, Laboratoire Ecologie et Evolution, Université Pierre et Marie Curie, 7 Quai St. Bernard 75005, Paris, France.

² CNRS ENS, UMS 3194, CEREEP – Ecotron IleDeFrance, Ecole Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours.

Titre court : Conséquences démographiques des effets cohortes

Référence : Mugabo, M. & Le Galliard, J.-F. 2011. « Mechanisms of cohort effects and their consequences for population dynamics ». Manuscrit en préparation pour soumission à *Proceedings of the Royal Society B-Biological Sciences*.

RÉSUMÉ

Des effets cohortes surviennent dans les populations quand la variation des conditions environnementales produit des différences entre des cohortes entières d’individus (c’est-à-dire groupes d’individus nés pendant le même épisode de reproduction). Deux grands groupes d’effets cohortes ont été identifiés par les écologistes des populations. Premièrement, la variation environnementale peut générer des effets cohortes numériques directs en produisant une importante variation des taux de survie et des trajectoires de croissance des nouveaux-nés et donc du recrutement. Deuxièmement, la variation environnementale produit des effets cohortes qualitatifs décalés quand les conditions passées expérimentées par les cohortes ont des effets prolongés sur leurs performances démographiques. Les effets cohortes peuvent affecter de manière substantielle la dynamique des populations à travers leur influence sur la variation d’histoire de vie et sur la structure de population. Ces effets démographiques peuvent impliquer des effets environnementaux directs sur la variation d’histoire de vie (c’est-à-dire des facteurs densité indépendants) et/ou des effets indirects sur l’intensité de la compétition intraspécifique (c’est-à-dire des facteurs densité dépendants) via des interactions sociales symétriques et asymétriques. Au cours des dernières décennies, des effets cohortes numériques et qualitatifs ont été décrits chez de nombreuses espèces. Cependant, leurs mécanismes sous-jacents et leurs conséquences pour la dynamique des populations restent souvent inexplorés. Nous présentons ici les routes potentielles d’influence des effets cohortes pour la structure d’histoire de vie et la dynamique des populations. Ensuite, nous examinons de manière critique les études et les cadres théoriques utilisés pour quantifier les conséquences démographiques des effets cohortes à travers des mécanismes densité indépendants et densité dépendants.

Mots-clés : variation cohorte, histoire de vie, densité indépendance, densité dépendance, compétition asymétrique, dynamique de population.

Mechanisms of cohort effects and their consequences for population dynamics

Marianne Mugabo,¹ & Jean-François Le Galliard,^{1,2}

¹ CNRS UPMC ENS, UMR 7625, Laboratoire Ecologie et Evolution, Université Pierre et Marie Curie, 7 Quai St. Bernard 75005, Paris, France.

² CNRS ENS, UMS 3194, CEREEP – Ecotron IleDeFrance, Ecole Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours.

Running title: Demographic consequences of cohort effects

Reference: Mugabo, M. & Le Galliard, J.-F. 2011. Mechanisms of cohort effects and their consequences for population dynamics. Manuscript in preparation for submission to the *Proceedings of the Royal Society B-Biological Sciences*.

ABSTRACT

Cohort effects arise in populations when variation in environmental conditions produces differences among entire cohorts of individuals (i.e., group of individuals born during the same reproductive pulse). Two broad kinds of cohort effects have been identified by population ecologists. First, environmental variation can generate direct numerical cohort effects by producing an important variation in survival rates and growth trajectory of newborns and thus in recruitment. Second, environmental variation can give rise to delayed quality cohort effects when past conditions experienced by cohorts have long-lasting effects on their demographic performances. Cohort effects have the potential to substantially affect population dynamics through their influence on life-history variation and population structure. These demographical effects can involve direct environmental effects on life-history variation (i.e., density-independent factors) and/or indirect effects on the intensity of intraspecific competition (i.e., density-dependent factors) through symmetric and asymmetric social interactions. Over the last decades, numerical and quality cohort effects have been described in a large set of species. However, their underlying mechanisms and consequences for population dynamics often remained unexplored. Here we present the potential routes of influence of cohort effects for life-history structure and population dynamics. Then, we critically review case studies and model frameworks used to quantify the demographic consequences of cohort effects through density-independent and density-dependent mechanisms.

Keywords: cohort variation, life history, density independence, density dependence, asymmetric competition, population dynamics.

The relevance of cohort effects in wild populations of plants and animals

Variation among individuals is ubiquitous in nature and can affect the life-history traits (e.g., survival, growth, or reproduction) that determine the growth and dynamics of populations (Benton et al., 2006). In particular, cohort effects emerge when environmental factors generate life history variation among entire birth cohorts, i.e., groups of individuals born during the same breeding pulse (Beckerman et al., 2003, Gaillard et al., 2003, Lindström, 1999). Climate conditions, population density, resource availability and habitat quality are key environmental factors causing cohort effects in plant and animal populations (e.g., Albon et al., 1987, Forchhammer et al., 2001, Reid et al., 2003, Roach, 2003). For instance, the life history of female red squirrels varies between cohorts due to differences in food availability, population density and temperature experienced during birth year (Descamps et al., 2008).

Two broad categories of cohort effects have been identified in nature. First, variation in environmental conditions during development can cause variation in the survival and growth trajectory of individuals prior to sexual maturation. These effects generate variable recruitment rates among cohorts and have therefore been called direct numerical cohort effects or numerical effects (Gaillard et al., 2003). Numerical cohort effects are extremely widespread in animal and plant populations (e.g., in reptiles, Le Galliard et al., 2010, mammals, Wittmer et al., 2007, birds, Reid et al., 2003, and plants, Roach, 2003). For instance, most populations of wild ungulates studied to date exhibit significant variation in juvenile survival between birth cohorts (reviewed in Gaillard et al., 2003). Second, environmental conditions may also lead to long-lasting differences in the performances or quality of individuals among cohorts that can be transmitted to the next generations through parental environmental effects (e.g., Plaistow et al., 2006, Marquis et al., 2008). These long-lasting environmental effects have been called delayed quality cohort effects or quality effects (Gaillard et al., 2003). Most attempts to characterize quality effects have focused on early life conditions (e.g., Lindström, 1999, Forchhammer et al., 2001, Mugabo et al., 2010) but quality effects can also arise from environmental conditions experienced late in life after sexual maturation (Beckerman et al., 2003, Mugabo et al., 2011).

Table 1. Empirical evidence of numerical (NE) and quality (QE) cohort effects (CE) in a reptile, three ungulate, a rodent and a bird species. Breeding success refers to the total number of offspring produced during the reproductive life.

Species	CE	Life-history traits	Environmental factors	Effect	Location	Ref.	
Common lizard <i>Zootoca vivipara</i>	NE	Juvenile growth	Rainfall when <i>in utero</i>	+	Mont Lozère (France)	1	
			Rainfall during the first month of life	-			
		Body size at one year old	Unknown				
		Early juvenile survival	Rainfall when <i>in utero</i>	+			
			Yearling survival	Unknown			
			Yearling growth	Temperature during the juvenile stage	+		
	QE	Body size at two years old		Temperature during the juvenile stage	+		
			Adult growth	Unknown			
Adult body size			Unknown				
Parturition date			Unknown				
Roe deer <i>Capreolus capreolus</i>	NE	Summer survival of fawns	Population density	-	Chizé & Trois	2	
			Rainfall in spring	+	Fontaines (France)		
	QE	Annual breeding success	Population density	-	Trois Fontaines		
Red deer <i>Cervus elaphus</i>	NE	Male calf winter survival	Density of females	-	Isle of Rum (Scotland)	3	
		Male yearling survival	Cohort mean birth date	-			
	QE	Male adult survival	Population density of females	+			
			Cohort mean birth date	+			
	Male lifetime breeding success	Rainfall during the spring of birth year	+				
Soay sheep <i>Ovis aries</i>	NE	Juvenile survival	Population density & climate when <i>in utero</i> *	-	St Kilda archipelago (Scotland)	4	
		Age at maturity	Population density & climate when <i>in utero</i> *	-			

Table 1. (continued)

Species	CE	Life-history traits	Environmental factors	Effect	Location	Ref.
Soay sheep	QE	Adult survival	Climate when <i>in utero</i> *	+		4
<i>Ovis aries</i>			Population densities when <i>in utero</i> & after birth	-		
		Lifetime Breeding success	Climate when <i>in utero</i> *	+		
			Timing of first reproduction	-		
		Birth weight, birth date, litter size	Population density & climate when <i>in utero</i> *	-		
Red squirrel <i>Tamiasciurus hudsonicus</i>	NE	Early juvenile survival	Food availability at birth	+	Kluane Lake area (Canada)	5
		Juvenile growth				
	QE	Lifetime breeding success	Population density at birth	-		6
		Longevity	Population density at birth	-		
		Annual survival	Population density at birth	-		
		Annual breeding success	Food availability at birth	+		
			Spring temperature during birth year	+		
		Body mass at maturity	Yearling food availability	+		
			Population density at birth	-		
Red-billed chough <i>Pyrrhocorax pyrrhocorax</i>	NE	Juvenile & yearling survival	Quality of natal habitat**	+	Island of Islay (Scotland)	7
		Recruitment				
	QE	Age at first breeding	Population density at maturity	-		
		Breeding longevity	Quality of natal habitat**	+		
		Breeding success in 3-year old males	Quality of natal habitat**	+		
		Lifetime breeding success	Quality of natal habitat**	+		

* The climate was estimated by the annual winter state of the North Atlantic Oscillation, NAO.

** The mean population breeding success was used as an index of habitat quality. It increased with temperature during late summer and decreased with late winter rainfall prior breeding.

1. (Le Galliard et al., 2010); 2. (Gaillard et al., 2003); 3. (Rose et al., 1998); 4. (Forchhammer et al., 2001); 5. (Humphries & Boutin, 2000); 6. (Descamps et al., 2008); 7. (Reid et al., 2003).

A precise quantification of cohort effects in nature requires the long-term monitoring of known-age individuals and the identification of relevant environmental factors (Descamps et al., 2008, Gaillard et al., 2003, Le Galliard et al., 2010). An increasing number of studies documented the occurrence of both numerical and quality cohort effects and some of the mechanisms driving cohort effects have been uncovered (Table 1). Yet, the demographical consequences of cohort effects for populations in variable environments have not been summarized previously. We argue that cohort effects have the potential to affect population dynamics through two non-exclusive sets of mechanisms and thus can give rise to complex patterns of demographic variation (Beckerman et al., 2002, Benton et al., 2006). First, in stochastic environments, cohort variation, autocorrelation and covariation in life-history variation influence the mean stochastic population growth through density-independent processes (Caswell, 2001, Tuljapurkar, 1990). Second, any variation in the number and quality of individuals among cohorts can influence social interactions and thus density-dependent population dynamics (Beckerman et al., 2002, Lindström & Kokko, 2002, Claessen et al., 2000, Webster, 2004). These density-dependent cohort effects can involve symmetric social interactions between individuals with similar competitive abilities from the same birth cohort, i.e., intracohort competition, or from different birth cohorts, i.e., intercohort competition (Beckerman et al., 2003, Lindström & Kokko, 2002). Importantly, however, density-dependent cohort effects usually involve asymmetric social interactions between individuals differing in their competitiveness and belonging to different cohorts, such as cannibalism and exploitative competition among different sized individuals (e.g., Claessen et al., 2000, Persson et al., 1998). The aims of this review are (i) to describe the density-independent and density-dependent demographic effects of cohort variation and (ii) to critically discuss case studies and model frameworks that have been used to investigate these demographic effects.

Cohort effects: pathways from environmental variation to demographic variation

Cohort variation, covariation and autocorrelation of life-history traits

Numerical and quality effects can influence life-history variation and therefore stochastic population dynamics through density-independent mechanisms. For example, cohort variation in pre-breeding survival leads to temporal variation in recruitment and age-structure that decreases the mean of population growth rate in stochastic environments (Tuljapurkar, 1990).

More generally, cohort effects imply cohort variation and also potential covariation of demographic traits and individual autocorrelation, which can all affect the mean of population growth in stochastic environments (Box 1, Haridas & Tuljapurkar, 2005, Pfister & Stevens, 2003, Doak et al., 2005, Tuljapurkar et al., 2009).

Box 1. Stochastic population dynamics: population growth in variable environments

Population matrix models predict that temporal variation in vital rates influences the fitness of individuals and the stochastic population growth rate, defined as the long-run growth rate of a population in a temporally varying environment (Tuljapurkar, 1990). For iid environments (i.e., no between-year correlation in vital rates) and a small temporal variability, the log of the stochastic growth rate can be approximated by

$$\log \lambda_s \approx \log \lambda_1 - \frac{V(\log \lambda_1)}{2\lambda_1^2} \quad (1),$$

where λ_1 is the dominant eigenvalue of the average projection matrix and $V(\log \lambda_1)$ is the variance of $\log \lambda_1$ (Tuljapurkar, 1990, Caswell, 2001). Equation (1) can also be written as a function of elasticities of λ_s with respect to the variability of matrix elements

$$\log \lambda_s \approx \log \lambda_1 + \frac{1}{2} T^\sigma \quad (2),$$

where T^σ is the sum of the elasticities of λ_s for each matrix element and is always negative (Haridas & Tuljapurkar, 2005). From this equation, we can conclude that an increase in temporal variability of a matrix element will lead to a proportional decrease in the log stochastic growth rate. These equations can be used to predict the demographic consequences of numerical cohort effects for the stochastic growth rate. However, it is more difficult to predict the consequences of delayed quality effects, since they give rise to correlations between vital rates within years and to between-year correlations (i.e., autocorrelation) within cohorts (see the main text). The negative demographic effects of temporal variance are increased in the presence of positive correlations between vital rates, whereas a positive autocorrelation can either decrease or increase the stochastic growth rate (Doak et al., 2005, Tuljapurkar et al., 2009).

Substantial cohort variation of demographic traits is often predicted to arise from environmental conditions experienced early in life (Lindström, 1999, Metcalfe & Monaghan, 2001, Gaillard et al., 2003). The reason is that environmental conditions experienced during development can have organizational effects on physiological and morphological

determinants of life-history traits, while environmental conditions late in life have activational effects (Lindström, 1999, Forchhammer et al., 2001, Monaghan, 2008). However, variation in environmental conditions experienced by mature stages can also have long-lasting and intergenerational effects, as demonstrated in experimental populations of soil mites (Beckerman et al., 2003, Plaistow et al., 2006) and in natural and experimental populations of common lizards *Zootoca vivipara* (Marquis et al., 2008, Mugabo et al., 2011).

A particular type of quality cohort effects, called the “silver spoon effect” (Grafen, 1988), implies that individuals born under favourable conditions maintain advantages during their entire life compared to individuals born under adverse conditions, whatever the subsequent environmental conditions (Albon et al., 1987, Grafen, 1988, Madsen & Shine, 2000, Plaistow et al., 2006). Silver spoon effects induce marked positive individual autocorrelation of life-history traits throughout life and positive cohort covariation among traits – this results in strong temporal variation in population growth rate (Reid et al., 2006, Zuidema et al., 2009). A silver spoon effect has been reported for growth trajectories and adult body size of water pythons in response to prey availability early in life (Madsen & Shine, 2000). Because body size influence many aspects of life history such as metabolism, foraging capacities, reproduction and survival (e.g., Kooijman, 2000, Bystrom & Garcia-Berthou, 1999, Mugabo et al., 2010), temporal variation in prey abundance during development is expected to produce positive covariation between growth rate and traits determining fitness (e.g., age at first reproduction, fecundity, number of mates, longevity, etc). Cohort covariation among life history traits can also be due to shared environmental plasticity between life-history traits (Albon et al., 2000, Coulson et al., 2005, Doak et al., 2005). For instance, the contribution of changes in birth rate and adult winter survival to the variance in population growth rate was reinforced by positive covariations between these variables and between calf winter survival and these variables in a population of red deer (Albon et al., 2000).

Patterns of cohort variation and covariation can be complicated by additional developmental and life history mechanisms. Physiological trade-offs between life-history traits (e.g., between current fecundity and future survival) may occur and compensatory responses may be observed when environmental conditions improve (Metcalf & Monaghan, 2001). These individual responses can buffer the delayed life-history effects or may even lead to negative covariation among life-history traits, thus weakening the demographic consequences of cohort effects. Moreover, because compensatory responses can be costly (reviewed in Metcalfe & Monaghan, 2001), cohort effects induced by environmental

conditions may lead to complex pattern of autocorrelation and cohort covariation among life-history traits. For example, temporarily harsh conditions early in life may reduce growth and survival, but be followed by growth compensation later in life together with reduced adult survival. Furthermore, the sensitivity of one life-history trait to the environment can change throughout life (Coulson et al., 2001, Benton et al., 2006, Beckerman et al., 2003) or from one generation to the next (Plaistow et al., 2006). In the common lizard *Zootoca vivipara*, a food deprivation at the juvenile stage had long-term positive effects on immunocompetence (Mugabo et al., 2010) whereas a food deprivation later in life had immunosuppressive effects (Mugabo et al., 2011). Also, the persistence of delayed life-history effects may be modulated by an interaction between past and current environmental effects (Monaghan, 2008 and references therein). In water pythons, the magnitude of the silver spoon effect on growth trajectories and adult body size varied with the current food availability. Therefore, past and present conditions contributed similarly to variations in growth and body size (Madsen & Shine, 2000). In other species, current environmental conditions may override delayed life-history effects (e.g., in a plant, Weiner et al., 1997, and in a small rodent, Ergon et al., 2001).

Heterogeneity among individuals within a birth cohort can also affect demographic variation. The most frequent situation arises from sexual differences in sensitivity to environmental conditions because of sex-specific energetic requirements or physiological costs (Lindström, 1999, Coulson et al., 2001). In sexually dimorphic ungulates, numerical and quality effects were more pronounced for males than for females. For instance, cohort variation in breeding success was more than three times greater among cohorts of males than among cohorts of females (Rose et al., 1998). Another important source of intracohort life-history variation arises from maternal effects with known consequences for demographic traits (Benton et al., 2008). Therefore, intracohort heterogeneities could modulate the consequences of cohort effects for population dynamics.

Cohort effects and density dependence: symmetric interactions

Density dependence can stabilize or destabilize population dynamics. Population models have shown that the shape of the relationship between population growth rate and density has strong effects on population dynamics (e.g., reviewed in Henle et al., 2004, Sibly et al., 2005). We envision three different ways by which cohort effects affect density dependence through symmetric social interactions. First, in a stochastic environment, numerical cohort effects due to environmental fluctuations (e.g., climate conditions) change the number of individuals within cohorts, which modifies the intensity of immediate or future density dependence.

Second, even in the absence of stochastic environmental fluctuations, population density itself may induce numerical and quality cohort effects, leading to delayed density dependence (Beckerman et al., 2002). Indeed, in stage-structured populations, the time needed for newborns to recruit give rise to time lags of the length of immature stages in the response of population growth to a modification of population density. For instance, in the white-tailed deer, recruitment rate respond to a change in density with a 3-year lag (Fryxell et al., 1991). Furthermore, density at birth may have long-lasting effects on the performances of reproductive individuals. For instance, Pettorelli *et al.* (2002) demonstrated in two natural populations of roe deer that the density experienced by individuals during their first year of life induced marked differences of body mass among adults belonging to different birth cohorts. This delayed density dependence of adult body mass is likely to influence population growth since body mass is a critical factor determining survival and reproduction in ungulates (e.g., Clutton-Brock, 1988, Gaillard et al., 1997). In *Daphnia*, exposure to chemical clues of population density during the early development changed their age at maturity and fecundity, with observed consequences for the population growth rate (Carvajal-Salamanca et al., 2008).

Third, conditions experienced early in life can influence the quality of individuals and therefore their sensitivity to population density (Beckerman et al., 2002, Lindström & Kokko, 2002, Plaistow et al., 2006). This mechanism generates a situation where the current density dependence is influenced by environmental conditions experienced in the past (Lindström & Kokko, 2002). For instance, Beckerman *et al.* (2003) demonstrated in soil mites that the density dependence of fecundity was influenced by rearing food conditions but only at low and moderate adult densities. This illustrates the fact that past and present conditions can also interact to determine the strength of density dependence. Thus, it can prove difficult to disentangle the exact mechanisms of population regulation and density dependence without proper assessments of cohort effects.

Cohort variation and density dependence: asymmetric intercohort interactions

Asymmetric competition between cohorts of a population occurs when (i) cohorts share limited resources (e.g., food, space, etc.), and (ii) individuals from different cohorts differ in their competitive abilities to access and exploit shared limited resources (Webster, 2004). In general, competitive ability depends on foraging efficiency and energetic requirements for maintenance, structural growth and reproduction, which are both strongly related to body size (Bystrom & Andersson, 2005, Kooijman, 2000, Persson et al., 1998 and references therein). It is therefore expected that asymmetric competition between cohorts depends on the resource

availability and the size distribution of competitors (de Roos et al., 2003, Claessen et al., 2000). Consequently, in size-structured populations, cohort effects could influence the intensity and the outcome of intercohort asymmetric competition through (i) effects on body size, (ii) effects on the number of individuals in each cohort, as well as through (iii) population feedbacks on resource availability (Claessen et al., 2000, de Roos et al., 2003, Mugabo et al., 2010, Persson et al., 1998).

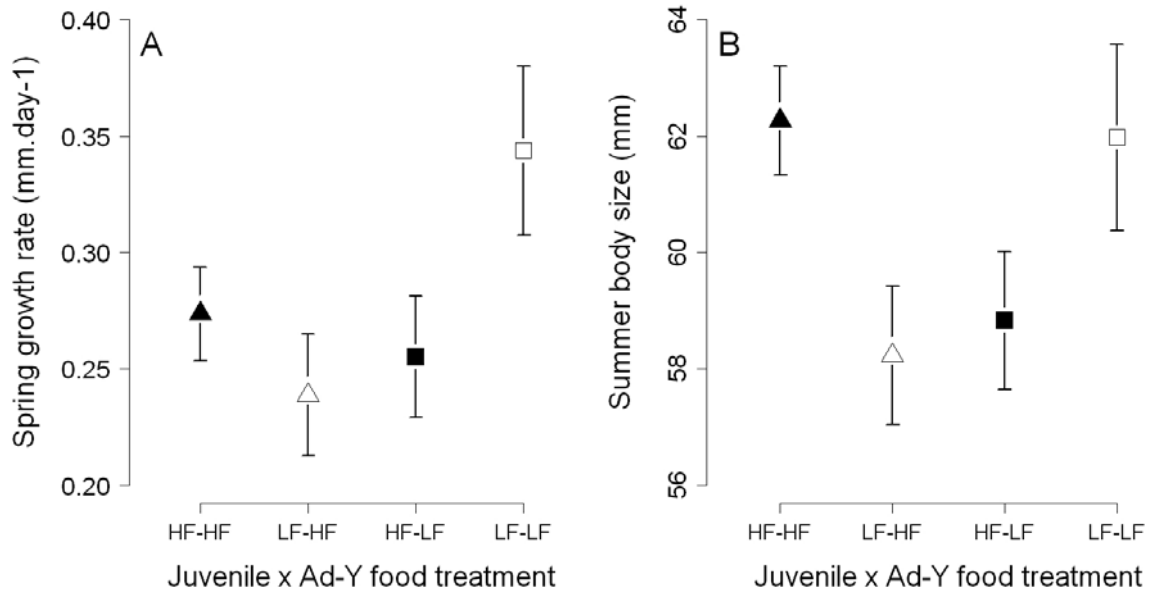


Figure 1. Delayed effects of a food deprivation early in life on spring juvenile growth rates and summer body size at the yearling stage in common lizards (*Zootoca vivipara*). We manipulated food availability in the laboratory for juveniles immediately after birth and for yearlings and adults. Individuals were either fully fed (treatment “High Food”) or food deprived (treatment “Low food”) and were then released in outdoor enclosures following a fully-crossed factorial design: juveniles from the same food treatment were released with fully fed or with food deprived yearlings and adults (i.e., 4 groups of experimental populations). Experimental populations were then monitored during the following two years. Estimates are given as mean growth rate and body size (\pm s.e.) per group. HF: High Food treatment, LF: Low food treatment; Ad: adult, Y: yearling. After Figure 3 in (Mugabo et al., 2010).

Models exploring these forms of density dependence usually distinguish exploitative from interference competition as they can lead to contrasted population dynamics (Claessen et al., 2000, Claessen et al., 2002, Persson et al., 1998). The former involves indirect interactions between competitors through the exploitation and depletion of a shared resource, whereas the latter involves direct interactions between competitors (e.g., cannibalism Bystrom & Garcia-Berthou, 1999, Persson et al., 2000). Empirical and theoretical studies have emphasized the importance of asymmetric competition between cohorts for life-history variation and population dynamics (e.g., Bystrom & Andersson, 2005, Claessen et al., 2000, Claessen et al.,

2002, Persson et al., 1998). However, very few studies have investigated the influence of stochastic environments on the outcome of asymmetric intercohort competition. Recently, we demonstrated in age-structured populations of common lizards that food conditions experienced by individuals had delayed effects on life history involving both direct effects of food availability through individual quality and indirect effects through intercohort interactions (Mugabo et al., 2010, Mugabo et al., 2011). Food deprivation in one cohort had delayed effects on growth rates, body size and survival that varied from positive to negative depending on food conditions experienced by another cohort. For instance, in the presence of fully fed yearlings and adults, fully fed juveniles maintained their body size advantages over food deprived juveniles, whereas in the presence of food deprived yearlings and adults, food deprived juveniles displayed overcompensatory growth and reach a larger body size at the yearling stage than fully fed juveniles (Mugabo et al., 2010, Figure 1). Thus, environmental fluctuations can interact with asymmetric social interactions to shape patterns of life history and population dynamics in size-structured populations.

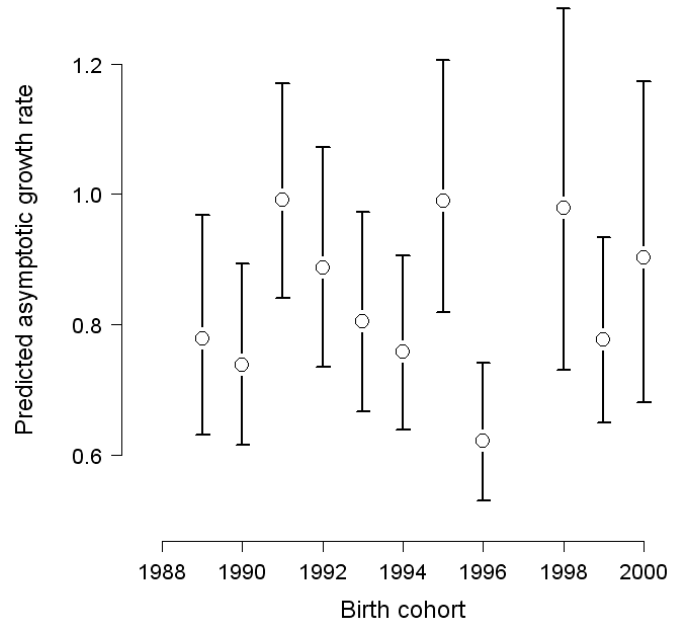
Cohort effects: quantifying demographic consequences

Density-independent mechanisms

To our knowledge, three empirical studies have quantified the consequences of cohort effects for density-independent population growth (Gaillard et al., 2003, Le Galliard et al., 2010, Wittmer et al., 2007). These studies used age-structured projection matrix models to identify the demographic rates that have the strongest influence on population dynamics (Caswell, 2001). Despite contrasted model species (an ungulate and a small viviparous lizard with stable dynamics, and a small predatory mammal with cyclic dynamics), two similar conclusions were reached. First, significant cohort variation in asymptotic growth rates were found in all cases (e.g., in the common lizard, Figure 2). Second, population dynamics were generally more affected by numerical effects, i.e., variation in early survival rates, than by delayed quality effects, i.e., variation in fecundity rates or in survival rates in mature individuals. For instance, in the roe deer, generation time was 1.4 lower in good cohorts than in bad cohorts due to much lower recruitment in poor cohorts (Gaillard et al., 2003). Likewise, in the common lizard, asymptotic growth rate was most sensitive to a change in juvenile annual survival, followed by adult and yearling annual survival and was weakly affected by a change in adult fecundity (Le Galliard et al., 2010). In the European stoat, the trend over the entire population cycle was a higher sensitivity of the asymptotic growth rate to changes in survival

rates, with the survival of immatures being more important than the survival of older individuals. However, the asymptotic growth rate was also sensitive to variation in fecundity of yearlings during some periods of the cycle (Wittmer et al., 2007).

Figure 2. Cohort variation in asymptotic growth rate of a population of common lizards (*Zootoca vivipara*) located in the Mont Lozère area in southern France (44°30’N, 3°45’E). For each combination of cohort-specific vital rates estimated from field data (i.e., annual juvenile, yearling and adult survival and fecundity), we calculated the mean and 95 % CI of the asymptotic growth rate using an age-structured matrix population model. After model and results in Le Galliard et al. (2010).



The use of projection matrix models parameterized with empirical observations provides some understanding of the density-independent consequences of cohort effects for population dynamics (Gaillard et al., 2003, Le Galliard et al., 2010, Wittmer et al., 2007). However, some limitations of this method must be recognized. The projection matrix models developed in these studies did not include any form of individual autocorrelation and covariation of demographic rates, which can arise from quality effects, and do not allow the calculation of the stochastic population growth rate. Yet, temporal variance, within-year correlation and between year correlations in life history traits can influence the stochastic population growth (Box 1). For instance, in a population of red deer, the contribution of numerical effects to variation in population growth rate was not always dominant when accounting for covariation between demographic rates (Albon et al., 2000). Pfister *et al.* (2003) and Coulson *et al.* (2005) demonstrated that projection matrix methods often provide a good approximation of the demographic rate(s) associated most strongly with variation in population growth. However, Pfister *et al.* (2003) also pointed out that size-structured matrix models are poor descriptors of the dynamics of populations characterized by a strong autocorrelation in individual growth rate. For instance, Zuidema *et al.* (2009) showed that

persistently fast-growing juvenile trees contributed up to 2.4 more to population growth than slow-growing trees.

Density-dependent mechanism: the case of symmetric competition

Only two studies attempted to estimate the consequences of cohort effects for density-dependent population dynamics through symmetric intraspecific interactions (Lindström & Kokko, 2002, Beckerman et al., 2003). Lindström & Kokko (2002) used a discrete time population model with overlapping generations. In this model, population growth at time t depends on survival and fecundity of individuals which are influenced by density at time t . Response to density is determined by the shape of density dependence, the quality of the year t and the quality of birth year. Hence, this model assumes differences in competitiveness at birth among cohorts with subsequent effects for density dependence. In a stable environment, the model predicts stable or unstable dynamics depending on the shape of density dependence. Interestingly, in stochastic environments, the cohort variation which arose from fluctuations of the quality of birth year had destabilizing effects for the dynamics of a stable population but stabilizing effects for the dynamics of an unstable population. Compared to variation of the quality of year t , cohort variation had a lower destabilizing effect on stable dynamics but had a higher stabilizing effect on unstable dynamics. Assuming a non-linear relationship between vital rates and density (i.e., concave or convex), the authors proposed that these dynamical effects of cohort variation were due to a linearization of the shape of density dependence in vital rates. More precisely, at low density, poor cohorts are disproportionately affected by an increase in density relative to good cohorts and thus their vital rates decrease rapidly with density. At high density, the opposite pattern is observed (Figure 3 for a convex shape of density dependence). As a consequence, the shape of average density dependence will be shallower in a population made-up of distinct cohorts than in an unstructured population (see Figure 3).

This model was tested by a combination of experimental and theoretical approaches in a laboratory soil mites system (Beckerman et al., 2003). Experiments provided clear demonstrations of the delayed density dependence involving both long-term life history effects of density and differences in quality among birth cohorts. A predictive model fitted to the data and life cycle of soil mites provided several insights about how past conditions experienced by cohorts may affect the density-dependent population dynamics. In accordance with Lindström and Kokko (2002), environmental variation led to a linearization of the shape of the relationship between the demographic rates of mites and the current density. On the

contrary, variation of the density at birth increased the non-linearity of density dependence for fecundity and recruitment. These two forms of delayed density dependence interacted and led to an overall destabilization of the dynamics of soil mite populations.

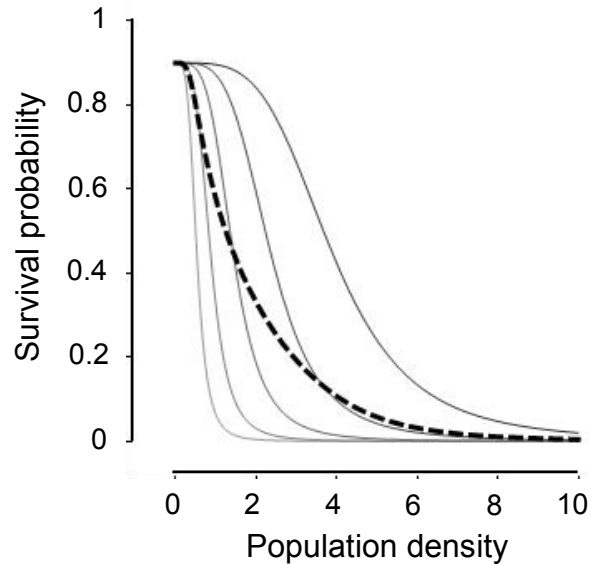


Figure 3. Effects of cohort variation on the density dependence of survival. Predicted curves were obtained from the population model developed by Lindström & Kokko (2002) in which survival of an individual from time t to time $t+1$ depends on the quality of its birth year i

following $p_{i,t} = \frac{p_0}{1 + (a_{i,t} \cdot N_t)^b}$ with $a_{i,t} = a_0 \exp\{-[\alpha \cdot q_i + (1 - \alpha)q_t]\}$, where p_0 is survival in

the absence of density dependence and N_t is population size at time t . $a_{i,t}$ specifies the strengths of density dependence which depends on the quality of birth year q_i and the quality of the year t q_t . The relative importance of the quality of the birth year and of year t is determined by the parameter α . b determines the shape of density dependence. Survival curves were calculated for $p_0 = 0.9$, $a_0 = 0.7$, $\alpha = 0.5$, $b = 4$, $q_t = 0$ and q_i varying from -2 to 2. The average shape of density dependence for a population composed of cohorts of different quality (i.e., mean $q_i = 0$) is represented by the dashed thick lines. A population without cohort variation and with the same mean quality ($q_i = 0$) would match the third thin curve.

Surprisingly, no other study published to date has been able to identify the particular form of delayed density dependence envisioned by Lindström and Kokko (2002), despite numerous studies on delayed life-history effects (e.g., reviewed in Beckerman et al., 2002, Pettorelli et al., 2002, Carvajal-Salamanca et al., 2008). Also, the conclusions about the density-dependent consequences of cohort effects for population dynamics may be highly model dependent (Lindström & Kokko, 2002). Yet, Beckerman *et al.* (2003) have shown that their conclusions were qualitatively robust to the introduction of age-structure in the model or to the addition of a time lag in density dependence. Finally, these models did not consider

intracohort variation in demographic rates. Consequently, they do not allow comparing the relative contribution of intracohort and intercohort variation to population dynamics which can both involve density-dependent mechanisms (Beckerman et al., 2002, Benton et al., 2006, Benton et al., 2008). For instance, it is known from a few populations that variation at the individual and maternal-level can contribute more to life history than cohort variation (e.g., Jones et al., 2005, Marquis et al., 2008).

Density-dependent mechanisms: the case of asymmetric competition

Studies investigating the consequences of asymmetric competition between cohorts for population dynamics have used stage-structured population models (e.g., Briggs et al., 2000) or physiologically structured population models (PSP models, e.g., Claessen et al., 2000, Claessen et al., 2002, and Persson et al., 1998). These models have been developed to explicitly link processes occurring at the individual level and at the population level in size-structured populations (de Roos et al., 2003 and references therein). At the individual level, vital rates are described as a function of the physiological state of individuals or *i*-state (e.g., size or stage). At the population level, the population state or *p*-state is represented by the distribution of individuals over the entire physiologically relevant *i*-state range (de Roos, 1997).

Persson *et al.* (1998) developed a PSP model to investigate the influence of the size scaling of the attack rate on population dynamics in a size-structured consumer-resource system. At the individual level, the model described foraging, metabolism, growth, mortality and reproduction as functions of the irreversible mass, the reversible mass of the individual (i.e., structural mass *versus* energy reserves) and the environment. Depending on the size scaling of the attack rate, juveniles had lower, higher or similar competitive abilities than adults. At the population level, the consumer-resource system assumed a coupled feedback loop between an unstructured prey population (zooplankton) and a size-structured predator population (a planktivorous fish). Resource density increased according to an intrinsic growth process and decreased with the size-dependent foraging of predators. Using this model, Persson *et al.* (1998) demonstrated that (i) differences in competitive abilities between size-classes give rise to cyclic population dynamics and that (ii) the characteristics of cycles depend on whether smaller or larger individuals are superior competitors. When juveniles had higher competitive abilities than adults, the foraging of juveniles decreased resource density below a starvation threshold for adults. As a consequence, population dynamics were characterized by regular juvenile-driven cycles. When juveniles and adults had similar

competitive abilities, i.e., no asymmetric competition, an equilibrium resource density was reached, allowing a stable coexistence of cohorts of juveniles and cohorts of adults. Finally, adult competitive dominance produced regular adult-driven cycles where most cohorts of juveniles were prevented to recruit through the depletion of resource density. In this population, adults did not starve to death and coexisted with the surviving cohorts of juveniles.

Several other similar studies predicted destabilizing effects of exploitative competition between cohorts for population dynamics (e.g., reviewed in de Roos et al., 2003). However, Persson *et al.* (1998) and Claessen *et al.* (2000) argue that size-dependent mortality can have a stabilizing effect on the dynamics of populations in the presence of asymmetric exploitative competition. For instance, size-dependent cannibalism can counteract the destabilizing effects of the juvenile competitive dominance in species where large cannibals share resources with their small victims. Claessen *et al.* (2000, 2002) showed that the stabilizing potential of cannibalism is determined by the lower limit of the range of prey size a cannibal of a given size can consume. For high values of the lower limit of this range, the predator population exhibited the same type of juvenile-driven cycles as described by Persson *et al.* (1998). Cannibals had a low influence on the density of newborns which depleted resources. At low values of the lower limit of this range, cannibalism regulated recruitment, allowing the coexistence of many cohorts and giving rise to stable cannibal-driven dynamics. Finally, at intermediate values, the interplay between size-dependent exploitative competition and size-dependent cannibalism gave rise to highly divergent life-history trajectories among large cohorts of dwarfs and small cohorts of giants. Consequently, population dynamics were alternatively driven by newborns and by cannibals producing regular dwarf-giant cycles. These predictions were supported by empirical data collected in natural populations of ontogenetic omnivorous fishes (Persson et al., 2000, Claessen et al., 2000, Claessen et al., 2002).

These theoretical studies have been extremely valuable to improve our understanding of size-dependent life history and population dynamics. However, an important drawback of PSP models lies in their large number of parameters and in their complexity (de Roos et al., 2003). In addition, most PSP models assumed that individuals belonging to the same cohort do not differ in their vital rates and were developed for constant environments (but see van Kooten et al., 2007). Recently, González-Suárez *et al.* (unpublished manuscript) developed PSP models based on the common lizard which included both intracohort and intercohort variation in vital rates. Models including intracohort life-history variation predicted similar

population dynamics than a standard PSP model without intracohort variation but provided new insights on the influence of intracohort individual variation on life history and population densities. In a consumer-resource system with exploitative competition and size-dependent cannibalism as the one studied by Classen *et al.* (2000, 2002), environmental stochasticity in resource density will introduce variation in the size distribution of competing cohorts. This can have major consequences for life-history trajectories and population dynamics since the size distribution of cohorts determines the intensity of intra and intercohort exploitative competition as well as the size-scaling of interactions between cohorts of cannibals and cohorts of newborns.

Conclusions

During the last decades, researches in ecology, evolutionary biology and population biology have brought a strong knowledge about the relationship between environmental conditions, life-history structure and population dynamics. Numerical and quality cohort effects, which correspond to a particular route between the environment and population dynamics, have been documented in a large number of species (e.g., Albon *et al.*, 1987, Descamps *et al.*, 2008, Gaillard *et al.*, 2003, Le Galliard *et al.*, 2010, Lindström, 1999). The combination of both forms of cohort effects has the potential to impact life history and population dynamics through direct and delayed density-independent and density-dependent phenomena (Albon *et al.*, 1987, Beckerman *et al.*, 2002, Benton *et al.*, 2006). Interactions between these different phenomena can give rise to complex patterns of variation of life history and population trajectories, thus hardening their identification and analysis (Mugabo *et al.*, 2010, Mugabo *et al.*, 2011). As a consequence, attempts to quantify the demographic consequences of cohort effects have been scarce and density-dependent and density-independent cohorts effects have been studied separately.

Yet, new insights about cohort effects have been obtained. Firstly, density-independent cohort effects are predicted to have more influence on population growth rate through numerical effects than through quality effects, at least in the three model species studied so far. Secondly, delayed density dependence arising from symmetric social interactions has the potential to either stabilize or destabilize population dynamics depending on the initial state of populations. Thirdly, asymmetric intercohort exploitative competition is predicted to destabilize dynamics whereas interference competition such as size-dependent cannibalism is predicted to have stabilizing effects. There is a real need to develop new models to study the additive and interactive effects of density-independent and density-

dependent cohort effects for population dynamics in structured populations. Physiologically structured population models, which explicitly link individual life history and population dynamics, provides the best framework to do so. Models of cohort effects should also include intracohort life-history variation in order to determine the relative importance of intracohort and intercohort variation for population dynamics in structured populations.

ACKNOWLEDGEMENTS

This research was supported by the Centre National de la Recherche Scientifique (CNRS), an Agence Nationale de la Recherche (ANR) grant (07-JCJC-0120) and a grant from the Région Île-de-France (Réseau de Recherche sur le Développement Soutenable R2DS 2007-006).

REFERENCES

- Albon, S. D., Cluttonbrock, T. H. & Guinness, F. E. 1987. Early development and population-dynamics in Red deer. 2. Density-independent effects and cohort variation. *Journal of Animal Ecology* **56**: 69-81.
- Albon, S. D., Coulson, T. N., Brown, D., Guinness, F. E., Pemberton, J. M. & Clutton-Brock, T. H. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. *Journal of Animal Ecology* **69**: 1099-1110.
- Beckerman, A., Benton, T. G., Lapsley, C. T. & Koesters, N. 2003. Talkin' 'bout my generation: environmental variability and cohort effects. *American Naturalist* **162**: 754-767.
- Beckerman, A., Benton, T. G., Ranta, E., Kaitala, V. & Lundberg, P. 2002. Population dynamic consequences of delayed life-history effects. *Trends in Ecology & Evolution* **17**: 263-269.
- Benton, T. G., Plaistow, S. J. & Coulson, T. N. 2006. Complex population dynamics and complex causation: devils, details and demography. *Proceedings of the Royal Society B-Biological Sciences* **273**: 1173-1181.
- Benton, T. G., St Clair, J. J. H. & Plaistow, S. J. 2008. Maternal effects mediated by maternal age: from life histories to population dynamics. *Journal of Animal Ecology* **77**: 1038-1046.
- Briggs, C. J., Sait, S. M., Begon, M., Thompson, D. J. & Godfray, H. C. J. 2000. What causes generation cycles in populations of stored-product moths? *Journal of Animal Ecology* **69**: 352-366.

- Bystrom, P. & Andersson, J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (*Arctic char*). *Oikos* **110**: 523-536.
- Bystrom, P. & Garcia-Berthou, E. 1999. Density dependent growth and size specific competitive interactions in young fish. *Oikos* **86**: 217-232.
- Carvajal-Salamanca, J. L., Aranguiz-Acuna, A., Ramos-Jiliberto, R. & Zuniga, L. R. 2008. Immediate and delayed life-history responses of *Daphnia ambigua* to conspecific cues. *Journal of Plankton Research* **30**: 1117-1122.
- Caswell, H. 2001. *Matrix population models*, 2 ed. Sinauer Associates, Sunderland.
- Claessen, D., de Roos, A. M. & Persson, L. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. *American Naturalist* **155**: 219-237.
- Claessen, D., Van Oss, C., de Roos, A. M. & Persson, L. 2002. The impact of size-dependent predation on population dynamics and individual life history. *Ecology* **83**: 1660-1675.
- Clutton-Brock, T. 1988. *Reproductive success*. The University of Chicago Press, Chicago.
- Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. & Grenfell, B. T. 2001. Age, sex, density, winter weather, and population crashes in soap sheep. *Science* **292**: 1528-1531.
- Coulson, T., Gaillard, J. M. & Festa-Bianchet, M. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. *Journal of Animal Ecology* **74**: 789-801.
- de Roos, A. M. (1997) A gentle introduction to physiologically structured population models. In: *Structured-population models in marine, terrestrial, and freshwater systems*, (Tuljapurkar, S. & Caswell, H., eds.) pp. 119-204. Chapman & Hall, New York.
- de Roos, A. M., Persson, L. & McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* **6**: 473-487.
- Descamps, S., Boutin, S., Berteaux, D., McAdam, A. G. & Gaillard, J. M. 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.
- Doak, D. F., Morris, W. F., Pfister, C., Kendall, B. E. & Bruna, E. M. 2005. Correctly estimating how environmental stochasticity influences fitness and population growth. *American Naturalist* **166**: E14-E21.
- Ergon, T., Lambin, X. & Stenseth, N. C. 2001. Life-history traits of voles in a fluctuating population respond to the immediate environment. *Nature* **411**: 1043-1045.

- Forchhammer, M. C., Clutton-Brock, T. H., Lindström, J. & Albon, S. D. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* **70**: 721-729.
- Fryxell, J. M., Hussell, D. J. T., Lambert, A. B. & Smith, P. C. 1991. Time lags and population fluctuations in white-tailed deer. *Journal of Wildlife Management* **55**: 377-385.
- Gaillard, J. M., Boutin, J. M., Delorme, D., VanLaere, 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., Loison, A., Toigo, C., Delorme, D. & Van Laere, G. 2003. Cohort effects and deer population dynamics. *Ecoscience* **10**: 412-420.
- Grafen, A. (1988) On the uses of data on lifetime reproductive success. In: *Reproductive Success*, (Clutton-Brock, T. H., ed.) pp. 454-471. University of Chicago Press, Chicago.
- Haridas, C. V. & Tuljapurkar, S. 2005. Elasticities in variable environments: Properties and implications. *American Naturalist* **166**: 481-495.
- Henle, K., Sarre, S. & Wiegand, K. 2004. The role of density regulation in extinction processes and population viability analysis. *Biodiversity and Conservation* **13**: 9-52.
- Humphries, M. M. & Boutin, S. 2000. The determinants of optimal litter size in free-ranging red squirrels. *Ecology* **81**: 2867-2877.
- Jones, O. R., Crawley, M. J., Pilkington, J. G. & Pemberton, J. M. 2005. Predictors of early survival in Soay sheep: cohort-, maternal- and individual-level variation. *Proceedings of the Royal Society B-Biological Sciences* **272**: 2619-2625.
- Kooijman, S. A. L. M. 2000. *Dynamic energy and mass budgets in biological systems*. Cambridge University Press, Cambridge.
- Le Galliard, J.-F., Marquis, O. & Massot, M. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology* **79**: 1296-1307.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* **14**: 342-348.
- Lindström, J. & Kokko, H. 2002. Cohort effects and population dynamics. *Ecology Letters* **5**: 338-344.

- Madsen, T. & Shine, R. 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.
- Marquis, O., Massot, M. & Le Galliard, J.-F. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. *Ecology* **89**: 2575-2583.
- Metcalf, N. B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution* **16**: 254-260.
- Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**: 1635-1645.
- Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. *Journal of Evolutionary Biology* **23**: 1886-1898.
- Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2011. Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. *Oecologia* **In press**.
- Persson, L., Bystrom, P. & Wahlstrom, E. 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology* **81**: 1058-1071.
- Persson, L., Leonardsson, K., de Roos, A. M., Gyllenberg, M. & Christensen, B. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology* **54**: 270-293.
- Pettorelli, N., Gaillard, J. M., Van Laere, G., Duncan, P., Kjellander, P., Liberg, O., Delorme, D. & Maillard, D. 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 B-Biological Sciences* **269**: 747-753.
- Pfister, C. A. & Stevens, F. R. 2003. Individual variation and environmental stochasticity: implications for matrix model predictions. *Ecology* **84**: 496-510.
- Plaistow, S. J., Lapsley, C. T. & Benton, T. G. 2006. Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. *American Naturalist* **167**: 206-215.
- Reid, J. M., Bignal, E. M., Bignal, D. I., McCracken, D. I. & Monaghan, P. 2006. Spatial variation in demography and population growth rate: the importance of natal location. *Journal of Animal Ecology* **75**: 1201-1211.

- Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. & Monaghan, P. 2003. Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology* **72**: 36-46.
- Roach, D. A. 2003. Age-specific demography in plantago: Variation among cohorts in a natural plant population. *Ecology* **84**: 749-756.
- Rose, K. E., Clutton-Brock, T. H. & Guinness, F. E. 1998. Cohort variation in male survival and lifetime breeding success in red deer. *Journal of Animal Ecology* **67**: 979-986.
- Sibly, R. M., Barker, D., Denham, M. C., Hone, J. & Pagel, M. 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science* **309**: 607-610.
- Tuljapurkar, S. 1990. *Population dynamics in variable environments*. Springer-Verlag, New York.
- Tuljapurkar, S., Gaillard, J. M. & Coulson, T. 2009. From stochastic environments to life histories and back. *Philosophical Transactions of the Royal Society B-Biological Sciences* **364**: 1499-1509.
- van Kooten, T., Persson, L. & de Roos, A. M. 2007. Size-dependent mortality induces life-history changes mediated through population dynamical feedbacks. *American Naturalist* **170**: 258-270.
- Webster, M. S. 2004. Density dependence via intercohort competition in a coral-reef fish. *Ecology* **85**: 986-994.
- Weiner, J., Martinez, S., Muller-Scharer, H., Stoll, P. & Schmid, B. 1997. How important are environmental maternal effects in plants? A study with *Centaurea maculosa*. *Journal of Ecology* **85**: 133-142.
- Wittmer, H. U., Powell, R. A. & King, C. M. 2007. Understanding contributions of cohort effects to growth rates of fluctuating populations. *Journal of Animal Ecology* **76**: 946-956.
- Zuidema, P. A., Brienens, R. J. W., During, H. J. & Guneralp, B. 2009. Do persistently fast-growing juveniles contribute disproportionately to population growth? A new analysis tool for matrix models and its application to rainforest Trees. *American Naturalist* **174**: 709-719.

CHAPITRE 2 – Effets de l’environnement nutritif précoce sur
l’histoire de vie dans des populations
structurées en cohortes

Effets immédiats et décalés d’une privation de nourriture précoce sur l’histoire de vie chez un lézard non-longévif

Marianne Mugabo *, Olivier Marquis *, Samuel Perret † & Jean-François Le Galliard *†

* CNRS UPMC ENS, UMR 7625 Ecologie et Evolution 75005 Paris France

† CNRS ENS, UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78
rue du Château, 77140 St-Pierre-lès-Nemours

Titre court : Effets d’une privation de nourriture sur l’histoire de vie

Référence : Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2010. « Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard ». *Journal of Evolutionary Biology* **23** : 1886-1898.

RÉSUMÉ

Les études détaillées des mécanismes responsables des réponses de l’histoire de vie à la disponibilité en nourriture sont de première importance pour comprendre l’évolution de la plasticité phénotypique et la capacité des organismes à produire des meilleurs phénotypes. La disponibilité en nourriture peut influencer les trajectoires d’histoire de vie à travers trois mécanismes non exclusifs : (i) des effets immédiats et décalés sur la qualité individuelle et des effets décalés indirects sur les interactions sociales (ii) intra-cohortes et (iii) inter-cohortes. Nous avons étudié chez le lézard vivipare (*Zootoca vivipara*) l’influence d’une privation de nourriture pendant les deux premiers mois de la vie sur l’histoire de vie (croissance, survie, reproduction) et les traits de performance (immunocompétence, performances locomotrices) jusqu’à l’âge adulte. Nous avons examiné les mécanismes sous-jacents et leurs possibles interactions en manipulant conjointement la disponibilité en nourriture chez une cohorte de nouveaux-nés et chez des cohortes de conspécifiques plus âgés. La privation de nourriture à la naissance a affecté la croissance de manière directe, immédiate et négative et l’immunocompétence de manière directe, décalée et positive. La privation de nourriture a également eu des effets indirects décalés sur la croissance, la taille corporelle, la survie précoce et la reproduction provoqués par une interaction entre ses effets directs sur la qualité individuelle et ses effets indirects sur l’intensité des interactions sociales entre cohortes. Ces effets ont été combinés à de la densité dépendance sur la taille corporelle. Ces résultats démontrent que les interactions entre les effets directs et sociaux des environnements passés influencent l’évolution de l’histoire de vie dans les populations structurées en taille et en stades.

Mots-clés : disponibilité de nourriture, effets cohortes, populations structurées en stades, densité dépendance, compétition asymétrique, compromis d’allocation, histoire de vie, traits de performance, *Zootoca vivipara*.

**Immediate and delayed life history effects caused by food deprivation early
in life in a short-lived lizard**

Marianne Mugabo *, Olivier Marquis *, Samuel Perret † & Jean-François Le Galliard *†

* CNRS UPMC ENS, UMR 7625 Ecologie et Evolution 75005 Paris France

† CNRS ENS, UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78
rue du Château, 77140 St-Pierre-lès-Nemours

Running title: Life history effects of food deprivation

Reference: Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. *Journal of Evolutionary Biology* **23**: 1886-1898.

ABSTRACT

Detailed studies of the mechanisms driving life history effects of food availability are of prime importance to understand the evolution of phenotypic plasticity and the capacity of organisms to produce better adapted phenotypes. Food availability may influence life history trajectories through three non-exclusive mechanisms: (i) immediate and long-lasting effects on individual quality, and indirect delayed effects on (ii) intra-cohort and (iii) inter-cohort interactions. Using the common lizard (*Zootoca vivipara*), we tested whether a food deprivation during the two first months of life influence life history (growth, survival, reproduction) and performance traits (immunocompetence, locomotor performances) until adulthood. We investigated the underlying mechanisms and their possible interactions by manipulating jointly food availability in a birth cohort and in cohorts of older conspecifics. Food deprivation had direct immediate negative effects on growth but positive long-lasting effects on immunocompetence. Food deprivation had also indirect delayed effects on growth, body size, early survival and reproduction mediated by an interaction between its direct effects on individual quality and its delayed effects on the intensity of inter-cohort social interactions combined with density dependence on body size. These results demonstrate that interactions between direct and socially-mediated effects of past environments influence life-history evolution in size- and stage-structured populations.

Keywords: food availability, cohort effects, stage-structured populations, density dependence, asymmetric competition, allocation trade-offs, life history, performance traits, *Zootoca vivipara*.

INTRODUCTION

Food availability early in life is a major factor of life-history variation that determines how individuals allocate energy among competing demands for growth, immunity, or maturation (Metcalf & Monaghan, 2001, Taborsky, 2006). In particular, food deprivation during development has both immediate effects on juvenile survival and growth and delayed effects on adult body size, survival, and reproductive performances (e.g., Madsen & Shine, 2000, Beckerman et al., 2003, Lindström, 1999). Thus, detailed studies of the mechanisms driving immediate and delayed effects of food availability are of prime importance to understand the evolution of plastic life history strategies and the capacity of organisms to produce better adapted phenotypes (Monaghan, 2008).

Currently, three potential mechanisms of delayed life-history effects have been identified. First, food availability can have direct, long-lasting effects on individual quality, including body size, body condition and immunity (Birkhead et al., 1999, Taborsky, 2006). An extreme form of long-lasting effects arises from “silver spoon effects”, when favourable early conditions lead to consistent fitness advantages throughout life (Grafen, 1988). Such silver spoon effects will affect the life-history trajectories of entire birth cohorts of individuals and lead to significant cohort effects (Lindström, 1999). For example, Madsen and Shine (2000) demonstrated that a high abundance of rats during the birth year results in cohorts of consistently larger water pythons. Second, food availability may change the number and body size of juveniles, and thus alter social interactions within a birth cohort (Beckerman et al., 2003). For example, poor nutritional conditions early in life may decrease juvenile survival and therefore lead to weaker density dependence at the adult stage (e.g., in a fish, van de Wolfshaar et al., 2008). Third, food availability can also influence social interactions between juveniles and older individuals. Competition, cannibalism or inhibition of sexual maturation between cohorts may in turn influence growth and maturation strategies, as demonstrated in fishes (Szabo, 2002, Aday et al., 2006, Claessen et al., 2000).

Delayed life-history effects of food availability experienced early in life are now documented in numerous animal species (e.g., Le Galliard et al., 2005, Madsen & Shine, 2000, Beckerman et al., 2003). Unfortunately, few studies have investigated the delayed effects of environmental variation on life-history trajectories through intra-cohort and inter-cohort interactions. Detailed laboratory experiments with soil mites indicate that rearing conditions during early development influence not only individual quality but also density

dependence at the adult stage (Beckerman et al., 2003). Asymmetric interactions between cohorts are also commonly seen in nature where they often result from size-dependent competition or predation (e.g., in fishes, Claessen et al., 2000, in lizards, Pafilis et al., 2009). Yet, despite the strong effects of food deprivation early in life on growth trajectories and therefore size-dependent behaviours (Monaghan, 2008), the influence of food availability on inter-cohort interactions remains to be investigated. In fact, little is known about how direct effects of food availability early in life and indirect effects mediated by social interactions combine to shape life-history trajectories (Beckerman et al., 2003). This is unfortunate because cohort interactions can strongly influence the dynamics of structured populations and the evolution of life history traits (Claessen et al., 2000, Claessen & Dieckmann, 2002, de Roos et al., 2003).

Here, we report a study of the immediate and delayed effects of food availability on life-history variation in the common lizard (*Zootoca vivipara* Jacquin 1787), a short-lived reptile (3-4 years life expectancy) with a plastic life history (Marquis et al., 2008). Typical immediate responses to malnutrition in this species include structural growth repression and reduced energy storage in body fat reserves (Avery, 1971, Le Galliard et al., 2005). Long-lasting direct effects of food deprivation on survival and reproduction may therefore be mediated by silver spoon effects on body size and stored energy (Massot et al., 1992, Le Galliard et al., 2005, Figure 1A). However, these direct effects may be buffered if individuals can compensate for a bad start when conditions subsequently improve (Metcalf & Monaghan, 2001, Birkhead et al., 1999). Animals with a continuous growth such as common lizards could in fact maintain the ability to compensate for poor early conditions over their entire life. Nevertheless, such compensatory responses may be associated with ecological and physiological costs (e.g., increase of predation risk or of metabolic rate, Anholt & Werner, 1998, Criscuolo et al., 2008) that could reduce survival and/or reproduction (Figure 1A).

Natural populations of the common lizard are characterised by substantial size variation, asymmetric competition between juveniles and older individuals, and strong density dependence (Massot et al., 1992). This implies that indirect effects involving density dependence within a cohort and inter-cohort interactions may influence life history plasticity to food availability early in life (Figure 1A). Firstly, high survival early in life in a favourable environment may lead to stronger density dependence and reduced performances at the adult stage. Secondly, asymmetric competition between cohorts may occur when food availability is limited and the niche overlapping between cohorts is substantial. Food deprived older conspecifics should therefore compete more strongly with juveniles than fully fed older

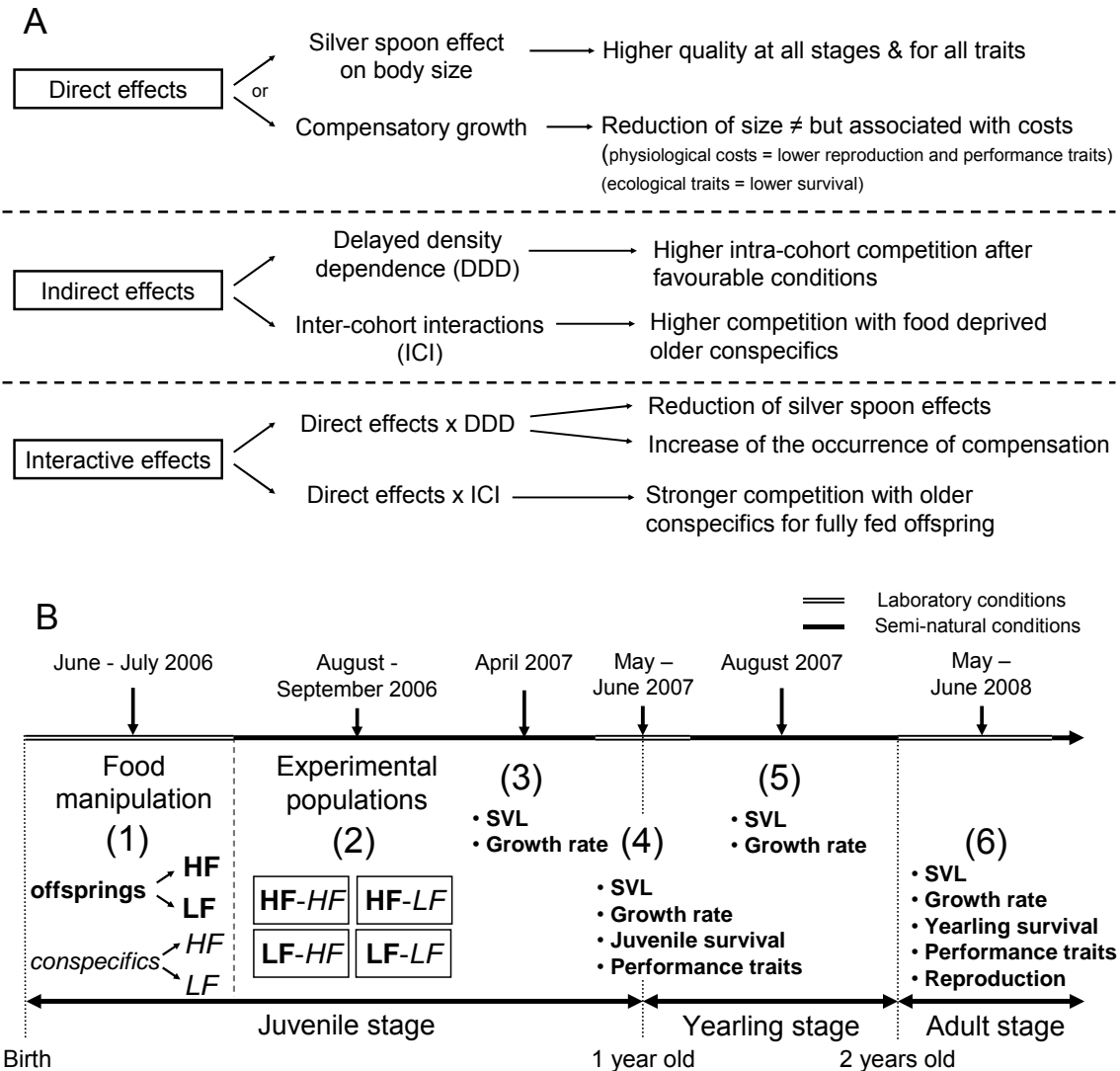


Figure 1. Predicted effects of food deprivation early in life on life history trajectories in the common lizard (A) and schematic representation of our experimental design (B). (A) Direct life history effects should cause lower performances of food deprived individuals, possibly buffered by compensatory growth responses throughout life. Such compensatory responses may involve physiological and ecological costs. Indirect effects through delayed-density dependence (DDD) are predicted if fully fed lizards have a higher juvenile survival than food deprived lizards. Inter-cohort interactions (ICI) are also predicted if food deprived conspecifics compete more with juveniles than fully fed conspecifics. Thus, direct effects of early food conditions may interact with delayed density dependence and with inter-cohort interactions if fully fed offspring are larger and compete more with older conspecifics. (B) During step 1, food deprivation was simulated in an entire birth cohort (offspring food treatment) and in cohorts of yearlings and adults (conspecific food treatment). After 50 days of laboratory manipulation (around August-September 2006), juveniles and conspecifics were released in 16 outdoor enclosures according to a fully-crossed factorial design (step 2). Life history traits were monitored in the cohort of offspring during four capture sessions carried out in April 2007 (step 3), May-June 2007 (step 4), August 2007 (step 5), and May-June 2008 (step 6). HF = high-food treatment group, LF = low-food treatment group.

conspecifics if they increase their food intake and/or prey on juveniles (Avery, 1971, Pafilis et al., 2009). In addition, large and fast-growing juveniles should be more sensitive to competition with older conspecifics than small and slow-growing juveniles due to a larger niche overlapping (Keren-Rotem et al., 2006). Asymmetric competition with older individuals should reduce body growth at the juvenile stage, size at maturation and reproductive outputs and may also reduce survival when social interactions are agonistic (Claessen et al., 2000, Pafilis et al., 2009). Thus, direct and indirect effects of early food conditions can interact to shape life-history trajectories of common lizards (Figure 1A).

We tested whether life history effects of food availability involved direct effects on individual quality and/or indirect effects by manipulating food availability during approximately two months in the laboratory for an entire birth cohort of offspring and for cohorts of older individuals (Figure 1B). Offspring from each food treatment were released in outdoor enclosures with food deprived or fully fed cohorts of older lizards in a fully-crossed factorial design. Experimental populations were monitored during two years and cohort densities were recorded. We compared the life histories of fully fed and food deprived offspring until adulthood according to their social environment. Several life-history traits (growth rates, body size, survival and reproductive performances) and two performance traits (immunocompetence and locomotor performances) were measured in males and females to evaluate the sensitivity of various demographic traits to food availability (Figure 1B). This experimental design enabled us to examine (i) direct immediate and delayed effects of early food conditions on individual quality, (ii) indirect effects by inter-cohort interactions and delayed density dependence within a cohort, and (iii) interactions between direct and indirect effects.

METHODS

Experimental design

From the 19th of June until the 13th of September 2006, we manipulated the daily food consumption in the laboratory of 460 juvenile lizards for 50 days from their day of birth. Offspring were fed with crickets *Acheta domesticus* obtained from Kreca Inc. (Ermelo, Holland). We used two food treatments, as in our previous studies (Le Galliard et al., 2004, Le Galliard et al., 2005). In the “high food” treatment (HF), individuals were fully fed with 100 mg.day⁻¹ of food, whereas individuals in the “low food” treatment (LF) were maintained under a food deprivation with a diet of 40 mg.day⁻¹. Prey items were weighed prior to feeding

and non-consumed prey was removed each week. Offspring were obtained from 42 gravid females captured in outdoor enclosures (CEREER, 48°17'N, 2°41'E; $n = 209$ offspring) and from 58 gravid females captured in two natural populations (Mont Lozère, 44°27'N, 3°44'E; $n = 251$). However, all lizards were from genetic strains originating from the same geographic area around the Mont Lozère. Immediately after birth, offspring were marked by toe clipping, sexed by counting ventral scales, measured for snout-vent length (SVL, to the nearest mm) and weighed (to the nearest mg). Clutches of offspring were split into two groups randomly assigned to each food treatment. Offspring food-treatment groups did not differ initially for SVL, body condition (residuals of a linear regression of body mass against body size) or sex ratios (ANOVA, all $P > 0.80$). To identify fathers, we performed microsatellite marker-based paternity analyses following the protocols described in Laloï et al. (2004). We used 5 highly polymorphic microsatellite loci (Lv-3-19, Lv-4-72, Lv-4-alpha, Lv-4-X and Lv-4-115, Boudjemadi et al., 1999) and carried out paternity assignments with a likelihood approach in the Cervus 3.0 software (<http://www.fieldgenetics.com/>). We could assign fathers to 202 offspring ($n = 21$ fathers and 41 mothers) in litters born from gravid females captured at CEREER but to no offspring from the natural populations since candidate fathers were not all sampled in natural populations.

At the same time, we also manipulated the daily food consumption of 263 older individuals for 50 days in the laboratory (144 yearlings and 119 adults; adults are ≥ 2 years old and sexually mature individuals, Figure 1B). We fed lizards with a combination of crickets and moth larvae (*Pyralis farinalis*). Food treatments for yearlings and adults (hereafter named “conspecific food treatments”) were adjusted according to food consumption data from the wild (Avery, 1971). Half of the individuals were fully fed with an average of 200 mg.day⁻¹ (HF treatment) and the remaining half were maintained under a food deprivation with an average of 100 mg.day⁻¹ (LF treatment). Animals were captured in outdoor enclosures (CEREER, $n = 214$) and in two natural populations (Mont Lozère, $n = 49$), and half of the animals of each origin were randomly assigned to each food treatment. The treatment groups did not differ initially for SVL, body condition or sex ratios (ANOVA, all $P > 0.45$) but body condition was significantly higher in the HF treatment after the manipulation ($F_{1,259} = 49.85$, $P < 0.0001$). Food manipulation for adult females started the day after parturition. The number of yearlings and adults starting the experiment each day was adjusted to the number of females in order to maintain the age and sex structure of each treatment.

At the end of the laboratory manipulation, lizards were measured for body size (SVL) and released into 16 outdoor enclosures each measuring 10 m by 10 m and located in a wet meadow at the CEREEP. We generated populations of lizards by mixing offspring from the same food-treatment group with yearlings and adults from a food deprived or a fully fed treatment group following a fully-crossed factorial design (Figure 1B). Offspring from the same clutch and food treatment were released into the same enclosure. Four outdoor enclosures were randomly selected for each treatment group and initial populations had similar age and sex structure (4-5 adult females, 3 adult males, 4-6 yearling females, 4-5 yearling males, 28-34 juveniles, juvenile sex ratio = 51 % of males \pm 2 s.e.). Outdoor enclosures provided lizards with natural food supplies, shelters and basking sites, and were protected by nets to avoid avian predation.

Measurements of life history traits

We monitored populations during four successive capture sessions each lasting 5-20 days to obtain data on growth, body size, survival and female reproductive performances in the cohort of offspring (Figure 1B). At each recapture, animals were measured for SVL, broken tail (intact vs. recently broken tail, used as an indicator of predation attempts, Pafilis et al., 2009) and ectoparasite load (number of ticks *Ixodes ricinus* around the neck and forelimbs, used to evaluate ectoparasite pressure, Moyer et al., 2002). Growth rates were calculated as the change in SVL divided by the time interval, calculated as the number of days elapsed between the initial measurement and the focal measurement minus the number of days spent in hibernation and emergence (assumed to be from the 1st of October 1 to the 15th of March). Because recapture probabilities are close to one in our experimental system, annual survival probabilities were estimated from recapture data at the juvenile stage (from release in summer 2006 to May 2007) and at the yearling stage (from May 2007 to May 2008). In late spring 2008, gravid females were maintained until parturition in the laboratory to assess their reproductive characteristics. We measured the quantity (total number of eggs) and quality (body size at birth) of the first generation (F1) of offspring born from manipulated females. In late spring 2007, 14 yearling females (8 HF and 6 LF) were obviously gravid upon capture but were not maintained in the laboratory because this would have changed their growth trajectories (Le Galliard, personal observation). We therefore could not include reproductive data from 2007 in our analyses.

Measurements of performance traits

We assessed immunocompetence and locomotor performances of manipulated offspring in late spring 2007 and 2008 (Figure 1B). Immunocompetence was estimated by measuring the delayed inflammatory response to the injection of the mitogen phytohaemagglutinine (PHA), which evaluates acquired T cell-mediated immunity characterised by a local T-cell proliferation (Tella et al., 2008). This procedure was preferred over alternative methods to measure innate and specific immunity that necessitate substantial blood samples. We injected all individuals ($n = 166$ in 2007 and 90 in 2008) subcutaneously in the right posterior leg with a solution of phosphate buffered saline (PBS, Sigma, reference D5773) containing 2.5 mg.mL^{-1} PHA (Sigma, reference L2880). We inject 0.04 mL in 2007 and 0.08 mL in 2008 to match the size increase of lizards from the yearling to the adult stage. Just before and 12 hours after the injection, we measured the thickness of the right posterior leg to the nearest 0.01 mm with a spessimeter (Mitutoyo ABSOLUTE ID-C1012BS, Japan). The inflammatory response was calculated as the difference in thickness of the leg (mm) between 12h after and before the injection. A larger value indicates a higher T cell-mediated immune response (Tella et al., 2008).

We also measured maximal sprint speed and endurance capacity at an optimal body temperature for locomotion ($31\text{-}33^{\circ}\text{C}$) and in a post-absorption state (after three days without food). Sprint speed measurements were done with a 3-meter long racetrack equipped with 12 pairs of photoreceptor cells, one pair placed every 0.25 m, to register running speed as described by Sorci et al. (1997). Maximal sprint speed was calculated from three successive trials separated by a minimum resting time of 30 minutes. Endurance capacity of the same individuals was measured with a motorised treadmill (Panlab LE 8700, Bioseb, France) as described by Le Galliard et al. (2004). Measurements were performed at a running speed of $7\text{-}8 \text{ m.s}^{-1}$ in 2007 and $8\text{-}11 \text{ m.s}^{-1}$ in 2008 to match the size increase of lizards and obtain data at ecologically relevant running speeds (Le Galliard et al., 2004). Pregnancy alters locomotor performances in the common lizard, so we measured the locomotor performances of 43 pregnant females after parturition in 2008.

Statistical analyses

We first analysed immediate effects of food availability on growth rate in SVL and SVL at the end of the experiment (hereafter named “final SVL”) with mixed-effects linear models. Fixed effects included offspring food treatment, sex, and their first-order interactions, as well

as additive effects of SVL at birth, date of birth and geographic origin of the mother. Clutch identity was included as a random effect influencing both the intercept and the food treatment effect. Next, we used similar models to study the delayed effects of food availability on life-history traits (growth rates in SVL, SVL and reproductive traits) and performance traits (immunocompetence, sprint speed and endurance capacity). These mixed-effects linear models also included (i) a conspecific food-treatment effect and its interaction with the offspring food-treatment effect to account for the food manipulation of older conspecifics, (ii) a fixed effect of the number of activity days since release when analysing SVL, (iii) a fixed effect of initial SVL when analysing growth rates to control for decelerating growth curves (Andrews, 1982) and second-order interactions between initial SVL and offspring and conspecific food treatment to test for context-dependent selection on growth rate. Locomotor performances increase with body size in the common lizard (Le Galliard et al., 2004, Sorci & Clobert, 1997). We therefore tested separately for the effects of treatments and the effects of body size on maximal sprint speed and endurance capacity. The random part of these models included an effect of enclosure identity, and, whenever necessary a clutch identity effect nested in the enclosure effect. Model parameters and test statistics were estimated with a restricted maximum likelihood approach in the *lme* procedure in R 2.9.2 software (<http://cran.r-project.org/>) as described by Pinheiro and Bates (2000). Minimum adequate models were selected by removing non-significant terms in a backward procedure using marginal F tests. Assumptions of normality were fulfilled but Bartlett tests detected variance heterogeneity between treatments and sexes in some analyses. We accounted for heterogeneous variances with a *varIdent* function in *lme* (chapter 5.2 in Pinheiro & Bates, 2000).

We analysed annual survival probabilities at the juvenile and yearling stages with mixed-effects logistic regressions including a logit link and binomial error terms. Models included fixed effects of offspring food treatment, conspecific food treatment, sex, and their first-order interactions, as well as additive effects of date of birth and geographical origin and a random enclosure effect. We tested for context-dependent selection on SVL by including in the models second-order interactions between initial SVL centred at its grand mean (linear and quadratic effects), offspring and conspecific food treatment. Model parameters were estimated with a Laplace approximation of the maximum likelihood in *lmer* and fixed effects were tested with Wald Z tests (Bolker et al., 2009). A minimum adequate model was obtained by backward elimination of non significant terms. All estimates are provided with standard errors unless otherwise stated.

RESULTS

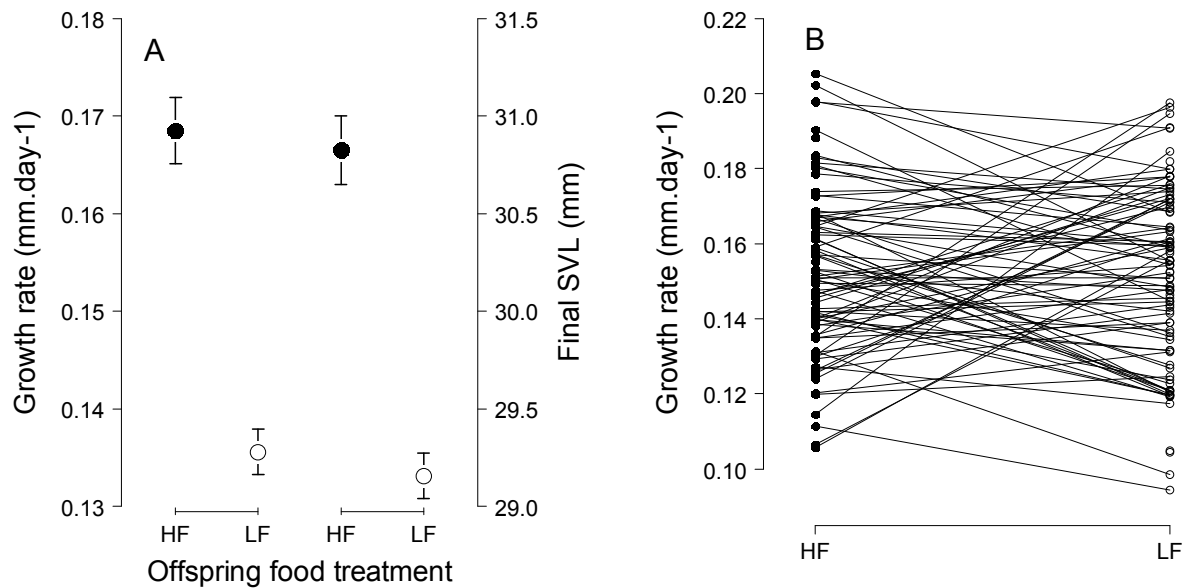


Figure 2. Immediate effects of offspring food treatment on growth rate and final SVL. (A) Mean (\pm s.e) growth rate (on the left) and final SVL (on the right) and (B) familial reaction norms for growth rate according to offspring food treatment. (B) Data are given as mean predicted growth rates per family and were obtained from the minimum adequate models selected (see main text).

Immediate effects

Food deprivation had immediate, negative effects on growth rate in SVL and final SVL (growth rate: $F_{1,357} = 77.77$, $P < 0.0001$; SVL: $F_{1,357} = 77.28$, $P < 0.0001$; Figure 2A), and variability in both traits was greater in the HF treatment group (growth rate: Bartlett’s K-squared = 41.97, $df = 1$, $P < 0.0001$, variance ratio = 1.59; SVL: Bartlett’s K-squared = 42.73, $df = 1$, $P < 0.0001$, variance ratio = 1.59, Figure 2A). Sex influenced growth rate and final SVL independently of food treatment (food treatment \times sex: all $P > 0.68$; sex: all $P = 0.02$). Growth rate and final SVL also varied significantly between clutches (growth rate: likelihood ratio test (LRT) = 53.85, $P < 0.0001$; SVL: LRT = 55.10, $P < 0.0001$).and, more importantly, growth sensitivity to food availability differed between clutches (growth rate: LRT = 5.95, $P = 0.05$; SVL: LRT = 6.58, $P = 0.04$). This was well illustrated by the crossing familial reaction norms for growth rate (Figure 2B). We investigated whether this variability could be explained by paternal effects in a sub-sample of offspring with known paternal lineage ($n = 202$), but this was not the case (LRT, all $P > 0.78$). Furthermore, the growth sensitivity to food treatment of a family was not correlated with mean offspring SVL at birth, birth date or clutch sex ratio (F tests, all $P \geq 0.10$).

Table 1. Analysis of growth rates of lizards (mm.day⁻¹) throughout their two first years of life according to the offspring (offsp.) food treatment, the conspecific (consp.) food treatment, sex, initial SVL, date of birth and the origin of the mother. Results in bold indicate significant effects. The F and P values were obtained by backward selection from the full models and LRT values were obtained for the minimum adequate model selected. Initial SVL refers to the SVL at the beginning of the studied period.

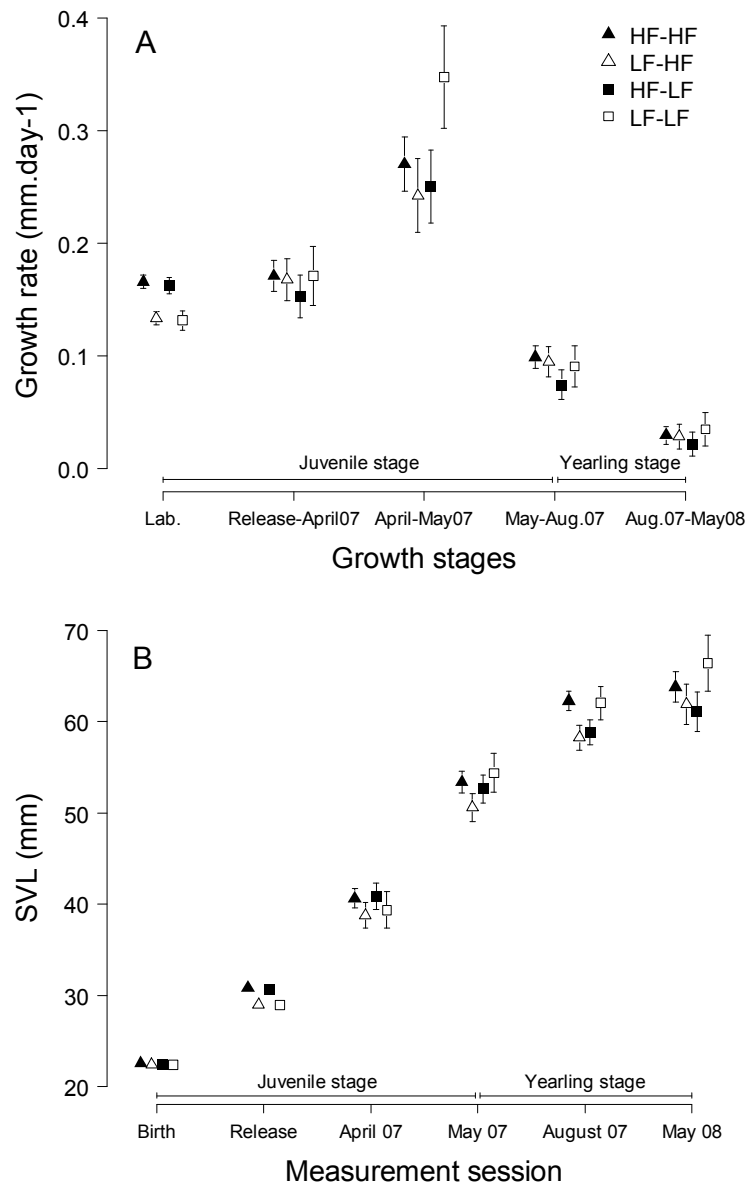
Effect	Release - April 07	April - May 07	May - August 07	August 07 - May 08
<i>Fixed effect</i>	<i>F</i> _{ndf,ddf}	<i>F</i> _{ndf,ddf}	<i>F</i> _{ndf,ddf}	<i>F</i> _{ndf,ddf}
Offsp. food treatment	F _{1,13} = 0.05	F _{1,12} = 1.96	F _{1,13} = 0.12	F _{1,14} = 0.22
Consp. food treatment	F _{1,14} = 1.25	F _{1,12} = 0.44	F _{1,14} = 0.53	F _{1,13} = 0.02
Offsp. × consp. food treatment	F _{1,12} = 0.76	F_{1,12} = 10.17^{**}	F _{1,12} = 3.05	F _{1,12} = 3.61 [†]
Sex	F _{1,154} = 0.62	F_{1,126} = 70.00^{****}	F_{1,128} = 46.25^{****}	F_{1,68} = 74.27^{****}
Offsp. food treatment × sex	F _{1,151} = 0.00	F _{1,119} = 0.63	F _{1,124} = 0.08	F _{1,63} = 1.21
Consp. food treatment × sex	F _{1,153} = 2.66	F _{1,120} = 1.33	F _{1,123} = 0.06	F _{1,62} = 0.18
Initial SVL (mm)	F _{1,152} = 1.63	F_{1,126} = 26.03^{****}	F_{1,128} = 19.49^{****}	F_{1,68} = 19.82^{****}
Offsp. food treatment × SVL	F _{1,151} = 1.46	F _{1,124} = 0.19	F _{1,127} = 0.09	F _{1,66} = 0.07
Consp. food treatment × SVL	F _{1,150} = 0.01	F _{1,125} = 1.03	F_{1,128} = 5.95[*]	F _{1,67} = 0.58
Offsp. × consp. food treatment × SVL	F _{1,149} = 0.10	F _{1,123} = 2.68	F _{1,126} = 2.88 [†]	F _{1,65} = 2.22
Birth date (days)	F_{1,155} = 13.83^{***}	F _{1,121} = 1.30	F_{1,128} = 26.16^{****}	F _{1,64} = 1.35
Origin of the mother	F _{1,155} = 3.15 [†]	F _{1,122} = 1.26	F _{1,125} = 0.43	F_{1,68} = 6.02[*]
<i>Random effect</i>	<i>LRT</i>	<i>LRT</i>	<i>LRT</i>	<i>LRT</i>
Enclosure	16.58^{****}	11.10^{***}	25.00^{****}	12.66^{***}

[†]P < 0.10, *P < 0.05, **P < 0.01, ***P < 0.001, ****P < 0.0001.

Delayed effects on body size

Growth rates from release to adulthood did not differ between offspring food-treatment groups (see the main effect in Table 1). However, growth rate in spring 2007 was affected by a significant interaction between offspring and conspecific food treatment (Table 1) as LF lizards maintained in populations with LF conspecifics grew about 0.1 mm.day⁻¹ faster than the other lizards (Figure 3A). Growth rate in summer 2007 was affected by an interaction between conspecific food treatment and SVL in May 2007 (Table 1): growth rate of individuals decreased less importantly with SVL when they were maintained with HF conspecifics (-0.003 ± 0.0007 , $F_{1,56} = 11.84$, $P = 0.001$) than with LF conspecifics (-0.005 ± 0.0006 , $F_{1,70} = 55.28$, $P < 0.0001$).

Figure 3. Growth rates (A) and SVL (B) in each treatment group. (A) Growth rates in the laboratory (Lab.: $n = 460$), from release in summer 2006 to April 2007 (Release-April07: $n = 173$), from April to May 2007 (April-May07: $n = 144$), from May to August 2007 (May-Aug.07: $n = 148$) and from August 2007 to May 2008 (Aug.07-May08: $n = 87$). (B) SVL at birth, at release, in April, May ($n = 167$) and August 2007 ($n = 152$) and in May 2008 ($n = 90$). (A, B) Estimates were obtained from linear mixed effects models with offspring and conspecific food treatment and their interaction as fixed factors. Black symbols: HF offspring food treatment; white symbols: LF offspring food treatment; triangles: HF conspecific food treatment; squares: LF conspecific food treatment.



Differences in SVL between HF and LF lizards were of the same order of magnitude in April 2007 as after the laboratory manipulation (Figure 3B) but were only marginally significant due to larger inter-individual variation (Table S1). From May 2007 onwards, SVL was affected by an interaction between offspring and conspecific food treatment (Table S1). Post-hoc tests revealed that LF lizards grew to be larger than HF lizards when maintained with LF conspecifics, but grew to be smaller when maintained with HF conspecifics (Fig 3B, Table S1). Cohort density did not explain differences in growth rates but partially explained differences in SVL. SVL in May 2008 was negatively correlated with cohort density in August 2007 ($F_{1,14} = 10.91$, $P = 0.005$) and treatment effects on SVL were no longer significant when cohort density was taken into account ($F_{1,11} = 2.97$, $P = 0.11$). We also found sexual differences in growth rates and SVL after spring 2007 independently of offspring food treatment (Table 1, Table S1).

Delayed effects on survival

Juvenile survival was affected by a significant interaction between offspring and conspecific food treatment ($Z = -4.17$, $P < 0.0001$). Survival was less than half for HF juveniles as for LF lizards when juveniles were maintained with HF conspecifics (post-hoc test: $Z = 3.61$, $P = 0.0003$), but was slightly longer for HF lizards when juveniles were maintained with LF conspecifics (post-hoc test: $Z = -2.19$, $P = 0.03$, Figure 4A). Among survivors, the frequency of broken tails was similar between treatment groups in May 2007 (logistic regression: $Z = 0.28$, $P = 0.78$) as well as the ectoparasite load (logistic regression: $Z = 0.99$, $P = 0.32$). Survival increased with SVL at release up to a plateau, indicating quadratic selection on SVL ($SVL = 0.2857 \pm 0.054$, $Z = 4.98$, $P < 0.0001$; $SVL^2 = -0.0374 \pm 0.0141$, $Z = -2.66$, $P = 0.008$, Figure 4B).

Yearling survival was similar between treatment groups (offspring \times conspecific food treatment: $Z = 0.10$, $P = 0.91$; offspring food treatment: $Z = -1.23$, $P = 0.22$; Figure 4C) and was influenced by a marginal interaction between offspring food treatment and a quadratic SVL effect (offspring food treatment \times SVL^2 : $Z = 1.91$, $P = 0.06$). Selection on SVL at the yearling stage was stabilising around the mean SVL in the HF offspring treatment group ($SVL = 0.0269 \pm 0.0803$, $Z = 0.34$, $P = 0.74$; $SVL^2 = -0.0190 \pm 0.0095$, $Z = -2.01$, $P = 0.05$) but no selection on SVL was found in the LF offspring treatment group (SVL : $Z = -0.29$, $P = 0.77$; SVL^2 : $Z = 0.22$, $P = 0.83$; Figure 4D).

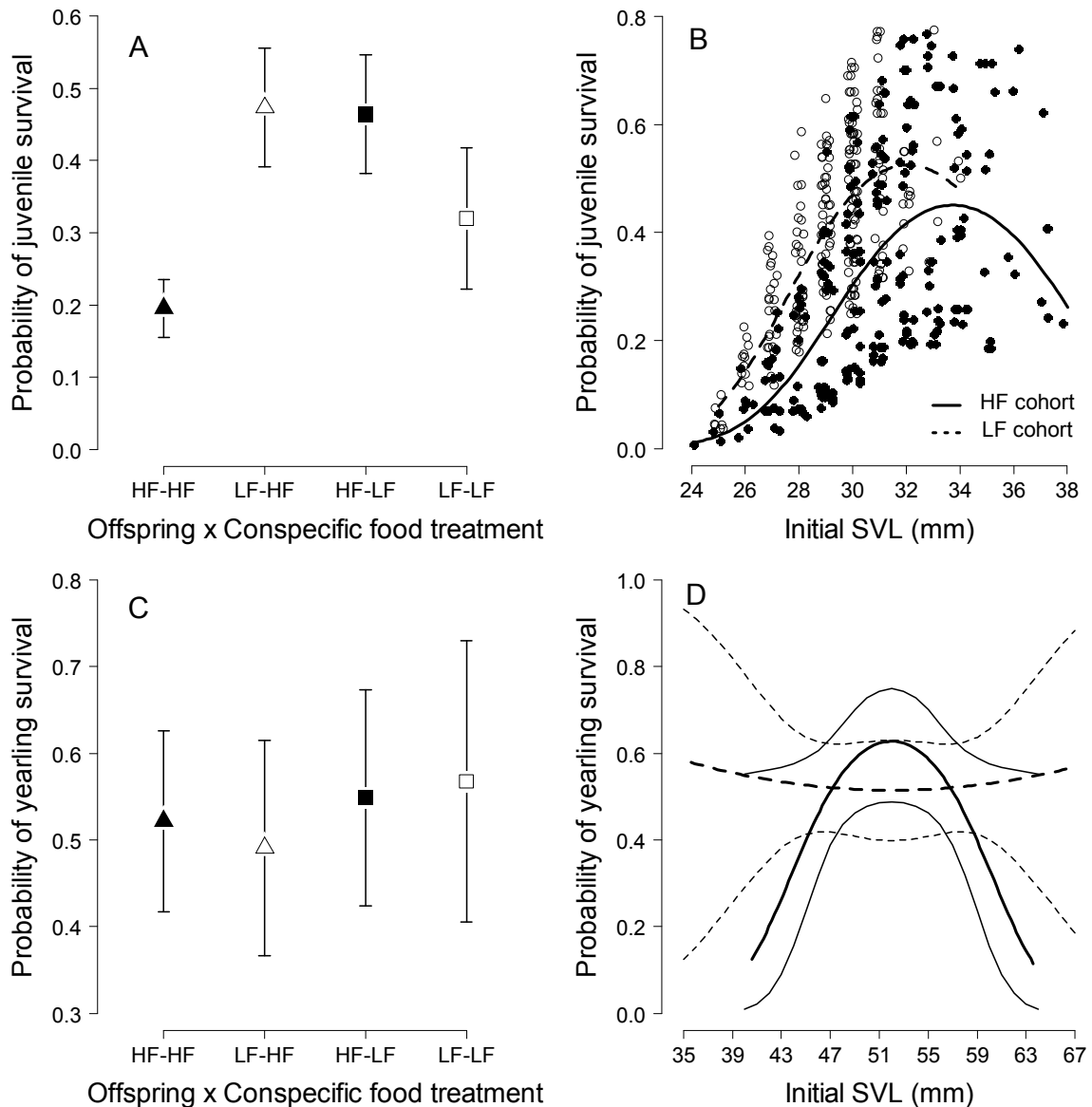


Figure 4. Annual survival probabilities for treatment groups at the juvenile stage (A) and yearling stage (C), as well as effects of initial SVL on juvenile survival (B, size at release) and yearling survival (D, size in May 2007). (A) The annual survival probability of fully fed juveniles maintained with fully fed older conspecifics was lower than the average annual juvenile survival probability observed in our experimental system from 1999 to 2003 (0.33 [0.23, 0.45] 95 % CI, $n = 1743$ juveniles). (A, C) Estimates were obtained from generalised mixed effects models with offspring and conspecific food treatment and their interaction as fixed factors. (B) Fitted values and predicted curves were obtained from the minimum adequate model (see main text) including an interaction between the quadratic body size effects and offspring food treatment. (D) Predicted curves (and 95 % CI) were drawn from the estimates of the minimum adequate model (see main text). Symbols as in Figure 3.

Delayed effects on reproductive performances

Fecundity was affected by a significant interaction between offspring and conspecific food treatment ($F_{1,11} = 21.48$, $P = 0.0007$). Females from the HF offspring food-treatment group

produced on average three more offspring than LF females when maintained with HF conspecifics, but the reverse was observed when females were maintained with LF conspecifics (Figure 5A). These treatment effects were importantly explained by differences in female SVL between treatment groups (female SVL: $F_{1,25} = 7.95$, $P = 0.009$; offspring \times conspecific food treatment controlling for SVL: $F_{1,11} = 4.35$, $P = 0.06$). In addition, SVL of produced offspring differed significantly between treatment groups after controlling for the trade-off between offspring quantity and quality (offspring \times conspecific food treatment: $F_{1,11} = 7.69$, $P = 0.02$; fecundity: $F_{1,14} = 14.89$, $P = 0.002$). For a given fecundity, females from the HF offspring treatment group produced offspring in average of 1 to 2 mm larger than those produced by LF females when maintained with HF conspecifics, but the reverse was observed when they were maintained with LF conspecifics (Figure 5B). Again, differences in female SVL between treatment groups explained importantly these treatment effects (offspring \times conspecific food treatment: $F_{1,11} = 4.18$, $P = 0.07$; fecundity controlled for female SVL: $F_{1,13} = 15.17$, $P = 0.002$; female SVL: $F_{1,13} = 4.08$, $P = 0.06$). Cohort density measured in May 2008 did not explain variation in reproductive performances (F tests, all $P > 0.40$).

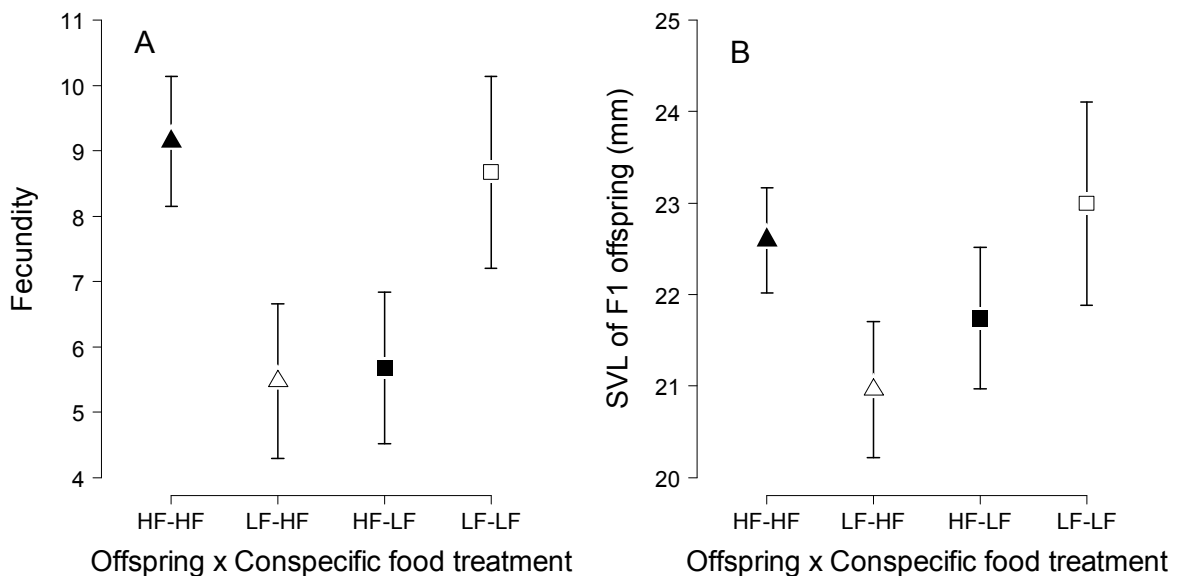


Figure 5. Female reproductive performances in 2008. (A) Fecundity ($n = 43$) and (B) SVL of the offspring ($n = 212$) produced in each treatment group. Estimates were obtained from the minimum adequate model (see main text) and (B) were calculated for a mean fecundity.

We combined data from all demographic traits to estimate the asymptotic growth rate (λ) of an age-structured population parameterised with treatment-specific estimates of each vital rate (see Appendix S2). Monte Carlo simulations indicate that λ did not differ from 1 in any treatment group and would not differ between treatment groups if observed differences in

fecundity at age 2 are consistent throughout life (Figure S2A). However, if differences in fecundity are compensated for after age 2, for example due to growth compensation, the λ of a population of HF offspring maintained with HF conspecifics would be significantly smaller than the λ of other treatment groups (Figure S2B).

Delayed effects on performances traits

Offspring food treatment had a delayed effect on immunocompetence at the yearling and adult stages (respectively, $F_{1,14} = 5.07$, $P = 0.04$; $F_{1,14} = 4.04$, $P = 0.06$). The inflammatory response was significantly higher in LF than in HF offspring food-treatment groups at the yearling stage (HF = $0.0589 \text{ mm} \pm 0.00657$, LF = 0.0805 ± 0.0078) and marginally higher at the adult stage (HF = 0.1076 ± 0.0107 , LF = 0.1366 ± 0.0144). Inflammatory response at the yearling stage did not correlate with future survival (logistic regression: $Z = 0.19$, $P = 0.85$), growth (linear regression: $F_{1,63} = 2.85$, $P = 0.10$) or fecundity (linear regression: $F_{1,23} = 0.01$, $P = 0.91$) and with current ectoparasite load (Poisson regression: $Z = 0.40$, $P = 0.69$).

Locomotor performances at the yearling and adult stages were not affected by offspring food treatment (all $P > 0.12$) and only maximal sprint speed at the yearling stage increased with body size ($F_{1,44} = 10.42$, $P = 0.0015$, other tests: $P > 0.45$). Males ran faster and were more enduring than females (all $P < 0.02$). Performance traits in 2007 and 2008 were positively correlated (Pearson's product correlation for immunocompetence: $r = 0.20$ [-0.01, 0.41] 95 % CI, $P = 0.07$; maximal sprint speed: $r = 0.34$ [0.13, 0.51] 95 % CI, $P = 0.002$; endurance capacity: $r = 0.38$ [0.19, 0.55] 95 % CI, $P = 0.0003$).

DISCUSSION

Immediate effects of food availability

Spatial and temporal variations in food availability are common in nature and play a major role in life-history variation (Metcalf & Monaghan, 2001). Here, we found that growth and body size during the first weeks of life responded quickly to food deprivation as in our previous study (Le Galliard et al., 2005). However, offspring raised under favourable conditions displayed more residual variation than lizards raised under food deprivation for growth rate and body size in the laboratory but not in the outdoor enclosures. This illustrates a clear example of context-dependent expression of phenotypic variation. Hoffmann (1999) explained this reduction in phenotypic variation under unfavourable conditions by a limitation

of the genetic potential of organisms – a hypothesis validated for morphometric traits by the meta-analysis of Charmantier and Garant (2005).

In addition, contrary to a previous study involving a smaller number of families (Le Galliard et al., 2005), we found that growth rate sensitivity to food availability varied significantly between families. This variation was substantial as growth did not improve, or even responded negatively to full feeding in some families (see Figure 2B). Maternal (reviewed in Mousseau & Fox, 1998) and paternal effects (Galloway, 2001) may contribute to changes in the ranking of families across environments. However, such parental effects are unlikely here because no paternal effects on phenotypic plasticity were found and none of the maternal effects on phenotypic plasticity tested were significant. Low genetic correlations across environments have already been demonstrated in the common lizard for survival and growth plasticity along altitudinal and humidity gradients (Lorenzon et al., 2001, Sorci et al., 1996) and are common in the wild (reviewed in Charmantier & Garant, 2005). Altogether, context-dependent expression of phenotypic variation and genotype-environment interactions may contribute to the maintenance of phenotypic plasticity in resource allocation strategies in this species (Hoffmann & Merilä, 1999, Charmantier & Garant, 2005).

Long lasting effects of food availability on life-history traits

We hypothesized that food deprivation early in life should have long-lasting effects on body size and would therefore affect size-dependent life-history traits such as growth, juvenile survival and reproductive performances (Figure 1A). If individuals were able to compensate, we expected them to face physiological costs through trade-offs between competing functions as well as ecological costs that may reduce their survival, performances traits or reproduction (Metcalfé & Monaghan, 2001, Figure 1A). We also predicted that these direct effects of food availability could be modulated by indirect effects caused by changes in the intensity of competition within and between cohorts (van de Wolfshaar et al., 2008, Pafilis et al., 2009, Claessen et al., 2000, Fig 1A). Our findings partially support these qualitative predictions.

When food deprived offspring were maintained with food deprived conspecifics, they overcompensated for their bad growth start during the juvenile stage and thus reached a larger body size at adulthood, which enabled them to produce more offspring than fully fed lizards. This growth overcompensation was associated with a juvenile survival that was slightly lower than that for fully fed lizards. In sharp contrast, fully fed lizards released with fully fed yearlings and adults maintained their body size advantage over food deprived offspring at the juvenile stage and thus reached a larger size at the yearling stage. As expected, the

reproductive performances of adult females were highly dependent on their body size (Massot et al., 1992). However, a silver spoon effect existed for the reproductive performances of fully fed females maintained with fully fed conspecifics: those females produced more and larger offspring than food deprived females despite their similar body size (Taborsky, 2006). At the same time, juvenile survival of fully fed individuals maintained with fully fed conspecifics was less than half that of food deprived individuals. Thus, life-history trajectories were shaped by an interaction between the direct effects of food availability early in life on individual quality and some indirect effects on the intensity of inter-cohort interactions. However, contrary to our qualitative predictions, fully fed older conspecifics inhibited compensatory responses in juveniles (Figure 1A). These results suggest that fully fed yearlings and adults with a higher condition (unpub. data) were greater competitors for juveniles than conspecifics that experienced a prolonged food deprivation (Keren-Rotem et al., 2006). In turn, competition with fully fed conspecifics may have selected for higher investment in body growth according to body size in juveniles and could explain why growth rates decelerated more weakly with body size for juveniles maintained with fully fed conspecifics.

Compensatory growth responses to poor early environmental conditions have been demonstrated in several species, where it may be an adaptive mechanism to reduce the fitness costs associated with poor early development (Metcalfé & Monaghan, 2001, Birkhead et al., 1999). Yet, the ability to compensate for a bad start varies between and within species (Metcalfé & Monaghan, 2001, Tschirren et al., 2009). In the common lizard, this ability depends on the population structure. Our previous studies have shown that strong competition within a cohort can prevent individuals from compensating for growth restriction at the juvenile and at the yearling stage (Le Galliard et al., 2005, Massot et al., 1992). Here, we demonstrated that food deprived lizards displayed compensatory growth only when they were maintained with food deprived older conspecifics. Thus, the ability to compensate can be modulated by inter-cohort interactions in size and stage-structured populations. Furthermore, despite their fitness advantages, compensatory growth strategies are often associated with short-term costs, such as an increased metabolic rate (Criscuolo et al., 2008) or risks of predation and parasitism (Anholt & Werner, 1998, Crouch & Lubin, 2000), and/or with long-term physiological costs, such as cellular damages (reviewed in Metcalfé & Monaghan, 2001). Here, growth overcompensation for a bad start that led to a higher maturation body size and fecundity was also associated with the immediate cost of reduced juvenile survival. This lower survival was not apparently due to higher predation and parasitic risks as assessed from the proportion of broken tails (Pafilis et al., 2009), ectoparasite load

(Moyer et al., 2002) and immune performances (see below). However, these variables were measured only on surviving individuals and may therefore not be reliable indicators of causes of mortality at the individual level.

Silver spoon effects from being born under favourable conditions are assumed to be associated with increased lifetime reproductive success (Grafen, 1988, Monaghan, 2008), but our analysis led to a different picture. Here, fully fed lizards benefited from a silver spoon effect on body size and female reproduction when they were maintained with fully fed yearlings and adults. However, these positive effects of early food conditions were associated with a strong negative effect on juvenile survival. Since fully fed juveniles did not display higher growth rates than food deprived lizards, their low juvenile survival cannot be explained by ecological or physiological costs associated with fast growth (Criscuolo et al., 2008, Anholt & Werner, 1998). Alternatively, we predicted that a low juvenile survival could be due to viability selection against larger individuals (Figure 1A). Indeed, juvenile survival depended on body size and the effect of body size was non-linear, indicating that some fitness costs counter-balanced the survival benefits of being larger early in life (Figure 4B). Yet, we failed to detect differential natural selection on body size between treatments (offspring \times conspecific food treatment \times initial SVL (linear and quadratic): all $P < 0.10$). Thus, the low juvenile survival of fully fed offspring cannot be explained by selection against larger individuals. Moreover, we did not find evidence of more aggression or predation attempts as assessed from the proportion of broken tails, and fully fed juveniles maintained with fully fed yearlings and adults did not suffer from a higher parasitic exposure. Thus, fully fed yearlings and adults imposed some undetected mortality factors on fully fed juveniles, which may be driven by behavioural interactions (Webster, 2004).

In summary, life history consequences of food availability were caused by statistical interactions between direct effects on individual quality and indirect effects on inter-cohort interactions. In addition, intra-cohort density dependence varied between experimental populations as a consequence of differences in juvenile survival and contributed to maintain body size differences between populations but did not influence yearling survival and reproductive performances. These results suggest that the dynamical effects of fluctuations in food supply should depend on cohort interactions, which could generate cohort cycles and complex population dynamics (de Roos et al., 2003). Also, our analysis of lifetime reproductive success suggests that the fitness benefits and costs of fast growth under favourable conditions early in life depend significantly on cohort interactions. The general picture was one of a lower lifetime reproductive success for fully fed juveniles maintained

with fully fed older conspecifics. Thus, cohort interactions may constrain the evolution of rapid growth rates early in life and should be considered in future studies of growth strategies in this and other species with structured populations.

Long-lasting effects of food availability on performance traits

Several laboratory studies investigated long-lasting effects of food deprivation on performance traits and hypothesized that these traits are surrogates of demographic performances in the wild (e.g., Le Galliard et al., 2004, Birkhead et al., 1999, Hoi-Leitner et al., 2001). However, our results show that effects of food deprivation on the performance traits investigated here (locomotor performances and immunocompetence) were independent of the effects on demographic traits. Performance traits were insensitive to social interactions between cohorts and to density-dependent interactions within a cohort. Also, locomotor performances were not influenced by food availability experienced early in life and a positive allometric relationship between locomotor performances and body size was significant only for maximal sprint speed at the yearling stage. Thus, factors not tested here, for example maternal genetic effects, the quality and the quantity of muscle or the length of the limbs, were more important determinants of locomotor capacities than body size and food availability early in life (Vanhooydonck et al., 2001, Le Galliard et al., 2004).

In addition, our results clearly indicate long-lasting effects of food deprivation on immunity, measured as the delayed inflammatory response to PHA injection. Other studies have demonstrated that food deprivation during early development has immediate immunosuppressive effects (e.g., Hoi-Leitner et al., 2001, Birkhead et al., 1999). However, individuals may be able to compensate or even overcompensate for these immunosuppressive effects (e.g., in the zebra finch, Birkhead et al., 1999, Tschirren et al., 2009). Here, offspring raised under food deprivation displayed higher inflammatory responses later in life than fully fed offspring but we cannot affirm that they overcompensated since we did not measure immediate effects of food deprivation on immunocompetence. The maintenance of a strong immunity requires substantial energy expenditure and thus should trade off with growth, fecundity and/or survival (reviewed in Lochmiller & Deerenberg, 2000). This cost of overcompensation was not detected in our experiment until adulthood; however, physiological costs may appear later in life and affect senescence patterns (Lochmiller & Deerenberg, 2000). Alternatively, the maintenance of a strong immunity may be an adaptive response to compensate for the survival costs associated with a reduced early growth since stronger immune responses allows individuals to fight parasites more efficiently (Tella et al.,

2008, Cote et al., 2010). Yet, we found no evidence of direct survival advantages to higher immunocompetence in this study.

Conclusion

Our study demonstrates complex cohort effects of food availability early in life mediated by direct effects on growth, long-lasting effects on immune performances, and an interaction between direct effects on body size and indirect effects on growth, survival and reproduction. The effects of food deprivation on performance traits were clearly independent of those on demographic traits, suggesting that findings concerning performance traits in laboratory studies should be interpreted with caution. In accordance with a previous study (Le Galliard et al., 2005), life history effects did not differ between sexes despite the existence of a sexual dimorphism in growth and body size. In addition, the early environment influenced population growth through variation in juvenile survival mediated by social interactions between cohorts. Interactions between direct and indirect effects of environmental variation may play a major role in the evolution of life history traits within size- and stage-structured populations characterised by strong asymmetric competition for food and space between cohorts as in many species of fish (Claessen et al., 2000, Szabo, 2002, Webster, 2004).

AKNOWLEDGMENTS

We thank B. Decenci re, M. Paquet and all students for assistance in the field and M. Richard and P. Federici for help with genetic analyses. We are grateful to S. Meylan and M. Massot for their helpful suggestions. Two anonymous reviewers and the Editor made useful suggestions to improve the quality of a previous version of this article. This research was supported by the *Centre National de la Recherche Scientifique* (CNRS), an *Agence Nationale de la Recherche* (ANR) grant (07-JCJC-0120) to J.F.L.G., grants from the *Institut Federatif Ecologie-Biodiversit -Evolution-Environnement* (IFR 101) to T.T. and a grant from the R gion Ile-De-France (*R seau de Recherche sur le D veloppement Soutenable R2DS 2007-006*) to J.-F. L.G. and M. M. Experimental protocols were validated by the *Regional ethics committee in animal experiment N 3 of the R gion Ile-De-France* (file p3/2006/10).

REFERENCES

- Aday, D. D., Philipp, D. P. & Wahl, D. H. 2006. Sex-specific life history patterns in bluegill (*Lepomis macrochirus*): interacting mechanisms influence individual body size. *Oecologia* **147**: 31-38.
- Andrews, R. M. (1982) Patterns of growth in reptiles. In: *Biology of the Reptilia*, Vol. 13 (Gans, G. & Pough, F. H., eds.). pp. 273-320. Academic Press, New York.
- Anholt, B. R. & Werner, E. E. 1998. Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. *Evolutionary Ecology* **12**: 729-738.
- Avery, R. A. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology* **40**: 351-365.
- Beckerman, A., Benton, T. G., Lapsley, C. T. & Koesters, N. 2003. Talkin' 'bout my generation: environmental variability and cohort effects. *American Naturalist* **162**: 754-767.
- Birkhead, T. R., Fletcher, F. & Pellatt, E. J. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proceedings of the Royal Society B-Biological Sciences* **266**: 385-390.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**: 127-135.
- Boudjemadi, K., Martin, O., Simon, J. C. & Estoup, A. 1999. Development and cross-species comparison of microsatellite markers in two lizard species, *Lacerta vivipara* and *Podarcis muralis*. *Molecular Ecology* **8**: 518-520.
- Charmantier, A. & Garant, D. 2005. Environmental quality and evolutionary potential: lessons from wild populations. *Proceedings of the Royal Society B-Biological Sciences* **272**: 1415-1425.
- Claessen, D., de Roos, A. M. & Persson, L. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. *American Naturalist* **155**: 219-237.
- Claessen, D. & Dieckmann, U. 2002. Ontogenetic niche shifts and evolutionary branching in size-structured populations. *Evolutionary Ecology Research* **4**: 189-217.
- Cote, J., Clobert, J., Poloni, L. M., Haussy, C. & Meylan, S. 2010. Food deprivation modifies corticosterone-dependent behavioural shifts in the common lizard. *General and Comparative Endocrinology* **166**: 142-151.

- Criscuolo, F., Monaghan, P., Nasir, L. & Metcalfe, N. B. 2008. Early nutrition and phenotypic development: 'catch-up' growth leads to elevated metabolic rate in adulthood. *Proceedings of the Royal Society B-Biological Sciences* **275**: 1565-1570.
- Crouch, T. E. & Lubin, Y. 2000. Effects of climate and prey availability on foraging in a social spider, *Stegodyphus mimosarum* (Araneae, Eresidae). *Journal of Arachnology* **28**: 158-168.
- de Roos, A. M., Persson, L. & McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* **6**: 473-487.
- Galloway, L. F. 2001. The effect of maternal and paternal environments on seed characters in the herbaceous plant *Campanula americana* (Campanulaceae). *American Journal of Botany* **88**: 832-840.
- Grafen, A. (1988) On the uses of data on lifetime reproductive success. In: *Reproductive Success*, (Clutton-Brock, T. H., ed.). pp. 454-471. University of Chicago Press, Chicago.
- Hoffmann, A. A. & Merilä, J. 1999. Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology & Evolution* **14**: 96-101.
- Hoi-Leitner, M., Romero-Pujante, M., Hoi, H. & Pavlova, A. 2001. Food availability and immune capacity in serin (*Serinus serinus*) nestlings. *Behavioral Ecology and Sociobiology* **49**: 333-339.
- Keren-Rotem, T., Bouskila, A. & Geffen, E. 2006. Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). *Behavioral Ecology and Sociobiology* **59**: 723-731.
- Laloi, D., Richard, M., Lecomte, J., Massot, M. & Clobert, J. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellite markers. *Molecular Ecology* **13**: 719-723.
- Le Galliard, J.-F., Clobert, J. & Ferrière, R. 2004. Physical performance and darwinian fitness in lizards. *Nature* **432**: 502-505.
- Le Galliard, J.-F., Ferrière, R. & Clobert, J. 2005. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* **111**: 368-376.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* **14**: 342-348.
- Lochmiller, R. L. & Deerenberg, C. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos* **88**: 87-98.

- Lorenzon, P., Clobert, J. & Massot, M. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. *Evolution*: 392-404.
- Madsen, T. & Shine, R. 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.
- Marquis, O., Massot, M. & Le Galliard, J.-F. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. *Ecology* **89**: 2575-2583.
- Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**: 1742-1756.
- Metcalfe, N. B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution* **16**: 254-260.
- Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**: 1635-1645.
- Mousseau, T. A. & Fox, C. W. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution* **13**: 403-407.
- Moyer, B. R., Drown, D. M. & Clayton, D. H. 2002. Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos* **97**: 223-228.
- Pafilis, P., Meiri, S., Foufopoulos, J. & Valakos, E. 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Naturwissenschaften* **96**: 1107-1113.
- Pinheiro, J. C. & Bates, D. M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer Verlag, New York.
- Sorci, G. & Clobert, J. 1997. Environmental maternal effects on locomotor performance in the common lizard (*Lacerta vivipara*). *Evolutionary Ecology* **11**: 531-541.
- Sorci, G., Clobert, J. & Belichon, S. 1996. Phenotypic plasticity of growth and survival in the common lizard *Lacerta Vivipara*. *Journal of Animal Ecology* **65**: 781-790.
- Szabo, A. R. 2002. Experimental tests of intercohort competition for food and cover in the tidepool sculpin (*Oligocottus maculosus* Girard). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **80**: 137-144.
- Taborsky, B. 2006. The influence of juvenile and adult environments on life-history trajectories. *Proceedings of the Royal Society B-Biological Sciences* **273**: 741-750.

- Tella, J. L., Lemus, J. A., Carrete, M. & Blanco, G. 2008. The PHA test reflects acquired T-cell mediated immunocompetence in birds. *Plos One* **3**: 9.
- Tschirren, B., Rutstein, A. N., Postma, E., Mariette, M. & Griffith, S. C. 2009. Short- and long-term consequences of early developmental conditions: a case study on wild and domesticated zebra finches. *Journal of Evolutionary Biology* **22**: 387-395.
- van de Wolfshaar, K. E., de Roos, A. M. & Persson, L. 2008. Population feedback after successful invasion leads to ecological suicide in seasonal environments. *Ecology* **89**: 259-268.
- Vanhooydonck, B., van Damme, R. & Aerts, P. 2001. Speed and stamina trade-off in Lacertid lizards. *Evolution* **55**: 1040-1048.
- Webster, M. S. 2004. Density dependence via intercohort competition in a coral-reef fish. *Ecology* **85**: 986-994.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Analysis of SVL (mm) of male and female lizards throughout their two-first years of life according to the offspring (offsp.) food treatment, the conspecifics (consp.) food treatment, the age (number of activity days since day of birth) and the origin of the mother.

Appendix S1 Methods: projection matrix model.

Figure S1 Predicted asymptomatic growth rate (k) in each treatment group.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be reorganized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Table S1. Analysis of SVL (mm) of male and female lizards throughout their two first years of life according to the offspring (offsp.) food treatment, the conspecific (consp.) food treatment, the age (number of activity days since day of birth) and the origin of the mother. Results in bold indicate significant effects. The F and P values were obtained by backward selection from the full models and LRT values were obtained for the minimum adequate model selected.

Effect	April 2007	May 2007	August 2007	May 2008
<i>Fixed effect</i>	<i>F</i> _{ndf,ddf}	<i>F</i> _{ndf,ddf}	<i>F</i> _{ndf,ddf}	<i>F</i> _{ndf,ddf}
Offsp. food treatment	F _{1,14} = 3.50 [†]	F _{1,12} = 3.38 [†]	F_{1,12} = 4.66*	F _{1,12} = 1.94
Consp. Food treatment	F _{1,13} = 0.42	F _{1,12} = 0.34	F _{1,12} = 2.57	F _{1,12} = 2.28
Offsp. × consp. food treatment	F _{1,12} = 0.27	F_{1,12} = 5.57*	F_{1,12} = 6.96*	F_{1,12} = 5.23*
Sex	F_{1,154} = 4.19*	F_{1,148} = 64.79****	F_{1,133} = 125.10****	F_{1,71} = 262.82****
Offsp. food treatment × sex	F _{1,152} = 0.05	F _{1,147} = 0.89	F _{1,131} = 0.14	F _{1,69} = 0.09
Consp. food treatment × sex	F _{1,153} = 0.91	F _{1,146} = 1.44	F _{1,132} = 0.10	F ₁₇₀ = 0.13
Age (activity days)	F_{1,154} = 86.64***	F_{1,148} = 40.84****	F_{1,133} = 20.04****	F_{1,71} = 17.26***
Origin of the mother	F_{1,154} = 11.70[†]	F_{1,148} = 11.17**	F_{1,133} = 16.16***	F_{1,71} = 25.28****
<i>Random effect</i>	<i>LRT</i>	<i>LRT</i>	<i>LRT</i>	<i>LRT</i>
Enclosure	19.50****	6.98**	11.59***	19.48****

[†]P < 0.10, *P < 0.05, **P < 0.01, ***P < 0.001, ****P < 0.0001

Appendix S1. Methods: Projection matrix model

We used a matrix projection model to calculate the asymptotic growth rate (λ), which corresponds to lifetime reproductive success when the population is at equilibrium. Our model assumed a post-breeding census, birth pulse dynamics, and included only the female portion of the population (Caswell, 2001). We considered three age classes (juveniles, yearlings and adults) in a transition matrix that included juvenile survival, yearling survival, adult survival and fecundity. Juvenile survival varied between treatment groups but yearling survival did not (see the main text) and adult survival was assumed to be equal to yearling survival. For fecundity, we first hypothesized that differences between treatments observed at age 2 were consistent throughout life. Alternatively, we hypothesized that fecundity after age 2 did not differ between treatments and used mean fecundity at age 2 as an estimate of fecundity after age 2. We calculated λ as the dominant eigenvalue of the transition matrix fitted and estimated the 95% confidence limits with Monte Carlo simulations (1000 projection matrix, see Alvarez-Buylla & Slatkin, 1991).

References

- Alvarez-Buylla, E. R. & Slatkin, M. 1991. Finding confidence-limits on population-growth rates. *Trends in Ecology & Evolution* **6**: 221-224.
- Caswell, H. 2001. *Matrix population models*, 2 ed. Sinauer Associates, Sunderland.

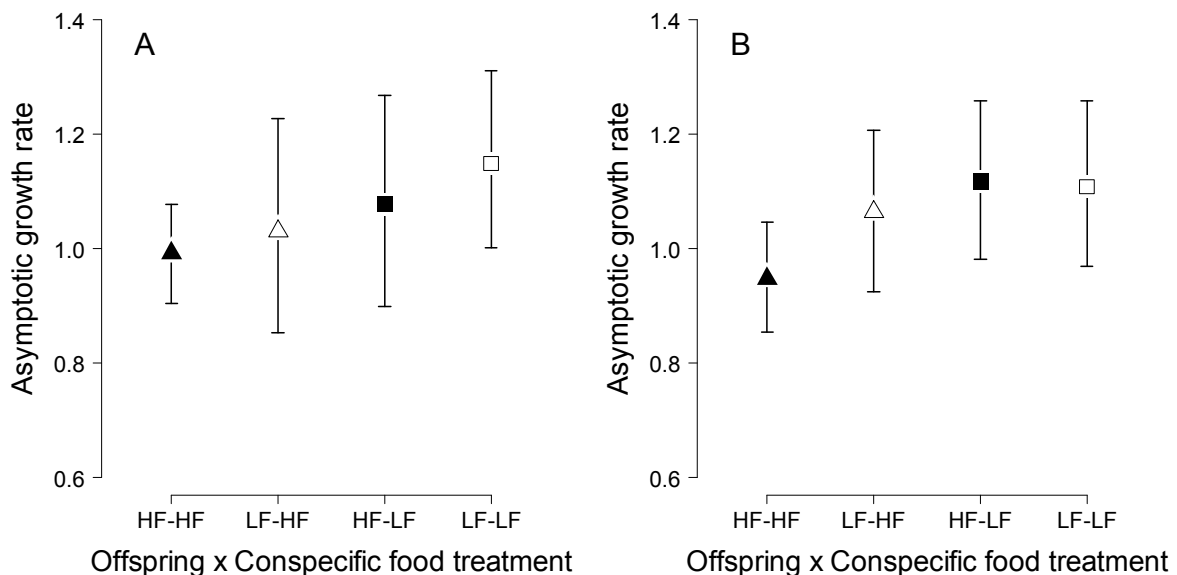


Figure S1. Lifetime reproductive success of each treatment group was estimated by the asymptotic growth rate. The calculation assumes that treatment groups differ for juvenile survival and adult fecundity. Fecundity differences observed at age 2 are maintained throughout life in (A) and are compensated for after age 2 in (B). Symbols as in Figure 3 from the main text.

**CHAPITRE 3 – Effets de l’environnement nutritif tardif sur l’histoire
de vie dans des populations structurées en cohortes**

Effets directs et sociaux de la disponibilité en nourriture tard dans la vie sur la variation d’histoire de vie chez un lézard non-longévif

Marianne Mugabo, *, Olivier Marquis, *, Samuel Perret † & Jean-François Le Galliard *†

* CNRS, UMR 7625, Laboratoire Ecologie et Evolution, Université Pierre et Marie Curie, 7 Quai St. Bernard, 75005, Paris, France.

† CNRS/ENS UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours

Titre court : Effets directs et sociaux de la disponibilité en nourriture sur l’histoire de vie

Référence : Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2011. « Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard ». *Oecologia* **In press**.

RÉSUMÉ

La disponibilité en nourriture est un facteur environnemental majeur qui peut influencer l’histoire de vie au sein d’une génération et entre générations via des effets directs sur la qualité individuelle et des effets indirects sur l’intensité de la compétition intra- et inter-cohortes. Ici, nous avons étudié chez des lézards vivipares sub-adultes et adultes (*Zootoca vivipara*) les effets d’histoire de vie directs et immédiats d’une privation de nourriture prolongée en laboratoire. Nous avons généré à la fin de la saison de reproduction des groupes de sub-adultes et d’adultes bien nourris ou mal nourris. Ces lézards ont ensuite été lâchés dans seize enclos extérieurs avec des sub-adultes et des adultes du même traitement de nourriture et avec des juvéniles bien ou mal nourris, créant ainsi quatre types de populations expérimentales. Ces populations expérimentales ont ensuite été suivies pendant deux ans, ce qui a révélé des effets complexes de la nourriture sur les trajectoires d’histoire de vie. La disponibilité en nourriture a eu des effets directs sur la morphologie et des effets indirects décalés sur l’immunocompétence et la condition corporelle des femelles à la sortie d’hibernation. De plus, le taux de survie annuel des mâles et le taux de croissance et la taille corporelle des femelles ont été affectés par une interaction entre les effets directs de la disponibilité en nourriture et les effets indirects sur la compétition asymétrique avec les juvéniles. Les performances reproductives n’ont pas été affectées par la disponibilité en nourriture, ce qui suggère que les femelles n’utilisent pas uniquement de l’énergie stockée à long terme lors de la reproduction. Pour finir, les conditions de nourriture ont eu des effets intergénérationnels d’origine sociale sur la survie et la croissance précoce via ses effets sur l’intensité de la compétition intraspécifique. Cette étude souligne l’importance des interactions sociales entre cohortes sur les trajectoires d’histoire de vie et la dynamique de populations dans les populations structurées en stades.

Mots-clés : privation de nourriture, stratégies d’allocation, compétition asymétrique, densité dépendance, *Zootoca vivipara*

Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard.

Marianne Mugabo, *, Olivier Marquis, *, Samuel Perret † & Jean-François Le Galliard *†

* CNRS, UMR 7625, Laboratoire Ecologie et Evolution, Université Pierre et Marie Curie, 7 Quai St. Bernard, 75005, Paris, France.

† CNRS/ENS UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours

Running title: Direct and socially-mediated life-history effects of food availability

Reference: Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2011. Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. *Oecologia* **In press**.

ABSTRACT

Food availability is a major environmental factor that can influence life history within and across generations through direct effects on individual quality and indirect effects on the intensity of intra and intercohort competition. Here, we investigated in yearling and adult common lizards (*Zootoca vivipara*) the immediate and delayed life-history effects of a prolonged food deprivation in the laboratory. We generated groups of fully fed or food deprived yearlings and adults at the end of one breeding season. These lizards were released in sixteen outdoor enclosures together with yearlings and adults from the same food treatment and with food deprived or fully fed juveniles, creating four types of experimental populations. Experimental populations were then monitored during two years, which revealed complex effects of food on life-history trajectories. Food availability had immediate direct effects on morphology and delayed direct effects on immunocompetence and female body condition at winter emergence. Also, male annual survival rate and female growth rate and body size were affected by an interaction between direct effects of food availability and indirect effects on asymmetric competition with juveniles. Reproductive outputs were insensitive to past food availability, suggesting that female common lizards do not solely rely on stored energy to fuel reproduction. Finally, food conditions had socially-mediated intergenerational effects on early growth and survival of offspring through their effects on the intensity of competition. This study highlights the importance of social interactions among cohorts for life-history trajectories and population dynamics in stage-structured populations.

Reference:

Keywords: food deprivation, allocation strategies, asymmetric competition, density dependence, *Zootoca vivipara*

INTRODUCTION

Food availability can have major consequences for life history by affecting the intrinsic quality of individuals. For instance, food deprivation during sexual maturation can have long-term consequences for fecundity, body size and survival (e.g., Beckerman et al., 2003). Likewise, adverse food conditions during the breeding season can compromise the fecundity, immunity, survival and future reproduction of individuals (e.g., Koskela et al., 1998, Martin et al., 2007, Saino et al., 1999, Brommer et al., 2004) and can also influence the performances of their descendants through intergenerational effects (e.g., Plaistow et al., 2006). In some species, poor nutrition during the inter-breeding period may further compromise the restoration of body fat reserves, structural growth, survival until the next breeding and the energy available for future reproduction (Drent & Daan, 1980). The extent to which conditions during breeding and inter-breeding periods are influential depend on resource allocation strategies since income breeders rely on resources acquired recently whereas capital breeders rely on stored energy (Drent & Daan, 1980).

By potentially influencing both the quality and the number of survivors, food availability can affect competition within a population (van de Wolfshaar et al., 2008, de Roos et al., 2003, Beckerman et al., 2003, Mugabo et al., 2010). For example, intraspecific competition is strongly influenced by the size distribution of competitors (Claessen et al., 2000, Bystrom & Andersson, 2005). Therefore, the competitive interactions within and between cohorts of individuals should be influenced by food conditions experienced in the past if these have lasting effects on size distribution. It is well-known that competition plays a major role in life-history evolution and influences importantly the dynamics of size and stage-structured populations (e.g., Claessen et al., 2000, de Roos et al., 2003, Bystrom & Andersson, 2005, van de Wolfshaar et al., 2008). Surprisingly, however, little is known about the effects of past environmental conditions on the intensity and the outcome of intraspecific competition and the consequences of this for life-history variation in structured populations (Mugabo et al., 2010).

Using the common lizard (*Zootoca vivipara*, Jacquin 1787) as a model system, we investigated life-history effects of a food deprivation experienced at the end of the reproductive period and aimed to identify the underlying mechanisms of life-history variation. As many ectotherms, the common lizard can use stored energy to fuel its reproduction (Bleu et al. unpublished data, Avery, 1975), but some data indicate that recently acquired resources

may also be influential (Avery, 1975, Massot & Clobert, 1995). To unravel immediate and delayed life-history effects, we manipulated food availability in the laboratory of yearling and adult males and females. Fully fed and food deprived lizards were then released separately in outdoor enclosures and experimental populations were monitored during two years, thus spanning two breeding seasons. Natural populations of the common lizard are checked by density dependence and asymmetric competition between juveniles, yearlings and adults has been reported (Massot et al., 1992, Lecomte et al., 1994, Mugabo et al., 2010). To unravel how asymmetric interactions between juveniles on one side and adults and yearlings on the other side influence food-mediated life-history effects, adults and yearlings from each food treatment were released in outdoor enclosures with fully fed or food deprived juveniles from the laboratory in a full-factorial design.

In the manipulated cohort of juveniles, we demonstrated earlier that food deprivation in the laboratory had direct immediate negative effects on structural growth but positive long-lasting effects on immunocompetence (Mugabo et al., 2010). Also, food deprivation had indirect delayed effects on the growth, body size, early survival and future reproduction of juveniles mediated by an interaction between its direct effects on individual quality and its indirect effects on the intensity of intercohort social interactions combined with density dependence on body size. In populations with fully fed yearlings and adults, fully fed juveniles maintained their body size advantage over food deprived juveniles until the yearling stage and fully fed females also benefited from a reproductive advantage as they produced more and larger offspring than food deprived females despite similar body size at adulthood. However, fully fed lizards suffered from a lower survival at the juvenile stage than food deprived lizards. In sharp contrast, in populations with food deprived yearlings and adults, food deprived juveniles overcompensated during the following spring for their limited growth early in life. This compensatory growth at the juvenile stage enabled them to reach a larger body size at adulthood and to produce more offspring than fully fed juveniles but was associated with a reduction of juvenile survival (Mugabo et al., 2010).

Here we hypothesize that food deprivation at the yearling and adult stages has strong immediate effects on body condition and to a lesser extent on body size since size growth is limited in adults (Andrews, 1982). Contrary to results obtained in juveniles (Mugabo et al., 2010), males and females should differ in their sensitivity to food conditions because sexes have different energetic requirements and resource allocation strategies at the yearling and adult stages (Le Galliard et al., 2005, González-Suárez et al., 2011). In particular, we predict stronger direct delayed effects of food deprivation in females than in males since this sex

invests more in reproduction (e.g., Aubret et al., 2002). As previously reported for the manipulated cohort of juveniles (Mugabo et al., 2010) and as expected for size-structured populations (see above), life-history variation in yearlings and adults could depend on food conditions experienced by the juveniles they interact with. For instance, faster growth in juveniles could be associated with a larger niche overlapping with yearlings and adults and affect performances of the latter through exploitative competition (Bystrom & Andersson, 2005). If so, we expect males to be less sensitive to competition than females as they are socially dominant over females and juveniles (Lecomte et al., 1994).

METHODS

Model species

Zootoca vivipara is a small (adult snout-vent-length, SVL: 50-75 mm) ovoviviparous lizard inhabiting humid habitats across northern Eurasia. This lacertid species is characterized by a 3-4 years life expectancy, continuous growth and plastic life history that is sensitive to food availability (Le Galliard et al., 2005, Mugabo et al., 2010). Natural populations are structured in three stage classes: juveniles (newborn individuals), yearlings (1-2 years old individuals) and adults. In our study site, males start to emerge from hibernation around the beginning of March, followed shortly by juveniles and by females few weeks later. Reproductive investment (i.e., spermatogenesis and vitellogenesis) occurs within few weeks after winter emergence and the mating period starts shortly after emergence of females (Bauwens et al., 1989, Bauwens & Verheyen, 1985). From June to July, females lay an average of five non-calcified eggs (range 1-12). Offspring hatch shortly after parturition and are immediately autonomous. Lizards enter hibernation in October.

Experimental design

From the 16 June 2006 to the 19 September 2006, we manipulated in the laboratory the daily food consumption of 263 yearling and adult lizards during 50 days. We fed lizards with a combination of larvae of the cricket *Acheta domesticus* and of the moth *Pyralis farinalis* obtained from Kreca Inc. (Ermelo, Holland). We used two food treatments adjusted with food consumption data of wild common lizards (Avery, 1971). In the “high food” treatment group (HF), individuals were fully fed with an average of 200 mg.day⁻¹ whereas in the “low food” treatment group (LF) lizards were maintained under a dietary restriction with an average of 100 mg.day⁻¹. Prey items were weighed each day prior to feeding and non-consumed prey was

removed each week. Animals were captured in outdoor enclosures at the Centre de Recherche en Ecologie Expérimentale et Prédictive (CEREEP, northern France, 48°17'N, 2°41'E; $n = 214$) and in two natural populations (Mont Lozère, 44°27'N, 3°44'E; $n = 49$). Half of the individuals from each origin were randomly assigned to each food treatment and adult females were manipulated from the day after parturition. Before the beginning of the food manipulation, all individuals were marked by toe clipping, sexed, measured for snout-vent length (to the nearest mm) and weighed (to the nearest mg). Food-treatment groups of adults and yearlings did not differ initially in SVL, body condition (estimated from an analysis of covariance of body mass including SVL as a covariate) or sex ratios (ANOVA, all $P > 0.45$). During the manipulation, lizards were kept in individual cages under standardized conditions with optimal thermal and humidity conditions.

At the same time, we manipulated in the laboratory the daily food consumption of 460 juvenile lizards during 50 days from their birth day (detailed procedures are described in Mugabo et al., 2010). Juvenile food treatments did not differ initially in SVL, body condition or sex ratios (ANOVA, all $P > 0.80$) but body size was significantly higher in the HF treatment group than in the LF treatment group after the manipulation ($F_{1,357} = 77.28$, $P < 0.0001$, as previously reported in Mugabo et al., 2010).

At the end of the laboratory manipulation, yearling and adult lizards were measured for body size (SVL) and body mass and then released in 16 outdoor enclosures measuring each 10 by 10 m and located in a natural meadow at the CEREEP. Yearlings and adults from each food treatment (hereafter named “main food treatment”) were released with food deprived or with fully fed juveniles (hereafter named “juvenile food treatment”), generating four different types of experimental populations with four replicates each (i.e., “fully fed” populations in which all lizards have been fully fed, “food deprived” populations, and two types of mixed populations, see Figure 1b in Mugabo et al., 2010). Outdoor enclosures were randomly selected for each treatment group and initial populations had similar age and sex structure (4-5 adult females, 3 adult males, 4-6 yearling females, 4-5 yearling males, 28-34 juveniles). Outdoor enclosures provided lizards with natural food supply, shelters and basking sites, and were protected by nets to avoid avian predation.

Measurements of life-history traits and immunocompetence

Populations were monitored during three successive capture sessions to obtain data of growth in SVL, body condition, survival, reproduction and immunocompetence of yearlings and adults. Capture sessions were from 2 to 5 April 2007 ($n = 110$), from 15 to 31 May 2007 ($n =$

112) and from 19 May to 5 June 2008 ($n = 56$). Growth rates in SVL were calculated as the change in SVL divided by the time interval (number of days elapsed between the initial measurement and the focal measurement minus the number of days spent in hibernation and emergence, assumed to be from the 1 October to 15 March in the study site). We estimated annual survival probabilities in 2007 and in 2008 between release in summer 2006 and May 2007 and between May 2007 and May 2008 respectively. Survival probabilities were directly obtained from recapture data since the catchability (i.e., capture probability) in our experimental system is very close to 1 at this time of the year (Le Galliard et al., 2005). In late spring 2007 and 2008, all females were maintained until parturition in the laboratory to assess their reproductive characteristics. Five of the 69 females recaptured in May 2007 and two of the 43 females recaptured in May 2008 were not gravid. Reproductive characteristics of gravid females were estimated by measuring fecundity (total number of eggs) and postpartum body condition.

We also assessed immunocompetence of manipulated lizards in late spring 2007 and 2008. Immunocompetence was measured by the skin-swelling in response to the injection of a mitogen, the phytohaemagglutinin (PHA), as described by Mugabo et al. (2010). The skin-swelling was calculated as the difference in thickness of the leg (mm) between 12h after and before the injection. This procedure triggers a haemagglutination and lymphoproliferation and evaluates the ability of an individual to mount an inflammatory response (Vinkler et al., 2010 and references therein).

In addition, we gathered data on intergenerational effects of food availability by measuring the SVL at birth of offspring produced by manipulated lizards during the first and second year of the study, and by measuring the body growth and juvenile survival of the cohort of offspring produced during the first year of the study. Numbers of released adults and yearlings, of released juveniles and of offspring born during the experiment were recorded for each population at each capture session to test for density dependence.

Statistical analyses

We analyzed immediate effects of food availability on body condition and SVL at the end of the manipulation with linear models. Explanatory variables included main food treatment (i.e., food treatment of yearlings and adults), sex, age class (yearling and adult classes), and their first-order interactions, as well as additive effects of date at the beginning of the manipulation and geographical origin.

We used mixed-effects linear models to analyze the delayed effects of food treatments on growth rates in SVL, SVL, body condition, female reproductive characteristics and immunocompetence. These models included fixed effects of (i) main food treatment in interaction with juvenile food treatment to account for the manipulation of juveniles, (ii) second-order interactions with sex to test for sexual differences of sensitivity to food treatments, (iii) initial age class (yearling or adult) and first-order interactions with food treatments (iv), as well as additive effects of date at the beginning of the manipulation and geographical origin. A first-order interaction between SVL and sex was included when analyzing body condition to control for sex-specific slopes between body mass and SVL. A fixed effect of initial SVL was included when analyzing growth rates to control for decelerating growth curves (Andrews, 1982) and the number of activity days was included when analyzing SVL to control for differences in release and capture dates. Fecundity generally increases with female’s SVL (Avery, 1975). We therefore tested for effects of treatments on fecundity without and with additive effects of SVL. The random part of all these models included an effect of enclosure identity. We used the restricted maximum likelihood approach of the *lme* procedure to estimate model parameters and test statistics following Pinheiro & Bates (2000). Minimum adequate models were selected by removing non-significant terms in a backward procedure using marginal F tests. Assumptions of normality were fulfilled but Bartlett tests detected variance heterogeneity in some analyses. In these cases, we accounted for heterogeneous variances with a *varIdent* function in *lme* (chapter 5.2 in Pinheiro & Bates, 2000).

Annual survival probabilities in 2007 and 2008 were analyzed with mixed-effects logistic regressions including a logit link and binomial error terms. Models included fixed effects of (i) main food treatment, juvenile food treatment, sex, initial age class and their first-order interactions, (ii) additive effects of initial SVL centered at its grand mean (linear and quadratic effects) to evaluate selection on body size and (iii) additive effects of geographical origin and date at the beginning of the manipulation. The random part of all these models included an enclosure effect. Model parameters were estimated with a Laplace approximation of the maximum likelihood in *lmer* and fixed effects were tested with Wald Z tests (Bolker et al., 2009). A minimum adequate model was obtained by backward elimination of non-significant terms.

We used similar mixed-effects models to analyze intergenerational effects of food treatments on SVL at birth of offspring born during the experiment and on annual growth rate and survival of offspring born in 2007. These models included additive effects of (i) date of

birth of the offspring, (ii) clutch size corrected for female’s SVL (residuals of linear regression of clutch size against SVL) when analyzing SVL at birth of juveniles and (iii) SVL at birth of the offspring when analyzing growth rate (linear effect) and probability of annual survival (linear and quadratic effects). Clutch size was included to control for the classical trade off between offspring quantity and offspring size in lizards (Olsson & Shine, 1997). The random part of all these models included a clutch identity effect nested in an enclosure effect.

Whenever significant effects of food treatments were observed, we tested for density-dependent effects. When analyzing delayed effects of food treatments, we used current numbers of yearlings and adults and numbers of juveniles from each population as covariates. When analyzing intergenerational effects on the growth rates and survival of offspring produced in 2007, we used numbers of offspring and numbers of older conspecifics. All models were implemented in R 2.10.1 software (<http://cran.r-project.org/>) and estimates are provided with standard errors.

Table 1. Immediate effects of food availability on body condition and SVL (mm) at the end of the manipulation in yearlings ($n = 144$) and adults ($n = 119$). LF indicates low food treatment, M indicates males, Y indicates yearlings and C indicates origin CEREEP.

Body condition (body mass controlled for SVL)			
<i>Effects</i>	Estimate ± s.e.	$F_{ndf,ddf}$	<i>P</i> value
Intercept	0.12 ± 0.07	$F_{1,255} = 3.01$	0.08
SVL (mm)	0.10 ± 0.01	$F_{1,255} = 241.37$	<.0001
Sex	M: 0.47 ± 0.05	$F_{1,255} = 84.74$	<.0001
SVL × sex	M: 0.02 ± 0.01	$F_{1,255} = 5.86$	0.02
Main food treatment	LF: -0.44 ± 0.07	$F_{1,255} = 37.36$	<.0001
Age class	Y: -0.59 ± 0.09	$F_{1,255} = 45.93$	<.0001
Main food treatment × age class	LF-Y: 0.26 ± 0.08	$F_{1,255} = 9.57$	0.002
Origin	C: 0.22 ± 0.08	$F_{1,255} = 6.69$	0.01
SVL (mm)			
<i>Effects</i>	Estimate ± s.e.	$F_{ndf,ddf}$	<i>P</i> value
Intercept	59.05 ± 0.56	$F_{1,258} = 10882.84$	<.0001
Main food treatment	LF: -1.08 ± 0.40	$F_{1,258} = 7.29$	0.007
Sex	M: -3.96 ± 0.48	$F_{1,258} = 88.01$	<.0001
Age class	Y: -9.93 ± 0.48	$F_{1,258} = 420.06$	<.0001
Origin	C: 6.23 ± 0.63	$F_{1,258} = 98.70$	<.0001

RESULTS

Immediate effects on morphology

Dietary restriction had immediate, negative effects on the body condition and SVL at the end of the laboratory experiment (Table 1, Figure 1A). Body condition was influenced by an interaction between main food treatment and age class (Table 1). The effect of main food treatment on body condition was stronger in adults than in yearlings (Figure 1A). In addition, SVL at the end of the manipulation was about 1mm larger in fully fed than in food deprived lizards (Table 1). Sex affected both traits independently of main food treatment (main food treatment \times sex: F tests, all $P > 0.09$; see Table 1 for details on sexual differences). Variability in body condition was also greater for adults than for yearlings (Bartlett’s K-squared = 17.72, $df = 1$, $P < 0.0001$, variance ratio = 1.53, Figure 1A).

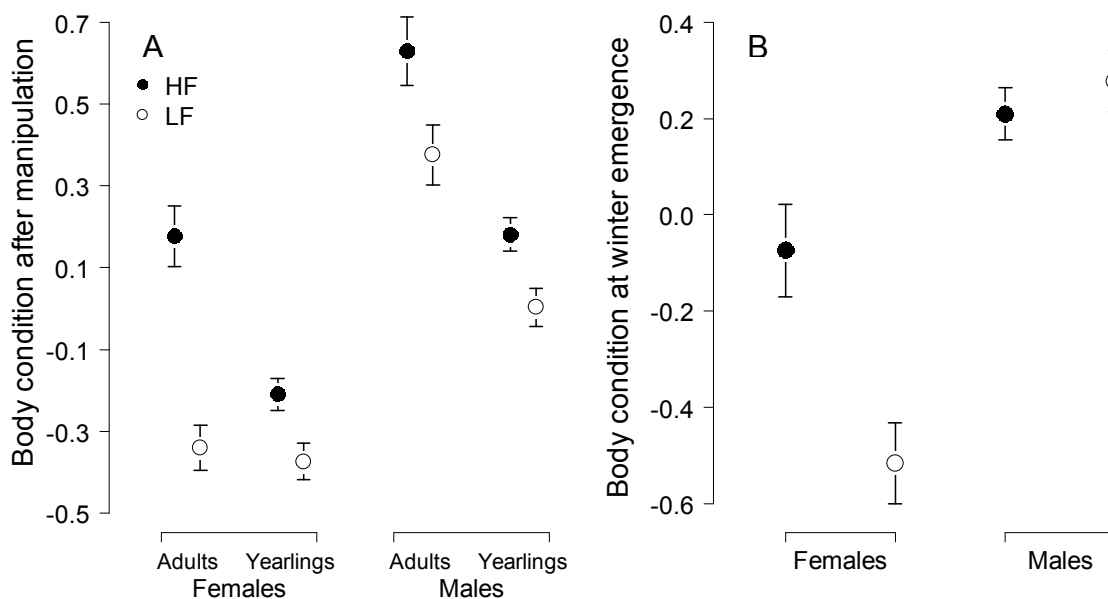


Figure 1. (A) Immediate effects of main food treatment on body condition in female and male adult and yearling common lizards and (B) delayed effects on body condition at winter emergence in females and in males. Data are given as mean values per food-treatment group in each stage \pm s.e. Black symbols: HF main food treatment; white symbols: LF main food treatment.

Delayed effects on life history and immunocompetence

Delayed effects on morphology

Body condition at winter emergence in April 2007 was affected by an interaction between main food treatment and sex ($F_{1,87} = 13.88$, $P = 0.0003$). LF females were less corpulent than

HF females (*post-hoc* test: $F_{1,13} = 12.15$, $P = 0.004$) whereas in males body condition was similar between food-treatment groups ($F_{1,13} = 0.13$, $P = 0.72$, Figure 1B). In addition, body condition at winter emergence was significantly higher ($F_{1,87} = 18.15$, $P = 0.0001$, Figure 1B; sex-specific slopes between body mass and SVL: $F_{1,83} = 0.69$, $P = 0.41$) but less variable (Bartlett's K-squared = 5.68, $df = 1$, $P = 0.02$, variance ratio = 0.77) in males than in females.

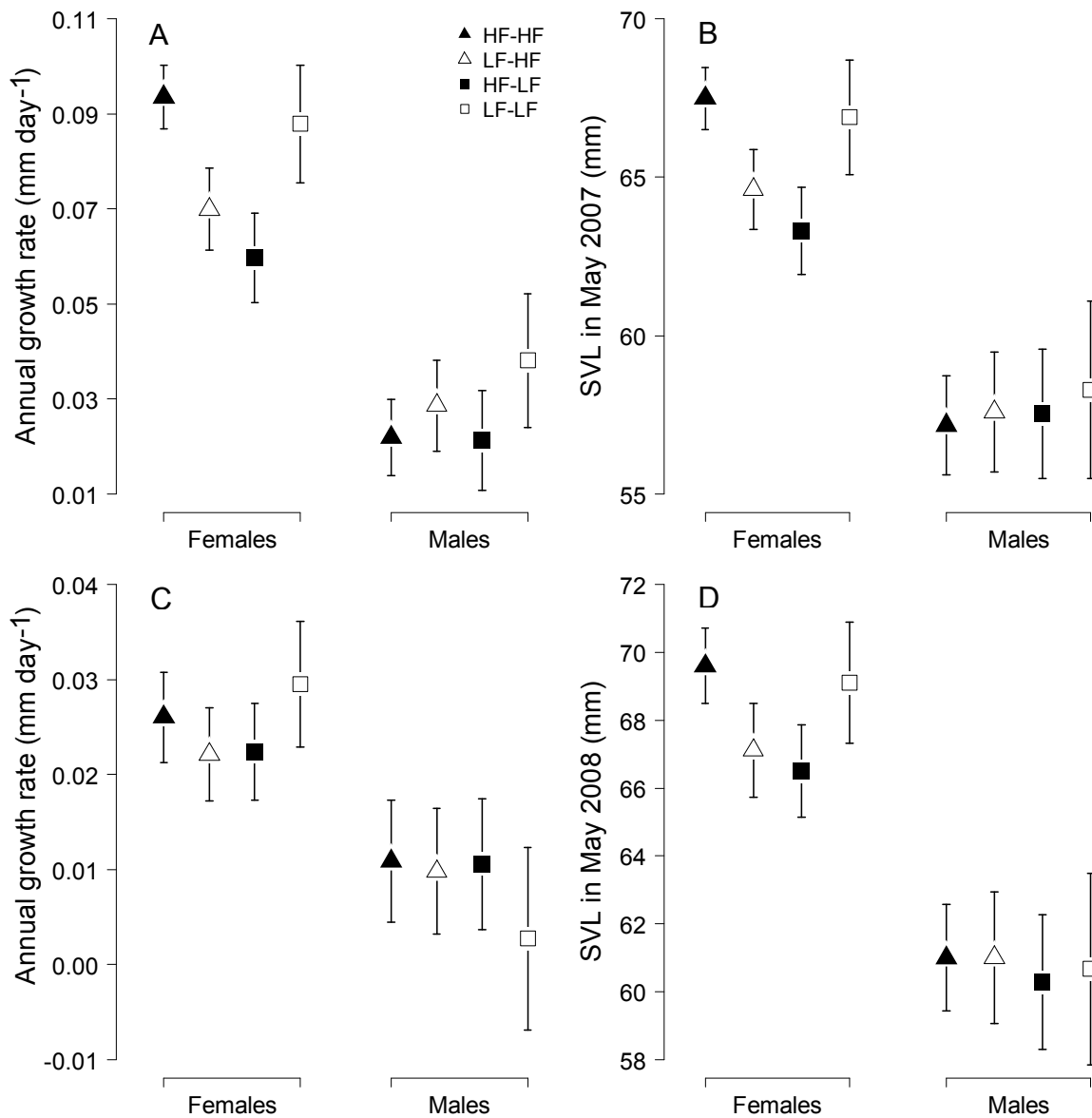


Figure 2. Delayed effects of main food treatment and juvenile food treatment on the annual growth rates and SVL of females and males during the (A, B) first and the (C, D) second year of the experiment. (A-D) Estimates were obtained from linear mixed effect models with fixed effects of main food treatment, juvenile food treatment, sex and their second-order interactions and (A, C) additive effects of initial SVL centered at its grand mean. (C) The negative values of annual growth rate are due to measurement errors (± 1 mm in adults). Black symbols: HF main food treatment; white symbols: LF main food treatment; triangles: HF juvenile food treatment; squares: LF food treatment.

Annual growth rates during the first year of the field experiment and SVL in May 2007 were both affected by a three-way interaction between main food treatment, juvenile food treatment and sex (respectively: $F_{1,90} = 11.19$, $P = 0.001$ and $F_{1,90} = 7.08$, $P = 0.009$). When maintained with HF juveniles, HF females grew to be larger than LF females (*post-hoc* tests for growth rate: $F_{1,6} = 11.96$, $P = 0.01$; for SVL: $F_{1,6} = 5.41$, $P = 0.06$, Figure 2) whereas the opposite was observed when females were maintained with LF juveniles (growth rate: $F_{1,6} = 13.57$, $P = 0.01$; SVL: $F_{1,6} = 6.44$, $P = 0.04$, Figure 2). These effects were not observed in males (growth rate and SVL, main \times juvenile food treatment: $F_{1,7} = 1.11$, $P = 0.33$ and $F_{1,7} = 0.11$, $P = 0.75$). Growth rate was marginally higher in LF than in HF males ($F_{1,9} = 3.78$, $P = 0.08$) and SVL was similar between LF and HF males ($F_{1,9} = 0.41$, $P = 0.54$, Figure 2). Numbers of conspecifics in May 2007 did not explain this variation of annual growth rate and SVL in males and females.

During the second year of the experiment, annual growth rate and SVL were no longer affected by the three-way interaction (respectively: $F_{1,38} = 3.57$, $P = 0.07$; $F_{1,37} = 1.79$, $P = 0.19$) nor by main food treatment effects (respectively: $F_{1,10} = 0.01$, $P = 0.95$; $F_{1,11} = 0.75$, $P = 0.41$). However, the pattern of body growth and SVL for females was very similar to the one of the first year (Figure 2), suggesting that we lacked power to detect a significant effect. In both years, females grew more and were larger than males (F tests, all $P < 0.0001$) and growth rates decreased with initial SVL (F tests, all $P < 0.0001$).

Delayed effects on annual survival

Probability of annual survival during the first year of the experiment was affected by an interaction between main food treatment, juvenile food treatment and sex ($Z = -2.64$, $P = 0.008$). Annual survival was affected by an interaction between main food treatment and juvenile food treatment only in males (in females: $Z = -0.21$, $P = 0.83$; in males: $Z = -2.23$, $P = 0.02$). Fully fed males but not females had a lower annual survival rate than food deprived males when maintained with fully fed juveniles (*post-hoc* tests in males: $Z = 2.08$, $P = 0.04$; in females: $Z = 1.00$, $P = 0.32$) but not in populations with food deprived juveniles (*post-hoc* tests in males: $Z = -1.09$, $P = 0.27$; in females: $Z = 0.91$, $P = 0.36$, Figure 3A). Annual survival during the first year was higher in yearlings than in adults (yearlings = 0.48 ± 0.07 , adults = 0.32 ± 0.08 ; $Z = 2.67$, $P = 0.008$), with no significant influence of body size (SVL: $Z = 1.77$, $P = 0.08$; SVL²: $Z = 0.47$, $P = 0.64$). During the second year of the experiment, annual survival rates were not affected by food treatments (Wald Z tests, all $P > 0.11$) and males and females had similar survival rates ($Z = 1.38$, $P = 0.17$, Figure 3B).

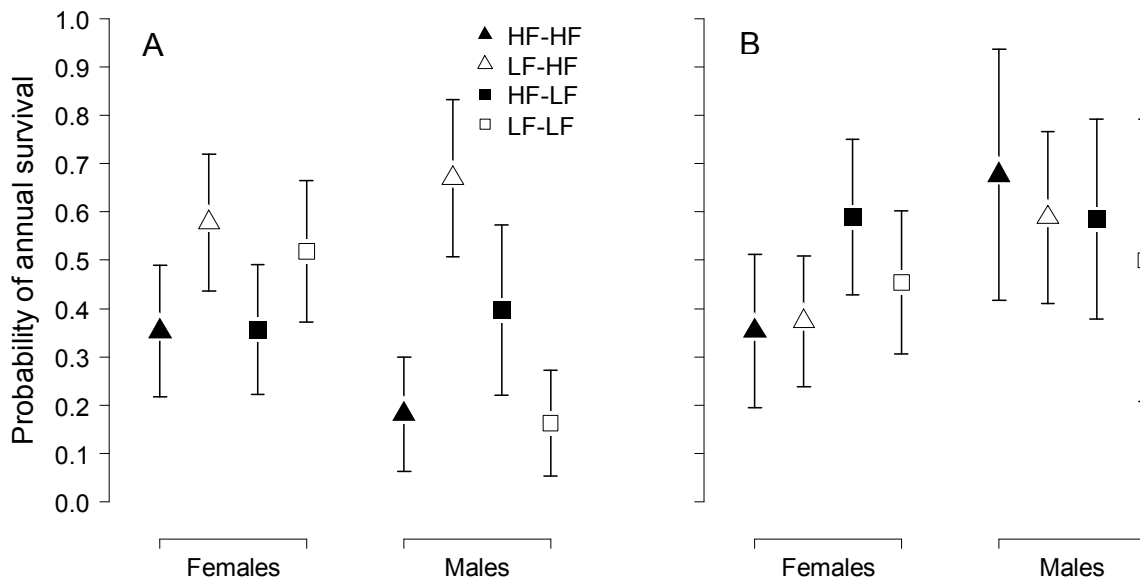


Figure 3. Delayed effects of main food treatment and juvenile food treatment on the probability of annual survival of females and males during (A) the first and (B) the second year of the experiment. Estimates were obtained from generalized mixed effect models with main and juvenile food treatment and their interaction as fixed factors. Symbols as in Figure 2.

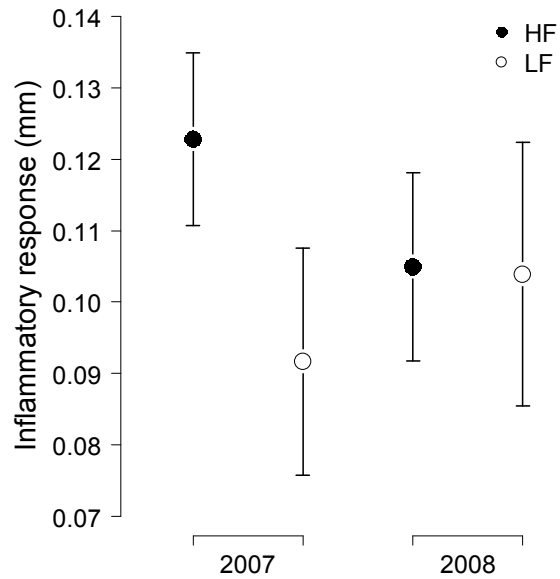
Delayed effects on reproduction

Fecundity recorded in 2007 was not affected by food treatments, despite a strong positive effect of body size (fecundity not controlled for SVL: F tests, all $P > 0.14$; fecundity controlled for SVL: F tests, all $P > 0.08$; SVL: $F_{1,51} = 33.12$, $P < 0.0001$). Similarly, fecundity in 2008 was not affected by food treatments when controlling or not for SVL of females (F tests, all $P > 0.10$). In addition, postpartum body condition in 2007 and 2008 was not affected by food treatments (F tests, all $P > 0.11$). Postpartum body condition was lower in yearlings than in adults in 2007 ($F_{1,49} = 17.61$, $P = 0.0001$) but not in 2008 ($F_{1,18} = 2.56$, $P = 0.13$).

Delayed effects on immune performances

Main food treatment marginally affected immune performances in 2007 ($F_{1,14} = 3.83$, $P = 0.07$) and had no effect in 2008 ($F_{1,10} = 0.15$, $P = 0.70$). In 2007, HF lizards displayed a higher inflammatory response than LF lizards (Figure 4). Immune performances in 2007 and 2008 were not correlated (Pearson’s product moment correlation: $r = 0.03$ [-0.29, 0.34], $P = 0.87$) and did not differ between sexes and age classes (F tests, all $P > 0.13$).

Figure 4. Delayed effects of main food treatment on inflammatory response in 2007 and 2008. Data are given as mean values per group \pm s.e.



Intergenerational effects

The SVL at birth of offspring born from manipulated lizards in 2007 and in 2008 was not affected by food treatments (F tests, all $P > 0.16$, Figure 5A). SVL at birth decreased with clutch size in 2007 ($F_{1,44} = 10.14$, $P = 0.003$) but not in 2008 ($F_{1,13} = 2.11$, $P = 0.17$) and was lower for male offspring (in 2007: $F_{1,249} = 92.36$, $P < 0.0001$; in 2008: $F_{1,162} = 57.76$, $P < 0.0001$). In addition, growth rate of offspring born in 2007 during their first year of life was not affected by food treatments (Figure 5B), irrespective of whether we controlled for density dependence (F tests, all $P > 0.23$) or not (F tests, all $P \geq 0.1$). Growth rate of offspring decreased with the number of older conspecifics (slope: -0.0014 ± 0.0003 , $F_{1,11} = 28.00$, $P = 0.0003$) and female offspring grew faster than males ($F_{1,80} = 14.55$, $P = 0.0003$).

In contrast, annual survival of offspring born in 2007 was affected by a two-way interaction between main food treatment and juvenile food treatment ($Z = -2.34$, $P = 0.02$). When maintained with HF juveniles, offspring born from HF females had a lower survival than those born from LF females ($Z = 2.07$, $P = 0.04$) whereas such a difference was reverse but not significant when offspring were maintained with LF juveniles ($Z = 1.26$, $P = 0.21$, Figure 5c). We found no effect of cohort densities, SVL at birth (linear and quadratic) and date of birth on offspring survival (Wald Z tests, all $P > 0.26$), but male offspring survived better than females ($Z = 2.03$, $P = 0.04$).

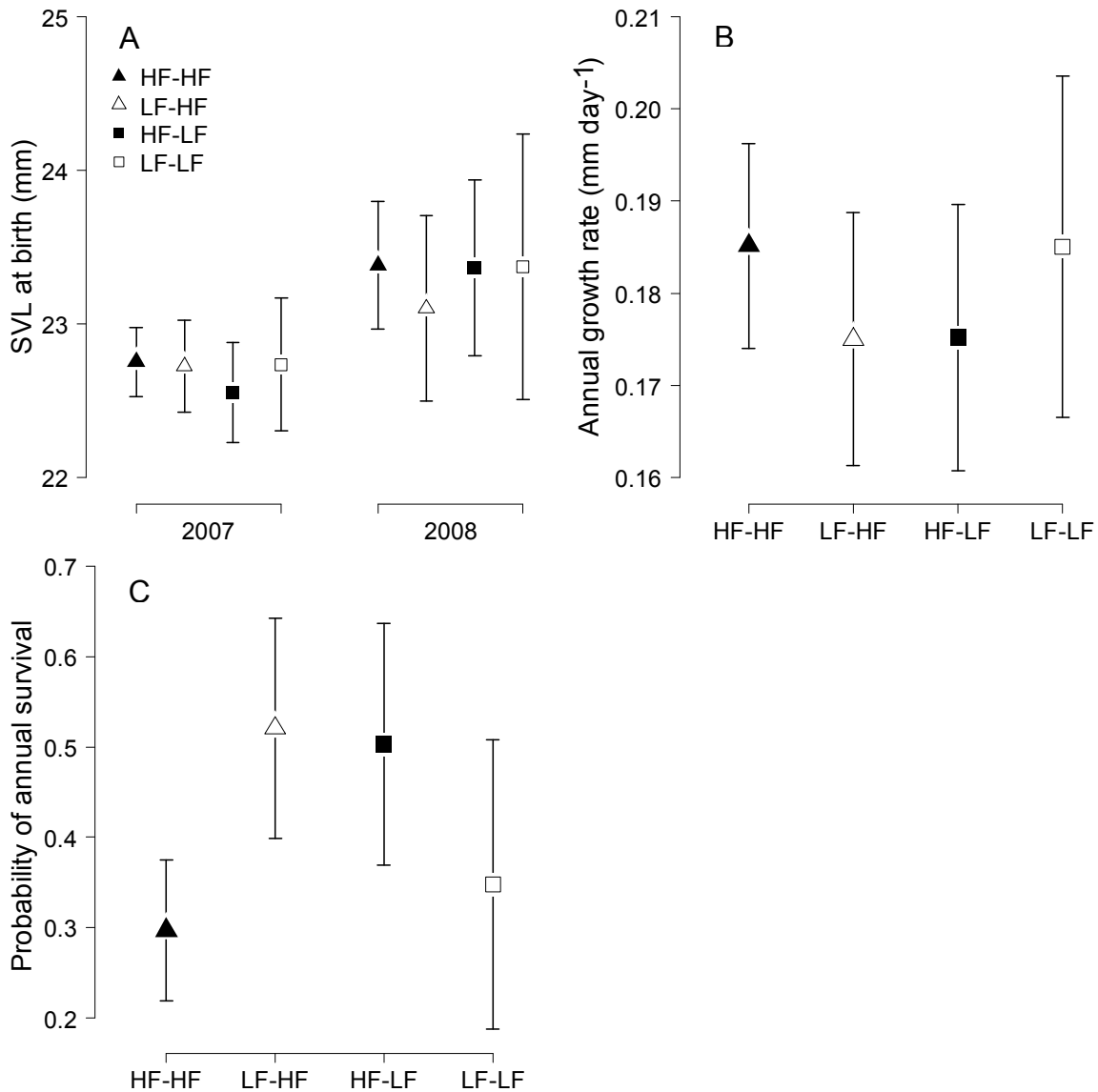


Figure 5. Intergenerational effects of main food treatment and juvenile food treatment on (A) the SVL at birth of offspring born in 2007 and 2008 and (B) on the annual growth rate and (C) annual survival probability of offspring born in 2007 during their first year of life. (A, B) Estimates (\pm se) were obtained from linear mixed effects models including main food treatment, juvenile food treatment and their interaction as fixed factors. (C) Estimates (\pm se) were obtained from generalized mixed effects models including main food treatment, juvenile food treatment and their interaction as fixed factors. Symbols as in Figure 2.

DISCUSSION

Immediate effects of food availability on morphology

A prolonged food deprivation during the summer had immediate negative effects on body condition and body size of yearlings and adults, which emphasizes a classical reduction of body fat reserves, muscular mass and structural growth at low food availability (Kooijman, 2000). These immediate effects of food deprivation on body condition were stronger in adults

than in yearlings. During the food manipulation, yearlings and adults received the same amounts of food. Yet, yearlings were substantially smaller than adults and thus had less energetic requirements for maintenance than adults (Kooijman, 2000), which allow them to capitalize more efficiently on available resources. Furthermore, the immediate effects of food deprivation were similar in males and females despite the existence of substantial sexual differences in body size and body condition (males are smaller but more corpulent than females) and thus in body composition (e.g., in muscles and body fat, Kratochvil et al., 2003). This result indicates that male and female lizards have a similar flexibility of their energy allocation strategy to body condition and structural growth at that time of the year. This is surprising because female common lizards spend large amounts of energy in vitellogenesis and gestation and body size is important for their fecundity, whereas energetic investment of males in production of gametes is less important (Avery, 1975, Nagy, 1983). We would therefore expect stronger sensitivity of growth allocation in females than in males. However, male mating behaviors can be costly in this species. Mating activity (e.g., mate searching and acquisition and multiple copulations) may limit the food intake of males (González-Suárez et al., 2011) and male-male aggressions have been reported in a mating experiment (Fitze et al., 2008). Body size is also an important determinant of the mating success of male common lizards (Fitze & Le Galliard, 2008). In addition, males emerge from hibernation few weeks before females and expose themselves to adverse food and climatic conditions where body fat reserves and muscular mass are critical for survival. Therefore, male and female common lizards may experience similar selection for an optimal body condition and body size (Schwarzkopf, 1994), thus explaining their parallel flexibility to food availability.

Direct delayed effects of food availability on life history

In accordance with our expectations, some lasting effects of food deprivation were seen for body condition in females, indicating that males but not females were able to fully compensate before hibernation for the immediate effects of food deprivation. Since males and females did not differ in their immediate sensitivity to food deprivation, this result suggests that sexes differed in their acquisition and/or allocation of energy before and during wintering. For example, food deprived yearling and adult males may have limited compensatory responses in females through dominance in competition for food (Lecomte et al., 1994, Massot et al., 1992). However, even in females, main effects of food deprivation did not last until the end of spring following winter emergence, since food deprived and fully fed females had similar fecundity and postpartum body condition during the two years of the

experiment. This ability to compensate for a lower body condition at the onset of reproduction and to invest similar amounts of energy in reproduction throughout life demonstrates that, as female geckos (Kubicka & Kratochvil, 2009), female common lizards can use energy acquired during vitellogenesis to fuel reproduction, i.e., an income breeder strategy. This result agrees with a study by Avery (1975) which suggested that female common lizards invest in egg production energy acquired during vitellogenesis and to a lesser extent stored energy.

Socially mediated delayed effects of food availability on life history

During the first year of the field experiment, annual growth rates and body size of females and annual survival rates of males were affected by an interaction between food conditions they experienced in the past and food conditions experienced by juveniles from the same population. Altogether, these results indicate that the delayed life-history effects of food deprivation for yearlings and adults depended on social interactions with juveniles and not on intracohort interactions (traits were insensitive to cohort densities). Comparable socially-mediated life-history effects were found for juveniles, except that no sexual differences were detected (see Mugabo et al., 2010 and our introduction). Yet, substantial life-history differences existed between the adults and yearlings on one side and the juveniles on the other side, suggesting that different mechanisms may be involved.

A similar pattern of survival was observed for juveniles and for yearling and adult males but not for females. In the common lizard, yearling and adult males and juveniles have similar activity periods that differ from the activity period of females. Males and juveniles emerge from hibernation in late winter, few weeks before yearling and adult females, when environmental conditions are suboptimal and risks of starvation are high (Bauwens et al., 1989, Bauwens & Verheyen, 1985). This difference of phenology may explain why annual survival of females was not affected by food treatments. In “fully fed” populations (i.e., HF-HF treatment group), fully fed yearling and adult males and juveniles suffered from a lower survival than after a food deprivation. This result suggests that the intensity of competition was increased when both juveniles and older lizards experienced favorable past food conditions. Since males are socially dominant over females and juveniles (Lecomte et al., 1994) and since females were not affected, we hypothesized that this increased competition gave rise to survival costs within the few weeks after winter emergence of juveniles and males and before emergence of females. We also speculate that a combination of two mechanisms may have contributed to this high level of competition between juveniles and yearlings and

adults in “fully fed” populations compared to other populations (Mugabo et al., 2010). First, large juveniles should be more affected by competition with older conspecifics than small juveniles due to a larger niche overlapping. Second large and corpulent yearlings and adults may compete more with juveniles than small and thin individuals due to the higher social rank and to the energetic requirements associated with a larger body mass (Kooijman, 2000). Exploitative competition (Bystrom & Andersson, 2005) more than an increase of aggressive behaviors (Claessen et al., 2000) or a change in resource exploitation behaviors (Lecomte et al., 1994) could be responsible for the mortality of juveniles and yearling and adult males. Indeed, juveniles from “fully fed” populations did not suffer from more aggression or predation attempts than juveniles from other populations (estimated by tail loss, Mugabo et al., 2010). However, behavioral data combined with estimates of food consumption and resource availability would be needed to validate these hypotheses. In “food deprived” populations (i.e., LF-LF treatment group), food deprived juveniles (Mugabo et al., 2010) but not adult and yearling males suffered from a significant reduction in survival relative to fully fed lizards. In these populations, Mugabo et al. (2010) observed that juveniles showed a strong overcompensatory growth, whereas males only showed a marginal compensatory growth in this study. Thus, some physiological costs of compensation (reviewed in Metcalfe & Monaghan, 2001) rather than ecological costs of competition could be responsible for the lower survival of food deprived juveniles in these populations (Mugabo et al., 2010).

Similar patterns of growth rates and body size were observed for juveniles and for yearling and adult females but not for males. Two non-exclusive mechanisms could explain this. First, investment in structural growth may be too limited in reproductive males to be substantially affected by competition with juveniles (Schwarzkopf, 1994, Andrews, 1982). Second, when environmental conditions were more favorable for body growth (i.e., from April-May to September), male performances may have been insensitive to competition due to their social dominance (Lecomte et al., 1994). When maintained with food deprived conspecifics (i.e., LF-LF treatment group), both food deprived old females (this study) and food deprived juveniles (Mugabo et al., 2010) displayed overcompensatory growth. In these populations, a limited level of competition for food between juveniles and yearling and adult females may have provided favorable conditions for compensatory responses to occur. In sharp contrast, when maintained with fully fed conspecifics (i.e., HF-HF treatment group), both fully fed females (this study) and fully fed juveniles (Mugabo et al., 2010) benefited from a “silver spoon effect” on body size, i.e., long-term fitness advantages of past favorable conditions (Grafen, 1988). They reached a higher body size than food deprived females and

juveniles and fully fed females even displayed higher growth rate. In juveniles, we hypothesized previously that competition with fully fed yearlings and adults prevented food deprived juveniles from compensating for their limited growth early in life (Mugabo et al., 2010). Fully fed juveniles thus maintained the body size advantage they acquired in the laboratory over food deprived juveniles. Here, we suggest that fully fed females were able to maintain higher growth rates than food deprived females even after the food manipulation because of their higher competitive abilities than juveniles (Lecomte et al., 1994). Another possibility is that juveniles invest more energy in structural growth whereas older individuals invest more energy in body condition (Andrews, 1982). Contrary to juveniles, fully fed females did accumulate additional stored energy during the food manipulation and were able to reinvest a substantial part of this energy in structural growth during the following spring. This result raises the need for a better understanding of energy allocation strategies in this species (Kooijman, 2000).

Female fecundity during the first year of the experiment was similar between treatment groups, despite the existence of significant differences in body size and significant effects of body size on reproductive outputs. This result differs from what was observed in the manipulated cohort of juveniles (Mugabo et al., 2010). Contrary to juveniles, fast growth in yearling and adult females facilitated by full-feeding may entail reproductive costs rather than survival costs, e.g., a negative trade-off between growth rate and future reproduction (Schwarzkopf, 1994, Heino & Kaitala, 1999). Altogether, these results demonstrate that females are not more affected than males by competition with juveniles but that sensitivity of life-history traits to competition with juveniles is contrasted between sexes. Differences in phenology and in energy acquisition and allocation could explain this heterogeneity between sexes and traits.

Direct delayed effects of food availability on immunocompetence

In sharp contrast with life-history traits, immunocompetence was affected by lasting effects of the main food treatment but was insensitive to juvenile food treatment. Such a discrepancy was also observed in the manipulated cohort of juveniles (see Mugabo et al., 2010) and suggests a decoupling between immunity and life-history variation in the common lizard. The lasting effects of food deprivation were opposite for yearlings and adults (this study) than for juveniles (Mugabo et al., 2010): food deprivation had marginal immunosuppressive effects in yearlings and adults after one year in the field, whereas food deprived juveniles had higher immune responses during the two years of the field study. Developmental plasticity may be

responsible for these age-specific effects of a food deprivation on immunocompetence (Bateson et al., 2004). Indeed, in developing individuals, a food deprivation may alter the construction of the immune system leading to a higher investment in immunity throughout life compared to individuals which experienced early good conditions (Birkhead et al., 1999, Tschirren et al., 2009). In grown and non-developing individuals, a decrease of energetic resources is expected to inhibit immune responses (Martin et al., 2007). In addition, differences of the inflammatory responses of yearlings and adults between the first and the second year of the field experiment could be explained by the activation of different components of the immune system between the first and the second encounter with PHA (e.g., activation of acquired immunity at the second encounter Vinkler et al., 2010 and references therein).

Intergenerational effects of food availability

Intergenerational effects of the environment experienced by the mother have been described in many taxa (e.g., in humans, Lummaa & Clutton-Brock, 2002, in squamates, Marquis et al., 2008, and in soil mites, Plaistow et al., 2006). Here, contrary to our expectations, quality at birth and early performances of offspring were not affected by past food conditions experienced by mothers. However, early performances of offspring were influenced by our treatments through similar, socially-mediated effects than the one detected for juveniles (Mugabo et al., 2010) and for adults and yearlings (this study). First, offspring early growth rate was negatively affected by the number of older conspecifics (i.e., manipulated adults, yearlings and juveniles) inside the population of birth. Second, offspring early survival varied similarly to survival in males and juveniles, suggesting an intergenerational effect of past food conditions through the intensity of intercohort competition. These results indicate that food conditions have the potential to influence the performances of individuals across generations not only through direct effects on the intrinsic quality of individuals (Plaistow et al., 2006) but also through indirect effects on their social environment.

ACKNOWLEDGEMENTS

We thank B. Decencière, M. Paquet and all students for assistance in the field. Raoul Van Damme and two anonymous reviewers made useful suggestions to increase the quality of a previous version of this article. This research was supported by the *Centre National de la Recherche Scientifique* (CNRS), an *Agence Nationale de la Recherche* (ANR) grant (07-JCJC-0120) to J.F.L.G., grants from the *Institut Federatif Ecologie-Biodiversité-Evolution-*

M. Mugabo – Caractérisation des interactions entre la structure de population et l'histoire de vie

Environnement (IFR 101) and a grant from the Région Île-de-France (*Réseau de Recherche sur le Développement Soutenable* R2DS 2007-006) to J.-F. L.G. and M. M.

REFERENCES

- Andrews, R. M. (1982) Patterns of growth in reptiles. In: *Biology of the Reptilia*, Vol. 13 (Gans, G. & Pough, F. H., eds.). pp. 273-320. Academic Press, New York.
- Aubret, F., Bonnet, X., Shine, R. & Lourdais, O. 2002. Fat is sexy for females but not males: the influence of body reserves on reproduction in snakes (*Vipera aspis*). *Hormones and Behavior* **42**: 135-147.
- Avery, R. A. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology* **40**: 351-365.
- Avery, R. A. 1975. Clutch size and reproductive effort in the lizard *Lacerta vivipara* Jacquin. *Oecologia* **19**: 165-170.
- Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R. A., Gluckman, P., Godfrey, K., Kirkwood, T., Lahr, M. M., McNamara, J., Metcalfe, N. B., Monaghan, P., Spencer, H. G. & Sultan, S. E. 2004. Developmental plasticity and human health. *Nature* **430**: 419-421.
- Bauwens, D., van Damme, R. & Verheyen, R. F. 1989. Synchronization of spring molting with the onset of mating behavior in male lizards, *Lacerta vivipara*. *Journal of Herpetology* **23**: 89-91.
- Bauwens, D. & Verheyen, R. F. 1985. The timing of reproduction in the lizards *Lacerta vivipara*: differences between individual females. *Journal of Herpetology* **19**: 353-364.
- Beckerman, A., Benton, T. G., Lapsley, C. T. & Koesters, N. 2003. Talkin' 'bout my generation: environmental variability and cohort effects. *American Naturalist* **162**: 754-767.
- Birkhead, T. R., Fletcher, F. & Pellatt, E. J. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proceedings of the Royal Society B-Biological Sciences* **266**: 385-390.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**: 127-135.
- Brommer, J. E., Karell, P. & Pietiainen, H. 2004. Supplementary fed Ural owls increase their reproductive output with a one year time lag. *Oecologia* **139**: 354-358.

- Bystrom, P. & Andersson, J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (*Arctic char*). *Oikos* **110**: 523-536.
- Claessen, D., de Roos, A. M. & Persson, L. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. *American Naturalist* **155**: 219-237.
- de Roos, A. M., Persson, L. & McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* **6**: 473-487.
- Drent, R. H. & Daan, S. 1980. The prudent parent - energetic adjustments in avian breeding. *Ardea* **68**: 225-252.
- Fitze, P. S., Cote, J., Martinez-Rica, J. P. & Clobert, J. 2008. Determinants of male fitness: disentangling intra- and inter-sexual selection. *Journal of Evolutionary Biology* **21**: 246-255.
- Fitze, P. S. & Le Galliard, J.-F. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. *Ecology Letters* **11**: 432-439.
- González-Suárez, M., Mugabo, M., Decencièrè, B., Perret, S., Claessen, D. & Le Galliard, J. F. 2011. Disentangling the effects of predator body size and prey density on prey consumption in a lizard. *Functional Ecology* **25**: 158-165.
- Grafen, A. (1988) On the uses of data on lifetime reproductive success. In: *Reproductive Success*, (Clutton-Brock, T. H., ed.). pp. 454-471. University of Chicago Press, Chicago.
- Heino, M. & Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology* **12**: 423-429.
- Kooijman, S. A. L. M. 2000. *Dynamic energy and mass budgets in biological systems*. Cambridge University Press, Cambridge.
- Koskela, E., Jonsson, P., Hartikainen, T. & Mappes, T. 1998. Limitation of reproductive success by food availability and litter size in the bank vole, *Clethrionomys glareolus*. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**: 1129-1134.
- Kratochvil, L., Fokt, M., Rehak, I. & Frynta, D. 2003. Misinterpretation of character scaling: a tale of sexual dimorphism in body shape of common lizards. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **81**: 1112-1117.

- Kubicka, L. & Kratochvil, L. 2009. First grow, then breed and finally get fat: hierarchical allocation to life-history traits in a lizard with invariant clutch size. *Functional Ecology* **23**: 595-601.
- Le Galliard, J.-F., Ferrière, R. & Clobert, J. 2005. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* **111**: 368-376.
- Lecomte, J., Clobert, J., Massot, M. & Barbault, R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. *Ecoscience* **1**: 300-310.
- Lummaa, V. & Clutton-Brock, T. 2002. Early development, survival and reproduction in humans. *Trends in Ecology & Evolution* **17**: 141-147.
- Marquis, O., Massot, M. & Le Galliard, J.-F. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. *Ecology* **89**: 2575-2583.
- Martin, L. B., Navara, K. J., Weil, Z. M. & Nelson, R. J. 2007. Immunological memory is compromised by food restriction in deer mice *Peromyscus maniculatus*. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology* **292**: R316-R320.
- Massot, M. & Clobert, J. 1995. Influence of maternal food availability on offspring dispersal. *Behavioral Ecology and Sociobiology* **37**: 413-418.
- Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**: 1742-1756.
- Metcalf, N. B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution* **16**: 254-260.
- Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. *Journal of Evolutionary Biology* **23**: 1886-1898.
- Nagy, K. A. (1983) Ecological energetics. In: *Lizard ecology: studies of a model organism*, (Huey, R. B., Pianka, E. R. & Schoener, T. W., eds.). pp. 24-54. Harvard University Press, Cambridge.
- Olsson, M. & Shine, R. 1997. The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). *American Naturalist* **149**: 179-188.
- Pinheiro, J. C. & Bates, D. M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer Verlag, New York.

- Plaistow, S. J., Lapsley, C. T. & Benton, T. G. 2006. Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. *American Naturalist* **167**: 206-215.
- Saino, N., Calza, S., Ninni, P. & Moller, A. P. 1999. Barn swallows trade survival against offspring condition and immunocompetence. *Journal of Animal Ecology* **68**: 999-1009.
- Schwarzkopf, L. (1994) Measuring trade-offs: a review of studies of cost of reproduction in lizards. In: *Lizard ecology: historical and experimental perspectives*, (Vitt, L. J. & Pianka, E. R., eds.). pp. 7-29. Princeton University Press, Princeton.
- Tschirren, B., Rutstein, A. N., Postma, E., Mariette, M. & Griffith, S. C. 2009. Short- and long-term consequences of early developmental conditions: a case study on wild and domesticated zebra finches. *Journal of Evolutionary Biology* **22**: 387-395.
- van de Wolfshaar, K. E., de Roos, A. M. & Persson, L. 2008. Population feedback after successful invasion leads to ecological suicide in seasonal environments. *Ecology* **89**: 259-268.
- Vinkler, M., Bainova, H. & Albrecht, T. 2010. Functional analysis of the skin-swelling response to phytohaemagglutinin. *Functional Ecology* **24**: 1081-1086.

CHAPITRE 4 – Densité de population et interactions trophiques proies-prédateurs

Dénouer les effets de la taille du prédateur et de la densité de proies sur la consommation de proies chez un lézard

Manuela González-Suárez^{1,2}, Marianne Mugabo¹, Beatriz Decencièrè³, Samuel Perret³, David Claessen^{1,4}, & Jean-François Le Galliard^{1,3}

¹ CNRS/UPMC/ENS 7625, Écologie & Évolution, Université Pierre et Marie Curie, 7 Quai St Bernard, 75005 Paris, France.

²Current address: Department of Conservation Biology, Estación Biológica de Doñana-CSIC, Calle Américo Vespucio s/n, 41092 Sevilla, Spain.

³ CNRS/UPMC/ENS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours, France.

⁴CERES-ERTI, École Normale Supérieure, 24 Rue Lhomond, 75005 Paris, France.

Titre courant : Prédation densité- et taille-dépendante

Référence : González-Suárez, M., Mugabo, M., Decencièrè, B., Perret, S., Claessen, D. & Le Galliard, J.-F. 2011. « Disentangling the effects of predator body size and prey density on prey consumption in a lizard ». *Functional Ecology* **25** : 158-165.

RÉSUMÉ

1. Comprendre les déterminants proximaux des taux de prédation est une question centrale en écologie. Les études utilisent souvent des modèles de réponse fonctionnelle (densité dépendants) ou des modèles allométriques (masse dépendants) mais les approches considérant des facteurs multiples sont cruciales pour saisir la complexité des interactions proie-prédateur.
2. Des estimations de la consommation de nourriture et de l’abondance de proies ont été obtenues dans 21 populations semi-naturelles du lézard *Zootoca vivipara*. Nous avons identifié la fonction de taux d’alimentation la plus parcimonieuse parmi des modèles allométriques, de réponse fonctionnelle simple et de réponse fonctionnelle allométrique. Chaque groupe incluait des effets du sexe et des conditions climatiques.
3. Les modèles allométriques révèlent l’importance de la masse et du sexe du prédateur. Les modèles de réponse fonctionnelle montrent que l’effet de la densité de proies est le mieux représenté par un modèle de réponse Holling de type II incluant un taux d’attaque masse-, sexe et climat-dépendant et un temps de manipulation constant. Cependant, le meilleur modèle de réponse fonctionnelle a reçu un soutien modéré comparé à des modèles allométriques plus simples basés uniquement sur la masse et le sexe du prédateur.
4. En dépit de cet effet limité des densités de proies sur le taux d’alimentation, nous avons détecté une relation significativement négative entre un index de biomasse des proies préférées et la densité de lézards.
5. Les modèles de réponse fonctionnelle qui ignorent la variation individuelle sont susceptibles de mal représenter les interactions trophiques. Cependant, des modèles plus simples basés sur des traits individuels pourraient recevoir un meilleur support par certaines données que des réponses fonctionnelles allométriques complexes. Ces résultats illustrent l’importance de considérer des effets individuels, populationnels et environnementaux en explorant également des modèles simples.

Mots-clés : expérience de terrain, réponse fonctionnelle, Lacertidés, parcimonie, interaction proie-prédateur, effet taille.

Disentangling the effects of predator body size and prey density on prey consumption in a lizard

Manuela González-Suárez^{1,2}, Marianne Mugabo¹, Beatriz Decencièrè³, Samuel Perret³, David Claessen^{1,4}, & Jean-François Le Galliard^{1,3}

¹ CNRS/UPMC/ENS 7625, Écologie & Évolution, Université Pierre et Marie Curie, 7 Quai St Bernard, 75005 Paris, France.

² Current address: Department of Conservation Biology, Estación Biológica de Doñana-CSIC, Calle Américo Vespucio s/n, 41092 Sevilla, Spain.

³ CNRS/UPMC/ENS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours, France.

⁴ CERES-ERTI, École Normale Supérieure, 24 Rue Lhomond, 75005 Paris, France.

Running title: Density- and size-dependent predation

Reference: González-Suárez, M., Mugabo, M., Decencièrè, B., Perret, S., Claessen, D. & Le Galliard, J.-F. 2011. Disentangling the effects of predator body size and prey density on prey consumption in a lizard. *Functional Ecology* **25**: 158-165.

ABSTRACT

1. Understanding proximate determinants of predation rates is a central question in ecology. Studies often use functional response (density dependent) or allometric (mass dependent) models but approaches that consider multiple factors are critical to capture the complexity in predator-prey interactions. We present a novel comprehensive approach to understand predation rates based on field data obtained from a vertebrate predator.
2. Estimates of food consumption and prey abundance were obtained from 21 semi-natural populations of the lizard *Zootoca vivipara*. We identified the most parsimonious feeding rate function exploring allometric, simple functional response, and allometric functional response models. Each group included effects of sex and weather conditions.
3. Allometric models reveal the importance of predator mass and sex: larger females have the highest natural feeding rates. Functional response models show that the effect of prey density is best represented by a Holling type II response model with a mass, sex and weather dependent attack rate and a constant handling time. However, the best functional response model only received moderate support compared to simpler allometric models based only on predator mass and sex.
4. Despite this limited effect of prey densities on feeding rates, we detected a significant negative relationship between an index of preferred prey biomass and lizard density.
5. Functional response models that ignore individual variation are likely to misrepresent trophic interactions. However, simpler models based on individual traits may be best supported than complex allometric functional responses by some data. These results illustrate the importance of considering individual, population, and environmental effects while also exploring simple models.

Keywords: Field experiment, functional response, Lacertidae, parsimony, prey-predator interaction, size-effect.

INTRODUCTION

The study of prey-predator interactions and foraging behaviour can provide critical insights into the structure of food webs, population dynamics, and species interactions (e.g., Abrams, 2000, de Roos et al., 2003, Gilg et al., 2003, Miller et al., 2006, Persson et al., 1998). The foraging ability of a predator determines its energy acquisition and ability to grow, survive, and reproduce, but can also influence the fitness of conspecifics as predators may aid or interfere with each other (Arditi & Akcakaya, 1990). Predation also has a large effect on prey populations influencing their dynamics, behaviour, and spatial distribution (Gilg et al., 2003, Reeve, 1997). Predation rates are determined by several factors including prey and predator densities, body size, habitat structure and weather conditions (e.g., Angilletta, 2001, Avery, 1971, Miller et al., 2006, Pitt & Ritchie, 2002). The field of foraging ecology has emphasized density-dependent effects defining functional responses that estimate prey consumption by an average predator as a function of prey, and in some cases predator, density (Hassell & Varley, 1969, Holling, 1959). However, these generalized functions fail to represent natural variation among individuals. Body size usually varies significantly among individuals with important consequences for the dynamics of prey-predator systems (Claessen et al., 2000, de Roos et al., 2003, Persson et al., 1998).

In most species, variation in body size influences both foraging ability and risk of predation (Aljetlawi et al., 2004, Tripet & Perrin, 1994, Werner & Hall, 1988). To incorporate this size dependence, feeding rates may be defined using allometric functions that incorporate the effects of predator and/or prey body size with simple power laws (e.g., Kooijman, 2000, Vucic-Pestic et al., 2010). These allometric functions take into account that a predator body size influences most aspects of its feeding behaviour. For example, size often determines the mobility and endurance of lizards affecting their ability to search for and pursue a prey (Le Galliard et al., 2004). Strength and bite force are also size-dependent and affect a lizard's ability to capture and handle prey (Herrel & O'Reilly, 2006). However, allometric functions often fail to incorporate density effects (but see Aljetlawi et al., 2004, Vucic-Pestic et al., 2010, Wahlstrom et al., 2000) and ignore other relevant environmental effects (e.g., climate conditions in ectothermic vertebrates). Thus, both simple allometric relationships and classic functional response equations ignore the complexities in predator-prey interactions and make unrealistic assumptions about how predators consume resources (Brose, 2010). Realistic estimates of feeding rates also require conducting experiments under natural conditions as

laboratory experiments may not accurately reflect field behaviours (e.g., Witz, 1996). Laboratory experiments often fail to capture ecological complexity in habitat structure, prey diversity, and social dynamics, and these experiments frequently use model species that do not represent complex predators, such as most vertebrates. Unfortunately, direct observation of food acquisition in natural conditions is difficult and natural environmental variability often leads to noise and co-variation in data from field studies.

To circumvent these previous limitations of foraging ecology studies, it is important to conduct experiments in natural conditions to obtain realistic estimates that capture the effects of body size, density and climate conditions on the foraging success of diverse species. This study achieves this important goal by investigating natural feeding rates of the European common lizard *Zootoca vivipara* Jacquin (Figure 1) in outdoor enclosures. *Z. vivipara* is a small ovoviviparous lizard that preys opportunistically on diverse invertebrate species (Avery, 1966, see also Appendix S1 in Supporting Information). Our goals were to: 1) gain an understanding of the factors influencing prey consumption in *Z. vivipara* by using a comprehensive approach that incorporates individual, population, and environmental effects; 2) identify the most parsimonious feeding rate function considering diverse allometric and density-dependent functions; and 3) investigate the effect of varying lizard densities and thus, predation pressure, on the invertebrate community. The importance of our study hinges on exploring a novel comprehensive approach to define prey-predator interactions using field data from a complex vertebrate predator. Our results highlight the importance of exploring diverse approaches using field data to advance our understanding of foraging dynamics.

Figure 1. Adult male of the species *Zootoca vivipara* (European common lizard) at an outdoor enclosure in the CEREEP, France (48°17'N, 2°41'E). Photo credit: M. González-Suárez.



METHODS

Lizard populations: enclosures

During the summer of 2008, we established five experimental density treatments of *Z. vivipara* in 24 outdoor enclosures at the Centre de Recherche en Ecologie Expérimentale et Prédictive (CEREPEP, 48°17'N, 2°41'E). Initial densities were equivalent to 700-3,500 adults + yearlings per ha and sex ratios were close to 1:1. Surviving lizards (N = 326) from all treatments were recaptured in May-June 2009 (93% of recaptures occurred on 4 days in May) and a final population density (P) per enclosure was calculated. After capture, we estimated body mass for each lizard and classified female reproductive status as pregnant or non pregnant. We also obtained an estimate of sunshine duration (I , in hours day⁻¹) from a Campbell Scientific (Courtaboeuf, France) CSD3 solar radiation sensor located within 300 m of the enclosures. Sunshine duration is defined as total time with direct solar radiation exceeding 120 Wm⁻² (W.M.O., 2008) and was calculated over 10 minute intervals. Although both air temperature and solar radiation influence activity in reptiles, based on previous studies we expected sunshine duration would influence activity (and hence, feeding) more directly than temperature in this species (Avery, 1971, House et al., 1980). Additional details of the enclosures, the density manipulation, and lizard captures are provided in Appendix S1.

Prey populations

Invertebrate abundance was estimated by a combination of pitfall trapping and sweep-net capture techniques (Brennan et al., 2005) after all lizards had been captured to avoid injuries to the lizards, i.e., drowning in a pit trap. Invertebrates were classified into order following Chinery (2005) and dried to determine dry biomass (in mg) per order in each enclosure. Estimated biomass represents an index as not all invertebrates in each enclosure were captured. We computed a total biomass index including all invertebrate groups, a preferred prey biomass index (N_p), which includes the orders Araneae, Homoptera, Heteroptera, and Orthoptera (Avery, 1966), and a spider biomass index (N_s , Araneae). Spiders were considered independently because they are the principal food of *Z. vivipara* (Avery, 1966, Le Galliard et al., 2005a) and also were the most common invertebrate group in the enclosures (Figure S1). Additional details of the invertebrate captures are provided in Appendix S1 (Supporting Information).

Estimation of feeding rates

We inferred natural feeding rates from measured faecal production using a standard relationship between faecal production and food consumption. This relationship was defined using data from a laboratory feeding experiment (see Appendix S1, Supporting Information). We also measured faecal production for 107 lizards captured in the outdoor enclosures. After capture these lizards were housed in individual terraria and kept without food for 3 days. All faecal pellets produced since capture were dried and weighed. Using the experimental relationship between faecal production and food consumption we estimated natural feeding rates (in mg of live prey day⁻¹). Experimental procedures are described in more detail in Appendix S1 (Supporting Information).

Data analysis: feeding rates

Using the laboratory data, we explored several models aiming to predict faecal production from food intake (E). Some models included effects of S (sex as male or female) and/or M (lizard mass in g). The best fitting model was selected using an information-theoretic approach described below. The selected model was used to infer natural feeding rates from the measured faecal output of the animals captured in the outdoor enclosures.

We investigated the effects of predator body mass (M) and sex (S), predator (P) and prey (N) densities, and sunshine duration (I) on the estimated natural feeding rates, applying allometric functions and functional responses. The simplest allometric function considered was $f(M) = AM^B$, in which feeding rates only depend on M . The allometric coefficient A and exponent B are estimated from the data. Alternative allometric functions were derived from this function by allowing the A and/or B parameter to vary between males and females, or introducing a linear effect of sunshine duration (e.g., $f(I, M) = AIM^B$). In total, we explored 11 allometric functions.

In addition, we formulated a group of functional response models considering Holling type I and type II response models (Holling, 1959) and a ratio dependent model (Hassell & Varley, 1969). The type I response model assumes a linear increase in predation with increasing prey density (N), $f(N) = bN$, where b is the attack rate. The type II response model assumes an asymptotic relationship of feeding rate with prey density, $f(N) = \frac{bN}{1 + bT_h N}$, where b is the attack rate and T_h the handling time. The Hassell-Varley flexible ratio function is a modified Holling type II model in which predation rate is influenced by prey (N) and predator

density (P), $f(N, P) = \frac{b(N/P^m)}{1 + bT_h(N/P^m)}$, where b is the attack rate, T_h the handling time, and m

an exponent that determines the strength of the predator density effect. In all models, prey densities (N) were defined as either preferred prey biomass (N_p) or spider biomass (N_s).

These three basic functional response equations were modified to include more complex attack rates that incorporate effects of predator body mass and sex, as well as sunshine duration. Attack rates are expected to increase with predator size as larger lizards have greater sensory acuity and locomotor ability (Garland, 1984). In *Z. vivipara* prey size has been observed to increase with lizard size (Avery, 1966) and we used an allometric attack rate function $b(M) = b_1 M^{b_2}$ where b_1 is an allometric coefficient and b_2 an allometric exponent. In some models we also included an effect of predator sex (e.g., $b(M, S) = b_1(S) \cdot M^{b_2(S)}$) and sunshine duration (e.g., $b(I, M) = b_1 I \cdot M^{b_2}$). Although handling time (T_h) may vary with body size (Persson et al., 1998), a recent study found these rates were relatively constant except for the smallest predators (Aljetlawi et al., 2004). We therefore assumed that handling time is constant. In total, we explored 54 functional response models.

All models were fitted using the non-linear procedure NLS in R 2.10.0 (R Development Core Team 2009). The best fitting model(s) was selected using an information-theoretic approach (Burnham & Anderson, 2002) considering Akaike’s information criterion corrected for small sample sizes (AIC_c), model support as the difference in AIC_c between each model and the model with the lowest AIC_c (Δ), and AIC_c weight (w_i). Total w_i was calculated as the cumulative weight of all models including a particular variable or type of functional response (e.g., Holling type I response), which is similar to the variable weight w_j proposed by Burnham & Anderson (2002). All models with $\Delta < 2$ were considered to be supported. We also estimated the percentage deviance explained as (model deviance-null model deviance/null model deviance)·100, where the null model is an intercept only model.

Data analysis: impact on invertebrate communities

First, we explored the relationship between invertebrate biomass index (total, N_p or N_s) and predator density (P) using linear regression. Second, we defined an invertebrate community similarity matrix among enclosures based on pairwise Bray-Curtis indices. Bray-Curtis indices were calculated as the absolute difference in invertebrate order biomass between two enclosures, summed over for all orders and divided by the total biomass in all enclosures and orders (Bray & Curtis, 1957). To detect changes in community structure (biomass and

composition) due to lizard density we used a test analogous to a multivariate analysis of variance called ADONIS (Oksanen et al., 2009). ADONIS returns a statistic R , which is a measure of separation among groups (0 indicates complete mixing and 1 represents full separation), and a P -value estimated by repeated permutations of the data. We used the ADONIS procedures in the VEGAN package in R.2.10.0 (R Development Core Team 2009) with 999 permutations. Although enclosures had overall similar habitat and environmental conditions, we expected a gradient of soil humidity due to differences in proximity to a nearby creek. Therefore, we introduced creek proximity, a proxy for humidity, as an additional regression variable to explain invertebrate biomass and as a block in the ADONIS procedure. Enclosures were distributed in five rows running more or less parallel to the creek, thus creek proximity was ranked from 1 to 5 with 1 assigned to the row of enclosures closest to the creek (~30 m) and 5 to those furthest (~90 m).

RESULTS

Experimental relationship between feeding rate and faecal production

Table 1. Selection results of models exploring faecal output in *Zootoca vivipara* kept in the laboratory for the complete dataset ($N = 41$) and for a dataset excluding pregnant females ($N = 35$). We report number of parameters (k), Akaike’s information criteria (AIC_c), model support (Δ), model weights (w_i), and percentage deviance explained. Supported models are in bold.

Model*	k	AIC_c	Δ	w_i	% deviance explained
All data					
<i>faecal output</i> = $\beta \cdot E$	2	213.469	0.000	0.4741	29.705
<i>faecal output</i> = $\beta(S) \cdot E$	3	214.788	1.318	0.2453	31.423
<i>faecal output</i> = $\beta \cdot M^R E$	3	215.347	1.877	0.1854	30.482
<i>faecal output</i> = $\beta(S) \cdot M^R E$	4	216.681	3.212	0.0952	32.369
Excluding pregnant females					
<i>faecal output</i> = $\beta \cdot E$	2	182.276	0.000	0.5505	26.805
<i>faecal output</i> = $\beta(S) \cdot E$	3	184.488	2.212	0.1822	27.599
<i>faecal output</i> = $\beta \cdot M^R E$	3	184.293	2.017	0.2008	27.195
<i>faecal output</i> = $\beta(S) \cdot M^R E$	4	186.504	4.228	0.0665	28.317

*In the models: E = experimental food intake, M = lizard body mass, S = lizard sex. β is the allometric coefficient and R is the allometric exponent.

The best model to explain faecal production includes only food intake (E). However, there were two additional models supported by the data (Table 1) that include mass and sex. At the time of this experiment, six females were in an advanced stage of pregnancy and ate

considerably less than expected based on their body mass because their abdominal cavity was largely occupied by developing eggs. We repeated our analysis excluding these individuals and found that a single model, including only E , was supported (Table 1). Therefore, we used the function $faecal\ output = \beta \cdot E$ ($\beta = 0.072$, $SE = 0.006$, $P < 0.0001$, deviance explained = 29.7%), where E is in mg of live prey day^{-1} and $faecal\ output$ is a daily mean estimated over 3 days (dry $mg\ day^{-1}$).

Natural feeding rates

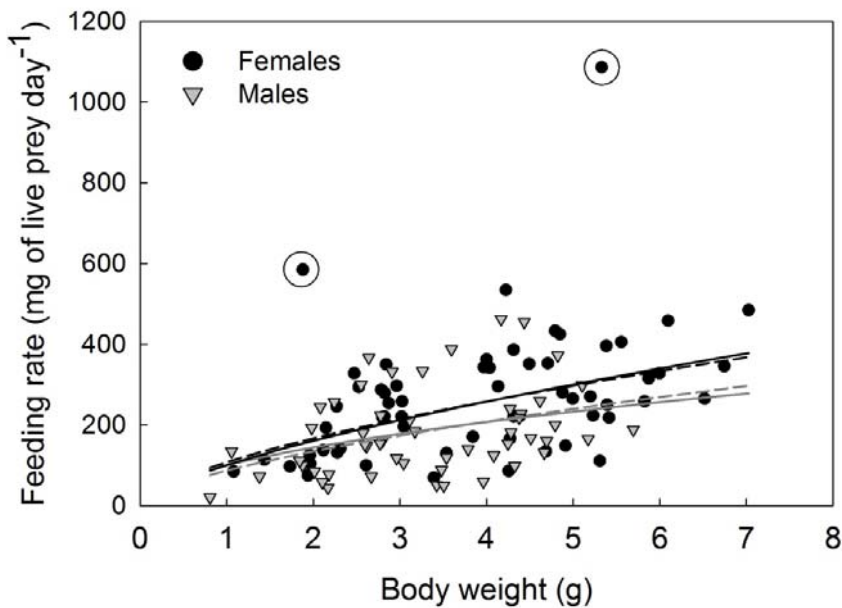


Figure 2. Feeding rate as a function of body mass and sex in *Zootoca vivipara*. The two best supported models, which received nearly identical support (Table 2), are represented by solid (top model) and dashed lines (second model). Two identified outliers are circled and were not used to define the regression function.

All individuals captured in the field produced faeces, which indicates that all had eaten prior to capture. There was no effect of capture date on food intake (Anova $F_{3,105} = 2.15$, $P = 0.10$). Two females had a faecal output much larger than expected based on their body mass (see Figure 2) and were identified as outliers during the analysis of the data. Reported results do not include these outliers because parameter estimates were different (particularly the allometric exponent) even though selected models were similar in both datasets. In the allometric function group, two models were supported while only four had $w_i > 10\%$ (Table 2). Both supported models include the same predictors: sex (S) and body mass (M); however, they differ in how the sex effect was introduced (either modifying the allometric coefficient A or the exponent B . Table 3). Supported models were nearly identical in their AIC_c value and

the resulting curves largely overlapped, predicting the highest feeding rates for larger female lizards (Table 3 and Figure 2, deviance explained = 31.4%). Mean (\pm SE) food intake was 182.68 ± 15.605 mg day⁻¹ for males and 251.51 ± 15.135 mg day⁻¹ for females. We found no differences between natural feeding rates of pregnant and non-pregnant females controlling for body mass (residuals of a mass model, Student $t = 0.75$, $df = 56$, $P = 0.457$). Models including an effect of sunshine duration (I) received low support (total $w_i = 0.07$).

Table 2. Selection results of simple allometric functions and functional responses describing feeding rates under semi-natural conditions in *Zootoca vivipara*. We present the top models with the number of parameters (k), Akaike’s information criteria (AIC_c), model support (Δ), model weights (w_i), and percentage deviance explained. Supported models are in bold.

Model*	k	AICc	Δ	wi	% deviance explained
Simple allometric functions					
$f(M, S) = A \cdot M^{B(S)}$	4	1264.258	0.000	0.371	31.382
$f(M, S) = A(S)M^B$	4	1264.286	0.027	0.366	31.400
$f(M, S) = A(S)M^{B(S)}$	5	1266.388	2.130	0.128	31.450
$f(M) = A \cdot M^B$	3	1267.814	3.556	0.063	27.560
$f(I, M, S) = A \cdot I \cdot M^{B(S)}$	4	1269.132	4.874	0.032	28.141
$f(I, M, S) = A(S) \cdot I \cdot M^B$	4	1269.413	5.155	0.028	27.948
$f(I, M, S) = A(S) \cdot I \cdot M^{B(S)}$	5	1271.321	7.063	0.011	28.152
Functional responses					
$f(I, N_p, M, S) = \frac{b_1(S)I \cdot M^{b_2(S)} N_p}{1 + b_1(S)I \cdot M^{b_2(S)} T_h N_p}$	6	1267.204	0.000	0.325	32.380
$f(I, N_p, P, M, S) = \frac{b_1 I \cdot M^{b_2(S)} N_p / P^m}{1 + b_1 I \cdot M^{b_2(S)} T_h N_p / P^m}$	6	1268.749	1.545	0.150	31.378
$f(I, N_p, P, M, S) = \frac{b_1(S)I \cdot M^{b_2(S)} N_p / P^m}{1 + b_1(S)I \cdot M^{b_2(S)} T_h N_p / P^m}$	7	1269.354	2.150	0.111	32.475
$f(I, N_p, M, S) = \frac{b_1(S)I \cdot M^{b_2} N_p}{1 + b_1(S)I \cdot M^{b_2} T_h N_p}$	5	1269.581	2.376	0.099	29.333
$f(N_p, M, S) = \frac{b_1 M^{b_2(S)} N_p}{1 + b_1 M^{b_2(S)} T_h N_p}$	5	1270.141	2.936	0.075	28.956
$f(N_p, M, S) = \frac{b_1(S)M^{b_2(S)} N_p}{1 + b_1(S)M^{b_2(S)} T_h N_p}$	6	1270.812	3.608	0.053	30.016
$f(I, N_s, M, S) = \frac{b_1 I \cdot M^{b_2(S)} N_s}{1 + b_1 I \cdot M^{b_2(S)} T_h N_s}$	5	1271.698	4.493	0.034	27.894

* I = sunshine duration, N_p = preferred prey biomass, N_s = spider biomass, P = lizard abundance, M = lizard body mass, S = lizard sex. A , B , b_1 , and b_2 , are allometric coefficients and exponents. The exponent m describes the strength of a predator density effect.

In the functional response group, two models were supported and only three models had $w_i > 10\%$ (Table 2). The top model was based on a Holling type II function for preferred prey biomass (N_p) with a M -, S -, and I -dependent attack rate (Table 3). The second supported

model also included a M -, S -, and I -dependent attack rate but was based on a Hassell-Varley function (Table 3). However, the exponent m , which describes the effect of predator density, was not significantly different from zero (Table 3). It is important to note that we did not have cross-treatments in which both prey and predator densities were controlled and varied. As a result prey and predator densities were correlated (P - N_p Pearson $r = -0.69$, P - N_s $r = -0.56$) and parameters in the Hassell-Varley models may not have been estimated adequately.

Table 3. Parameter estimates for the best models defining natural feeding rates in *Zootoca vivipara* considering simple allometric functions and functional responses. See table 2 for model selection.

Model*	Parameter \pm SE†	P
Simple allometric functions		
$f(M, S) = A \cdot M^{B(S)}$	A = 100.47 \pm 18.050	< 0.0001
	B _{fem} = 0.70 \pm 0.119	< 0.0001
	B _{male} = 0.52 \pm 0.146	< 0.001
$f(M, S) = A(S)M^B$	A _{fem} = 107.85 \pm 20.508	< 0.0001
	A _{male} = 87.02 \pm 15.259	< 0.0001
	B = 0.63 \pm 0.124	< 0.0001
Functional responses		
$f(I, N_p, M, S) = \frac{b_1(S)I \cdot M^{b_2(S)} N_p}{1 + b_1(S)I \cdot m^{b_2(S)} T_h N_p}$	T _h = 0.003 \pm 0.0003	< 0.0001
	b _{1fem} = 0.03 \pm 0.043	= 0.448
	b _{1male} = 0.17 \pm 0.100	= 0.098
	b _{2fem} = 3.58 \pm 1.51	= 0.020
	b _{2male} = 1.28 \pm 0.544	= 0.020
$f(I, N_p, P, M, S) = \frac{b_1 I \cdot M^{b_2(S)} N_p / P^m}{1 + b_1 I \cdot M^{b_2(S)} T_h N_p / P^m}$	T _h = 0.003 \pm 0.0004	< 0.0001
	b ₁ = 0.17 \pm 0.185	= 0.361
	b _{2fem} = 2.44 \pm 0.825	= 0.004
	b _{2male} = 1.58 \pm 0.600	= 0.009
	m = 0.03 \pm 0.290	= 0.907

* I = sunshine duration, N_p = preferred prey biomass, N_s = spider biomass, P = lizard abundance, M = lizard body mass, S = lizard sex.

†Subscripts indicate *fem*: parameter value for females, *male*: parameter value for males

Overall, models based on a Holling type II response had more support (total $w_i = 0.65$) than those based on the Hassell-Varley function (total $w_i = 0.34$), while Holling type I response models received no support (total $w_i < 0.0001$). Models based on N_p had higher weights (total $w_i = 0.89$) than models based on spider biomass only (N_s ; total $w_i = 0.11$). Models including M - and S -dependent attack rates were strongly supported (total $w_i > 0.99$ and total $w_i = 0.98$, respectively). In contrast to the results from the allometric group, functional response models including an effect of I were supported (total $w_i = 0.79$). Density-

dependent models not including individual traits (M and S) received no support ($\Delta > 34.34$, $w_i < 0.0001$).

Because both groups of models used the same database, we could also compare them to determine the most parsimonious model overall. The top two allometric functions including S and M (Tables 2 and 3) were identified as the only supported models when combining both groups of functions. The best functional response model had $\Delta = 4.5$ (Table 2), suggesting limited support for a density effect on natural feeding rates.

Impacts of lizard density on invertebrate populations

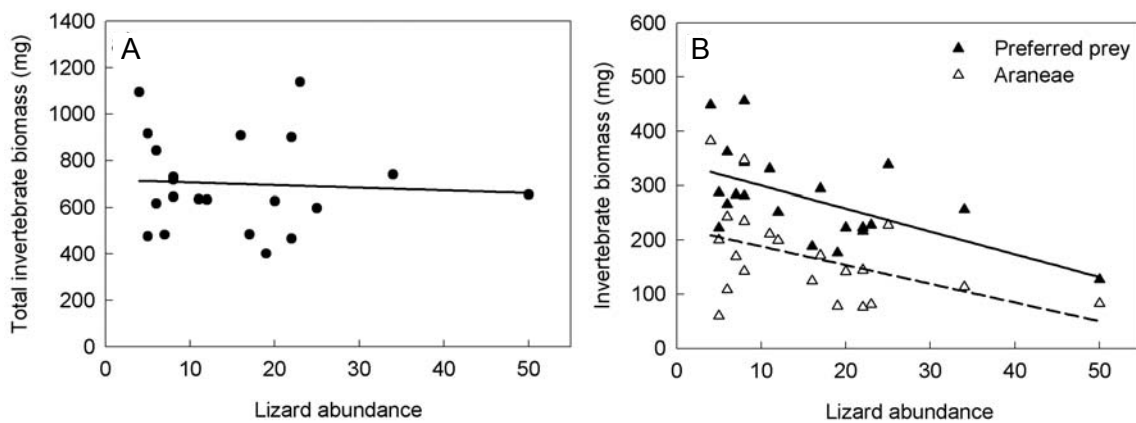


Figure 3. Invertebrate biomass and lizard abundance on 21 outdoor experimental enclosures. (A) Total invertebrate biomass. (B) Preferred lizard prey (orders: Araneae, Heteroptera, Homoptera, and Orthoptera), and spider biomass (Araneae). Note different scale of the y-axis.

We captured and identified invertebrates from 17 different orders. The most abundant group was *Araneae* (Figure S1), while *Ephemeroptera*, *Neuroptera*, and *Odonata* were rare (found in < six enclosures and representing < 0.5 % of the total biomass). There was no relationship between the total invertebrate biomass index and lizard density or creek proximity ($F_{5,15} = 2.00$, $P = 0.14$; adjusted $R^2 = 0.20$. Figure 3A). However, we found a significant negative effect of lizard density on biomass of preferred lizard prey N_p ($\beta = -3.29$, $SE = 1.305$. Figure 3B) with no effect of creek proximity (overall regression $F_{5,15} = 4.84$, $P = 0.008$, adjusted $R^2 = 0.49$). There was also an effect of lizard density on spider biomass N_s ($\beta = -1.69$, $SE = 1.393$. Figure 3B) with no effect of creek proximity (overall regression $F_{5,15} = 4.49$, $P = 0.011$, adjusted $R^2 = 0.47$). Despite these differences for particular invertebrate groups, we did not detect differences in invertebrate community structure with lizard density, although there was a weak but significant effect of creek proximity (density: $R = 0.05$, $P = 0.38$; creek proximity: $R = 0.14$, $P = 0.05$). Results did not change if the rare orders: *Ephemeroptera*, *Neuroptera*, and *Odonata*, were excluded.

DISCUSSION

Intrinsic factors influencing feeding rates

Both lizard body mass and sex had important effects on individual feeding rates. Larger predators consume more prey than smaller individuals as previously reported for *Z. vivipara* (Avery, 1971, Pilorge, 1982) and many other species (Aljetlawi et al., 2004, Tripet & Perrin, 1994, Vucic-Pestic et al., 2010). A new finding is that females consume greater amounts of food than males, even after controlling for differences in body mass. Previous studies of *Z. vivipara* failed to detect (Avery, 1971) or to consider (Van Damme et al., 1991) these sex differences. However, our results suggest they may be important.

There are several possible non-exclusive explanations for these sex differences. Females could have increased feeding rates to compensate for their recent investment in reproduction (Avery, 1974). However, we found that pregnant and non-pregnant females had similar feeding rates. Alternatively males may spend less time foraging because they engage in reproductive behaviours during this time of the year. On the other hand, females and males may have different diets due to distinct energy requirements and investment strategies. For example, juvenile female *Z. vivipara* invest more in body length growth, while males invest in body condition (mass adjusted for length, Le Galliard et al., 2005b). Whether these differences in energy investments influence feeding rates remains to be determined.

Extrinsic factors influencing feeding rates and functional response functions

Feeding rates generally increase with sunshine duration (see also Avery, 1971, House et al., 1980). However, the effect of sunshine was only noticeable within the functional response model group, suggesting attack rates (search and detection of prey) increase in sunnier days. Future experimental studies may be necessary to clarify the role of weather conditions in *Z. vivipara* feeding rates. Similarly, evidence of prey density effects in feeding rates was limited. Prey densities in semi-natural conditions cannot be easily manipulated. Instead prey biomass was expected to vary due to the experimental manipulation of lizard density. Although variability in prey was observed, there was only a weak effect of prey density in feeding rates. It is possible that prey densities remained sufficiently high to prevent strong food limitation even at the highest lizard densities.

Which functional response models better represent natural dynamics is a debated issue that this study directly addresses (Abrams & Ginzburg, 2000, Schenk et al., 2005). We found

best support for a Holling type II functional response in *Z. vivipara* suggesting feeding rates reach a limit at high prey densities. However, unlikely previous studies (Miller et al., 2006, Schenk et al., 2005), we only found limited support for an effect of predator density. The common lizard is a non-territorial species with overlapping home ranges and conspecific interference during predation may be rare (Massot et al., 1992). Alternatively, the correlation between prey and predator densities may have limited our ability to correctly fit models including both density effects.

Most parsimonious feeding rate functions

A primary goal of this study was to identify the most parsimonious feeding rate function following a comprehensive approach that includes both allometric and functional responses. Many studies consider only one group of models and thus create a dichotomy that does not exist in reality (Brose, 2010). Our results show that both prey density and body mass influence feeding rates, but that individual traits, mass and sex, are much better predictors. Recent studies have shown the importance of considering both density and body mass effects and have suggested the use of allometric functional response models in which attack rates and/or handling times are size dependent (Aljetlawi et al., 2004, Vucic-Pestic et al., 2010). Allometric functional responses provide an important tool to represent individual and population level effects (Brose, 2010). However, for empirical studies and generalist predators, simpler allometric functions may provide a more parsimonious description of the data than complex allometric functional response models. Even though at some level prey density must affect feeding rates and functional response models are an important contribution to the field of ecology (Abrams, 2000), variation in prey consumption may be better explained by individual differences than by natural variation in prey density. In light of these results, we urge researchers to explore diverse types of function, including allometric functional responses and simpler functions, while considering the effects of multiple individual traits such as mass and sex, prey and predator population densities, and whenever possible environmental variables.

Despite a weak effect of prey density on consumption rates, our study documents a negative effect of lizard density on preferred prey and in particular on spider biomass, presumably as a consequence of feeding pressure. A negative effect of lizard density on spider abundance has been previously reported (Le Galliard et al., 2005a, Spiller & Schoener, 1998). This effect may be potentially important for community diversity and structure because spiders are themselves predators that can influence other invertebrates and habitat conditions

(Greenstone, 1999, Schmitz, 2008). Therefore, lizards could directly, via predation, and indirectly, via their effect on spiders, influence the composition and biomass of the invertebrate communities (Spiller & Schoener, 1998). Although in our study, we did not find a significant effect of lizard density on invertebrate community structure, which instead appears to respond to creek proximity (a proxy of humidity), effects may occur at different densities of lizards and/or spiders.

One caveat in our study is that prey and lizard densities could not be estimated at the same time. This time lag may have limited our ability to identify existing effects of prey density on lizard feeding rates or of lizard density on prey communities. Regrettably, we could not estimate prey biomass until after all lizards were captured to avoid injuring lizards inside insect traps and thus, we could not estimate prey and lizard densities simultaneously. These difficulties are drawbacks of field studies. Nevertheless, we detected an expected effect of lizard density on prey abundance, suggesting measured prey densities did reflect, at least to some extent, enclosure conditions prior to lizard removal.

Finally, the observation that prey consumption depends only weakly on prey density is both interesting and puzzling. This result poses the question of how common lizard populations and their prey are regulated (Abrams, 2000, Massot et al., 1992). If populations are regulated through prey depletion as typically assumed in population dynamic models, prey consumption should decrease with predator density due to a decrease in prey abundance. We indeed found a negative effect of lizard density on preferred prey and spider biomass. However, the associated reduction in predation rate was less evident. This might imply that other ecological interactions, which remain unexplored, are involved in the regulation of these lizard populations.

ACKNOWLEDGEMENTS

We would like to thank all personnel at the CEREEP field station for their help. Three anonymous reviewers and the associate editor provide helpful suggestions to improve an earlier version of this manuscript. This study was funded by the Région Île-de-France R2DS program (grant 2007-06), the Agence Nationale de la Recherche (ANR grant 07-JCJC-0120), the Centre National de la Recherche Scientifique (CNRS), the Spanish Ministry of Science and Innovation (Project: CGL2009-07301/BOS), and the European Community’s Seventh Framework Programme (FP7/2007-2013) under grant agreement n° 235897. The protocol of

this study was approved by the Ile-De-France Regional Ethics Committee for Animal Experimentation N°3 (file p3/2008/008).

REFERENCES

- Abrams, P. A. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* **31**: 79-105.
- Abrams, P. A. & Ginzburg, L. R. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution* **15**: 337-341.
- Aljetlawi, A. A., Sparrevik, E. & Leonardsson, K. 2004. Prey-predator size-dependent functional response: derivation and rescaling to the real world. *Journal of Animal Ecology* **73**: 239-252.
- Angilletta, M. J. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology* **82**: 3044-3056.
- Arditi, R. & Akcakaya, H. R. 1990. Underestimation of mutual interference of predators. *Oecologia* **83**: 358-361.
- Avery, R. A. 1966. Food and feeding habits of common lizard (*Lacerta vivipara*) in West of England. *Journal of Zoology* **149**: 115-121.
- Avery, R. A. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology* **40**: 351-365.
- Avery, R. A. 1974. Storage lipids in lizard *Lacerta vivipara*: a quantitative study. *Journal of Zoology* **173**: 419-425.
- Bray, J. R. & Curtis, J. T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* **27**: 326-349.
- Brennan, K. E. C., Majer, J. D. & Moir, M. L. 2005. Refining sampling protocols for inventorying invertebrate biodiversity: influence of drift-fence length and pitfall trap diameter on spiders. *Journal of Arachnology* **33**: 681-702.
- Brose, U. 2010. Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology* **24**: 28-34.
- Burnham, K. P. & Anderson, D. R. 2002. *Model selection and multimodel inference. A practical information-theoretic approach*. Springer, New York.
- Chinery, M. 2005. *Insectes de France et d'Europe occidentale*. Flammarion, Paris, France.
- Claessen, D., de Roos, A. M. & Persson, L. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. *American Naturalist* **155**: 219-237.

- M. Mugabo – Caractérisation des interactions entre la structure de population et l'histoire de vie
- de Roos, A. M., Persson, L. & McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* **6**: 473-487.
- Garland, T. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. *American Journal of Physiology* **247**: R806-R815.
- Gilg, O., Hanski, I. & Sittler, B. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. *Science* **302**: 866-868.
- Greenstone, M. H. 1999. Spider predation: How and why we study it. *Journal of Arachnology* **27**: 333-342.
- Hassell, M. P. & Varley, G. C. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* **223**: 1133-&.
- Herrel, A. & O'Reilly, J. C. 2006. Ontogenetic scaling of bite force in lizards and turtles. *Physiological and Biochemical Zoology* **79**: 31-42.
- Holling, C. S. 1959. Some characteristics of simple type of predation and parasitism. *The Canadian Entomologist* **91**: 385-398.
- House, S. M., Taylor, P. J. & Spellerberg, I. F. 1980. Patterns of daily behavior in two lizard species *Lacerta agilis* L. and *Lacerta vivipara* Jacquin. *Oecologia* **44**: 396-402.
- Kooijman, S. A. L. M. 2000. *Dynamic energy and mass budgets in biological systems*. Cambridge University Press, Cambridge.
- Le Galliard, J.-F., Clobert, J. & Ferrière, R. 2004. Physical performance and darwinian fitness in lizards. *Nature* **432**: 502-505.
- Le Galliard, J.-F., Ferrière, R. & Clobert, J. 2005a. Effect of patch occupancy on immigration in the common lizard. *Journal of Animal Ecology* **74**: 241-249.
- Le Galliard, J.-F., Ferrière, R. & Clobert, J. 2005b. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* **111**: 368-376.
- Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**: 1742-1756.
- Miller, D. A., Grand, J. B., Fondell, T. E. & Anthony, M. 2006. Predator functional response and prey survival: direct and indirect interactions affecting a marked prey population. *Journal of Animal Ecology* **75**: 101-110.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. 2009. *VEGAN: Community ecology package*. R. package version 1.15-4 <http://CRAN.R-project.org/package=vegan>.

- Persson, L., Leonardsson, K., de Roos, A. M., Gyllenberg, M. & Christensen, B. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology* **54**: 270-293.
- Pilorge, T. 1982. Ration alimentaire et bilan énergétique individuel dans une population de montagne de *Lacerta vivipara*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **60**: 1945-1950.
- Pitt, W. C. & Ritchie, M. E. 2002. Influence of prey distribution on the functional response of lizards. *OIKOS* **96**: 157-163.
- R Development Core Team (2009) R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reeve, J. D. 1997. Predation and bark beetle dynamics. *Oecologia* **112**: 48-54.
- Schenk, D., Bersier, L. F. & Bacher, S. 2005. An experimental test of the nature of predation: neither prey- nor ratio-dependent. *Journal of Animal Ecology* **74**: 86-91.
- Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* **319**: 952-954.
- Spiller, D. A. & Schoener, T. W. 1998. Lizards reduce spider species richness by excluding rare species. *Ecology* **79**: 503-516.
- Tripet, F. & Perrin, N. 1994. Size-dependent predation by *Dugesia lugubris* (Turbellaria) on *Physa acuta* (Gastropoda): experiments and model. *Functional Ecology* **8**: 458-463.
- Van Damme, R., Bauwens, D. & Verheyen, R. F. 1991. The thermal dependence of feeding behavior, food consumption and gut passage time in the lizard *Lacerta vivipara* Jacquin. *Functional Ecology* **5**: 507-517.
- Vucic-Pestic, O., Rall, B. C., Kalinkat, G. & Brose, U. 2010. Allometric functional response model: body masses constrain interaction strengths. *Journal of Animal Ecology* **79**: 249-256.
- W.M.O. 2008. *WMO guide to meteorological instruments and methods of observation*. World Meteorological Organization, Geneva, Switzerland.
- Wahlstrom, E., Persson, L., Diehl, S. & Bystrom, P. 2000. Size-dependent foraging efficiency, cannibalism and zooplankton community structure. *Oecologia* **123**: 138-148.
- Werner, E. E. & Hall, D. J. 1988. Ontogenetic habitat shifts in bluegill sunfish: the foraging rate-predation risk tradeoff. *Ecology* **69**: 1352-1366.
- Witz, B. W. 1996. The functional response of *Cnemidophorus sexlineatus*: laboratory versus field measurements. *Journal of Herpetology* **30**: 498-506.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1 Extended methods.

Figure S1 Total invertebrate biomass per experimental enclosure.

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Appendix S1: Extended Methods

Study species

Zootoca vivipara is a small (adult snout-vent length: 50-70 mm) ovoviviparous Lacertidae species found in humid habitats across northern Eurasia. This lizard is a diurnal active forager that preys opportunistically on invertebrate species (Avery, 1966, Pilorge, 1982). Natural populations can be divided into three main age classes: juveniles (< 1 year old), yearlings (1-2 years old) and adults (> 2 years old). In our study lizards were individually marked by toe clipping at birth and their age was known. In the study area, individuals emerge from hibernation in late March or April. Females lay an average of five (range 1 - 12) non-calcified eggs from early June to early July. Hatching usually occurs within a few minutes of egg laying. Individuals enter hibernation in late September. Natural populations range in density from 200 to 2,000 adults + yearlings per ha (Massot et al., 1992).

Lizard density manipulation

During the summer of 2008, we established experimental populations of *Z. vivipara* in 24 outdoor enclosures in the Centre de Recherche en Ecologie Expérimentale et Prédictive (CEREEP, 48°17'N, 2°41'E). Enclosures were 10 x 10 m, located in a wet meadow, and provided lizards with natural prey sources, shelters, and basking sites (see Le Galliard et al., 2005c for further details). Lizards could not move among enclosures, but dispersal of invertebrate prey among enclosures and from natural surroundings was only partially limited. In 2008 we established five density treatments equivalent to 700-3,500 adults + yearlings per ha. In low density enclosures we released three adults, four yearlings, and 10-11 juveniles. The remaining density treatments were defined by increasing abundance by a factor of 2, 3, 4 or 5, e.g., we released 15 adults, 20 yearling, and 50-55 juveniles in the high density treatment. In all enclosures the sex ratio for all age classes was close to 1:1. We adjusted the number of replicates per treatment to maintain the same total number of lizards per density group, i.e., there were fewer replicates of the higher density treatments. For example we had 10 replicates of the lowest density vs. 2 replicates of the highest density treatment. Enclosures and lizards were randomly assigned to density treatments.

From May 11-June 14, 2009 all surviving lizards (N = 326) were recaptured. More than 93% of the recaptures occurred on 4 days in May (11th, 12th, 13th, and 18th), with only a few remaining individuals from different enclosures captured on later days. Lizards in the same enclosure were generally captured on the same day. After capture we estimated body mass to the nearest 2 mg and classified the reproductive status of each female as pregnant or

non pregnant. Reproductive status was later confirmed by parturition in the laboratory. Afterwards lizards were kept under standard laboratory conditions (see Le Galliard et al., 2003).

Prey populations

In June 2, 2009 we placed four pitfall traps, plastic cylinders (120 mm x 75 mm) filled with water, in each enclosure. Traps were monitored every morning until they were removed on June 5. Sweep-net sampling in all enclosures was done in one day, June 4, by sweeping a 300-mm diameter net in close proximity to the ground 30 times covering the entire enclosure area. Trapped adult invertebrates were stored in 70 % ethanol and later classified into order following the taxonomy in Chinery (2005). Trapped larvae were not identified. We considered that a classification to order was sufficient to capture most of the variation in prey size, structure, and palatability for an opportunistic forager like *Z. vivipara*. Identified specimens were dried at 60 °C for 17 hours in a drying oven (Memmert, Schwabach, Germany) to determine dry biomass (in mg) per enclosure for each order.

Estimation of feeding rates

A laboratory experiment was used to define a standard relationship between faecal production and food consumption. We used 41 lizards (9 adult females, 10 adult males, 10 yearling males, and 12 yearling females) kept under standard laboratory conditions for an average of 43 days (range: 25-48) after their capture in the outdoor enclosures. On June 23 we relocated all animals to individual terraria prepared with bloating paper, a water dish, and a refuge for thermoregulation. For 5 days, lizards were kept under standard laboratory conditions and were given a daily ration of live crickets *Acheta domesticus*, 400 mg for adult lizards and 200 mg for yearlings. Uneaten food was removed daily and weighed to the nearest 2 mg to estimate experimental food intake rate in mg of live prey day⁻¹ (hereafter *E*). On the sixth day we removed uneaten food, faeces, and food particles. Lizards were then kept without food for 3 days after which all faecal pellets were collected. The faecal matter was separated from the solid excretory component which was discharged (Avery, 1971). Faecal matter was then dried at 65 °C for 24 hrs and weighed to the nearest 0.1 mg.

We also measured faecal production for 107 lizards: 29 adult females, 22 adult males, 29 yearling females, and 27 yearling males. These lizards were captured on 21 of the 24 experimental enclosures during 4 days (May 11th, 12th, 13th, and 18th) from 11:00 to 18:00. We did not include lizards from three of the enclosures because only one or two individuals

were found and these lizards were mostly captured after the beginning of our experiment. Lizard masses covered a wide range (0.81-7.03 g) and there were approximately equal numbers of both sexes and age classes from the five density treatments. After capture lizards were housed in individual terraria (described above) and kept without food for 3 days. All faecal pellets produced since the capture were dried and weighed as described above. Because unfed lizards produced no faeces after ~3 days, we inferred measured faecal production reflects feeding rates over a period of 3 days. Mean daily sunshine duration (I in hours day⁻¹) was estimated for the same 3 day period.

References

- Avery, R. A. 1966. Food and feeding habits of common lizard (*Lacerta vivipara*) in West of England. *Journal of Zoology* **149**: 115-121.
- Avery, R. A. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology* **40**: 351-365.
- Chinery, M. 2005. *Insectes de France et d'Europe occidentale*. Flammarion, Paris, France.
- Le Galliard, J.-F., Fitze, P. S., Ferrière, R. & Clobert, J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 18231-18236.
- Le Galliard, J.-F., Le Bris, M. & Clobert, J. 2003. Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. *Functional Ecology* **17**: 877-885.
- Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**: 1742-1756.
- Pilorge, T. 1982. Ration alimentaire et bilan énergétique individuel dans une population de montagne de *Lacerta vivipara*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **60**: 1945-1950.

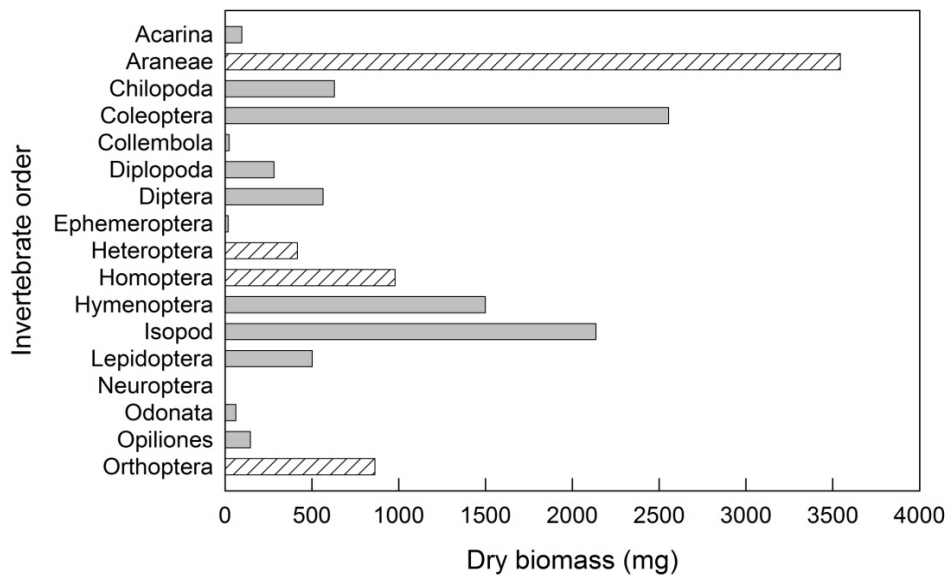


Figure S1. Total biomass of 17 orders of invertebrates captured in 21 experimental enclosures. Hatched columns indicate orders considered as preferred lizard prey.

CHAPITRE 5 – Densité dépendance de l’histoire de vie et risque d’extinction

Histoire de vie densité-dépendante et la dynamique des petites populations

Marianne Mugabo, ¹, Samuel Perret, ², Stéphane Legendre, ³, & Jean-François Le Galliard ^{1,2}.

¹ CNRS/UPMC, UMR 7625, Laboratoire Ecologie et Evolution, Université Pierre et Marie Curie, 7 Quai St. Bernard, 75005, Paris, France.

² CNRS/ENS, UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours, France.

³ CNRS/ENS, UMR 7625, Laboratoire Ecologie et Evolution, Ecole Normale Supérieure, 46 Rue d'Ulm, 75005, Paris, France.

Titre court : Densité dépendance et extinction

Référence : Mugabo, M., Perret, S., Legendre, S. & Le Galliard, J.-F. 2011. « Density-dependent life history and the dynamics of small populations ». Manuscrit en préparation pour soumission à *American Naturalist*.

RÉSUMÉ

La dynamique de population dépend de manière importante de la force et de la forme de la densité dépendance. Malheureusement, le manque de données d’histoire de vie fiables empêche l’établissement de prédictions démographiques correctes sur les petites populations régulées par densité dépendance. Nous avons créé un gradient allant de faibles à de fortes densités dans des petites populations isolées de lézards vivipares (*Zootoca vivipara*) et avons étudié la forme de la densité dépendance de l’histoire de vie pendant un cycle d’une année. La croissance corporelle, les performances reproductrices et l’immunocompétence ont diminué quasiment linéairement avec la densité tandis que la date de parturition présentait un effet Allee à faibles densités. La survie et la taille corporelle à la naissance de la première génération de descendants étaient densité-indépendants. Nous avons utilisé ces données pour créer des modèles de populations déterministes et stochastiques à un sexe et à deux sexes. Les analyses d’élasticité des modèles densité-dépendant et densité-indépendant ont indiqué les classes juvénile et sub-adulte comme les plus influentes, mais ont produit des résultats divergents sur l’influence des taux démographiques. Les simulations stochastiques ont démontré que la densité dépendance négative tamponne les effets de la densité initiale sur la probabilité d’extinction, a des effets positifs sur la persistance des populations de faible densité et interagit avec les fluctuations du sexe ratio pour modeler les dynamiques d’extinction des populations denses. Notre étude démontre l’importance de prendre en compte les régulations densité-dépendantes pour établir des prédictions correctes sur l’extinction des petites populations.

Mots-clés : densité dépendance, histoire de vie, modèles de populations structurées en âge, système d’appariement, effets Allee, petites populations, *Zootoca vivipara*.

Density-dependent life history and the dynamics of small populations

Marianne Mugabo, ¹, Samuel Perret, ², Stéphane Legendre, ³, & Jean-François Le Galliard ^{1,2}.

¹ CNRS/UPMC, UMR 7625, Laboratoire Ecologie et Evolution, Université Pierre et Marie Curie, 7 Quai St. Bernard, 75005, Paris, France.

² CNRS/ENS, UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours, France.

³ CNRS/ENS, UMR 7625, Laboratoire Ecologie et Evolution, Ecole Normale Supérieure, 46 Rue d'Ulm, 75005, Paris, France.

Running title: Density dependence and extinction

Reference: Mugabo, M., Perret, S., Legendre, S. & Le Galliard, J.-F. 2011. Density-dependent life history and the dynamics of small populations. Manuscript in preparation for submission to the *American Naturalist*.

ABSTRACT

Population dynamics depend importantly on the strength and shape of density dependence. Unfortunately, the lack of reliable life-history data often prevents to make accurate demographic predictions about small populations regulated by density dependence. We created a gradient from low to high densities in small isolated populations of common lizards (*Zootoca vivipara*) and investigated the shape of density dependence of life history during a yearly cycle. Body growth, reproductive performances and immunocompetence decreased almost linearly with density, while parturition date showed evidences of an Allee effect at low densities. Survival and body size at birth of the first generation of offspring were density-independent. We used these data to design deterministic and stochastic one-sex and two-sex population models. Elasticities analyses of the density-dependent and density-independent models pinpointed the juvenile and yearling classes as the most influential, but rose different results about the influence of vital rates. Stochastic simulations demonstrated that negative density dependence buffers the effects of initial density on extinction probability, has positive effects on the persistence of sparse populations, and interacts with sex ratio fluctuations to shape extinction dynamics of dense populations. Our study demonstrates the importance of accounting for density-dependent regulations to draw accurate predictions about the extinction of small populations.

Keywords: density dependence, life history, age-structured population models, mating system, Allee effects, small populations, *Zootoca vivipara*.

INTRODUCTION

Density dependence is one of the major mechanisms of population regulation and dynamics. Population density can have both negative (e.g., Massot et al., 1992) and positive effects on components of population growth (i.e., Allee effects, e.g., Angulo et al., 2007). Negative density dependence arises from intraspecific competition for limited resources such as food and space, whereas Allee effects arise from a reduction of cooperative interactions at low densities (reviewed in Courchamp et al., 2008). Researchers in population management have highlighted the importance of density dependence for population viability along with demographic and environmental stochasticity (e.g., Lande et al., 2003, Morris & Doak, 2002, Grant & Benton, 2000, Grant & Benton, 2003, Schoener et al., 2003). For example, negative density dependence can stabilize the population at low densities where the risk of extinction remains high (Morris & Doak, 2002, Lande et al., 2003). A demographic Allee effect implies an unstable equilibrium below which population goes deterministically extinct (i.e., Allee threshold Courchamp et al., 2008).

A wide range of functions has been used to describe density dependence and quantify its consequences for population dynamics and extinction risk (reviewed in Henle et al., 2004 and Courchamp, 2008 #720). In most cases, the choice of a density-dependent function has been driven by mathematical concerns rather than by solid biological knowledge. Yet, depending on the shape and strength of negative density dependence, models can either predict an increase, a decrease or no modification of extinction risk compared to density-independent models and models using different functions can produce inconsistent predictions (e.g., Henle et al., 2004, Morris & Doak, 2002, Runge & Johnson, 2002). In addition, functions differ in their ability to describe a demographic Allee effect and analyses that ignore Allee effects tend to under-estimate extinction probabilities (e.g., in harvested populations of fishes, Roughgarden & Smith, 1996). To draw accurate predictions of the persistence of populations, it is therefore crucial to identify the demographic rates that are most sensitive to population density and to determine the shape of density dependence (Henle et al., 2004, Pascual et al., 1997, Runge & Johnson, 2002). Unfortunately, the characterization of the shape of density dependence in natural populations can be extremely difficult, especially in threatened species where demographic data are often available over a limited range of densities (Morris & Doak, 2002, Courchamp et al., 2008). Therefore, there is a need to implement empirical studies that span a large range of population densities and realistic

demographic models that link life-history responses to density with long-term population dynamics.

Using the common lizard (*Zootoca vivipara*, Jacquin 1787) as a model species, we investigated the consequences of density dependence for the growth and dynamics of small experimental populations. This species is currently not endangered but populations at warm margins of the range are put at higher risks of extinction by climate warming (Sinervo et al., 2010). Density dependence is an important regulatory mechanism in natural populations and several components of population growth are negatively affected by an experimental density increase (e.g., growth rate, body size, survival rate, reproduction and dispersal Cote et al., 2008, Lecomte et al., 1994, Lecomte et al., 2004, Le Galliard et al., 2006, Massot et al., 1992, Meylan et al., 2007, Dreiss et al., 2010). For instance, a density increase has negative effects on clutch size and access to reproduction in juveniles and a weak negative effect on juvenile survival (Dreiss et al., 2010, Meylan et al., 2007, Massot et al., 1992). In this species, adult survival is lower in males than in females and the adult sex ratio in natural populations is on average female-biased with significant spatial and temporal variation (Le Galliard et al., 2005). Therefore, a shortage of mates could also impact population growth in small isolated populations. Unfortunately, previous studies were not designed to examine the shape of density dependence and quantify its dynamical consequences.

Here, we seeded outdoor enclosures with small populations of common lizards following a gradient from low to high densities. Experimental populations were monitored to characterize the shape and the strength of the relationship between the initial population density and life-history traits, including body growth and size, survival, reproductive performances and immunocompetence. We compared the support of three alternative density dependent functions: a step function appropriate to model threshold effects, a linear function, and a quadratic function appropriate to model non-linear effects. A quadratic function allows to detect positive density-dependence at low densities (e.g., Angulo et al., 2007) or may be used to model a decelerating negative density dependence (e.g., for growth rate Jenkins et al., 1999). Using this empirical knowledge, we constructed deterministic and stochastic one-sex and two-sex matrix population models to investigate the dynamical consequences of density dependence. The comparison of one-sex with two-sex models that incorporate a mating function allowed us to investigate the main dynamical effects of density dependence and its effects when combined with stochastic fluctuations in the adult sex ratio and mating pair formation. Such fluctuations arise from a complex interplay between demographic

stochasticity, sex-specific survival rates and mating system, and are important to consider in small populations (Bessa-Gomez et al., 2004, Engen et al., 2003, Legendre et al., 1999).

METHODS

Model species

The common lizard is a small (adult snout-vent-length, SVL: 50-75 mm) ovoviviparous species inhabiting humid habitats across northern Eurasia. The species is characterized by a short life expectancy (3-4 years), a continuous growth and a polygynandrous mating system. Females produce one clutch per year with one to six genetic mates whereas males can successfully mate with up to fourteen females (Fitze et al., 2005). Natural populations can be divided into three age classes: juveniles (newborn individuals), yearlings and adults (≥ 2 years old). In our study site, age at first reproduction is plastic and varies between one to three years old (see Mugabo et al., 2010). In natural populations from where individuals originate (Mont Lozère, southern France, 44°27’N, 3°44’E), mean density ranges from 200 to 2000 adults and yearlings per ha (Massot et al., 1992). In our experimental system, the pre-breeding equilibrium population size is estimated around 2000 yearlings + adults per ha (Lecomte et al., 2004).

Manipulation of population density

During the summer 2008, we manipulated the initial density of 24 experimental populations maintained in outdoor enclosures at our experimental facility (48°17’N, 2°41’E). Enclosures measuring 10 × 10 m each were located in a natural meadow and provided lizards with natural food, shelters and basking sites (see Le Galliard et al., 2005). Enclosure size corresponds to the average home range of an adult in natural populations (Lecomte et al., 2004). Populations were established post-breeding following five density levels. The smallest populations (i.e., density level 1) had 1 adult male, 2 adult females, 2 yearling males, 2 yearling females, and 5-6 and 4-5 juvenile males and females respectively (i.e., initial density N_0 equivalent to 700 adults + yearlings per ha). Density levels 2 to 5 differed from density level 1 by a multiplicative factor of 2 to 5, respectively, and had similar age and sex structures (i.e., density gradient from N_0 to $5N_0$). The number of enclosures per treatment was adjusted to maintain a similar total number of individuals per treatment (density level 1: $N=10$, level 2: $N=5$, level 3: $N=4$, level 4: $N=3$, level 5: $N=2$). Enclosures were randomly assigned to treatments.

Adults and yearlings were captured in outdoor enclosures in May 2008 and all newborns were obtained from the captured gravid females. Individuals were sexed, measured for SVL to the nearest mm and weighted to the nearest 0.01 g. Adults ($n=162$) and yearlings ($n=216$) were randomly assigned to experimental populations. Juveniles ($n=549$) were released according to a split-clutch design such that juveniles from the same clutch were equally distributed among density levels in different enclosures. At the beginning of the experiment, treatment groups did not differ in SVL and body condition (estimated from an analysis of covariance of body mass including SVL as a covariate; ANOVA, all $P>0.34$). Adult and yearling males and non reproductive females were released in outdoor enclosures on the 12th and 13th of June whereas post-reproductive females and their juveniles were released right after parturition (from the 11th of June to the 23rd of July). Experimental populations were then monitored during one year.

Measurements of life history traits and immunocompetence

Individual data were collected during two successive capture sessions carried out in late summer 2008 (from the 25th of August to the 11th of September, $n=763$), hereafter referred as 'August 2008' and in late spring 2009 (from to the 11th of May to the 14th of June, $n=321$), hereafter referred as 'May 2009'. Growth rates in SVL were calculated as the change in SVL divided by the time interval as defined in Mugabo *et al.* (2010). Annual survival probabilities were estimated from recapture data in late spring 2009 when the catchability is close to one. In May 2009, all reproductive females ($n=104$) were kept in the laboratory until parturition to assess their clutch size (total number of eggs), date of parturition, body condition after parturition and the SVL at birth of their viable offspring. Not all females started to breed at the age of one year, and we therefore estimated the proportion of breeders within the group of released juveniles.

In addition, immunocompetence was assessed by the skin-swelling in response to the injection of a mitogen, the phytohaemagglutinin (PHA), as described by Mugabo *et al.* (2010). Measurements were done for yearlings and adults before release and for all recaptured individuals in May 2009. The skin-swelling was calculated as the difference in thickness of the leg (to the nearest 0.01 mm) between 12h after and right before the injection. This procedure triggers a haemagglutination and lymphoproliferation and evaluates the ability of an individual to mount an inflammatory response (Vinkler *et al.*, 2010 and references therein). Immunocompetence of yearlings and adults before release did not differ between treatments (F tests, all $P>0.22$).

Statistical analyses

We investigated the relationship between population density on one hand and life-history traits and immunocompetence on the other hand using three alternative shapes of density dependence: a step function (density level as a factor), a linear function (covariate in a linear regression) and a quadratic function (covariate in a quadratic regression). For each model, we calculated the Akaike Information Criterion corrected for small sample size (AIC_c) the ΔAIC_c (difference with AIC_c of the best model) and the AIC_c weight (w , a measure of the degree of support relative to the set of alternative models tested). One model was considered to provide the best fit of the data if ΔAIC_c was ≥ 2 (Burnham & Anderson, 2002).

Density dependence in growth rates, body size, reproductive characteristics and immunocompetence was investigated with mixed-effects linear models in R 2.10.1 (<http://cran.r-project.org/>) following Pinheiro & Bates (2000). Density dependence in survival and access to reproduction was investigated with mixed-effects generalized linear models with a logit link function and binomial error terms following Bolker *et al.* (2009). All models included a random effect of enclosure identity and models of SVL at birth included a clutch identity effect nested in the enclosure effect. In addition, models describing juveniles’ traits included a random effect of clutch identity to test for differences among families. The family reaction norms of growth rates and survival in response to density were further quantified by including an interaction between the clutch identity random effect and the density effect following Nussey *et al.* (2005).

The fixed part of all models included a treatment effect (see above), a sex effect and their first-order interaction and the additive effect of release date. Models of yearlings’ and adults’ traits and models of reproductive performances (females from all age classes) included also an additive effect of age class and the first-order interaction between age class and treatment. Additional fixed effects were (i) a linear effect of initial SVL when analyzing growth rates to control for decelerating growth curves, (ii) a linear effect of recapture date when analyzing SVL at recapture, (iii) linear and quadratic effects of initial SVL when analyzing annual survival to control for natural selection on body size, and (iv) a clutch size effect corrected for female SVL (residuals of a linear regression) and a date of birth effect when analyzing SVL at birth of offspring. Parturition date and clutch size are usually affected by SVL in the common lizard (Le Galliard *et al.*, 2010, Mugabo *et al.*, 2010). We thus run two sets of models that included or did not include a linear effect of SVL and estimated the

contribution of SVL to density-dependence by comparing the percentage deviance explained by models with or without SVL effects.

For normally distributed responses and nested random effects, we used a maximum likelihood approach in the *lme* procedure and tested for significance of fixed effects with marginal F tests (Pinheiro & Bates, 2000). For normally distributed responses and additive random effects and for non-normally distributed responses, we used a Laplace approximation of the maximum likelihood in the *lmer* procedure and fixed effects were tested with likelihood-ratio tests (LRT) and Wald-Z tests (Bolker et al., 2009). In all cases, a minimum adequate model was obtained by backward elimination of non-significant terms. Assumptions of normality were fulfilled but Bartlett tests revealed significant variance heterogeneity between groups that we accounted for with a *varIdent* function in *lme* (results not shown). All estimates are provided with standard errors unless otherwise stated and degrees of freedom (d.f.) of LRT are indicated when different than one.

Population model

Dynamical effects of density dependence were investigated using an age-classified matrix population model with three age classes (juveniles, yearlings and adults). The model assumed a post-breeding census and a birth pulse reproduction (Caswell, 2001). We analyzed seven versions of this model (see Appendix A for further details). First, we developed deterministic one-sex models with or without density dependence to estimate the elasticity of population growth rate and equilibrium density for each vital rate (Grant & Benton, 2000). Second, we developed a deterministic density-dependent two-sex model to predict the density and age and sex-structures at equilibrium. Third, we developed four stochastic versions including demographic stochasticity on all vital rates: (i) a density-independent one-sex model, (ii) a density-dependent one-sex model, (iii) a density-independent two-sex model, (iv) a density-dependent two-sex model. Two-sex models assumed a male and female coupled life cycle and a polygynous mating system with a harem size of 4 (i.e., a single male mates on average with 4 females Fitze et al., 2005). Model parameters were estimated from our experimental data (Table A1). The initial age and sex structures were similar to the ones carried out in our experiment and the best supported density-dependent function was used. Simulations were carried out using ULM (Legendre & Clobert, 1995).

RESULTS

Growth rate and body size

Table 1. Long-term effects of density on annual growth rate (mm.day⁻¹) and body size in May 2009 (mm) in yearlings and adults ($n=113$). Results are from the minimum adequate models. The best models include a linear effect of density (annual growth rate: $AIC_c=-656.11$, $w=0.999$, SVL in May 2009: $AIC_c=495.98$, $w=0.9998$).

Annual growth rate (mm.day⁻¹)			
<i>Fixed effects</i> *	Estimate \pm s.e.	$F_{ndf,ddf}$	<i>P</i> value
Intercept	0.0579 \pm 0.0064	$F_{1,86}=82.52$	< 0.0001
Initial SVL (mm)	-0.0043 \pm 0.0003	$F_{1,86}=210.71$	< 0.0001
Sex	M: -0.0429 \pm 0.0052	$F_{1,86}=67.31$	< 0.0001
Age class	Y: 0.0176 \pm 0.0057	$F_{1,86}=9.54$	0.003
Density	-0.0020 \pm 0.0017	$F_{1,20}=1.37$	0.26
Density \times sex	M: 0.0033 \pm 0.0014	$F_{1,86}=5.33$	0.02
Density \times age class	Y: -0.0050 \pm 0.0014	$F_{1,86}=13.10$	0.0005
<i>Random effects</i>	Estimate [95% CI]	LRT (d.f.=1)	<i>P</i> value
Enclosure identity	0.0061 [0.0034, 0.0108]	5.64	0.02
Residuals	0.0053 [0.0037, 0.0076]		
SVL in May 2009 (mm)			
<i>Fixed effects</i>	Estimate \pm s.e.	$F_{ndf,ddf}$	<i>P</i> value
Intercept	69.21 \pm 0.89	$F_{1,87}=6000.79$	< 0.0001
Sex	M: -8.73 \pm 0.84	$F_{1,87}=107.87$	< 0.0001
Age class	Y: 0.06 \pm 0.77	$F_{1,87}=0.01$	0.93
Density	-0.44 \pm 0.25	$F_{1,20}=2.94$	0.10
Density \times sex	M: 0.77 \pm 0.24	$F_{1,87}=10.18$	0.002
Density \times age class	Y: -0.78 \pm 0.22	$F_{1,87}=12.30$	0.0007
<i>Random effects</i>	Estimate [95% CI]	LRT (d.f.=1)	<i>P</i> value
Enclosure identity	0.27 [0.002, 31.38]	0.04	0.83
Residuals	0.97 [0.67, 1.40]		

Density=linear effect, M=males, Y=yearlings, SVL=snout-vent length, LRT=likelihood-ratio test, CI=confidence interval.

* Estimates are given for a mean value of the initial SVL.

Density had negative short-term and long-term effects on body growth and size in juveniles and in adults and yearlings (Appendix B and C and Table 1). During the summer, juvenile growth rate and body size decreased linearly with density and density dependence was similar

in males and females (density \times sex: LRT, all $P > 0.76$; Table B1, Figure B1). On the long term, annual growth rate and body size in May 2009 decreased non-linearly with density, and juvenile females were more affected than males (Table C1, Figure 1). Summer and annual growth rates and SVL varied between clutches (Table B1 and Table C1, LRT, all $P < 0.02$). In the analysis of family reaction norms of growth rates, clutches also differed significantly in their responses to density on the short but not on the long term. This effect was due to a negative correlation between the intercept and the slope of reaction norms (see estimates of correlation terms in Table 2) and implies that, on the short term, fast-growing clutches at low densities were more sensitive to a density increase than slow-growing clutches.

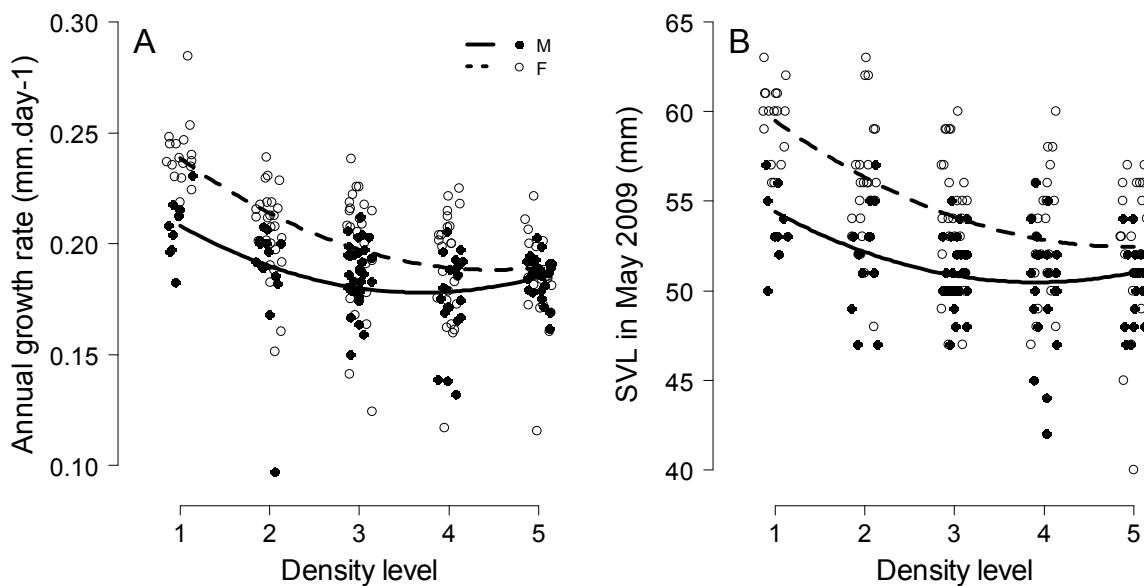


Figure 1. Long-term effects of density on body growth (A) and SVL at the end of the experiment (B) for juveniles. Estimates of the regression lines were obtained from the minimum adequate models (see Table C1). F: females, M: males. The graphical function *jitter* in R was used to separate overlapping points.

In adults and yearlings, short-term and long-term density dependence in growth and body size differed between sexes and age classes (Appendix B and Table 1). Body growth and body size in males were not significantly affected by density (*post-hoc* F tests, all $P > 0.09$, Appendix B; Table 1), but our sample size at the end of the experiment was small ($n=30$). In females, growth rate during the summer decreased non-linearly with density in adults but not in yearlings (*post-hoc* F tests for density² in adults: $F_{1,21}=6.00$, $P=0.02$, in yearlings: $F_{1,21}=1.44$, $P=0.24$; for density: all $P < 0.001$), whereas annual growth rate and body size decreased linearly with density in both classes (*post-hoc* F tests, all $P < 0.003$; Appendix B; Table 2). On average, growth rate and SVL were higher in females (F tests, all $P < 0.0001$). On

the short-term, density dependence of growth rate was more linear in yearlings than in adults (Table B2) and on the long-term, density dependence of growth rate and SVL was stronger in yearlings than in adults (Table 1).

Table 2. Estimates of family reaction norms of growth rates (mm.day⁻¹) in response to density on the short term (i.e., early growth rate, $n=428$ juveniles from 83 clutches) and on the long term (i.e., annual growth rate, $n=192$ juveniles from 57 clutches). Results are from models as in Table B1 and Table C1, additionally including random variation between clutches in the intercept and slope of a linear density-dependent growth model. Correlation term refers to the correlation between the clutch intercept and the clutch slope on density.

<i>Random effects</i>	Early growth rate				Annual growth rate			
	Estimate	LRT	d.f.	P value	Estimate	LRT	d.f.	P value
Clutch intercept	0.0394	45.49	1	< 0.0001	0.0086	7.25	1	0.007
Clutch slope on density	0.0072	<0.01	1	0.99	0.0013	0.10	1	0.75
Correlation term	-0.8650	5.90	1	0.02	-0.2200	< 0.01	1	0.99
Residuals	0.0330				0.0170			

LRT=Likelihood ratio test.

Annual survival

Annual survival of juveniles, yearlings and adults was not affected by density (LRT, all $P>0.12$). Juvenile survival increased with body size at birth up to a plateau, as indicated by the significant quadratic effect of SVL (SVL= 4.15 ± 2.0 , LRT=4.71, $P=0.03$; SVL²= -0.085 ± 0.043 , LRT=4.17, $P=0.04$). Yearling and adult survival decreased linearly with SVL at release (SVL= -0.062 ± 0.017 , LRT=13.58, $P=0.0002$; SVL²: LRT=2.81, $P=0.09$), indicating a negative directional selection on body size. Annual survival was much lower in males than in females for adults and yearlings (juveniles: LRT=2.05, $P=0.15$; adults and yearlings: LRT=332.83, $P<0.0001$) and did not differ between adults and yearlings (LRT=0.21, $P=0.64$). In juveniles, clutches had similar annual survival (LRT<0.01, $P=0.99$) and did not differ in density dependence (clutch \times density: LRT=0.06, d.f.=2, $P=0.97$).

Reproduction

The proportion of breeding females among released juveniles decreased linearly on the logit scale with density (AIC_c weight $w=0.80$; logit slope= -0.80 ± 0.21 , LRT=12.81, $P=0.0003$), even after controlling for a positive effect of SVL on breeding probability (SVL: logit slope= 0.32 ± 0.09 , LRT=22.18, $P=0.0002$; density: log slope= -0.45 ± 0.21 , LRT=4.85, $P=0.03$; Figure 2A). Controlling for the positive effect of SVL on breeding probability increased the percentage of deviance explained by the fitted model from 9.1 % to 24.9 %.

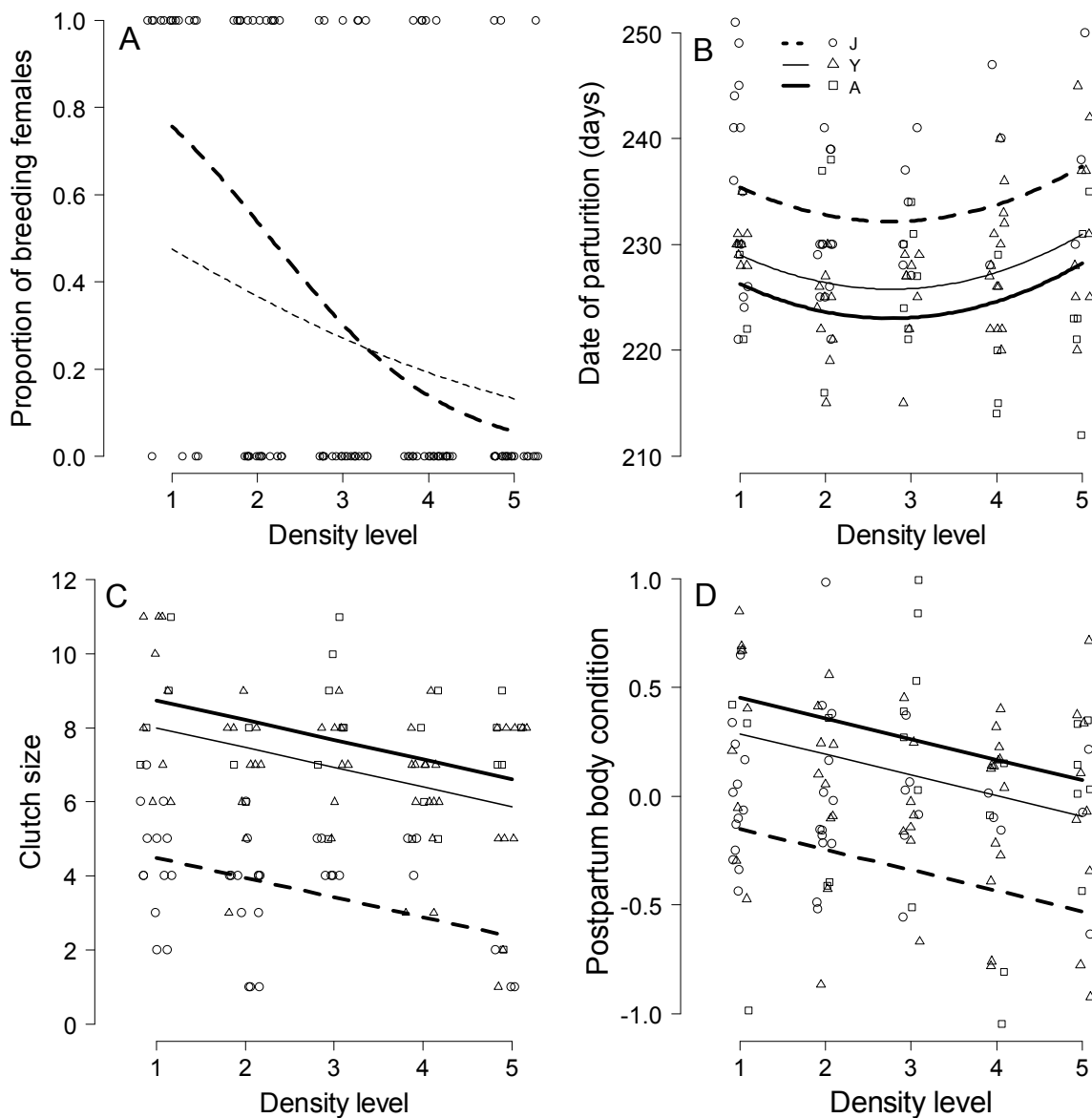


Figure 2. Density-dependence of the proportion of breeding females among released juveniles (A, $n=116$), the date of parturition (B, $n=112$), the clutch size (C, $n=114$) and the postpartum body condition (D, $n=111$) in juvenile, yearling and adult females. Estimates of regression lines were obtained from the minimum adequate models. In panel (A), the thin line corresponds to a model accounting for SVL effects and the thick line to a model without SVL effects. J: juveniles, Y: yearlings, A: adults.

Parturition date varied non-linearly with density ($w=0.80$; density: -5.74 ± 2.42 , $F_{1,19}=5.61$, $P=0.03$; density²: 1.04 ± 0.40 , $F_{1,19}=6.64$, $P=0.02$) and was lower at the intermediate level of density (Figure 2B). Juveniles laid eggs $6.40 (\pm 1.57)$ days later on average than yearlings and $9.16 (\pm 1.90)$ days later than adults ($F_{2,88}=13.41$, $P<0.0001$, multiple comparisons: juveniles *versus* yearlings and adults, all $P<0.0001$, yearlings *versus* adults: $P=0.24$). Clutch size was not affected by density when controlling for a positive effect

of SVL (density: $F_{1,20}=2.13$, $P=0.16$; $SVL=0.3460 \pm 0.0319$, $F_{1,91}=117.83$, $P<0.0001$; 15.5% deviance explained) and was not different between age classes ($F_{2,89}=2.65$, $P=0.08$). When not controlling for SVL, clutch size varied significantly with density and age class, and the percentage of deviance explained by the model was similar (14.45 %). The best model indicated a linear decrease of clutch size with density (slope= -0.53 ± 0.14 , $F_{1,20}=13.95$, $P=0.001$, Figure 2C) but the linear model and the step model were equally supported by the data (respectively $w=0.57$ and $w=0.43$, $\Delta AIC_c=0.53$). Finally, postpartum body condition decreased linearly with population density ($w=0.95$, density= -0.09 ± 0.04 , $F_{1,19}=6.71$, $P=0.02$; $n=111$; Figure 2D) and was lower in juveniles than in yearlings and adults ($F_{2,87}=4.54$, $P=0.01$, multiple comparisons: juveniles *versus* yearlings and adults, all $P<0.01$, yearlings *versus* adults: $P=0.39$).

The SVL at birth of viable offspring was not affected by density ($F_{1,19}=0.13$, $P=0.72$, $n=556$ juveniles from 95 females). SVL at birth decreased with residual fecundity (slope= -0.1493 ± 0.0559 , $F_{1,71}=7.14$, $P=0.009$) and was lower in males ($F_{1,460}=175.52$, $P<0.0001$). SVL at birth was also larger in offspring produced by yearlings and adults than in offspring produced by juveniles ($F_{1,71}=6.20$, $P=0.003$, multiple comparisons: juveniles *versus* yearlings and adults, all $P<0.03$, yearlings *versus* adults: $P=0.88$).

Immunocompetence

Immunocompetence was not affected by density in juveniles ($F_{1,22}=0.31$, $P=0.58$, $n=202$) but decreased with density in yearlings and adults. The quadratic model and the linear model were equally supported ($\Delta AIC_c=0.02$, quadratic model $w=0.43$, linear model $w=0.43$; density²= -0.0019 ± 0.0008 , $F_{1,19}=4.90$, $P=0.04$; density= -0.018 ± 0.0053 , $F_{1,19}=4.88$, $P=0.04$; $n=101$). Immunocompetence was also significantly lower in males than in females for yearlings and adults (juveniles: $F_{1,177}=2.74$, $P=0.10$; yearlings and adults: $F_{1,79}=11.16$, $P=0.001$). Immunocompetence before and after the experiment were not correlated ($r=0.11$ [-0.09, 0.30] 95% CI, $P=0.27$).

Population dynamics and extinction risk

The density-dependent deterministic model predicted a stable equilibrium of 52 lizards including 16 juvenile females, 16 juvenile males, 7 yearling females, 7 yearling males, 5 adult females and 1 adult male. Elasticity analyses indicated that the asymptotic growth rate λ and density at equilibrium N_{eq} were most affected by a change in juvenile survival, followed by yearling survival (Table 3). Contrary to λ , N_{eq} was equally affected by a change in yearling

survival and fecundity and was also highly sensitive to a change in juvenile fecundity (Table 3). In addition, N_{eq} was importantly affected by a change in the slope of density dependence acting on the percentage of breeders among juveniles (Table 3).

Table 3. Elasticity of the asymptotic growth rate (λ) and population size at equilibrium (N_{eq}) for each vital rate. Estimates of elasticity of λ are from the density-independent one-sex model. Estimates of elasticity of N_{eq} are from the density-dependent one-sex model. For density-dependent vital rates (proportion of breeding juveniles and clutch size), a linear relationship between the vital rate and density on the scale of the regression (logit scale and log scale respectively) was best supported by our experimental data (see the main text). Here, we therefore refer to the density-dependent function $f(x_i)$ on the logit or the log scale with $x_i(n) = a_i - b_i n$, where x_i is the vital rate and b_i the slope of the density dependence (see Table A1). Values in bold are elasticities of vital rates. Values between brackets give the ratio of the elasticity of vital rates with the highest elasticity (i.e., annual juvenile survival in both cases).

Vital rates	Elasticity of λ	Elasticity of N_{eq}
Annual juvenile survival	0.503 (1)	1.699 (1)
Annual yearling survival	0.373 (0.74)	1.364 (0.80)
Annual adult survival	0.124 (0.25)	0.481 (0.28)
Juvenile fecundity ($\gamma_j \times f_j \times h_{s_j} \times sr_j$)	0.130 (0.26)	0.960 (0.57)
Percentage of breeders (γ_j)		0.770
Slope of the density-dependence of (γ_j)		-0.568
Total clutch size (f_j)		0.358
Slope of the density dependence of (f_j)		-0.077
Hatching success (h_{s_j})		0.331
Primary ex ratio (sr_j)		0.326
Yearling fecundity ($\gamma_y \times f_y \times h_{s_y} \times sr_y$)	0.280 (0.56)	1.366 (0.80)
Percentage of breeders (γ_y)		1.004
Total clutch size (f_y)		1.361
Slope of the density dependence of (f_y)		-0.260
Hatching success (h_{s_y})		1.010
Primary sex ratio (sr_y)		1.006
Adult fecundity ($\gamma_a \times f_a \times h_{s_a} \times sr_a$)	0.093 (0.18)	0.391 (0.23)
Percentage of breeders (γ_a)		0.346
Total clutch size (f_a)		0.398
Slope of the density dependence of (f_a)		-0.092
Hatching success (h_{s_a})		0.363
Primary sex ratio (sr_a)		0.353

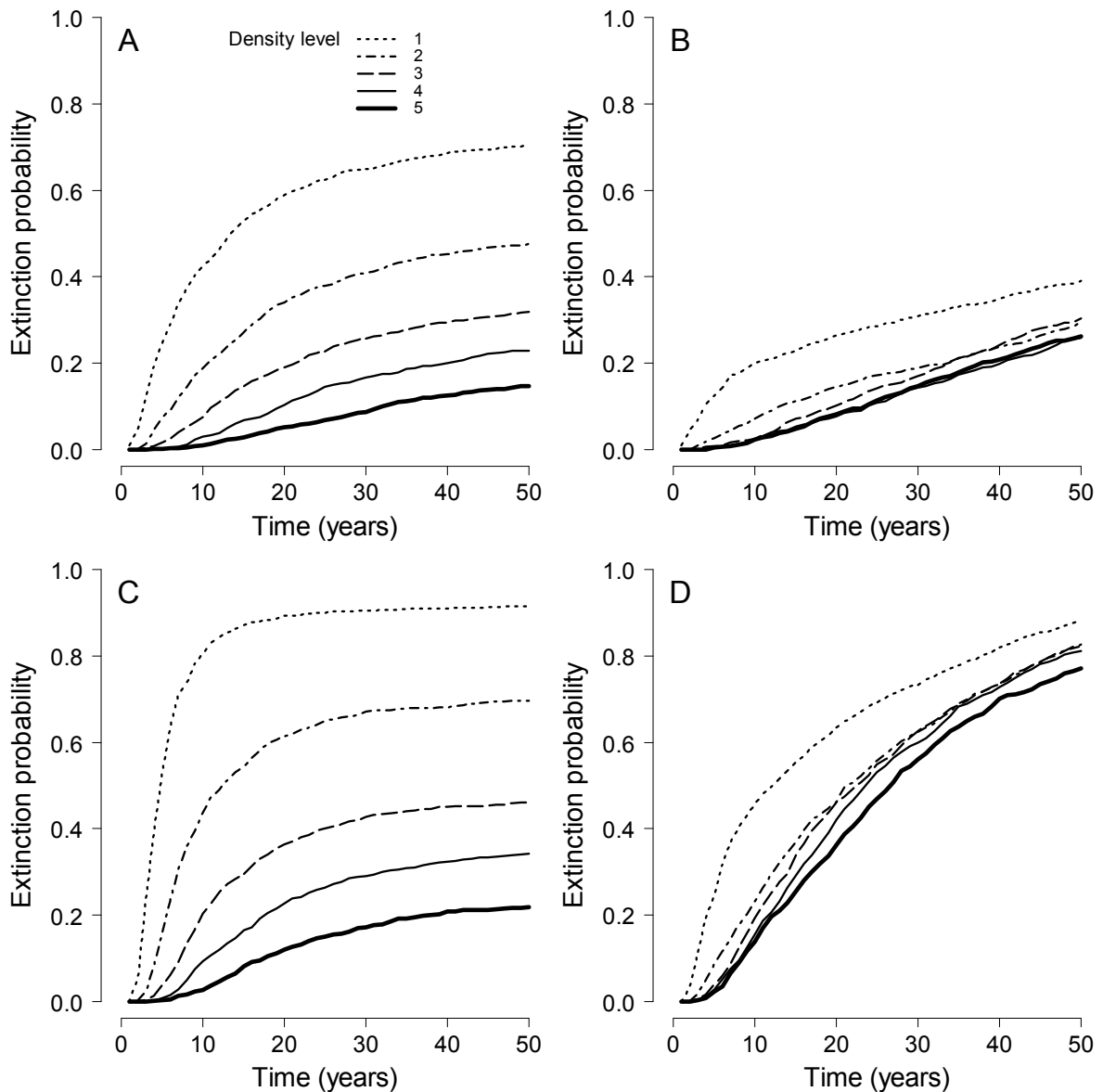


Figure 3. Cumulated extinction probability over time according to initial density for (A) a density-independent one-sex model, (B) a density-dependent one-sex model, (C) a density-independent two-sex model and (D) a density-dependent two-sex model. The structure and parameterization of each model is described in Appendix A. Results are from Monte Carlo simulations of 1000 trajectories.

Stochastic simulations demonstrate that negative density dependence buffers differences in extinction probabilities among populations starting with different densities (or numbers) of lizards. In the one-sex density-independent model, the extinction risk gradually decreased with initial population density, as expected (Figure 3A-B). In the density-dependent model, extinction probabilities were more similar among populations except for the populations starting at low initial densities. As a consequence, density dependence had a positive effect on the extinction risk in populations at low and moderate initial densities, and no or a weakly negative effect in initially dense populations. As expected, accounting for

males and sex ratio fluctuations increased importantly the extinction probability, though this effect was much stronger in density-dependent models and interacted with density dependence (Figure 3C-D). In two-sex models, density dependence decreased the extinction risk in initially sparse populations but increased it importantly in initially dense populations. To understand this interaction between density dependence and sex ratio fluctuations, we ran simulations of a two-sex density-dependent model with an unrestricted harem size (males are not limiting reproduction) or with no sex bias in mortality (yearling and adult males survive similarly than females, see Appendix D). Assuming an unrestricted harem size did not change the results, but increasing survival of males produced patterns of extinction similar to those predicted by the one-sex density-dependent model (Figure D1).

DISCUSSION

Mechanisms of density dependence

Among the nine traits studied here, seven were negatively and almost linearly affected by population density and one of them (parturition date) also showed evidences of an Allee effect at low densities. Negative density-dependence of life history can be triggered by trophic interactions, physiological processes and behavioral changes (Edeline et al., 2010). In crowded environments, competition for food can reduce individual feeding rates and thus the amount of energy available for structural growth, maintenance, immunity and reproduction (Amundsen et al., 2007). Lizard feeding rates during late spring are weakly affected by prey density and lizard abundance has a negative effect on the biomass of preferred preys (González-Suárez et al., 2011). Therefore, trophic interactions may be responsible for a part of the observed life-history responses to density. High levels of social competition can also be associated with physiological (e.g., increase in circulating levels of glucocorticoids) and behavioral responses (e.g., increase in aggressiveness) that divert energy from growth, immunity, or reproduction (e.g., Edeline et al., 2010, Hawley et al., 2006, Comendant et al., 2003). For example, chronic enhancement of circulating corticosterone levels increases behavioral activity and metabolic rates in common lizards (e.g., Cote et al., 2006, Meylan et al., 2010). Therefore, density-dependent increases in corticosterone levels could be responsible for the life-history responses to population density observed here. The link between corticosterone, population density and life history remains however to be investigated. On the other hand, the absence of detectable component Allee effects for reproductive traits such as breeding frequency and clutch size in this and other empirical

studies (Courchamp et al., 2008, Gregory et al., 2010) should be interpreted with caution. We may not have reached sufficiently low densities or used sufficiently large enclosures to detect Allee effects, even though male availability at low densities constrained breeding schedules.

Patterns and shape of density dependence

Growth rate and body size decreased linearly or weakly non-linearly with density depending on the study period, the sex and the age class. A decelerating density dependence on body growth has been well described in salmonids (e.g., Grant & Imre, 2005, Amundsen et al., 2007, Jenkins et al., 1999) and is classically explained by a curvilinear variation of feeding rates with density (Amundsen et al., 2007, González-Suárez et al., 2011). Thus, according to our growth data, population density may have negatively affected annual feeding rates in juveniles as well as summer feeding rates in yearling and adult females. In addition, our study revealed differences among clutches in the plasticity of body growth to density during the early juvenile stage. This result is in accordance with a previous laboratory study showing interfamilial variation in growth sensitivity to food availability (Mugabo et al., 2010) and was explain by the fact that fast-growing clutches at low densities were more affected by density than slow-growing clutches. These findings suggest the existence of a polymorphism in the acquisition and/or allocation of energy to structural growth early in life. Further investigations are needed to determine if interfamilial variation in phenotypic plasticity is driven by maternal effects or genetic variation (Mugabo et al., 2010, Nussey et al., 2005). On the overall juvenile stage, we did not detect interfamilial variation in the plasticity of body growth. This could be due to the change of the shape of density dependence on body growth between the early and the late juvenile stage, which suggests a change in the patterns of allocation of energy to growth in response to density; a loss of statistical power or selection against families that were more sensitive to high densities.

Access to reproduction in juveniles and clutch size decreased linearly with density. These are expected life-history responses in organisms with a fast life history, a plastic age at sexual maturation and a plastic reproductive effort, such as the common lizard and many other species (e.g., Massot et al., 1992, Both, 1998, Forrester et al., 2011). Density dependence on reproduction was importantly driven by positive effects of body size on age at first reproduction and clutch size. These results contrast with those of a field experiment by Massot et al (1992) where an experimental increase of density had weak effects on body size of breeding females but strong effects on their fecundity. Therefore, reproductive performances in crowded environments are probably limited both by body size and by other

physiological constraints (e.g., body reserves). The postpartum body condition decreased also with density. Female common lizards use a mixed energy allocation strategy to fuel reproduction based on long-term energy store (i.e., capital breeding) and energy acquired during vitellogenesis (i.e., income breeding Mugabo et al., 2011). A low postpartum condition at high densities could therefore diminish their future survival and reproduction.

Parturition dates showed evidences of an Allee effect at low density and negative density dependence from moderate to high densities. To our knowledge, only one study in a colonial seabird reported positive density dependence in breeding dates, which was explained by a social stimulation of reproduction and a social facilitation of foraging (Votier et al., 2009). Common lizards are not cooperative breeders or foragers, but it is likely that a limited access to breeding males at low densities can delay the onset of reproduction of females. At high densities, the timing of reproduction may be constrained by food intake and aggressive social interactions (see e.g., Le Galliard et al., 2005). The fitness of reproductive individuals and their offspring is often negatively correlated with parturition and hatching dates (e.g., Le Galliard et al., 2010, Mugabo et al., 2011). For instance, hatching dates are negatively correlated with offspring body size and growth during the first year of life (Le Galliard et al., 2010), but also with juvenile survival and clutch size at first reproduction (unpublished data, respectively Wald-Z=-3.17, P=0.001 and $F_{1,25}=9,28$, P=0.005). Therefore, positive and negative density dependence acting on the parturition date could substantially affect population dynamics.

In accordance with a previous finding (Massot et al., 1992), growth rate was more sensitive to density in juvenile females, followed by juvenile males, yearling females, yearling males and adult females. Body growth was insensitive to density in adult males. Adult male common lizards are socially dominant and asymmetric competition for food and space has been reported (Lecomte et al., 1994, Massot et al., 1992, Mugabo et al., 2010, 2011). Therefore, asymmetric competition could be responsible for the sex and age-specific responses of growth to density. On the contrary, immunocompetence, measured by the inflammatory response, decreased with density in yearling and adult males and females but was density-independent for juveniles. A similar age-dependent sensibility of immunity has been described for food availability and was explained by different allocation strategies to immunity in developing (i.e., juveniles) and non-developing individuals (Mugabo et al., 2010, 2011). Alternatively, this result could be explained by the activation of different components of the immune system between the first and the second encounter with PHA (i.e., innate

versus acquired immunity Vinkler et al., 2010), since yearlings and adults but not juveniles had been exposed twice to PHA.

Density independent life history

Survival probabilities and body size at birth of the first generation of offspring were not affected by population density. Density independence of adult and yearling survival has already been demonstrated by Massot et al (1992). However, inconsistent effects of density are seen for juvenile survival in natural populations (negative in Massot et al., 1992 and positive for females in), which suggest that density can interact with other environmental factors that are not entirely understood. Effects of density on body size at birth are consistent with those of other studies where the quality at birth of offspring was density-independent (Massot et al., 1992, Meylan et al., 2007, Dreiss et al., 2010). This demonstrates that female common lizards maintained at a high density compromise the quantity but not the quality of their progeny. This allocation strategy is expected to occur in species with a variable clutch size, a trade-off between offspring number and size at birth, and a positive directional selection on body size at birth (e.g., Du, 2006). This is the case in the common lizard because clutch size is plastic and size at birth is positively correlated with early survival and body size at adulthood (Mugabo et al., 2010, Le Galliard et al., 2010).

Dynamical consequences of density-dependence

The deterministic two-sex density-dependent model produced smooth dynamics towards a stable equilibrium and realistic predictions of the equilibrium characteristics. Predicted density of adults and yearlings at equilibrium matched those observed previously in the same experimental set-up (Lecomte et al., 2004). The adult sex ratio (ASR=proportion of males) shifted from 0.33 in initial populations to 0.25 at equilibrium and the proportion of adults changed from 0.43 to 0.32. This equilibrium age- and sex-structure falls within the range of variation observed in the natural populations from where the lizards originated (ASR range = 0-0.80, mean=0.18 \pm 0.18 SD Le Galliard et al., 2005, proportion of adults range = 0.35-0.57, mean=0.47 \pm 0.09 SD Massot et al., 1992, Meylan et al., 2007).

We combined elasticity analyses with simulations including demographic stochasticity to investigate the consequences of density dependence for the deterministic and stochastic dynamics. Elasticity analyses of density-independent models are often used to determine the most influential stages of an organism life cycle and manage populations (Caswell, 2001). Elasticity analyses of the asymptotic growth rate λ and of the density at equilibrium N_{eq}

revealed that λ was affected most importantly by variations in juvenile and yearling survival, while N_{eq} was also affected by variations in juvenile and yearling fecundity. Thus, elasticities of λ and N_{eq} pinpointed the same most influential stage classes but rose different results for each demographic rate. In addition, N_{eq} was sensitive to the strength of density dependence acting on the percentage of breeders among juveniles: uncertainty in the shape of this density-dependent function may thus lead to erroneous predictions of N_{eq} . According to theory, elasticity of N_{eq} is proportional to elasticity of λ if (i) the population has a stable equilibrium, (ii) density dependence is a function of the total number of individuals and (iii) density dependence operates in the same way in all the age classes (Grant & Benton, 2000). Here, only the two first conditions were verified since maturation and percentage of breeders was density-dependent in juveniles but yearlings and adults had density-independent breeding frequencies. These results confirm the utility of accounting for density dependence to draw conclusions about the most influential life stages and demographic traits (Grant & Benton, 2000, Grant & Benton, 2003).

In addition, our stochastic simulations yielded three major results. First, negative density dependence buffers the effects of initial density on the persistence of small populations. Second, density dependence alone has positive effects on the persistence of sparse populations. These two effects of the negative density dependence acting on reproduction are due to the fact that the influence of demographic stochasticity on the time to extinction in density-dependent populations is dependent on (i) the upper limit on population density introduced by the negative density dependence, (ii) the long-term population growth rate and (iii) the shape of density-dependence (Lande, 1993, Lande et al., 2003). For instance, a linear negative density dependence acting on body growth, maturation and fecundity as described here implies that reproductive rates increase in declining populations and thus act as a rescue effect allowing sparse populations to rapidly move away from a zone of high extinction risks due to demographic stochasticity (Morris & Doak, 2002, Henle et al., 2004). Third, density dependence interacts with sex ratio fluctuations to shape extinction dynamics of dense populations. In accordance with previous studies (e.g., Bessa-Gomez et al., 2004, Legendre et al., 1999, Engen et al., 2003), we found that stochastic fluctuations in sex ratios and mating pair formation increase substantially the risks of extinction of small populations. Therefore, demographic stochasticity can lead to a shortage of males in small lizard populations and thus to a demographic Allee effect. More interestingly, the comparison of one-sex and two-sex models showed that the negative density dependence acting on fecundity combined with sex ratio fluctuations to generate higher extinction risk in initially dense

populations, while initially sparse populations were less at risks of extinction from density dependence. This unexpected result is because of a higher probability that no breeding male survived to inseminate breeding females in initially dense populations regulated by density dependence around their equilibrium than in unregulated populations.

Density-dependence has received less attention in the field of population management than sex ratio fluctuations (but see La Montagne et al., 2002, Schoener et al., 2003). Our experiment and modeling exercise demonstrate the importance of density-dependent regulations even for small populations influenced by demographic stochasticity. Furthermore, density dependence can also affect mating systems and sex ratio fluctuations through density-dependent effects on intrasexual and intersexual competition (Kokko & Rankin, 2006 and references therein). Interactions between the population density and the mating system, such as the one found in this study, are therefore likely to be general and should be considered when attempting to predict the dynamics of populations.

ACKNOWLEDGEMENTS

We are thankful to B. Decencière, M. Paquet, M. Cisel, M. González-Suárez, S. Meylan and all students and personnel at the CEREEP for assistance in the field. This study was funded by the Centre National de la Recherche Scientifique (CNRS), the Agence Nationale de la Recherche (ANR, grant 07 –JCJC-0120 to J.F.L.G.) and the Région Île-de-France R2DS program (grant 2007-06 to J.F.L.G. and M.M.) and was validated by the Regional ethics committee in animal experiment N°3 of the Région Île-de-France (file p3/2008/008).

REFERENCES

- Amundsen, P. A., Knudsen, R. & Klemetsen, A. 2007. Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *Journal of Animal Ecology* **76**: 149-158.
- Angulo, E., Roemer, G. W., Berec, L., Gascoigne, J. & Courchamp, F. 2007. Double Allee effects and extinction in the island fox. *Conservation Biology* **21**: 1082-1091.
- Bessa-Gomez, C., Legendre, S. & Clobert, J. 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecology Letters* **7**: 802-812.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**: 127-135.

- Both, C. 1998. Experimental evidence for density dependence of reproduction in great tits. *Journal of Animal Ecology* **67**: 667-674.
- Burnham, K. P. & Anderson, D. R. 2002. *Model selection and multimodel inference. A practical information-theoretic approach*. Springer, New York.
- Caswell, H. 2001. *Matrix population models*, 2 ed. Sinauer Associates, Sunderland.
- Comendant, T., Sinervo, B., Svensson, E. I. & Wingfield, J. 2003. Social competition, corticosterone and survival in female lizard morphs. *Journal of Evolutionary Biology* **16**: 948-955.
- Cote, J., Boudsocq, S. & Clobert, J. 2008. Density, social information, and space use in the common lizard (*Lacerta vivipara*). *Behavioral Ecology* **19**: 163-168.
- Cote, J., Clobert, J., Meylan, S. & Fitze, P. S. 2006. Experimental enhancement of corticosterone levels positively affects subsequent male survival. *Hormones and Behavior* **49**: 320-327.
- Courchamp, F., Brec, L. & Gascoigne, J. 2008. *Allee effects in ecology and conservation*. Oxford University Press, Oxford.
- Dreiss, A. N., Cote, J., Richard, M., Federici, P. & Clobert, J. 2010. Age- and sex-specific response to population density and sex ratio. *Behavioral Ecology* **21**: 356-364.
- Du, W. G. 2006. Phenotypic plasticity in reproductive traits induced by food availability in a lacertid lizard, *Takydromus septentrionalis*. *Oikos* **112**: 363-369.
- Edeline, E., Haugen, T. O., Weltzien, F. A., Claessen, D., Winfield, I. J., Stenseth, N. C. & Vollestad, L. A. 2010. Body downsizing caused by non-consumptive social stress severely depresses population growth rate. *Proceedings of the Royal Society B-Biological Sciences* **277**: 843-851.
- Engen, S., Lande, R. & Saether, B.-E. 2003. Demographic stochasticity and Allee effects in populations with two sexes. *Ecology* **84**: 2378-2386.
- Fitze, P. S., Le Galliard, J.-F., Federici, P., Richard, M. & Clobert, J. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. *Evolution* **59**: 2451-2459.
- Forrester, G., Harmon, L., Helyer, J., Holden, W. & Karis, R. 2011. Experimental evidence for density-dependent reproductive output in a coral reef fish. *Population Ecology* **53**: 155-163.
- González-Suárez, M., Mugabo, M., Decencière, B., Perret, S., Claessen, D. & Le Galliard, J.-F. 2011. Disentangling the effects of predator body size and prey density on prey consumption in a lizard. *Functional Ecology* **25**: 158-165.

- Grant, A. & Benton, T. G. 2000. Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* **81**: 680-693.
- Grant, A. & Benton, T. G. 2003. Density-dependent populations require density-dependent elasticity analysis: an illustration using the LPA model of *Tribolium*. *Journal of Animal Ecology* **72**: 94-105.
- Grant, J. W. A. & Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *Journal of Fish Biology* **67**: 100-110.
- Gregory, S. D., Bradshaw, C. J. A., Brook, B. W. & Courchamp, F. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. *Ecology* **91**: 2151-2161.
- Hawley, D. M., Lindstrom, K. & Wikelski, M. 2006. Experimentally increased social competition compromises humoral immune responses in house finches. *Hormones and Behavior* **49**: 417-424.
- Henle, K., Sarre, S. & Wiegand, K. 2004. The role of density regulation in extinction processes and population viability analysis. *Biodiversity and Conservation* **13**: 9-52.
- Jenkins, T. M., Diehl, S., Kratz, K. W. & Cooper, S. D. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology* **80**: 941-956.
- Kokko, H. & Rankin, D. J. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B-Biological Sciences* **361**: 319-334.
- La Montagne, J. M., Irvine, R. L. & Crone, E. E. 2002. Spatial patterns of population regulation in sage grouse (*Centrocercus spp.*) population viability analysis. *Journal of Animal Ecology* **71**: 672-682.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**: 911-927.
- Lande, R., Engen, S. & Saether, B. E. 2003. *Stochastic population dynamics in ecology and conservation*. Oxford University Press, Oxford.
- Le Galliard, J.-F., Fitze, P. S., Ferrière, R. & Clobert, J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 18231-18236.
- Le Galliard, J.-F., Marquis, O. & Massot, M. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology* **79**: 1296-1307.

- Le Galliard, J.-F., Massot, M., Landys, M. M., Meylan, S. & Clobert, J. 2006. Ontogenic sources of variation in sexual size dimorphism in a viviparous lizard. *Journal of Evolutionary Biology* **19**: 690-704.
- Lecomte, J., Boudjemadi, K., Sarrazin, F., Cally, K. & Clobert, J. 2004. Connectivity and homogenisation of population sizes: an experimental approach in *Lacerta vivipara*. *Journal of Animal Ecology* **73**: 179-189.
- Lecomte, J., Clobert, J., Massot, M. & Barbault, R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. *Ecoscience* **1**: 300-310.
- Legendre, S. & Clobert, J. 1995. ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics* **22**: 817-834.
- Legendre, S., Clobert, J., Moller, A. P. & Sorci, G. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *American Naturalist* **153**: 449-463.
- Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**: 1742-1756.
- Meylan, S., Clobert, J. & Sinervo, B. 2007. Adaptive significance of maternal induction of density-dependent phenotypes. *Oikos* **116**: 650-661.
- Meylan, S., Haussy, C. & Voituren, Y. 2010. Physiological actions of corticosterone and its modulation by an immune challenge in reptiles. *General and Comparative Endocrinology* **169**: 158-166.
- Morris, D. L. & Doak, D. F. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates Inc., Sunderland.
- Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. *Journal of Evolutionary Biology* **23**: 1886-1898.
- Mugabo, M., Marquis, O., Perret, S. & Le Galliard, J.-F. 2011. Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. *Oecologia* **In press**.
- Nussey, D. H., Clutton-Brock, T. H., Elston, D. A., Albon, S. D. & Kruuk, L. E. B. 2005. Phenotypic plasticity in a maternal trait in red deer. *Journal of Animal Ecology* **74**: 387-396.

- Pascual, M. A., Kareiva, P. & Hilborn, R. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* **11**: 966-976.
- Pinheiro, J. C. & Bates, D. M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer Verlag, New York.
- Roughgarden, J. & Smith, F. 1996. Why fisheries collapse and what to do about it. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 5078-5083.
- Runge, M. C. & Johnson, F. A. 2002. The importance of functional form in optimal control solutions of problems in population dynamics. *Ecology* **83**: 1357-1371.
- Schoener, T. W., Clobert, J., Legendre, S. & Spiller, D. A. 2003. Life-history models of extinction: A test with island spiders. *American Naturalist* **162**: 558-573.
- Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Cruz, M. V. S., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M. L., Meza-Lazaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibarquengoytia, N., Puntriano, C. A., Massot, M., Lepetz, V., Oksanen, T. A., Chapple, D. G., Bauer, A. M., Branch, W. R., Clobert, J. & Sites, J. W. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**: 894-899.
- Vinkler, M., Bainova, H. & Albrecht, T. 2010. Functional analysis of the skin-swelling response to phytohaemagglutinin. *Functional Ecology* **24**: 1081-1086.
- Votier, S. C., Hatchwell, B. J., Mears, M. & Birkhead, T. R. 2009. Changes in the timing of egg-laying of a colonial seabird in relation to population size and environmental conditions. *Marine Ecology-Progress Series* **393**: 225-233.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix A – Stage-structured projection matrix model.

Appendix B – Summer body growth and body size.

Appendix C – Annual juvenile growth rate and body size at the yearling stage.

Appendix D – Consequences of density for the persistence of populations.

Appendix A – Stage-structured projection matrix model

Model assumptions

We used age-structured matrix population models with post-breeding census and birth pulse dynamics (Caswell, 2001). We first considered a one-sex model (female based) with three age-classes (juveniles, yearlings and adults) and projection matrix

$$A = \begin{pmatrix} s1 \times F1 & s2 \times F2 & s3 \times F3 \\ s1 & 0 & 0 \\ 0 & s2 & s3 \end{pmatrix},$$

where $s1$ is the annual juvenile survival, $s2$ the annual yearling survival, $s3$ the annual adult survival, $F1$ the juvenile fecundity, $F2$ the yearling fecundity and $F3$ the adult fecundity. Fecundity in each age class was the product of the proportion of breeders (γ), the stage-specific total clutch size (f_i), the hatching success (hs), and the primary sex ratio (sr ; the proportion of male offspring at birth). Estimates of vital rates were obtained from our experimental data except for the primary sex ratio which was assumed to be balanced (Table A1). The proportion of breeders among juveniles and the total clutch size of juveniles, yearlings and adults were density-dependent. In each case, we used the best density-dependent function supported by our experimental data, i.e., the linear function on the scale of the regression used to analyze the data: (see Results section in the main text and Table A1). Starting conditions of the simulations were similar to the ones carried out in the experiment. A two-sex version of this deterministic model was developed to predict the density and age and sex-structures at equilibrium.

The consequences of population density for the extinction risk were investigated using stochastic one-sex and two-sex models. One-sex models assumed a female census while two-sex models assumed a male and female coupled life cycle and a polygynous mating system. In two-sex models, potential breeders of all age classes mated randomly. The number of clutches per generation was calculated either as the minimum of the number of potentially breeding females and four times the number of potentially breeding males (i.e., harem size=4), following the mating function $M(N_m, N_f) = \min(hN_m, N_f)$ where N_m is the number of males, N_f the number of females and h the harem size; or as the number of potentially breeding females except when there were no males in which case it was equal to zero (i.e., unrestricted harem size). A harem size of four corresponds to a conservative estimate of the average number of females inseminated by a single breeding male in this species (Fitze et al., 2005). In this case, the number of breeding male is limiting when it is lower than one quarter of the number of breeding females. An unrestricted harem size implies that a single breeding male can

inseminate all the breeding females present in the population whatever the population density. In this case, the number of males is limiting only when there is no breeding male in the population.

Elasticity analyses

We carried out density-independent and density-dependent elasticity analyses. Elasticities of λ and elasticities of N_{eq} predict the proportional change in λ and in N_{eq} respectively, given a small proportional change in a parameter of the model while all other parameters remain constant (Caswell, 2001). Elasticities of N_{eq} are proportional to elasticities of λ if (i) the population has a stable equilibrium, (ii) density dependence acting on vital rates is a function of the total number of individuals within the population and (iii) density dependence operates in the same way in all age classes (Grant & Benton, 2000). Here, only the first two conditions were met since the percentage of breeders was density-dependent in juveniles but not in yearlings and adults. The computations were carried out using ULM (Legendre & Clobert, 1995).

Demographic stochasticity

We performed individual-based simulations by incorporating demographic stochasticity on all demographic events. Survival probabilities, breeding probabilities, mating probabilities, sex at birth and the number of mating events were drawn from binomial distributions while the number of offspring produced was drawn from Poisson distributions.

Literature cited

- Caswell, H. 2001. *Matrix population models*, 2 ed. Sinauer Associates, Sunderland.
- Fitze, P. S., Le Galliard, J.-F., Federici, P., Richard, M. & Clobert, J. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. *Evolution* **59**: 2451-2459.
- Grant, A. & Benton, T. G. 2000. Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* **81**: 680-693.
- Legendre, S. & Clobert, J. 1995. ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics* **22**: 817-834.

Table A1. Parameter estimates for density-dependent and density-independent one-sex and two-sex models. Estimates of the proportion of breeders and hatching success are given on the logit scale [$f(x_i) = \frac{1}{1 + \exp(-x_i)}$] and estimates of the total clutch size are given on the log scale [$f(x_i) = \exp(x_i)$]. In the density-independent model, estimates were calculated over the entire data set, independently of the density level. In the density-dependent model, $x_i(n) = a_i - b_i n$, where a_i is the intercept (at $n=0$), b_i the slope of the density dependence and n the density level. Estimates in bold are for females, estimates in italic are for males and other estimates are for both sexes.

Vital rates	Density-independent model		Density-dependent model	
	One-sex model	Two-sex model	One-sex model	Two-sex model
Annual juvenile survival	0.409	0.409 , <i>0.409</i>	0.409	0.409 , <i>0.409</i>
Annual yearling survival	0.519	0.519 , <i>0.186</i>	0.519	0.519 , <i>0.186</i>
Annual adult survival	0.260	0.260 , <i>0.186</i>	0.260	0.260 , <i>0.186</i>
Juvenile fecundity				
Percentage of breeders		-0.422	1.664 - 0.803 × n	
Total clutch size		1.338	1.521 - 0.080 × n	
Hatching success		1.910	1.910	
Yearling and adult fecundity *				
Percentage of breeders		2.290	2.290	
Total clutch size		1.966	2.217 - 0.080 × n	
Hatching success		1.910	1.910	

* Yearling and adult females did not differ in their fecundity (see the main text).

Appendix B – Summer body growth and body size**Table B1.** Short-term effects of density on growth rate during the summer 2008 (mm.day⁻¹) and on SVL in August 2008 (SVL in mm) in juveniles ($n=436$ from 91 clutches). Results are from the minimum adequate models. The best models included a linear effect of density (growth rate: AIC_c=-1512.76, $w=0.81$, SVL: AIC_c=2060.76, $w=0.83$).

Growth rate during summer 2008 (mm.day⁻¹)				
<i>Fixed effects</i>	Estimate ± s.e.	LRT	d.f.	<i>P</i> value
Intercept	0.4649 ± 0.0148	93.21	1	< 0.0001
Density	-0.0241 ± 0.0054	15.18	1	< 0.0001
<i>Random effects</i>	Estimate *	LRT	d.f.	<i>P</i> value
Enclosure identity	0.0341	180.86	1	< 0.0001
Clutch identity	0.0256	46.25	1	< 0.0001
Residual	0.0348			
SVL in late summer 2008 (mm)				
<i>Fixed effects</i> **	Estimate ± s.e.	LRT	d.f.	<i>P</i> value
Intercept	51.21 ± 0.84	123.27	1	< 0.0001
Density	-1.41 ± 0.30	16.19	1	< 0.0001
Sex	M: -1.27 ± 0.22	31.83	1	< 0.0001
Release date (days)	-0.36 ± 0.03	103.33	1	< 0.0001
<i>Random effects</i>	Estimate *	LRT	d.f.	<i>P</i> value
Enclosure identity	1.89	131.06	1	< 0.0001
Clutch identity	1.65	60.43	1	< 0.0001
Residual	2.07			

Density=linear effect, M=males, SVL=snout-vent length, LRT=likelihood-ratio test.

* Confidence interval estimates are not available in the *lmer* procedure in R. Estimation of confidence intervals requires estimates of the exact maximum likelihood. Yet, in the *lmer* procedure all methods of estimation of maximum likelihood are approximations.

** Estimates are given for a mean value of release date (days).

Table B2. Short-term effects of density on growth rate during summer 2008 (mm.day⁻¹, $n=318$) and on body size in late summer 2008 (mm, $n=320$) in yearlings and adults. Results are from the minimum adequate models. The best models included a quadratic effect for growth rate ($AIC_c=-1397.22$, $w=0.81$) and a linear effect for body size ($AIC_c=1449.98$, $w=0.99$).

Growth rate during summer 2008 (mm.day⁻¹)			
<i>Fixed effects</i> *	Estimate ± s.e.	F_{ndf,ddf}	P value
Intercept	0.1453 ± 0.0156	F _{1,287} =86.92	< 0.0001
Initial SVL (mm)	-0.0075 ± 0.0004	F _{1,287} =334.41	< 0.0001
Sex	M: -0.1073 ± 0.0137	F _{1,287} =61.70	< 0.0001
Age class	Y: 0.0235 ± 0.0062	F _{1,287} =14.23	0.0002
Release date (days)	-0.0003 ± 0.0001	F _{1,287} =4.04	0.04
Density	-0.0337 ± 0.0126	F _{1,21} =7.12	0.01
Density ²	0.0045 ± 0.0022	F _{1,21} =4.18	0.05
Density × sex	M: 0.0294 ± 0.0101	F _{1,287} =8.53	0.004
Density ² × sex	M: -0.0038 ± 0.0016	F _{1,287} =5.34	0.02
Density ² × age class	Y: -0.0008 ± 0.0003	F _{1,287} =6.17	0.01
<i>Random effects</i>	Estimate [95% CI]	LRT (d.f.=1)	P value
Enclosure identity	0.0145 [0.0095, 0.0220]	32.11	< 0.0001
Residuals	0.0203 [0.0178, 0.0230]		
SVL in August 2008 (mm)			
<i>Fixed effects</i>	Estimate ± s.e.	F_{ndf,ddf}	P value
Intercept	70.99 ± 0.55	F _{1,292} =16491.68	< 0.0001
Sex	M: -9.30 ± 0.66	F _{1,292} =197.29	< 0.0001
Age class	Y: -4.73 ± 0.38	F _{1,292} =154.18	< 0.0001
Density	-0.79 ± 0.17	F _{1,22} =22.47	0.0001
Age class × sex	Y-M: 2.68 ± 0.51	F _{1,292} =27.85	< 0.0001
Density × sex	M: 0.58 ± 0.18	F _{1,292} =10.83	0.001
<i>Random effects</i>	Estimate [95% CI]	LRT (d.f.=1)	P value
Enclosure identity	0.67 [0.03, 1.26]	6.65	0.01
Residuals	1.81 [1.60, 2.05]		

Density=linear effect, Density²=quadratic effect, M=males, Y=yearlings, LRT=likelihood-ratio test, CI=confidence interval.

* Estimates are given for a mean value of the initial SVL and release date.

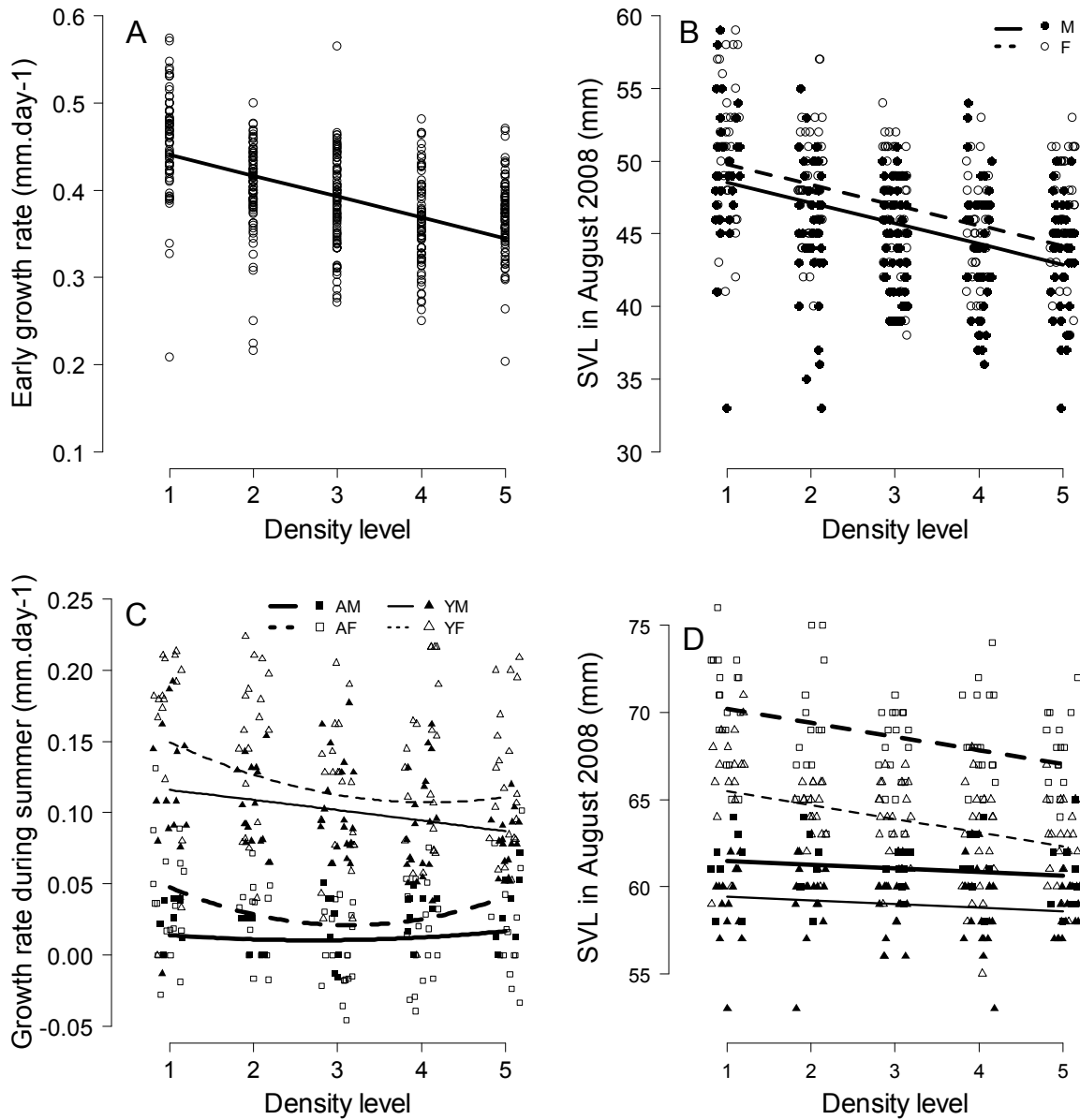


Figure B1. Short-term effects of density on growth rate during the summer 2008 and body size (SVL) in August 2008 in the juvenile age class (A, B) and in the yearling and adult age classes (C, D). Estimates of the regression lines were obtained from the minimum adequate models.

Appendix C – Annual juvenile growth rate and body size at the yearling stage

Table C1. Long-term effects of density on annual growth rate (mm.day⁻¹) and SVL (mm) in May 2009 in juveniles ($n=211$ from 77 clutches). Results are from the minimum adequate models. The best model included a quadratic effect of population density (growth rate: $AIC_c=-1052.91$, $w=0.88$, SVL: $AIC_c=1009.49$, $w=0.71$). Estimates are given for mean values of all the covariates.

Annual growth rate (mm.day⁻¹)				
<i>Fixed effects</i>	Estimate ± s.e.	LRT	d.f.	<i>P</i> value
Intercept	0.2716 ± 0.0107	87.37	1	< 0.0001
Initial SVL (mm)	-0.0030 ± 0.0013	5.15	1	0.02
Sex	M: -0.0370 ± 0.0071	27.17	1	< 0.0001
Density	-0.0372 ± 0.0084	16.22	1	< 0.0001
Density ²	0.0041 ± 0.0014	8.01	1	0.005
Density × sex	M: 0.0065 ± 0.0020	10.81	1	0.001
<i>Random effects</i>	Estimate *	LRT	d.f.	<i>P</i> value
Population identity	0.0084	17.44	1	< 0.0001
Clutch identity	0.0084	8.04	1	0.004
Residual	0.0167			
SVL in May 2009 (mm)				
<i>Fixed effects</i>	Estimate ± s.e.	LRT	d.f.	<i>P</i> value
Intercept	63.56 ± 1.36	114.28	1	< 0.0001
Sex	M: -6.01 ± 0.92	62.26	1	< 0.0001
Density	-4.54 ± 1.06	15.60	1	< 0.0001
Density ²	0.46 ± 0.18	6.66	1	0.01
Density × sex	M: 0.91 ± 0.26	11.98	1	0.0005
Release date (days)	-0.21 ± 0.03	38.21	1	< 0.0001
Recapture date (days)	0.06 ± 0.01	51.47	1	< 0.0001
<i>Random effects</i>	Estimate *	LRT	d.f.	<i>P</i> value
Population identity	1.01	11.50	1	0.0007
Clutch identity	1.17	6.56	1	0.01
Residual	2.21			

Density=linear effect, Density²=quadratic effect, M=males, SVL=snout-vent length, LRT=likelihood-ratio test.

* Confidence interval estimates are not available in the *lmer* procedure in R (explanation provided in Table B1).

Appendix D – Consequences of density for the persistence of populations

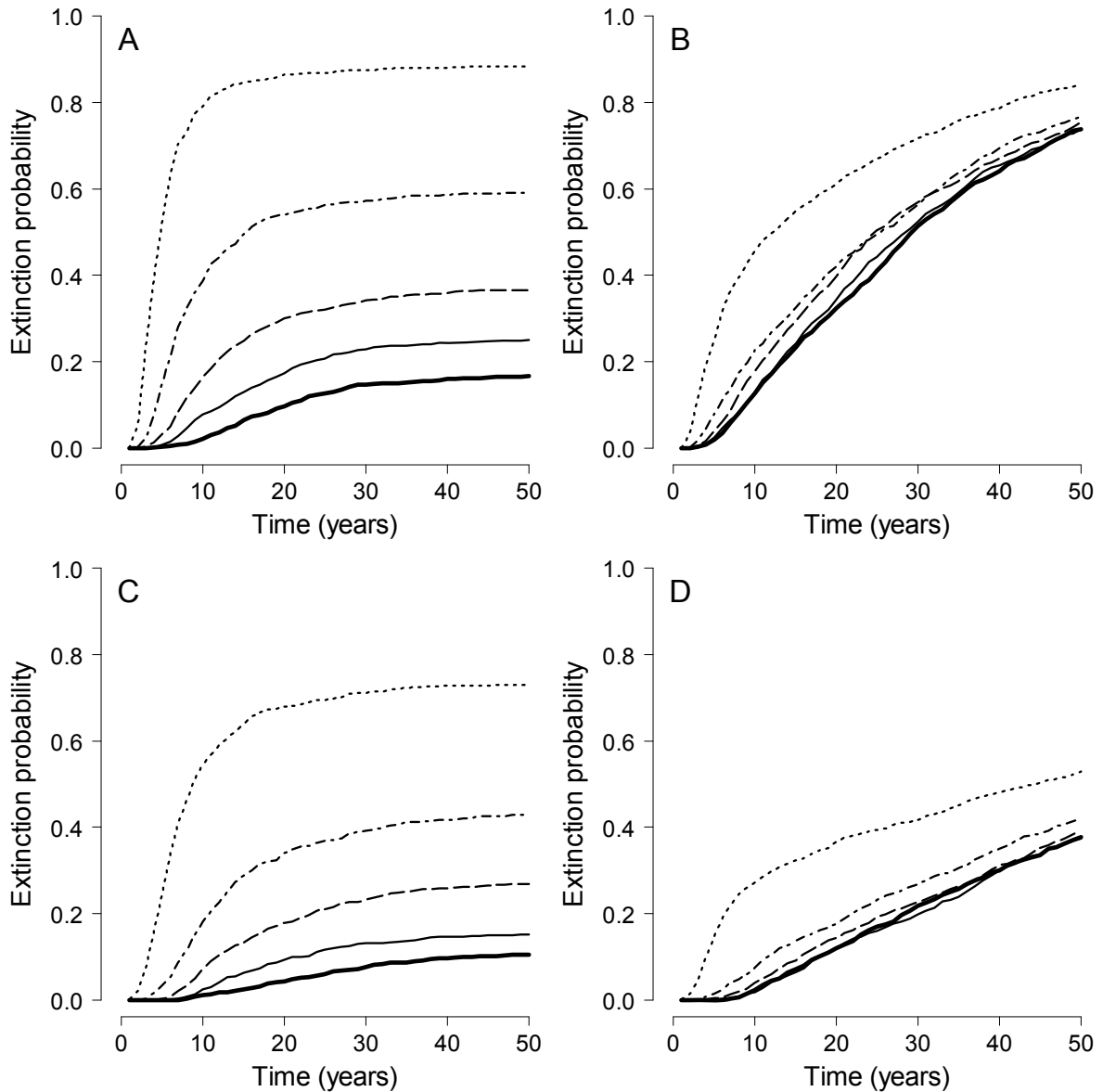


Figure D1. Cumulated extinction probability over time according to initial population density for density-independent (A, C) and density-dependent (B, D) two-sex models. In (A) and (B), the models assumed a polygynous mating system with an unrestricted harem size. In (C) and (D), the models assumed a polygynous mating system with a harem size of 4 as in Figure 3 C-D but with a male annual survival similar to the one of females. Results are from Monte Carlo simulations of 1000 trajectories. Legends as in Figure 3.

RÉSUMÉ

La structure des populations influence de manière importante le taux de croissance des populations et donc leurs capacités à faire face à des changements environnementaux. En effet, elle détermine la part d’individus qui contribuent au renouvellement des générations ainsi que l’intensité des interactions sociales compétitives et coopératives. Utilisant le lézard vivipare (*Zootoca vivipara*, Jacquin 1787) comme modèle d’étude, mon travail de thèse consiste à caractériser la relation entre la structure de population (en termes de cohortes, densité et classes d’âge et de sexe), l’histoire de vie et la dynamique de petites populations isolées. Pour cela, nous combinons des approches expérimentales en conditions semi-naturelles à des approches théoriques utilisant des modèles populationnels à un et deux sexes structurés en classes d’âge. Une analyse critique de la littérature montre que la variabilité environnementale peut générer des différences d’histoire de vie entre cohortes de naissance, ou effets cohortes, à travers son influence sur la qualité des individus et sur l’intensité de la compétition intraspécifique au sein d’une cohorte et entre cohortes. Un premier travail empirique démontre que ces trois mécanismes induisent de la variation d’histoire de vie entre cohortes, mais met également en évidence que les effets directs de la variabilité environnementale sur la qualité des individus interagissent de manière complexe avec des effets indirects sur l’intensité de la compétition entre individus. Au cours d’une deuxième étude empirique, nous analysons les processus et conséquences démographiques de ces interactions compétitives. Une élévation de la densité augmente la compétition trophique et pourrait également induire des réponses hormonales au stress social, ce qui ralentit la croissance corporelle et la reproduction. Un modèle stochastique démontre que cette densité dépendance de l’histoire de vie interagit avec les fluctuations stochastiques du sexe ratio pour façonner la dynamique d’extinction des petites populations de lézards. Ces prédictions seront affinées par l’analyse d’une troisième étude empirique impliquant une manipulation conjointe de la densité et du sexe ratio de la population. Nos résultats, intégrés dans le contexte général de l’écologie des populations, soulignent l’importance de prendre en compte la structure de la population et l’hétérogénéité de l’histoire de vie pour établir des prédictions fiables sur le devenir des petites populations et mettre en place des mesures de gestion efficaces.

Mots-clés : effets cohortes, densité dépendance, structure d’âge, sexe ratio adulte, histoire de vie, système d’appariement, sélection sexuelle.