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Influence of ecological traits on movement of ungulates across environmental gradients: an intra- and interspecific evaluation

Kamal Atmeh

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Influence of ecological traits on movement of ungulates across
environmental gradients

An intra- and interspecific evaluation

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Influence of ecological traits on movement of ungulates
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An intra- and interspecific evaluation

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21/03/2022

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ABSTRACT

Of the many behaviors that an animal exhibits, movement is one of the main studied components of organisms. Investigating the intricacies of movement can contribute to our understanding of the mechanisms connecting spatial behavior to population demography. Animals must move in the landscape to select habitats containing the necessary resources for their survival and to maximize their reproductive success. Choosing the right habitat however is not a simple task since individuals must account for predators, conspecifics, and landscape configuration to decide on how and where to move. Additionally, the movement of animals in their environment may depend on their morphological, physiological, and ecological traits. Until now, most studies related home range size and movement to environmental variables, with few relating these two spatial components to the internal state of the animal. During my thesis, I tried to resolve this issue by evaluating how the intertwined relationship between environmental and individual-specific constraints influence movement at various spatiotemporal scales. I concentrated my research on ungulates because of their vast distribution across multiple settings, their significant differences in life-history traits, and the availability of studies and GPS data from this taxonomic group. In the first part of my thesis, I summarized past research on the intraspecific drivers of home range size in ungulates and evaluated whether previous findings depend on the ecological traits of the species. Second, using data on 23 species and the robust framework of continuous-time stochastic movement models (CTMM), I investigated how female ungulates respond geographically to the spatial variation in productivity while accounting for the neonatal anti-predator tactic of their offspring. This should lead to a better understanding of the elements that influence the movement of animals during periods of high energy requirement when they have to balance their demands for safety and food. Third, I used the CTMM framework to determine the influence of mating tactics on the movement of male ungulates during the rut. I also provided a key metric that may be used to distinguish between the different mating tactics. All of the findings provided in this thesis have contributed to a better understanding of the variables that influence home range size and movement in various ungulate species at key moments of their biological cycle.

Keywords: ungulate, movement, home range, life-history trait, diet, productivity, neonatal anti-predator tactic, mating tactic

RÉSUMÉ

Parmi les nombreux comportements que présente un animal, le mouvement est l'une des principales composantes étudiées des organismes. L'étude des particularités du mouvement peut contribuer à notre compréhension des mécanismes reliant le comportement spatial à la démographie des populations. Les animaux doivent se déplacer dans le paysage pour sélectionner les habitats contenant les ressources nécessaires à leur survie et pour maximiser leur succès reproducteur. Choisir le bon

habitat n'est cependant pas une tâche simple car les individus doivent tenir compte des prédateurs, des congénères et de la configuration du paysage pour décider comment et où se déplacer. De plus, le déplacement des animaux dans leur environnement peut dépendre de leurs caractéristiques morphologiques, physiologiques et écologiques. Jusqu'à présent, la plupart des études reliaient la taille du domaine vital et les déplacements à des variables environnementales, et peu d'entre elles reliaient ces deux composantes spatiales à l'état interne de l'animal. Au cours de ma thèse, j'ai tenté de résoudre cette question en évaluant comment la relation entre les contraintes environnementales et les contraintes spécifiques à l'individu influencent le mouvement à différentes échelles spatio-temporelles. J'ai concentré mes recherches sur les ongulés en raison de leur vaste distribution dans de multiples contextes, de leurs différences significatives dans les traits de l'histoire de vie, et de la disponibilité d'études et de données GPS de ce groupe taxonomique. Dans la première partie de ma thèse, j'ai résumé les recherches antérieures sur les facteurs intraspécifiques de la taille du domaine vital chez les ongulés et j'ai évalué si les résultats précédents dépendent des caractéristiques écologiques de l'espèce. Ensuite, en utilisant des données sur 23 espèces et en profitant du cadre robuste des modèles de mouvement stochastiques à temps continu (CTMM), j'ai étudié comment les femelles ongulées répondent géographiquement à la variation spatiale de la productivité tout en tenant compte de la tactique néonatale anti-prédateur de leurs petits. Cela devrait permettre de mieux comprendre les éléments qui influencent le mouvement des animaux pendant les périodes de besoin énergétique élevé où ils doivent équilibrer leurs demandes de sécurité et de nourriture. Troisièmement, j'ai utilisé le cadre CTMM pour déterminer l'influence des tactiques d'accouplement sur les mouvements des ongulés mâles pendant le rut. J'ai également fourni une métrique clé qui peut être utilisée pour distinguer les différentes tactiques d'accouplement. Tous les résultats fournis dans cette thèse ont contribué à une meilleure compréhension des variables qui influencent la taille du domaine vital et les mouvements chez diverses espèces d'ongulés à des moments clés de leur cycle biologique.

Mots-clés: ongulé, mouvement, domaine vital, trait d'histoire de vie, régime alimentaire, productivité, tactique néonatale anti-prédateur, tactique de reproduction

In the sphere of natural science let us remember that we have always to deal with an insoluble problem. Let us prove keen and honest in attending to anything which is in any way brought to our notice, most of all when it does not fit in with our previous ideas. For it is only thereby that we perceive the problem, which does indeed lie in nature, but still more in man.

—Johann Wolfgang von GOETHE, *THE MAXIMS AND REFLECTIONS OF GOETHE*

Contents

Preface	xix
I General Introduction	1
1 Theoretical context	3
1.1 The road towards a movement paradigm	3
1.2 The habitat concept	6
1.2.1 A dualistic definition	6
1.2.2 Habitat selection as a hierarchical process	6
1.2.3 From hierarchical scales to hierarchical factors	7
1.3 Home range	8
1.3.1 A complex definition	8
1.3.2 Inter- and intraspecific factors shaping home range size	10
1.3.3 Choosing the right scale of observation	11
1.4 A triptych of interactive landscapes shaping movement	12
1.4.1 Resource landscape	12
1.4.2 Energy landscape	14
1.4.3 Landscape of fear	15
1.5 Social sampling and sociality	17
1.6 Intra-annual changes in movement related to the biological cycle	18
1.6.1 Parturition and caring for offspring	18
1.6.2 Mating season	19
2 Aim of the thesis	21
2.1 Ungulates as a case study	21
2.2 Main questions	23

II	Core research	25
3	A systematic review of within-population variation in the size of home range across ungulates: What do we know after 50 years of telemetry studies?	27
3.1	Introduction	31
3.2	Material and methods	35
3.2.1	Literature survey	35
3.2.2	Literature analysis and retrieval of article and species metadata	36
3.2.3	Extraction of results	38
3.2.4	Descriptive and statistical analysis	40
3.3	Results	40
3.3.1	Studies and species	40
3.3.2	Telemetry and estimators of the sizes of home ranges	41
3.3.3	Descriptive summary of studied variables	41
3.3.4	Methodological co-variables and seasonal variation influencing papers' results	44
3.3.5	Influence of species-specific life history traits on findings	46
3.4	Discussion	46
3.4.1	More support to the resource than to the landscape heterogeneity hypothesis	46
3.4.2	Study design and statistical considerations	46
3.4.3	Temporal and spatial scales	48
3.4.4	Accounting for life history traits	50
3.4.5	Other drivers of variation in the sizes of individual home ranges	51
3.4.6	Recommendations	52
	References	55
	Supplementary Information	66
4	Spatial constraints of raising offspring drive movement tactics of female ungulates around parturition	79
4.1	Introduction	83
4.2	Results	84
4.2.1	Neonatal tactics and residency in relation to parturition	84
4.2.2	Neonatal tactics and shift in female movements	86
4.3	Discussion	88
4.4	Material and methods	91
4.4.1	Study sites and GPS data	91
4.4.2	Defining reproductive periods	91
4.4.3	Continuous-time stochastic movement models and model fitting	93
4.4.4	Covariates	96
4.4.5	Statistical analysis	97
	References	99
	Supplementary Information	104

5	Mating tactics of male ungulates mark fine-scale movement signature in GPS data	139
5.1	Introduction	143
5.2	Material and methods	145
5.2.1	Data collection	145
5.2.2	Establishing rut periods	150
5.2.3	Fitting of continuous-time stochastic movement models	150
5.2.4	Statistical analysis	151
5.3	Results	152
5.4	Discussion	153
5.4.1	Movement processes linked to mating in males	154
5.4.2	Other drivers of movement processes	155
	References	159
	Supplementary Information	165
III	Synthesis and Perspectives	175
6	Summary and discussion of results	177
6.1	Home range studies: factors and limitations	177
6.2	A fine-scale look at the balance between movement, resource acquisition, and care for offspring	179
6.3	Inferring mating strategies	182
6.4	The multipotential of continuous-time stochastic movement models	182
7	Perspectives for future research	185
7.1	Hiders in seasonal environments	185
7.2	A link to breeding strategies	187
7.3	Maternal investment along the hider-follower continuum	188
7.4	Phenology of mating	189
7.5	Concluding remarks	189
	Bibliography	191
	Appendices	229
A	Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape	231

List of Tables

3	A systematic review of within-population variation in the size of home range across ungulates: What do we know after 50 years of telemetry studies?	
3.1	Information on the 33 selected papers.	37
3.2	Characteristics of the species included in the 33 selected papers.	39
3.3	Biological interpretations provided by authors to explain results that were retained as opposite to initial biological hypothesis, per category of variable.	49
3.4	Recommendations for authors that should help quantitative studies aiming at evaluating the effect of the environment and life history traits on the size of home range.	54
S3.1	Information on the variables used in the 33 selected papers (productive and non-productive season). For each variable, we assigned the unit and the category (Resource, Heterogeneity and Risk) for both productive and non-productive seasons.	66
S3.2	Characteristics of species of the 33 selected papers (productive and non-productive season) and references associated. Species were ranked by Latin name.	69
S3.3	Model selection table summarizing the different models explaining the level of support for ecological drivers.	70
S3.4	Model selection table summarizing the different models explaining the level of support for ecological drivers. These models include the baseline model of Supplementary Table S3.3	70
S3.5	Model selection table summarizing the different models explaining the level of support for ecological drivers, performed on the subset of case studies focusing on the effect of resources and studying the two seasons.	70

4	Spatial constraints of raising offspring drive movement tactics of female ungulates around parturition	
4.1	Glossary of parameters and movement processes of interest, adapted from Péron et al. (2017)	94
S4.1	Species, study sites, and contact information. <i>NT</i> : neonatal anti-predator tactic of the species (hider = H, follower = F). <i>BM</i> : female body mass. <i>Nb</i> : number of individuals.	105
S4.2	Information on reproduction for each study population along with the type of cut-off date used for the analysis. The 5% cut-off dates were retrieved either using published data or using material provided by the data owners.	119
S4.3	Acknowledgments for each dataset. To be completed for some populations.	126
5	Mating tactics of male ungulates mark fine-scale movement signature in GPS data	
5.1	Common mating tactics of male ungulates	144
5.2	Summary variables of species and populations.	147
5.3	Model selection for the variation in home range size (a), diffusion (b), and frequency of return to a central place (c).	153
S5.1	Estimates and associated standard errors retrieved from the model averaging of the best retained models assessing the link between home range size, mating tactic, and period. Values in bold are significant. . . .	165
S5.2	Estimates and associated standard errors retrieved from the model averaging of the best retained models assessing the link between diffusion, mating tactic, and period. Values in bold are significant. . . .	165
S5.3	Estimates and associated standard errors retrieved from the model averaging of the best retained models assessing the link between frequency of return to a central place, mating tactic, and period. Values in bold are significant.	166
A	Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape	
A.1	Summary statistics from the model averaging procedure (1).	244
A.2	Summary statistics from the model averaging procedure (2).	245
A.3	Summary statistics from the model averaging procedure (3).	247
SA.1	Overlap between the post-dispersal range and the adult range for 15 individuals monitored both as a juvenile and an adult – Overlap was measured using a 50 % kernel – ID : individual identity ; a value of 0 indicates the ranges did not overlap.	256
SA.2	Overlap between successive adult annual ranges for GPS-tracked adult roe deer – Overlap was measured using a 50 % kernel – ID : individual identity ; a value of 0 indicates the ranges did not overlap	257

SA.3	generalised linear models in a ΔAICc of 2 describing individual propensity to adopt a progressive dispersal tactic	259
SA.4	Candidate generalised linear models in a ΔAICc of 2 describing individual propensity to adopt a multi-range tactic	259
SA.5	Candidate generalised linear models in a ΔAICc of 2 describing individual propensity to adopt an aborted dispersal tactic.	260
SA.6	Candidate multinomial models describing individual propensity to adopt one of the four alternative tactics.	260
SA.7	Summary statistics from the model averaging procedure based on multinomial models discriminating all dispersal tactics.	261
SA.8	Mean duration of segments for each dispersal tactic identified.	268
SA.9	Mean departure date from each segment for each dispersal tactic identified.	269
SA.10	Principal Component Analysis scores and proportion of variance explained by the three axes of the PCA on landscape characteristics of the natal range for 146 monitored juvenile roe deer.	270
SA.11	Mean phenotypic and landscape descriptors in the natal range (with their standard deviations) for each behavioural tactic identified during the dispersal phase.	271
SA.12	Repeatability models for each class and each movement parameter (τ_p , σ^2 and D).	273

List of Figures

1	Theoretical context	
1.1	A general conceptual framework for movement ecology	4
1.2	Habitat selection, represented as a hierarchical process spanning four spatio-temporal scales.	7
1.3	Three main classes of factors are expected to influence animal movement decisions shaping the home range.	9
1.4	Schematic illustration of different migratory movement tactics when confronted with the green wave.	13
3	A systematic review of within-population variation in the size of home range across ungulates: What do we know after 50 years of telemetry studies?	
3.1	Schematic summary of the methodological framework.	34
3.2	PRISMA flow diagram.	36
3.3	Descriptive summary of the articles and species retained.	42
3.4	Descriptive summary of tracking and home range estimation methods.	43
3.5	Descriptive summary of biological metrics used in published papers.	44
3.6	Effect of sample size, number of metrics tested, positioning system and diet on the probability of gaining support for a biological hypothesis.	45
S3.1	Proportions of metrics consistent with hypothesis (“Same as expected”), not-consistent with hypothesis (“Contrary to expected”), and unknown because we only have non-significant <i>p</i> -values or a non-selected variable in a model selection.	71
S3.2	Venn diagrams representing the number of relationships tested for each category of variables.	72
4	Spatial constraints of raising offspring drive movement tactics of female ungulates around parturition	

4.1	Conceptual framework of movement patterns of reproductive females in ungulate species in relation to the environment and to their offspring's neonatal anti-predator tactics.	85
4.2	Predicted probabilities of being stationary for movement of females of 23 species of ungulates in response to parturition and spatial range of variability in productivity.	86
4.3	Predicted mean values for diffusion rate and frequency of return for females of 23 species of ungulates.	88
4.4	Overview of the species and populations.	92
S4.1	Percentage of Ornstein-Uhlenbeck models (stationarity) for pre-parturition (plain bars) and post-parturition (dashed bars) for each studied population.	112
S4.2	Means of the posterior distribution for phylogenetic heritability H^2 and fixed effects, along with their 95% highest posterior density intervals (HPDI), extracted from Bayesian Phylogenetic Mixed Models assessing the relationship between neonatal tactic, reproductive period, seasonality and the probability of being stationary. Values excluding 0 are statistically significant.	113
S4.3	Means of the posterior distribution and 95% highest posterior density intervals (HPDI) of the fixed effects retrieved from the most parsimonious Bayesian Phylogenetic Mixed Models determining factors impacting the variation of home range size, diffusion, and the frequency of return to a central place. Values excluding 0 are statistically significant.	114
S4.4	Reconstructed slopes for mean (a-c) and range (d-f) NDVI from the most parsimonious Bayesian Phylogenetic Mixed models for home range size, diffusion, and frequency of return for each neonatal anti-predator tactic and period. Blue chamois kid and red roe deer fawn represent followers and hidiers, respectively.	115

S4.5	Predicted values of the three movement components (home range size [a,b], diffusion [c,d], and frequency of return [e,f]) of 23 species of ungulates, retrieved from the most parsimonious Bayesian phylogenetic mixed models depicting the effect of the interplay between neonatal anti-predator tactic, pre- and post-parturition, productivity (mean NDVI; left panels) and spatial range of resource variation (range NDVI; right panels). Low, mean and high classes represent the 10%, mean and 90% quantiles of each environmental variable (0.18, 0.41 and 0.72 for mean NDVI, and 0.25, 1.33 and 6.5 km for range NDVI). Predicted values for each parameter were computed for an animal of 60 kg, and the mean value of one environmental variable was fixed when predicting the effect of the other environmental variable for each class. Solid and blank points represent mean predicted values for pre- and post-parturition, respectively. Dark and light shadings represent pre- and post-parturition, respectively. Red roe deer fawn and blue chamois kid represent hider and follower species, respectively. The increase in the size of points represent higher values of environmental variables.	116
S4.6	Linear regression between the range of NDVI and the euclidean distance between the centroids of the locations of each period for every individual year. Blue and red represent followers and hidiers respectively.	117
S4.7	The 5% cut-off date	118
S4.8	GPS location (points) and semivariograms of Brownian Motion and Ornstein-Uhlenbeck movement behavior.	125
5	Mating tactics of male ungulates mark fine-scale movement signature in GPS data	
5.1	Expected variation of home range size as a resultant of diffusion and frequency of return to a central place for non-territory (red) and territory-based (blue) mating strategies.	145
5.2	Changes in home range size, diffusion, and frequency of return behavior of males around the rutting period according to the mating tactic (non-territorial vs territorial) of 14 species. The x and y axes are on the logarithmic scale. Body mass was fixed at the mean body mass in the dataset equaling 98.5 kg.	154
5.3	Conceptual framework and perspectives for future analyses.	158
S5.1	Density of home range size (km^2) values for each population during reference, pre-rut, and rut periods. The x-axis is on the logarithmic scale and fixed for all panels. The y-axis varies for each population.	167
S5.2	Density of diffusion ($m^2.s^{-1}$) values for each population during reference, pre-rut, and rut periods. The x-axis is on the logarithmic scale and fixed for all panels. The y-axis varies for each population.	168

S5.3	Density of the frequency of return (day^{-1}) values for each population during reference, pre-rut, and rut periods. The x-axis is on the logarithmic scale and fixed for all panels. The y-axis varies for each population.	169
S5.4	Percentage of stationary tracks during each period of reference, pre-rut, and rut for each population and according to mating tactic. Lines represent mean values for each period.	170
S5.5	Log of the ratio of home range size between mating periods (i.e. pre-rut and rut) and the reference period. A value of 0 represents no change in home range size during pre-rut and rut compared to the reference period.	171
S5.6	Log of the ratios of both frequency of return and diffusion between the pre-rut and the reference period. A value of 0 represents no change in parameters during pre-rut compared to the reference period.	172
S5.7	Log of the ratios of both frequency of return and diffusion between the rut and the reference period. A value of 0 represents no change in parameters during rut compared to the reference period.	173
6	Summary and discussion of results	
6.1	The 10 most common home range estimators used per year in studies retained for analysis ($n = 1,203$) in a review of terrestrial home range literature published between 2000 and 2019.	180
7	Perspectives for future research	
7.1	The probability of being a hider in relation to seasonality in the environment.	186
A	Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape	
A.1	Classification steps to discriminate between alternative movement tactics of juvenile roe deer during the dispersal phase.	239
A.2	Examples of the six alternative movement tactics exhibited by juvenile roe deer during the dispersal phase.	243
A.3	Variation in the propensity of juvenile roe deer to (a) progressively disperse, (b) adopt the multirange tactic, (c) abort their dispersal attempt (versus classically disperse) as a function of increasing landscape heterogeneity, availability of crops and meadows and anthropogenic disturbance.	246
SA.1	Examples of overlap between the location at death and locations from GPS devices.	258
SA.2	Additional examples of individual trajectories for each movement tactic exhibited by roe deer.	262

SA.3	Plot of the first and second principal components and the proportion of the total variance explained from the PCA of landscape structure in the natal range.	270
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Preface

My brothers and I were always, in a way or another, in contact with nature, from occasional picnics to playtime in my grandmother's garden. But to say I was fascinated by nature would be an overstatement. I enjoyed it. Fascination, in my opinion, comes from a deep understanding of the intricacy of the subject in question. It is when looking closely into *The Music Lesson* and noticing the meticulously painted rug knots that one is bewitched by Vermeer. In nature, as it is in arts, it is only after delving into the sheer complexity of its mechanisms that we enter the realm of fascination.

The following thesis is the story of that journey. Its genesis began long before I arrived, and evolved into what it is now. It is somehow like an incomplete metamorphosis, started as an egg, a small idea in the minds of great researchers, morphed into a nymph when I joined, only to become a mature adult through various external and internal feedback without losing its shape or essence. A Kafkaesque metamorphosis nonetheless, full of nightmarish recurrent analyses and tedious chasing of my tail. This is the Gregor Samsa of the past four years of my life.

When I first started working on this thesis, I was new to the field of "movement ecology", but I was confident that I had adequate scientific support to guide me. I was not wrong. In an ingenious move, my supervisors decided to initiate me through the course of a systematic review. As I went deep into the literature and reviewed all the published papers on home range size, I realized that the subject is complex with many inconsistencies. This discovery led to my first paper. At the same time, I was working on a side project on two species to understand continuous-time stochastic movement models. Following multiple discussions with my supervisors, however, we decided to dig deeper to understand the mechanisms of movement more thoroughly, understand its components, and how species move differently based on internal and external constraints. And, in the blink of an eye, my initially minor project exploded into an international collaboration that provided me with data on 23 species. This leap was equivalent to fighting a boss in a video game without finishing any of the side

quests: arduous. But, with the right feedback and despite it being a laborious birth, the second and third papers came to life. These represent the three pillars of the thesis that is presented to you in this document. This is the result of various encounters and interactions with eminent researchers and humans, without whom I would not be here.

Similar to this thesis, movement was at the core of my journey, which was much like natal dispersal, consisting of three stages: departure, transience, and settlement. Having left my home country for a Master's in France, my natal dispersal began. During my first year abroad, I had the opportunity to conduct an internship in Sweden at Grimsö Wildlife Research Station, which I can confidently say was the catalyst to this entrancing interest in wildlife and ungulates, and which opened up the door for the events that unfolded in later years. For that, I am extremely grateful to Petter Kjellander, Madeleine Christensson, and Malin Teräväinen for guiding me during my stage of transience. My settlement, however, was nowhere in sight. Another experience seemed mandatory to consolidate my appeal for wildlife research. Thus came my internship on least weasels at the Mammal Research Institute in Poland with Karol Zub, and I knew by the end of it that a thesis is what I was seeking. Sitting in my small room in Białowieża at the border of Belarus, a thesis proposal on movement ecology at the *Laboratoire de Biométrie et Biologie Evolutive* grabbed my attention. I would be working with names that I have been reading for the past years, pioneers in ungulate ecology! With no hesitation, I sent my application only to be contacted swiftly by Anne Loison, sending me her approval. And so, following a successful application to the doctoral school, I settled in Lyon.

I always thought I was a perfectionist until I worked with Anne Loison. When I would feel like I did my best, she was always there to remind me that I can do better. I cannot recount the number of times I modified the figures, the analyses, the writing, anything really. Her perceptive eye for small details and theoretical problems, as well as her thorough knowledge of relevant literature, have been pivotal for the construction of all three papers. Ideas never fell on deaf ears when I would discuss them with her, and she never failed to encourage me in times of doubt, even when I was at my lowest. Unquestionably, Anne Loison has my sincere gratitude for her limitless patience and support throughout these past four years. I only hope my work was up to her expectations.

If this thesis was a movie, Christophe Bonenfant would win the Academy Award for Best Supporting Supervisor. Following a rocky first act when I was overwhelmed by immense data manipulation, Christophe Bonenfant jumped in at the right moment during the second act to lend me a hand with the Bayesian models when things were going awry. His expertise in life-history traits led to fruitful discussions around the second and third papers, which would not have been the same without his contribution. His benevolence and understanding provided me with a stream of motivation to reach the closure of the thesis' third act, and, for that, I am extremely thankful to him.

To the collaborators I had the pleasure to work with, whether in France within the MovIt consortium or globally, I am most grateful for their approval to use their data, for their constructive comments, for their time, and especially for their patience when

papers were overdue. I have been lucky to learn at an early stage in my academic career—*if I can call it that*—the basis of a functional collaborative environment with worldwide renowned scientists. I would also like to thank in particular Guillaume Péron for taking the time to explain the framework of the continuous-time stochastic movement models and for helping me with the methodology of the second and third papers.

For the constant moral support, my deepest gratitude goes to the lovely colleagues and friends in Lyon, Chambéry, and abroad. It was a privilege to be surrounded by and work with considerate people, whether they were students, researchers, technicians, engineers, or administrative employees. Their encouragement throughout this thesis is immeasurable, and no matter what I do, I will not be able to pay it back.

Finally, I am here because of the unconditional support of my two lifelong exceptional supervisors. They go by the name of Mom and Dad. For them, and my brothers, there is no ‘thank you’ I can give that would be enough.

At the dawn of my last academic exam, I ask myself, am I an expert now? Have I reached the balance where I have enough knowledge and confidence? I do not think so. There will always be things that will slip past the learning funnel. The path to academia goes through a rugged bumpy terrain packed with impeding self-doubt. But, at the end of the day, life is just an incomplete metamorphosis for all of us, where we will never attain the last stage of absolute knowledge and we just have to keep pushing forward.

KAMAL ATMEH

2022

PART I

GENERAL INTRODUCTION



1

Theoretical context

1.1 The road towards a movement paradigm

MOVEMENT represents a means for mobile animals to access and acquire any type of resources such as forage, mates, and refuge areas. Understanding the intricacies of movement can enhance our knowledge of the mechanisms that upscale from small-scale and rapid behavioral choices of resource selection and use, to population dynamics (Gaillard et al., 2010; Morales et al., 2010; Turchin, 1991). Consequently, this knowledge can be used to improve conservation and management measures (Allen and Singh, 2016). For instance, how species navigate the landscape can be a pertinent indicator of factors that limit individual performance, allowing researchers, managers, and stakeholders to anticipate the negative consequences of changing environments on the fitness of animals (Bastille-Rousseau et al., 2019; Owen-Smith and Cain, 2007).

In the 1960s-'70s, behavioral studies relied on evolutionary models, investigating the foraging behavior of animals in relation to their environment and food distribution (Charnov, 1976a; Emlen, 1966; Fretwell and Lucas, 1969; MacArthur and Pianka, 1966). Although the animals' ability to move is assumed most of the time, these studies did not focus on movement *per se*. Only several decades after did movement come to complement research on behavior and its link to the environment (Nathan et al., 2008). Most previous research has focused solely on the link between movement and external variables (e.g. landscape configuration, resource distribution), with little attention paid to how the interaction between external factors and individual characteristics (e.g. life-history traits, reproductive status) drive movement behavior (Holyoak et al., 2008; Joo et al., 2020). An individual's response to environmental stimuli will largely depend on its internal state and characteristics, which in return can be modified by the environment. For instance, an animal may require more resources during the reproductive period than outside of it due to the high energetic demands of gestation and lactation (Clutton-Brock, Albon, and Guinness, 1989; Clutton-Brock et al., 2009). Also, the presence of a predator may

increase stress levels for prey which will then favor habitats providing refuge over forage. Focusing solely on one type of variable, whether it is environmental or internal, may not provide a comprehensive understanding of the drivers of movement behavior.

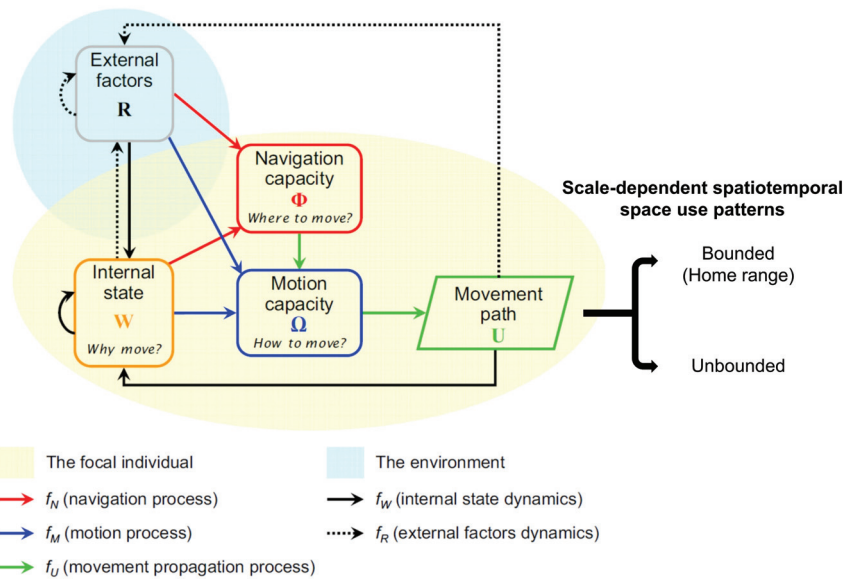


FIGURE 1.1: A general conceptual framework for movement ecology, composed of three basic components (yellow background) related to the focal individual (internal state, motion capacity, and navigation capacity) and a fourth basic component (turquoise background) referring to external factors affecting its movement. Relationships among components related to the processes by which they affect each other, with arrows indicating the direction of impact. The resulting movement path feeds back to the internal and external components (Nathan et al., 2008). Depending on the spatio-temporal scale of observation, movement paths upscale to bounded (i.e. home range) or unbounded spatial behavior. The colored left figure is taken from Nathan et al. (2008) and the elements added to the right are adapted from Börger, Dalziel, and Fryxell (2008).

To tackle this complexity in movement decision, Nathan et al. (2008) proposed the ‘movement ecology paradigm’ (Figure 1.1) in which an individual is described by three components relating to its internal state (e.g., physiological requirements driving movement), navigation capacity (e.g., sensory traits enabling orientation), and motion capacity (e.g., biomechanical traits enabling movement). These three components allow researchers to answer the questions of “why move?”, “where to move?”, and “how to move?”, respectively. In this paradigm, external factors represent a major fourth component to take into account environmental and social features such as resource, predation, or conspecifics which can affect the behavior of individuals (Figure 1.1). It is through the interplay of these four components that movement patterns emerge, leading to either a bounded home range or an unbounded spatial behavior each as a result of the spatio-temporal scale of observation (Börger, Dalziel, and Fryxell, 2008; Nathan et al., 2008).

The movement paradigm represents a turning point for studies on movement. With its inception and with the development of robust statistical methods dealing with high-resolution data from GPS and accelerometers (Benoit et al., 2020; Fleming et al., 2015;

Gurarie et al., 2016; Noonan et al., 2019) (Box 1.1), ecologists are turning the page on home range studies and shifting their focus towards investigating fine-scale movement and trajectories (Joo et al., 2020). It is thus timely to summarize the findings of the past decades on home range size and pinpoint advances and limitations of this field. Furthermore, the global deployment of GPS devices with fine-scale resolution on a large diversity of species makes it convenient to evaluate and compare movement around key periods of an animal's life (e.g. reproduction). Only by doing so can we understand the evolutionary pressures on spatial behavior since movement upscales to habitat selection and home range size (Van Moorter et al., 2016), both influencing the fitness of individuals (Gaillard et al., 2010; McLoughlin et al., 2007).

Box 1.1. TECHNOLOGICAL AND STATISTICAL HURDLES IN MOVEMENT RESEARCH

Until now, empirical evidence on movement was hindered by the lack of technological and statistical advances that allow collecting and analyzing movement data. Animal locations were mostly retrieved via field observations or Very High Frequency (VHF) devices, leading to coarse datasets (Kays et al., 2015). Subsequently, VHF data focused on evaluating home range, ignoring the underlying components of movement at fine spatio-temporal scales (Cagnacci et al., 2010; Joo et al., 2020; Kays et al., 2015). Another constraint lay in the weight of VHF and, later on, Global Positioning System (GPS) devices which were too bulky—and even expensive—to be deployed on small- to medium-sized animals, thus limiting data to a handful of large species (Kays et al., 2015). However, determining ultimate evolutionary mechanisms and proximate (*sensu* Mayr, 1961) external and internal factors shaping movement requires not only high-resolution data (Kays et al., 2015) but also data from a wide range of species distributed globally.

Over the years, loggers became smaller, cheaper, and provided finer data resolution leading to an upsurge in the number of species equipped with GPS. Despite this development, statistical methods were still unadapted for data with high spatio-temporal correlation. Consequently, a variety of debatable methods were developed to deal with this data (e.g. home range estimators, Kie et al., 2010; Noonan et al., 2019), leading to very heterogeneous studies over the years. Furthermore, linking fine-scale movement to landscape features faced new challenges since the resolution of vegetation maps did not correspond anymore to the fine-scale sampling of locations; a crucial element in landscape ecology (Bissonette, 1997). All these hurdles combined have led to a lack of consensus over the factors dictating movement.

1.2 The habitat concept

1.2.1 A dualistic definition

Even though central to ecology, the term ‘habitat’ has been subject to much debate and scrutiny. Often confused with the niche concept (*sensu* Hutchinson, 1957), it has received a variety of definitions (Hall, Krausman, and Morrison, 1997; Odum, 1971; Whittaker, Levin, and Root, 1973) which led to its misuse in multiple academic publications (Darracq and Tandy, 2019; Kirk et al., 2018) and ultimately to questioning its usefulness (Mitchell, 2005). The current most used definition partitions habitat into two components of structure and functionality (Gaillard et al., 2010). The structural habitat is limited to a human-made discrete or continuous description of vegetation type and categories (Hutto, 1985), which may or may not be of value for the studied species (Gaillard et al., 2010; Wiens, 1976). The main problem in the structural definition of habitat is that it does not account for spatial and temporal scales. For instance, a grassland for a giraffe (*Giraffa camelopardalis*) does not represent a similar habitat for a bark beetle (*Dendroctonus ponderosae*) that chooses structural components at much smaller scales. Nevertheless, this definition represents the main knot in a chain of processes pertaining to habitat selection. As animals select vegetation types to maximize their energy gain, these decisions at small spatio-temporal scales will end up determining their survival and maintenance over evolutionary time and at broader scales, leading to the functional habitat (Figure 1.2). In that sense, the functional definition of habitat draws from the niche concept (Hutchinson, 1957) and is defined as a mixture of biotic (e.g. predators, food items) and abiotic (e.g. rain) environmental variables (Hall, Krausman, and Morrison, 1997; Whittaker, Levin, and Root, 1973) that are accessible to the animal and which determine population and species dynamics (Gaillard et al., 2010). Consequently, the term “resource” does not refer only to food items but also other biotic and abiotic components of the environment such as refuge, water sources, and temperature (Hall, Krausman, and Morrison, 1997). Both definitions of habitat remain therefore closely interlinked and provide detailed information on habitat selection since they reflect biological processes at different spatio-temporal scales (Gaillard et al., 2010).

1.2.2 Habitat selection as a hierarchical process

Habitat selection has been defined by Johnson (1980) as a hierarchical process resulting from complex decisions and transcending multiple spatial scales. There are mainly four hierarchical levels: the selection of the range of distribution of the species (1st-order selection), and within that range, animals select their home range area (2nd-order selection). These first two levels are pertinent at the region and landscape scale and for individuals and populations. Going into a finer resolution, animals select a patch within the home range (3rd-order selection) and subsequently select food items within the chosen patch (4th-order selection) (Figure 1.2).

The development of this framework recognizes the multi-scale aspect of habitat selection (Gaillard et al., 2010) and implies that the choice of habitats at large spatial

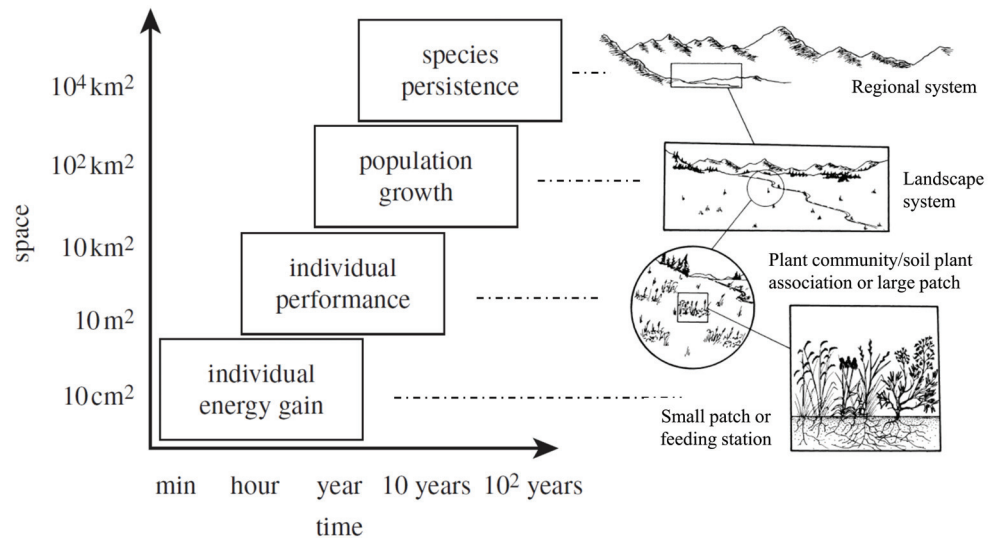


FIGURE 1.2: Habitat selection, represented as a hierarchical process spanning four spatio-temporal scales. The left figure is taken from Gaillard et al. (2010) and the right figure is taken from Senft et al. (1987).

scales has considerable impacts on the levels of selection at smaller spatial scales (Senft et al., 1987). However, distinguishing the hierarchical levels from food item to region is not as straightforward as it may seem. Even though the structural habitat is mostly used to assess the resources that are important for the energy gain of animals (Gaillard et al., 2010), using it to distinguish between spatial scales may be inadequate. Senft et al. (1987) argue that “a basic postulate of hierarchy theory is that functional parameters, the frequencies and rates of activities, are often more useful for defining hierarchical scales than are physical structures (Allen and Starr, 1982). Scales in an ecological hierarchy are separated by identifying frequencies or rates of pertinent processes”. It is therefore important to investigate behavioral processes (i.e. foraging, movement) at different spatio-temporal scales to understand the fitness consequences of habitat selection and how individuals perceive the landscape and their environment.

1.2.3 From hierarchical scales to hierarchical factors

Despite being represented as distinct hierarchical scales, there is almost consistently an interaction between the different levels of selection. This stems from the fact that different resources and factors are distributed and vary over multiple scales, leading animals to have different goals at each scale (Senft et al., 1987). For instance, shelter and water points may be concentrated at the patch level while forage may be found dispersed at the landscape scale. As a result, the animal ends up foraging in areas around water points due to their limited availability at the landscape scale (Owen, 1996; e.g. khulan *Equus hemionus*; Nandintsetseg et al., 2016). The spatial distribution of complementary resources at one scale can thus lead to considerable movement and behavioral constraints at another scale which then translate into habitat selection at the different hierarchical levels (Gaillard et al., 2010; Wiens, 1989). Habitat selection can therefore be viewed as a trade-off between the different needs of an animal, where

some factors are favored over others depending on the extent of their availability and the amplitude of their consequences on fitness.

Following this reasoning, one can expect that factors should also be organized in a hierarchy based on their limiting effect. This was proposed by Rettie and Messier (2000) in their paper on woodland caribou (*Rangifer tarandus*) where they found that females reduced the risk of predation by wolves (*Canis lupus*) by selecting less risky habitats at broad spatial scales (i.e. landscape), all the while selecting forage at fine spatial scales (i.e. within the home range). Following their findings, they suggest that factors that are the most limiting to the fitness of individuals should be avoided at the broader spatio-temporal scale. However, empirical studies were not consistent, with some providing support for the hypothesis (moose *Alces alces*: Dussault et al., 2005b, grizzly bears *Ursus arctos*: McLoughlin et al., 2002) and others not (sage-grouse *Centrocercus urophasianus*: Aldridge and Boyce, 2008). Limiting factors are not static and differ based on the temporal variation of the environment (e.g. between seasons) and also on the focal organism. For instance, water availability can be most limiting during the dry season in African savannas but its limiting effect may depend on the diet of the species (Redfern et al., 2003). Acquiring the most limiting factor for their fitness (i.e. in the case of resources) or avoiding it (i.e. in the case of predators) can be possible if animals have deep knowledge of their environment. This can be rendered impossible if the environment changes stochastically with no apparent pattern since memory is ineffective in such landscapes (Fagan et al., 2013; McNamara and Houston, 1987). The validity of Rettie and Messier's (2000) hypothesis may thus be restricted to animals in predictable environments and when the different limiting factors present similar spatial heterogeneity across scales (Gaillard et al., 2010). Therefore, to understand biological processes, both the spatial and temporal scales at which they are analyzed should correspond to the spatio-temporal scale of the biological question (Gaillard et al., 2010). This notion of scale has been transferred to movement ecology since animals adapt their behavior to limiting factors by moving in the landscape. Choosing the scale of observation, such as home range, fine- or broad-scale movements, should be determined by the biological hypothesis at hand.

1.3 Home range

1.3.1 A complex definition

To survive in heterogeneous and often unpredictable landscapes, an animal trades off resources, predator avoidance, mate search, movement costs, and social interactions (Péron, 2019), leading to an area-restricted space use commonly called a home range (Figure 1.3). Out of all the scales of habitat selection, the home range has been one of the most studied variables of animal space-use behavior (Joo et al., 2020; Kays et al., 2015) due to its relative importance for species distribution (Gautestad and Myrsetrud, 2005), community structure (Fagan, Lutscher, and Schneider, 2007), and conservation decisions (Schofield et al., 2010; Zeale, Davidson-Watts, and Jones, 2012). Burt (1943) defined

the home range as the “*area traversed by the individual in its normal activities of food gathering, mating, and caring for young*”, adding that “*occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range*”. Home range behavior emerges from movement patterns and routine activities in a familiar landscape, where memory is an essential driver for finding previously located food items, refuge, mates, and other resources (Fagan et al., 2013; McNamara and Houston, 1987; Van Moorter et al., 2009b). However, home range is not a static feature but can be viewed as a dynamic property emerging from movement. Its shape, size, and location vary with time since internal and external drivers of home range change temporally throughout the animal’s life (Börger, Dalziel, and Fryxell, 2008; Morellet et al., 2013). The relationship between these factors and movement is therefore bound to vary based on the spatio-temporal scale (Kie et al., 2002) and even on the level of observation (i.e. species, population, individual) of the question at hand (McCloughlin and Ferguson, 2000). For instance, mule deer (*Odocoileus hemionus*) home range sizes vary in relation to environmental features within a 2000m radius from their center than to environmental features within a 250m radius (Kie et al., 2002).

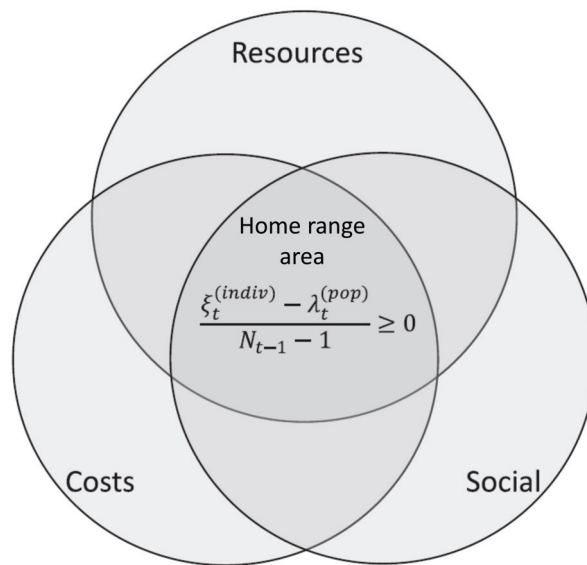


FIGURE 1.3: Three main classes of factors are expected to influence animal movement decisions shaping the home range: (1) food and shelter resources for maintenance and reproduction; (2) social interactions with congeners, including reproduction, competition, and sociality; (3) costs of and constraints on movement, including energy expenditure, environmental barriers, and cognitive biases. In this Venn diagram inspired by an analogy with the mechanistic drivers of species distribution (Soberón, 2007), the illustrated principle is that individuals look for the intersection that contains enough resources, that can be acquired at a low-enough cost, for the individual to perform as good as or better than its competitors, as measured by its contribution to population growth rate (*sensu* Coulson et al., 2006). ξ denotes the sum of the individual’s survival plus its surviving offspring at the end of the focal time period t . λ denotes the population growth rate over that period. N here denotes the population size at the beginning of the period. Taken and adapted from Péron (2019).

Nevertheless, Burt’s (1943) definition, although very clear, remained centered around resources and did not provide a precise spatio-temporal scale to analyze the home

range, which made it open to different interpretations (Péron, 2019). At the same time, ecologists focused mostly on the technological and statistical aspects for defining home range rather than on the conceptual side (Powell and Mitchell, 2012). As a result of this asynchronous development of theory, technology, and statistical methods, and despite the numerous studies, we still need a general comparative approach to comprehensively understand variations in home range size (Börger, Dalziel, and Fryxell, 2008; Kie et al., 2010; Péron, 2019; Powell and Mitchell, 2012). Unless the effect of the spatial and temporal scales, as well as individual traits, are investigated simultaneously (Börger, Dalziel, and Fryxell, 2008; Campioni et al., 2013), studies will continue to face a lack of consensus on factors shaping home range size. In his recent review, Péron (2019) advocates for a definition of home range as the area that would allow the animal to contribute to population growth rate (Figure 1.3). He suggests that other definitions of timeframes should not be called home range to make a clear distinction between the demographic relevance of a home range and the spatial behavior of an animal. Thus, understanding which factors influence and limit home range size the most (Mcloughlin and Ferguson, 2000), and at which spatio-temporal scales (van Beest et al., 2011), becomes crucial as home ranges upscale to impact population dynamics (Morales et al., 2010) and animal fitness (Gaillard et al., 2010).

1.3.2 Inter- and intraspecific factors shaping home range size

Examining factors that dictate inter- and intraspecific variation in home range size would allow us to grasp the ultimate and proximate causes of space use. Body mass, trophic level, and movement capacity should explain most of the variation in home range size across species than within species, as a result of evolutionary pressures. Resource distribution and internal factors, conversely, should be much more adequate in explaining intraspecific variation in home range size (Mcloughlin and Ferguson, 2000).

Across species variation in home range size is largely attributed to differences in body mass (McNab, 1963). This allometric relationship reflects size-dependent metabolic rate, where animals choose areas containing enough resources to satisfy their energetic needs. McNab (1963) reported that home range size scales with body mass in a similar manner to basal metabolic rate. However, even after accounting for body mass, there remain differences in home range size between species. This has been proven in consequent studies where scaling exponents differed significantly from the expected metabolic exponents of species (Gittleman and Harvey, 1982; Harestad and Bunnell, 1979; Lindstedt, Miller, and Buskirk, 1986; Mcloughlin and Ferguson, 2000). The observed allometric relationship between home range size and body mass changes with the lifestyle of the focal species (Kelt and Vuren, 1999). Social organization (Damuth, 1981; Jetz et al., 2004), trophic level (Gittleman and Harvey, 1982; Tamburello, Côté, and Dulvy, 2015), diet (Mysterud, Pérez-Barbería, and Gordon, 2001), habitat productivity (Lindstedt, Miller, and Buskirk, 1986), and openness (Ofstad et al., 2016) can have a significant effect on the scaling exponent and elevation of the home range-body mass relationship.

Intraspecific variation in home range size is less well understood than interspecific variation (Börger, Dalziel, and Fryxell, 2008; Kjellander et al., 2004). A variety of internal and external factors have been reported to shape intraspecific variation in home range size, with the main ones being age and sex (Cederlund and Sand, 1994), individual traits (Campioni et al., 2013), quantity of food (Andrzejewski and Mazurkiewicz, 1976), landscape configuration (Brambilla et al., 2006; de Beer and van Aarde, 2008), and predation risk (Desy, Batzli, and Liu, 1990; Tufto, Andersen, and Linnell, 1996). These factors have seldom been analyzed simultaneously at different spatio-temporal scales (van Beest et al., 2011), and still face considerable debate as to how they should be measured (Li and Reynolds, 1994; Murwira, 2003; Nilsen, Herfindal, and Linnell, 2005). This leads to a lack of consensus over which factors are the most limiting and even underestimates their complementary effects on home range size. Furthermore, and unlike for interspecific analyses, how a species' life-history and ecological traits (e.g. diet, group size) shape the intraspecific relationship between home range and environmental variables, has been less explored.

1.3.3 Choosing the right scale of observation

As movement capacities vary across species, the emergence of bounded home ranges for different species may arise over different temporal scales. For instance, a mouse may define its home range over a few weeks while elephant home ranges may emerge over months. Even the same animal can show bounded and unbounded movement at different spatio-temporal scales (Börger, Dalziel, and Fryxell, 2008; Powell et al., 1997). Mongolian gazelle exhibit nomadic movement patterns when monitored over short times but visit previously visited sites at longer temporal scales, which eventually lead to bounded home ranges (Nandintsetseg et al., 2019). Therefore, inter- and intraspecific comparisons of home ranges from different spatio-temporal scales may be complex (Börger, Dalziel, and Fryxell, 2008; Péron, 2019), especially when home range estimators are not adapted for comparing heterogeneous datasets (Börger, Dalziel, and Fryxell, 2008; Kie et al., 2010; Noonan et al., 2019; Noonan et al., 2020; Péron, 2019).

Concurrently, even though a home range may seem stable, the underlying movement behavior may be varying over time (Campioni et al., 2013; Courriot et al., 2018). Depending on the question at hand, choosing home range as the scale of observation may therefore not be the most informative. For instance, the distances traveled by male eagle owls (*Bubo bubo*) are significantly larger during the incubation and nestling periods compared to the rest of the season. Nevertheless, despite these marked increases in movement, their home range sizes remain stable over the whole season (Campioni et al., 2013). Interestingly, the extent of the effect of internal and external factors can depend on the spatio-temporal scale. Whereas the biological cycle leads to increased movement within the home range, external factors such as population density may prevent home range expansion (Campioni et al., 2013).

Therefore, understanding the full extent of spatial behavior requires more studies on the drivers of movement using empirical data at different spatio-temporal scales.

Consequently, and with the development of robust statistical methods (Börger, Dalziel, and Fryxell, 2008; Dunn and Gipson, 1977; Fleming et al., 2016; Fleming et al., 2014), researchers are not solely analyzing home range size but are also focusing on movement, trajectories, and the underlying parameters of home range to evaluate relevant biological questions (Moorcroft, Lewis, and Crabtree, 1999; Moorcroft, Lewis, and Crabtree, 2006; Moorcroft, 2012; Van Moorter et al., 2009b).

1.4 A triptych of interactive landscapes shaping movement

1.4.1 Resource landscape

Food resources can be characterized by their abundance, timing, ephemerality, and predictability which upscale to determine their spatio-temporal configuration and variance in the landscape (i.e. resource landscape; Abrahms et al., 2021). As food resources become heterogeneous, and to maximize their energy gain, animals may shift their diet to the more abundant rich food (e.g. black bear *Ursus americanus*: McDonald and Fuller, 2005) or move to access all the required resources for their survival (e.g. birds: Thorup et al., 2017). while reducing costs of movement and search (i.e. optimal foraging theory: Charnov, 1976a; Emlen, 1966; MacArthur and Pianka, 1966). In that sense, the optimal foraging theory stipulates that animals should always choose the most adapted foraging behavior that maximizes the net gain of energy per unit of time for the lowest possible movement cost (Schoener, 1971).

To maximize their energy gain through food acquisition, individuals exhibit a diversity of movement patterns, including nomadic, migratory, or sedentary behavior, primarily in response to the spatio-temporal variation in resource distribution (Mueller and Fagan, 2008; Singh et al., 2012). For instance, stationary behavior such as range residency is prevalent in fine-scale heterogeneous and predictable landscapes (Mueller and Fagan, 2008) and nomadism is mostly observed in resource-poor and unpredictable environments (Mueller and Fagan, 2008; Teitelbaum and Mueller, 2019). Many animals track resources spatially allowing them to temporally extend access to food which would have been limited if individuals remained in the patches they occupied initially (Abrahms et al., 2021; Hebblewhite, Merrill, and McDermid, 2008; Sawyer and Kauffman, 2011). For instance, blue whales (*Balaenoptera musculus*) have been shown to track phytoplankton blooms using climatological gradients along the west coast of North America (Abrahms et al., 2019). Similarly, ungulates use spring green-up of vegetation to time their migration with waves of plant growth, also called surfing the green wave (i.e. green wave hypothesis, Aikens et al., 2017; Bischof et al., 2012; Drent, Ebbinge, and Weijand, 1978) (Figure 1.4), and thus acquire high-quality forage (i.e. forage maturation hypothesis, Fryxell, 1991; Hebblewhite, Merrill, and McDermid, 2008).

However, resource tracking is not limited to large-scale movements such as migration. Not all individuals in a population, nor do all ungulates, migrate (Bischof et al., 2012; Middleton et al., 2018; Mysterud et al., 2011). Animals may track resources at a much finer scale if the grain of variation occurs at the patch level rather than at the

landscape level (Couriot et al., 2018; Duparc et al., 2019; Middleton et al., 2018). For instance, roe deer adopt a multi-range tactic (i.e. sub-seasonal functional home ranges) to track variation in resources at the within-home range scale (Couriot et al., 2018). Resource tracking presents considerable benefits to animals, ranging from increased food consumption (e.g. bears: Service et al., 2019) to higher fat gain in migrants compared to residents (e.g. red deer *Cervus elaphus*: Middleton et al., 2018), all of which have a significant positive impact on the fitness of individuals (Gaillard et al., 2000).

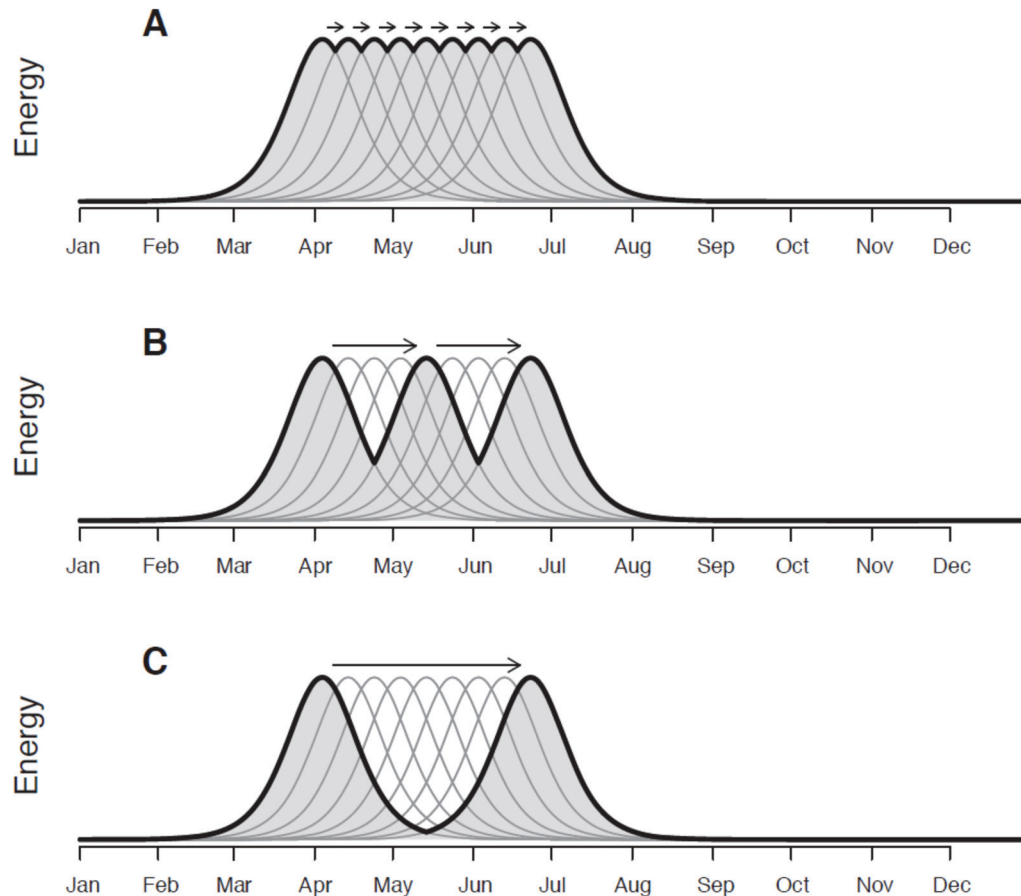


FIGURE 1.4: Schematic illustration of different migratory movement tactics (thick black lines) when confronted with the green wave, represented by snapshots of peaks in energy (nutrient) availability (thin gray lines) moving across the landscape during the growing season. Individuals surfing the green wave (A) may do so by gradually sliding or moving in small spatial increments along with the wave, thereby tightly matching phenological development. Individuals jumping the green wave (C), experience the passing of the green wave at one location and then transition to a new location to capture the green wave, but without sliding along its leading edge, having a considerable mismatch in speed compared to plant phenological development. Green-wave pursuit patterns depicted in B are intermediate, with migrants using more or less frequent stopover sites to intersect the leading edge of the wave at different locations. Gray areas represent the cumulative “springness” experienced by migrants following each tactic. Taken from Bischof et al. (2012).

Accordingly, due to the many benefits of acquiring high-quality food resources, one can assume that all animals should aggregate in the most suitable habitat to them

(Fretwell and Lucas, 1969). In doing so, animals would maximize their survival and reproductive success by increasing their net energy gain. One of the limits of optimality theory, however, that made it subject to wide criticism (Pierce and Ollason, 1987; Pyke, 1984), is that individuals face constraints due to external and internal factors which do not allow them to exhibit maximal fitness for all features. An animal shares its surroundings with conspecifics and other species, which may be helpful or harmful to its survival (Charnov, 1976b; Kie, 1999). These interactions are therefore bound to render some habitats unavailable – with availability referring “*to the accessibility and procurability of physical and biological components of a habitat by animals*” (Hall, Krausman, and Morrison, 1997). The interplay between the multiple biotic and abiotic constraints leads individuals to select only available habitats even if their preference lay elsewhere. These interactions are therefore bound to modify the animal’s behavior and may hinder its movements. To maximize their net energy gain, and in turn their fitness, animals do not solely rely on acquiring rich resources but take advantage of abiotic features in their environment to reduce movement costs, and adopt behaviors that would reduce their risk of mortality and that of their offspring in the presence of predators. Consequently, the recent ‘optimal movement theory’ advocates for the study of movement by merging the resource landscape with energy and fear landscapes, assuming that animals maximize their energy depending on all three landscapes (Williams and Safi, 2021).

1.4.2 Energy landscape

Animals may also choose habitats that can minimize the energetic costs of movement which would allow them to increase their net energy gain. These habitats are mostly related to a set of abiotic and physical components (e.g. slopes, updrafts, airflows) which end up defining the physical energy landscape (Shepard et al., 2013; Williams and Safi, 2021). For instance, soaring birds choose habitats at certain altitudes to take advantage of atmospheric uplifts, allowing them to glide through the landscape with minimal movement costs (Scacco et al., 2019; Williams and Safi, 2021). Furthermore, resource tracking is not limited to tracking forage. Animals can track abiotic components which represent cues for future resources. For instance, female caribou track snowmelt in a similar manner to ungulates surfing green-waves, allowing individuals to reach calving ground and benefiting from spring green-up while minimizing the costs of movement that can arise from impeding snow cover (Laforge, Bonar, and Wal, 2021). However, animals do not move in relation to solely one of the resource or energy landscapes but adapt their behavior to both. In some cases, resource distribution in the landscape may require broad-scale movements which may be costly, and depending on the species’ locomotion capacity, these movement costs may limit resource tracking (Abrahms et al., 2021; Shepard et al., 2013). However, these costs of movement can be compensated by a trade-off between resource intake and physiology. For instance, juvenile Pacific bluefin tuna (*Thunnus orientalis*) subject to a marine heatwave shifted their migration to cool waters optimizing their metabolic expenditures and simultaneously increasing their energy intake from foraging (Carroll et al., 2021).

Nevertheless, the resource and energy landscapes remain incomplete in explaining the spatial behavior of animals since they omit constraints of risk avoidance on movement (Gallagher et al., 2017; Halsey, 2016).

1.4.3 Landscape of fear

Many species are prey subject to predation pressures, limiting their populations through direct killing or indirect costs (Creel, 2018; LaManna and Martin, 2016; Preisser, Bolnick, and Benard, 2005; Say-Sallaz et al., 2019; Sinclair, Mduma, and Brashares, 2003). To maximize survival, animals may behave proactively by fleeing (Caro, 2005), increasing vigilance (Brown, 1999; Creel, Schuette, and Christianson, 2014), or choosing less risky habitats (Brown, 1999; Charnov, 1976b; Hernández and Laundré, 2005; Lima and Dill, 1990), which can induce considerable costs (Creel, 2018). For instance, when increasing their vigilance, bison (*Bison bison*) and elk (*Cervus canadensis*) decreased their bite rate while foraging (Fortin et al., 2004). The presence of predators can also limit access to highly favorable habitats and species may be forced to choose suboptimal unpreferred habitats as a trade-off between food and safety. For instance, bottlenose dolphins (*Tursiops aduncus*) choose habitats with lower food availability when tiger sharks (*Galeocerdo cuvier*) are present in high densities, leading to a food-safety trade-off (Heithaus and Dill, 2002). Temporal shift of activities can also be a strategic behavior to avoid predation. Plains zebras (*Equus quagga*), for example, minimize the danger of being attacked by lions (*Panthera leo*) at night by foraging near waterholes solely during the day (Courbin et al., 2019).

Non-lethal risk, through antipredator responses, may be as costly to individuals (non-consumptive effects; Say-Sallaz et al., 2019) as lethal risk (Preisser, Bolnick, and Benard, 2005; Schmitz, Beckerman, and O'Brien, 1997) since it can affect reproduction, growth, and survival (Creel et al., 2007; Creel, Christianson, and Winnie, 2011; LaManna and Martin, 2016; Proffitt et al., 2014). The prey's perception of predation risk leads therefore to the establishment of the landscape of fear (Gaynor et al., 2019; Laundré, Hernández, and Altendorf, 2001; Laundré, Hernandez, and Ripple, 2010) which varies spatially due to different environmental (Camp et al., 2012), sensory (Kuijper et al., 2014), or social (Danchin et al., 2004) cues. Similarly, the temporal variation of risk (e.g. dry and wet season, Owen-Smith, 2008) and its predictability dictate the prey's foraging response as well as its intensity (predation-risk allocation hypothesis, Lima and Bednekoff, 1999).

Nevertheless, animals maximize energy gain and survival by adapting their movement behavior in relation to all three of the resource, energy, and fear landscapes. For instance, elk, in the presence of wolves, shift their habitat selection from rich meadows to safe forests, but at the same time do not select for higher elevation or slopes thus minimizing costs of movement (Creel et al., 2005; Gallagher et al., 2017). Therefore, understanding the full extent of movement requires an evaluation of the interaction between these landscapes.

Some species migrate long distances to avoid predation and give birth in safe habitats (predation risk avoidance hypothesis, Bergerud, Butler, and Miller, 1984; Fryxell, Greever, and Sinclair, 1988), even though there is a high risk of being predated on in migratory corridors (e.g. elk: Hebblewhite and Merrill, 2007; Hebblewhite and Merrill, 2009). At the same time, predation risk can have significant effects on the ability of species to track resources, possibly dictating whether individuals jump or surf the greenwave (e.g. red deer: Bischof et al., 2012). For instance, reindeer *Rangifer tarandus* in Sweden when exposed to high densities of brown bears (*Ursus arctos*) deviated their movement from the spring green-up by using safer habitats (Rivrud et al., 2018). Nonetheless, avoiding predators by shifting habitat may not be sufficient in a multi-predator ecosystem, because prey may be putting themselves at risk of being predated on by another species. Elk reduce the risk of direct predation by wolves by moving to another habitat, but this, in turn, increases the risk of predation by cougars (*Puma concolor*) (Atwood, Gese, and Kunkel, 2009). Similarly, caribou mothers avoiding habitats used by wolves increased the risk of predation by black bears on their offspring (Leblond et al., 2016). Predation is also the most important cause of mortality in neonates (see Linnell, Aanes, and Andersen, 1995 for a review on ungulates), leading them to adapt their movement behavior accordingly (Lent, 1974).

In this matrix of risk, anthropogenic disturbances and even direct predation actions by humans induce strong behavioral responses of species (e.g. hunting, Chassagneux et al., 2019), and represent as much of a risk to animals as natural predators (Frid and Dill, 2002). This leads animals to avoid habitats with high human concentration, reduce their movement (Tucker et al., 2018), and even synchronize their activity and movement patterns with periods of low human disturbance (Bonnot et al., 2013). For instance, coyotes (*Canis latrans*) and maned wolves (*Chrysocyon brachyurus*) adopt periodic movements of one week, where they reduce activity during weekdays and resume normal behavior during the weekends probably due to lower human disturbance (Péron et al., 2017). Anthropogenic constructions can also alter the use of the energy landscape in animals. Herring gulls (*Larus argentatus*) do not take advantage of the highest updraughts generated by onshore winds due to their closeness to buildings, but instead use updraughts that are further away from constructions to reduce the risk of collision (Gallagher et al., 2017; Shepard, Williamson, and Windsor, 2016). Road densities and the risk of death by collision can also shift habitat use of species to less risky habitats, but at the cost of food resources (Basille et al., 2013). At the same time, anthropogenic linear features represent semi-permeable, and in some cases even impermeable (e.g. fences) barriers that can render resource tracking and green-wave surfing complicated by deviating animals from their optimal migration routes (Sawyer et al., 2013). Since the benefits of migration are considerable (Fryxell and Sinclair, 1988; Fryxell, Greever, and Sinclair, 1988; Middleton et al., 2018), anthropogenic barriers can lead to a decrease in the fitness of individuals (Kauffman et al., 2021b). Indirect effects of human disturbance on species' mortality can also be seen at stop-overs where migrating species, reaching unknown grounds, rely on sensory cues to detect predators,

a behavior sometimes impeded by anthropogenic noise and light disturbance (Dominoni et al., 2020).

Overall, the spatial behavior that results from the animal's interaction with the resource, energy, and fear landscapes should form a fitness landscape, where animals should adopt the best behavior while accounting for all constraints. In theory, this should help explain the observed movement patterns and provide a comprehensive understanding of how movement upscales to population dynamics.

1.5 Social sampling and sociality

Navigating ecological landscapes may be difficult and animals may not be able to maximize energy gain when they have little knowledge of their environment. Social sampling refers to the process of observing social cues, thus leading individuals to have a wider range of perception due to the transfer of social information when in uncertain conditions (Williams and Safi, 2021). Individuals share their environment with con- and heterospecifics which can provide information on optimal habitats, rendering search and movement in the three ecological landscapes less costly (Spiegel and Crofoot, 2016; Williams and Safi, 2021). Evaluating how animals navigate ecological landscapes while simultaneously gaining information from social interactions represents a comprehensive framework to understand the emergence of movement patterns and grouping behavior (Williams and Safi, 2021).

Information gained from conspecifics and other species can help individuals improve their search for resources, reduce their movement costs, and increase their survival by providing cues for predators and risk. Newly translocated alpine ibex (*Capra ibex*), for instance, used resident ibex as an indicator of high-quality resources and then occupied and used similar habitats (Scillitani et al., 2013). Species can also modify the physical energy landscape by creating tracks and footsteps in costly substances, which other species can later on use to reduce their costs of movement (Spiegel and Crofoot, 2016; Williams and Safi, 2021). Social information extends also to providing cues for detecting predators (i.e. many eyes effect, Pulliam, 1973) and species can evolve group-living as a way of diluting predation risk (Beauchamp and Ruxton, 2008). In mixed-species herds, zebras eavesdrop on behavioral cues from giraffes which allows them to reduce predation risk (Schmitt, Stears, and Shrader, 2016). Defassa waterbuck (*Kobus ellipsiprymnus*) synchronize their vigilant behavior with other group members, creating waves of vigilance that maximize predator detection (Pays et al., 2007). Caribou can detect high predation risk in habitats with high moose density since the latter species is considered the main prey for wolves (Gaynor et al., 2019). Also, by observing density cues, individuals arriving at new areas can identify refuge habitats that are still unknown to them (Sabal et al., 2021).

Nevertheless, not all social interactions are beneficial. Interference competition can lead some subordinate individuals to end up in poor habitats with negative impacts on their fitness (i.e. source-sink habitats, Pulliam, 1988). For instance, dominant adult male Great Tits (*Parus major*) occupy resource-rich hedgerows and restrict yearling males to

occupying suboptimal woodlands that negatively impact their fitness (Krebs, 1971). In group-living species, large group formations can lead to competition over forage and faster depletion of food patches, thus leading to higher movement costs to find other suitable foraging areas (Chapman, 1990; Johnson et al., 2015). Conversely, group-living can also lead to significant constraints on the movement of individuals, which hampers their exploration of new possibly profitable patches (Pays et al., 2012). Whether group-living implies costs through the first or second pathway depends, however, on the diet of the species (Doran-Sheehy et al., 2004) and the availability and quality of forage (Johnson et al., 2015). It is therefore important to evaluate movement across ecological landscapes through an inter- and intraspecific comparative lens while accounting for social interactions and ecological traits.

Differences in movement, however, are not solely driven by environmental and social variables. How species respond to the ecological landscapes depends largely on their internal state (Nathan et al., 2008) which fluctuates markedly in time, especially during key periods of the biological cycle.

1.6 Intra-annual changes in movement related to the biological cycle

1.6.1 Parturition and caring for offspring

Around parturition, there is an increased need for high-quality safe habitats to offset the energetic requirements of parturition and to increase the survival of the newborn offspring (Trivers, 1974). However, having both rich and safe habitats can incur significant costs on movement since refuge and food resources can be unevenly distributed in the landscape, thus impacting the three ecological landscapes. For instance, in species displaying central place-foraging, mothers of altricial young are obliged to return to their den or burrow after a foraging bout to feed their young at regular intervals (Lariviere and Messier, 1997; Oftedal, Boness, and Tedman, 1987). In contrast, species that give birth to precocious offspring, which are more mobile, may have their mobility constrained by the movement abilities or needs of their young (Bustnes, 1996). The presence of an offspring at heel in ungulates can lead to reduced movement of mothers (Ciuti et al., 2006; Clutton-Brock et al., 2009; Saïd et al., 2005) which may constrain her from reaching high-quality habitats. Female ungulates even migrate before parturition to give birth in safe and high-quality habitats before being limited by the movement of their young (Lendrum et al., 2014).

Also, as foraging and protection attributes are rarely maximized in the same habitat type, mothers may be forced to feed on low-quality forage (Festa-Bianchet, 1988) or trade-off their safety and their offspring's for high-quality habitats (Jarnemo, 2004; Panzacchi et al., 2010) around parturition, all of which can negatively impact the individual's fitness. Furthermore, migration to new grounds with rich forage can be quite costly for the offspring since, in some species, neonatal predation can be high during large-scale movements (Berg et al., 2021). Nevertheless, the effect of resource

distribution on the spatial behavior of parturient animals has seldom been accounted for in movement ecology (Long et al., 2009). Therefore, we still lack a general understanding of how animals balance resource acquisition while being constrained by the limited mobility of their offspring, especially in very heterogeneous environments which require large movement behavior.

1.6.2 Mating season

While females generally invest their energy in the rearing of offspring, males allocate resources to develop characteristics that would allow them to compete against other males for the access of reproductive females (Trivers, 1972). In that sense, how males acquire mating opportunities can be an effective factor determining their reproductive success and spatial behavior (Clutton-Brock, 1988; Clutton-Brock, 1989; Emlen and Oring, 1977). Of the most common behavior depicting the link between internal state and movement (Nathan et al., 2008), mating exploits are one of the most evident. As the internal hormonal clock reaches its peak time during the mating season (Santiago-Moreno et al., 2005; Whitehead and McEwan, 1973), animals exhibit significant increases in their movement to access mates. For instance, the total daily movements of white-tailed deer (*Odocoileus virginianus*) are 20% higher during the rut than after it since they are continuously in search of mates (Webb et al., 2010). Adult male water voles (*Arvicola amphibius*) expand their home ranges during the reproductive season to include as many mates as possible and thus increase their reproductive success (Frafjord, 2016). Large movements during the mating season may lead males to end up in unfamiliar environments due to their exploratory behavior (Shakeri, White, and Waite, 2021). Male mountain goats (*Oreamnos americanus*), for example, exhibited low site fidelity during winter following the rut probably due to seasonal carry-over effects (Shakeri, White, and Waite, 2021). Consequently, there are considerable impacts of mating behavior on gene flow (Portanier et al., 2018) and disease spread (Marchand et al., 2017) in a population.

Changes in movement during the mating season, however, are not solely limited to males in a species. Increased movements in females have been detected in some species in relation to the mating season. Female roe deer (*Capreolus capreolus*) had at least one notable excursion during the rut, with traveled distances greater than the average diameter of male home ranges, implying a strategy to avoid mating with relatives, given that males remain immobile throughout the rut (Debeffe et al., 2014). However, movement of females during the mating season is not always driven by mate availability, but also by the distribution of food resources in the landscape (e.g. reindeer: Djaković et al., 2015). Interestingly, the distribution of females, whether as a response to mates or resources, leads to the rise of different male mating tactics (Clutton-Brock, 1989; Emlen and Oring, 1977; Ims, 1988). Depending on the spatial availability of females, males can be territorial, where they remain sedentary to defend rich food resources (Clutton-Brock, 1989; Johansson, 1996), or non-territorial where they move in the landscape in search of mates (Bon et al., 1992; Bowyer et al., 2020; Willis and Neuhaus, 2009). Accordingly, both tactics can impact differently the movement of animals. For instance,

both territorial roe deer and non-territorial mouflon (*Ovis gmelini musimon*) increased their home range sizes during the rut, but the extent of increase was lower in the former than in the latter (Malagnino et al., 2021). Nevertheless, how fine-scale movements of distinct mating tactics drive differences in home range size is still understudied and requires further investigation.

2

Aim of the thesis

UNDERSTANDING the movement patterns of animals, especially in the context of climate change, can contribute to improving conservation and management policies (Allen and Singh, 2016). As seen throughout the previous chapter, movement behavior, habitat selection, and the size of home range can incur significant consequences on the individuals' fitness and dynamics of a population (Gaillard et al., 2010; Morales et al., 2010). However, despite numerous studies, we still need robust comparisons of the factors determining home range size and movement patterns at different spatio-temporal scales. Furthermore, how ecological and life-history traits drive movement behavior needs to be investigated further both across and within species. Within this framework, I chose to focus my research on ungulates because of their ability to modify ecosystems (Apollonio, Andersen, and Putman, 2010), their abundant telemetry data (Kauffman et al., 2021a), and their marked inter- and intraspecific variability in movement (Kauffman et al., 2021a; Naidoo et al., 2012) as well as in ecological and life-history traits (Fritz and Loison, 2006).

2.1 Ungulates as a case study

The Smithsonian Institution recognizes 257 species of ungulates —*meaning having hooves or an enlarged toenail*— with recent taxonomies identifying over 450 species (Groves and Grubb, 2011). Ungulate species belong to the orders Perissodactyla, Artiodactyla, and Proboscidea. They first appeared over 50 million years ago in forested habitats and later spread to occupy grasslands and savannas (Janis, 2008). Nowadays, ungulates are present across all biomes, from highly to poorly productive environments (Fritz and Loison, 2006). Species occupy open and closed habitats, deserts, savannas, and arctic tundra. This diversity of environments makes it attractive to study their movement across environmental gradients. Furthermore, there is considerable variation in the body size of ungulates, with marked sexual dimorphism (Loison et al., 1999; Pérez-Barbería, Gordon, and Pagel, 2002), ranging from ungulates below 2kg (e.g. Java mouse-deer

Tragulius javanicus) to species having a body mass over 1000kg (e.g. giraffe) (Pérez-Barbería and Gordon, 2000).

These differences in body mass translate to differences in feeding style (Gordon and Illius, 1994; Pérez-Barbería and Gordon, 1999) since body mass is a major determinant of energetic requirements. The Jarman-Bell principle (Bell, 1971; Geist, 1974; Jarman, 1974) states that because of their higher “metabolism requirement/gut capacity” ratio, smaller species have higher energetic requirements compared to larger species. Consequently, large species can compensate for their energetic expenditure by feeding on abundant lower quality forage such as grass, while smaller species are much more selective and require high-quality forage such as twigs and plant parts. To distinguish among feeding styles, Hofmann (1989) categorized ungulates into three classes: browsers, grazers, and intermediate feeders. The first one encompasses small species feeding on twigs and shrubs. The second one contains large species which feed on herbaceous plants. Finally, the third class encompasses species that feed on both types of forage. However, certain exceptions do not fit the body size-feeding style classification. For instance, the largest ungulate, the giraffe, is a browser. Ungulate species below 10kg sometimes forage on fruits (Fritz and Loison, 2006). Therefore, the browser-grazer classification should be restricted to the diet of the species, while the species itself should be characterized by the morphology of its rumen, where two types are expected: moose-type and cattle-type (Codron and Clauss, 2010).

Ungulates also vary in their social organization. Some species remain solitary or in pairs throughout their whole life (e.g. Japanese serow *Capricornis crispus*: Bro-Jørgensen, 2008), while others live in groups and herds formed by more than 25 individuals (e.g. Mongolian saiga *Saiga tatarica*: Bro-Jørgensen, 2008). There is a close link between group size, feeding style, body mass (Jarman, 1974), and even habitat openness (Fritz and Loison, 2006). Small ungulates are found to be more solitary while larger species are found to create larger groups. Consequently, due to the relation between feeding style and body size, we can deduce that browsers occur in smaller groups than grazers. This can be a reflection of the spatial distribution of shrubs and grass, where the former are more dispersed while the latter are more clumped (Searle, Hobbs, and Gordon, 2007; Searle and Shipley, 2008) thus causing the emergence of the observed social pattern. The more striking relationship, however, exists between group size and habitat (Fritz and Loison, 2006). Larger groups of ungulates are more abundant in open habitats while smaller groups and solitary individuals are more present in forests and closed environments. This can represent an antipredator behavior as a way of diluting predation risk in more open risky habitats.

Habitat type has been a major explanation for the emergence of different neonatal anti-predator tactics in ungulates (Fisher, Blomberg, and Owens, 2002). Predation is one of the major reasons for offspring mortality in ungulates (Linnell, Aanes, and Andersen, 1995) which can cause considerable consequences on population dynamics (Gaillard, Festa-Bianchet, and Yoccoz, 1998). Consequently, ungulate neonates developed neonatal tactics with different implications on their mobility. Lent (1974) identified a hider and

a follower tactic. Hider neonates remain hidden in concealed spots during the first weeks after birth and have very limited mobility which imposes constraints on the mother (Ciuti et al., 2006). Due to their need for concealment, this tactic has evolved in closed habitats (Fisher, Blomberg, and Owens, 2002). Follower neonates can follow the mother directly after birth and therefore only limit her movement with their limited movement capacity. Offspring with a follower tactic rely mostly on contact maintenance as a defense strategy against predators (Green, 1992), and since they do not require concealment, they are more present in open habitats (Fisher, Blomberg, and Owens, 2002). Therefore, it has been suggested that larger females (Jarman, 1974) and group sizes (Estes and Estes, 1979; Ralls, Kranz, and Lundrigan, 1986) are more efficient in defending follower offspring. While the group size hypothesis has been confirmed with phylogenetic analyses, the body mass theory did not receive a lot of support (Fisher, Blomberg, and Owens, 2002).

Mating systems in ungulates are also diverse and we can observe both monogamy and polygyny among species (Fritz and Loison, 2006). There is a close relationship between both systems and body size, whereas small species are found to be monogamous and large ones polygynous (Loison et al., 1999). The observed variation in mating systems is the result of low paternal investment in the rearing of the young and the spatial distribution of females across the landscape which determines their defensibility (Clutton-Brock, 1989). The distribution of females depends however on the distribution of resources. Ungulates exhibit resources-defense strategies, leks, harems, and tending bonds during the rut period. There is also marked intraspecific variation in mating strategies, where some individuals of the same species display leks while others resort to harem defense or territorial mating strategies (e.g. fallow deer *Dama dama* and red deer, Carranza, Garcia-Muñoz, and de Dios Vargas, 1995; Clutton-Brock, 1989). These differences may be due to variation in resources which then drive female distribution thus cascading to differences in mating strategies (Carranza, Garcia-Muñoz, and de Dios Vargas, 1995). Intraspecific variation can also arise due to age-specific differences between males. For instance, adult ibex exhibit a tending bond with females while younger males resort to coursing tactics to access mates as they are not able to compete with the bigger males (Willisch and Neuhaus, 2009).

These large differences in ecological and life-history traits make it convenient to test multiple hypotheses as to how species adapt their movement and space use behavior across environmental gradients.

2.2 Main questions

First, contrary to previous studies at the interspecific level, we still lack a consensus over the factors driving intraspecific variation in home range size. To address this issue, we conducted a systematic review of home range studies of ungulates to try and reach conclusions as to the effect of food resources, lethal and non-lethal risk of predation and anthropization, and landscape heterogeneity on home range size at the within-population level. We also tested whether the observed patterns were affected by the

temporal scale of home range, diet, group size of the focal species, and statistical and technological methods used in the studies (i.e. home range estimators, VHF, and GPS).

Second, understanding the constraint of offspring on the movement of females around parturition is essential. Female ungulates have to balance their energetic needs and their offspring's safety. However, offspring have limited mobility and may constrain ungulate mothers from reaching the necessary forage (Ciuti et al., 2006; Lendrum et al., 2014; Shakeri, White, and Waite, 2021). We thus conducted an interspecific study to understand the extent of the limitation of offspring. We analyzed the movement of females with hider and follower neonates in environments with contrasting degrees of productivity. To bypass the hurdles of home range estimation and interspecific comparison of heterogeneous datasets, we used the robust continuous-time stochastic movement models. Most importantly, these models proved efficient in providing a general understanding of the underlying movement patterns that drive home range size.

Third, if biological cycles are more evident at small spatial scales (Campioni et al., 2013) then one can assume that particular biological events can be reciprocally inferred from GPS trajectories. This has been the case for the detection of parturition dates from GPS data (Marchand et al., 2021). However, there are almost no studies on the inference of mating tactics from location data, although these tactics present marked movement signatures. Using continuous-time stochastic movement models and data from multiple species, we investigated whether movement parameters of diffusion and frequency of return allow detecting signature movements of mating tactics (i.e. territoriality, leks, tending, harem).

At the end of this dissertation, I discuss the limitations and obstacles that impede our understanding of the drivers of home range size. I also propose theories on how females of hidere and followers adapt their movement in relation to offspring presence and resources. Lastly, I summarize my research by providing a new method for discriminating between different mating tactics using two movement parameters extracted from GPS data.

PART II

CORE RESEARCH



3

A systematic review of within-population variation in the size of home range across ungulates: What do we know after 50 years of telemetry studies?

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Abstract

Studying the factors determining the sizes of home ranges, based on body mass, feeding style, and sociality level, is a long-standing goal at the intersection of ecology and evolution. Yet, how species-specific life history traits interact with different components of the landscape to shape differences in individual home ranges at within-population level has received much less attention. Here, we review the empirical literature on ungulates to map our knowledge of the relative effects of the key environmental drivers (resource availability, landscape heterogeneity, lethal and non-lethal risks) on the sizes of individual home ranges within a population and assess whether species' characteristics (body mass, diet, and social structure), account for observed variation in the responses of the sizes of individual home ranges to local environmental drivers. Estimating the sizes of home ranges and measuring environmental variables raise a number of methodological issues, which complicate the comparison of empirical studies. Still, from an ecological point of view, we showed that (1) a majority of papers (80%) supported the habitat productivity hypothesis, (2) the support for the influence of landscape heterogeneity was less pervasive across studies, (3) the response of cattle-type to variation in food availability was stronger than the response of moose-type, and (4) species-specific body mass or sociality level had no detectable effect on the level of support to the biological hypotheses. To our surprise, our systematic review revealed a dearth of studies focusing on the ecological drivers of the variation in the sizes of individual home ranges (only about 1% of articles that dealt with home ranges), especially in the later decade where more focus has been devoted to movement. We encourage researchers to continue providing such results with sufficient sample sizes and robust methodologies, as we still need to fully understand the link between environmental drivers and individual space use while accounting for life-history constraints.

Keywords: ungulate, diet, complementary resource, landscape structure, life history trait, landscape heterogeneity, habitat, body mass.

How the size of a home range responds to environmental changes has been the focus of many empirical studies across taxa (“home range,” singular or plural, returns 12,389 hits as a Topic on *Web of Science* Core Collection by 24 Nov 2020) including many studies on ungulates. Finding the drivers of variation in the sizes of home ranges within a given species across different habitats would indeed allow understanding higher-level processes such as population range expansion and restriction in the context of global changes. The size of an individual’s home range (*sensu* Burt, 1943; i.e., “area traversed by the individual in its normal activities of food gathering, mating, and caring for young”) should adjust to the different components of the environment, as a result of the movements and habitat selection by this individual (Van Moorter et al., 2016). The relationship between the size of a home range and food resources, which corresponds to the habitat productivity hypothesis proposed by Harestad and Bunnell (1979), is expressed as:

$$H = R/P \tag{1}$$

with H the size of the home range, R the overall energy requirements of an individual of a given mass (in kilo-calories [kcal] per day) and P the rate of usable energy (kcal per day per unit area). Nonetheless, this formulation does not account explicitly for resources other than food (e.g., water, shelter), for avoidance of risk of death, or for social interactions. As habitats are heterogeneous (e.g., Wiens, Crawford, and Gosz, 1985), the size of a home range should also depend on the spatial distribution of the amount and quality of resources (Mitchell and Powell, 2004). This was explicitly mentioned by Harestad and Bunnell (1979) but simply as an allometric constraint of large animals forced indirectly to include non-resource habitats within their home range because of the need to forage over large areas to satisfy all energy requirements. With highly dispersed resources, interstitial patches connecting food plots occur in the habitat matrix. This leads to increased exploitation costs for individuals, hence to a need for larger home ranges (Péron, 2019). While a home range with highly dispersed food patches can still be perceived by an individual as being of high quality (Mitchell and Powell, 2008), the expected relationship between classic estimates of the size of a home range (Laver and Kelly, 2008) and resources within the home range would appear negative. Furthermore, not only food resource distribution matters. Animals also face lethal risks (hunting, predation, and vehicle collision) and nonlethal disturbances perceived as risks (human presence in nature for other reasons than hunting; Berger-Tal and Saltz, 2019; Ciuti et al., 2012 that vary in space and time. These lethal and non-lethal risks generate the so-called landscape of fear (Laundré, Hernández, and Altendorf, 2001),

which can lead to changes in the sizes of home ranges through, for instance, the need to include more refuge areas (Powell et al., 1996; Taylor, 1988). Lastly, when habitats ensuring different functions (Camp et al., 2013; Dunning, Danielson, and Pulliam, 1992) are far from each other, home ranges should increase to include all these habitats. Therefore, the habitat productivity hypothesis (Harestad and Bunnell, 1979) which is only based on food resources for a given mass, appears to be too restricted. Within a population, the relationship between the sizes of home ranges and environmental variables should indeed result from the interplay of individual responses to all types of resources and risks and to landscape heterogeneity. Exploring the complexity of these responses has been the goal of modeling and simulation endeavors (Börger, Dalziel, and Fryxell, 2008; Buchmann et al., 2013; Mitchell and Powell, 2004; Moorcroft, Lewis, and Crabtree, 1999), paralleling the upsurge of empirical studies. After five decades of technological improvements (Kays et al., 2015; Wilson, Shepard, and Liebsch, 2008), it is timely to evaluate whether empirical knowledge acquired on a panel of diverse species and environments support hypotheses about the ecological drivers of the size of an individual's home range.

For a given ecological context, the sizes of home ranges should differ among individuals of different species in relation to body mass and life history tactics (Ofstad et al., 2016). Hence, the overall responses of the sizes of home ranges to changes in environmental features across individuals within a population are framed within these species-specific constraints. The main constraints should result from body mass, which determines energy requirements (see, e.g., Robinson, Peters, and Zimmermann, 1983) and the potential distance covered during a unit of time (at least within a taxonomic group), and to life style, which determines resource acquisition (Dobson, 2007). As metabolic rates are hypo-allometrically scaled with body mass, large individuals need less food per mass unit than small ones, so that R in subsection 5.2.3 scales with an allometric exponent of ca. 0.75 (Brody, 1945) and are also less selective in terms of food quality than small ones (Demment and Van Soest, 1985). In addition, as habitat features are independent of species size, the available energy per area does not change with body mass (Jetz et al., 2004) but the rate of acquisition does, which leads P in subsection 5.2.3 to have the dimension of frequency (with an allometric exponent close to -0.25 , e.g., Robinson, Peters, and Zimmermann, 1983). This difference in allometric exponents leads the size of a home range for a given resource requirement to decrease much faster with increasing resource availability in large than in small individuals, and thereby to expect the decrease of the size of an individual's home range with increasing P to be weaker in small than in large species.

Among lifestyle traits that determine resource acquisition, diet is of prime importance (Searle and Shipley, 2008) and strongly influences the sizes of home ranges across mammals (Harestad and Bunnell, 1979; Tucker, Ord, and Rogers, 2014). Ungulates are mostly herbivores with a generalist diet, but they differ in their morpho-physiological characteristics, which cascades into how flexible their diet can be. Codron and Clauss (2010) distinguished species with a "moose-like" rumen, which have a suit of morpho-

physiological features that restrict them to feed on browse material, and species with a “cattle-like” rumen, which allows them to have a more flexible diet. Individuals of species with moose-type rumen should therefore be more sensitive to variation in resource availability than individuals with cattle-type rumen, which have a wider diet niche (Codron and Clauss, 2010). In addition, as browse material represents more sparsely distributed resources (Gordon, 2003; Jarman, 1974), the sizes of home ranges of individuals with moose-type rumen, which are browsers, should be most sensitive to changes in landscape heterogeneity.

Studies performed across species have long pointed out that the sizes of home ranges should also vary with home range overlap among individuals (Jetz et al., 2004; Péron, 2019), and then according to the average group size typical of a species (Damuth, 1981; Mcloughlin, Ferguson, and Messier, 2000). Hence, the size of an individual’s home range for a given resource availability should be larger in group-living individuals than in solitary individuals. In populations with diverse group sizes (a common feature of group-living ungulates; Prox and Farine, 2020), the variation in the number of individuals sharing home ranges should weaken the influence of resource availability on the sizes of home ranges.

One last aspect to consider for identifying the relative roles of resources, landscape heterogeneity, and lethal and non-lethal risk on the sizes of home ranges is the seasonality of the resources, as ungulate populations face a succession of productive and nonproductive seasons. The signature of food resources on the sizes of home ranges should therefore be stronger in the limiting than in the productive season (Volampeno, Masters, and Downs, 2011), even though this effect could be dampened in some species by the ability of individuals to acquire fat reserves during the productive season, allowing them to cope with a limited access to resources during the lean season (Mautz, 1978; Stephenson et al., 2020).

Based on a systematic literature review of the variation in the sizes of individual home ranges at the within-population level in ungulates, we aimed at assessing (1) the empirical support for an impact of the different ecological drivers (resource availability, landscape heterogeneity, and lethal or non-lethal risk) on the size of an individual’s home range and (2) whether the level of support found in the different publications depended on the lifestyle traits (body mass, diet, and social structure) of the species studied. Ungulates occupy all biomes, are central in terrestrial trophic networks (Montgomery et al., 2019), display a large range of both body mass and ecological traits (Fritz and Loison, 2006), and have been the focus of studies on the sizes of home ranges at the individual, population, and species levels since the 1970s (e.g., Dunn and Gipson, 1977; Estes, 1974; Jarman, 1974; McNab, 1963; Owen-Smith, 1977). Thus, ungulate home ranges have been studied by direct observation for decades and by the use of telemetry from the early days of its development for wildlife (e.g., Dunn and Gipson, 1977). Collars with VHF and now GPS and biologgers (Kays et al., 2015) have been deployed on an ever-growing number of species, providing a rich literature on the sizes of home ranges (for interspecific overviews, see, e.g., Mysterud, Pérez-Barbería, and Gordon, 2001;

Ofstad et al., 2016). Yet, to map the determinants of the sizes of home ranges among individuals across species, methodological questions arise about how the sizes of home ranges are estimated from location data, and how environmental variables are measured (Nilsen, Herfindal, and Linnell, 2005). These are not trivial issues as attested by the substantial literature focusing on the meaning and definition of a home range (Fieberg and Börger, 2012; Kie et al., 2010; Péron, 2019; Powell and Mitchell, 2012), as well as on statistical methods to estimate not only the sizes of home ranges (Börger et al., 2006b; Kie et al., 2010; Noonan et al., 2019; Péron, 2019) but also resource availability (from the field, Flombaum and Sala, 2007; Redjadj et al., 2012; or remotely, Garrouste, Hansen, and Lawrence, 2016; Pettorelli et al., 2005; Pettorelli et al., 2006; and more specifically, the edible portion of the biomass, Duparc et al., 2020) and landscape heterogeneity (Sundell-Turner and Rodewald, 2008).

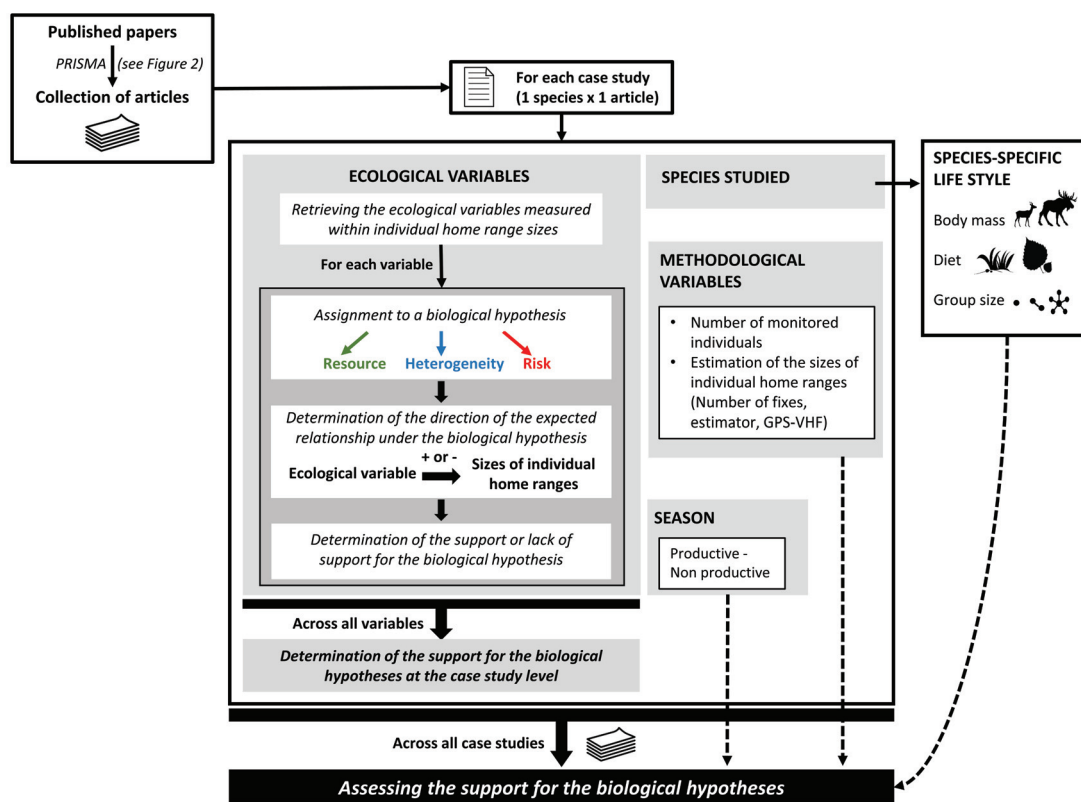


FIGURE 3.1: Schematic summary of the methodological framework. We tested biological hypotheses derived from a review of the empirical literature regarding (1) the ecological drivers of the sizes of individual home ranges (resource, landscape heterogeneity, and risk) and how (2) species-specific lifestyle traits (body mass, group size, and diet) and (3) seasonal resource variation (productive vs. non-productive season) impact the level of support to each hypothesis, while taking into account methodological variables. Each article was assessed to determine whether the relationship between the sizes of individuals' home ranges and the ecological metrics were consistent with hypotheses about the ecological drivers. The results in the article were considered supporting the hypothesis concerning ecological drivers if at least one metric was retained. The probability to support a hypothesis was evaluated using the data collected across all case studies from the review. Pictograms downloaded from <http://www.phylopic.org> or from the personal collection of authors.

In the midst of these ecological and methodological challenges, we reviewed the empirical support for the impact of three main ecological drivers (resources, landscape

heterogeneity, and risks), on the variation in the sizes of individual home ranges, accounting for article-specific confounding methodological variables (sample size, positioning system, number of locations, number of metrics considered, home range estimator). Comparing the results across all articles, we then tested whether the effect of resources on the sizes of home ranges was supported more pervasively during the productive than during the non-productive season. Furthermore, we checked whether lifestyle traits such as body mass, group size and diet explained the level of support to the ecological hypotheses found in published articles (Figure 3.1). After mapping the state of our knowledge after five decades of upsurge in the number of studies on the sizes of home ranges in ungulates, and in times when new technologies revolutionize the fine-scale monitoring of animal movement and behavior (Kays et al., 2015; Wilson, Shepard, and Liebsch, 2008), we identify the remaining challenges and raise guidelines for future studies.

3.2 Material and methods

3.2.1 Literature survey

We conducted the literature survey using the Web of Science Core Collection, and then applied the PRISMA procedure (Liberati et al., 2009; Figure 3.2) to select a collection of comparable papers (Figure 3.1). We used the following keywords (“home range” OR “range use” OR “spatial distribution” OR “space use” OR “spatial variation” OR “area use” OR “habitat use” OR “ranging behavior”) AND (“ungulate*” OR “herbivore*” OR “mammal*” OR “deer” OR “chamois” OR “ibex” OR “mouflon” OR “bison” OR “capreolus”) and obtained a total of 7,454 articles (Figure 3.2). We deliberately added a few names of species as keywords to incorporate older studies, which usually used the name of species in titles or keywords instead of broader taxonomic (e.g., ungulates) or ecological (e.g., herbivores) terms. We restricted the results of our search to the topics Ecology, Zoology, Environmental, and Behavioral sciences. The survey included articles published up to October 2019.

Our selection followed three steps (Figure 3.2). We first retained for further consideration only articles for which data on the sizes of home ranges were provided for ungulates and at the population level. We restricted our review to herbivorous ungulates, hence removing articles on the wild boar (*Sus scrofa*), an omnivorous species, but included articles on elephant (*Loxodonta africana*), which is an herbivorous sub-ungulate. This led us to keep 216 articles out of the 7,454. Second, we retained only articles providing a continuous relationship between the sizes of individual home ranges and an independent ecological metric measured at the individual home range level. This led us to remove 165 and retain 53 articles. Two of the discarded articles (Börger et al., 2006a on roe deer *Capreolus capreolus*, and Brook, 2010 on elk *Cervus canadensis*) provided the sizes of home ranges for individuals assigned *a priori* to habitat categories defined by their dominant vegetation type, which were synthetic proxies of differences in all ecological drivers (resource, landscape heterogeneity, risk). We could therefore

not derive results concerning the relationship between the size of an individual's home range and an ecological metric of resource, landscape heterogeneity or risk from these articles that would compare with the other retained articles. Third, we considered only articles that provided the sizes of seasonal home ranges to test the hypothesis that the expected effect of resources on the sizes of individual home ranges should get more support during the non-productive than during the productive season. Although we recognize that there are several meanings and definitions of home range in the literature (see [Introduction](#)), here we have had to accept by default the definition adopted by the authors in each of the selected studies.

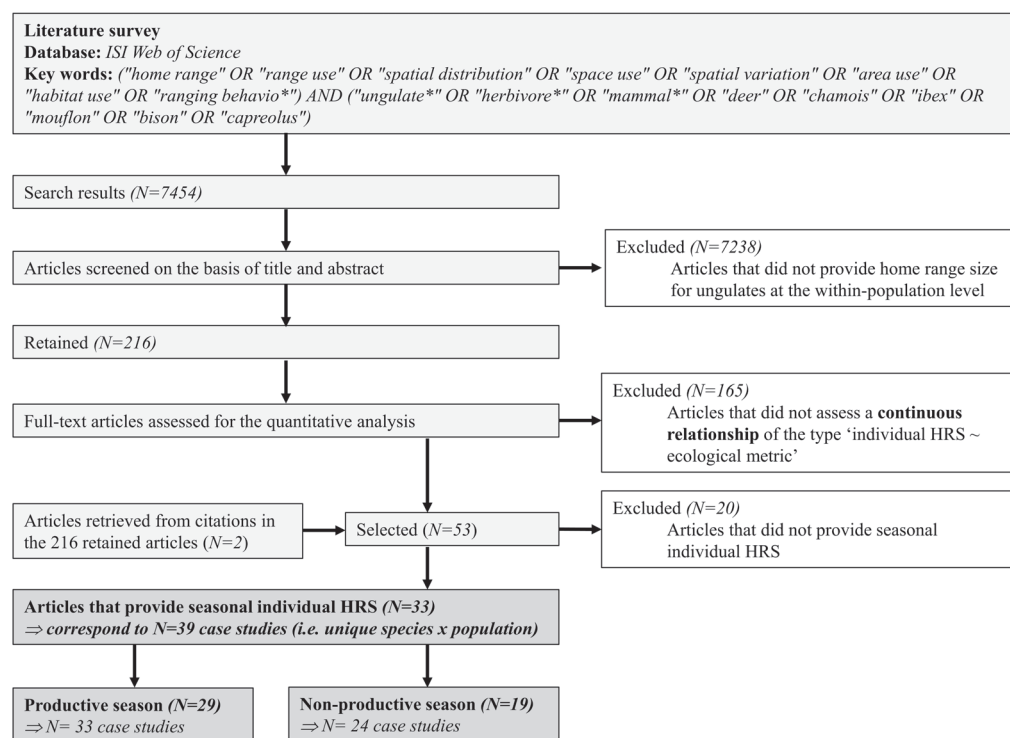


FIGURE 3.2: PRISMA flow diagram, according to the PRISMA statement by Liberati et al. (2009) and recommended by Nakagawa and Poulin (2012).

3.2.2 Literature analysis and retrieval of article and species metadata

For each retained article, we started by recording the basic information required to identify each article (i.e., title, first author, year of publication, journal), the species studied and study sites. When an article considered several species or several study sites, we split it accordingly, as our unit of interest for retrieving the environmental-to-home range relationship was the species-specific population. Then, we called a “case-study” each unique species-population, which became our unit of study. We retrieved data related to animal sampling (sample size, age, and sex), duration and period of monitoring (e.g., all year round, during which season) ([Table 3.1](#)). We also recorded information about the location data: type of collars used (VHF or GPS) and number of fixes used per

TABLE 3.1: Information on the 33 selected papers (productive and non-productive seasons).

References	Study duration (year)	Comment	n	Species	Sex	Resource	Risk	Landscape heterogeneity
Anderson et al. (2005)	4	Population	10	Elk	Female	×		
Anderson et al. (2005)	4	Population	32	Elk	Female	×		
Anderson et al. (2005)	4	Population	57	Elk	Female	×		
Bartlam-Brooks et al. (2013)	1		14	Zebra	Female	×		×
Bender et al. (2007)	2		40	Mule deer	Female	×		
Bevanda et al. (2015)	8	Species	32	Red deer	Combined	×		
Bevanda et al. (2015)	6	Species	40	Roe deer	Combined	×		×
Bjørneraas et al. (2012)	2	Sex	108	Moose	Female	×		
Bjørneraas et al. (2012)	2	Sex	108	Moose	Male	×		
Brashares and Arcese (2002)	0.5		161	Oribi	Female	×		
Hansen et al. (2009b)	2		29	Svalbard reindeer	Female	×		
Hansen et al. (2009a)	2		26	Svalbard reindeer	Female	×		
Daleszczyk et al. (2007)	11	Population	9	European bison	Combined	×		
Daleszczyk et al. (2007)	11	Population	25	European bison	Combined	×		
de Beer and van Aarde (2008)	2	Population	6	African bush elephant	Female		×	×
de Beer and van Aarde (2008)	2	Population	4	African bush elephant	Female		×	×
de Beer and van Aarde (2008)	2	Population	4	African bush elephant	Female			×
Dussault et al. (2005a)	2		8	Moose	Combined	×		
Grainger et al. (2005)	21	Sex	7	African bush elephant	Male	×		×
Grainger et al. (2005)	21	Sex	8	African bush elephant	Female	×		×
Grignolio et al. (2003)	2		14	Alpine ibex	Male	×		
Kilpatrick et al. (2011)	2		56	White-tailed deer	Female	×	×	×
Lamberti et al. (2006)	1	Sex	4	Roe deer	Female	×		
Lamberti et al. (2006)	1	Sex	9	Roe deer	Combined	×		
Lamberti et al. (2006)	1	Sex	5	Roe deer	Male	×		
Laurian et al. (2008)	3		47	Moose	Combined	×		
Leach and Edge (1994)	2		13	White-tailed deer	Female	×		
Massé and Côté (2012)	5	Season	19	White-tailed deer	Female	×		×
Massé and Côté (2012)	5	Season	13	White-tailed deer	Female	×		×
Moe and Wegge (1994)	2		10	Axis deer	Female	×		
Morellet et al. (2013)	1.5-8		190	Roe deer	Female	×		
Naidoo et al. (2012)	3		31	African buffalo	Combined	×	×	
Nicholson et al. (1997)	3		43	Mule deer	Combined	×	×	
Quinn et al. (2013)	2	Season/sex	32	White-tailed deer	Female			×
Quinn et al. (2013)	2	Season/sex	15	White-tailed deer	Male			×
Quinn et al. (2013)	2	Season/sex	33	White-tailed deer	Female			×
Quinn et al. (2013)	2	Season/sex	17	White-tailed deer	Male			×
Rivrud et al. (2010)	3		47	Red deer	Female	×		
Saïd and Servanty (2005)	2		24	Roe deer	Female			×
Saïd et al. (2005)	2		37	Roe deer	Female	×		
Scillitani et al. (2012)	6		28	Alpine ibex	Male	×		
Tufto et al. (1996)	5		35	Roe deer	Female	×		
van Beest et al. (2011)	2		24	Moose	Female	×		
Vercauteren and Hygnstrom (1998)	3		30	White-tailed deer	Female	×		
Viana et al. (2018)	3		18	Iberian ibex	Combined	×		
Walter et al. (2009)	7		257	White-tailed deer	Female	×	×	×
Widmer et al. (2004)	2		6	Roe deer	Female	×		

The column "comment" indicates the study of several populations. The last three columns indicate the category of variables (resource, landscape heterogeneity, and risk) tested in each paper (see Figure 3.1).

animal to estimate the size of its home range. Then, we classified each paper according to the method used to estimate the sizes of home ranges (Minimum Convex Polygon [MCP], Kernel Density Estimation [KDE], Local Convex Hull [LoCoH], Harmonic Mean [HM], and Brownian Bridge [BB]), thereafter regrouped into three classes: MCP, KDE *vs.* other methods for further analysis. We also classified papers according to time frame (i.e., day, week, month, season, or year), and spatial scale in terms of isopleths (e.g., 50 or 90% of utilization distribution). We discarded estimates at a time frame lower than one month, because the ecological meaning of very short-term home ranges is debatable (Péron, 2019), and at annual time frame because we were interested in testing the impact of seasonal variation in resources on the support for ecological drivers. It is worth noting that the few articles estimating the sizes of home ranges at the daily or weekly levels also provided estimates at a longer time frame, so we did not discard any case study for this reason. We did not retain sizes of home ranges estimated with <70% of locations.

As a second step, we listed all the ecological variables studied in a case study. For each of these variables, we retrieved the unit of measurement, the spatial scale at which it was estimated (e.g., at the home range scale or in a buffer around the home range), and whether it was log-transformed before being included in the analyses. Indeed, the relationship between the sizes of home ranges and productivity becomes linear only when both of them are log-transformed (subsection 5.2.3). We faced a huge diversity of metrics (Supplementary Table S3.1), which we classified as measures of resource, landscape heterogeneity, or risk (Figure 3.1; Supplementary Table S3.1). We then counted the number of metrics for a given category of variables (resource, landscape heterogeneity, risk) and a given season (productive and non-productive season) studied per case study. We did not consider the following metrics: index of snow severity (Ramanzin, Sturaro, and Zanon, 2007), snow cover (Grignolio et al., 2003), snow depth (Scillitani et al., 2012; van Beest et al., 2011), elevation (Bevanda et al., 2015; Hansen et al., 2009a), and slope (Anderson et al., 2005), since these factors were only relevant to some specific environments (e.g., mountainous and arctic regions). Based on the species' ecology and information given in each article, we associated each metric to the expected slope direction of its relationship with the sizes of home ranges: increase, i.e., positive effect size, or decrease, i.e., negative effect size. For example, to be in line with the resource hypothesis, we expected a negative relationship between the sizes of individual home ranges and resource metrics reflecting good quality forage (e.g., grass nitrogen content, Brashares and Arcese, 2002), but a negative relationship when resource metrics were related to poor-quality forage (e.g., fiber content, Brashares and Arcese, 2002).

As a third step, we retrieved species-specific traits from the literature, such as adult body mass for both sexes, type of physio-digestive system (moose-type *vs.* cattle-type), sociality level, and phylogenetic information (see Table 3.2). We did not use phylogenetic information in our models due to the low number of species (15 species) finally retrieved in our sample (see Results section 3.3). For ranking species on the generalist-specialist gradient, we used the type of physio-digestive system (moose-type *vs.* cattle-type), as proposed by Codron and Clauss (2010). For the social structure, we classified species as living in small groups (solitary to small groups up to five individuals) and in large groups (six or more), following the classification proposed by Prox and Farine (2020).

3.2.3 Extraction of results

In the retained articles, independent variables were considered to influence the sizes of home ranges either based on an information theory approach (usually comparing models with an information criterion, such as Akaike Information Criterion [AIC]) or by inferential procedures based on statistical tests and *p*-values. Retrieving standardized effect sizes required for a meta-analysis was not possible because independent variables were mostly included in multi-variable models, were not systematically scaled or log-transformed, and statistics needed to calculate effect sizes were not all (or not at all) provided in the article (especially for variables found to have no statistically significant effect or that were not included in the best models). Consequently, we summarized the

TABLE 3.2: Characteristics of the species included in the 33 selected papers (productive and non-productive seasons).

Species	Latin name	♀BM (kg)	♂BM (kg)	Group size	Habitat	Diet
Moose	<i>Alces alces</i>	440	320	4	Boreal and mixed forest	Moose-type
Axis deer	<i>Axis axis</i>	80	55	25	Grassland forest	Cattle-type
European bison	<i>Bison bonasus</i>	710	420	20	Mixed forests	Cattle-type
Ibex	<i>Capra ibex</i>	95	45	11	Alpine grassland	Cattle-type
Iberian ibex	<i>Capra pyrenaica</i>	70	35	7	Shrubland areas	Cattle-type
Roe deer	<i>Capreolus capreolus</i>	28	26	2	Mixed	Moose-type
Elk	<i>Cervus canadensis</i>	312	238	4	Grassland	Cattle-type
Red deer	<i>Cervus elaphus</i>	163	107	6	Mixed	Cattle-type
Zebra*	<i>Equus burchelli</i>	280	190	10	Grassland-savannah	Cattle-type
African bush elephant*	<i>Loxodonta africana</i>	8000	3700	12	Dry wood/shrublands	Moose-type
Mule deer	<i>Odocoileus hemionus</i>	80	50	3	Mixed	Moose-type
White-tailed deer	<i>Odocoileus virginianus</i>	72	48	3	Mixed	Moose-type
Oribi	<i>Ourebia ourebi</i>	14	13	2	Mixed	Cattle-type
Svalbard reindeer	<i>Rangifer tarandus</i>	136	88	6	Open taiga	Cattle-type
African buffalo	<i>Syncerus caffer</i>	700	500	30	Savannas	Cattle-type

Species are ranked by Latin name. See Supplementary Table S3.2 for references. *These two species are not ruminants, and therefore should not be classified following the “moose-type” and “cattle-type” typology of Codron and Clauss (2010). Nevertheless, the respective diets of these species, grazer for zebra and mixed-feeder for elephant, correspond to the use of resources of moose-type and cattle-type species, respectively, while with strong physiological differences (McNaughton and Georgiadis, 1986).

results in a categorical way instead of reporting the estimated values of effect sizes (i.e., slopes and standard errors). For each metric (Figure 3.1), we recorded, whether the analyses reported in the article supported our biological hypotheses regarding resource, landscape heterogeneity, or risk, i.e., whether the relationship between the sizes of home ranges and the ecological variable was in the same direction as expected, in the opposite direction, or not retained. For independent variables without detectable effect or not included in the selected model, we sought whether the slope was nevertheless in the expected direction, or opposite to the expected direction, when given. Therefore, we ended up with variables assigned to five different result categories: “as expected and detected or retained in the best models”, “as expected and not detected or not retained in the best model”, “opposite and detected or retained in the best model”, “opposite and not detected or not retained in the best model”, or “direction unknown and not detected or not retained in the best model”. The distribution of the five different categories of results is provided in Supplementary Figure S3.1. For the rest of our analyses, we classified the result of each metric as being supporting or not supporting the biological hypothesis it was assigned to (Figure 3.1). Importantly, we considered that a biological hypothesis was supported in a case study if at least one of its metrics was supporting the given biological hypothesis, independently of the number of metrics tested. We are aware that a statistical hypothesis can only be rejected or not rejected, but for greater clarity throughout the manuscript, we use the terms “supporting” the biological and ecological hypotheses tested for “rejecting” the null statistical hypothesis, and “not supporting” the biological and ecological hypotheses tested for “not rejecting” the null statistical hypothesis.

3.2.4 Descriptive and statistical analysis

We performed an in-depth analysis of the probability for a study to support each of the biological hypotheses. Using generalized linear models (GLMs), we first tested whether methodological co-variables influenced the probability of support for a given biological hypothesis, considered as a binomial response variable (Figure 3.1). The methodological variables tested were sample size (for a given expected effect size, large sample size should positively influence the likelihood to detect a relationship), the number of variables studied (the larger the number of variables considered, the more likely one would be retained), and all technical aspects expected to increase the accuracy of estimates of the sizes of individual home ranges (number of re-locations; positioning system, VHF *vs.* GPS; statistical method used to estimate the sizes of home ranges). We then assessed if the level of support for a biological hypothesis differed for resource, landscape heterogeneity, or risk and whether it was more important for resource during the non-productive season than during the productive season. Note that due to the few case studies focusing on risk (and none on risk only), we did not include this category in models, hence we were not able to assess the level of empirical support for our hypothesis that individual exposure to risk should affect the sizes of individual home ranges. We included a two-way interaction between the ecological driver (resource and landscape heterogeneity) and the number of metrics tested, as this number was generally higher for landscape heterogeneity. We compared models accounting for methodological variables using the Akaike Information Criterion and selected the model with the lowest AIC value.

Then, we assessed whether the lifestyle variables (Figure 3.1) could influence the level of support to each ecological driver: body mass (expecting an increased support with increasing body mass), diet (expecting a stronger support for species with moose-type digestive features), and social structure (expecting a reduced support in large group-living species).

We fitted GLMs with a binomial distributed error structure and a *logit* link function, using the *glm* function implemented in the package *stats* of R 3.3.3 (Team, 2017). We ranked candidate models using the Akaike Information Criterion for small sample sizes (AICc) as implemented in the R package *AICcmodavg* (Mazerolle, 2020) and calculated $\Delta AICc$ and $\Delta AICc$ weights. Models with $\Delta AICc \leq 2$ were considered equivalent (Burnham and Anderson, 2002), and when models had a $\Delta AICc \leq 2$, we kept the most parsimonious one. Results are depicted using the *sjPlot* (Lüdtke, 2019) and *visreg* (Breheny and Burchett, 2017) R-packages.

3.3 Results

3.3.1 Studies and species

We retained 33 articles, published in 26 different scientific journals that met our two first criteria of selection (Figure 3.2), covering both the productive (29 articles) and non-productive (19 articles) seasons. Most studies were published during the early

2000-2010, with a noticeable decrease post-2013 (Figure 3.3A). Fifteen species were studied during at least one of the productive and non-productive seasons (Figure 3.3B). These species belong mostly to the order Artiodactyla, and are essentially members of the families Bovidae (five species) and Cervidae (eight species). The remaining two species belong to the Equidae (*Equus burchelli*) and Elephantidae (*Loxodonta africana*) (Figure 3.3B). Among these species, some have been studied more than others, as 19 of the 33 articles (57%) focused on only three species: roe deer *Capreolus capreolus* (eight articles), white-tailed deer *Odocoileus virginianus* (seven articles), and moose *Alces alces* (four articles). Individuals from different species were contrasted in terms of body mass, group size, habitat, and percentage of grass in the diet (mean = 45.9 ± 29.5): six species were classified as having individuals forming low group sizes and nine as having highly social individuals (Table 3.2).

Almost all studies have been conducted in North America ($N = 10$) and Europe ($N = 17$), with only five studies located in Southern Africa (Figure 3.3C). We retrieved only one study conducted in Asia (axis deer *Axis axis* in Nepal, (Moe and Wegge, 1994)). Among the 33 retained articles, three included several populations of the same species (Anderson et al., 2005; Daleszczyk et al., 2007; de Beer and van Aarde, 2008) and one article studied two species (Bevanda et al., 2015). Overall, this led to 39 independent case studies (Table 3.1).

3.3.2 Telemetry and estimators of the sizes of home ranges

Animal locations were obtained either by GPS or VHF positioning system. Before 2000, all studies used VHF collars (Figure 3.4A). GPS collars came into use in 2000 and dominated until after 2010 (Figure 3.4A). Before 2000 (five case studies), MCP dominated, and two methods (KDE and Harmonic Mean method as the only “other methods”) were used equivalently (Figure 3.4B). During the 2001–2010 (23 case studies), KDE took over MCP, with 63% of articles using KDE. Since 2011 (11 case studies), methods used have diversified, leading to a decrease in the occurrence of MCP and KDE. The increased use of other methods in the later years corresponded to the development of alternative home range estimators such as LoCoH or Brownian Bridge methods. Twenty five case studies (65%) were based on <20 marked animals, while only six case studies (15%) had sample sizes above 50 (Figure 3.4C). The number of relocations used to estimate the sizes of home ranges also revealed a strong variability among the 39 case studies (Figure 3.4D). On average, about 852 locations per month were used to compute the sizes of home ranges, but with a wide range, with minimum and maximum numbers of locations being six and 5,040 locations, respectively.

3.3.3 Descriptive summary of studied variables

Most case studies focused on variables related to “resource” ($N = 34$), followed by “landscape heterogeneity” ($N = 12$) and lethal or non-lethal “risk” ($N = 6$; Figure 3.5A). No case study focused solely on lethal or non-lethal risk, and this factor was always tested in conjunction with one of the other two categories of variables or with both of

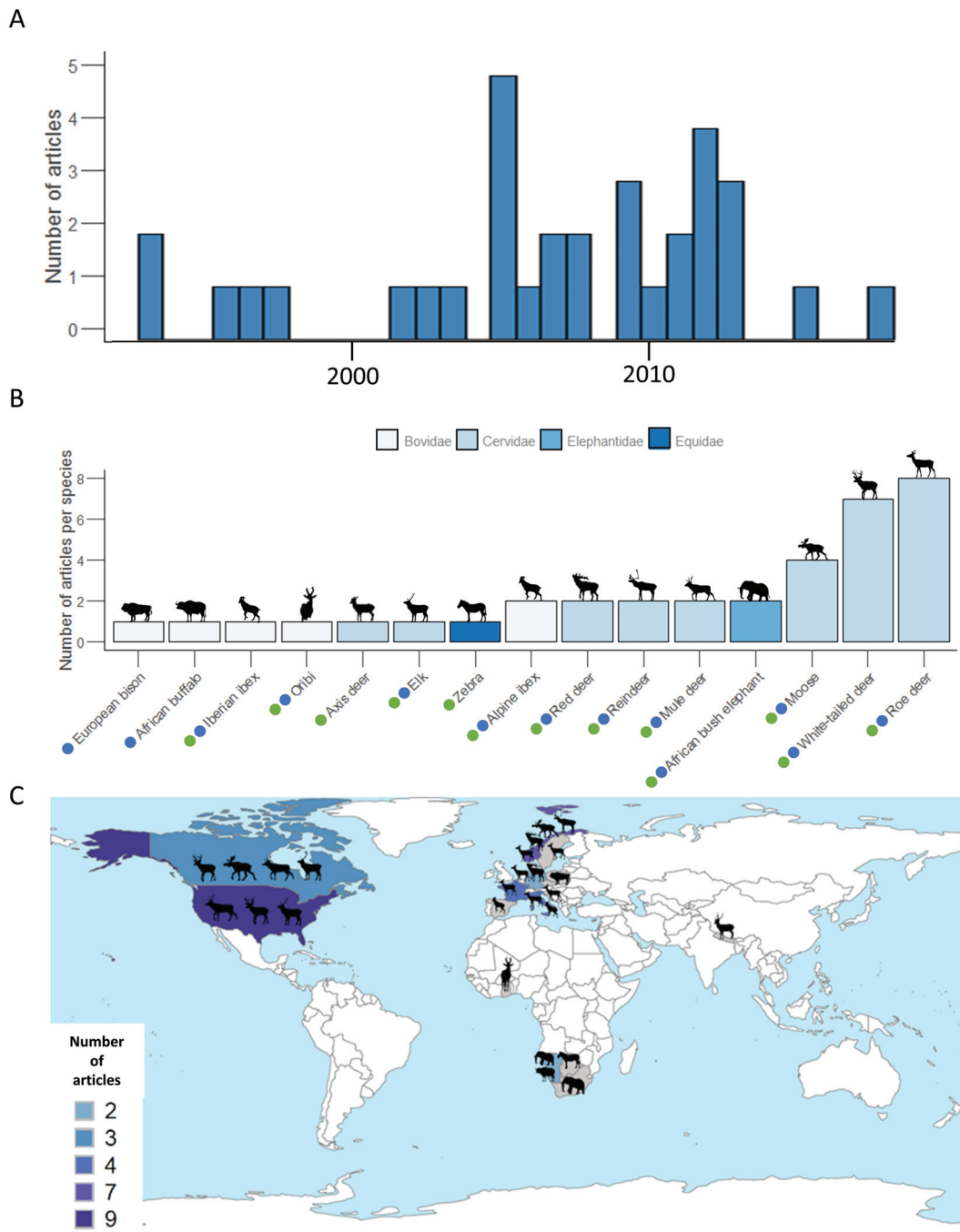


FIGURE 3.3: (A) Number of articles published each year. (B) Number of articles per species. Dots depict species for which we were able to retrieve information on seasonal relationships between the sizes of home ranges and biomass of vegetation during the productive (green dots) and non-productive (blue dots) periods and retained in the final comparative analysis (see PRISMA; Figure 3.2). (C) Map of the countries where studies took place. Numbers of publications per country are indicated by different colors.

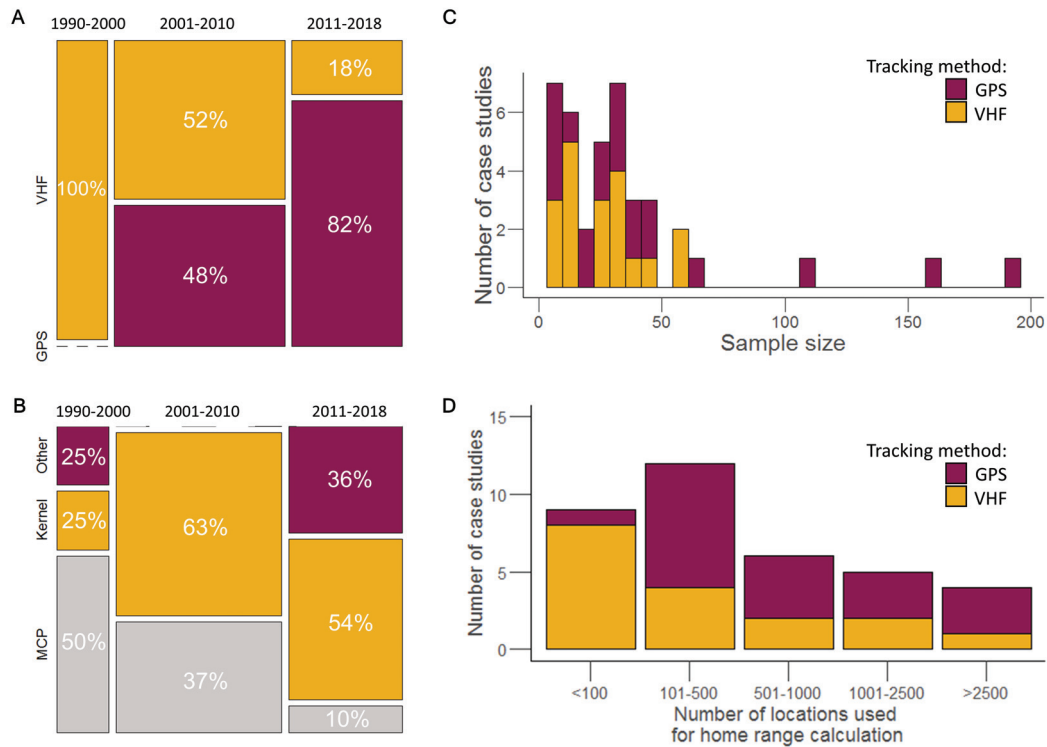


FIGURE 3.4: (A) Evolution of tracking methods used in the 33 selected articles (GPS, VHF) according to a 10-year time period. The width of the bars corresponds to the percentage of articles by time period. The percentages given in the bars represent the percentage of articles with data collected with GPS vs. VHF per time period. (B) Evolution of home range estimators used in the 33 articles according to time period. The percentages correspond to the proportions of articles per time period for each home range estimator. (C) Distribution of the number of individuals per case study ($N = 39$) according to tracking method. (D) Distribution of the number of locations used for home range calculation in the 39 case studies according to the tracking method.

them. All variables considered as metrics of risk by the authors were distance or density of linear features (e.g., road) (Supplementary Table S3.1). The majority of case studies investigated the effect of several independent variables on the sizes of home ranges with on average 2.6 relationships tested per case study for resource (range: 1–12), 7.8 for landscape heterogeneity (range: 1–12), and 1.3 for risk (range: 1–3) (Figure 3.5B). As too few studies assessed the influence of lethal or non-lethal risk, this ecological driver was excluded from the analyses. We retrieved 123 slopes characterizing the link between the sizes of home ranges and resource, 152 for the category of landscape heterogeneity variables, and eight for risk metrics. Only 15 papers out of the 33 log-transformed the sizes of home ranges.

The results at the metric level supported one of the biological hypotheses and were detected or retained for 37% of the metrics across all studies, whereas they were opposite to the initial expectation and detected or retained for 13% of the metrics (Supplementary Figure S3.1). Not detected or not retained metrics were reported for 50% of the metrics (16% were consistent and 16% opposite to the direction expected under the biological hypotheses and finally 18% were unknown, Supplementary Figure S3.1).

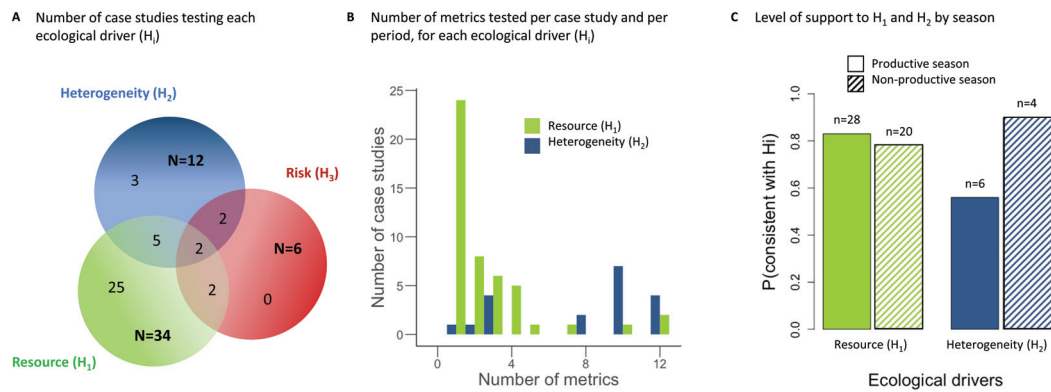


FIGURE 3.5: (A) Venn diagrams for the number of case studies testing a relationship between the sizes of home ranges and resource, landscape heterogeneity or risk indices, and combinations of these. (B) Number of metrics tested per case study, per period, and for each ecological driver. (C) Proportion of case studies that contained at least one metric supporting the biological hypothesis, for each ecological driver and season.

3.3.4 Methodological co-variables and seasonal variation influencing papers' results

Eighty percent of the 33 case studies focusing on resource metrics (28 in the productive season and 20 in the non-productive seasons) concluded that the habitat productivity hypothesis was supported (i.e., at least one variable tested supported the expected impact of resources on the sizes of home ranges). This percentage was 73% for the 12 case studies studying landscape heterogeneity (nine in the productive season, and 10 in the non-productive season; Figure 3.5C).

The probability for a case study to support the biological hypotheses increased with sample size ($\beta = 0.23 \pm 0.30$, log scale; Figure 3.6A) and was influenced by the two-way interaction between the number of metrics and the biological hypothesis considered ($\beta = 1.21 \pm 0.52$ for resource, $\beta = -0.07 \pm 2.02$ for landscape heterogeneity; Figure 3.6B) and by the positioning system ($\beta_{VHF \text{ vs. } GPS} = 1.51 \pm 1.27$; Figure 3.6C and see Supplementary Table S3.3 for details). Neither the number of locations per individual nor the estimation method of the sizes of home ranges (KDE, MCP, and others) was retained in the best models (all $\Delta AICc > 2$; see Supplementary Table S3.3). When looking at the prediction from the best model, the percentage of studies supporting the expected relationship between the sizes of home ranges and resources were close to 100%, when animals were monitored by VHF or by GPS (mostly from papers after 2010, Figure 3.4), as long as enough resource metrics (roughly > 4) were measured (Figure 3.6B). Landscape heterogeneity influenced the sizes of home ranges in about 96% of studies based on individuals monitored by VHF but in only about 75% for individuals monitored by GPS, whatever the number of studied metrics. Neither the season nor the interaction between season and category of variables were retained in the best model for resources (Supplementary Table S3.3).

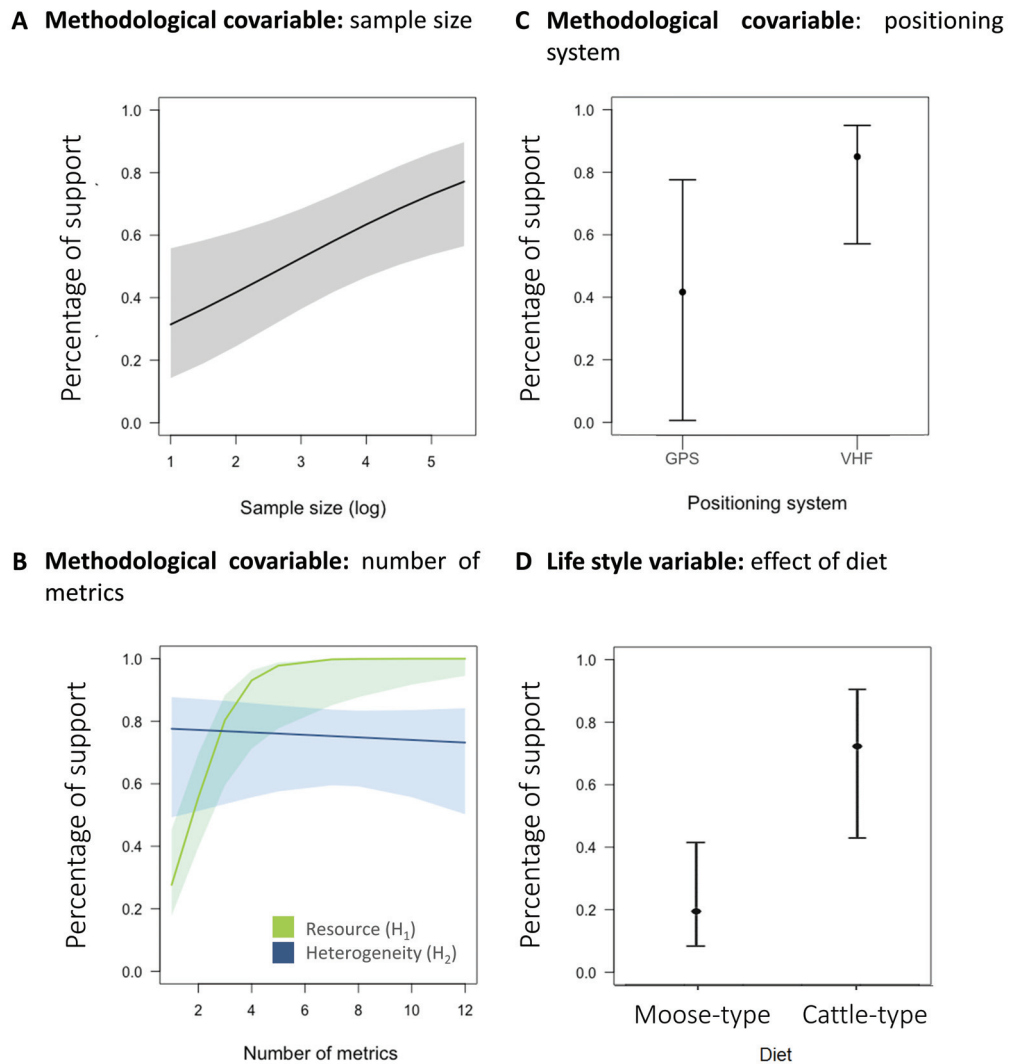


FIGURE 3.6: Effect of (A) the sample size (log-transformed; if the positioning system was GPS, the season was the non-productive season, the number of metrics was 4.07 and the ecological driver was the resource one); (B) the number of metrics tested (if the sample size was 3.06 [log-transformed], the positioning system was GPS and the season was the non-productive season) on the probability to have at least one metric supporting the biological hypotheses. These results correspond to the model that explains the probability of support for each hypothesis according to the different methodological features accounted for differences among case studies. (C) Effect of the positioning system (if the season was the non-productive one, the number of metrics was 4.07, the ecological driver was the resource one, and the sample size was 3.07 [log-transformed]). (D) Effect of diet (if the positioning system was GPS, the sample size was 3.18 [log-transformed] and the season was the non-productive season) on the probability to have at least one metric supporting biological hypothesis. This model was performed on a subset of our sample with the resource hypothesis only and the case studies studying the two seasons. The response variable for the four panels is binomial, whereby 0 means that the authors concluded that their hypothesis was not supported, and one otherwise (see Figure 3.1). The shades in (A and B) represent the 95% confidence interval.

3.3.5 Influence of species-specific life history traits on findings

We added body mass (log-transformed), group size, and diet to the baseline model selected above to test for the life style-related hypotheses (Figure 3.1). Body mass, group size, and diet did not affect the level of support for the biological hypothesis in models where both resources and landscape heterogeneity were considered together (Supplementary Table S3.4). Only the variables of the baseline model (i.e., sample size, positioning system, and the two-way interaction between the number of metrics and the ecological driver) were retained.

We then focused on the metrics from the resource category only to test more specifically the resource hypothesis and whether the support for the resource hypothesis was larger in species with a moose-type than a cattle-type rumen (model selection table in Supplementary Table S3.5). We actually found the opposite, as the support to the resource hypothesis was larger for species with a cattle-type rumen ($\beta = 0.81 \pm 0.62$; Figure 3.6D) than for moose-type ($\beta = -1.48 \pm 0.43$).

3.4 Discussion

3.4.1 More support to the resource than to the landscape heterogeneity hypothesis

The size of an individual's home range should vary according to a triptych of factors composed by resources, landscape heterogeneity, and risk (Bonnot et al., 2013; Creel, Schuette, and Christianson, 2014; Desy, Batzli, and Liu, 1990; Haskell, Ritchie, and Olf, 2002; Kittle et al., 2008). Assessing the level of support to each of these drivers of variation in the sizes of individual home ranges from a literature review has however proven more challenging than we had anticipated, for many reasons. First, a dearth of studies provided exploitable results on the variation of the sizes of home ranges with ecological drivers (<1%). Second, methodological issues included the rampant debate on how to estimate both the sizes of home ranges and independent metrics, issues which are far from trivial. Third, the limited number of species studied and the limited geographic distribution of study sites, tied with the methodological concerns, are hurdles in our ability to test whether species-specific lifestyles explain the different sensitivity of individuals from each species to the main ecological drivers.

3.4.2 Study design and statistical considerations

Resource metrics, especially food resources, have been studied more than metrics of landscape heterogeneity (Figure 3.5A). The majority of articles found that the sizes of individual home ranges were decreasing with increasing amounts of resources (Figure 3.5C), supporting the Habitat Productivity Hypothesis. On the other hand, support for the effect of landscape heterogeneity on the sizes of home ranges was more limited (Figure 3.5C). Landscape heterogeneity includes several components (local diversity, landscape complementarity, or landscape-level fragmentation; Dunning,

Danielson, and Pulliam, 1992), each of which should be measured explicitly (Turner, 2005). The lower proportion of papers supporting that landscape heterogeneity affects the sizes of home ranges may therefore result from the difficulty to identify and measure the proper metric and scale at which it should be measured (Bevanda et al., 2015).

Sample size and the problem of statistical power

Articles were more likely to support the biological hypotheses when the studies included a large number of animals (Figure 3.6A), due to a higher statistical power (Steidl, Hayes, and Schaubert, 1997). Interestingly, the effect size linking environmental variables and the sizes of home ranges varied with life history traits (Figure 3.6D). Authors should therefore anticipate the statistical power of their study accounting for the biology of individuals of the studied species and their life history, to enhance the probability of finding an effect. Biological conclusions based on small samples should not be over-interpreted to avoid erroneous conclusions (Steidl, Hayes, and Schaubert, 1997). Fortunately, as the cost of telemetry collars are decreasing, we can expect the number of animals per study to increase for a given budget.

Technological improvements and estimates of the sizes of home ranges

The technology to monitor individuals has greatly improved during the last 30 years (Kays et al., 2015) and, accordingly, the publications after 2010 rely mostly on GPS-collared individuals. GPS collars are more expensive than VHF collars but provide a larger number of predetermined fixes, which should ensure a better delimitation and estimation of the size of a home range (Kie et al., 2010; Laver and Kelly, 2008; Pellerin, Saïd, and Gaillard, 2008). Yet, studies relying on GPS collars supported biological hypotheses to a lower extent than studies where animals were VHF collared. A tendency to publish non-significant results to a greater extent in more recent years might account for this surprising result. In parallel to the change in technology, methods to estimate the sizes of home ranges have shifted from MCP to a large range of methods, which undermines the comparison and repeatability of studies (Laver and Kelly, 2008). While we did not detect any effect of the estimation method, the low number of case studies prevented us from testing for all interactions, leading us to interpret this finding with caution. Recent articles studying habitat selection or animal movements tend to skip providing the sizes of home ranges, focusing on smaller spatial scale movement behavior. This probably explains why, despite recent evaluation of the robustness of estimators of the sizes of home ranges (e.g., Noonan et al., 2019), we have retrieved fewer articles and data over the last few decades than we had hoped.

Environmental variables: Their number, measurement, and meaning

The large diversity of metrics used to measure resource availability and landscape heterogeneity, as well as the restricted number of variables assessing risk, were problematic (Supplementary Table S3.1). The few risk-related metrics interpreted by the

authors to be risky were mostly landscape features (see [Table 3.1](#)) and almost no studies fitted our selection criteria for evaluating individual exposure to natural predation or hunting risks ([Figure 3.1](#)). The complexity to evaluate risk metrics at the individual level renders empirical studies of the possible effect of both lethal and non-lethal risk on the sizes of individual home ranges particularly challenging.

The proportion of relationships supporting biological hypotheses was quite low: 52% with resource metrics and only 21% with landscape heterogeneity metrics ([Supplementary Figure S3.2](#)). Quantifying resources that are edible for ungulates is tricky as it requires information on individual energetic requirements and nutritional state, diet, and diet selection ([Duparc et al., 2020](#)). Metrics used to measure these factors, derived from remote sensing, field measurements, and proportion of rich or poor habitat available, are often quite crude ([Pettorelli, 2013](#)), far from the species-specific foodscape (*sensu* [Duparc et al., 2020](#); [Searle, Hobbs, and Gordon, 2007](#)). Likewise, the fragmentation perceived by an individual ([Sundell-Turner and Rodewald, 2008](#)) is difficult to measure from geographic databases where habitats are human-derived categories of land cover and would not necessarily reflect how animals perceive their surrounding landscape ([Baguette and Van Dyck, 2007](#); [Li and Reynolds, 1994](#); [Van Dyck, 2007](#)). These difficulties to measure meaningful metrics may explain also why the probability for a case study to conclude opposite to the expectation (i.e., at least one metric tested contradicting the initial hypothesis) was quite high. The papers with such surprising results were mainly those with a large number of metrics tested. With the continuing increases in map resolution and the growing easiness to analyze patterns in a landscape through dedicated software and packages (e.g., [Fragstats](#), [Fourier transforms](#), [Rocchini et al., 2013](#)), researchers are tempted to include a plethora of variables, which is not advisable ([Streiner and Norman, 2011](#)). This problem probably explains the low proportion of variables found to be statistically significant, the high probability of obtaining at least one variable with an effect opposite to what is expected, and the *ad hoc* explanation of significant relationships. A better understanding of the energetic requirements, diet needs, and the multiple components of landscape heterogeneity as perceived by an individual is badly required and should be the focus of renewed empirical effort in the future.

3.4.3 Temporal and spatial scales

Seasonality

Contrary to our expectations, the influence of resources on variation in the sizes of home range was not supported to a greater extent during the non-productive than during the productive season. This result was surprising, given that most studies took place in areas with marked seasonality ([Figure 3.3C](#)). Environmental constraints might account for this discrepancy, as movements can be restricted during winter, especially at high latitude and high elevation, preventing the sizes of individual home ranges from responding to reduced food resources during the lean season ([Rivrud, Loe, and Mysterud, 2010](#)). Moreover, the ability for some species to store fat reserves may relax the requirements

to resort to immediately available food resources during the lean season (Mautz, 1978), so that an extension of the size of the home range may not be required. Hence, while seasonal expansion-contraction of the sizes of home ranges occurs in ungulates (Börger et al., 2006a; Morellet et al., 2013), among-individual variation in home range sizes does not appear to be triggered by food resources to a greater extent in the lean season.

Temporal definition of seasonal period

Another reason why seasonal differences did not affect home range sizes may be that estimates of the sizes of home ranges were calculated over varying time windows. For the sake of comparison, we simply attributed a season to an estimate of the size of a home range, but this classification may itself cover various periods of time, from the peak period of productivity (i.e., within a few weeks), to the productive season on its whole (i.e., over several months). The estimates of both the sizes of home ranges (Börger, Dalziel, and Fryxell, 2008) and the metrics of resources may vary with the time window. For instance, van Beest et al. (2011) reported that the lack of consistency in the effects of individual attributes and environmental conditions (resource and climate) on the sizes of home ranges could be due to the inadequate choice of the temporal scale (Table 3.3). A relevant choice of spatial and temporal scales is essential and should be suited to the biology of the species, in terms of how individuals perceive the environment (Cushman and McGarigal, 2004) and stationarity (Laver and Kelly, 2008; Péron, 2019).

TABLE 3.3: Biological interpretations provided by authors to explain results that were retained as opposite to initial biological hypothesis, per category of variable.

	Variables	Expected	Interpretations given by authors	Species
Resources	Proportion of grassland ^a	Negative	Complementarity (Animals searched cover or refuge)	Mule deer
	Proportion of crop ^b	Negative		White-tailed deer
	Proportion of open area ^c	Negative		Axis deer
	Browse density ^d	Positive	Scale, Disturbance period	Moose
	NDVI band 1 ^e	Positive	Quality (Difference between poor and rich habitat, generalist search quality in rich areas and quantity in poor areas)	Svalbard reindeer
	Grass fibre content ^f	Negative	Small ruminant look for low rate of fiber to digest faster	Oribi
	Proportion of barren land ^g	Positive	Low productivity	Moose
	Mean foraging biomass ^h	Negative	None	Elk
	Proportion of deciduous forest ⁱ	Negative	None	Red deer/Roe deer
	Proportion of acacia woodland ^j	Positive	None	Zebra
	Proportion of lacustrine woodland ^j	Positive	None	Zebra
	NDVI ^e	Negative	None	Svalbard reindeer
	Distance to forest ^b	Negative	None	White-tailed deer
	Distance to water ^k	Positive	None	Mule deer
	Proportion of low-productivity coniferous forest ^g	Negative	None	Moose
	Vegetation index ^l	Negative	None	African buffalo
	Landscape heterogeneity	Patch number ^j	Positive	Many patches in a poor quality environment can cause an increase of home range
Interspersion-juxtaposition index ^j		Positive	None	Zebra
Largest patch index ^m		Positive	None	African bush elephant
Mean edge contrast ^m		Negative	None	African bush elephant
Patch density of developed types ⁿ		Positive	None	White-tailed deer
Shannon diversity index ^o		Negative	None	White-tailed deer

^aBender et al., 2007; ^bWalter et al., 2009; ^cMoe and Wegge, 1994; ^dvan Beest et al., 2011; ^eHansen et al., 2009a; ^fBrashares and Arcese, 2002; ^gBjørneraas et al., 2012; ^hAnderson et al., 2005; ⁱBevanda et al., 2015; ^jBartlam-Brooks et al., 2013; ^kNicholson et al., 1997; ^lNaidoo et al., 2012; ^mGrainger et al., 2005; ⁿKilpatrick et al., 2011; ^oQuinn et al. 2013.

3.4.4 Accounting for life history traits

Body mass

Species' body mass did not influence how the sizes of home ranges responded to environmental factors, despite the range of body mass varying from 13 to 8,000 kg, thus covering the range of body mass of ungulates (Fritz and Loison, 2006). We expected the pathways through which environmental variables cascade to the sizes of individual home ranges to be much more complex in large than small species (Haskell, Ritchie, and Olf, 2002), but we did not find such evidence. In a recent paper, (Noonan et al., 2020) provide evidence that investigating allometric relationship of the sizes of home ranges from conventional KDE method could be misleading as the sizes of home ranges tend to be increasingly underestimated as species body mass increases. This exemplifies that the endeavor of reviewing the variation in the sizes of home ranges requires first and foremost the development of a rigorous and accepted methodology for estimating the sizes of home ranges, while the conceptual framework is already well-anchored since the theoretical approaches developed in the late 1960s (Jetz et al., 2004; McNab, 1963).

Group size

Unlike what we posited, the support for the biological hypotheses did not decrease in species with large group size. Our rough categories of group size at the species level and the low number of species included in our review might have prevented us from detecting the influence of group size on the relationship between resource availability or landscape heterogeneity and the sizes of home ranges. In most group-living species, the situation is complex (Prox and Farine, 2020) because groups vary in size (e.g., fission-fusion societies, Aureli et al., 2008). The lability of group sizes and also the varying degree of home range overlap among individuals of a given social unit (McLoughlin, Ferguson, and Messier, 2000) may however prevent detecting a resource-to-home range size relationship, when group size is not controlled.

Diet

The support to the resource hypothesis was higher for species with a "cattle-type" rumen (Codron and Clauss, 2010), which contradicted our expectation. This could be caused by the difficulty to obtain a reliable metric for resource availability in moose-type species (mostly browsers, Codron and Clauss, 2010), whose resources are difficult to evaluate using remote sensing. In addition, grass (consumed by individuals of species with cattle-type rumen to different degrees) produces most of its rich foliage during a limited time frame and quickly disappears when passing into the non-productive season, while browse such as ivy or bramble, due to their deep roots, can continue to produce some buds and foliage even after the end of the productive season (Jarman, 1974; Shipley, 1999). This difference in growth rates of resources can render cattle-type species to be more sensitive to resource availability. As broached earlier, a proper assessment of species-specific foodscape and of the search and exploitation balance in time budget

and movements is required for a better understanding of how resource availability and landscape heterogeneity shape the sizes of home ranges in species with different diets (Shipley, 1999) and morpho-digestive constraints (Clauss, Lechner-Doll, and Streich, 2003).

3.4.5 Other drivers of variation in the sizes of individual home ranges

Individual attributes

We only analyzed the effect of resource availability and landscape heterogeneity on the variation in the sizes of home ranges in relation to species-specific diet and group size. Nonetheless, other factors shape among-individual variation in the sizes of home ranges, such as individual attributes (e.g., sex, age, or body condition). As critical periods in terms of energetic expenditures differ between sexes (i.e., mating in males, late gestation-early lactation in females) and because females cannot move a lot after parturition, intraspecific variation in the sizes of home ranges emerges (e.g., Bowyer, 2004; Ruckstuhl, 2007). The size of an individual's home range can also vary as a function of age (Tao, Börger, and Hastings, 2016), either because individuals gain more experience and a better knowledge of resource distribution when aging (Saïd et al., 2009) or because they are increasingly less efficient at exploiting a large area (Froy et al., 2018). More generally, intraspecific variation in the internal state of individuals could lead to contrasted costs of movement (McNab, 1963) and therefore to different responses of the sizes of home ranges to changes in environmental variables.

Population density

We omitted population density as a possible driver of the size of individual home range, as we considered population density to be an emergent property of combined individual home ranges and overlap among individuals (Damuth, 1981). Even though the sizes of home ranges can decrease with density, as shown by Kjellander et al. (2004) on roe deer, changes in home range overlap could blur this relationship (Jetz et al., 2004). More generally, a detailed appraisal of the social system should be inseparable from the study of the home range-to-density relationship (Damuth, 1981; Mcloughlin, Ferguson, and Messier, 2000).

Coexisting with other species

In addition, most individuals share their home ranges with members of sympatric species with overlapping niches, which leads to potential competing or facilitating relationships (Buchmann et al., 2013; du Toit and Olf, 2014). Individuals living in a multi-species environment, where resources are depleted at a fast rate, should have larger home ranges than individuals living alone in a given area (Buchmann et al., 2013). The inverse may happen when facilitation occurs (du Toit and Olf, 2014). The reason the community setting is seldom considered in single species studies of variation in the sizes of home ranges may be the strong bias of studies from the northern hemisphere,

where the research tradition is more single species based, in contrast to Africa where comprehensive species and community approaches are more common (e.g., starting in the early 1970s with the works of Estes, 1974). Ungulates are also prey to various predators in all ecosystems (Montgomery et al., 2019). The impact of natural predation and human hunting on the sizes of individual home ranges within a population remains to be evaluated, accounting for both ungulate life history traits (Hopcraft, Olf, and Sinclair, 2010) and predator hunting modes (cursorial *vs.* ambush, Say-Sallaz et al., 2019).

3.4.6 Recommendations

We acknowledge that in the last 15 years, several authors have reviewed in depth the concept of home range and its estimation, providing important recommendations regarding the methodology and reporting of information in published studies (for recent studies, Noonan et al., 2019; Noonan et al., 2020; Péron, 2019). More than 10 years ago, Laver and Kelly (2008) urged researchers to follow a unified methodology for estimating animal home ranges and recommended a minimal report of information for a better reproducibility and robust comparisons among studies. Likewise, we can only insist that it would be most useful, for comparative endeavors like ours, that authors provide estimates of the sizes of home ranges obtained with different methods, if only as Supplementary Information. In addition, previous reviews provided insightful information and critical perspectives regarding the definition of a home range and the estimation of its size (Börger, Dalziel, and Fryxell, 2008; Fieberg and Börger, 2012; Péron, 2019). In a prospective review, Börger, Dalziel, and Fryxell (2008) advocated for the development of a general mechanistic model of animal home range behavior that would unify movement, individual resource requirements, and statistical models of home ranges. While this review did not directly provide guidelines on how to enhance the reporting and standardization of results of home range studies, it proposed a general approach, unifying our understanding of links between small-scale movements and home range behavior. We refer the readers to these previous reviews for discussion about the concept of home range, its definition and estimation, and the future avenues of research regarding the up-scaling of movements to home ranges. In our systematic review, we encountered other hurdles, such as the methodological and biological inconsistencies regarding the independent variables and the statistical models. This led us to summarize some recommendations (Table 3.4) that should help future empirical studies aiming at evaluating the effect of the resource availability, landscape heterogeneity, and risk on the sizes of home ranges mediated by species-specific lifestyle. These recommendations pertain to (1) study design and methodology, (2) the choice and estimation of the candidate drivers of the sizes of home ranges, although we are aware of the persistence of some challenges and disagreement across the literature on the most appropriate and meaningful metrics, for example of landscape heterogeneity, (3) general statistical considerations, and (4) the need of considering life history traits when evaluating variation in the sizes of home ranges within a population. Understanding

processes at the community level requires a better grasp of how individual movements, triggered by resources, landscape heterogeneity, predation, and coexistence with other species, lead to home range formation and space sharing (Bhat, Kempes, and Yeakel, 2020; Buchmann et al., 2013). Our review brings to the fore that the last 50 years of telemetry studies are actually only the first steps into finding the link between environmental factors, life-history constraints, and individual space use that could feed our understanding of larger-scale processes. Therefore, we urge researchers on movement ecology to continue providing results on individual home ranges in their articles.

TABLE 3.4: Recommendations for authors that should help quantitative studies aiming at evaluating the effect of the environment and life history traits on the size of home range.

Recommendations
<p>A. Study design and methodology related to estimating home ranges (see also, Laver and Kelly, 2008)</p> <ul style="list-style-type: none"> • Sample size is crucial: mark enough individuals; • The choice of home range estimator is crucial and for comparative purposes, repeating the analyses with different estimators (to be provided as Appendix for example) would be helpful; • State the bandwidth and the kernel used when making kernel home range estimates. Without both information, comparisons of kernel estimates of utilization distributions or estimates of sizes cannot be made. If, however, bandwidth and kernel are presented, then biases of estimates can be known and used when making comparisons; • Evaluate the movement stationarity vs. time-window relationship to choose a meaningful temporal scale regarding (1) the definition of a home range, (2) the temporal and spatial scales at which environmental variables are estimated (see also, Börger et al., 2006a), and (3) the body mass of the species. <p>B. Identifying and measuring environmental variables</p> <ul style="list-style-type: none"> • The effect of food resource availability should not be studied without accounting for other complementary resources and landscape structure; • Evaluate the species' foodscape when selecting metrics of food resources; • Consider the different components of landscape heterogeneity explicitly (i.e., fragmentation, diversity, complementation) and express specific hypotheses for each component; • Consider reducing the number of metrics of landscape heterogeneity and formulating clear hypotheses on expected causal relationships. <p>C. General statistical considerations</p> <ul style="list-style-type: none"> • Scale variables to allow comparison across studies; • Report standardized β estimates of models for a better comparative approach; • Always report β estimates even in cases where the effect was not statistically significant; • Report the transformation used on variables; • Evaluate the log-log relationship between home range, body mass and biomass; • Correct for multiple testing when multiple metrics are evaluated, and especially when these metrics are correlated (e.g., Fragstats metrics); • Express the expected relationship in formal mathematical terms; • Take into consideration bias when measuring the metric value (e.g., Metric value = True value + bias + error). <p>D. Biological considerations</p> <ul style="list-style-type: none"> • Provide a clear definition of home range and of the rationale behind its studied properties (size, shape, temporal scale, spatial scale—see also, recommendations in A.) (see also, Börger, Dalziel, and Fryxell, 2008; Péron, 2019). • For social species, consider the sociality level (overlap with other con-specific, group size, group stability) for each individual (Péron, 2019); • Evaluate the individual exposure to lethal (predation, hunting, collision) and to non-lethal (disturbances) risks at the individual level; • Account for sympatric species of the same guild and overlapping trophic niche that could lead to modification of individual space use through competition (interference, exploitation) or facilitation processes.

Data availability

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

JS-F, KA, GY, and AL conceived this work and designed the methodology with inputs from J-MG, MG, and NM. JS-F and KA collected and analyzed the data with inputs from VR. JS-F, KA, GY, and AL led the initial writing of the manuscript. All authors contributed critically to the manuscript and gave final approval for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- Anderson, D. P. et al. (2005). "Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes." In: *Landscape Ecology* 20.3, pp. 257–271.
- Aureli, F. et al. (2008). "Fission-Fusion Dynamics: New Research Frameworks." In: *Current Anthropology* 49.4, pp. 627–654.
- Baguette, M. and Van Dyck, H. (2007). "Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal." In: *Landscape Ecology* 22.8, pp. 1117–1129.
- Bartlam-Brooks, H. L. A., Bonyongo, M. C., and Harris, S. (2013). "How landscape scale changes affect ecological processes in conservation areas: external factors influence land use by zebra (*Equus burchelli*) in the Okavango Delta." In: *Ecology and Evolution* 3.9, pp. 2795–2805.

- Bender, L. C., Lomas, L. A., and Kamienski, T. (2007). "Habitat Effects on Condition of Doe Mule Deer in Arid Mixed Woodland-grassland." In: *Rangeland Ecology & Management* 60.3, pp. 277–284.
- Berger-Tal, O. and Saltz, D. (2019). "Invisible barriers: anthropogenic impacts on inter- and intra-specific interactions as drivers of landscape-independent fragmentation." In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 374.1781, p. 20180049.
- Bevanda, M., Fronhofer, E. A., Heurich, M., Müller, J., and Reineking, B. (2015). "Landscape configuration is a major determinant of home range size variation." In: *Ecosphere* 6.10, art195.
- Bhat, U., Kempes, C. P., and Yeakel, J. D. (2020). "Scaling the risk landscape drives optimal life-history strategies and the evolution of grazing." In: *Proceedings of the National Academy of Sciences* 117.3, pp. 1580–1586.
- Bjørneraas, K., Herfindal, I., Solberg, E. J., Sæther, B.-E., van Moorter, B., and Rolandsen, C. M. (2012). "Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore." In: *Oecologia* 168.1, pp. 231–243.
- Bonnot, N. et al. (2013). "Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer." In: *European Journal of Wildlife Research* 59.2, pp. 185–193.
- Börger, L., Dalziel, B. D., and Fryxell, J. M. (2008). "Are there general mechanisms of animal home range behaviour? A review and prospects for future research: Home range modelling." In: *Ecology Letters* 11.6, pp. 637–650.
- Börger, L. et al. (2006a). "An Integrated Approach to Identify Spatiotemporal and Individual-Level Determinants of Animal Home Range Size." In: *The American Naturalist* 168.4, pp. 471–485.
- Börger, L. et al. (2006b). "Effects of sampling regime on the mean and variance of home range size estimates." In: *Journal of Animal Ecology* 75.6, pp. 1393–1405.
- Bowyer, R. T. (2004). "Sexual Segregation in Ruminants: Definitions, Hypotheses, and Implications for Conservation and Management." In: *Journal of Mammalogy* 85.6, pp. 1039–1052.
- Brashares, J. S. and Arcese, P. (2002). "Role of forage, habitat and predation in the behavioural plasticity of a small African antelope." In: *Journal of Animal Ecology* 71.4, pp. 626–638.
- Breheny, P. and Burchett, W. (2017). "Visualization of Regression Models Using visreg." In: *The R Journal* 9.2, pp. 56–71.
- Brody, S. (1945). "Bioenergetics and Growth, Reinhold Publ." In: *Co., New York*, pp. 265–266.

- Brook, R. K. (2010). "Habitat selection by parturient elk (*Cervus elaphus*) in agricultural and forested landscapes." In: *Canadian Journal of Zoology* 88.10, pp. 968–976.
- Buchmann, C. M., Schurr, F. M., Nathan, R., and Jeltsch, F. (2013). "Habitat loss and fragmentation affecting mammal and bird communities—The role of interspecific competition and individual space use." In: *Ecological Informatics*. The analysis and application of spatial ecological data to support the conservation of biodiversity 14, pp. 90–98.
- Burnham, K. P. and Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. New York: Springer-Verlag.
- Burt, W. H. (1943). "Territoriality and Home Range Concepts as Applied to Mammals." In: *Journal of Mammalogy* 24.3, pp. 346–352.
- Camp, M., Rachlow, J., Woods, B., Johnson, T., and Shipley, L. (2013). "Examining functional components of cover: the relationship between concealment and visibility in shrub-steppe habitat." In: *Ecosphere* 4.2, pp. 1–14.
- Ciuti, S. et al. (2012). "Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear." In: *PLoS ONE* 7.11.
- Clauss, M., Lechner-Doll, M., and Streich, W. J. (2003). "Ruminant diversification as an adaptation to the physicommechanical characteristics of forage." In: *Oikos* 102.2, pp. 253–262.
- Codron, D. and Clauss, M. (2010). "Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species." In: *Canadian Journal of Zoology* 88.11, pp. 1129–1138.
- Creel, S., Schuette, P., and Christianson, D. (2014). "Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community." In: *Behavioral Ecology* 25.4, pp. 773–784.
- Cushman, S. A. and McGarigal, K. (2004). "Patterns in the species–environment relationship depend on both scale and choice of response variables." In: *Oikos* 105.1, pp. 117–124.
- Daleszczyk, K., Krasieńska, M., Krasieński, Z., and Bunevich, A. (2007). "Habitat structure, climatic factors, and habitat use by European bison (*Bison bonasus*) in Polish and Belarusian parts of the Białowieża Forest, Poland." In: *Canadian Journal of Zoology* 85.2, pp. 261–272.
- Damuth, J. (1981). "Home range, home range overlap, and species energy use among herbivorous mammals." In: *Biological Journal of the Linnean Society* 15.3, pp. 185–193.
- De Beer, Y. and van Aarde, R. J. (2008). "Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas?" In: *Journal of Arid Environments* 72.11, pp. 2017–2025.

- Dechen Quinn, A. C., Williams, D. M., and Porter, W. F. (2013). "Landscape structure influences space use by white-tailed deer." In: *Journal of Mammalogy* 94.2, pp. 398–407.
- Demment, M. W. and Van Soest, P. J. (1985). "A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores." In: *The American Naturalist* 125.5, pp. 641–672.
- Desy, E. A., Batzli, G. O., and Liu, J. (1990). "Effects of Food and Predation on Behaviour of Prairie Voles: A Field Experiment." In: *Oikos* 58.2, pp. 159–168.
- Dobson, F. S. (2007). "A lifestyle view of life-history evolution." In: *Proceedings of the National Academy of Sciences* 104.45, pp. 17565–17566.
- Dunn, J. E. and Gipson, P. S. (1977). "Analysis of Radio Telemetry Data in Studies of Home Range." In: *Biometrics* 33.1, pp. 85–101.
- Dunning, J. B., Danielson, B. J., and Pulliam, H. R. (1992). "Ecological Processes That Affect Populations in Complex Landscapes." In: *Oikos* 65.1, pp. 169–175.
- Duparc, A., Garel, M., Marchand, P., Dubray, D., Maillard, D., and Loison, A. (2020). "Through the taste buds of a large herbivore: foodscape modeling contributes to an understanding of forage selection processes." In: *Oikos* 129.2, pp. 170–183.
- Dussault, C., Courtois, R., Ouellet, J.-P., and Girard, I. (2005a). "Space use of moose in relation to food availability." In: *Canadian Journal of Zoology* 83.11, pp. 1431–1437.
- Du Toit, J. T. and Olf, H. (2014). "Generalities in grazing and browsing ecology: using across-guild comparisons to control contingencies." In: *Oecologia* 174.4, pp. 1075–1083.
- Estes, R. D. (1974). "Social organization of the African Bovidae." In: *The behaviour of ungulates and its relation to management* 1, pp. 166–205.
- Fieberg, J. and Börger, L. (2012). "Could you please phrase "home range" as a question?" In: *Journal of Mammalogy* 93.4, pp. 890–902.
- Flombaum, P. and Sala, O. E. (2007). "A non-destructive and rapid method to estimate biomass and aboveground net primary production in arid environments." In: *Journal of Arid Environments* 69.2, pp. 352–358.
- Fritz, H. and Loison, A. (2006). "Large herbivores across biomes." In: *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Ed. by Danell, K., Bergström, R., Duncan, P., and Pastor, J. Conservation Biology. Cambridge University Press, pp. 19–49.
- Froy, H. et al. (2018). "Declining home range area predicts reduced late-life survival in two wild ungulate populations." In: *Ecology Letters* 21.7, pp. 1001–1009.
- Garrouette, E. L., Hansen, A. J., and Lawrence, R. L. (2016). "Using NDVI and EVI to Map Spatiotemporal Variation in the Biomass and Quality of Forage for Migratory Elk in the Greater Yellowstone Ecosystem." In: *Remote Sensing* 8.5, p. 404.

- Gordon, I. J. (2003). "Browsing and grazing ruminants: are they different beasts?" In: *Forest Ecology and Management* 181.1-2, pp. 13–21.
- Grainger, M., Aarde, R. v., and Whyte, I. (2005). "Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa." In: *African Journal of Ecology* 43.4, pp. 369–375.
- Grignolio, S., Parrini, F., Bassano, B., Luccarini, S., and Apollonio, M. (2003). "Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*." In: *FOLIA ZOOLOGICA-PRAHA* 52.2, pp. 113–120.
- Hansen, B. B., Aanes, R., Herfindal, I., Sæther, B.-E., and Henriksen, S. (2009a). "Winter habitat–space use in a large arctic herbivore facing contrasting forage abundance." In: *Polar Biology* 32.7, pp. 971–984.
- Hansen, B. B., Herfindal, I., Aanes, R., Sæther, B.-E., and Henriksen, S. (2009b). "Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore." In: *Oikos* 118.6, pp. 859–872.
- Harestad, A. S. and Bunnell, F. L. (1979). "Home Range and Body Weight—A Reevaluation." In: *Ecology* 60.2, pp. 389–402.
- Haskell, J. P., Ritchie, M. E., and Olf, H. (2002). "Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges." In: *Nature* 418.6897, pp. 527–530.
- Hopcraft, J. G. C., Olf, H., and Sinclair, A. R. E. (2010). "Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas." In: *Trends in Ecology & Evolution* 25.2, pp. 119–128.
- Jarman, P. J. (1974). "The Social Organisation of Antelope in Relation To Their Ecology." In: *Behaviour* 48.1-4, pp. 215–267.
- Jetz, W., Carbone, C., Fulford, J., and Brown, J. H. (2004). "The Scaling of Animal Space Use." In: *Science* 306.5694, pp. 266–268.
- Kays, R., Crofoot, M. C., Jetz, W., and Wikelski, M. (2015). "Terrestrial animal tracking as an eye on life and planet." In: *Science* 348.6240.
- Kie, J. G. et al. (2010). "The home-range concept: are traditional estimators still relevant with modern telemetry technology?" In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1550, pp. 2221–2231.
- Kilpatrick, H. J., Labonte, A. M., and Barclay, J. S. (2011). "Effects of landscape and land-ownership patterns on deer movements in a suburban community." In: *Wildlife Society Bulletin* 35.3, pp. 227–234.

- Kittle, A. M., Fryxell, J. M., Desy, G. E., and Hamr, J. (2008). "The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates." In: *Oecologia* 157.1, pp. 163–175.
- Kjellander, P., Hewison, A. J. M., Liberg, O., Angibault, J.-M., Bideau, E., and Cargnelutti, B. (2004). "Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies." In: *Oecologia* 139.3, pp. 478–485.
- Lamberti, P., Mauri, L., Merli, E., Dusi, S., and Apollonio, M. (2006). "Use of space and habitat selection by roe deer *Capreolus capreolus* in a Mediterranean coastal area: how does woods landscape affect home range?" In: *Journal of Ethology* 24.2, pp. 181–188.
- Laundré, J. W., Hernández, L., and Altendorf, K. B. (2001). "Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A." In: *Canadian Journal of Zoology* 79.8, pp. 1401–1409.
- Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M., and Breton, L. (2008). "Behavioral Adaptations of Moose to Roadside Salt Pools." In: *Journal of Wildlife Management* 72.5, pp. 1094–1100.
- Laver, P. N. and Kelly, M. J. (2008). "A Critical Review of Home Range Studies." In: *Journal of Wildlife Management* 72.1, pp. 290–298.
- Leach, R. and Edge, W. (1994). "Summer Home-Range and Habitat Selection by White-Tailed Deer in the Swan-Valley, Montana." In: *Northwest Science* 68.1, pp. 31–36.
- Li, H. and Reynolds, J. F. (1994). "A Simulation Experiment to Quantify Spatial Heterogeneity in Categorical Maps." In: *Ecology* 75.8, pp. 2446–2455.
- Liberati, A. et al. (2009). "The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate health care interventions: explanation and elaboration." In: *PLoS medicine* 6.7, e1000100.
- Lüdecke, D. (2019). "sjstats: Statistical functions for regression models (version 0.17.4)." In: *R package: <https://www.cran.r-project.org/package=sjstats>*. doi 10.
- Massé, A. and Côté, S. D. (2012). "Linking habitat heterogeneity to space use by large herbivores at multiple scales: From habitat mosaics to forest canopy openings." In: *Forest Ecology and Management* 285, pp. 67–76.
- Mautz, W. W. (1978). "Sledding on a Bushy Hillside: The Fat Cycle in Deer." In: *Wildlife Society Bulletin (1973-2006)* 6.2, pp. 88–90.
- Mazerolle, M. J. (2020). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*.

- Mcloughlin, P. D., Ferguson, S. H., and Messier, F. (2000). "Intraspecific Variation in Home Range Overlap with Habitat Quality: A Comparison among Brown Bear Populations." In: *Evolutionary Ecology* 14.1, pp. 39–60.
- McNab, B. K. (1963). "Bioenergetics and the Determination of Home Range Size." In: *The American Naturalist* 97.894, pp. 133–140.
- McNaughton, S. J. and Georgiadis, N. J. (1986). "Ecology of African Grazing and Browsing Mammals." In: *Annual Review of Ecology and Systematics* 17, pp. 39–65.
- Mitchell, M. S. and Powell, R. A. (2004). "A mechanistic home range model for optimal use of spatially distributed resources." In: *Ecological Modelling* 177.1, pp. 209–232.
- (2008). "Estimated home ranges can misrepresent habitat relationships on patchy landscapes." In: *Ecological Modelling* 216.3, pp. 409–414.
- Moe, S. R. and Wegge, P. (1994). "Spacing behaviour and habitat use of axis deer (*Axis axis*) in lowland Nepal." In: *Canadian Journal of Zoology* 72.10, pp. 1735–1744.
- Montgomery, R. A., Moll, R. J., Say-Sallaz, E., Valeix, M., and Prugh, L. R. (2019). "A tendency to simplify complex systems." In: *Biological Conservation* 233, pp. 1–11.
- Moorcroft, P. R., Lewis, M. A., and Crabtree, R. L. (1999). "Home Range Analysis Using a Mechanistic Home Range Model." In: *Ecology* 80.5, pp. 1656–1665.
- Morellet, N. et al. (2013). "Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe." In: *Journal of Animal Ecology* 82.6, pp. 1326–1339.
- Mysterud, A., Pérez-Barbería, F. J., and Gordon, I. J. (2001). "The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants." In: *Oecologia* 127.1, pp. 30–39.
- Naidoo, R., Preez, P. D., Stuart-Hill, G., Chris Weaver, L., Jago, M., and Wegmann, M. (2012). "Factors affecting intraspecific variation in home range size of a large African herbivore." In: *Landscape Ecology* 27.10, pp. 1523–1534.
- Nakagawa, S. and Poulin, R. (2012). "Meta-analytic insights into evolutionary ecology: an introduction and synthesis." In: *Evolutionary Ecology* 26.5, pp. 1085–1099.
- Nicholson, M. C., Bowyer, R. T., and Kie, J. G. (1997). "Habitat Selection and Survival of Mule Deer: Tradeoffs Associated with Migration." In: *Journal of Mammalogy* 78.2, pp. 483–504.
- Nilsen, E. B., Herfindal, I., and Linnell, J. D. C. (2005). "Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity?" In: *Écoscience* 12.1, pp. 68–75.
- Noonan, M. J. et al. (2019). "A comprehensive analysis of autocorrelation and bias in home range estimation." In: *Ecological Monographs* 89.2, e01344.

- Noonan, M. J. et al. (2020). "Effects of body size on estimation of mammalian area requirements." In: *Conservation Biology* 34.4, pp. 1017–1028.
- Ofstad, E. G., Herfindal, I., Solberg, E. J., and Sæther, B.-E. (2016). "Home ranges, habitat and body mass: simple correlates of home range size in ungulates." In: *Proceedings of the Royal Society B: Biological Sciences* 283.1845, p. 20161234.
- Owen-Smith, N. (1977). "On Territoriality in Ungulates and an Evolutionary Model." In: *The Quarterly Review of Biology* 52.1, pp. 1–38.
- Pellerin, M., Saïd, S., and Gaillard, J.-M. (2008). "Roe deer *Capreolus capreolus* home-range sizes estimated from VHF and GPS data." In: *Wildlife Biology* 14.1, pp. 101–110.
- Péron, G. (2019). "The time frame of home-range studies: from function to utilization." In: *Biological Reviews* 94.6, pp. 1974–1982.
- Pettorelli, N. (2013). *The Normalized Difference Vegetation Index*. OUP Oxford.
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., and Stenseth, N. C. (2005). "Using the satellite-derived NDVI to assess ecological responses to environmental change." In: *Trends in Ecology & Evolution* 20.9, pp. 503–510.
- Pettorelli, N. et al. (2006). "Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer." In: *Oikos* 112.3, pp. 565–572.
- Powell, R. A., Zimmerman, J. W., Seaman, D. E., and Powell, C. (1996). *Ecology and Behaviour of North American Black Bears: Home Ranges, Habitat and Social Organization*. Chapman & Hall Wildlife Ecology and Behaviour Series. Springer Netherlands.
- Powell, R. A. and Mitchell, M. S. (2012). "What is a home range?" In: *Journal of Mammalogy* 93.4, pp. 948–958.
- Prox, L. and Farine, D. (2020). "A framework for conceptualizing dimensions of social organization in mammals." In: *Ecology and Evolution* 10.2, pp. 791–807.
- Ramanzin, M., Sturaro, E., and Zanon, D. (2007). "Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps." In: *Canadian Journal of Zoology* 85.2, pp. 280–289.
- Redjadj, C. et al. (2012). "Estimating herbaceous plant biomass in mountain grasslands: a comparative study using three different methods." In: *Alpine Botany* 122.1, pp. 57–63.
- Rivrud, I. M., Loe, L. E., and Mysterud, A. (2010). "How does local weather predict red deer home range size at different temporal scales?" In: *Journal of Animal Ecology* 79.6, pp. 1280–1295.
- Robinson, W. R., Peters, R. H., and Zimmermann, J. (1983). "The effects of body size and temperature on metabolic rate of organisms." In: *Canadian Journal of Zoology* 61.2, pp. 281–288.

- Rocchini, D., Metz, M., Ricotta, C., Landa, M., Frigeri, A., and Neteler, M. (2013). "Fourier transforms for detecting multitemporal landscape fragmentation by remote sensing." In: *International Journal of Remote Sensing* 34.24, pp. 8907–8916.
- Ruckstuhl, K. E. (2007). "Sexual segregation in vertebrates: proximate and ultimate causes." In: *Integrative and Comparative Biology* 47.2, pp. 245–257.
- Säid, S. and Servanty, S. (2005). "The Influence of Landscape Structure on Female Roe Deer Home-range Size." In: *Landscape Ecology* 20.8, pp. 1003–1012.
- Säid, S. et al. (2005). "Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland." In: *Journal of Zoology* 267.3, pp. 301–308.
- Säid, S. et al. (2009). "What shapes intra-specific variation in home range size? A case study of female roe deer." In: *Oikos* 118.9, pp. 1299–1306.
- Say-Sallaz, E., Chamailé-Jammes, S., Fritz, H., and Valeix, M. (2019). "Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg." In: *Biological Conservation* 235, pp. 36–52.
- Scillitani, L., Sturaro, E., Monaco, A., Rossi, L., and Ramanzin, M. (2012). "Factors affecting home range size of male Alpine ibex (*Capra ibex ibex*) in the Marmolada massif." In: *Hystrix, the Italian Journal of Mammalogy* 23.2, pp. 19–27.
- Searle, K. R., Hobbs, N. T., and Gordon, I. J. (2007). "It's the "Foodscape", not the Landscape: Using Foraging Behavior to Make Functional Assessments of Landscape Condition." In: *Israel Journal of Ecology and Evolution* 53.3-4, pp. 297–316.
- Searle, K. R. and Shipley, L. A. (2008). "The Comparative Feeding Behaviour of Large Browsing and Grazing Herbivores." In: *The Ecology of Browsing and Grazing*. Ed. by Gordon, I. J. and Prins, H. H. T. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 117–148.
- Shipley, L. A. (1999). "Grazers and browsers: how digestive morphology affects diet selection." In: *Grazing behavior of livestock and wildlife* 70, pp. 20–27.
- Steidl, R. J., Hayes, J. P., and Schaubert, E. (1997). "Statistical Power Analysis in Wildlife Research." In: *The Journal of Wildlife Management* 61.2, pp. 270–279.
- Stephenson, T. R. et al. (2020). "Linking population performance to nutritional condition in an alpine ungulate." In: *Journal of Mammalogy*. Ed. by Barboza, P., gya091.
- Streiner, D. L. and Norman, G. R. (2011). "Correction for Multiple Testing: Is There a Resolution?" In: *Chest* 140.1, pp. 16–18.
- Sundell-Turner, N. M. and Rodewald, A. D. (2008). "A comparison of landscape metrics for conservation planning." In: *Landscape and Urban Planning* 86.3, pp. 219–225.

- Tao, Y., Börger, L., and Hastings, A. (2016). "Dynamic Range Size Analysis of Territorial Animals: An Optimality Approach." In: *The American Naturalist* 188.4, pp. 460–474.
- Taylor, R. D. (1988). "Age determination of the African buffalo, *Syncerus coffer* (Sparrman) in Zimbabwe." In: *African Journal of Ecology* 26.3, pp. 207–220.
- Team, R. D. C. (2017). "R development core team." In: *RA Lang Environ Stat Comput* 55, pp. 275–286.
- Tucker, M. A., Ord, T. J., and Rogers, T. L. (2014). "Evolutionary predictors of mammalian home range size: body mass, diet and the environment." In: *Global Ecology and Biogeography* 23.10, pp. 1105–1114.
- Tufto, J., Andersen, R., and Linnell, J. (1996). "Habitat Use and Ecological Correlates of Home Range Size in a Small Cervid: The Roe Deer." In: *Journal of Animal Ecology* 65.6, pp. 715–724.
- Turner, M. G. (2005). "Landscape Ecology: What Is the State of the Science?" In: *Annual Review of Ecology, Evolution, and Systematics* 36.1, pp. 319–344.
- Van Dyke, F. (2007). "Colonization of non-traditional range in dispersing elk, *Cervus elaphus nelsoni*, populations." In: *The Canadian field-naturalist* 121.2, pp. 133–141.
- Van Moorter, B., Rolandsen, C. M., Basille, M., and Gaillard, J.-M. (2016). "Movement is the glue connecting home ranges and habitat selection." In: *Journal of Animal Ecology* 85.1, pp. 21–31.
- Van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M., and Mysterud, A. (2011). "What determines variation in home range size across spatiotemporal scales in a large browsing herbivore?" In: *Journal of Animal Ecology* 80.4, pp. 771–785.
- Vercauteren, K. C. and Hygnstrom, S. E. (1998). "Effects of Agricultural Activities and Hunting on Home Ranges of Female White-Tailed Deer." In: *The Journal of Wildlife Management* 62.1, pp. 280–285.
- Viana, D. S. et al. (2018). "Linking seasonal home range size with habitat selection and movement in a mountain ungulate." In: *Movement Ecology* 6.1, pp. 1–11.
- Volampeno, M. S. N., Masters, J. C., and Downs, C. T. (2011). "Home range size in the blue-eyed black lemur (*Eulemur flavifrons*): A comparison between dry and wet seasons." In: *Mammalian Biology* 76.2, pp. 157–164.
- Walter, W. D. et al. (2009). "Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer." In: *Landscape Ecology* 24.10, pp. 1405–1420.
- Widmer, O., Saïd, S., Miroir, J., Duncan, P., Gaillard, J.-M., and Klein, F. (2004). "The effects of hurricane Lothar on habitat use of roe deer." In: *Forest Ecology and Management* 195.1, pp. 237–242.

Wiens, J. A., Crawford, C. S., and Gosz, J. R. (1985). "Boundary Dynamics: A Conceptual Framework for Studying Landscape Ecosystems." In: *Oikos* 45.3, pp. 421–427.

Wilson, R. P., Shepard, E. L. C., and Liebsch, N. (2008). "Prying into the intimate details of animal lives: use of a daily diary on animals." In: *Endangered Species Research* 4.1-2, pp. 123–137.

Supplementary Information

Supplementary Tables

TABLE S3.1: Information on the variables used in the 33 selected papers (productive and non-productive season). For each variable, we assigned the unit and the category (Resource, Heterogeneity and Risk) for both productive and non-productive seasons.

Variables	Units	Non-productive season	Productive season
NDVI	undimensionless	Resource	
INDVI	undimensionless		Resource
biomass	g/m ²		Resource
grass biomass	g/m ³	Resource	Resource
grass nitrogen content	percentage	Resource	Resource
grass fibre content	percentage	Resource	Resource
mean foraging biomass	g/m ²	Resource	Resource
food density	g/m ²		Resource
browse density	g/ha	Resource	Resource
corn development	undimensionless	Resource	Resource
resource availability	percentage	Resource	
salt pools	n		Resource
supplemental feeding	n		Resource
vegetation index	undimensionless		Resource
density of windblown fir trees	n/ha	Resource	
distance to forest	m	Resource	Resource
distance to human development	km		Resource
distance to water	km		Resource
edge density of forest land	m/ha	Resource	
grassland slope	degree		Resource
mean occurrence of forbs	percentage		Resource
mean occurrence of shrubs	percentage		Resource
natural water source	n/100km ²	Resource	Resource
proportion of crop	percentage	Resource	Resource
proportion of agricultural land	percentage		Resource
proportion of barren land	percentage		Resource
proportion of clear cut	percentage	Resource	
proportion of crop	percentage		Resource
proportion of deciduous forest	percentage		Resource
proportion of fir	percentage	Resource	
proportion of floodplain	percentage	Resource	
proportion of food-rich habitat	percentage	Resource	Resource
proportion of forest (high productivity)	percentage	Resource	
proportion of forest land	percentage	Resource	
proportion of grassland	percentage	Resource	Resource
proportion of high-productivity coniferous forest	percentage		Resource
proportion of meadow	percentage		Resource
proportion of open area	percentage	Resource	Resource
proportion of pastures	percentage	Resource	
proportion of peatland	percentage		Resource
proportion of unlogged riparian habitat	percentage		Resource

proportion of woodland	percentage		Resource
slope	degree	Resource	Resource
elevation	m	Resource	
altitude	m		Resource
band 1	undimensionless	Resource	
band 5	undimensionless	Resource	
mean band 5	percentage		Resource
patch density of developed types	n/ha	Resource	
proportion of acacia woodland	percentage	Resource	
proportion of alderwood	percentage		Resource
proportion of bare ground	percentage		Resource
proportion of bog	percentage		Resource
proportion of chamise	percentage		Resource
proportion of developed land	percentage	Resource	
proportion of forest cover	percentage	Resource	Resource
proportion of lacustrine woodland	percentage	Resource	
proportion of sagebrush	percentage		Resource
proportion of mopane woodland	percentage	Resource	
proportion of logged riparian habitat	percentage		Resource
proportion of low productivity forest	percentage	Resource	
proportion of low-productivity coniferous forest	percentage		Resource
proportion of coniferous forest	percentage		Resource
proportion of forage-poor area	percentage	Resource	
ruggedness	undimensionless	Resource	
configuration	percentage		Heterogeneity
contrast-weighted edge density	m/ha	Heterogeneity	Heterogeneity
edge density	m/ha and km/km ²	Heterogeneity	Heterogeneity
edge density between clear cuts and balsam fir and spruce stands	m/ha		Heterogeneity
edge density between clear cuts and balsam fir stands	m/ha	Heterogeneity	
edge density between peatlands and balsam fir and spruce stands	m/ha		Heterogeneity
edge density of all habitat types	m/ha	Heterogeneity	
edge density of developed land	m/ha	Heterogeneity	
interspersion-juxtaposition index	undimensionless	Heterogeneity	Heterogeneity
landscape shape index	undimensionless	Heterogeneity	Heterogeneity
mean edge contrast	percentage	Heterogeneity	Heterogeneity
number of patch	n	Heterogeneity	
patch density	n/km ² and n/ha	Heterogeneity	Heterogeneity
patch density of forest types	n/ha	Heterogeneity	
patch richness density	n/100ha	Heterogeneity	Heterogeneity
coefficient of variation of patch size	percentage	Heterogeneity	Heterogeneity
ressource dispersion	undimensionless	Heterogeneity	Heterogeneity
shanon diversity index	undimensionless	Heterogeneity	Heterogeneity
simpsons diversity index	undimensionless	Heterogeneity	
contagion index	percentage	Heterogeneity	Heterogeneity
largest patch index	percentage	Heterogeneity	Heterogeneity
mean patch size	ha	Heterogeneity	Heterogeneity
proportion of cohesion	percentage	Heterogeneity	Heterogeneity
proportion of contagion	percentage	Heterogeneity	Heterogeneity

shape index	undimensionless	Heterogeneity	Heterogeneity
mean shape index	undimensionless	Heterogeneity	Heterogeneity
road density	m/ha	Risk	Risk
distance to roads	m	Risk	Risk
mean field distance	m		Risk
mean barrier distance	m		Risk
mean river distance	m		Risk

TABLE S3.2: Characteristics of species of the 33 selected papers (productive and non-productive season) and references associated. Species were ranked by Latin name.

Species	Latin name	♂BM (kg)	♀BM (kg)	Group size	Habitat	References
Moose	<i>Alces Alces</i>	440	320	4	Boreal and mixed forest	Codron and Clauss, 2010; Hofmann, 1989; Mysterud, Pérez-Barbería, and Gordon, 2001; Ofstad et al., 2016; Ripple et al., 2015; van Beest et al., 2011; van Wieren, 1996
Axis deer	<i>Axis axis</i>	80	55	25	Grassland forest	Ables, 1974; Azad, Hossain, and Bhuiyan, 2005; Barrette, 2009a; Barrette, 2009b; Chapple, English, and Mulley, 1993; Codron and Clauss, 2010; Mishra and Wemmer, 1987; Miura, 1981; Moe and Wegge, 1997; Oulthavon et al., 2009; Raman, 1997; Sankar and Acharya, 2004; van Wieren, 1996
European bison	<i>Bison bonasus</i>	710	420	20	Mixed forests	Codron and Clauss, 2010; Krasnińska, Krasniński, Bunevich, et al., 2000; Krasnińska and Krasniński, 1995; Mysterud, Pérez-Barbería, and Gordon, 2001; Ofstad et al., 2015; van Wieren, 1996
Ibex	<i>Capra ibex</i>	95	45	11	Alpine grassland	Codron and Clauss, 2010; Hofmann, 1989; Ofstad et al., 2016; van Wieren, 1996
Iberian ibex	<i>Capra pyrenaica</i>	70	35	7	Shrubland areas	Acevedo and Cassinello, 2009; Alados, 1986; Codron and Clauss, 2010; Fandos, Vigal, and Fernandez-Lopez, 1989; Santiago-Moreno et al., 2007; van Wieren, 1996
Roe deer	<i>Capreolus capreolus</i>	28	26	5	Mixed	Codron and Clauss, 2010; Hofmann, 1989; Loison et al., 1999; Mysterud, Pérez-Barbería, and Gordon, 2001; Ofstad et al., 2016; van Wieren, 1996
Elk	<i>Cervus canadensis</i>	312	238	4	Grassland	Anderson et al., 2005; Codron and Clauss, 2010; Hofmann, 1989; Mysterud, Pérez-Barbería, and Gordon, 2001; van Wieren, 1996
Red deer	<i>Cervus elaphus</i>	163	107	6	Mixed	Clutton-Brock, Albon, and Guinness, 1989; Clutton-Brock, Guinness, and Albon, 1982; Codron and Clauss, 2010; Gebert and Verheyden-Tixier, 2001; Mattioli et al., 2003; Sommer et al., 2008; van Wieren, 1996
Zebra	<i>Equus burchelli</i>	280	190	10	Grassland-savannah	Bartlam-Brooks, Bonyongo, and Harris, 2013; Codron and Clauss, 2010; Courbin et al., 2016; Creel, Schuette, and Christianson, 2014; Ripple et al., 2015; Schmitt, Stears, and Shrader, 2016; Schmitt et al., 2014; van Wieren, 1996
African elephant	<i>Loxodonta africana</i>	8000	3700	12	Dry wood and shrublands	Archie, Moss, and Alberts, 2006; Bates et al., 2008; Blanc, 2007; Caughley, 1976; Cerling et al., 2009; Codron and Clauss, 2010; Owen-Smith, 1988; van Wieren, 1996
Mule deer	<i>Odocoileus hemionus</i>	80	50	3	Mixed	Anderson, Medin, and Bowden, 1974; Anderson and Wallmo, 1984; Codron and Clauss, 2010; Crete and Daigle, 1999; Geist, 1998; Hofmann, 1989; Kie and Czech, 2000; Mysterud, Pérez-Barbería, and Gordon, 2001; Ofstad et al., 2016; van Wieren, 1996; Wallmo, 1981
White-tailed deer	<i>Odocoileus virginianus</i>	72	48	3	Mixed	Codron and Clauss, 2010; Hofmann, 1989; Mysterud, Pérez-Barbería, and Gordon, 2001; Ofstad et al., 2016; van Wieren, 1996
Oribi	<i>Ourebia ourebi</i>	14	13	2	Mixed	Codron and Clauss, 2010; Estes, 1991; Skinner and Chimimba, 2005; Van Teylingen and Kerley, 1995; van Wieren, 1996
Svalbard reindeer	<i>Rangifer tarandus</i>	136	88	6	Open taiga	Baskin and Danell, 2003; Codron and Clauss, 2010; Crete and Daigle, 1999; Cronin, MacNeil, and Patton, 2005; Geist, 1998; Lincoln and Tyler, 1994; Loe et al., 2007; Miller, 2003; van Wieren, 1996
African buffalo	<i>Syncerus caffer</i>	700	500	30	Savannas	Beekman and Prins, 1989; Blancou, 1935; Codron and Clauss, 2010; Mahaney, 1987; Prins, 1996; Sinclair, 1977; Taylor, 1988; Turner, Jolles, and Owen-Smith, 2005; Van Hooff et al., 2010; Van Hooff, Groen, and Prins, 2000; Van Hooff, Groen, and Prins, 2002; van Wieren, 1996; Winterbach, 1998

TABLE S3.3: Model selection table summarizing the different models explaining the level of support for ecological drivers. These models include the effect of season (productive vs non-productive) and categories of variables (resource and landscape heterogeneity, "Cat") and methodological features: the number of variables tested ("#Var"), the home range estimator (KDE, MCP, or other, denoted "estHR"), the number of locations used to compute the home range ("#XY"), the sample size (number of individuals collared, "#Indiv"), and the positioning system (GPS vs VHF, denoted "Pos"). "k" represents the degrees of freedom of each model, " $\Delta AICc$ " is the difference in AICc between the focal model and the model with the lowest AICc, and "Weight" is conditional probabilities for each model.

Season	Cat	Season:Cat	#Var	Cat:#Var	estHR	#XY	#Indiv	Pos	k	$\Delta AICc$	Weight
	+		+	+	+		+	+	7	0	0.297
	+		+	+			+	+	6	0.07	0.287
	+		+	+	+		+	+	8	1.74	0.124
	+		+	+		+		+	8	1.95	0.112
	+		+	+	+			+	7	2.19	0.099
									1	5.6	0.012

TABLE S3.4: Model selection table summarizing the different models explaining the level of support for ecological drivers. These models include the baseline model of Supplementary Table S3.3: categories of variables (resources and heterogeneity, "Cat") and methodological features: the number of variables tested ("#Var"), the sample size (number of individuals collared, "#Indiv"), the positioning system (GPS vs. VHF, denoted "Pos"), and life history traits: group size ("Gs"), the diet (Diet) and body mass (BM, log-transformed). "k" is the degrees of freedom of each model, " $\Delta AICc$ " is the difference in AICc between the focal model and the model with the lowest AICc, and "Weight" is conditional probabilities for each model.

Cat	#Var	Cat:#Var	#Indiv	Pos	Gs	Diet	BM	k	$\Delta AICc$	Weight
+	+	+	+	+				7	0	0.44
+	+	+	+	+		+	+	10	1.27	0.34
+	+	+	+	+			+	8	1.67	0.19
+	+	+	+	+	+		+	9	2.38	0.14

TABLE S3.5: Model selection table summarizing the different models explaining the level of support for ecological drivers, performed on the subset of case studies focusing on the effect of resources and studying the two seasons. These models include the variables selected in Supplementary Table S3.3: the effect of season (productive vs non-productive) and methodological features: the number of variables tested ("#Var"), the sample size (number of individuals collared, "#Indiv"), the positioning system (GPS vs VHF, denoted "Pos"), to which we added the diet (Diet) and body mass (BM, log-transformed). "k" is the degrees of freedom of each model, " $\Delta AICc$ " is the difference in AICc between the focal model and the model with the lowest AICc, and "Weight" is conditional probabilities for each model.

Season	#Var	#Indiv	Pos	Diet	BM	k	$\Delta AICc$	Weight
	+			+		4	0	0.415
	+	+		+		5	2.11	0.153
	+		+	+		5	2.21	0.137
+	+			+		5	2.37	0.127
	+			+	+	5	2.66	0.109
						1	12.15	0.001

Supplementary Figures

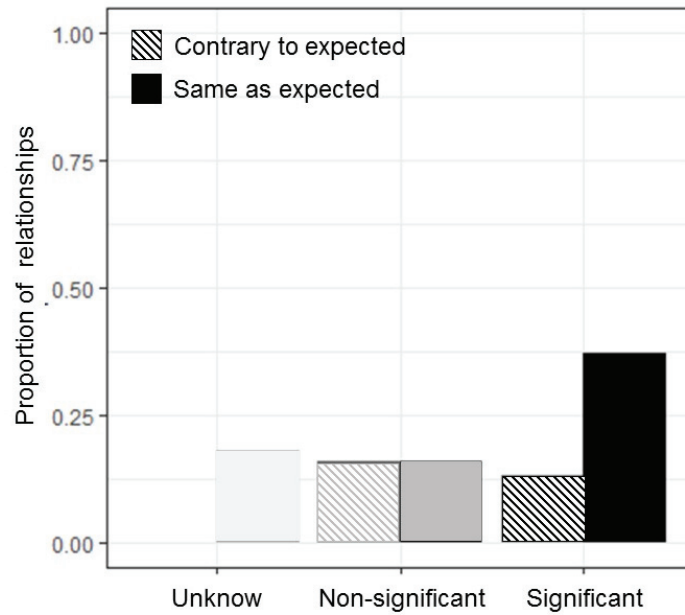


FIGURE S3.1: Proportions of metrics consistent with hypothesis (“Same as expected”), not-consistent with hypothesis (“Contrary to expected”), and unknown because we only have non-significant p -values or a non-selected variable in a model selection. For metrics consistent or not-consistent with hypothesis, we further distinguished significant from non-significant relationships. All the metrics included in our study were used to construct this graph.

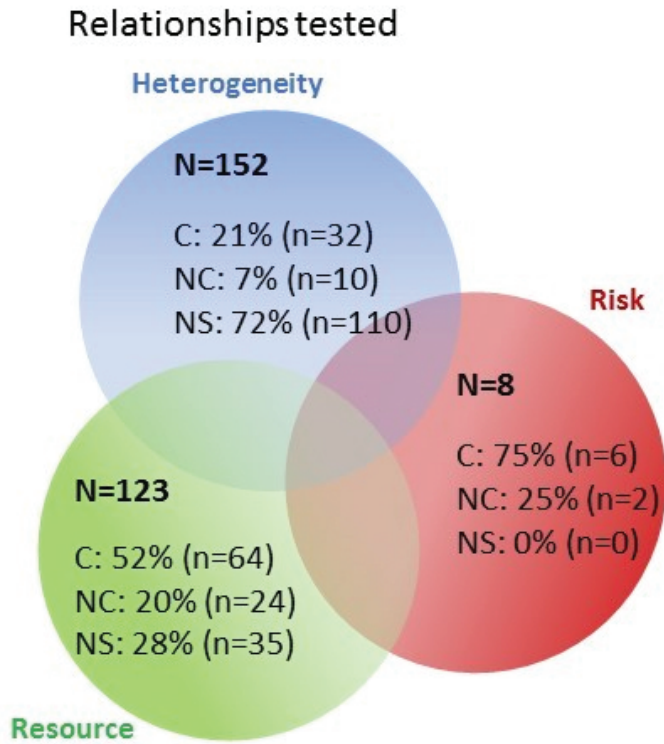


FIGURE S3.2: Venn diagrams representing the number of relationships tested for each category of variables (“N”). “C” represents the number of consistent relationships with initial authors’ expectations for each tested category of variables (resource, risk and/or heterogeneity; see Introduction), “NC” represents the non-consistent relationships and “NS” the non-significant/retained relationships.

References in Supplementary Information

- Ables, E. (1974). "The Axis deer in Texas. The Caesar Kleberg Research Programme. The Texas Agricultural Experiment Station." In: *A & M University System. Texas*.
- Acevedo, P. and Cassinello, J. (2009). "Biology, ecology and status of Iberian ibex *Capra pyrenaica*: a critical review and research prospectus." In: *Mammal Review* 39.1, pp. 17–32.
- Alados, C. L. (1986). "Aggressive behaviour, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenaica*)." In: *Behavioural Processes* 12.2, pp. 145–158.
- Anderson, A. E., Medin, D. E., and Bowden, D. C. (1974). "Growth and Morphometry of the Carcass, Selected Bones, Organs, and Glands of Mule Deer." In: *Wildlife Monographs* 39, pp. 3–122.
- Anderson, A. E. and Wallmo, O. C. (1984). "Odocoileus hemionus." In: *Mammalian Species* 219, pp. 1–9.
- Anderson, D. P. et al. (2005). "Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes." In: *Landscape Ecology* 20.3, pp. 257–271.
- Archie, E. A., Moss, C. J., and Alberts, S. C. (2006). "The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants." In: *Proceedings of the Royal Society B: Biological Sciences* 273.1586, pp. 513–522.
- Azad, M., Hossain, M., and Bhuiyan, A. (2005). "Feeding and management of spotted deer at Dhaka zoo." In: *International Journal of Zoological Research* 1.1, pp. 48–52.
- Barrette, C. (2009a). "Antler eating and antler growth in wild Axis deer." In: *Mammalia* 49.4, pp. 491–500.
- (2009b). "The size of Axis deer fluid groups in Wilpattu national park, Sri Lanka." In: *Mammalia* 55.2, pp. 207–220.
- Bartlam-Brooks, H. L. A., Bonyongo, M. C., and Harris, S. (2013). "How landscape scale changes affect ecological processes in conservation areas: external factors influence land use by zebra (*Equus burchelli*) in the Okavango Delta." In: *Ecology and Evolution* 3.9, pp. 2795–2805.
- Baskin, L. and Danell, K. (2003). *Ecology of ungulates: a handbook of species in Eastern Europe and Northern and Central Asia*. Springer Science & Business Media.
- Bates, L. A., Sayialel, K. N., Njiraini, N. W., Poole, J. H., Moss, C. J., and Byrne, R. W. (2008). "African elephants have expectations about the locations of out-of-sight family members." In: *Biology Letters* 4.1, pp. 34–36.
- Beekman, J. H. and Prins, H. H. T. (1989). "Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo, *Syncerus coffer*." In: *African Journal of Ecology* 27.2, pp. 129–147.

- Blanc, J. J. (2007). *African elephant status report 2007: an update from the African elephant database*. 33. Iucn.
- Blancou, L. (1935). "Buffles de l'Oubangui-Chari-Tchad." In: *La Terre et la vie*.
- Caughley, G. (1976). "The elephant problem—an alternative hypothesis." In: *African Journal of Ecology* 14.4, pp. 265–283.
- Cerling, T. E., Wittemyer, G., Ehleringer, J. R., Remien, C. H., and Douglas-Hamilton, I. (2009). "History of Animals using Isotope Records (HAIR): A 6-year dietary history of one family of African elephants." In: *Proceedings of the National Academy of Sciences of the United States of America* 106.20, pp. 8093–8100.
- Chapple, R. S., English, A. W., and Mulley, R. C. (1993). "Characteristics of the oestrous cycle and duration of gestation in chital hinds (*Axis axis*)." In: *Reproduction* 98.1, pp. 23–26.
- Clutton-Brock, T. H., Albon, S. D., and Guinness, F. E. (1989). "Fitness costs of gestation and lactation in wild mammals." In: *Nature* 337.6204, pp. 260–262.
- Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red deer: behavior and ecology of two sexes*. University of Chicago press.
- Codron, D. and Clauss, M. (2010). "Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species." In: *Canadian Journal of Zoology* 88.11, pp. 1129–1138.
- Courbin, N. et al. (2016). "Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale." In: *Oikos* 125.6, pp. 829–838.
- Creel, S., Schuette, P., and Christianson, D. (2014). "Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community." In: *Behavioral Ecology* 25.4, pp. 773–784.
- Crete, M. and Daigle, C. (1999). "Management of indigenous North American deer at the end of the 20th century in relation to large predators and primary production." In: *Acta Veterinaria Hungarica* 47.1, pp. 1–16.
- Cronin, M. A., MacNeil, M. D., and Patton, J. C. (2005). "Variation in Mitochondrial DNA and Microsatellite DNA in Caribou (*Rangifer tarandus*) in North America." In: *Journal of Mammalogy* 86.3, pp. 495–505.
- Estes, R. (1991). *The behavior guide to African mammals*. Vol. 64. University of California Press Berkeley.
- Fandos, P., Vigal, C., and Fernandez-Lopez, J. (1989). "Weight estimation of Spanish ibex, *Capra pyrenaica*, and chamois, *Rupicapra rupicapra* (Mammalia, Bovidae)." In: *Z. Suetierkunde* 54, pp. 239–242.

- Gebert, C. and Verheyden-Tixier, H. (2001). "Variations of diet composition of Red Deer (*Cervus elaphus* L.) in Europe." In: *Mammal Review* 31.3-4, pp. 189–201.
- Geist, V. (1998). *Deer of the world: their evolution, behaviour, and ecology*. Stackpole books.
- Hofmann, R. R. (1989). "Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system." In: *Oecologia* 78.4, pp. 443–457.
- Kie, J. G. and Czech, B. (2000). "Mule and black-tailed deer." In: *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey, USA, pp. 629–657.
- Krasińska, M., Krasiński, Z. A., Bunevich, A. N., et al. (2000). "Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Białowieża Forest." In: *Acta Theriologica* 45.3, pp. 321–334.
- Krasińska, M. and Krasiński, Z. A. (1995). "Composition, group size, and spatial distribution of European bison bulls in Białowieża Forest." In: *Acta Theriologica* 40, pp. 1–21.
- Lincoln, G. A. and Tyler, N. J. C. (1994). "Role of gonadal hormones in the regulation of the seasonal antler cycle in female reindeer, *Rangifer tarandus*." In: *Reproduction* 101.1, pp. 129–138.
- Loe, L. E. et al. (2007). "Activity pattern of arctic reindeer in a predator-free environment: no need to keep a daily rhythm." In: *Oecologia* 152.4, pp. 617–624.
- Loison, A., Gaillard, J.-M., Pélabon, C., and Yoccoz, N. G. (1999). "What factors shape sexual size dimorphism in ungulates?" In: *Evolutionary Ecology Research* 1.5, pp. 611–633.
- Mahaney, W. C. (1987). "Behaviour of the African buffalo on Mount Kenya." In: *African Journal of Ecology* 25.3, pp. 199–202.
- Mattioli, S., Fico, R., Lorenzini, R., and Nobili, G. (2003). "Mesola red deer: physical characteristics, population dynamics and conservation perspectives." In: *Hystrix, the Italian Journal of Mammalogy* 14.1-2.
- Miller, F. (2003). "Caribou–*Rangifer tarandus*. Wild Mammals of North America: Biology, Management, and Conservation." In: *The Johns Hopkins University Press, Baltimore, MD*. G. Samelius et al. *Ostfeld, RS & Keesing, F.(2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution* 15, pp. 232–237.
- Mishra, H. and Wemmer, C. (1987). "The comparative breeding ecology of four cervids in Royal Chitwan National Park. Biology and management of the Cervida." In: *Research symposia of the National Zoological Park*. Smithsonian Institution Press, Washington DC.

Miura, S. (1981). "Social behaviour of the axis deer during the dry season in Guindy Sanctuary, Madras." In.

Moe, S. R. and Wegge, P. (1997). "The effects of cutting and burning on grass quality and axis deer (*Axis axis*) use of grassland in lowland Nepal." In: *Journal of Tropical Ecology* 13.2, pp. 279–292.

Mysterud, A., Pérez-Barbería, F. J., and Gordon, I. J. (2001). "The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants." In: *Oecologia* 127.1, pp. 30–39.

Ofstad, E. G., Herfindal, I., Solberg, E. J., and Sæther, B.-E. (2016). "Home ranges, habitat and body mass: simple correlates of home range size in ungulates." In: *Proceedings of the Royal Society B: Biological Sciences* 283.1845, p. 20161234.

Ouithavon, K., Bhumpakphan, N., Denduangboripant, J., Siritroonrat, B., Trakulnaleamsai, S., et al. (2009). "An Analysis of the Phylogenetic Relationship of Thai Cervids Inferred from Nucleotide Sequences of Protein Kinase C Iota (PRKCI) Intron." In: *Kasetsart Journal, Natural Sciences* 43.4, pp. 709–719.

Owen-Smith, R. N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge university press.

Prins, H. (1996). *Ecology and behaviour of the African buffalo: social inequality and decision making*. Vol. 1. Springer Science & Business Media.

Raman, T. R. S. (1997). "Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India." In: *Journal of Biosciences* 22.2, pp. 203–218.

Ripple, W. J. et al. (2015). "Collapse of the world's largest herbivores." In: *Science Advances* 1.4, e1400103.

Sankar, K. and Acharya, B. (2004). "Spotted Deer or Chital.(K. Sankar, & SP Goyal, Eds.)" In: *ENVIS Bulletin: Wildlife and Protected Areas* 7.1, pp. 171–180.

Santiago-Moreno, J., Toledano-Díaz, A., Pulido-Pastor, A., Gómez-Brunet, A., and López-Sebastián, A. (2007). "Horn quality and postmortem sperm parameters in Spanish ibex (*Capra pyrenaica hispanica*)." In: *Animal Reproduction Science* 99.3, pp. 354–362.

Schmitt, M. H., Stears, K., and Shrader, A. M. (2016). "Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe." In: *Behavioral Ecology* 27.4, pp. 1073–1077.

Schmitt, M. H., Stears, K., Wilmers, C. C., and Shrader, A. M. (2014). "Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds." In: *Animal Behaviour* 96, pp. 151–158.

Sinclair, A. R. E. (1977). "The African buffalo; a study of resource limitation of populations." In.

- Skinner, J. D. and Chimimba, C. T. (2005). *The mammals of the southern African sub-region*. Cambridge University Press.
- Sommer, R. S., Zachos, F. E., Street, M., Jöris, O., Skog, A., and Benecke, N. (2008). "Late Quaternary distribution dynamics and phylogeography of the red deer (*Cervus elaphus*) in Europe." In: *Quaternary Science Reviews* 27.7, pp. 714–733.
- Taylor, R. D. (1988). "Age determination of the African buffalo, *Syncerus caffer* (Sparman) in Zimbabwe." In: *African Journal of Ecology* 26.3, pp. 207–220.
- Turner, W. C., Jolles, A. E., and Owen-Smith, N. (2005). "Alternating sexual segregation during the mating season by male African buffalo (*Syncerus caffer*)." In: *Journal of Zoology* 267.3, pp. 291–299.
- Van Hooft, P. et al. (2010). "Rainfall-driven sex-ratio genes in African buffalo suggested by correlations between Y-chromosomal haplotype frequencies and foetal sex ratio." In: *BMC Evolutionary Biology* 10.1, p. 106.
- Van Hooft, W. F., Groen, A. F., and Prins, H. H. T. (2000). "Microsatellite analysis of genetic diversity in African buffalo (*Syncerus caffer*) populations throughout Africa." In: *Molecular Ecology* 9.12, pp. 2017–2025.
- (2002). "Phylogeography of the African buffalo based on mitochondrial and Y-chromosomal loci: Pleistocene origin and population expansion of the Cape buffalo subspecies." In: *Molecular Ecology* 11.2, pp. 267–279.
- Van Teylingen, K. E. and Kerley, G. I. H. (1995). *Habitat characteristics of increasing and decreasing oribi subpopulations in Eastern Cape Province, South Africa*. Text.
- Van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M., and Mysterud, A. (2011). "What determines variation in home range size across spatiotemporal scales in a large browsing herbivore?" In: *Journal of Animal Ecology* 80.4, pp. 771–785.
- Van Wieren, S. E. (1996). "Do large herbivores select a diet that maximizes short-term energy intake rate?" In: *Forest Ecology and Management. Ungulates in Temperate Forest Ecosystems* 88.1, pp. 149–156.
- Wallmo, O. C. (1981). "Mule and black-tailed deer in North America. A Wildlife Management Institute book." In.
- Winterbach, H. E. K. (1998). *Research review : The status and distribution of Cape buffalo *Syncerus caffer caffer* in southern Africa*. Text.

4

Spatial constraints of raising offspring drive movement tactics of female ungulates around parturition

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Abstract

Caring for newborn offspring hampers resource acquisition of mammalian females, curbing their ability to meet the high energy expenditure of early lactation. Because newborns are particularly vulnerable, large herbivores have evolved a continuum of neonatal anti-predator tactics, ranging from immobile hider to highly mobile follower offspring. How these tactics constrain female behavior around parturition is unknown, particularly within the current context of increasing habitat fragmentation and advancing plant phenology due to climate change. Using a comparative analysis across 54 populations of 23 species, we fill this knowledge gap, showing that the response of mothers in terms of movement behaviour to variation in resource productivity and heterogeneity depends on their offspring's neonatal tactic. In particular, mothers with hider offspring are unable to exploit poor quality and spatially heterogeneous habitats. The neonatal tactic is a neglected, but likely crucial, component of life history for predicting how species will cope with environmental change.

Keywords: attraction, reproductive tactic, resource heterogeneity, diffusion, follower, hider, home range size, neonate, ungulates.

FOR female mammals that provide extensive maternal care, access to high quality or abundant forage, is of prime importance to fulfill the marked increase in energetic demands during late gestation and early lactation (Clutton-Brock, Albon, and Guinness, 1989). Many species synchronize birth events with the seasonal flush of resources when resources become of highest quality and available in large quantity (Rutberg, 1987). At that time, the temporal dynamics and the spatial distribution of resources may require reproductive females to move and track patches of suitable forage (Fauchald, 1999; Mueller et al., 2008; Oftedal, Boness, and Tedman, 1987; Teitelbaum et al., 2015), leading, in some environments, females to migrate. Following parturition, the movement of mothers might however be restricted by the limited mobility of their offspring. In addition, in precocial species, such as ungulates, early development of offspring occurs outside a nest or burrow (excluding suids), making them highly vulnerable to predation (Linnell, Aanes, and Andersen, 1995). Parturient females, hence, face trade-offs involving providing maternal care and acquiring sufficient energy, while keeping their offspring safe (Trivers, 1974). At the evolutionary timescale, ungulate neonates have evolved a diversity of anti-predator tactics ranging from being immobile and concealed (“hider” tactic *sensu* Lent, 1974) to being mobile and following the mother (“follower” tactic *sensu* Lent, 1974). Being a species with a hider or a follower offspring imposes different constraint on females movement. In “hider” species, the offspring’s bed sites correspond to central places to which the mother returns at regular intervals to provide care. In “follower” species, mothers have to maintain contact and adjust their daily ranging behavior to the movement capacity of their offspring. So far, we lack a comprehensive understanding of how the neonate’s anti-predator tactic interacts with the environment to drive fine- and large-scale movements of reproductive females, which have to balance their own energetic needs and offspring safety during a period when their foodscape is usually highly dynamic in space and time (Searle, Hobbs, and Gordon, 2007).

Our aim was therefore to investigate how neonatal tactics affect movement patterns of female ungulates around parturition, across gradients of productivity and spatial variation in resource availability. We performed an interspecific comparison of 23 ungulate species with contrasting neonatal anti-predator tactics distributed worldwide in 54 populations. We used continuous-time stochastic movement models, chosen for their ability to overcome the hurdles of inter-population comparisons of movement, and to provide several movement parameters, which we interpreted biologically as proxies of residency, diffusion, and frequency of return to a central place (see glossary in [Box 4.1](#)).

Box 4.1. GLOSSARY OF BIOLOGICAL TERMS USED IN THE PAPER

Vegetation productivity: derived from Normalized Difference Vegetation Index (NDVI) and a proxy of vegetation biomass, denoted "Mean NDVI".

Spatial variation in vegetation productivity: determined by the fine-scale and broad-scale spatial variation in NDVI values. The scale of spatial variation is denoted "Range NDVI".

Stationarity: usually representing the property of a time series. However, in this paper, we use it as a measure that allows us to determine the propensity of species to migrate (i.e., non-stationary) or not (i.e., stationary).

Home range: even though the use of "home range" is best adapted for an annual time-scale (Péron, 2019), in this paper it represents a proxy of the monthly space use around parturition of stationary individuals, only.

Diffusion: a surface velocity defining the movement spread of an individual over an area. It is the equivalent of a random movement in the landscape.

Frequency of return to central place: the propensity for an individual to return to a central location after a diffusion bout.

We first expected that the level of residency should increase with resource productivity and decrease with the scale of spatial variation in resource productivity, irrespective of the neonatal tactics. However, following parturition, species with hider offspring should become more resident, regardless of the environment (Figure 4.1 – 1st step). Second, we predicted females of hider species to increase the frequency with which they return to their newborn, to a greater degree in the poorest environments or those with broad scale variability in resources. In contrast, reproductive females of follower species should only reduce the extent of their movement, and only in populations with large-scale variation in resource availability or low productivity (Figure 4.1 – 2nd step).

4.2 Results

4.2.1 Neonatal tactics and residency in relation to parturition

Across all the studied populations of 23 ungulate species (11 generally classified as followers and 12 as hidere), $79 \pm 11\%$ (range = 20.7%-100%) of trajectories conformed to a stationary signal during the pre-parturition period, and $83 \pm 11\%$ (range = 0%-100%) during the post-parturition period. Hiders exhibited on average higher stationarity in their trajectories than followers during both periods, although it was not statistically significant (pre-parturition: Hiders = $81 \pm 14\%$; Followers = $77 \pm 16\%$; post-parturition: Hiders = $88 \pm 16\%$; Followers = $76 \pm 16\%$) (Supplementary Figures S4.1 and S4.2).

We failed to detect a statistically significant effect of body mass on the probability of being stationary ($LowerCredibleIntervalMeanUpperCredibleInterval = -0.614_{0.057,0.811}$), and the phylogenetic signal was weak ($H^2 = 0.000_{0.088,0.369}$). Among the environmental

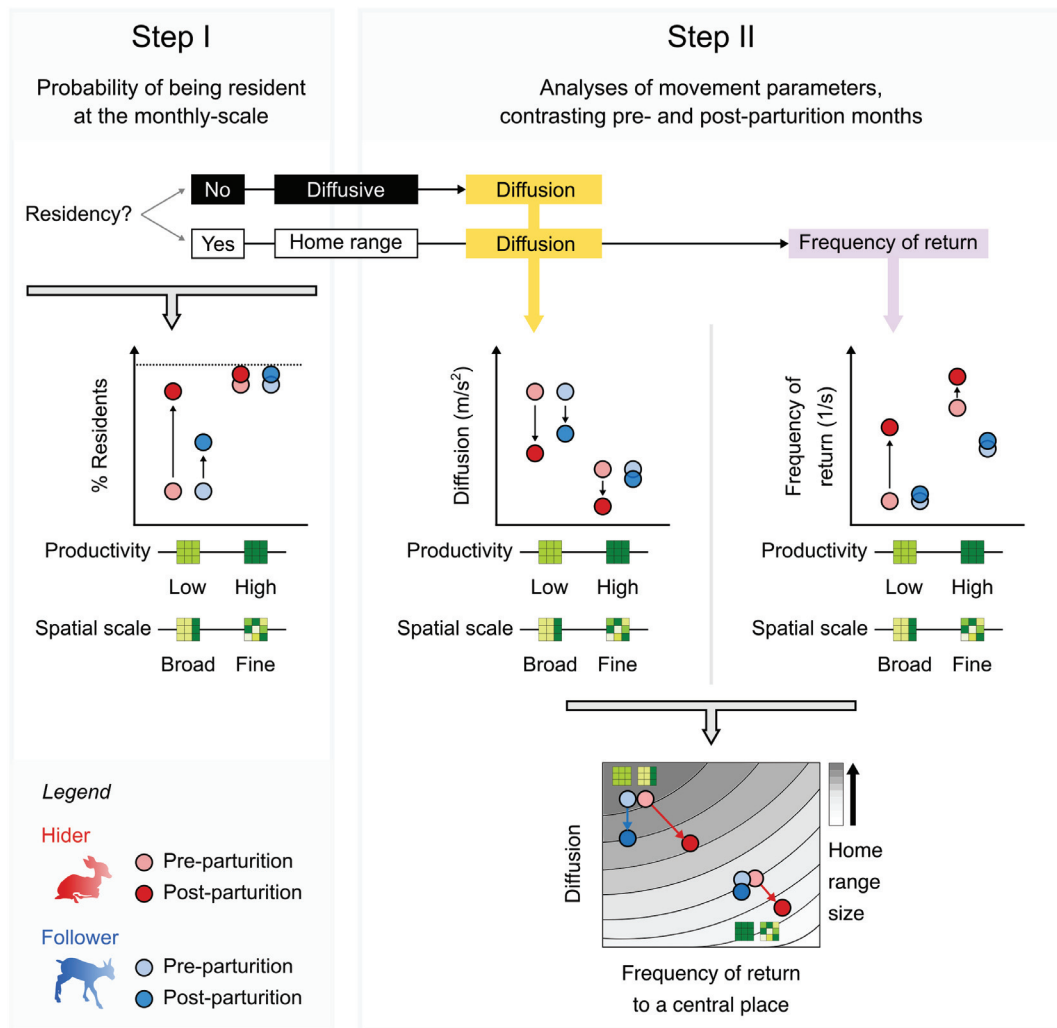


FIGURE 4.1: Conceptual framework of movement patterns of reproductive females in ungulate species in relation to the environment and to their offspring's neonatal anti-predator tactics. Step I) We first determine whether an animal is stationary in a focal period. We expect the percentage of residents to vary based on the neonatal anti-predator tactic, period, productivity, and spatial scale of variation in productivity. Step II) If an animal is found to be non-stationary in the focal track, we only extract the diffusion parameter. If an animal is found to be resident, we extract both diffusion and frequency of return in the focal track. We expect both movement parameters to change following parturition in relation to the neonatal anti-predator tactic and environmental variables. Red roe deer fawn and blue chamois kid represent hider and follower species, respectively.

variables, and contrary to our expectation, productivity had no effect on the degree of stationarity, regardless of parturition period or neonatal anti-predator tactic (Supplementary Figure S4.2). On the other hand, increasing spatial variation of vegetation productivity led to decreasing stationarity, but to different extents between periods and tactics (Figure 4.2, Supplementary Figure S4.2). This decrease was more stringent in hiders ($-2.786-2.53-2.272$) than followers ($-1.540-1.276-1.037$) during pre-parturition, and was shallower overall during post-parturition and similar in both tactics (followers = $-1.03-0.771-0.524$; hiders = $-1.149-0.926-0.696$). Consequently, the difference in stationarity between pre- and post-parturition was not the same between

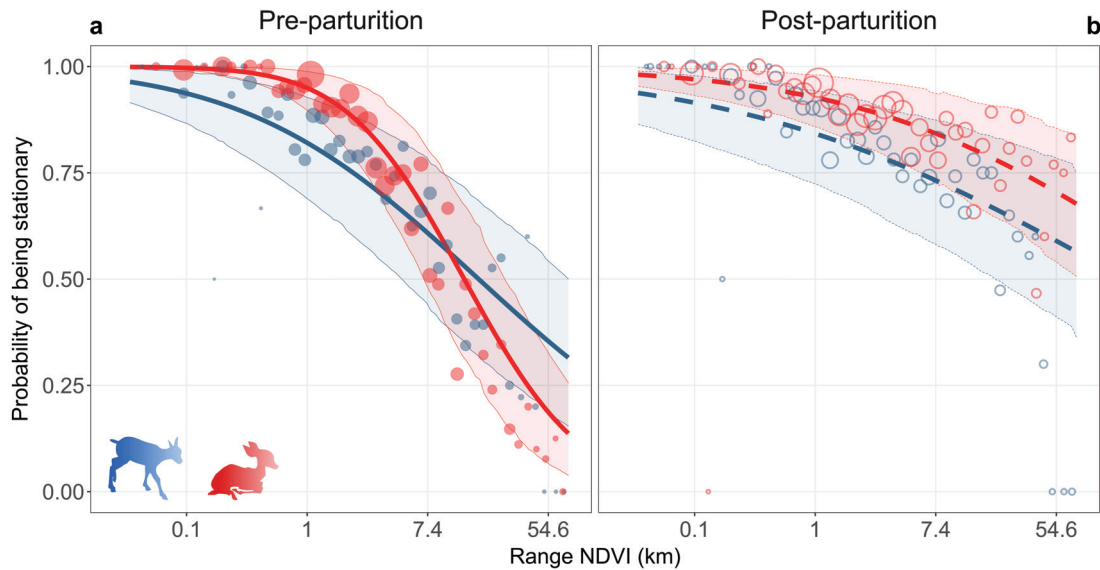


FIGURE 4.2: Predicted probabilities of being stationary for movement of females of 23 species of ungulates in response to parturition and spatial range of variability in productivity (a-b), retrieved from Bayesian phylogenetic mixed models, for hider (represented by the red roe deer fawn) and follower (represented by the blue chamois kid) species. Points, lines and shading represent mean probabilities, model fit and its associated 95% credible intervals, respectively. Size of points is proportionate to the number of individuals.

tactics. Accordingly, hidiers were 3.9 times more likely to be stationary during post-parturition compared to pre-parturition in environments with broad-scale spatial variation of productivity (range NDVI > 56km), while followers were only 1.7 times more likely to exhibit this behavior (Figure 4.2). This corroborates our expectation that females of hidiers become more stationary than females of followers after parturition especially for broad-scale spatial variation of vegetation productivity. Noticeably, however, a substantial proportion of females still exhibited non-stationary behavior after parturition in populations with large-scale spatial variation of productivity, even in species with hider offspring (e.g. up to 20% of pronghorns in the Northern Sagebrush Steppe and mule deer in Wyoming's Red Desert USA and western Washington USA).

4.2.2 Neonatal tactics and shift in female movements

Prior to parturition, diffusion rate was similar for hidiers and followers, irrespective of resource productivity (difference between tactics: $-0.102-0.0180_{0.068}$, Figure 4.3, model output in Supplementary Figures S4.3 and S4.4, Supplementary Figure S4.5c). Following parturition, contrary to our expectation, diffusion rate decreased more markedly in hidiers than in followers (difference between tactics: $-0.517-0.426_{-0.325}$, Figure 4.3). Diffusion also decreased with increasing resource productivity at a similar rate in both hidiers and followers (difference between tactics: $-0.277-0.194_{-0.106}$; Figure 4.3, Supplementary Figures S4.3 and S4.4). The impact of giving birth on the mother's diffusion rate was much lower when habitat productivity was low (4% increase in followers, 26% decrease in hidiers) than when it was high (38% decrease in followers, 56% in hidiers) (Figure 4.3). Spatial heterogeneity in resource productivity influenced

diffusion rate more markedly than mean productivity (model output in Supplementary Figures S4.3 and S4.4). Prior to parturition, diffusion rate increased more markedly with spatial heterogeneity in resource productivity for hidiers ($0.938_{0.996}^{1.054}$) compared to followers ($0.731_{0.807}^{0.889}$), but this relationship did not differ between hidiers ($0.273_{0.330}^{0.385}$) and followers ($0.291_{0.369}^{0.448}$) following parturition. When spatial heterogeneity in resource productivity was low, diffusion rate actually increased following parturition in both hidiers (by 41%) and followers (by 30%), but decreased markedly when spatial heterogeneity in resource productivity was intermediate or high, especially in hidiers (Supplementary Figure S4.5d).

As expected, hidiers had a consistently higher frequency of return than followers (Supplementary Figure S4.5e-f, Supplementary Figures S4.3 and S4.4). Prior to parturition, the frequency in return of mothers increased with habitat productivity to a similar degree in hidiers and followers (difference between tactics: $0.083_{0.166}^{0.241}$). This relationship persisted following parturition in followers, but disappeared in hidiers (slope: $-0.089_{0.005}^{0.085}$, Supplementary Figure S4.3). Thus, our expectation that the increase in the frequency of return following parturition should be more marked in hidiers than in followers was only supported when habitat productivity was low. Indeed, as the increase in the frequency of return lessened with productivity in hidiers (increase in return rate of 61%, 31% and 1% in low, intermediate, and high productivity habitats, respectively, Fig. 4.e) but not in followers (average increase of 12% across all values of habitat productivity), frequency of return was actually highest in hidiers in highly productive habitats.

For both neonatal tactics, the frequency of return decreased markedly as spatial heterogeneity in resource productivity increased, especially prior to parturition. The slope of this relationship was steeper in hidiers ($-0.791_{-0.724}^{-0.659}$) than followers ($-0.680_{-0.588}^{-0.494}$) such that the frequency of return differed to a greater extent between neonatal tactics when spatial heterogeneity in resource productivity was low (Supplementary Figure S4.5). Following parturition, although the negative relationship between frequency of return and spatial heterogeneity in resource productivity was attenuated for both neonatal tactics (model output in Supplementary Figures S4.3 and S4.4), the frequency of return still decreased with increasing spatial heterogeneity in resource productivity, albeit faster in hidiers ($-0.646_{-0.584}^{-0.521}$) than followers ($-0.543_{-0.458}^{-0.358}$, Supplementary Fig. S5). Thus, the increase in the frequency of return following parturition differed between tactics and depended on spatial heterogeneity in resource productivity (hidiers: increase of 11%, 31% and 53% for low, intermediate, and high values of heterogeneity, respectively; followers: decrease of 5% for low values, then increase of 12% and 31% for intermediate and high values of heterogeneity, respectively, Supplementary Figure S4.5f).

By decomposing home range size into its movement components (i.e. diffusion and frequency of return) (Figure 4.3), we assessed the interplay of resource productivity and neonatal tactic in determining parturition-related changes in movement behavior of mothers. Home range size increased with increasing diffusion rate and decreasing

frequency of return (Figure 4.3). Arrows were generally longer for hidere, clearly illustrating their more marked modifications in movement behaviour and home range size that occurred following parturition compared to followers. However, modifications in the movement parameters of followers could also be observed under particular environmental conditions, notably when resource productivity was both high and spatially heterogeneous.

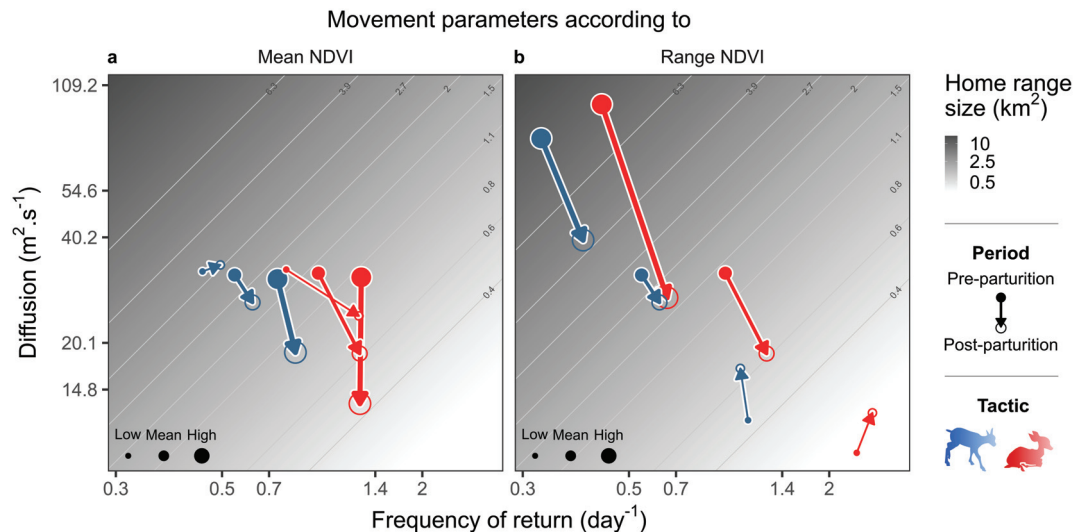


FIGURE 4.3: Predicted mean values for diffusion rate and frequency of return for females of 23 species of ungulates in relation to (a) mean resource productivity (mean NDVI) and (b) spatial variation in resource productivity (range NDVI) prior to and following parturition in hidere (red roe deer fawn) and followers (blue chamois kid). Low, mean, and high categories represent the 10%, mean, and 90% quantiles of each environmental variable, respectively (0.18, 0.41 and 0.72 for mean NDVI, and 0.25, 1.33 and 6.5 km for range NDVI). Arrows represent the change of each parameter from prior to (point) to following (arrow tip) parturition. Predicted values for each parameter were computed for an animal of 60 kg, and the mean value of one environmental variable was fixed when predicting the effect of the other environmental variable for every class.

4.3 Discussion

Reproductive mammalian females must cope with the conflicting constraints associated with keeping their offspring safe and the acquisition of food resources to offset the energetic demands of both reproduction and their own maintenance. The energetic constraint leads many species to match the timing of births with the seasonal peak of the resource flush (Linnell and Andersen, 1998a; Rutberg, 1987), and to track high quality resources through various movement patterns (Bischof et al., 2012; Fryxell et al., 2008; Mueller and Fagan, 2008; Singh et al., 2012) resulting from the spatio-temporal variation of resources in their landscape (Mueller and Fagan, 2008; Teitelbaum et al., 2015; Van Moorter et al., 2013). Habitat selection and movements of reproductive females have been shown to deviate from optimal resource tracking as a response to predation presence (Rivrud et al., 2018). However, how neonatal antipredator tactics, which have evolved at an evolutionary timescale (Fisher, Blomberg, and Owens, 2002), influence the

movement response of females in dynamic resource landscapes had not been extensively explored. Our study across 23 species of ungulates reveals that neonatal anti-predator tactics constrain females' responses to the productivity and spatial dynamics of their food resources.

The spatial variation in vegetation productivity was pivotal for determining the degree of stationarity and the spatial shifts in range use across all populations (see Supplementary Figure S4.6), which is in agreement with the results of previous comparative research (Mueller et al., 2011; Teitelbaum et al., 2015; Van Moorter et al., 2013). All reproductive females would bear some constraints in their movement after birth due to increased energetic demands and caring for their offspring, an explanation often brought forward to explain why some species may jump the green-wave rather than surfing it (Lendrum et al., 2014). However, a hider or a follower offspring impose widely different constraints on female movements. Females with follower offspring are only constrained by being coupled with an individual of a much lower mobility capacity, but, in contrast to females with hider offspring, are not bound to return to a given place. Interestingly, at broad-scale spatial variation in productivity, the probability for a female to be stationary was lowest before parturition and highest after parturition in species with hider offspring. This suggests that migration may be more urgent for females with hider offspring than for females with follower offspring, thus anticipating the peak of the vegetation flush as well as the movement constraint imposed by their offspring. At the same time, migrating before parturition may be a less perilous movement strategy for hider mothers, as predation risk is already high during migration (Nicholson, Bowyer, and Kie, 1997) and would only be higher with the limited mobility of their young. Noticeably, the level of non-stationarity did not drop to zero even in hider species living in sites with broad-scale spatial variation in productivity like the saiga antelope and Mongolian gazelle in Mongolia, pronghorn in Wyoming USA, or mule deer from Western Washington USA. Caring for a hider offspring and non-stationarity could be compatible if neonates relocate their hiding site to mirror the foraging movements of females (Panzacchi et al., 2010) or if the hiding phase is short. Given the constraint imposed by caring for a concealed offspring, we need more comprehensive studies of how hider species cope in environments with a narrow temporal flush of resources over large-scale geographic gradients (Morellet et al., 2013) and whether the duration of the hiding phase is reduced in populations where females would need to track resources at a broad spatial scale.

Our results revealed how females adjusted two key movement processes, diffusion and the frequency of return visits, from pre- to post-parturition, with direct outcome on home range size. Even when not considering the neonatal antipredator tactics, the patterns of changes from pre- to post-parturition are complex, and contrast environments with high productivity and/or low spatial range of resource variation with environments with low productivity and/or high spatial range of resource variation, as exemplified by the different shifts in the diffusion-frequency of return space (Figure 4.3). The similar responses to parturition of females of both anti-predator tactics probably translate that

having an offspring, be it hider or follower, is a constraint on movement. Additionally, as the vegetation after birth reaches its peak production (English et al., 2012; Linnell and Andersen, 1998a; Sinclair, Mduma, and Arcese, 2000), females may not need to diffuse as far to forage, and return to the best feeding places. But here, we unveil that neonatal tactics lead to differences in the shifts on movement components, in most environments. The smaller home range sizes after parturition for females with hider neonates (documented in several single studies such as roe deer: Saïd et al., 2005, and fallow deer: Ciuti et al., 2006) results from a combination of a larger decrease in diffusion and increase in the frequency of return visits to a central location (Figure 4.3) than in females with follower neonates, as expected due to the need for females to go back frequently to their concealed offspring (Péron et al., 2018; Saïd et al., 2005; Van Moorter et al., 2009a). Females with follower offspring have also lower diffusion after parturition compared to pre-parturition, which could possibly arise from the relatively limited mobility of their neonates, but could also be a behavioral tactic of mothers to reduce the energetic costs of movement borne, not only by them, but also by the offspring (Carl and Robbins, 1988). Furthermore, the offspring's resting time and immobility during suckling adds constraints on female movement range (Green, 1992), not only in hider but also in follower species, possibly contributing to shifts in the post-parturition movement components variation in the latter species.

The evolution of neonatal anti-predator tactics in herbivores should be envisioned more comprehensively, because it might not have evolved solely as a response to differing predator guild (Estes and Estes, 1979; Rutberg, 1987) and habitat structure (Fisher, Blomberg, and Owens, 2002; Green, 1992). Indeed, offspring survival depends strongly on body mass at birth (Gaillard et al., 2000) and subsequent growth rate, which influence offspring ability to cope with weather variation (e.g. through thermoregulation) and vulnerability to predation. The crux is therefore to understand whether hider and follower species differ, and under which environmental conditions, in terms of birth and weaning body mass, growth rate, and eventually offspring survival. The energy allocation (to maintenance, movement, and growth for the neonate, and to maintenance, movement, and milk production for the female) are born differently by the female and its neonate depending on the tactics (Carl and Robbins, 1988; Fisher, Blomberg, and Owens, 2002). Hider neonates bear limited costs of movement (though the location of bed sites can change through time, Linnell et al., 1999; Van Moorter et al., 2009a) and can therefore allocate most of the energy provided by their mother to growth, while for follower offspring, neonates also deplete their own energy to remain in contact with their mother (Carl and Robbins, 1988). In turn, for females with hider offspring, commuting for nursing the offspring (which occur as often as every hour, Saito and Idani, 2018) can incur significant direct energetic costs due to movement and, possibly, indirect energetic costs in terms of missed possibility to reach high quality resources in heterogeneous habitats (Panzacchi et al., 2010). In follower species, females may therefore have to provide more energy than in hider species for the same relative offspring growth rate to offset their offspring's energy expenditure resulting from its movement. Whether

offspring body mass at weaning differs or not among tactics (with the latter found in controlled condition by Carl and Robbins, 1988), the interplay between energetic expenditure and acquisition for mother and neonates is not similar in hider and follower species, with potential consequences on how these species perform depending on the spatio-temporal dynamics of their resource landscape. The relative allocation of energy to somatic maintenance and reproduction in relation to the timing of breeding has led to rank species, within their taxon, along a continuum of income- to capital breeder species (Jönsson, 1997; Stephens et al., 2009), which results in differences in how species respond to environmental variation, especially, as emphasized by Stephens et al. (2009) in populations living in highly seasonal environment and/or migrating before reproduction. Given that neonatal antipredator tactics influence movement patterns in relation to large-scale spatiotemporal variation in resources, and that they may influence the pathway through which female energy acquisition is transferred to offspring, it would be enlightening to add the neonatal tactic as a potential lifestyle variable explaining how species cope with environmental variability.

4.4 Material and methods

4.4.1 Study sites and GPS data

We collected datasets either through the Movebank animal tracking database and repository available online (<https://www.movebank.org>), or by direct contact with the co-authors and data providers (Table S4.1). Because we were focusing on movement prior to and following parturition, we removed from our dataset adult females known for not having reproduced as well as individuals with no monitoring covering the entire reproductive period as well as individuals with known negative reproductive status. We removed outlier GPS locations using the method proposed by Bjørneraas et al. (2010). Following this selection procedure, our dataset contained 3,907,880 GPS locations of 23 ungulate species (11 generally classified as followers and 12 as hidere) from 54 worldwide populations distributed along longitudinal and latitudinal gradients (Figure 4.4), with 2,386 individuals monitored from 1997 to 2019, thus representing a total of 3,942 individual-years.

4.4.2 Defining reproductive periods

Because we wanted to investigate movement prior to and following parturition, and for the best precision, we defined timeframes that best capture the pre-parturition and post-parturition periods. When precise information on reproduction was available (12 populations), we used individual parturition dates to divide the monitoring into a one-month pre-parturition (parturition date – 30 days) and one-month post-parturition periods (parturition date + 30 days), hereafter referred to as tracks. Choosing a one-month window allowed us to cover the full timeframe when mother-infant interactions and neonatal behavior were at their peak, therefore sampling the period where it was most likely to observe clear changes in movement, even though the duration of

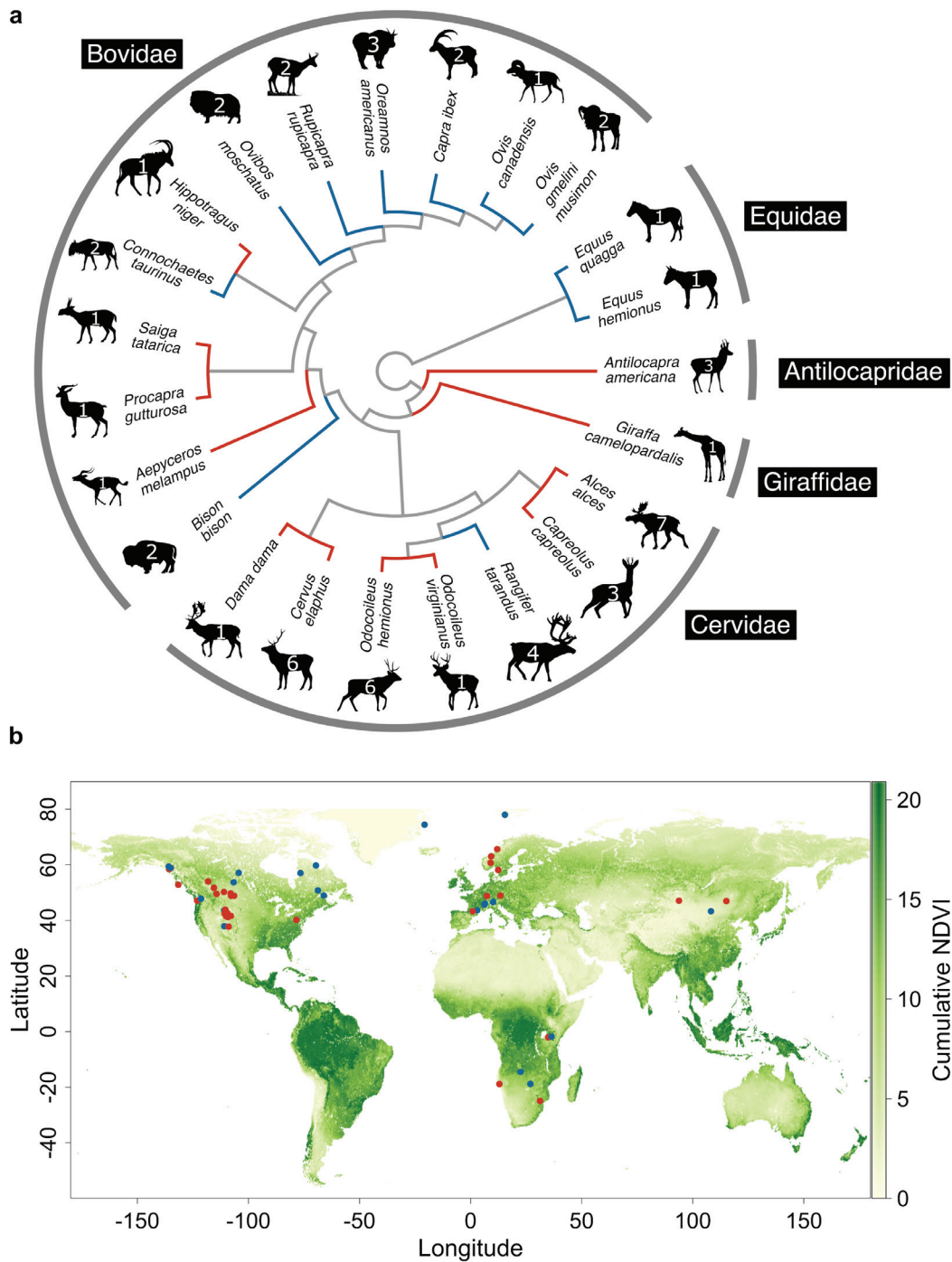


FIGURE 4.4: Overview of the species and populations. a) Phylogenetic tree of the 23 species of ungulate included in this study (see the [Phylogenetic analysis](#) section in the [Supplementary Information](#)). The number of populations for each species is indicated on each pictogram (downloaded from <http://www.phylopic.org> or from the personal collection of the authors). b) Average location of each population (see [Table S4.1](#)) on a composite map of cumulative Normalized Difference Vegetation Index (NDVI) values, retrieved from [Radeloff et al. \(2019\)](#), and used solely for presentation purposes. Red and blue represent hider and follower species, respectively.

these interactions vary across species. At the same time, our study focuses on the

asymptotic range residency behavior of movement (detailed in [next section](#)), which is most commonly achieved over a monthly time frame.

In the remaining 42 populations, individual parturition dates were unavailable. However, most ungulates exhibit pulsed breeding (English et al., 2012; Rutberg, 1987; Sinclair, Mduma, and Arcese, 2000), yielding a normal or log-normal distribution of birth dates. We therefore defined a population-based cut-off date, corresponding to 5% of birth events (Supplementary [Figure S4.7](#)), using both data previously published or a best informed estimate provided by data owners (Supplementary [Table S4.2](#)). With a 5% cut-off date, we made sure that most females did not give birth preceding that date but would eventually do so afterwards, thus leaving a small margin of error with the presumably 5% of females who had already given birth. This method was applied to females with no individual parturition dates (representing 2,906 or 73.72% of individual-year). In populations where individual parturition dates were not available for all females (10 out of 12 populations), we used the on-hand available individual parturition dates to compute the 5% cut-off.

4.4.3 Continuous-time stochastic movement models and model fitting

Continuous-time stochastic movement models (CTMM) offer more robust statistical approaches than discrete-time models by accounting for temporal autocorrelation (Calabrese, Fleming, and Gurarie, 2016; Fleming et al., 2014; Fleming, Subaşı, and Calabrese, 2015). They describe movement as continuous through time, with a stable process-mean accompanied by random deviations from the expected path (i.e. stochasticity). While the simplest of CTMM classes, the Brownian Motion model (BM), fails to account for the emergence of home ranges given its assumption of an infinite diffusion process (Blackwell, 1997) ([Table 4.1](#)), other classes of CTMM do actually lead to bounded home ranges, such as Ornstein-Uhlenbeck (OU) models (Dunn and Gipson, 1977). These models are especially attractive because the movement variance (usually denoted σ^2) can be decomposed into the contribution of diffusion (D) and position autocorrelation time (Fleming et al., 2014) (τ_p), two parameters of ecological interest ([Table 4.1](#)). The diffusion coefficient determines how animals move away from their expected paths, while being constantly attracted back to it at a rate defined by the position autocorrelation time, thus leading to a range-defined movement process. As a consequence, the net squared displacement (Börger and Fryxell, 2012; Fryxell et al., 2008) (i.e. squared Euclidean distance between start and end point of a trajectory) and the semivariogram of the location time series (Fleming et al., 2014) reach an asymptote that scales to the home range size (Supplementary [Figure S4.8](#)). In fact, the asymptotic value of the Gaussian distribution of the movement process represents σ^2 which is a proxy of home range size, and the rate of increase of the semivariance with time before it reaches σ^2 represents τ_p whose inverse represents the frequency of return to a central point.

Because the low number of parameters of OU models cannot resolve complex animal movement patterns at fine time scales, further classes of models have been

TABLE 4.1: Glossary of parameters and movement processes of interest, adapted from Péron et al. (2017)

Parameters and models	and Notations and acronyms	Biological meaning
Movement variance	$\sigma^2 (m^2)$	The non-random movement amplitude of the movement process, representing a proxy of home range size.
Instantaneous diffusion	$D (m^2.s^{-1})$	The rate at which the animal moves away from its expected path.
Position autocorrelation time	$\tau_p (s)$	Quantifies the rate at which the animal reverts back to its expected path after a random deviation. Its inverse represents the frequency of return of the animal to a central place.
Velocity autocorrelation time	$\tau_v (s)$	Quantifies the intensity of persistence in the direction and speed of movement.
Brownian motion	BM	An endlessly diffusing movement process described simply by the instantaneous diffusion parameter (D) and representing non-stationarity.
Ornstein-Uhlenbeck position movement process	OU	A stationary home range-bounded movement process described by two parameters: the instantaneous diffusion parameter and the position autocorrelation time.
Ornstein-Uhlenbeck-Foraging movement process	OUF	A stationary home range-bounded movement process, superficially similar to the Ornstein-Uhlenbeck position process, and described by three parameters: the instantaneous diffusion parameter, the position autocorrelation time, and the velocity autocorrelation time.

introduced (e.g. Ornstein-Uhlenbeck Foraging model: Fleming et al., 2014), and incorporate temporal autocorrelation in position (τ_p) and velocity (τ_v). Using these models and parameters, we head out to test our biological hypotheses when it comes to stationarity (stationary OU vs non-stationary BM), home range size (σ^2), diffusion, and frequency of return (inverse of τ_p). For each period (i.e. before/after parturition), we first determined whether the individual was stationary or not using empirical semivariograms (Supplementary Figure S4.8). The semivariance is a measure of the similarity in distance between two recorded locations, as a function of the time lag between them and calculated over all possible time lags (Fleming et al., 2014). The semivariogram is a useful diagnosis tool to categorize movement types. If the semivariance increases monotonically with the time lag, the movement is endlessly diffusive, like a Brownian Motion (BM). By contrast, if the semivariance exhibits an inflexion and reaches an asymptote for large time lags, the animal is stationary or home-

range-bounded, like an Ornstein-Uhlenbeck process (Calabrese, Fleming, and Gurarie, 2016; Dunn and Gipson, 1977; Fleming et al., 2014).

We selected only tracks with a median sampling interval not higher than 6 hours, with at least 14 days of data and a minimum of 60 locations per period (Börger et al., 2006b). We followed the method proposed by Bunnefeld et al. (2011) and fit competing non-linear models to the empirical semivariograms, selecting the best fit using the Akaike Information Criterion. In practice we fitted the BM and OU models, each corresponding to a known nonlinear semivariance model (Fleming et al., 2014). We fitted the OU process to the stationary tracks using the *ctmm.fit* routine in the *ctmm* package (Fleming and Calabrese, 2020) available in R (R Core Team, 2020). Given that velocity autocorrelation can bias the estimation of the movement amplitude (Fleming et al., 2014), we first fitted an OU-Foraging (OUF; includes velocity autocorrelation time τ_v) model to extract the diffusion parameter (D), position autocorrelation time (τ_p) and movement variance (σ^2). In some cases (1.6% of analyzed tracks), our data did not support the OUF model, probably because the velocity autocorrelation time was smaller or of the same order of magnitude as the sampling interval, thus we fitted the OU model and extracted the same focal parameters. For tracks identified as non-stationary BM, we only extracted the diffusion parameter D from fitting a theoretical semivariogram to the empirical one. All values were log-transformed. To remove potential outliers, we computed Z-scores for each population:

$$Z = \frac{(x_{ip} - \mu_{ip})}{\sigma_{ip}}$$

where x_{ip} is the parameter's i value in the period p , μ_{ip} is the mean of all the parameter's i values in period p and σ_{ip} (not to be confused with σ^2 of the OU movement model) is the standard deviation of all the parameter's i values in period p . We removed scores that were lower than -3 or higher than 3 which represented 1.14% ($N = 90$ out of 7,884) of all tracks and 0.2% ($N = 8$ out of 3,942) of all individual-years. If an OU track was identified as an outlier for a certain parameter, all parameters of that track were subsequently removed because we were interested in the combined, even though non-independent, variation of diffusion, frequency of return, and home range size. Some individual-years had only one of their periods removed as outliers. In these cases, we ended up removing all the individual-year ($N = 74$ out of 3,934) since analyzing changes in movement required both tracks. For BM models, only the diffusion coefficient D was used to compare changes between pre- and post-parturition periods.

Following all the above mentioned criteria, our extensive dataset included 2,342 reproductive females (Table S4.1) with 3,860 female-years covering the pre- and post-parturition periods (i.e., 7,720 tracks). The data covered 23 species, with between one and seven populations per species, located in a wide range of ecosystems, from the low productivity biomes of the Mongolian steppes to the highly productive systems found in the temperate regions of Europe (Figure 4.4b).

4.4.4 Covariates

Resource availability and distribution are known to influence animal movement, where individuals in low productive and highly heterogeneous environments move longer distances (Mueller et al., 2011; Teitelbaum et al., 2015), seeking necessary resources to satisfy their energetic needs. To evaluate the effect of resource productivity and spatial distribution on movement, we used the Normalized-Difference Vegetation Index (NDVI) MOD13Q1 v.006 images with a 250m resolution at a 16-day interval, derived from MODIS satellite imagery and available online (https://search.earthdata.nasa.gov/search?q=C194001241-LPDAAC_ECS). NDVI is an index of primary productivity measuring the green biomass of the canopy and grasslands (Boschetti, Bocchi, and Brivio, 2007; Santin-Janin et al., 2009), though previous studies (Borowik et al., 2013) also found a correlation between understory biomass and NDVI values in forest habitats.

We retrieved NDVI composite images spanning from February 2000 to December 2019, which correspond to the years when NDVI 250m was first available and the last year of monitoring in our dataset, respectively. We rescaled NDVI values to vary between $[-1,1]$, and modified and removed values based on pixel reliability provided with the MOD13Q1. Pixels with reliability values of -1 (no data) and 3 (cloudy) were removed, and those of 2 (snow/ice) were assigned to a NDVI value of 0. Following Teitelbaum et al. (2015), we set a minimum threshold of 0.05 to all NDVI values below that threshold which do not reflect resource availability for ungulates.

We computed, for each individual-year, the 95% Minimum Convex Polygon (MCP) of all GPS locations from both periods using the `adehabitatHR` package (Calenge, 2006) in R. Afterwards, we extracted, for each polygon, the mean annual NDVI for the corresponding year of monitoring as a proxy of resource availability, a temporal scale which has been shown to relate to seasonal migration distance (Teitelbaum et al., 2015). For individual-years monitored before 2000 ($N = 5$, Bison in Prince Albert National Park, Canada), we used the NDVI images from 2000. We also measured the spatial range of variation of resources by extracting, for each polygon, the mean annual NDVI (mean NDVI) values of each pixel for the corresponding year of monitoring and subsequently calculating the spatial range (m) of the autocorrelation in NDVI (range NDVI) values using the `variofit` function from the `geoR` package (Ribeiro Jr et al., 2007) available in R. High values of the spatial range of NDVI represent broad-scale variability in resources, whereas low values represent fine-scale variability (Van Moorter et al., 2013). For 421 out of the 3,860 individual-years, we randomly subsampled 6,000 of the 250x250m cells, following Teitelbaum et al. (2015), to avoid computational limitations due to the high number of cells retrieved in their polygons. Finally, using published papers, we retrieved the mean body mass of adult females for each species in our dataset (Table S4.1) to take into account the allometry of movement, because larger animals have bigger movement amplitudes and cover larger areas (Ofstad et al., 2016).

4.4.5 Statistical analysis

For all our analyses, we used Bayesian Phylogenetic Mixed-effect Models (BPMM), which are appropriate to perform phylogenetic analyses on large datasets with multiple measurements per species, and implemented in the `MCMCglmm` package (Hadfield, 2010) for R. It was essential to control for phylogeny as a way to correct for non-independence between species-specific data points that may arise from relatedness among species sharing common traits. We constructed our own phylogenetic tree using full mitogenome sequences retrieved from Genbank (Clark et al., 2016) (see the [Phylogenetic analysis](#) section in the [Supplementary Information](#) for full details).

We first tested the effect of neonatal tactic (hider *vs.* follower), resource availability, spatial variation, and period (pre- *vs.* post-parturition) on the probability of being stationary. We ran BPMM with a binomial distribution specified with the argument `family = categorical` using the function `MCMCglmm` to investigate the probability of being stationary in each track, defined as a binary response variable (0 = *non-stationary BM* and 1 = *stationary OU/OUF*). We included phylogeny (to which we attributed the variance-covariance matrix), species (since multiple measurements for a given species can share biological traits that do not arise from the phylogenetic relatedness), population nested in species, year nested in population, and individuals nested in population and species as random factors. We added two three-way interactions in the model as two fixed effects: the first between neonatal tactics, mean NDVI, and period, and the second one with the log-transformed range NDVI instead of the mean NDVI. The log-transformed body mass was added as an additive fixed effect to account for the allometric relation of movement (Noonan et al., 2020; Ofstad et al., 2016), along with the monitoring duration of the track (days) and number of locations since a finer and longer sampling procedure has a higher chance of detecting a stationary behavior. Both variables were also log-transformed. We first used a non-informative Inverse Wishart prior ($\nu = 0.02$ and $V = 1$) with a fixed residual variance ($V = 1$ and $fix = 1$). As a second step, we conducted a sensitivity analysis to verify that the prior did not impact our results and re-ran the model using a parameter extended prior ($\nu = 1$, $V = 1$, $alpha.mu = 0$, $alpha.V = 1,000$). We observed no difference between the results from each prior. We ran the model three times with 550,000 iterations ($burn-in = 50,000$ and $thinning = 100$) and conducted the Gelman-Rubin diagnostic (Gelman and Rubin, 1992) using the `gelman.diag` function from the package `coda` (Plummer et al., 2006) to confirm the convergence of the model. If any difference is observed between the three MCMC chains, the diagnostic concludes that the model did not converge. In our case, we did not detect any difference between our models.

To assess the effect of parturition and the environment on movement parameters in relation to neonatal tactic, we ran similar BPMM, in terms of random and fixed effects, but with home range size, diffusion and frequency of return as continuous response variables and a Gaussian distribution for the data. In the models on diffusion, we added the attributed model (BM or OU/OUF) as an additive fixed effect to control for differences in diffusion values between BM and OU, the former expressing larger

diffusion than the latter. For models on the frequency of return and home range size, we only included individuals with tracks identified as stationary Ornstein-Uhlenbeck during both periods. This led to the removal of Mongolian gazelles from the analyses because all individuals were non-stationary during the post-parturition period. We also added, as a statistical weight and for all models, the inverse of the error variance for each data point. We used the non-informative Inverse Wishart prior ($\nu = 0.02$ and $V = 1$) with no fixed residual variance and ran the model with 550,000 iterations (*burn-in* = 50,000 and *thinning* = 100). We also conducted a sensitivity analysis with an extended prior ($\nu = 1$, $V = 1$, $\alpha.\mu = 0$, $\alpha.V = 1,000$) and found no difference in our results from both priors. We ran the Gelman-Rubin diagnostic and found that our models did converge. To prepare [Figures 4.2](#) and [4.3](#), we predicted values for each parameter in relation to the 10%, mean and 90% quantiles of every environmental variable (mean and range NDVI) using individuals which were stationary (OU/OUF) during both periods. When predicting values for one environmental variable, we fixed the other at its mean. We fixed the body mass at 60 kg, representing the mean body mass of ungulates (Fritz and Loison, 2006), and which was log-transformed.

We calculated the phylogenetic heritability H^2 (Lynch, 1991) for each model mentioned above, which can be interpreted similarly as Pagel's phylogenetic signal λ (Pagel, 1999). A phylogenetic heritability of 0 indicates that no phylogenetic relatedness exists among effect sizes, while an $H^2 = 1$ indicates an exact proportional relationship between effect sizes among species and their phylogenetic relatedness (Nakagawa and Santos, 2012). We reported the mean of the posterior distribution for each effect along with its 95% credible interval of the highest posterior density distribution (HPDI). The significance of an effect was determined by the exclusion of 0 from its credible interval.

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Author contributions

K.A., G.P. and A.L. designed the study, C.B, J.M.G., M.G., A.J.M.H, P.M, N.M and S.S contributed to the study design through fruitful discussions, K.A. analyzed the data and

wrote the first draft. Co-authors collected and provided the datasets, participated in the writing process and approved the final version of the manuscript.

References

- Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., and Mysterud, A. (2012). "A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave?" In: *The American Naturalist* 180.4, pp. 407–424.
- Bjørneraas, K., Moorter, B. V., Rolandsen, C. M., and Herfindal, I. (2010). "Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics." In: *The Journal of Wildlife Management* 74.6, pp. 1361–1366.
- Blackwell, P. G. (1997). "Random diffusion models for animal movement." In: *Ecological Modelling* 100.1, pp. 87–102.
- Börger, L. and Fryxell, J. (2012). "Quantifying individual differences in dispersal using net squared displacement." In: *Dispersal Ecology and Evolution*. Ed. by Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M. Oxford University Press, pp. 222–230.
- Börger, L. et al. (2006b). "Effects of sampling regime on the mean and variance of home range size estimates." In: *Journal of Animal Ecology* 75.6, pp. 1393–1405.
- Borowik, T., Pettorelli, N., Sönnichsen, L., and Jędrzejewska, B. (2013). "Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats." In: *European Journal of Wildlife Research* 59.5, pp. 675–682.
- Boschetti, M., Bocchi, S., and Brivio, P. A. (2007). "Assessment of pasture production in the Italian Alps using spectrometric and remote sensing information." In: *Agriculture, Ecosystems & Environment* 118.1, pp. 267–272.
- Bunnefeld, N. et al. (2011). "A model-driven approach to quantify migration patterns: individual, regional and yearly differences." In: *Journal of Animal Ecology* 80.2, pp. 466–476.
- Calabrese, J. M., Fleming, C. H., and Gurarie, E. (2016). "ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process." In: *Methods in Ecology and Evolution* 7.9, pp. 1124–1132.
- Calenge, C. (2006). "The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals." In: *Ecological Modelling* 197.3, pp. 516–519.
- Carl, G. R. and Robbins, C. T. (1988). "The energetic cost of predator avoidance in neonatal ungulates: hiding versus following." In: *Canadian Journal of Zoology*.
- Ciuti, S., Bongi, P., Vassale, S., and Apollonio, M. (2006). "Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation." In: *Journal of Zoology* 268.1, pp. 97–107.

- Clark, K., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J., and Sayers, E. W. (2016). "GenBank." In: *Nucleic Acids Research* 44.Database issue, pp. D67–D72.
- Clutton-Brock, T. H., Albon, S. D., and Guinness, F. E. (1989). "Fitness costs of gestation and lactation in wild mammals." In: *Nature* 337.6204, pp. 260–262.
- Dunn, J. E. and Gipson, P. S. (1977). "Analysis of Radio Telemetry Data in Studies of Home Range." In: *Biometrics* 33.1, pp. 85–101.
- English, A. K., Chauvenet, A. L. M., Safi, K., and Pettorelli, N. (2012). "Reassessing the Determinants of Breeding Synchrony in Ungulates." In: *PLOS ONE* 7.7, e41444.
- Estes, R. D. and Estes, R. K. (1979). "The Birth and Survival of Wildebeest Calves." In: *Zeitschrift für Tierpsychologie* 50.1, pp. 45–95.
- Fauchald, P. (1999). "Foraging in a Hierarchical Patch System." In: *The American Naturalist* 153.6, pp. 603–613.
- Fisher, D. O., Blomberg, S. P., and Owens, I. P. F. (2002). "Convergent Maternal Care Strategies in Ungulates and Macropods." In: *Evolution* 56.1, pp. 167–176.
- Fleming, C. H., Calabrese, J. M., Mueller, T., Olson, K. A., Leimgruber, P., and Fagan, W. F. (2014). "From Fine-Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement Modes across Spatiotemporal Scales." In: *The American Naturalist* 183.5, E154–E167.
- Fleming, C. H., Subaşı, Y., and Calabrese, J. M. (2015). "Maximum-entropy description of animal movement." In: *Physical Review E* 91.3, p. 032107.
- Fleming, C. H. and Calabrese, J. M. (2020). *ctmm: Continuous-Time Movement Modeling*.
- Fritz, H. and Loison, A. (2006). "Large herbivores across biomes." In: *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Ed. by Danell, K., Bergström, R., Duncan, P., and Pastor, J. Conservation Biology. Cambridge University Press, pp. 19–49.
- Fryxell, J. M. et al. (2008). "Multiple movement modes by large herbivores at multiple spatiotemporal scales." In: *Proceedings of the National Academy of Sciences* 105.49, pp. 19114–19119.
- Gaillard, J.-M., Festa-Bianchet, M., Delorme, D., and Jorgenson, J. (2000). "Body mass and individual fitness in female ungulates: bigger is not always better." In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267.1442, pp. 471–477.
- Gelman, A. and Rubin, D. B. (1992). "Inference from Iterative Simulation Using Multiple Sequences." In: *Statistical Science* 7.4, pp. 457–472.
- Green, W. C. H. (1992). "The development of independence in bison: pre-weaning spatial relations between mothers and calves." In: *Animal Behaviour* 43.5, pp. 759–773.

- Hadfield, J. D. (2010). "MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package." In: *Journal of statistical software* 33.2, pp. 1–22.
- Jönsson, K. I. (1997). "Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction." In: *Oikos* 78.1, pp. 57–66.
- Lendrum, P. E., Anderson, C. R., Monteith, K. L., Jenks, J. A., and Bowyer, R. T. (2014). "Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality." In: *Mammalian Biology* 79.6, pp. 369–375.
- Lent, P. C. (1974). "Mother-infant relationships in ungulates." In: *The behaviour of ungulates and its relation to management* 1, pp. 14–55.
- Linnell, J. D. C. and Andersen, R. (1998a). "Timing and synchrony of birth in a hider species, the roe deer *Capreolus capreolus*." In: *Journal of Zoology* 244.4, pp. 497–504.
- Linnell, J. D. C., Aanes, R., and Andersen, R. (1995). "Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates." In: *Wildlife Biology* 1.1, pp. 209–223.
- Linnell, J. D. C., Nijhuis, P., Teurlings, I., and Andersen, R. (1999). "Selection of bed-sites by roe deer *Capreolus capreolus* fawns in a boreal forest landscape." In: *Wildlife Biology* 5.1, pp. 225–231.
- Lynch, M. (1991). "Methods for the Analysis of Comparative Data in Evolutionary Biology." In: *Evolution* 45.5, pp. 1065–1080.
- Morellet, N. et al. (2013). "Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe." In: *Journal of Animal Ecology* 82.6, pp. 1326–1339.
- Mueller, T. and Fagan, W. F. (2008). "Search and navigation in dynamic environments – from individual behaviors to population distributions." In: *Oikos* 117.5, pp. 654–664.
- Mueller, T., Olson, K. A., Fuller, T. K., Schaller, G. B., Murray, M. G., and Leimgruber, P. (2008). "In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity." In: *Journal of Applied Ecology* 45.2, pp. 649–658.
- Mueller, T. et al. (2011). "How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data." In: *Global Ecology and Biogeography* 20.5, pp. 683–694.
- Nakagawa, S. and Santos, E. S. A. (2012). "Methodological issues and advances in biological meta-analysis." In: *Evolutionary Ecology* 26.5, pp. 1253–1274.
- Nicholson, M. C., Bowyer, R. T., and Kie, J. G. (1997). "Habitat Selection and Survival of Mule Deer: Tradeoffs Associated with Migration." In: *Journal of Mammalogy* 78.2, pp. 483–504.

- Noonan, M. J. et al. (2020). "Effects of body size on estimation of mammalian area requirements." In: *Conservation Biology* 34.4, pp. 1017–1028.
- Ofstad, E. G., Herfindal, I., Solberg, E. J., and Sæther, B.-E. (2016). "Home ranges, habitat and body mass: simple correlates of home range size in ungulates." In: *Proceedings of the Royal Society B: Biological Sciences* 283.1845, p. 20161234.
- Oftedal, O. T., Boness, D. J., and Tedman, R. A. (1987). "The Behavior, Physiology, and Anatomy of Lactation in the Pinnipedia." In: *Current Mammalogy*. Ed. by Genoways, H. H. Boston, MA: Springer US, pp. 175–245.
- Pagel, M. (1999). "Inferring the historical patterns of biological evolution." In: *Nature* 401.6756, pp. 877–884.
- Panzacchi, M., Herfindal, I., Linnell, J. D. C., Odden, M., Odden, J., and Andersen, R. (2010). "Trade-offs between maternal foraging and fawn predation risk in an income breeder." In: *Behavioral Ecology and Sociobiology* 64.8, pp. 1267–1278.
- Péron, G. (2019). "The time frame of home-range studies: from function to utilization." In: *Biological Reviews* 94.6, pp. 1974–1982.
- Péron, G. et al. (2017). "Periodic continuous-time movement models uncover behavioral changes of wild canids along anthropization gradients." In: *Ecological Monographs* 87.3, pp. 442–456.
- Péron, G. et al. (2018). "Circadian periodicity in space use by ungulates of temperate regions: How much, when and why?" In: *Journal of Animal Ecology* 87.5, pp. 1299–1308.
- Plummer, M., Best, N., Cowles, K., and Vines, K. (2006). "CODA: convergence diagnosis and output analysis for MCMC." In: *R news* 6.1, pp. 7–11.
- R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Radeloff, V. C. et al. (2019). "The Dynamic Habitat Indices (DHIs) from MODIS and global biodiversity." In: *Remote Sensing of Environment* 222, pp. 204–214.
- Ribeiro Jr, P. J., Diggle, P. J., Ribeiro Jr, M. P. J., and Suggests, M. (2007). "The geoR package." In: *R news* 1.2, pp. 14–18.
- Rivrud, I. M., Sivertsen, T. R., Mysterud, A., Åhman, B., Støen, O.-G., and Skarin, A. (2018). "Reindeer green-wave surfing constrained by predators." In: *Ecosphere* 9.5, e02210.
- Rutberg, A. T. (1987). "Adaptive Hypotheses of Birth Synchrony in Ruminants: An Interspecific Test." In: *The American Naturalist* 130.5, pp. 692–710.
- Säid, S. et al. (2005). "Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland." In: *Journal of Zoology* 267.3, pp. 301–308.

- Saito, M. and Idani, G. (2018). "Giraffe Mother-Calf Relationships in the Miombo Woodland of Katavi National Park, Tanzania." In: *Mammal Study* 43.1, pp. 11–17.
- Santin-Janin, H., Garel, M., Chapuis, J.-L., and Pontier, D. (2009). "Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: a case study on the Kerguelen archipelago." In: *Polar Biology* 32.6, pp. 861–871.
- Searle, K. R., Hobbs, N. T., and Gordon, I. J. (2007). "It's the "Foodscape", not the Landscape: Using Foraging Behavior to Make Functional Assessments of Landscape Condition." In: *Israel Journal of Ecology and Evolution* 53.3-4, pp. 297–316.
- Sinclair, A. R. E., Mduma, S. A. R., and Arcese, P. (2000). "What Determines Phenology and Synchrony of Ungulate Breeding in Serengeti?" In: *Ecology* 81.8, pp. 2100–2111.
- Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., and Ericsson, G. (2012). "From migration to nomadism: movement variability in a northern ungulate across its latitudinal range." In: *Ecological Applications* 22.7, pp. 2007–2020.
- Stephens, P. A., Boyd, I. L., McNamara, J. M., and Houston, A. I. (2009). "Capital breeding and income breeding: their meaning, measurement, and worth." In: *Ecology* 90.8, pp. 2057–2067.
- Teitelbaum, C. S. et al. (2015). "How far to go? Determinants of migration distance in land mammals." In: *Ecology Letters* 18.6, pp. 545–552.
- Trivers, R. L. (1974). "Parent-Offspring Conflict." In: *American Zoologist* 14.1, pp. 249–264.
- Van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J., and Sæther, B.-E. (2013). "Understanding scales of movement: animals ride waves and ripples of environmental change." In: *Journal of Animal Ecology* 82.4, pp. 770–780.
- Van Moorter, B., Gaillard, J.-M., McLoughlin, P. D., Delorme, D., Klein, F., and Boyce, M. S. (2009a). "Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales." In: *Oecologia* 159.3, pp. 669–678.

Supplementary Information

Species and populations

TABLE S4.1: Species, study sites, and contact information. *NT*: neonatal anti-predator tactic of the species (hider = H, follower = F). *BM*: female body mass. *Nb*: number of individuals.

Species	Population	Average animal locations	NT	♀BM (kg)	Nb	Contact	Data institution
<i>Aepyceros melampus</i>	Serengeti National Park	2.1245S, 34.9456E	H	43.8	17	Co-author	Norwegian Institute for Nature Research (NINA)
<i>Alces alces</i>	Alberta – British Columbia	53.9604N, 118.3382W	H	365	7	Co-author	University of Montana (UMT)
	Alaska – Berners Bay	58.8630N, 134.9196W			22	Co-author	Alaska Department of Fish and Game (ADFG)
	Alaska – Gustavus	58.4481N, 135.7300W			27	Co-author	
	Jackson	43.8918N, 110.3630W			40	Co-author	Wyoming Cooperative Fish and Wildlife Research Unit (WYOCOOP)
	Sublette	42.9813N, 110.2795W			56	Co-author	

	Valdres & Hallingdal	60.7035N, 9.0140E			22	Co-author	NINA
	Vega Island	65.6589N, 11.9636E			48	Co-author	
<i>Antilocapra americana</i>	Northern Sagebrush Steppe	49.2217N, 108.3931W	H	46.8	139	Co-author via Movebank	UMT
	Red Desert	41.6054N, 107.9508W			116	Co-author	University of Wyoming (UWYO)
	Rock Springs	41.5178N, 109.7946W			33	Co-author	WYOCOOP
	Henry Mountains	38.0000N, 110.8610W	F	274.8	26	Co-author	Utah State University (USU)
<i>Bison bison</i>	Prince Albert National Park	53.7266N, 106.6663W			51	Co-author	Laval University (ULAAVAL)
	Bargy mountain range	45.9998N, 6.4642E	F	48.9	24	Co-author	Office Français de la Biodiversité (OFB)
<i>Capra ibex</i>	Swiss National Park	46.6108N, 10.1010E			10	Co-author	Swiss National Park (SNP)

<i>Capreolus capreolus</i>	Aurignac	43.2673N, 0.8660E	H	26.5	79	Co-author	National Institute for Agriculture, Food and Environment
	Bavarian Forest National Park	48.9388N, 13.3859E			21	Co-author	University of Freiburg
	Koberg estate	58.1515N, 12.4307E			8	Co-author	Swedish University Of Agricultural Sciences
<i>Cervus elaphus</i>	Bavarian Forest National Park	48.9651N, 13.4393E	H	125	50	Co-author	University of Freiburg
	La Petite Pierre National Hunting and Wildlife Reserve	48.8185N, 7.3309E			59	Co-author	OFB
	Multiple Norwegian counties	62.9536N, 8.4790E			15	Co-author	University of Oslo & Norwegian Institute of Bioeconomy Research
<i>Cervus elaphus canadensis</i>	Canadian Rockies	49.5247N, 114.3009W	H	238.7	98	Co-author	University of Alberta
	Little Mountain	41.1977N, 109.2604W			46	Co-author	Wyoming Cooperative Fish and Wildlife Research Unit (WYOCOOP)

	Ya Ha Tinda Ranch	51.7169N, 115.5565W		125	Co-author via Movebank	UMT
<i>Connochaetes taurinus</i>	Kenya – 3 National Parks	1.7132S, 36.3246E	F	184.9	19 Co-author via Movebank	Colorado State University
	Liuwa Plain National Park	14.5594S, 22.5280E		13	Co-author	Zambian Carnivore Programme
<i>Dama dama</i>	Koberg estate	58.1295N, 12.4135E	H	44	20 Co-author	Swedish University Of Agricultural Sciences
<i>Equus hemionus</i>	Mongolian Gobi	43.0219N, 108.3966E	F	230	17 Co-author	Wildlife Conservation Society Mongolia (WCS Mongolia), University of Veterinary Medicine Vienna (MedVetvienna) & NINA.
<i>Equus quagga</i>	Hwange National Park	18.8889S, 26.8467E	F	322	23 Co-author	Centre d'Ecologie Fonctionnelle et Evolutive (CEFE)
<i>Giraffa camelopardalis</i>	Namib desert	18.9912S, 13.0338E	H	700	5 Co-author	Giraffe Conservation Foundation

<i>Hippotragus niger</i>	Kruger National Park	24.6996S, 31.2303E	H	216.2	7	Co-author	University Witwatersrand	of
	Haida Gwaii	52.8443N, 131.5834W	H	55.5	15	Co-author	CEFE	
<i>Odocoileus hemionus</i>	Little Mountain	41.2305N, 109.1691W			92	Co-author	WYOCOOP	
	Red Desert	42.2931N, 109.2875W			101	Co-author		
	Southwest Colorado	37.7303N, 108.9252W			11	Co- author via Movebank	Colorado Parks and Wildlife (CPW), USDA- APHIS-WS, & Pennsylvania Cooperative Fish and Wildlife Research Unit (PACCOOP)	
	Western Washington	47.1033N, 123.0875W			152	Co- author via Movebank	Washington Department of Fish and Wildlife (WDFW)	
	Wyoming Range	42.3342N, 110.6724W			143	Co-author	WYOCOOP	

<i>Odocoileus virginianus</i>	Pennsylvania	40.2144N, 78.4453W	H	68.5	31	Co- author via Movebank	Pennsylvania Commission & PACOOP	Game
<i>Oreamnos americanus</i>	Alaska - Klukwan	59.4010N, 135.8817W	F	61	20	Co-author	ADFG	
	Alaska – Lynn Canal	59.0049N, 135.0880W			18	Co-author		
	Washington	47.6151N, 121.3694W			31	Co- author via Movebank	WDFW	
<i>Ovibos moschatus</i>	Zackenbergl	74.4654N, 20.6262W	F	266	28	Co-author	Aarhus University	
	Quebec	58.1965N, 73.5548W			18	Co-author	U LAVAL & Ministry of Forests, Fauna and Parks	
<i>Ovis canadensis</i>	Grand Teton	43.7210N, 110.8562W	F	57.9	2	Co-author	WYOCOOP	
<i>Ovis gmelini musimon</i>	Bauges hunting reserve	45.6970N, 6.2004E	F	37.1	16	Co-author	OFB	
	Caroux reserve	43.6321N, 2.9619E			75	Co-author		

<i>Procapra gutturosa</i>	Mongolian Steppe	47.2447N, 115.4887E	H	24	6	Co-author	WCS Mongolia
<i>Rangifer tarandus caribou</i>	Côte du Nord	50.8335N, 68.7283W	F	132	53	Co-author	ULAAVAL
	Gaspésie	48.9583N, 66.1316W			25	Co-author	Université du Québec à Rimouski
	Saskatchewan Boreal Shield	57.1532N, 104.3711W			86	Co-author	McLoughlin Lab in Population Ecology
<i>Rangifer platyrhynchus</i>	Svalbard	78.0478N, 15.4607E	F		49	Co-author	Norwegian University of Life Sciences
<i>Rupicapra rupicapra</i>	Bauges hunting reserve	45.6582N, 6.2190E	F	31.7	89	Co-author	OFB
	Swiss National Park	46.6464N, 10.1566E			22	Co-author	SNP
<i>Saiga tatarica</i>	Mongolian Steppe	47.0629N, 93.8708E	H	32.3	16	Co-author	WWF & WCS Mongolia

Phylogenetic analysis

We retrieved full mitogenome sequences from Genbank. Sequences were aligned using Kalign 2.0 (Lassmann and Sonnhammer, 2005), edited and visually inspected with SeaView 4.3.3 (Gouy, Guindon, and Gascuel, 2010). The models of DNA substitution were selected using the software Smart Model Selection (SMS) (Lefort, Longueville, and Gascuel, 2017), based on the Akaike Information Criterion (AIC). The GTR + G + I substitution model best fitted our mitogenome dataset. Based on this selected substitution model, a phylogenetic tree was constructed using a Maximum Likelihood (ML) approach applied on >16,700 aligned base pairs of full mitogenomes. ML heuristic searches were performed using PHYML 3.3 (Guindon et al., 2010), optimizing the tree topology with SPR, using a BioNJ starting tree and adding 5 SPR tree searches using random starting trees. The resulting unrooted tree was visualized and edited with FigTree 1.3.1 (<http://tree.bio.ed.ac.uk/software/figtree/>; Figure 4.4a). Finally, we extracted the covariance matrix among the species from the phylogenetic tree.

Stationarity

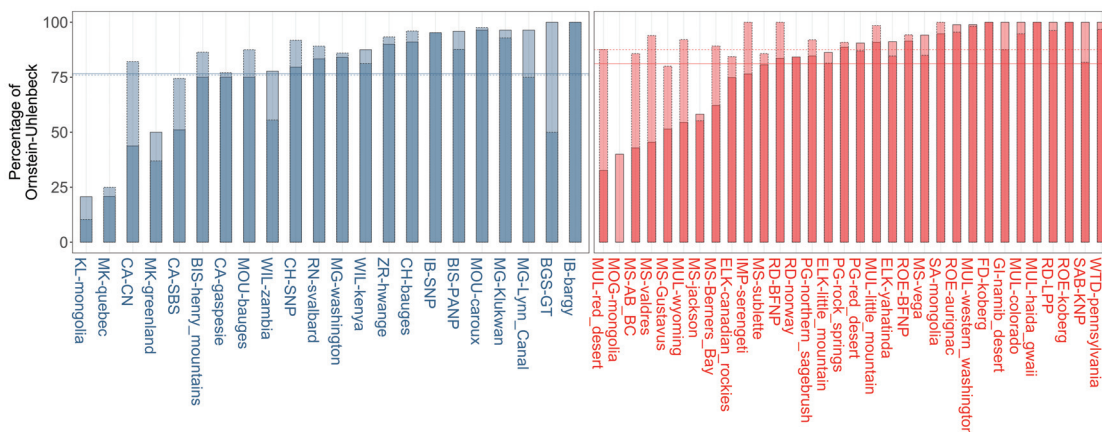


FIGURE S4.1: Percentage of Ornstein-Uhlenbeck models (stationarity) for pre-parturition (plain bars) and post-parturition (dashed bars) for each studied population. Horizontal lines represent the mean percentage of stationarity for each tactic and period. Blue and red represent followers and hidlers, respectively. BIS: American bison; BGS: Bighorn sheep; CA: Caribou; CH: Alpine chamois; ELK: Elk; FD: Fallow deer; GI: Giraffe; IB: Alpine ibex; IMP: Impala; KL: Khulan; MG: Mountain goat; MK: Muskox; MOG: Mongolian gazelle; MOU: European mouflon; MS: Moose; MUL: Mule deer; PG: Pronghorn; RD: Red deer; RN: Svalbard reindeer; ROE: Roe deer; SA: Saiga antelope; SAB: Sable antelope; WIL: Wildebeest; WTD: White-tailed deer; ZR: Plains zebra.

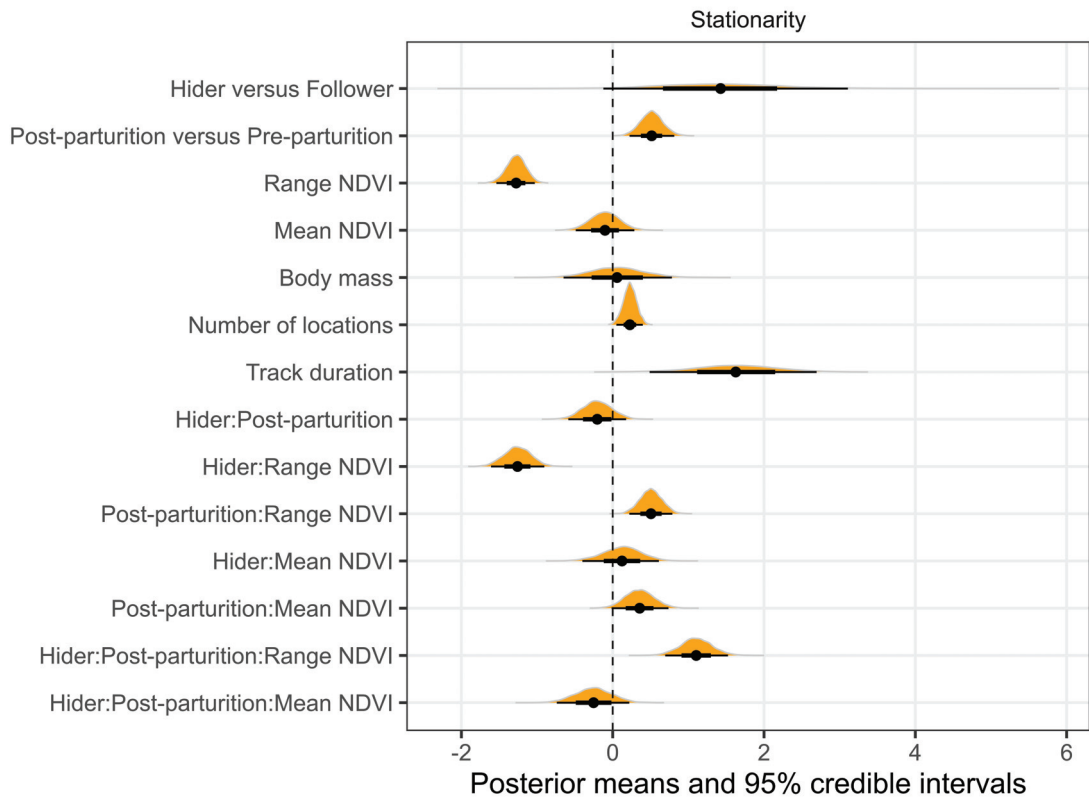


FIGURE S4.2: Means of the posterior distribution for phylogenetic heritability H^2 and fixed effects, along with their 95% highest posterior density intervals (HPDI), extracted from Bayesian Phylogenetic Mixed Models assessing the relationship between neonatal tactic, reproductive period, seasonality and the probability of being stationary. Values excluding 0 are statistically significant.

Model parameters

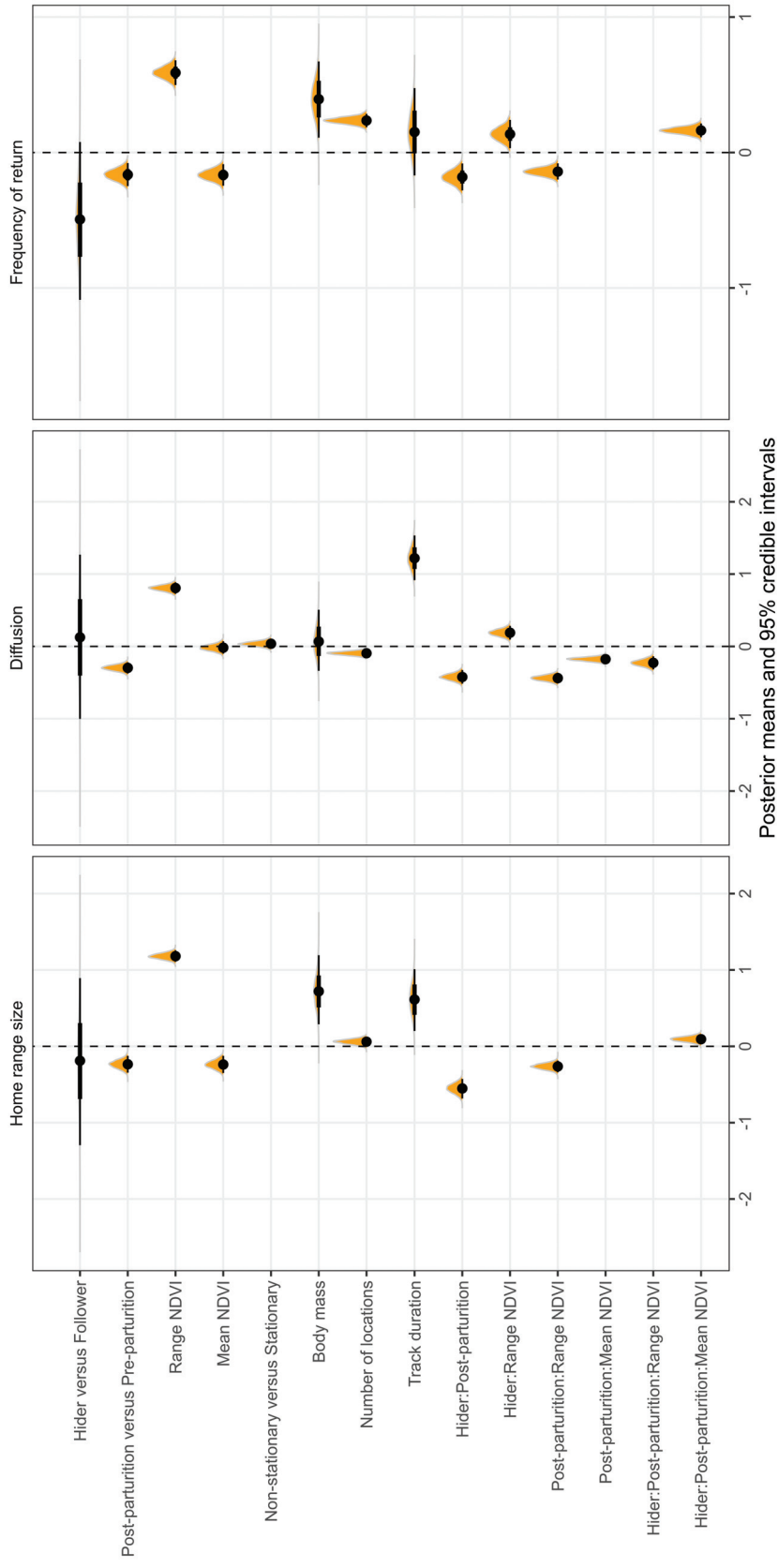


FIGURE S4.3: Means of the posterior distribution and 95% highest posterior density intervals (HPDI) of the fixed effects retrieved from the most parsimonious Bayesian Phylogenetic Mixed Models determining factors impacting the variation of home range size, diffusion, and the frequency of return to a central place. Values excluding 0 are statistically significant.

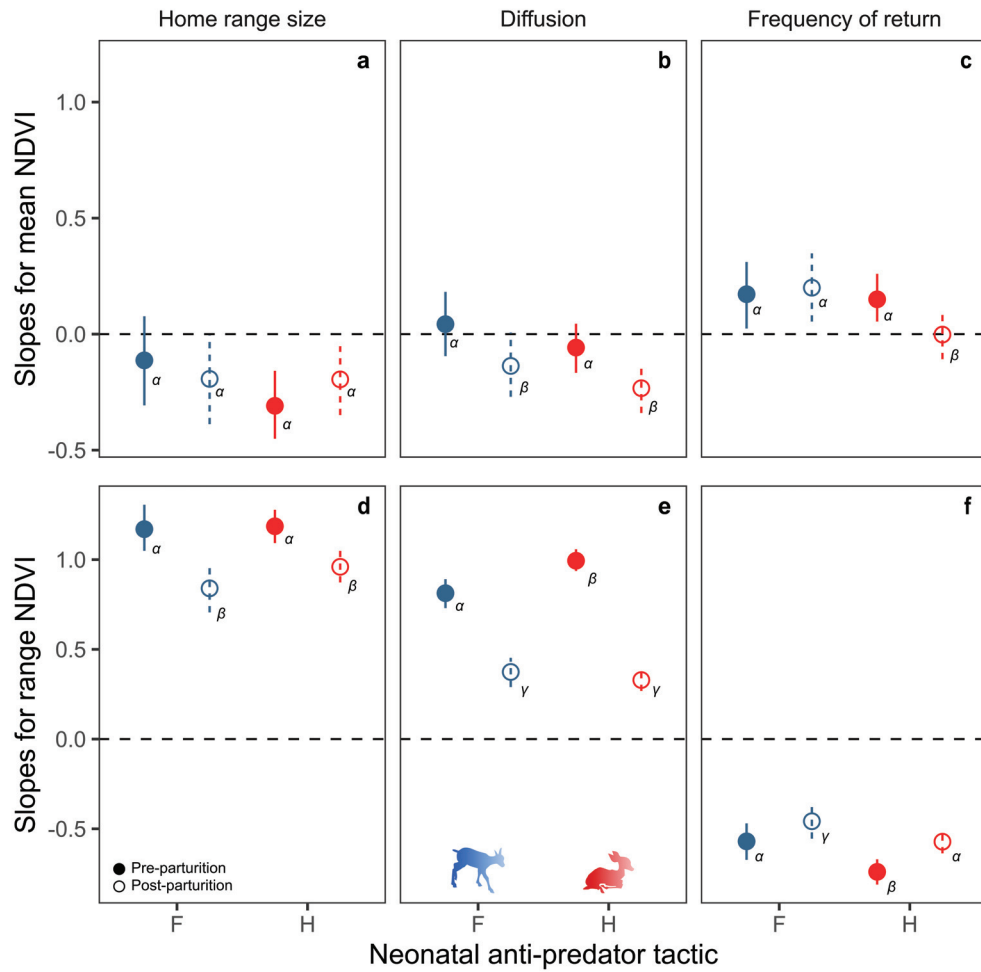


FIGURE S4.4: Reconstructed slopes for mean (a-c) and range (d-f) NDVI from the most parsimonious Bayesian Phylogenetic Mixed models for home range size, diffusion, and frequency of return for each neonatal anti-predator tactic and period. Blue chamois kid and red roe deer fawn represent followers and hiders, respectively.

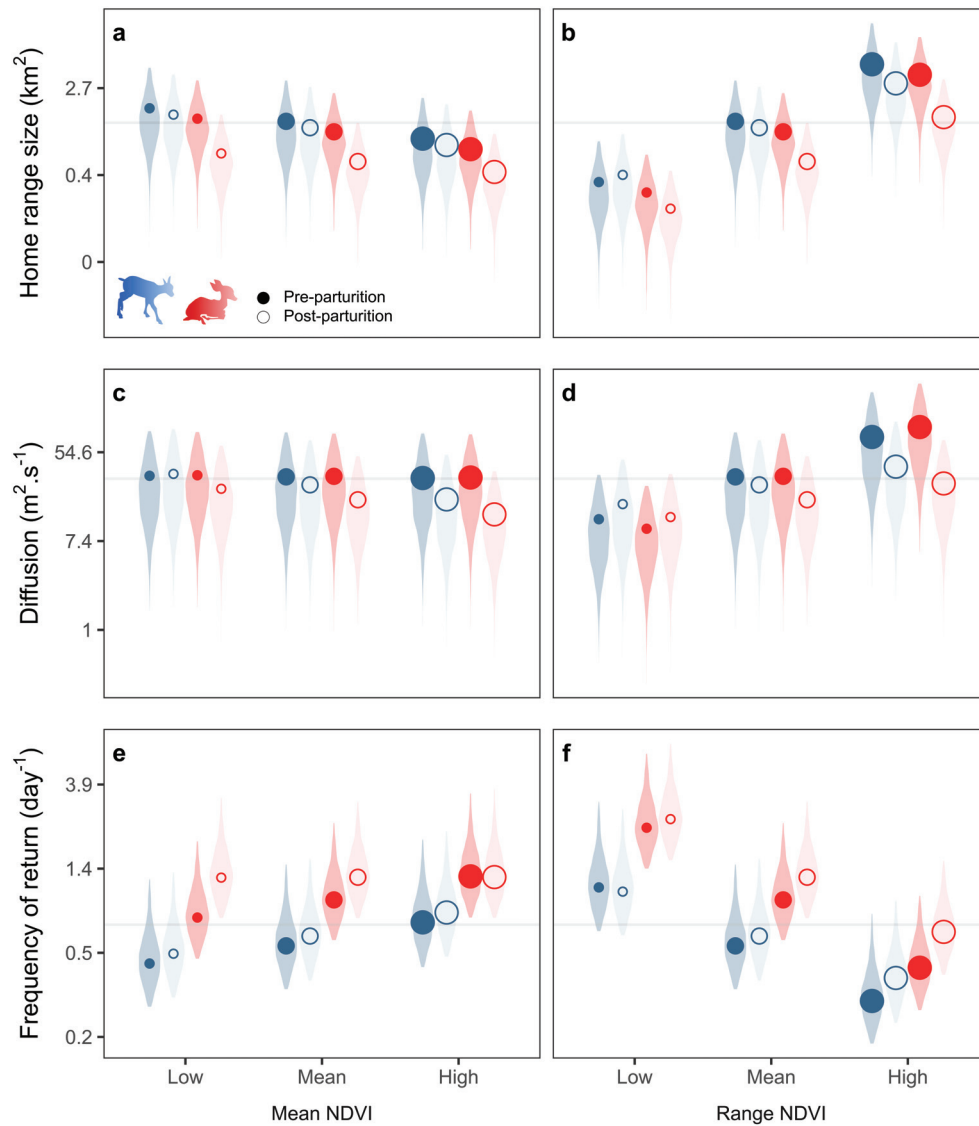


FIGURE S4.5: Predicted values of the three movement components (home range size [a,b], diffusion [c,d], and frequency of return [e,f]) of 23 species of ungulates, retrieved from the most parsimonious Bayesian phylogenetic mixed models depicting the effect of the interplay between neonatal anti-predator tactic, pre- and post-parturition, productivity (mean NDVI; left panels) and spatial range of resource variation (range NDVI; right panels). Low, mean and high classes represent the 10%, mean and 90% quantiles of each environmental variable (0.18, 0.41 and 0.72 for mean NDVI, and 0.25, 1.33 and 6.5 km for range NDVI). Predicted values for each parameter were computed for an animal of 60 kg, and the mean value of one environmental variable was fixed when predicting the effect of the other environmental variable for each class. Solid and blank points represent mean predicted values for pre- and post-parturition, respectively. Dark and light shadings represent pre- and post-parturition, respectively. Red roe deer fawn and blue chamois kid represent hider and follower species, respectively. The increase in the size of points represent higher values of environmental variables.

Distance between centroids

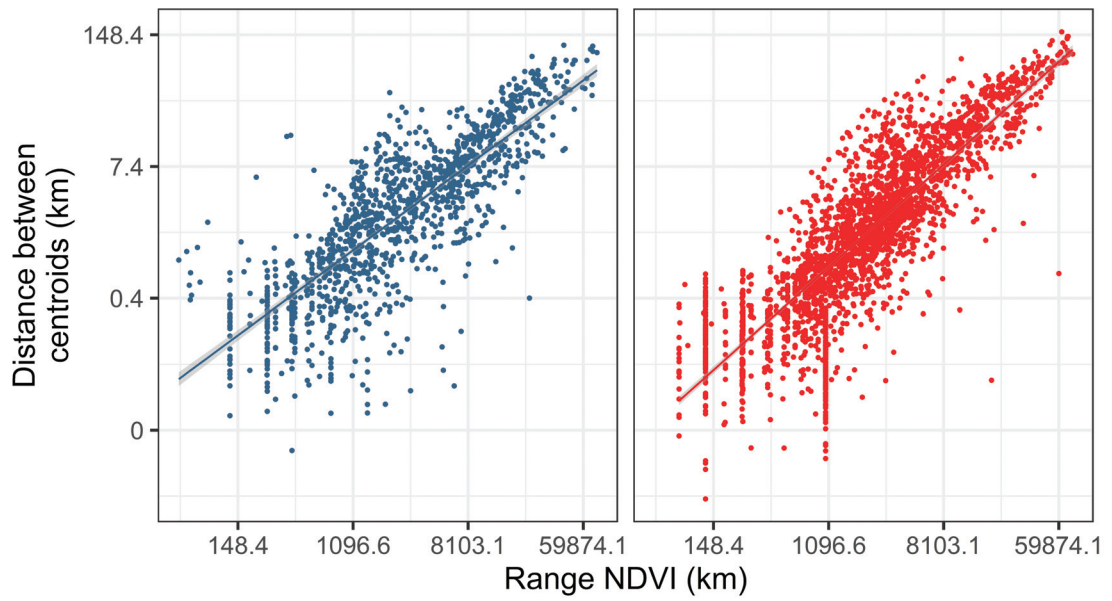


FIGURE S4.6: Linear regression between the range of NDVI and the euclidean distance between the centroids of the locations of each period for every individual year. Blue and red represent followers and hiders respectively.

Cut-off date

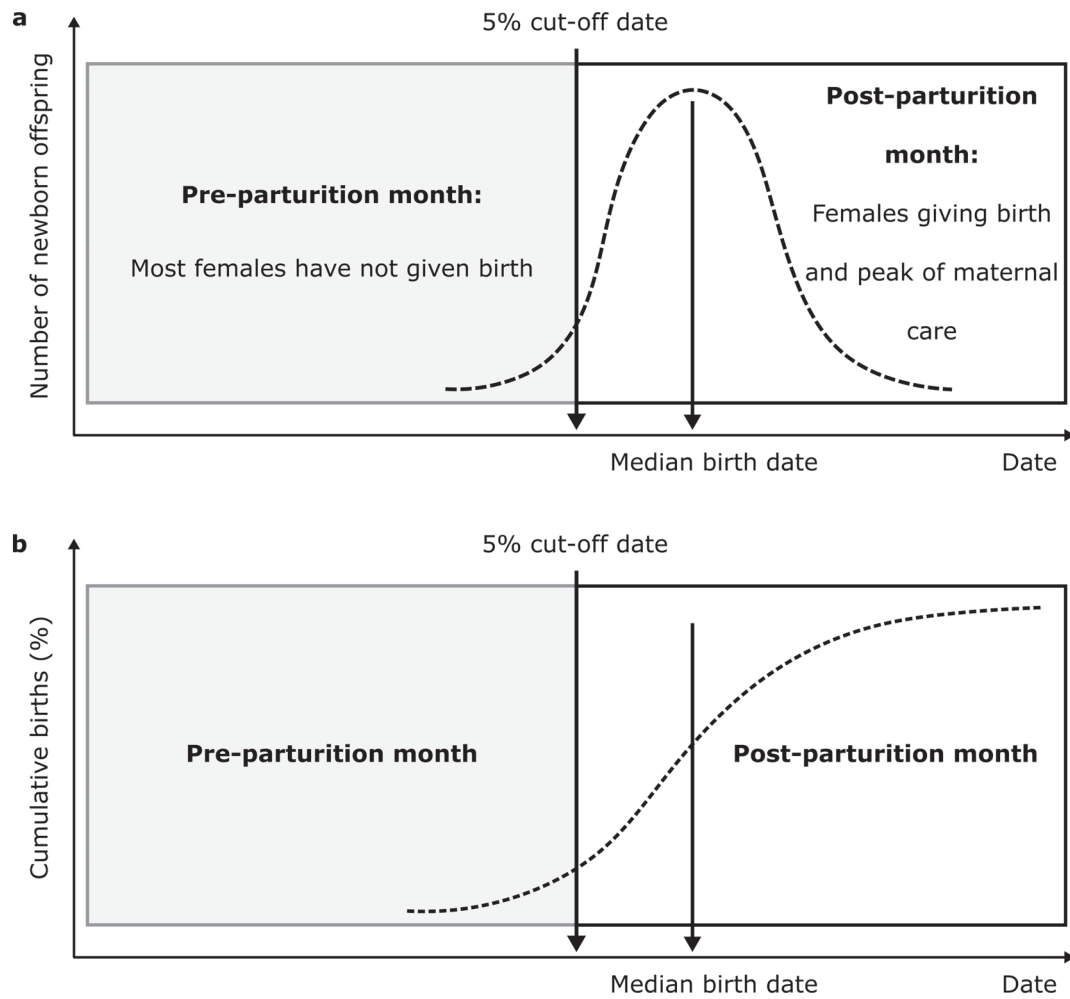


FIGURE S4.7: The 5% cut-off date from (a) the distribution of numbers of newborn offspring or from (b) cumulative percentage of birth events to determine pre- and post-parturition periods. The shape of both curves is hypothetical.

TABLE S4.2: Information on reproduction for each study population along with the type of cut-off date used for the analysis. The 5% cut-off dates were retrieved either using published data or using material provided by the data owners.

Species	Population	Reproduction information	Type of cut-off date	5% cut-off date	References
<i>Aepyceros melampus</i>	Serengeti National Park	Pregnancy	Population	1-October	Ogutu, Piepho, and Dublin, 2014
<i>Alces alces</i>	Alberta – British Columbia	None	Population	1-June	Sigouin, Ouellet, and Courtois, 1997
	Alaska – Berners Bay	Birth	Population	13-May	Guesstimate provided by data owner
	Alaska – Gustavus	Birth	Population	13-May	Guesstimate provided by data owner
	Jackson	Pregnancy & Birth	Population	14-May	Guesstimate provided by data owner
	Sublette	Pregnancy & Birth	Population	14-May	Guesstimate provided by data owner
	Valdres & Hallingdal	Birth	Population	20-May	Guesstimate provided by data owner
	Vega Island	Birth	Individual & Population	20-May	Computed using individual birth dates

<i>Antilocapra americana</i>	Northern Sagebrush Steppe	None	Population	12-May	Barrett, 1981
	Red Desert	Birth	Population	12-May	Panting, 2018
	Rock Springs	None	Population	22-May	Guesstimate provided by data owner
<i>Bison bison</i>	Henry Mountains	None	Population	1-April	Fuller et al., 2007
	Prince Albert National Park	Pregnancy at capture	Population	25-April	Meagher, 1986
<i>Capra ibex</i>	Bargy mountain range	Birth	Population	19-May	Catusse, 1996; Couturier, 1961
	Swiss National Park	Birth	Population	1-June	Guesstimate provided by data owner
<i>Capreolus capreolus</i>	Aurignac	Birth	Individual & Population	1-May	Computed using individual birth dates
	Bavarian Forest National Park	None	Population	1-May	Guesstimate provided by data owner
	Koberg estate	None	Population	15-May	Guesstimate provided by data owner
<i>Cervus elaphus</i>	Bavarian Forest National Park	None	Population	1-June	Guesstimate provided by data owner

	La Petite Pierre National Hunting and Wildlife Reserve	None	Population	11-May	Loe et al., 2005
	Multiple Norwegian counties	Birth	Individual & Population	1-June	Computed using individual birth dates
<i>Cervus elaphus canadensis</i>	Canadian Rockies	Pregnancy at capture	Population	20-May	Berg, 2019
	Little Mountain	Birth	Individual & Population	1-June	Computed using individual birth dates
	Ya Ha Tinda Ranch	Birth	Individual & Population	22-May	Berg, 2019
<i>Connochaetes taurinus</i>	Kenya – 3 National Parks	None	Population	1-February	Hopcraft, 2010
	Liuwa Plain National Park	Calf at heel	Population	10-October	Guesstimate provided by data owner
<i>Dama dama</i>	Koberg estate	Birth	Individual & Population	1-July	Computed using individual birth dates
<i>Equus hemionus</i>	Mongolian Gobi	None	Population	1-July	Guesstimate provided by data owner
<i>Equus quagga</i>	Hwange National Park	Birth	Population	1-October	Grange et al., 2015
<i>Giraffa camelopardalis</i>	Namib desert	None	Population	1-March	Hart et al., 2021

<i>Hippotragus niger</i>	Kruger National Park	None	Population	1-February	Guesstimate provided by data owner
<i>Odocoileus hemionus</i>	Haida Gwaii	None	Population	1-June	Guesstimate provided by data owner
	Little Mountain	Birth	Individual & Population	1-June	Computed using individual birth dates
	Red Desert	None	Population	1-June	Guesstimate provided by data owner
	Southwest Colorado	None	Population	1-June	Pojar and Bowden, 2004
<i>Odocoileus virginianus</i>	Western Washington	Birth	Individual & Population	20-May	Computed using individual birth dates
	Wyoming Range	Birth	Individual & Population	1-June	Computed using individual birth dates
	Pennsylvania	None	Population	15-May	Diefenbach et al., 2019
<i>Oreamnos americanus</i>	Alaska - Klukwan	Birth	Population	13-May	Guesstimate provided by data owner
	Alaska – Lynn Canal	Birth	Population	13-May	Guesstimate provided by data owner
	Washington	None	Population	18-May	Côté and Festa-Bianchet, 2001

<i>Ovibos moschatus</i>	Zackenberg	None	Population	15-April	Thing et al., 1987
	Quebec	Pregnancy at capture	Population	1-May	Guesstimate provided by data owner
<i>Ovis canadensis</i>	Grand Teton	None	Population	1-May	Guesstimate provided by data owner
<i>Ovis gmelini musimon</i>	Bauges hunting reserve	None	Population	1-April	Bon, Dardailon, and Estevez, 1993; Bourgoin et al., 2018
	Caroux reserve	None	Population	1-April	Bourgoin et al., 2018
<i>Procapra gutturosa</i>	Mongolian Steppe	None	Population	1-July	Olson et al., 2005
<i>Rangifer tarandus caribou</i>	Côte du Nord	Pregnancy at capture	Population	20-May	Pinard et al., 2012
	Gaspésie	Birth	Individual & Population	20-May	Computed using individual birth dates
	Saskatchewan Boreal Shield	Birth	Individual & Population	1-May	Computed using individual birth dates
<i>Rangifer platyrhynchus</i>	Svalbard	Birth	Individual & Population	1-June	Garfelt-Paulsen et al., 2021
<i>Rupicapra rupicapra</i>	Bauges hunting reserve	None	Population	15-May	Loison, 1995

<i>Saiga tatarica</i>	Swiss National Park	Birth	Population	15-May	Guestimate provided by data owner
	Mongolian Steppe	Birth	Population	13-June	Buuveibaatar et al., 2013

Semivariograms of movement models

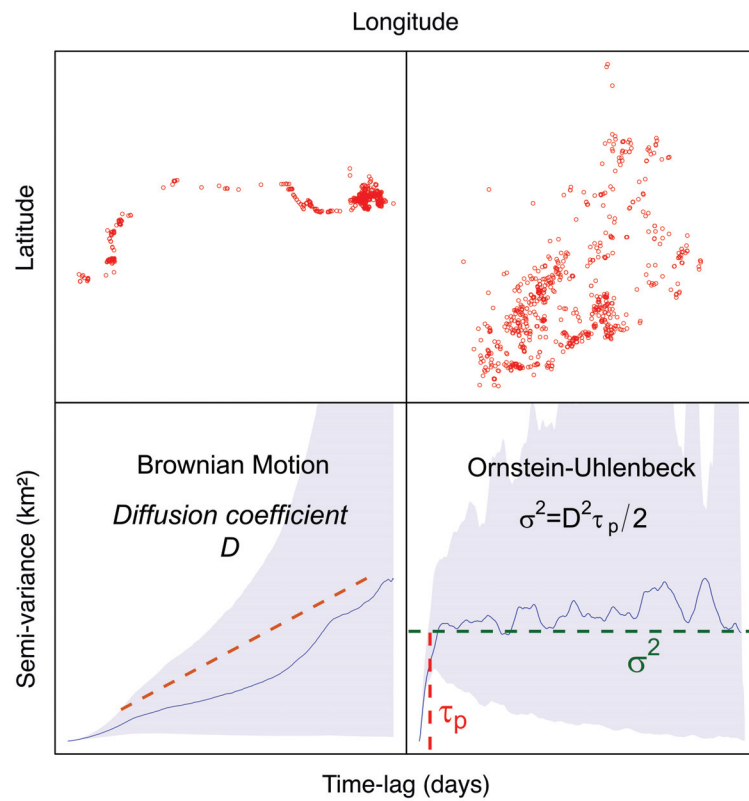


FIGURE S4.8: GPS location (points) and semivariograms of Brownian Motion and Ornstein-Uhlenbeck movement behavior. Only the diffusion coefficient D can be estimated from BM tracks. Ornstein-Uhlenbeck models lead to a home range with spatially bounded movements where σ^2 represents the asymptotic movement variance scaling to home range size, τ_p represents the home range crossing time or the time needed to reach the asymptote, and the diffusion coefficient D represents the rate of increase in the Mean Squared Displacement.

Extended acknowledgments

TABLE S4.3: Acknowledgments for each dataset. To be completed for some populations.

Species	Population	Acknowledgments
<i>Aepyceros melampus</i>	Serengeti National Park	This research was supported by the European Union's Horizon 2020 research and innovation program under grant agreement No. 641918 (AfricanBioServices).
<i>Alces alces</i>	Alberta – British Columbia	Funding provided by Alberta Fish and Wildlife, Canadian Association of Petroleum Producers, University of Montana, Alberta Conservation Association, and World Wildlife Fund.
	Alaska – Berners Bay & Gustavus	This research was funded by the Alaska Department of Fish and Game and the Alaska Department of Transportation and Public Facilities.
	Jackson & Sublette	
	Valdres & Hallingdal – Vega Island	The study was supported by the Research Council of Norway (project SUSTAIN 244647 and SFF-III 223257).

<i>Antilocapra americana</i>	Northern Sagebrush Steppe	<p>The NSS Pronghorn study was funded by the Alberta Antelope Guides, Alberta Conservation Association (ACA), Alberta Fish and Game Association, (Zone 1), Alberta Professional Outfitters Society, Alberta Sport Recreation Parks and Wildlife Foundation, Canadian Forces Base Suffield, Foundation for North American Wild Sheep - Eastern Chapter, MITACS Inc. - Accelerate Program, Montana Chapter of the Wildlife Society with Counter Assault Inc., Montana Fish, Wildlife & Parks (FWP), National Fish and Wildlife Foundation, Petro-Canada Sustainable Greasslands Applied Research Program, Safari Club International, Safari Club International Alberta Chapter & Northern Alberta Chapter, Sagebrush Science Initiative (a collaboration between U.S. Fish and Wildlife Services and Western Association of Fish and Wildlife Agencies), Saskaatchewan Ministry of Environment, University of Calgary, University of Montana, U.S. Bureau of Land Management (BLM), and World Wildlife Fund (WWF). Additional in-kind support was provided by The Miistakis Institute, The Nature Conservancy, FWP, ACA, BLM and WWF.</p>
	Red Desert	<p>Anadarko Petroleum Corporation, Black Diamond Minerals LLC, British Petroleum North America, Devon Energy, Linn Energy, Memorial Resource Development, Samson Resources, Warren Resources, Incorporated, the Bureau of Land Management-Rawlins Field Office, Wyoming Game and Fish Department, Wyoming Governor's Big Game License Coalition, and the University of Wyoming (Department of Ecosystem Science and Management, Office of Academic Affairs, and Wyoming Reclamation and Restoration Center) funded our research.</p>
	Rock Springs	

<i>Bison bison</i>	Henry Mountains Prince Albert National Park	
<i>Capra ibex</i>	Bargy mountain range Swiss National Park	We thank the rangers of the Swiss National Park for marking and observing the individuals.
<i>Capreolus capreolus</i>	Aurignac Bavarian Forest National Park Koberg estate	We would like to thank the local hunting associations, the Fédération Départementale des Chasseurs de la Haute Garonne, as well as all co-workers and volunteers for their involvement and the field technicians B. Cargnelutti, N. Cebe, J. Merlet, D. Picot and J.L. Rames, for their assistance in roe deer captures and tagging. The project was funded by the program Ziel ETZ Free State of Bavaria-Czech Republic (2014-2020) Interreg V (project number 184).
<i>Cervus elaphus</i>	Bavarian Forest National Park La Petite Pierre National Hunting and Wildlife Reserve Multiple Norwegian counties	This project was funded by the program Ziel ETZ Free State of Bavaria – Czech Republic 2014–2020 (INTERREG V) (project number 184). This data collection was funded by the Office Français de la Biodiversité. We would like to thank the wildlife technicians (J.-L. Hamann and V. Siat), the foresters, the 67 Départemental Service and the many volunteers for their help in the capture of deer.

<i>Cervus elaphus canadensis</i>	Canadian Rockies	This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Alberta Conservation Association.
	Little Mountain	Funding for this project was provided by Wyoming Game and Fish Department, Bureau of Land Management, Muley Fanatic Foundation Headquarters and the Southwest, Upper Green, Casper, and Flaming Gorge chapters of Muley Fanatic Foundation, Safari Club International Foundation, Rocky Mountain Elk Foundation, Wyoming Wildlife and Natural Resource Trust, Wyoming Animal Damage Management Board, Bowhunters of Wyoming, Wyoming Governor’s Big Game License Coalition. KSH was funded by National Science Foundation Graduate Research Fellowship.
	Ya Ha Tinda Ranch	Funding was provided by NSF LTREB Grant 1556248, Parks Canada, Alberta Conservation Association, Natural Sciences and Engineering Research Council, Rocky Mountain Elk Foundation, Safar Club International Foundation, Alberta Environment and Parks, University of Alberta, University of Montana.
<i>Connochaetes taurinus</i>	Kenya – 3 National Parks	This research was supported by the National Science Foundation (DEB Grant 0919383).
	Liuwa Plain National Park	
<i>Dama dama</i>	Koberg estate	The Swedish Environmental Protection Agency and The Marie-Claire Cronstedt foundation.

<i>Equus hemionus</i>	Mongolian Gobi	Movement data on khulan was collected within the framework of the Oyu Tolgoi LLC Core Biodiversity Monitoring Program, implemented by the Wildlife Conservation Society through a cooperative agreement with Sustainability East Asia LLC. During manuscript preparation Petra Kaczensky was funded by the Research Council of Norway (grant 251112).
<i>Equus quagga</i>	Hwange National Park	We thank the Director General of the Zimbabwe Parks and Wildlife Management Authority for providing the opportunity to carry out this research in Hwange National Park. This research was partly funded by the grants ANR-08-BLAN-0022, ANR-11-CEPS-003, ANR-16-CE02-0001-01. The support from the CNRS LTSEER Zone Atelier program is also acknowledged.
<i>Giraffa camelopardalis</i>	Namib desert	
<i>Hippotragus niger</i>	Kruger National Park	
<i>Odocoileus hemionus</i>	Haida Gwaii	Funding was provided by grant BAMBI-2010-BLAN-1718-0 of the French 'Agence Nationale de la Recherche', by Forest Renewal BC, South Moresby Forest Replacement Account, International Research Group (GRDI) Dynamics of Biodiversity and Life-History Traits, the French Ministry of Foreign Affairs, and the French Ecological Society (SFE). Logistic support was provided by the Haida Gwaii Watchmen, the Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site, the Research Group on Introduced Species and the Laskeek Bay Conservation Society.

Little Mountain	<p>Funding for this project was provided by Wyoming Game and Fish Department, Bureau of Land Management, Muley Fanatic Foundation Headquarters and the Southwest, Upper Green, Casper, and Flaming Gorge chapters of Muley Fanatic Foundation, Safari Club International Foundation, Rocky Mountain Elk Foundation, Wyoming Wildlife and Natural Resource Trust, Wyoming Animal Damage Management Board, Bowhunters of Wyoming, Wyoming Governor’s Big Game License Coalition. KSH was funded by National Science Foundation Graduate Research Fellowship.</p>
Red Desert	<p>The USDA National Wildlife Research Center, Colorado Habitat Partnership Program, Montelores Habitat Partnership Program, Rocky Mountain Elk Foundation, and the Colorado Auction/Raffle Grant program provided funding for this project. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.</p>
Western Washington	<p>Support for this work was from U.S. Fish and Wildlife Service under the State Wildlife Grants Program and Federal Aid in Wildlife Restoration.</p>

Wyoming Range	The Wyoming Range Mule Deer project is supported by Wyoming Game and Fish Department, Wyoming Game and Fish Commission, Bureau of Land Management, Muley Fanatic Foundation (including Southwest, Kemmerer, Upper Green, and Blue Ridge Chapters), Boone and Crockett Club, Wyoming Wildlife and Natural Resources Trust, Knobloch Family Foundation, Wyoming Animal Damage Management Board, Wyoming Governor's Big Game License Coalition, Bowhunters of Wyoming, Wyoming Outfitters and Guides Association, Pope and Young Club, U.S. Forest Service, and U.S. Fish and Wildlife Service.
<i>Odocoileus virginianus</i>	Work was approved by an Institutional Animal Care and Use Committee (IACUC) at The Pennsylvania State University under protocol numbers PROTO201800639 and 47054. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.
<i>Oreamnos americanus</i>	Research was supported by the Alaska Department of Fish and Game, Alaska Department of Transportation and Public Facilities, Bureau of Land Management and Coeur Alaska.
Washington	Support for this work was from U.S. Fish and Wildlife Service under the State Wildlife Grants Program and Federal Aid in Wildlife Restoration, the Wildlife Research Program of Seattle City Light, the Sauk-Suiattle Tribe, and the United States Forest Service Challenge Cost Share program.
<i>Ovibos moschatus</i>	Research was supported by 15. Juni Foundation, Copenhagen Zoo, the Danish Environmental Protection Agency and the Aarhus University Research Fund.

Quebec	<p>Our research is supported by the Québec Ministère des forêts, de la faune et des parcs and Caribou Ungava partners (in alphabetical order): Air Inuit, ArcticNet, Azimut Exploration, Centre d'Études Nordiques, Grand Council of Crees, Exploration Osisko, Canada Foundation for Innovation, GlenCore-Mine Raglan, Hydro-Québec, Makivik Corporation, TataSteel Minerals Canada Limited. Caribou Ungava was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC RDCPJ 46512-14). We thank V. Brodeur, C. Jutras, B. Lamglait, S. Lair, M. Leblond and A. Brodeur for assistance with the muskox project. We thank all the professionals and wildlife technicians of the Ministère des forêts, de la faune et des parcs of Québec government from the for assistance with the muskox project, fieldwork and data collection. In particular, C. Jutras and V. Brodeur. We thank the Centre québécois sur la santé des animaux sauvages for help and support, in particular B. Lamglait and S. Lair.</p>
<i>Ovis canadensis</i>	Grand Teton
<i>Ovis gmelini musimon</i>	Bauges hunting reserve & Caroux reserve
<i>Procapra gutturosa</i>	Mongolian Steppe
	<p>We are grateful to field assistants as well as World Wide Fund for Nature, Mongolia (WWF) for gazelle capture permissions. All animals were captured following standard protocols approved by the Ministry of Environment and Green Development in Mongolia (licenses: 6/5621, 5/4275). The project was funded by Robert Bosch Foundation.</p>

<i>Rangifer tarandus caribou</i>	Côte du Nord	<p>This research was supported by the Sentinel North program of Université Laval, made possible, in part, thanks to funding from the Canada First Research Excellence Fund, together with the Fonds de Recherche du Québec—Nature et Technologies, the Ministère des Forêts, de la Faune et des Parcs (MFFP), and the Université Laval Industrial Research Chair in Boreal Forest Silviculture.</p> <p>Thanks to B. Baillargeon, D. Grenier, J. Mainguy, and G. Tremblay for the capture and collaring of Atlantic-Gaspésie caribou. This work was supported by the Fonds de Recherche du Québec – Nature et Technologies (FRQNT), the Ministère des Forêts, de la Faune et des Parcs, the Canada Foundation for Innovation (John R. Evans Leaders Fund Grant # 26442 to M.-H. St-Laurent), the Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grant 3866661-2010 to M.-H. St-Laurent), the Société des Établissements de Plein Air du Québec, the Fondation de la Faune du Québec and the Université du Québec à Rimouski (Fonds Institutionnel de Recherche).</p>
	Gaspésie	
	Saskatchewan Boreal Shield	<p>Funded by a Collaborative Research and Development Grant from the Natural Sciences and Engineering Research Council (NSERC) Canada (CRDPJ 449509), with additional financial and in-kind support from Cameco Corporation, Environment and Climate Change Canada, the Government of Saskatchewan, the Saskatchewan Mining Association, SaskPower Inc., Golder Associates Ltd., Claude Resources Inc., Rio Tinto Group, Orano Resources Canada Inc., Golden Band Resources Inc., Masuparia Gold Corporation, Western Economic Diversification Canada, Omnia Ecological Services, and the University of Saskatchewan.</p>

<i>Rangifer platyrhynchus</i>	tarandus	Svalbard	COAT - Climate-ecological Observatory for Arctic Tundra; SIOS - Svalbard Integrated Arctic Earth Observing System.
<i>Rupicapra rupicapra</i>		Bauges hunting reserve	We also thank all the professionals and trainees from the Office Français de la Biodiversité who performed the monitoring of this population.
		Swiss National Park	We thank the rangers of the Swiss National Park for marking and observing the individuals.
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References in Supplementary Information

- Barrett, M. W. (1981). "Environmental Characteristics and Functional Significance of Pronghorn Fawn Bedding Sites in Alberta." In: *The Journal of Wildlife Management* 45.1, pp. 120–131.
- Berg, J. E. (2019). "Shifts in strategy: Calving and calf survival in a partially migratory elk population." In.
- Bon, R., Dardaillon, M., and Estevez, I. (1993). "Mating and Lambing Periods as Related to Age of Female Mouflon." In: *Journal of Mammalogy* 74.3, pp. 752–757.
- Bourgoin, G., Marchand, P., Hewison, A. J. M., Ruckstuhl, K. E., and Garel, M. (2018). "Social behaviour as a predominant driver of sexual, age-dependent and reproductive segregation in Mediterranean mouflon." In: *Animal Behaviour* 136, pp. 87–100.
- Buuveibaatar, B. et al. (2013). "Factors affecting survival and cause-specific mortality of saiga calves in Mongolia." In: *Journal of Mammalogy* 94.1, pp. 127–136.
- Catusse, M. (1996). *La grande faune de montagne*. Dubray.
- Côté, S. D. and Festa-Bianchet, M. (2001). "Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality." In: *Oecologia* 127.2, pp. 230–238.
- Couturier, M. A. (1961). "Ecologie et protection du bouquetin (*Capra aegagrus ibex ibex* L.) et du chamois (*Rupicapra rupicapra rupicapra* (L.) dans les Alpes." In: *La Terre et la vie*.
- Diefenbach, D. R., Alt, G. L., Wallingford, B. D., Rosenberry, C. S., and Long, E. S. (2019). "Effect of male age structure on reproduction in white-tailed deer." In: *The Journal of Wildlife Management* 83.6, pp. 1368–1376.
- Fuller, J. A., Garrott, R. A., White, P. J., Aune, K. E., Roffe, T. J., and Rhyan, J. C. (2007). "Reproduction and Survival of Yellowstone Bison." In: *The Journal of Wildlife Management* 71.7, pp. 2365–2372.
- Garfelt-Paulsen, I. M. et al. (2021). "Don't go chasing the ghosts of the past: habitat selection and site fidelity during calving in an Arctic ungulate." In: *Wildlife Biology* 2021.2, wlb.00740.
- Gouy, M., Guindon, S., and Gascuel, O. (2010). "SeaView Version 4: A Multiplatform Graphical User Interface for Sequence Alignment and Phylogenetic Tree Building." In: *Molecular Biology and Evolution* 27.2, pp. 221–224.
- Grange, S. et al. (2015). "Demography of plains zebras (*Equus quagga*) under heavy predation." In: *Population Ecology* 57.1, pp. 201–214.

- Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W., and Gascuel, O. (2010). "New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0." In: *Systematic Biology* 59.3, pp. 307–321.
- Hart, E. E., Fennessy, J., Wells, E., and Ciuti, S. (2021). "Seasonal shifts in sociosexual behaviour and reproductive phenology in giraffe." In: *Behavioral Ecology and Sociobiology* 75.1, p. 15.
- Hopcraft, J. G. C. (2010). *Ecological implications of food and predation risk for herbivores in the Serengeti*. University Library Groningen][Host].
- Lassmann, T. and Sonnhammer, E. L. (2005). "Kalign – an accurate and fast multiple sequence alignment algorithm." In: *BMC Bioinformatics* 6.1, p. 298.
- Lefort, V., Longueville, J.-E., and Gascuel, O. (2017). "SMS: Smart Model Selection in PhyML." In: *Molecular Biology and Evolution* 34.9, pp. 2422–2424.
- Loe, L. E. et al. (2005). "Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France." In: *Journal of Animal Ecology* 74.4, pp. 579–588.
- Loison, A. (1995). "Approches intra-et inter-spécifiques de la dynamique des populations: l'exemple du chamois." PhD thesis. Lyon 1.
- Meagher, M. (1986). "Bison bison." In: *Mammalian Species* 266, pp. 1–8.
- Ogotu, J. O., Piepho, H.-P., and Dublin, H. T. (2014). "Reproductive seasonality in African ungulates in relation to rainfall." In: *Wildlife Research* 41.4, pp. 323–342.
- Olson, K. A., Fuller, T. K., Schaller, G. B., Lhagvasuren, B., and Odonkhuu, D. (2005). "Reproduction, neonatal weights, and first-year survival of Mongolian gazelles (*Procapra gutturosa*)." In: *Journal of Zoology* 265.3, pp. 227–233.
- Panting, B. (2018). "Influence of Environmental Variables on Survival Rates of Pronghorn (*Antilocapra americana*) Neonates Across Idaho." In: *All Graduate Theses and Dissertations*.
- Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D., and Courtois, R. (2012). "Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape." In: *The Journal of Wildlife Management* 76.1, pp. 189–199.
- Pojar, T. M. and Bowden, D. C. (2004). "Neonatal Mule Deer Fawn Survival in West-Central Colorado." In: *The Journal of Wildlife Management* 68.3, pp. 550–560.
- Sigouin, D., Ouellet, J. .-, and Courtois, R. (1997). "Geographical variation in the mating and calving periods of moose." In: *Alces* 33.January 1997, pp. 85–95.
- Thing, H., Klein, D. R., Jingfors, K., and Holt, S. (1987). "Ecology of muskoxen in Jameson Land, northeast Greenland." In: *Ecography* 10.2, pp. 95–103.

5

Mating tactics of male ungulates mark fine-scale movement signature in GPS data

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& DATA PROVIDERS

WORK IN PROGRESS. THIS VERSION REPRESENTS A FIRST DRAFT AND HAS NOT BEEN READ BY
THE DATA PROVIDERS YET.

Abstract

A key objective for movement ecologists is to describe how movement tactics change in response to internal and external stimuli. To uncover such tactics, we need summary metrics that characterize different axes of covariation in movement rates. With that in mind, the continuous-time stochastic movement model framework allows decomposing the space use of animals into diffusion and frequency of return to a central place. We can thus uncover two different pathways through which animal manage space requirements and space use within their range. Using data from 12 species of ungulates, we aimed to uncover whether contrasting rutting behavior translate into different movement tactics during the breeding periods, at the inter-specific level. We found that in males, diffusion increased during the rut in all species, but the frequency of return to a central place decreased in the species and individuals with a tending behavior whereas it increased in the species and individuals with territorial behavior, indicating major changes in space use within the home range during the rut. By decomposing seasonal and individual variation in home range size into diffusion and frequency of return, the continuous-time modeling framework allows extracting more information about movement tactics and characterizing individual and species-specific signatures.

Keywords: attraction, reproductive tactic, resource heterogeneity, diffusion, follower, hider, home range size, neonate, ungulates.

THE choice of a mating tactic is paramount in determining a male's reproductive success, which is based on male preferential access to females and female mate choice. Mating tactics are related to sexual selection within populations and species since they contribute to the variance in reproductive success among males (Clutton-Brock, 1989; Emlen and Oring, 1977; Greenwood, 1980). After years of empirical and theoretical studies, it is now vastly supported that the different male mating strategies vary in response to specific spatial and temporal distribution of receptive mating females, which in turn are partly driven by resource distribution (Clutton-Brock, 1989). In a landscape where food patches are clumped and unequally distributed, males could monopolize access to resources essential for the rearing success of females (Clutton-Brock, 1989), thus leading to a resource defense system (Emlen and Oring, 1977; Greenwood, 1980). In cases where resources are distributed over large areas, females may distribute over large home ranges, so that males may not be able to adopt a resource defense system. Instead, they may move long distances (e.g. breeding dispersal, moving territory; Espmark, 1964) and adopt a mate defense strategy (Clutton-Brock, 1989; Greenwood, 1980). In mammals, a large array of mating tactics has accordingly been described, whereby males defend territories in some species (e.g. impala *Aepyceros melampus*: Murray, 1982; roe deer *Capreolus capreolus*: Johansson, 1996; Linnell and Andersen, 1998b) or drastically modify their space use patterns during the breeding season as they search for females and compete with other attending males (Bon et al., 1992; Lent, 1965; Willis and Neuhaus, 2009). Hence, the active search for mating partners and the defending of resource- or non-resource-based territories determine how males move between different habitats while interacting with other males and females. Hence, male behavior before (i.e. when dominance is assessed among males) and during the rut (i.e. when males copulate) plays a key role in animal populations by determining not only male fitness but also disease spread (e.g. Conner and Miller, 2004; Marchand et al., 2017) and gene flow within populations (e.g. Portanier et al., 2018). Mating strategies developed by animals are therefore of critical importance but remain poorly studied through the lens of movement ecology.

Male mating tactics vary widely across ungulate species (Clutton-Brock, 1989), as males can display territoriality, harem, leks, coursing, and tending tactics (Table 5.1), all with different implications on male movements before the mating season (i.e. during the pre-rutting period, when males compete with each other, perform temporary breeding excursions, or establish their mating territory) and during the mating (copulating) season *per se* (Carranza, Garcia-Muñoz, and de Dios Vargas, 1995; Clutton-Brock, Guinness, and Albon, 1982; Lincoln and Guinness, 1973). Until recently, mating strategies have

TABLE 5.1: Common mating tactics of male ungulates

	Male mating tactics	Definition
Territory-based	Territoriality	Establishment and defense of a single territory to which females are attracted by sensory cues
	Mating territories	Temporary territory placed in environments rich in resources as a way to intercept the movement of foraging females
	Lek	Competitive displays of multiple males on clustered territories
Non-territory-based	Tending	Males attend, follow, and defend females against competing individuals with no active defense of territories
	Coursing	Gaining temporary access to a female attended by another male by disturbing the pair and pursuing her
	Harem defense	Defense of a group of females by a single male with exclusive access to reproductive females. The male will follow the movement of females instead of being constrained in a single territory

been determined through observations of males during the breeding season (Bon et al., 1992; Mainguy et al., 2008). However, with the advent of fine-scale GPS monitoring and relevant statistical approaches (Cagnacci et al., 2010; Demšar et al., 2015; Kays et al., 2015), researchers have set out to identify and quantify these tactics using location data (Corlatti et al., 2013; Corlatti, Cotza, and Nelli, 2021). More specifically, continuous-time stochastic movement models (CTMM) represent an adequate approach to tackle this question and may provide insight on the implications of such mating tactics on fine-scale movement. In addition, the analysis of heterogeneous datasets from different species and populations is now possible since these models are robust against varying sampling resolutions (Blackwell, 1997; Fleming et al., 2014).

Using the CTMM framework, we investigated how movement varies during the mating season in 14 species having either a non-territorial or territorial mating tactic. We expected that home range size would increase markedly during the rut in non-territorial males as they continuously follow females with no constraint to return to previously visited sites. Territorial males, since they are sedentary during their defense of their territory, should not exhibit any changes in home range size. On a finer-scale of movement, we expected males, regardless of their mating tactic, to extend their movements during the mating season either to find females, to reach areas where females gather, or to repel other competing males: this should translate into an increase

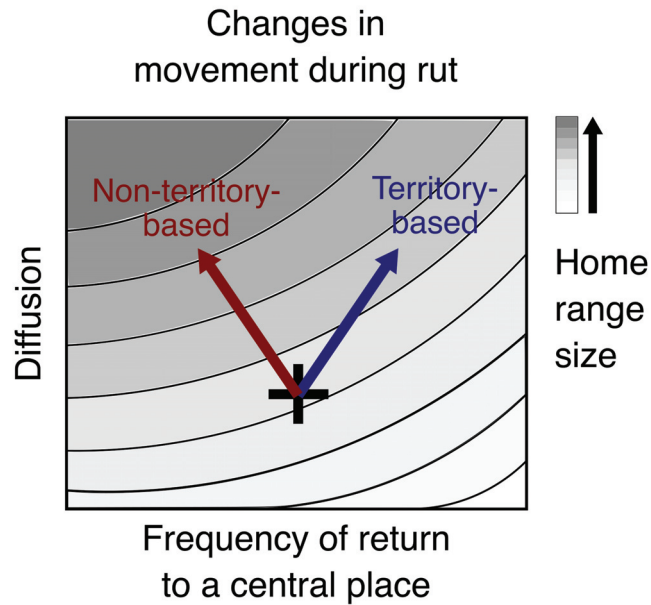


FIGURE 5.1: Expected variation of home range size as a resultant of diffusion and frequency of return to a central place for non-territory (red) and territory-based (blue) mating strategies. We expect diffusion to increase during the rut for both groups since males will move erratically to acquire mating opportunities. The frequency of return should increase during the rut for territory-based strategies as males return to their territory borders and defend them. Non-territory-based mating strategies are expected to show a decrease in the frequency of return since males will move and follow receptive females to acquire mating opportunities. These contrasted variation in diffusion and frequency of return should lead in difference in the variation in home range size for species with non-territory- and territory-based mating tactics.

of diffusion for all species (Figure 5.1). In territorial species, we expected an increase in the frequency of return to a central place as a way to increase the rate of return to territory borders as a defense strategy (Emlen and Oring, 1977; Liberg et al., 1998). In contrast, we expected no increase in the frequency of return in species with a non-territorial behavior (i.e. tending or harem) because their movement should increase when they guard and follow local groups of females and compete against other attending males (Figure 5.1). We expected that our comparative approach using CTMM would better bring to the fore the consequences of the male rutting tactics on movement-to-home-range processes.

5.2 Material and methods

5.2.1 Data collection

We retrieved GPS data from the Movebank repository (<https://www.movebank.org>) or by direct contact with data providers (Table 5.2; see also Table S4.1 in Chapter 4 for details on contact information corresponding to the data in this chapter). We analyzed improbable movement patterns in the GPS data to remove spatial outliers (Bjørneraas et al., 2010). We were only interested in male mating tactics and we therefore removed females from our dataset. Our final dataset contained 536 male individuals

($N = 699$ individual-year) monitored between 2002 and 2019. Our data represented 14 species from 25 populations with three different mating tactics: harem defense ($N_{\text{species}} = 2$; $N_{\text{populations}} = 5$; $N_{\text{individuals}} = 108$), territoriality ($N_{\text{species}} = 4$; $N_{\text{populations}} = 7$; $N_{\text{individuals}} = 171$), and tending ($N_{\text{species}} = 8$; $N_{\text{populations}} = 13$; $N_{\text{individuals}} = 257$). The male body mass of species ranged from 28 to 482.5 kg. The aforementioned numbers represent the final dataset following the selection criteria that we will present below.

TABLE 5.2: Summary variables of species and populations. *MT* = mating tactic, *BM* = body mass (kg), *GL* = Gestation length (days), *Nb_ind* = number of individuals, *Statio* = Stationary.

Species	<i>MT</i>	σBM (kg)	<i>GL</i> (days)	Population	Mean latitude	Birth date †	Rut date	cut-off	<i>Nb_ind</i>	
									All <i>Statio</i> ‡	
<i>Alces alces</i>	Tending ^a	482.5 ^c	243 ^h	Alberta – British Columbia	53.8°N	01-June	01-Oct		7	4
<i>Bison bison</i>	Tending ^b	469.9 ^f	274 ^h	Vega Island Henry Mountains	65.7°N 38°N	20-May 01-April	19-Sept 01-July		37	36
<i>Capra ibex</i>	Tending ^b	80.5 ^c	169 ^h	Bargy range	46°N	19-May	01-Dec		34	28
<i>Capreolus</i>	Territoriality ^b	28 ^a	290 ⁱ	Belledonne Swiss National Park Aurignac	45.2°N 46.6°N 43.3°N	01-June 01-June 01-May	14-Dec 14-Dec 15-July		24 10 84	13 7 80
<i>capreolus</i>				Bavarian National Park Koberg estate	48.9°N 58.2°N	01-May 15-May	15-July 29-July		25 3	24 3

<i>Cervus elaphus</i>	Harem ^a	250 ^a	245 ^h	Bavarian National Park	Forest	49°N	01-June	29-Sept	26	23
				Canadian Rockies		49.5°N	20-May	17-Sept	14	9
				Multiple counties	Norwegian	63°N	01-June	29-Sept	50	41
<i>Connochaetes taurinus</i>	Territoriality ^c	235.3 ^c	253 ^h	Kenya - National Parks	Three	1.7°S	01-Feb	24-May	11	10
<i>Dama dama</i>	Territoriality ^a	67 ^a	236 ^j	Koberg estate		58.1°N	01-July	07-Nov	12	11
<i>Odocoileus hemionus</i>	Tending ^a	87.5 ^f	207 ^h	Haida Gwaii		52.8°N	01-June	06-Nov	6	6
<i>Odocoileus virginianus</i>	Tending ^a	68 ^f	198 ^h	Pennsylvania		40.2°N	15-May	29-Oct	9	6
<i>Oreamnos americanus</i>	Tending ^b	95.9 ^c	184 ^h	Alaska - Klukwan		59.4°N	13-May	10-Nov	27	23
				Alaska - Lynn Canal		59°N	13-May	10-Nov	18	13
				Washington		47.6°N	18-May	15-Nov	10	9
<i>Ovibos moschatus</i>	Harem ^d	334 ^f	258 ^h	Hudson Bay		57°N	01-May	16-Aug	8	5
				Ungava Bay		59.5°N	01-May	16-Aug	10	3

<i>Ovis gmelini musimon</i>	Tending ^b	67.9 ^g	146 ^h	Caroux reserve	43.6°N	01-April	06-Nov	53	53
<i>Rangifer tarandus</i>	Tending ^e	136.7 ^f	228 ^h	Gaspésie	49°N	20-May	04-Oct	13	11
<i>Rupicapra rupicapra</i>	Territoriality ^c	40.3 ^c	170 ^k	Bauges reserve	45.7°N	15-May	26-Nov	24	21
				Swiss National Park	46.6°N	15-May	26-Nov	12	11

[†] Cut-off dates of birth are retrieved from Chapter 4

[‡] Number of individuals that were kept in the analysis. See section "Statistical analysis"

^a Plard, Bonenfant, and Gaillard, 2011; ^b Toigo and Gaillard, 2003; ^c Bro-Jørgensen, 2007; ^d Owen-Smith, 1977; ^e Lent, 1965; ^f Loison et al., 1999; ^g Pérez-Barbería and Gordon, 2000; ^h De Magalhães and Costa, 2009; ⁱ Lambert, 1999; ^j San José, Braza, and Aragón, 1999; ^k Serrano et al., 2015

5.2.2 Establishing rut periods

The main purpose of our study was to identify changes in movement during the rut. This required an accurate definition of reference and rut periods. For each population, we obtained a birth cut-off date representing 5% of birth events that have occurred in the population (see "Defining reproductive periods" in Chapter 4). To estimate the cut-off date for the rut period in each population, we subtracted the gestation length of the focal species from the population's cut-off date of 5% of births (Table 5.2). We assumed that subtracting the gestation length would provide us with a rut cut-off date where 5% of copulations have already happened. The "rut" period was defined over 30 days from the rut cut-off date (date + 30 days). We verified the accuracy of our rut periods by comparing them to previous findings. We did not define the reference period as being before the rut since male-male competition occurs around that time. We called that period the "pre-rut" (date – 30 days). Following this reasoning, the "reference" period was defined as the month occurring before the pre-rut (from date – 60 days to date – 30 days). We investigated how movement changed between the reference period and the pre-rut and rut periods.

5.2.3 Fitting of continuous-time stochastic movement models

Continuous-time stochastic movement models describe movement as continuous through time. In our study, we were interested in two classes of models. The Brownian Motion (BM) model represents an infinite diffusion trajectory with no bounded home range (Blackwell, 1997), characterized by a constant increase in the semivariogram of the location time series (Fleming et al., 2014). The Ornstein-Uhlenbeck (OU) models on the other hand do represent a stationary movement that typically leads to the emergence of a home range (Dunn and Gipson, 1977), characterized by an asymptote in the semivariogram. Even though we can retrieve the diffusion parameter (D) from BM models, we suggest in our hypothesis that discriminating between mating tactics may be possible using the frequency of return parameter which can only be retrieved from OU models. The frequency of return is the inverse of the position autocorrelation time (τ_p) which represents the time it takes for the semivariogram to reach its asymptote. The asymptote of the semivariogram noted σ^2 , scales to the home range size and is linked to diffusion and position autocorrelation time as follows:

$$\sigma^2 = D^2 \tau_p / 2$$

To retrieve the parameters, we first had to identify whether tracks for each period were stationary or not. For each period, we only chose tracks having a median sampling interval of fewer than 6 hours, at least 14 days of data, and at least 60 locations (Börger et al., 2006b). To determine whether each track was stationary, we fit competing non-linear models corresponding to BM and OU models (Fleming et al., 2014) to the tracks' empirical semivariograms, and then selected the best fit using the Akaike Information Criterion. After identifying whether a track was BM or OU, we fit the corresponding model using the *ctmm.fit* routine in the *ctmm* package (Calabrese, Fleming, and Gurarie,

2016) in R. In the case of a BM model we extracted the diffusion parameter of the track, and in the case of an OU model we extracted the home range size (σ^2), diffusion (D), and position autocorrelation time (τ_p).

We standardized each of σ^2 , D , and τ_p values by population and period and excluded scores that were lower than -3 or higher than 3 which were considered outliers. The removed data represented 1.31% of all tracks ($N = 40$) and 0.59% of all individuals ($N = 5$). For an OU track, if one of the parameters was considered an outlier, we ended up excluding the whole track since we were interested in the simultaneous variation of diffusion and frequency of return. Consequently, our selection process led to the removal of all periods for several individual-year or to the removal of one or two periods. Since our main interest was the change between the reference and rut periods, we removed individuals for whom we did not retain tracks in both periods, which represented 17.76% of all tracks ($N = 536$) and 24.47% of all individuals ($N = 207$). If an individual-year did not have a track during pre-rut due to a lack of monitoring or outlier removal, we still retained the tracks during the reference and rut periods.

5.2.4 Statistical analysis

We excluded juveniles from the data ($N=103$ accounting for 16.12% of all individuals) since they do not participate in the rut, and only kept individuals that were two years and older (column "All" in Table 5.2). We removed tracks that were identified as non-stationary ($N = 260$ representing 12.5% of all tracks) since we wanted to investigate the joint change in diffusion and frequency of return. Out of all these tracks, 17.7%, 44.6%, and 26.5% belonged to non-territorial males during the reference, pre-rut, and rut periods, respectively. The remaining 2.7%, 3.5%, and 5% of these tracks belonged to territorial males during the reference, pre-rut, and rut periods, respectively. If an individual-year had one of its reference or rut tracks removed, we ended up removing the whole individual-year. This process led to the removal of 80 individuals accounting for 14.93% of all individuals in the data (see Table 5.2 column "Stationary" representing the number of individuals included in the statistical analysis). We also combined harem defense and tending tactics into one category of non-territorial tactics since an initial analysis showed similar variation in their movement.

We fit three linear mixed models with a Gaussian distribution using the *glmmTMB* function available in the *glmmTMB* package (Brooks et al., 2017) to examine how home range size, diffusion, and frequency of return to a central place (Supplementary Figures S5.1–S5.3) vary with the period (reference, pre-rut, and rut), mating tactic of the species (non-territorial and territorial), and the interaction between period and tactic. We corrected each model for male body mass of the species, duration of monitoring, and number of locations in each track, all of which can affect the response variables. We log-transformed all the control variables. We also included the individual nested in population nested in species and year nested in population as random effects on the intercept to account for repeated measurements.

For home range size, diffusion, and frequency of return, we conducted a model selection using the *dredge* function in the MuMIn package (Barton, 2020). Models were evaluated based on Akaike's Information Criterion adjusted for small sample size (AICc), ΔAICc , and Akaike weights (Burnham and Anderson, 2002). We relied on the AICc to rank models and considered models with no more than 2 AIC units from the top model ($\Delta\text{AICc} \leq 2$) as being equally representative of the data. If more than one model had a $\Delta\text{AICc} \leq 2$, we conducted a model averaging over the retained models using the *model.avg* function, also available in MuMIn (Barton, 2020). It is important to emphasize that the frequency of return is the inverse of the position autocorrelation time τ_p (see section "Fitting of continuous-time stochastic movement models") which was our response variable on the logarithmic scale. To obtain estimates for the frequency of return we therefore inverse the sign of the effect size.

5.3 Results

Following our model selection, all the retained best models ($\Delta\text{AICc} \leq 2$) for home range size, diffusion, and frequency of return included mating tactic, period, body mass, and the two-way interaction between mating tactic and period (Table 5.3). Home range size and diffusion were both positively related to body mass (home range: $\beta_{\text{average}} = 1.81 \pm 0.27$; diffusion: $\beta_{\text{average}} = 1.08 \pm 0.25$) while the frequency of return to a central place decreased with increasing body mass ($\beta_{\text{average}} = -0.75 \pm 0.19$) (Tables S5.1–S5.3). There was no influence of the track's duration ($\beta_{\text{average}} = -0.01 \pm 0.01$) and number of locations in the focal track ($\beta_{\text{average}} = 0.02 \pm 0.03$) on diffusion, and only the duration of the track and not the number of locations explained some of the variation in home range size ($\beta_{\text{average}} = 0.12 \pm 0.03$) and the frequency of return ($\beta_{\text{average}} = -0.14 \pm 0.03$).

As expected, the spatial behavior of males changed during the rut period but the direction of change depended on the mating tactic of the species (Table S5.1). The home range size of non-territorial males increased significantly during the mating season and was 2.7 times higher during the pre-rut and 3 times higher during the rut when compared to the reference period. Territorial males, on the other hand, did not show a significant increase in home range size during the mating season, thus supporting our hypothesis. Home range size of territorial males was only 1.2 and 1.3 times higher during the pre-rut and rut compared to the reference period, respectively (Figure 5.2). Interestingly, the home range sizes of both tactics during the rut were equal with a ratio of only 1.01 times higher in non-territorial compared to territorial males.

Regardless of the mating tactic, males increased their diffusion during the pre-rut and rut periods as hypothesized, albeit to different extents (Table S5.2). Non-territorial males had a diffusion 1.7 times higher during pre-rut and 2.5 times higher during rut compared to the reference period. Territorial males on the other hand exhibited a diffusion 1.3 times higher during pre-rut and 1.8 times higher during the rut compared to the reference period (Figure 5.2). Overall, diffusion was highest during the rut period for all males.

TABLE 5.3: Model selection for the variation in home range size (a), diffusion (b), and frequency of return to a central place (c). The variables included in the models were mating tactic of the species (*MT*: Non-territorial, Territorial), the period of the track (*P*: Reference, Pre-rut, Rut), log-transformed body mass of the species (*BM*), duration of the track (*Du*), number of locations in each track (*Nb_loc*), and the two-way interaction between mating tactic and period (*MT * P*). Column *df* represents the degrees of freedom of each model. Models in bold have all been retained for the focal parameter.

		<i>Intercept</i>	<i>MT</i>	<i>P</i>	<i>BM</i>	<i>Du</i>	<i>Nb_loc</i>	<i>MT * P</i>	<i>df</i>	$\Delta AICc$	<i>Weight</i>
a) Home range size	Model 1	12.09	+	+	1.81	0.12		+	13	0	0.69
	Model 2	12.09	+	+	1.82	0.12	0.03	+	14	1.6	0.31
	Model 3	12.11	+	+	1.83		0.07	+	13	12.31	0
	Model 4	12.1	+	+	1.82			+	12	12.92	0
	Model 5	12.97	+	+		0.12		+	12	20.78	0
	Model 6	12.98	+	+		0.11	0.04	+	13	21.94	0
b) Diffusion	Model 1	1.21	+	+	1.08			+	12	0	0.37
	Model 2	1.21	+	+	1.09		0.04	+	13	0.59	0.27
	Model 3	1.21	+	+	1.09	-0.02	0.04	+	14	1.43	0.18
	Model 4	1.21	+	+	1.08	-0.01		+	13	1.48	0.18
	Model 5	1.76	+	+				+	11	10.68	0
	Model 6	1.77	+	+			0.04	+	12	11.23	0
c) Frequency of return	Model 1	11.56	+	+	0.75	0.14		+	13	0	0.72
	Model 2	11.56	+	+	0.75	0.14	0.01	+	14	1.95	0.27
	Model 3	11.91	+	+		0.14		+	12	9.76	0.01
	Model 4	11.92	+	+		0.14	0.02	+	13	11.62	0
	Model 5	11.67	+	+	0.75	0.13			11	24.19	0
	Model 6	11.46		+	0.92	0.13			10	24.42	0

The direction of change in the frequency of return to a central place was significantly different across both mating tactics (Table S5.3). Non-territorial males exhibited a frequency of return 1.6 times lower during pre-rut and 1.2 times lower during rut compared to the reference period. Conversely, territorial males displayed a frequency of return that was 1.13 times higher during pre-rut (although non-significant) and 1.45 times higher during rut compared to the reference period, thus supporting our hypothesis (Figure 5.2).

5.4 Discussion

Until now, mating tactics have been identified from observations in the wild, with little quantitative explanation of how different tactics impact male mobility throughout the rutting season. In this paper, we offered a new approach to quantify mating tactics behavior from movement data, using the robust framework of continuous-time stochastic movement models (CTMM) (Blackwell, 1997; Calabrese, Fleming, and Gurarie, 2016; Fleming et al., 2014). Comparing data on 14 species from 25 populations, we were able to provide for the first time, a quantified evaluation of territorial and non-territorial behaviors, through the means of two movement components: diffusion and frequency of return to a central place. Our findings, in particular, highlight the relevance of scale in movement ecology by demonstrating that, once body mass, the main determinant of home range size has been accounted for, male home range sizes during

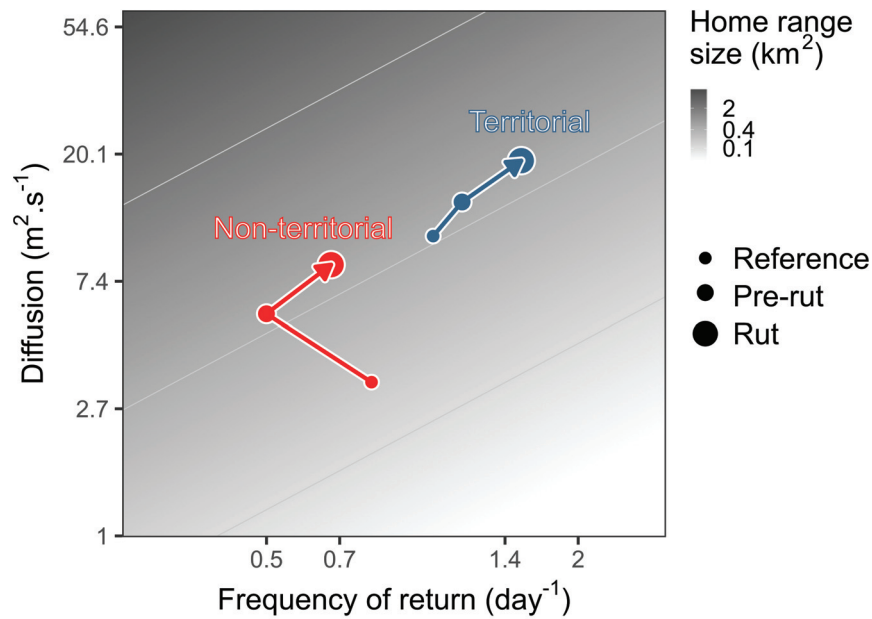


FIGURE 5.2: Changes in home range size, diffusion, and frequency of return behavior of males around the rutting period according to the mating tactic (non-territorial vs territorial) of 14 species. The x and y axes are on the logarithmic scale. Body mass was fixed at the mean body mass in the dataset equaling 98.5 kg.

the rut do not differ among species with different mating tactics, while the underlying movement components do.

5.4.1 Movement processes linked to mating in males

During the mating season, males tend to occupy larger home ranges than outside the rutting season (Cederlund and Sand, 1994; Malagnino et al., 2021; Vanpé et al., 2009). This is usually interpreted as males moving to mating areas, exploring female ranges, assessing their dominance, or as a stratagem to monopolize as many females as possible and increase mating opportunities. The rate of increase in home range size can however differ among species. For instance, mouflon, a non-territorial species, displayed a higher increase in home range size during the rut compared to the territorial roe deer (Malagnino et al., 2021). Observations at the home range scale can nevertheless obscure the behavioral pathways at the root of these contrasted variations.

Our results show that territorial species did not significantly modify their home range size during the rutting season in contrast with non-territorial species that expanded threefold their home range during the rut (Figure 5.2). However, unexpectedly, the home range sizes of both non-territorial and territorial males were similar during the rut period (Figure 5.2). One of the most important new aspects of our research is the decomposition of home range into diffusion and frequency of return, providing a deeper comprehension of these species variations. First, diffusion increased during the pre-rut and rut in all species, thus confirming our hypothesis (Figures 5.1 and 5.2). The increase in diffusion supports a link between movement rates and circulating androgens which also peak during the rut in all species (Alpine chamois: Corlatti

et al., 2012; Alpine ibex: Decristophoris, Hardenberg, and McElligott, 2007; mouflon: Lincoln, 1998; Santiago-Moreno et al., 2005; red deer: Pavitt et al., 2015; roe deer: Roelants et al., 2002; reindeer and caribou: Whitehead and McEwan, 1973). Also, the persistent chasing of competitors keeps the males almost continuously busy (Alados, 1986; Clutton-Brock, Guinness, and Albon, 1982; Espmark, 1964), leading to erratic movement and an increase in diffusion. Males with non-territory-based mating tactics (i.e. tending and harem) decreased their frequency of return during the rut (Figure 2) since their movement depends on the movement of females and is not constrained to a fixed territory in space. For instance, caribou (Espmark, 1964), mouflon (Bon et al., 1992), and Alpine ibex (Willisch and Neuhaus, 2009) do not defend territories within their ranges and are extremely mobile during the breeding season as they search and follow groups of moving females (Supplementary Figure S5.4). On the other hand, in species with territory-based mating tactics, and as hypothesized, the frequency of return to a central place increased during the rut (Figure 5.2), thus compensating for the effect of diffusion on home range size. An increase in the frequency of return may be due to frequent patrolling of and return to territory borders as a way to drive competitors away (Liberg et al., 1998; Linnell and Andersen, 1998b; Owen-Smith, 1977). Consequently, the simultaneous increase in diffusion and increase in the frequency of return in territorial males has led to the lower variations in their home range size compared to non-territorial animals (Figure 5.2).

Results from CTMM support the rutting behavior described earlier for these mating tactics but also allowed unveiling the setting up of rutting behavior during the pre-rut period. We found a larger decrease in the frequency of return of non-territorial males during the pre-rut than during the rut. Clutton-Brock, Guinness, and Albon (1982), for example, reported that in the early rut, red deer males relocate to traditional rutting grounds to form harems where they concentrate their mating activities in these particular areas. This could explain the lower frequency of return in the pre-rut due to long traveled distances. Interestingly, for territorial species, there was no difference in the frequency of return between the reference and pre-rut periods. The establishment of a territory can occur before the rutting season (e.g. roe deer become territorial in March: Hoem et al., 2007; Johansson, 1996) which can explain the lack of variation in the frequency of return during pre-rut. Nonetheless, it appears that the rut, in particular, intensifies the territorial behavior of species since the frequency of return did increase significantly during that period.

5.4.2 Other drivers of movement processes

Our method of using CTMM to extract the essence of movement from a few model parameters is promising for gaining a deeper grasp of the movement implications of ecological traits at the inter-specific level. We focused here on the reproductive season in males and found that the frequency of return appears to be the main parameter differentiating space use and movement patterns of territorial and non-territorial species. We, therefore, propose that the frequency of return can be used to characterize the

degree of territoriality. Nevertheless, it is important to discuss possible limitations of our approach as well as other factors that may have affected our movement patterns and which require future analyses.

Our approach requires choosing adequate reference and peak activity periods for each species and population, which is not as straightforward as it seems. In many species, rutting behavior devoted to male-male or male-female interactions and to prospecting movements may occur sometimes before actual copulations (Bon et al., 1992; Kojola, 1986; Willisch and Ingold, 2007). The duration and start of the pre-rut activities are not well known and may be a progressive process, though probably triggered in males by peaks in testosterone levels (Bubenik et al., 1997; Lincoln, 1998; Santiago-Moreno et al., 2005). It may be useful to use our method as a way of determining the start of mating activity for individuals as there are quite discernable shifts in our parameters throughout the rut.

Furthermore, we could only retrieve the frequency of return when movements were stationary over at least a 14-day scale, discarding migrating or nomadic males. This should however not affect the inter-specific patterns obtained here, as the vast majority of individuals had stationary movements (Supplementary Figure S5.4). Nevertheless, seasonal variation in resources may have influenced our estimated parameters. Most mating periods occur in autumn-winter (Table 5.2) when resources are scarce and heterogeneously distributed. Additionally, there may be marked differences in resource availability between the reference and rut periods, since the latter, in most cases, occur at the onset of autumn, thus requiring migration during the rut (Hebblewhite and Merrill, 2007; Mysterud et al., 2011). Our descriptive results on the percentage of stationary individuals show a trend of increased non-stationarity during the pre-rut and rut periods compared to the reference month, with higher migration, albeit descriptively, in non-territorial species (Supplementary Figure S5.4). Whether our movement parameters were impacted by changes in broad-scale movements remains to be investigated. This makes us question whether restricting our analyses to individuals having a home range is adequate since some animals display a rutting behavior during migration (e.g. reindeer: Espmark, 1964). Therefore, it would be interesting to evaluate the probability of being stationary for each mating tactic while accounting for resource distribution, since non-stationarity can also reveal a movement decision during the rut.

Hunting activities during the mating season are amongst the factors that can influence our movement parameters. In many populations, the hunting season overlaps with mating activities (e.g. moose on Vega island: Solberg et al., 2010; mouflon in the Caroux reserve: Marchand et al., 2014; red deer in Norway: Loe et al., 2005) which can lead to marked changes in the movement of animals (Chassagneux et al., 2020; Marchand et al., 2014). Moreover, recreational activities, such as skiing and hiking, may alter the behavior of animals (Duparc, 2016; Marchand et al., 2014). Whether hunting or other sources of human disturbance occur during the mating season should be accounted for in our models since they may explain part of the variation in the males' movements.

Mating tactics, however, are not always unique within a species. They are expected to vary within and among species, populations, and individuals, as a response to different environmental and social factors (Bowyer et al., 2020; Figure 5.3). For example, in fallow and red deer, some individuals engage in leks while others engage in harem defense or territorial mating behaviors (Carranza, Garcia-Muñoz, and de Dios Vargas, 1995; Clutton-Brock, 1989). Differences in mating tactics across populations and within populations may be due to variation in resources driving female distribution which, in turn, cascades to differences in mating tactics (Clutton-Brock, 1989). For instance, red deer males switched from harem to resource defense when food was provided in concentrated patches (Carranza, Garcia-Muñoz, and de Dios Vargas, 1995). Using the frequency of return parameter, it would be interesting to evaluate how mating tactics vary within species depending on the resource distribution across and within populations (Figure 5.3). In doing so, we may be able to provide individual-specific mating tactics and identify whether some species are more flexible in the mating tactics that they exhibit or not (Figure 5.3).

Internal variables of the focal individual (e.g. age, social status, and physical condition) can also lead to differences in mating tactics across species (Bowyer et al., 2020; Corlatti et al., 2013; Mainguy et al., 2008; Figure 5.3). For instance, male alpine ibexes exhibit alternative mating tactics, where coursing is predominant in individuals younger than four years old while a prevalent tending behavior is observed in older males (Willisch and Neuhaus, 2009). Age, along with resource variation between populations, may explain the large within-population variability in the movement parameters in some populations (Supplementary ??–S5.7). Therefore, another perspective would be to compare individuals in species exhibiting alternative mating tactics among age classes (e.g. chamois: Corlatti et al., 2013; Lovari, Sacconi, and Trivellini, 2006; von Hardenberg et al., 2000; mouflon: Bon et al., 1992; mountain goats: Mainguy et al., 2008) to adequately discern rutting behavior and evaluate how internal factors influence the movement of individuals (Figure 5.3).

In the light of our results, more complex development of CTMM, whereby the estimated parameters might depend on environmental and individual covariates, could offer new insights on behavioral processes. The appeal of the method is its ability to dissect space use into behaviorally meaningful movement parameters, thereby avoiding methodological limitations of home range estimations (Börger, Dalziel, and Fryxell, 2008; Laver and Kelly, 2008; Noonan et al., 2019; Seigle-Ferrand et al., 2021), a critical task in an evolving world of animal monitoring (Cagnacci et al., 2010; Demšar et al., 2015; Kays et al., 2015).

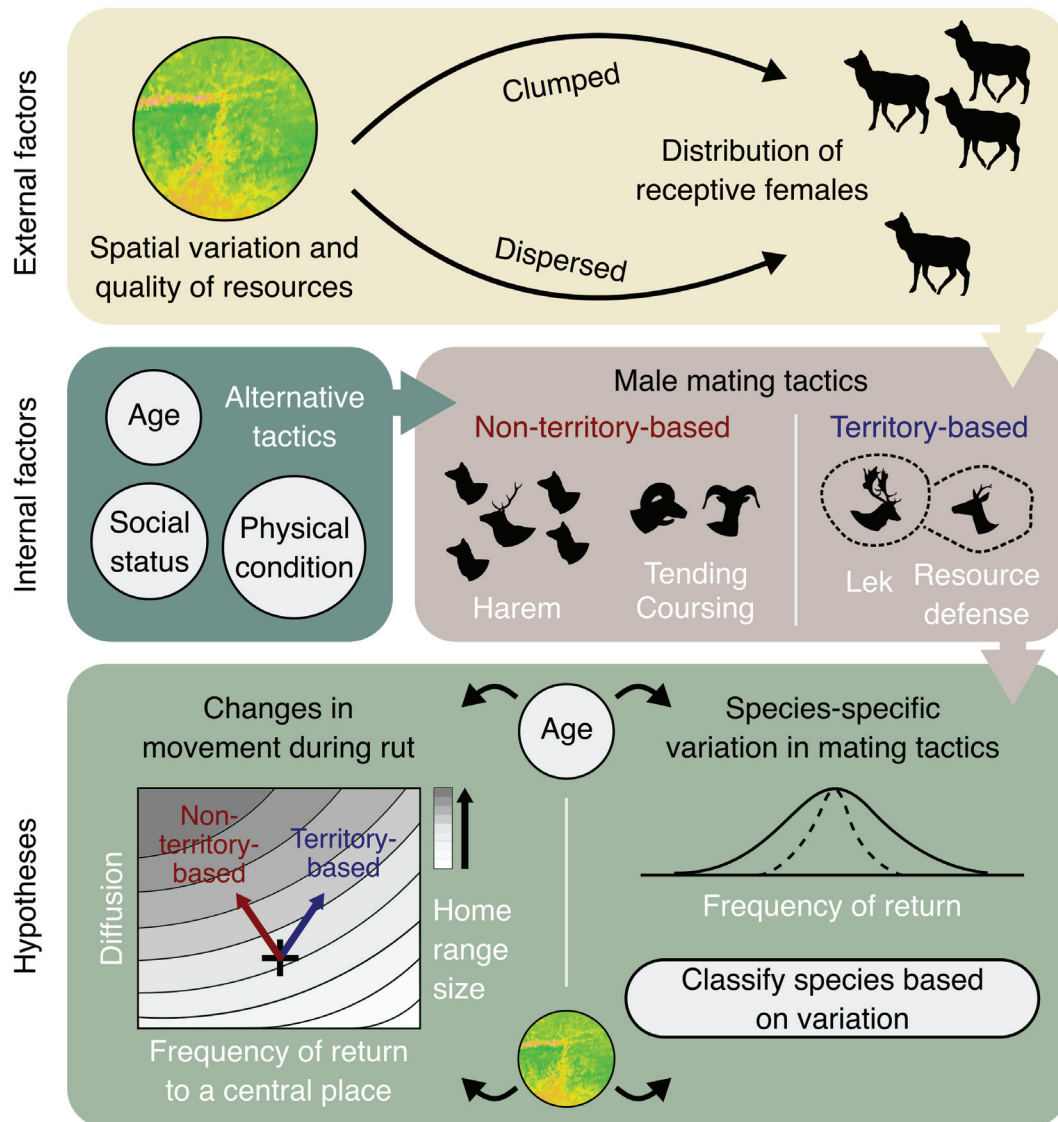


FIGURE 5.3: Conceptual framework and perspectives for future analyses. The spatial distribution of resources will lead to the spatial distribution of ungulate females. In turn, the mating strategy of males will be determined by the distribution of females in the landscape. Differences in the distribution of resources between populations of the same species may result in high intraspecific variability in mating tactics. However, alternative mating tactics may emerge as a result of the age, social status, and physical condition of the male. We expect to see an effect of age on the movement parameters, as well as on the intraspecific variation in the frequency of return. The extent of variation in the frequency of return for each species can help us qualify species on the strictly territorial to non-territorial spectrum.

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Author contributions

K.A., G.P. and A.L. designed the study, C.B, J.M.G., M.G., A.J.M.H, P.M, N.M and S.S contributed to the study design through fruitful discussions, K.A. analyzed the data and wrote the first draft. Co-authors collected and provided the datasets, participated in the writing process and approved the final version of the manuscript.

References

- Alados, C. L. (1986). "Aggressive behaviour, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenica*)." In: *Behavioural Processes* 12.2, pp. 145–158.
- Barton, K. (2020). *MuMIn: Multi-Model Inference*.
- Bjørneraas, K., Moorter, B. V., Rolandsen, C. M., and Herfindal, I. (2010). "Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics." In: *The Journal of Wildlife Management* 74.6, pp. 1361–1366.
- Blackwell, P. G. (1997). "Random diffusion models for animal movement." In: *Ecological Modelling* 100.1, pp. 87–102.
- Bon, R., Gonzalez, G., Bosch, M. D., and Cugnasse, J. M. (1992). "Ram rut-involvement in a hunted population of mouflons." In: *Acta Theriologica* 37.1-2, pp. 63–71.
- Börger, L., Dalziel, B. D., and Fryxell, J. M. (2008). "Are there general mechanisms of animal home range behaviour? A review and prospects for future research: Home range modelling." In: *Ecology Letters* 11.6, pp. 637–650.
- Börger, L. et al. (2006b). "Effects of sampling regime on the mean and variance of home range size estimates." In: *Journal of Animal Ecology* 75.6, pp. 1393–1405.
- Bowyer, R. T., McCullough, D. R., Rachlow, J. L., Ciuti, S., and Whiting, J. C. (2020). "Evolution of ungulate mating systems: Integrating social and environmental factors." In: *Ecology and Evolution* 10.11, pp. 5160–5178.
- Bro-Jørgensen, J. (2007). "The Intensity of Sexual Selection Predicts Weapon Size in Male Bovids." In: *Evolution* 61.6, pp. 1316–1326.
- Brooks, M. E. et al. (2017). "glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling." In: *The R Journal* 9.2, pp. 378–400.

Bubenik, G. A., Schams, D., White, R. J., Rowell, J., Blake, J., and Bartos, L. (1997). "Seasonal Levels of Reproductive Hormones and Their Relationship to the Antler Cycle of Male and Female Reindeer (*Rangifer tarandus*)." In: *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 116.2, pp. 269–277.

Burnham, K. P. and Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. New York: Springer-Verlag.

Cagnacci, F., Boitani, L., Powell, R. A., and Boyce, M. S. (2010). "Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges." In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1550, pp. 2157–2162.

Calabrese, J. M., Fleming, C. H., and Gurarie, E. (2016). "ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process." In: *Methods in Ecology and Evolution* 7.9, pp. 1124–1132.

Carranza, J., Garcia-Muñoz, A. J., and de Dios Vargas, J. (1995). "Experimental shifting from harem defence to territoriality in rutting red deer." In: *Animal Behaviour* 49.2, pp. 551–554.

Cederlund, G. and Sand, H. (1994). "Home-Range Size in Relation to Age and Sex in Moose." In: *Journal of Mammalogy* 75.4, pp. 1005–1012.

Chassagneux, A. et al. (2020). "Should I stay or should I go? Determinants of immediate and delayed movement responses of female red deer (*Cervus elaphus*) to drive hunts." In: *PLOS ONE* 15.3, e0228865.

Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red deer: behavior and ecology of two sexes*. University of Chicago press.

Clutton-Brock, T. H. (1989). "Review Lecture: Mammalian mating systems." In: *Proceedings of the Royal Society of London. B. Biological Sciences* 236.1285, pp. 339–372.

Conner, M. M. and Miller, M. W. (2004). "Movement Patterns and Spatial Epidemiology of a Prion Disease in Mule Deer Population Units." In: *Ecological Applications* 14.6, pp. 1870–1881.

Corlatti, L., Béthaz, S., von Hardenberg, A., Bassano, B., Palme, R., and Lovari, S. (2012). "Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs." In: *Animal Behaviour* 84.4, pp. 1061–1070.

Corlatti, L., Caroli, M., Pietrocini, V., and Lovari, S. (2013). "Rutting behaviour of territorial and nonterritorial male chamois: Is there a home advantage?" In: *Behavioural Processes* 92, pp. 118–124.

Corlatti, L., Cotza, A., and Nelli, L. (2021). "Linking alternative reproductive tactics and habitat selection in Northern chamois." In: *Ecology and Evolution* 11.11, pp. 7057–7068.

- De Magalhães, J. P. and Costa, J. (2009). "A database of vertebrate longevity records and their relation to other life-history traits." In: *Journal of Evolutionary Biology* 22.8, pp. 1770–1774.
- Decristophoris, P. M. A., Hardenberg, A. v., and McElligott, A. G. (2007). "Testosterone is positively related to the output of nematode eggs in male Alpine ibex (*Capra ibex*) faeces." In: *Evolutionary Ecology Research* 9.8, pp. 1277–1292.
- Demšar, U. et al. (2015). "Analysis and visualisation of movement: an interdisciplinary review." In: *Movement Ecology* 3.1, p. 5.
- Dunn, J. E. and Gipson, P. S. (1977). "Analysis of Radio Telemetry Data in Studies of Home Range." In: *Biometrics* 33.1, pp. 85–101.
- Duparc, A. (2016). "Dynamiques spatio-temporelles des ressources alimentaires et des activités humaines : impacts sur la sélection d'habitat d'un grand herbivore de montagne." PhD thesis. Université Grenoble Alpes.
- Emlen, S. T. and Oring, L. W. (1977). "Ecology, Sexual Selection, and the Evolution of Mating Systems." In: *Science* 197.4300, pp. 215–223.
- Espmark, Y. (1964). "Rutting behaviour in reindeer (*Rangifer tarandus* L.)" In: *Animal Behaviour* 12.1, pp. 159–163.
- Fleming, C. H., Calabrese, J. M., Mueller, T., Olson, K. A., Leimgruber, P., and Fagan, W. F. (2014). "From Fine-Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement Modes across Spatiotemporal Scales." In: *The American Naturalist* 183.5, E154–E167.
- Greenwood, P. J. (1980). "Mating systems, philopatry and dispersal in birds and mammals." In: *Animal Behaviour* 28.4, pp. 1140–1162.
- Hebblewhite, M. and Merrill, E. H. (2007). "Multiscale wolf predation risk for elk: does migration reduce risk?" In: *Oecologia* 152.2, pp. 377–387.
- Hoem, S. A., Melis, C., Linnell, J. D. C., and Andersen, R. (2007). "Fighting behaviour in territorial male roe deer *Capreolus capreolus*: the effects of antler size and residence." In: *European Journal of Wildlife Research* 53.1, pp. 1–8.
- Johansson, A. (1996). "Territory Establishment and Antler Cycle in Male Roe Deer." In: *Ethology* 102.4, pp. 549–559.
- Kays, R., Crofoot, M. C., Jetz, W., and Wikelski, M. (2015). "Terrestrial animal tracking as an eye on life and planet." In: *Science* 348.6240.
- Kojola, I. (1986). "Rutting behaviour in an enclosed group of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.)" In: *Rangifer*, pp. 173–179.

- Lambert, R. T. (1999). "Conceptus-endometrial interactions and reproductive hormone profiles during embryonic diapause and reactivation of the blastocyst in the European roe deer (*Capreolus capreolus*)." In: *Rangifer* 19.1, pp. 41–49.
- Laver, P. N. and Kelly, M. J. (2008). "A Critical Review of Home Range Studies." In: *Journal of Wildlife Management* 72.1, pp. 290–298.
- Lent, P. C. (1965). "Rutting behaviour in a barren-ground caribou population." In: *Animal Behaviour* 13.2, pp. 259–264.
- Liberg, O., Johansson, A., Andersen, R., and Linnell, J. D. C. (1998). "Mating system, mating tactics and the function of male territoriality in roe deer." In: *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp. 221–256.
- Lincoln, G. A. (1998). "Reproductive seasonality and maturation throughout the complete life-cycle in the mouflon ram (*Ovis musimon*)." In: *Animal Reproduction Science* 53.1, pp. 87–105.
- Lincoln, G. A. and Guinness, F. E. (1973). "The sexual significance of the rut in red deer." In: *Journal of Reproduction and Fertility. Supplement* 19, pp. 475–489.
- Linnell, J. D. and Andersen, R. (1998b). "Territorial fidelity and tenure in roe deer bucks." In: *Acta Theriologica* 43.1, pp. 67–75.
- Loe, L. E. et al. (2005). "Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France." In: *Journal of Animal Ecology* 74.4, pp. 579–588.
- Loison, A., Gaillard, J.-M., Pélabon, C., and Yoccoz, N. G. (1999). "What factors shape sexual size dimorphism in ungulates?" In: *Evolutionary Ecology Research* 1.5, pp. 611–633.
- Lovari, S., Sacconi, F., and Trivellini, G. (2006). "Do alternative strategies of space use occur in male Alpine chamois?" In: *Ethology Ecology & Evolution* 18.3, pp. 221–231.
- Mainguy, J., Côté, S. D., Cardinal, E., and Houle, M. (2008). "Mating Tactics and Mate Choice in Relation to Age and Social Rank in Male Mountain Goats." In: *Journal of Mammalogy* 89.3, pp. 626–635.
- Malagnino, A. et al. (2021). "Do reproductive constraints or experience drive age-dependent space use in two large herbivores?" In: *Animal Behaviour* 172, pp. 121–133.
- Marchand, P., Garel, M., Bourgoïn, G., Dubray, D., Maillard, D., and Loison, A. (2014). "Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area." In: *Biological Conservation* 177, pp. 1–11.
- Marchand, P. et al. (2017). "Sociospatial structure explains marked variation in brucellosis seroprevalence in an Alpine ibex population." In: *Scientific Reports* 7.1, p. 15592.

- Murray, M. G. (1982). "The Rut of Impala: Aspects of Seasonal Mating under Tropical Conditions." In: *Zeitschrift für Tierpsychologie* 59.4, pp. 319–337.
- Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. (2011). "Partial migration in expanding red deer populations at northern latitudes – a role for density dependence?" In: *Oikos* 120.12, pp. 1817–1825.
- Noonan, M. J. et al. (2019). "A comprehensive analysis of autocorrelation and bias in home range estimation." In: *Ecological Monographs* 89.2, e01344.
- Owen-Smith, N. (1977). "On Territoriality in Ungulates and an Evolutionary Model." In: *The Quarterly Review of Biology* 52.1, pp. 1–38.
- Pavitt, A. T., Walling, C. A., Möstl, E., Pemberton, J. M., and Kruuk, L. E. B. (2015). "Cortisol but not testosterone is repeatable and varies with reproductive effort in wild red deer stags." In: *General and Comparative Endocrinology* 222, pp. 62–68.
- Pérez-Barbería, F. J. and Gordon, I. J. (2000). "Differences in body mass and oral morphology between the sexes in the Artiodactyla: evolutionary relationships with sexual segregation." In: *Evolutionary Ecology Research* 2.5, pp. 667–684.
- Plard, F., Bonenfant, C., and Gaillard, J.-M. (2011). "Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver." In: *Oikos* 120.4, pp. 601–606.
- Portanier, E. et al. (2018). "Landscape genetics matches with behavioral ecology and brings new insight on the functional connectivity in Mediterranean mouflon." In: *Landscape Ecology* 33.7, pp. 1069–1085.
- Roelants, H., Schneider, F., Göritz, F., Streich, J., and Blottner, S. (2002). "Seasonal Changes of Spermatogonial Proliferation in Roe Deer, Demonstrated by Flow Cytometric Analysis of c-kit Receptor, in Relation to Follicle-Stimulating Hormone, Luteinizing Hormone, and Testosterone." In: *Biology of Reproduction* 66.2, pp. 305–312.
- San José, C., Braza, F., and Aragón, S. (1999). "The effect of age and experience on the reproductive performance and prenatal expenditure of resources in female fallow deer (*Dama dama*)." In: *Canadian Journal of Zoology* 77.11, pp. 1717–1722.
- Santiago-Moreno, J., Gómez-Brunet, A., González-Bulnes, A., Toledano-Díaz, A., Malpoux, B., and López-Sebastián, A. (2005). "Differences in reproductive pattern between wild and domestic rams are not associated with inter-specific annual variations in plasma prolactin and melatonin concentrations." In: *Domestic Animal Endocrinology* 28.4, pp. 416–429.
- Seigle-Ferrand, J. et al. (2021). "A Systematic Review of Within-Population Variation in the Size of Home Range Across Ungulates: What Do We Know After 50 Years of Telemetry Studies?" In: *Frontiers in Ecology and Evolution* 8.

Serrano, E. et al. (2015). "Border Disease Virus: An Exceptional Driver of Chamois Populations Among Other Threats." In: *Frontiers in Microbiology* 6, p. 1307.

Solberg, E. J., Rolandsen, C. M., Heim, M., Linnell, J. D. C., Herfindal, I., and Sæther, B.-E. (2010). "Age and sex-specific variation in detectability of moose (*Alces alces*) during the hunting season: implications for population monitoring." In: *European Journal of Wildlife Research* 56.6, pp. 871–881.

Toïgo, C. and Gaillard, J.-M. (2003). "Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness?" In: *Oikos* 101.2, pp. 376–384.

Vanpé, C., Morellet, N., Kjellander, P., Goulard, M., Liberg, O., and Hewison, A. M. (2009). "Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality." In: *Journal of Animal Ecology* 78.1, pp. 42–51.

Von Hardenberg, A., Bassano, B., Peracino, A., and Lovari, S. (2000). "Male Alpine Chamois Occupy Territories at Hotspots Before the Mating Season." In: *Ethology* 106.7, pp. 617–630.

Whitehead, P. E. and McEwan, E. H. (1973). "Seasonal variation in the plasma testosterone concentration of reindeer and caribou." In: *Canadian Journal of Zoology* 51.6, pp. 651–658.

Willisch, C. S. and Ingold, P. (2007). "Feeding or Resting? The Strategy of Rutting Male Alpine Chamois." In: *Ethology* 113.1, pp. 97–104.

Willisch, C. S. and Neuhaus, P. (2009). "Alternative Mating Tactics and Their Impact on Survival in Adult Male Alpine Ibex (*Capra ibex ibex*)." In: *Journal of Mammalogy* 90.6, pp. 1421–1430.

Supplementary Information

Supplementary Tables

TABLE S5.1: Estimates and associated standard errors retrieved from the model averaging of the best retained models assessing the link between home range size, mating tactic, and period. Values in bold are significant.

	Estimate	Standard error	<i>p</i> -value
Intercept [Non-territorial:Reference]	12.091	0.281	<0.01
Mating Tactic [Territorial]	0.848	0.538	0.115
Period [Pre-rut]	0.981	0.083	<0.01
Period [Rut]	1.086	0.08	<0.01
Body mass	1.812	0.268	<0.01
Number of locations	0.01	0.029	0.746
Duration	0.119	0.032	<0.01
Mating Tactic [Territorial]:Period [Pre-rut]	-0.833	0.142	<0.01
Mating Tactic [Territorial]:Period [Rut]	-0.86	0.138	<0.01

TABLE S5.2: Estimates and associated standard errors retrieved from the model averaging of the best retained models assessing the link between diffusion, mating tactic, and period. Values in bold are significant.

	Estimate	Standard error	<i>p</i> -value
Intercept [Non-territorial:Reference]	1.209	0.261	<0.01
Mating Tactic [Territorial]	1.146	0.5	<0.05
Period [Pre-rut]	0.536	0.052	<0.01
Period [Rut]	0.921	0.049	<0.01
Body mass	1.085	0.245	<0.01
Number of locations	0.018	0.028	0.529
Duration	-0.007	0.015	0.662
Mating Tactic [Territorial]:Period [Pre-rut]	-0.268	0.088	<0.01
Mating Tactic [Territorial]:Period [Rut]	-0.328	0.085	<0.01

TABLE S5.3: Estimates and associated standard errors retrieved from the model averaging of the best retained models assessing the link between frequency of return to a central place, mating tactic, and period. Values in bold are significant.

	Estimate	Standard error	p-value
Intercept [Non-territorial:Reference]	11.56	0.208	<0.01
Mating Tactic [Territorial]	-0.258	0.396	0.514
Period [Pre-rut]	0.441	0.071	<0.01
Period [Rut]	0.17	0.068	<0.05
Body mass	0.751	0.195	<0.01
Number of locations	0.003	0.021	0.88
Duration	0.138	0.026	<0.01
Mating Tactic [Territorial]:Period [Pre-rut]	-0.562	0.121	<0.01
Mating Tactic [Territorial]:Period [Rut]	-0.539	0.118	<0.01

Supplementary Figures

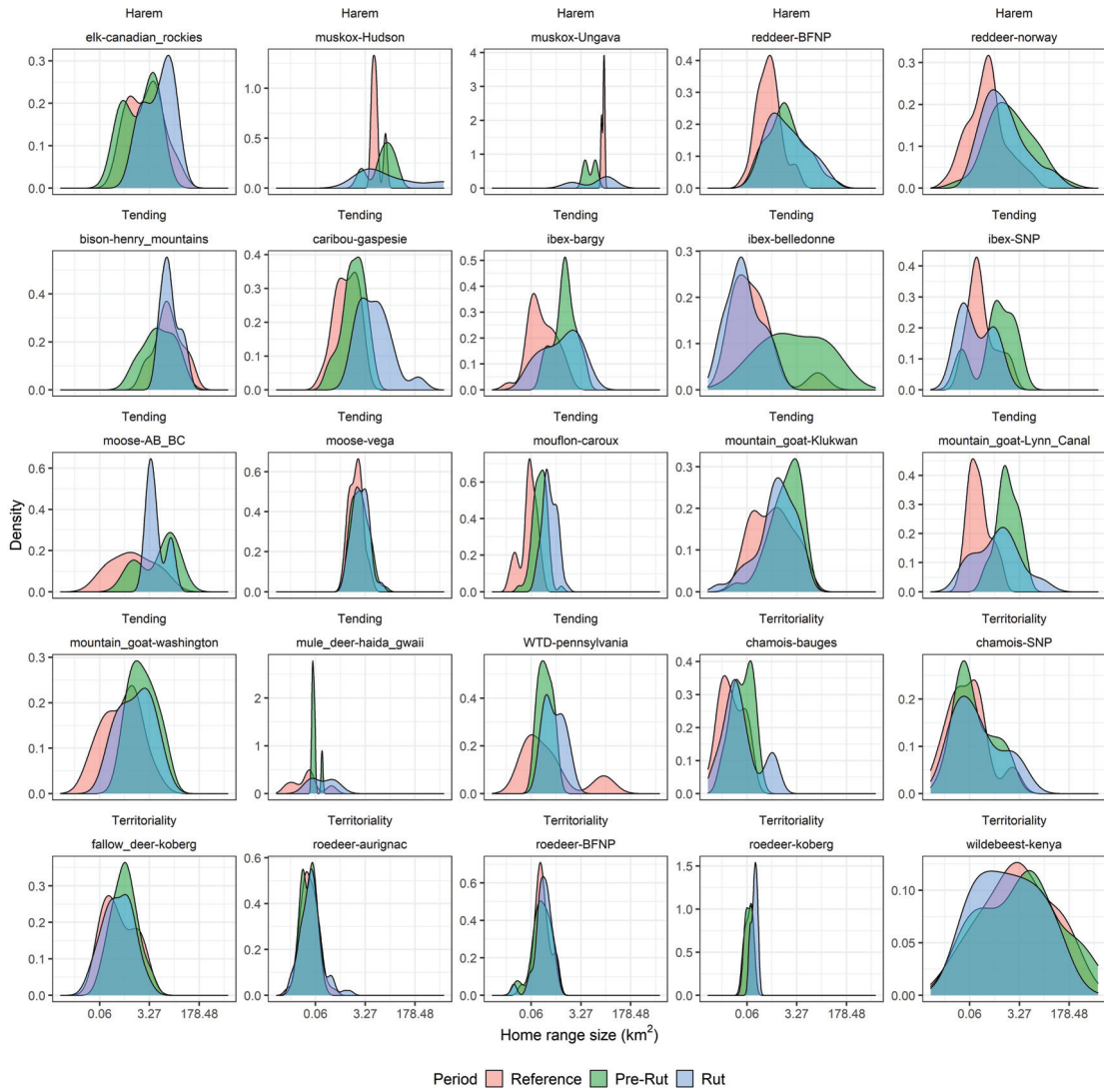


FIGURE S5.1: Density of home range size (km^2) values for each population during reference, pre-rut, and rut periods. The x-axis is on the logarithmic scale and fixed for all panels. The y-axis varies for each population.

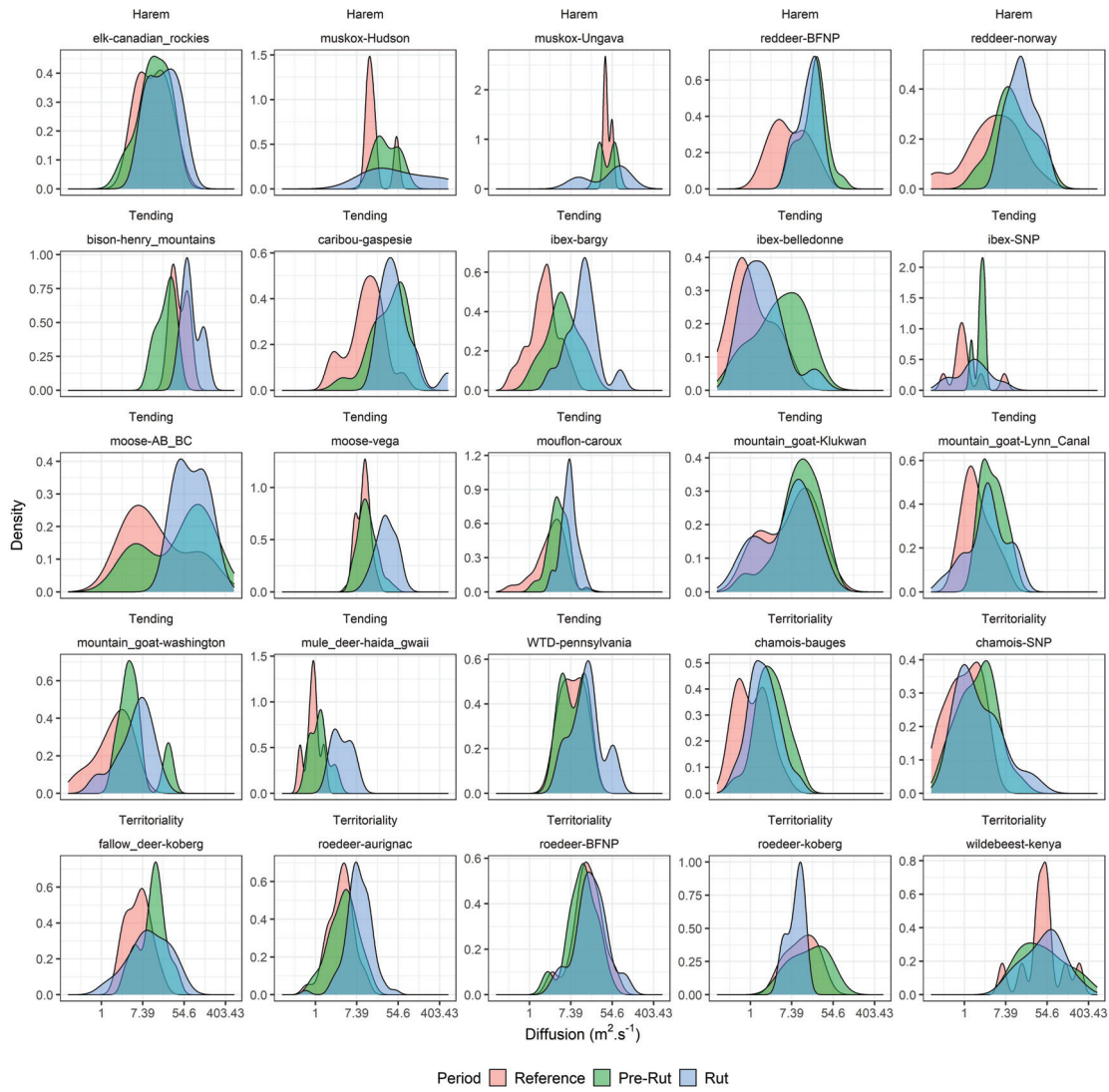


FIGURE S5.2: Density of diffusion ($m^2 \cdot s^{-1}$) values for each population during reference, pre-rut, and rut periods. The x-axis is on the logarithmic scale and fixed for all panels. The y-axis varies for each population.

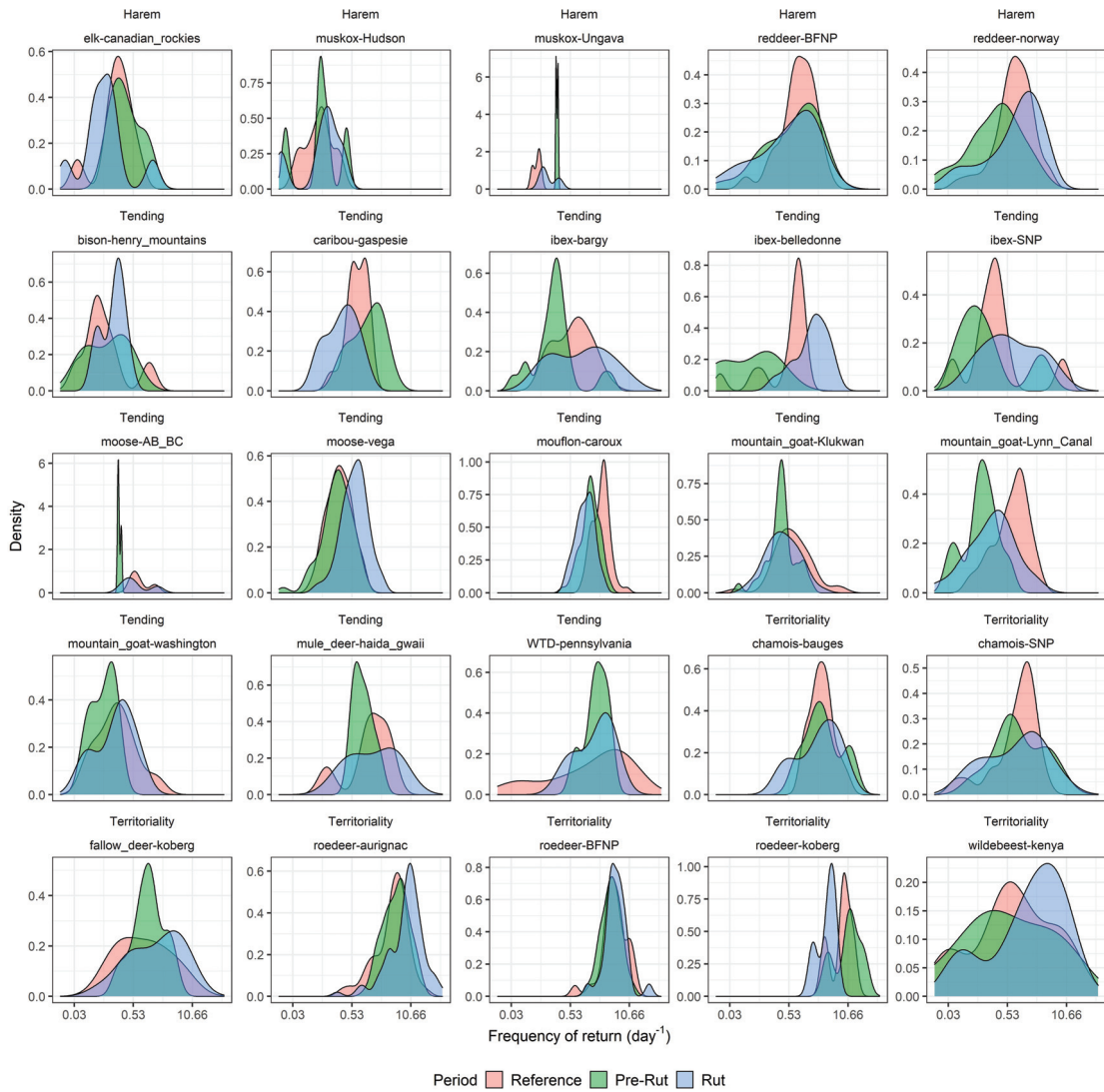


FIGURE S5.3: Density of the frequency of return (day^{-1}) values for each population during reference, pre-rut, and rut periods. The x-axis is on the logarithmic scale and fixed for all panels. The y-axis varies for each population.

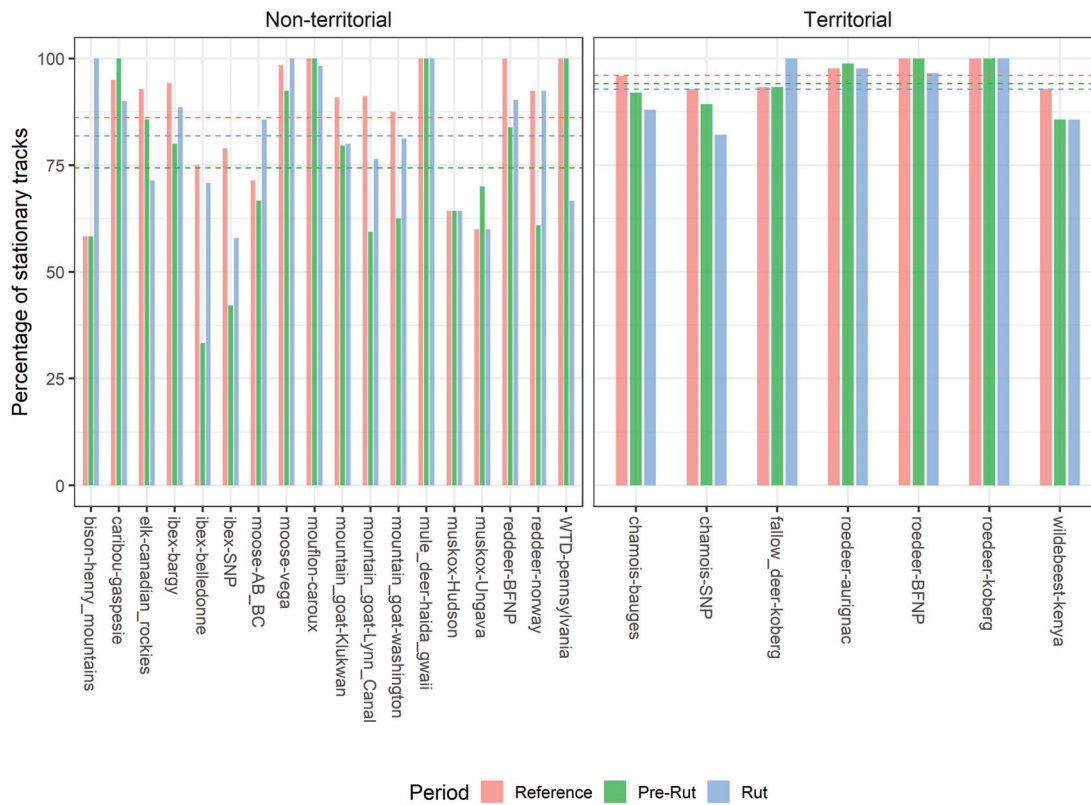


FIGURE S5.4: Percentage of stationary tracks during each period of reference, pre-rut, and rut for each population and according to mating tactic. Lines represent mean values for each period.

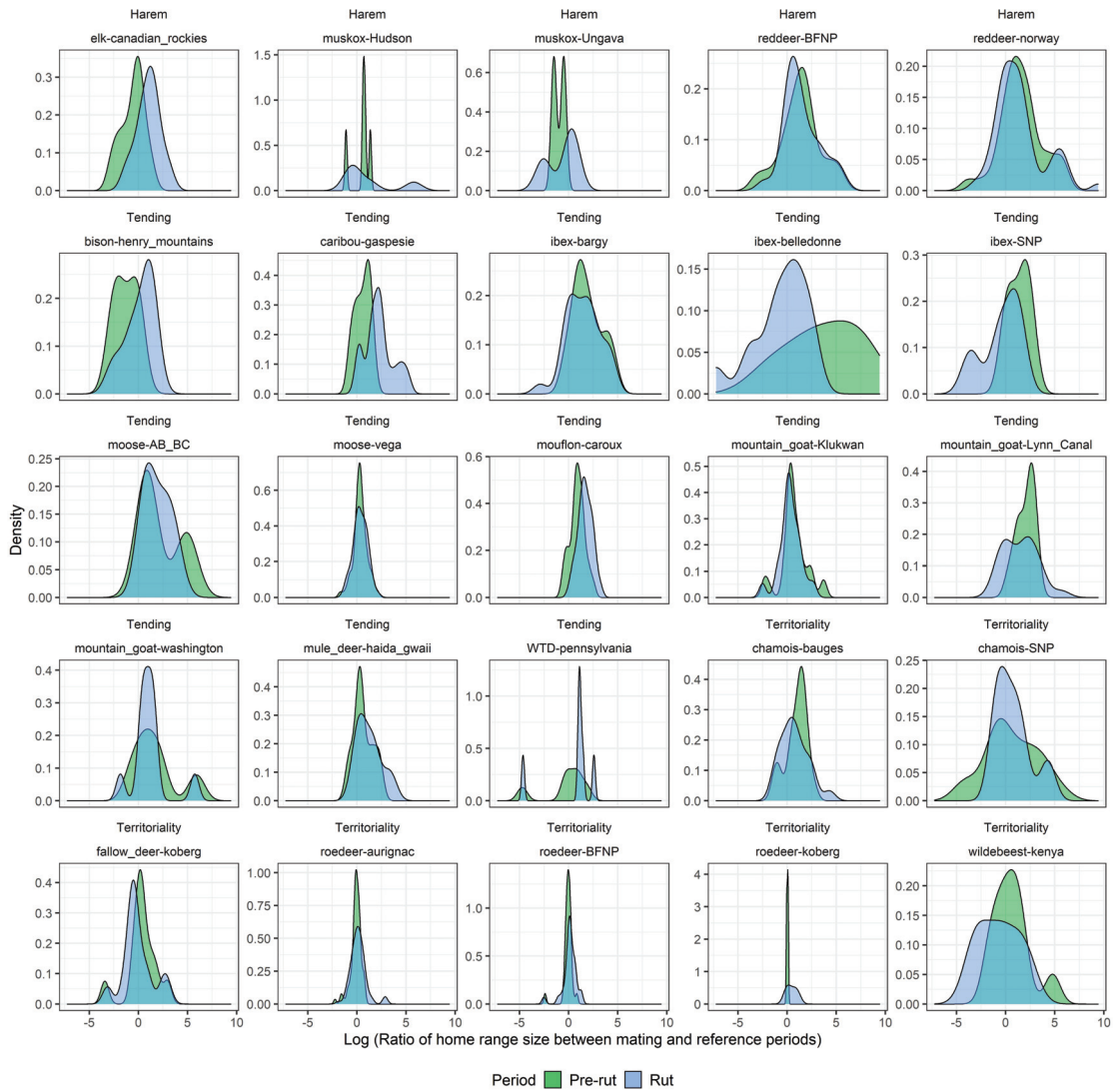


FIGURE S5.5: Log of the ratio of home range size between mating periods (i.e. pre-rut and rut) and the reference period. A value of 0 represents no change in home range size during pre-rut and rut compared to the reference period.

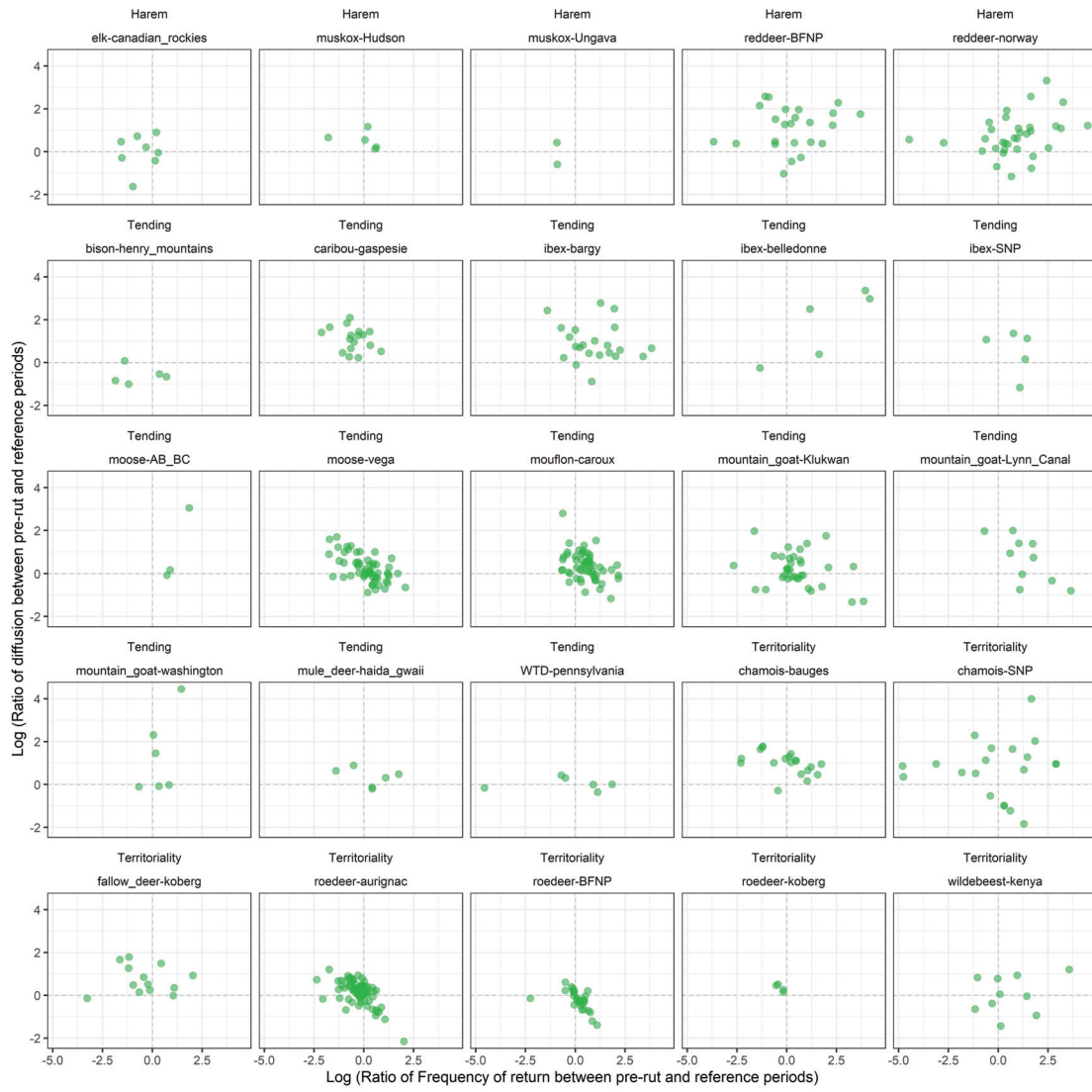


FIGURE S5.6: Log of the ratios of both frequency of return and diffusion between the pre-rut and the reference period. A value of 0 represents no change in parameters during pre-rut compared to the reference period.

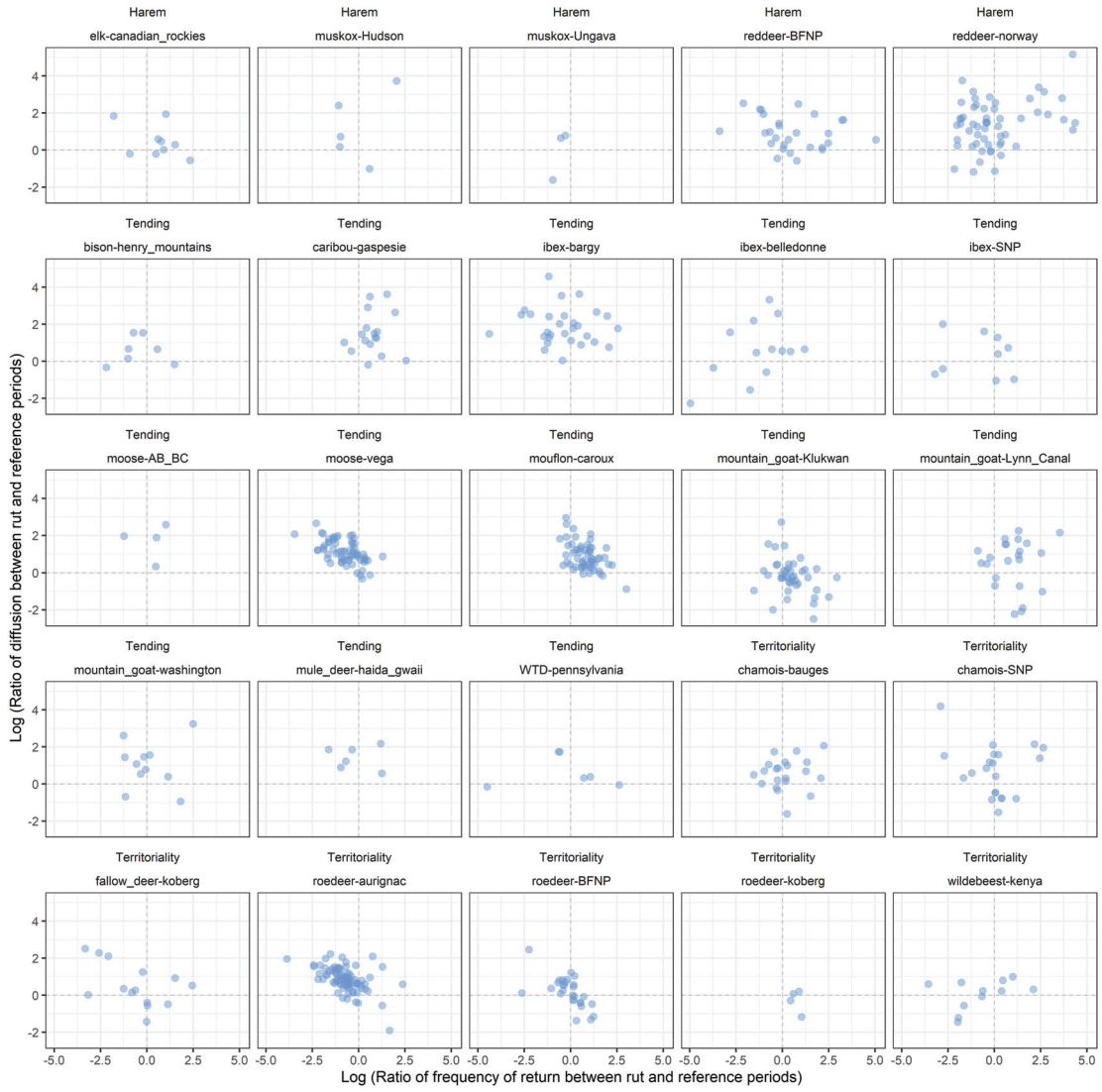


FIGURE S5.7: Log of the ratios of both frequency of return and diffusion between the rut and the reference period. A value of 0 represents no change in parameters during rut compared to the reference period.

PART III

SYNTHESIS AND PERSPECTIVES



6

Summary and discussion of results

THROUGHOUT the first chapter of this thesis, I posited that there is significant variation in movement among individuals which stems from multiple environmental and individual factors, leading to intra- and interspecific differences in fitness. These driving factors are also bound to vary with the spatio-temporal dynamics of the environment and the animal's needs throughout its biological cycle. The main purpose of this thesis was to reconcile these two aspects by evaluating how movement varies with the intertwined link between external and internal constraints at different spatio-temporal scales. Only by doing so can we understand the full scope of animal behavior and reach robust conclusions that would help theoretical, conservation, and management studies. I focused my research on ungulates because of their wide distribution across different environments, their considerable variation in life-history and ecological traits, as well as the availability of studies and GPS data from this taxonomic clade. My objective was threefold: bibliographical, empirical, and methodological. First, I summarized previous studies on the intraspecific drivers of home range size. Second, I evaluated how females respond spatially to the availability and distribution of resources while caring for offspring around parturition. Third, I aimed to identify the mating tactics of males during the rut from GPS data. In this chapter, I will provide a summary of the main results that I obtained, each followed by a quick discussion to highlight their importance in the field of movement ecology. Before concluding, I will also contribute a few ideas and perspectives that I believe can be important for future prospective studies.

6.1 Home range studies: factors and limitations

The tight link between home range size and population dynamics (Gaillard et al., 2010; Morales et al., 2010) makes it crucial to understand the drivers of variation in home range size. At the interspecific level, there is generally a consensus on the factors that lead to the observed differences in home range size. Factors such as body mass

(Harestad and Bunnell, 1979; McNab, 1963), diet (Mysterud, Pérez-Barbería, and Gordon, 2001), social organization (Damuth, 1981), habitat (Ofstad et al., 2016), and even the defensibility of the home range borders (Grant, Chapman, and Richardson, 1992) explain in large part the observed variation. At the intraspecific level, however, and despite the numerous studies on home range size since the '70s, how factors drive variation in home range size remain somewhat obscure. There is a consensus on a set of factors (Mcloughlin and Ferguson, 2000), however, the expected relationship is not always consistent across species. Whether the inconsistency of the expected relationship is an outcome of ecological or methodological aspects remained to be investigated. In our first paper, we conducted a systematic review to determine how food resources, landscape heterogeneity, and risk (lethal and non-lethal) drive intraspecific seasonal variation in home range size of ungulates, and whether the observed relationship depends on life-history and ecological traits such as body mass, diet, and social organization. We found that 80% of the retrieved studies provided support for the negative relationship between home range size and food availability. This was not the case, however, for the link between home range and landscape heterogeneity. Of the life-history traits that we tested, body mass and group size did not impact the observed relationship between food resources and home range size. Only diet seemed to determine whether there was support for the expected relationship, where home range sizes of cattle-type ungulates showed marked variation with food availability than moose-type ungulates.

Despite the interesting trends and results, we were not able to provide a consensus over the expected relationships between home range size and landscape heterogeneity or risk. Our paper, however, provided some insights into the problems in home range studies. Only 1% were available to be included in our analysis and they were restricted to a handful of species with limited geographic distribution. Additionally, only two studies measured the three variables (i.e. food, landscape heterogeneity, and risk) simultaneously. This is problematic, since home range, as shown in [Chapter 1](#), is a result of the interplay between all three (Péron, 2019). This could obscure the underlying relationships between environmental variables and home range size. We also identified multiple methodological problems that hindered our findings. It is quite difficult to quantify the level of risk in the landscape for ungulates, as attested by the multitude of metrics used in the literature (Moll et al., 2017; Prugh et al., 2019). For instance, the giving-up density (Brown, 1988) may be used to quantify risk, but it can be quite laborious to put in place over entire landscapes, and may not be as helpful for ungulates as it is for small rodents (Prugh et al., 2019). Also, it is difficult to determine how a variable is perceived by the animal. For instance, human presence has been used to determine the level of risk (Bonnot et al., 2013), but in some populations, human settlements may be considered a refuge from other predators (Hebblewhite and Merrill, 2009). Unless we take a holistic view of the system in which the animal lives and account for predators, heterospecifics, and conspecifics, we will continue to face difficulties when evaluating home range size. Moreover, measures of food resources and landscape heterogeneity are based on human-made observations and maps of categorical or continuous variables.

This could have no value for the species. This is why it is crucial to understand the foodscape of the animal (Duparc et al., 2020; Searle, Hobbs, and Gordon, 2007) to accurately quantify its food resources without having to use unclear proxies. Overall, we still lack a standardization to quantify landscape and risk and have difficulty linking these two variables to the correct scale of response. Most studies measure environmental variables within the home range, but this is entirely circular since there is already a higher level of selection that has occurred (Johnson, 1980; Kie et al., 2002). An animal perceives its environment and, based on the availability of forage and other resources, will define its home range size.

Bias in home range studies, however, has not been only an outcome of mismeasurement of environmental variables. One of the major problems is the estimation of home range size with inappropriate methods that are subject to different sources of bias such as telemetry error, autocorrelation, kernel smoothing, sample size, and spatial dimensionality (2D estimation rather than 3D) (Heit, Ortiz-Calo, and Montgomery, 2021). There is an increasing number of studies that started to address some of these problems by accounting for the bias in their home range estimation. Nevertheless, some sources of bias such as spatial dimensionality are still left aside. Overall, less than 1% of papers on terrestrial home ranges account for all sources of bias (Heit, Ortiz-Calo, and Montgomery, 2021). Therefore, it is not surprising that we still have trouble understanding the effect of external and internal factors on home range size (Chapter 3, Seigle-Ferrand et al., 2021). Additionally, and despite the many studies on the limitations of Kernel Density Estimators and Minimum Convex Polygon (Börger, Dalziel, and Fryxell, 2008; Kie et al., 2010; Laver and Kelly, 2008; Nilsen, Pedersen, and Linnell, 2008), researchers still rely on both estimators to measure home range size (Figure 6.1, for a review on terrestrial animals: Heit, Ortiz-Calo, and Montgomery, 2021, on ungulates: Seigle-Ferrand et al., 2021, on reptiles: Crane et al., 2021), even though new more robust estimators have been developed (auto-correlated Kernel Density Estimator AKDE: Fleming et al., 2016).

Underestimating the space use of an animal by using KDE or MCP (Noonan et al., 2019) can significantly alter the scaling exponents between home range and explanatory variables. For instance, the use of AKDE significantly changes the scaling of the allometric relationship of home range size (Noonan et al., 2020). Whether this has also an effect on the relationship between home range and environmental variables remains to be explored and requires researchers to revisit previous home range estimations (Noonan et al., 2020).

6.2 A fine-scale look at the balance between movement, resource acquisition, and care for offspring

So far, to characterize changes in movement behavior linked to reproduction, most studies have focused on the home range size (e.g. in Alpine ibex: Grignolio et al., 2007, in roe deer: Malagnino et al., 2021; Saïd et al., 2005, in fallow deer: Ciuti et al.,

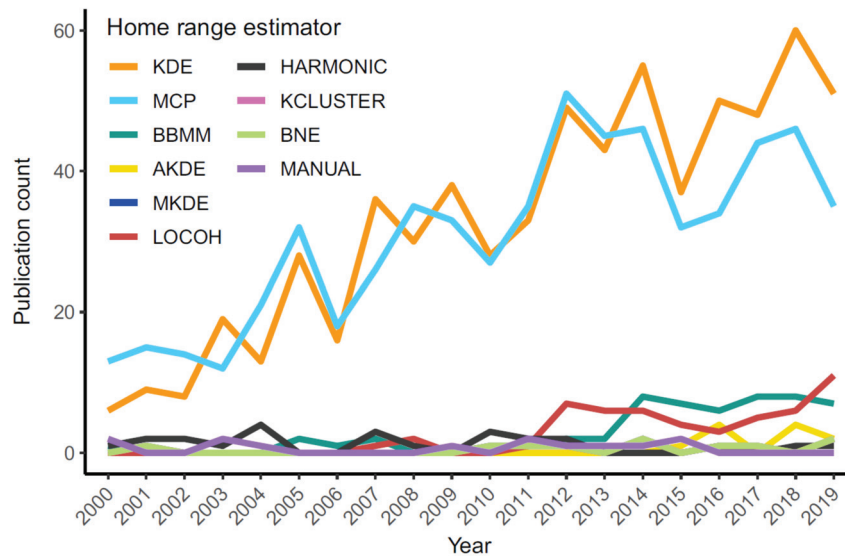


FIGURE 6.1: The 10 most common home range estimators used per year in studies retained for analysis ($n = 1,203$) in a review of terrestrial home range literature published between 2000 and 2019. Estimators include: kernel density estimation (KDE), minimum convex polygon (MCP), Brownian-bridge movement model (BBMM), autocorrelated KDE (AKDE), movement KDE (MKDE), local convex hull (LOCOH), harmonic mean (HARMONIC), k-cluster (KCLUSTER), and analog/manual (MANUAL). Taken from Heit, Ortiz-Calo, and Montgomery (2021).

2006), which may not capture all the relevant details of within-range behavior linked to reproductive tactics (Campioni et al., 2013). At the same time, focusing on home range assumes that individuals exhibit solely a restricted space use which could obscure our understanding of their movement during critical biological periods. Therefore, we decided in this thesis to evaluate the movement behavior of females around parturition, at a finer scale than home range. Efforts to acquire energy in a landscape with spatially heterogeneous resources can be hampered when females have a calf at heel. It is therefore important to accurately address how mothers adjust their movement with the spatial distribution of resources and limited mobility of their offspring around parturition.

Little was known about the relative constraint of neonatal anti-predator tactics on the movement of reproductive females as a function of the local environment, even less in an interspecific framework (but see Malagnino et al., 2021; Marchand et al., 2021; Péron et al., 2018). Conducting studies in an interspecific context, however, allows us to pinpoint the driving factors of movement (Nathan et al., 2008). Our study on 23 species of ungulates, is the first large-scale interspecific investigation of the constraints of offspring on female movement along the hider-follower continuum. As parturition is quite energetically costly, females require a large amount of resources to compensate for their energy expenditure (Clutton-Brock, Albon, and Guinness, 1989) and therefore need to be present at a particularly resource-rich location during the specific birth period. With high temporal variation and spatial heterogeneity of food resources, individuals are more likely to migrate (Bischof et al., 2012; Mueller and Fagan, 2008; Mysterud et al., 2011) because they make the most of the phenology gradient with latitude or altitude to find higher quality and quantity of forage. Our results highlight the movement

mechanisms that species use in relation to food distribution and show that females, in response to such effects, will adapt their spatial behavior according to the anti-predatory tactic of their offspring. It appears that females with hider offspring can anticipate their future need to access distant resources by moving one month before parturition, in sharp contrast to females with follower offspring. The limited mobility of hider neonates, once they are born, will thus force females to anticipate resource needs, leading therefore to increased directional diffusion in search of rich environments (Chapter 4; Bischof et al., 2012; Hebblewhite and Merrill, 2009; Lendrum et al., 2014) to reach before giving birth and becoming constrained by the offspring. Followers, on the other hand, appear to be less pressured to reach a rich environment before birth since their offspring would barely limit their movements as they can follow them shortly after birth.

We also found that species with offspring using both tactics reduced their movement after parturition, probably due to the constraints imposed by their offspring. The extent of the constraints was however more marked in hider than in follower species. Studies evaluating the effect of offspring presence on the movement of mothers report mostly a reduction in home range size (Ciuti et al., 2006; Grignolio et al., 2007; Malagnino et al., 2021; Saïd et al., 2005). One of the most important aspects of our results is the proof that even if space use is roughly similar between individuals, the underlying components of movement can vary based on the internal factors and ecological traits of the species. We detail that ungulate mothers adjust their space use through a combined change in their diffusion in the landscape and frequency of return to previously visited sites based on the neonatal anti-predator tactics of their offspring.

The way breeding mammalian females cope with opposing spatial constraints associated with parturition and the acquisition of food resources to offset the energetic demands of breeding (Clutton-Brock, Albon, and Guinness, 1989) has major biological and ecological consequences. From the newborn perspective, environmental conditions during early life, like the transfer of food resources from the mother, strongly impact the immediate development and survival of the dependent offspring (Guinness, Clutton-Brock, and Albon, 1978; Nilsen, Linnell, and Andersen, 2004). Long-term consequences of early life conditions also partly shape the offspring's future breeding success during adulthood (Lindström, 1999; Lummaa and Clutton-Brock, 2002). It is important to note, however, that our observed patterns are solely based on food resource variables. We did not account for the presence of predators, diet, or snow cover in each population which can lead to marked differences in the movement behavior of individuals (Geremia et al., 2019; Hebblewhite and Merrill, 2009; Laforge, Bonar, and Wal, 2021; Tucker et al., 2018). We found that females migrate to acquire resources but we did not test whether the choice of birth site is favorable for the offspring. Migrating elk, for instance, did not trade-off high-quality forage with a lower risk of predation and subjected their offspring to higher mortality (Berg et al., 2021). Additionally, the use of NDVI may be questionable as it cannot capture some resources which can affect the choice of migrating. For instance, non-resident elk did not surf the green wave probably due to irrigated fields of high-quality forage which were not detected with the instantaneous

green-up (Middleton et al., 2018). This may only be problematic for intraspecific studies however since the large variation in NDVI-based variables between populations can make it quite reliable to investigate movement patterns across species (Aikens et al., 2020; Mueller et al., 2011; Teitelbaum et al., 2015).

Nevertheless, the marked differences between hidiers and followers are a clear sign that neonatal anti-predator tactics should be accounted for in future studies and management decisions. As human settlements expand even more (Tucker et al., 2018) to the point of constraining migratory routes, there is a need to protect landscape corridors for migrating species (Allen and Singh, 2016; Kauffman et al., 2021b). From our results, it seems that maintaining connectivity may be more urgent for hider species in highly variable environments since they exhibit marked mobility around parturition. Evaluating whether this is an accurate assumption seems like an interesting venture for future migration studies (Kauffman et al., 2021b).

6.3 Inferring mating strategies

The fitness of animals relies not only on the survival of offspring but also on the mating success of male individuals. To access mates during the rut, male ungulates display a wide variety of mating tactics with distinct movement behavior (Clutton-Brock, 1988; Clutton-Brock, 1989). There are still, however, few studies that identified such behavior from GPS data (Malagnino et al., 2021). Taking advantage of the advanced methodology, our results, albeit descriptive, show that there is possibly a way to discriminate the different mating tactics using the frequency of return metric. We showed that ungulates with non-territory-based mating tactics (e.g. tending, coursing) exhibit a decrease or no change in their frequency of return. Species with territory-based mating tactics (e.g. territorial, lek), on the other hand, showed increases in the frequency of return probably due to intense patrol and defense of territory borders. Nevertheless, we still need to investigate further and take into account the resource distribution, social status, and age which can affect the choice of mating strategy (Bon et al., 1992; Bon, Dardaillon, and Estevez, 1993; Willis and Neuhaus, 2009). Also, hunting activity and snow cover can be two confounding factors that can change the movement behavior of individuals (Boldt and Ingold, 2005; Chassagneux et al., 2020), especially when the rut occurs in autumn and during hunting sessions, and should therefore be accounted for. We also suggest that our method can be used to determine the intraspecific variation in mating tactics which has been a long-standing debate in ecology.

6.4 The multipotential of continuous-time stochastic movement models

Overcoming inconsistencies in home range size estimates (Chapter 3, Crane et al., 2021; Heit, Ortiz-Calo, and Montgomery, 2021; Seigle-Ferrand et al., 2021) requires novel methods that can allow robust comparisons between individuals and species.

Several promising approaches (e.g. mechanistic home range analysis: Moorcroft, Lewis, and Crabtree, 2006; Moorcroft, 2012) have been developed to disentangle movement processes and identify the underlying factors resulting in home range formation (e.g. memory/familiarity: Van Moorter et al., 2009b; Wolf et al., 2009, the influence of physical or behavioral barriers in the landscape: Beyer et al., 2016). Among the most recent of such approaches, continuous-time stochastic movement models (CTMM) offer an exciting new avenue of research (Blackwell, 1997; Calabrese et al., 2018; Fleming et al., 2014), as they explicitly connect movement processes to home ranges while simplifying complex movements in a restricted number of parameters. With their relative simplicity, CTMM can help capture the essence of the movement-to-home range processes required to describe animal space use translated into fitness costs (Gaillard et al., 2010; McLoughlin et al., 2007; Morales et al., 2010). In addition, the used method is robust to varying sampling intervals (Calabrese, Fleming, and Gurarie, 2016; Fleming et al., 2014; Péron, 2019) while accounting for temporal and spatial autocorrelation, allowing us to compare heterogeneous datasets. Interestingly, the use of CTMM can be widened, not only to understand the underlying mechanisms of home range formation but also to relate the movement metrics to ecological and life-history traits. The underlying metrics proved efficient in discriminating movement between hidiers and followers (Chapter 4), mating tactics (Chapter 5), and even provided support for identifying alternative behavioral tactics of juvenile roe deer (Appendix A, Ducros et al., 2020). Throughout this thesis, therefore, we provided evidence of the multipotential of CTMM in interspecific studies. The framework is even more appealing because it is already implemented and quite straightforward to use, with no need for resampling data (Calabrese, Fleming, and Gurarie, 2016).

With the increasing fine-scale resolution of GPS data (Kays et al., 2015), there is no doubt that CTMM will continue to be a major robust framework for the analysis of movement. Using the diffusion and frequency of return metrics relies however on the asymptotic behavior of movement which is typically achieved over a weekly or monthly scale. Therefore, we may still not be able to adapt this to very fine daily scales. Nevertheless, the reliance of CTMM on the asymptotic behavior can help us recognize the temporal scale of species at which they reach a restricted space use in a robust comparative way. This would provide significant insight into the movement scale of each species, which is a long-standing goal in movement and conservation ecology (Allen and Singh, 2016; Börger, Dalziel, and Fryxell, 2008; Laver and Kelly, 2008; Péron, 2019).

7

Perspectives for future research

Results in this thesis open many lines of research for future studies. I decided however to limit myself in this chapter to ideas around the hider-follower continuum, and a quick thought on mating tactics. I spent almost the past three years working on the interspecific paper on neonatal anti-predator tactics. Due to this heavily invested time, I owe it to myself to express my ideas which arose during my study around this subject, as speculative as they may be. Most of the perspectives that I will present below relate to life-history traits and evolutionary questions rather than movement ecology. I believe that it is important to show that results on movement can help clarify and raise questions on larger areas of evolutionary ecology. I will briefly detail below my thoughts and why there is a need to investigate them in a much more thorough manner.

7.1 Hiders in seasonal environments

In [Chapter 4](#), I argue that the environment itself can act as a selective pressure on neonatal anti-predator tactics in addition to predation. I also put forward a new hypothesis for an environmentally driven hider-follower tactic, where the duration of the hiding phase should decrease with increasing heterogeneity and decreasing productivity, otherwise such environments will not be able to harbor hider species as the temporally restricted flush of resources would require constant movement, rendered complicated by the immobility of the offspring. Even though females with hider young were more stationary around parturition than before parturition, a substantial proportion of individuals living in environments with a coarse distribution of resources still exhibit non-stationary behavior ([Chapter 4](#)). I propose that some females may be able to move after parturition in seasonal environments because their offspring shortened the length of the hiding phase in these populations. Some studies evidence inter-population variability in the duration of hiding in large herbivores (Baharav, 1983; Ralls, Kranz, and Lundrigan, 1986), however nearly none correlated it to food resource seasonality. One study on Mountain and Dorcas gazelles (*Gazella gazella gazella* and

Gazella dorcas) showed a 15-day difference in hiding between two populations and attributed the reduction of hiding to unfavorable environmental conditions which led fawns to exit their hide earlier (Baharav, 1983).

At a very large spatial scale, highly seasonal environments are mostly open habitats (e.g. grasslands, tundra, taiga), unfavorable to hiding neonates which require moderately high vegetation cover to avoid detection by predators (Fisher, Blomberg, and Owens, 2002). Hence, as seasonality increases and habitats become more open to a point where hiding is no longer advantageous, we can expect a shorter hiding phase to reduce the predation risk on offspring. Similarly, the narrow spatio-temporal flush of resources characteristic of strongly seasonal environments would require imminent migration (Mueller and Fagan, 2008) for hider females following parturition to reconnect with the green wave (Aikens et al., 2017; Bischof et al., 2012) and monopolize resources required for lactation (Clutton-Brock, Albon, and Guinness, 1989), all the while constrained by their offspring. Because a reduction in hiding duration would allow breeding females to move to foraging areas (Baharav, 1983), I hypothesize that species with hider offspring should avoid seasonal environments, as hiding may be disadvantageous for resource acquisition of distant resources, which in turn would decrease the reproductive success of females. A preliminary analysis of a dataset on ungulates that I assembled shows an interesting trend that supports my hypothesis (Figure 7.1) but still requires further evaluation.

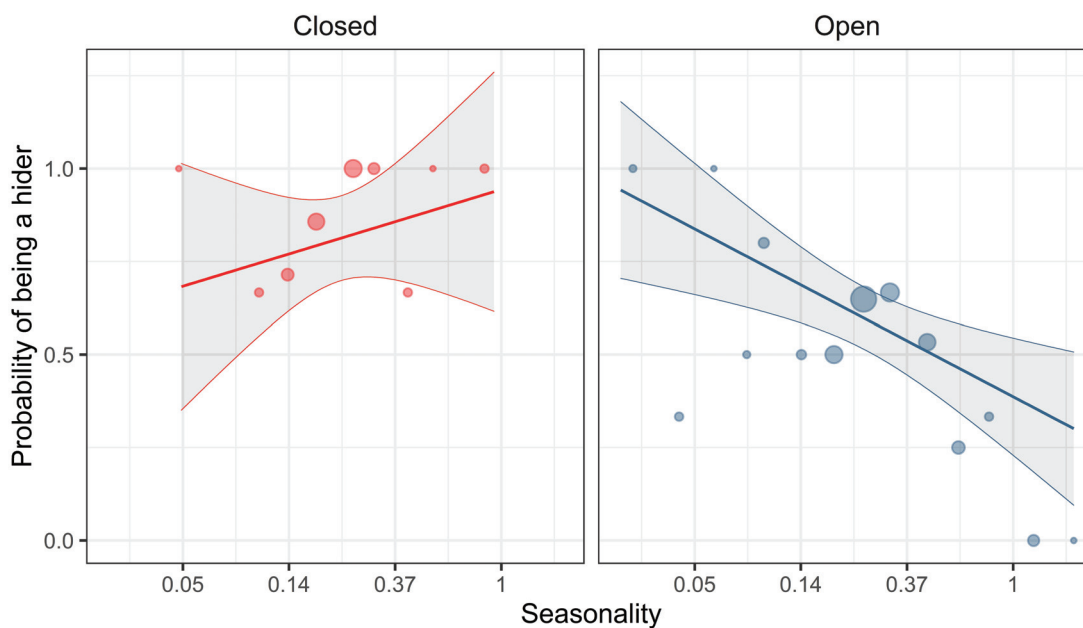


FIGURE 7.1: The probability of being a hider in relation to seasonality in the environment ($\beta_{closed} = 0.087, p = 0.41$; $\beta_{open} = -0.15, p < 0.05$) and the type of habitat (closed/open), estimated using a generalized linear model with a binomial response (follower = 0 and hider = 1) after accounting for the log-transformed body mass of females and group size of 176 species of ungulates (61 followers and 115 hidiers). Using the spatial ranges of distribution of species provided by the IUCN (2021), I retrieved the mean seasonality (coefficient of variation in productivity) for each species from maps with a 1 km resolution provided by Radeloff et al. (2019). The size of points represents the number of species, and the x-axis is on the logarithmic scale. Results have not yet been corrected for phylogenetic relatedness.

Until now, theories on the evolution of hider-follower tactics (Fisher, Blomberg, and Owens, 2002; Lent, 1974) have discussed the relative importance of habitat type (i.e. open vs. closed), body mass, and gregariousness, but the possible role of the spatio-temporal variability of resources on the evolution of anti-predator behavior of neonates remains to be explored. It would also be interesting to compare the hiding period of neonates across populations of the same species with contrasted seasonality to determine whether there is indeed an adaptive value for the duration of hiding. Estimating the time that offspring spend hiding may however be a laborious task as it requires intense fieldwork. There may be a way to identify changes in the movement of neonates through GPS data but this requires further miniaturization of GPS and telemetry devices (Cagnacci et al., 2010; Kays et al., 2015).

7.2 A link to breeding strategies

I posited in [Chapter 4](#) that hidiers move to rich sites before parturition in sharp contrast to followers. Following this explanation, it is quite normal to ask why followers do not exhibit such behavior. Do they not need enough resources to compensate for the energetically demanding parturition? Jönsson (1997) defined the capital-income breeding dichotomy where capital breeders store resources during gestation while income breeders rely on the on-hand available forage after parturition to care for the offspring. One of the main advantages of capital breeding is that feeding and reproduction are spatially and temporally decoupled. Interestingly, Jönsson (1997) even suggests that “*under unpredictable food conditions, food/time limitations, and risky foraging conditions*”, capital breeding is more beneficial.

Therefore, in line with my previous thought on followers being more present in seasonal environments with temporally limited resources, I suggest that there may be a close link between the evolution of capital breeding and the follower neonatal tactic. The contrast we found in the movement before parturition ([Chapter 4](#)) could be because females with follower offspring have already accumulated the required resources for birth and hence do not feel the pressure to be in a particularly rich environment. For instance, bighorn mothers, a capital breeder and follower species, store the required energy for parturition before the peak in environmental productivity in contrast to pronghorn, an income breeder and hider species, which time their birth peak as close as possible to the local environmental productivity optimum (Hogg et al., 2017). Additionally, in follower species, mothers reduce predation risk on their conspicuous mobile offspring through contact maintenance (Estes and Estes, 1979) and thus adapt their movement to the limited motor capacities of their young. However, contact maintenance may lead to increased energetic costs for females as their feeding time becomes limited by the offspring’s resting time. For instance, bison cows that remained close to their kids most likely grazed less (Green, 1992). A capital breeding strategy would therefore be more beneficial for follower species as it would compensate for the reduced feeding time, while hider species may develop an income breeding strategy since mothers can feed on resources while their offspring are concealed away

from them. Moreover, for species with hider neonates, most of the energetic costs of reproduction are thought to be mostly supported by females to sustain the high body growth rate for their immobile neonates while for follower offspring, neonates deplete their energy to move along with their mothers (Carl and Robbins, 1988). Hence, anticipated storage of resources in follower species should enable mothers to reduce their movement in search of additional resources, thus minimizing the mobility costs of their offspring which would lead to a positively significant reproductive success.

Evaluating whether this assumption holds or not can provide more knowledge into why some species surf the green wave and others do not. Most notably, it would be interesting to see if there is a higher propensity for hidiers to surf the green wave than followers, especially if the former are found to be income breeders and the latter capital breeders. Bison in Yellowstone did not surf the green wave because their grazing activity sustained a high forage quality (Geremia et al., 2019). There are however some obvious counter-arguments. For instance, red deer are capital breeders (Myserud et al., 2008) contradicting my hypothesis. Nonetheless, there is a need for global pattern analyses of hider-follower in relation to breeding strategy to better understand the evolution of such tactics.

7.3 Maternal investment along the hider-follower continuum

Parental care in reproduction (Trivers, 1974) is key to understanding the mechanisms of survival of offspring and parental fitness (Case, 1978; Gaillard et al., 1993; Gaillard et al., 1997; Lack, 1968). In mammals, for which most of the care is provided by females, energy allocated by mothers to their offspring is a major component of life-history traits and in turn, allows the distinction of different development stages of the neonates. Previous studies have shown that mammalian species with poorly-developed altricial newborns differ from species with highly-developed precocial ones by a shorter gestation length for females, lower weight of neonates at birth, and even higher growth rates (Martin and MacLarnon, 1985; Zveloff and Boyce, 1980; Zveloff and Boyce, 1986). This pattern has also been documented in birds, where precocial chicks were found to have lower growth rates than altricial ones (Olson, 1992).

Despite large herbivores being considered precocial species, the hider-follower continuum shows that there are differing levels of mobility in neonates (Lent, 1974). Due to the higher activity of followers linked to locomotion as a means of avoiding predators, energy allocation after birth is mostly focused on maintenance than on growth in comparison to hider species, leading therefore to higher growth rates in the latter (Carl and Robbins, 1988). However, in harsh conditions, energy allocated to maintenance may become limited, and as juvenile survival from predation depends on body mass (Linnell, Aanes, and Andersen, 1995), follower species with conspicuous offspring should invest in gestation to produce heavy neonates. Bigger follower offspring may be able to imitate more closely the larger movement rates of their mothers which rely mostly on contact maintenance as a defense strategy (Green, 1992) and thus reduce predation. Hider offspring mortality, on the other hand, due to their immobile behavior,

depends on the availability of cover in the occupied habitat. The differing levels of mobility between follower and hider species should therefore lead to differing levels of maternal investment in gestation.

It would be interesting to test whether evolution selected traits allowing juveniles with a follower anti-predator tactic to escape from predation as fast as possible. One way to do this would be to evaluate, for each of the two neonatal anti-predator tactics, the allometric relationship of gestation length and neonate weight divided by litter size, two measures previously shown to represent maternal investment at birth (Zeloff and Boyce, 1980). I predict that follower species should be characterized by longer gestation periods than hider species, due to the necessity of producing large neonates that have the locomotor capacities to accompany the mother (Sacher and Staffeldt, 1974).

7.4 Phenology of mating

The phenology of births has been largely studied in the literature (Linnell and Andersen, 1998b; Loe et al., 2005; Sinclair, Mduma, and Arcese, 2000) due to its importance in understanding the fitness and survival of offspring (Festa-Bianchet, 1988; Rutberg, 1987; Thel, Bonenfant, and Chamaillé-Jammes, 2021). There are many metrics used to estimate the level of synchrony in birth events (Thel, Chamaillé-Jammes, and Bonenfant, 2021), however, there are still very few methods to estimate the phenology of mating. The difficulty lies in the fact that mating events are mostly determined through fieldwork, which can be quite intense and laborious, and observations are even rare. Understanding the synchrony in mating is however essential to evaluate the adaptation of animals to future climate change. The dates of mating determine in return the dates of births which should synchronize with the peak of resources. In Chapter 5, I used CTMM to discriminate between mating tactics by observing marked changes in movement between a reference month and the expected month of the rut. Using CTMM, it would probably be possible to determine the phenology of mating from GPS data by using a moving window over the track of individuals and observing marked changes in their movement around the known months of the rut. Using the results for all individuals, we can determine whether changes in movement occur during a narrow or a large timeframe.

7.5 Concluding remarks

In this thesis, I set out on a quest to provide answers to questions that have been troubling researchers. By no means do I mean that I have answered them completely. That is inherently impossible. There will still be questions to answer and gaps to fill to complement our findings. Nevertheless, I hope that this thesis will provide at least some useful insights as to the direction in which studies should head in the future.

Bibliography

- Ables, E. (1974). "The Axis deer in Texas. The Caeser Kleberg Research Programme. The Texas Agricultural Experiment Station." In: *A & M University System. Texas*.
- Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., and Merkle, J. A. (2021). "Emerging Perspectives on Resource Tracking and Animal Movement Ecology." In: *Trends in Ecology & Evolution* 36.4, pp. 308–320.
- Abrahms, B. et al. (2019). "Memory and resource tracking drive blue whale migrations." In: *Proceedings of the National Academy of Sciences* 116.12, pp. 5582–5587.
- Acevedo, P. and Cassinello, J. (2009). "Biology, ecology and status of Iberian ibex *Capra pyrenaica*: a critical review and research prospectus." In: *Mammal Review* 39.1, pp. 17–32.
- Aikens, E. O., Kauffman, M. J., Merkle, J. A., Dwinnell, S. P. H., Fralick, G. L., and Monteith, K. L. (2017). "The greenscape shapes surfing of resource waves in a large migratory herbivore." In: *Ecology Letters* 20.6, pp. 741–750.
- Aikens, E. O. et al. (2020). "Wave-like Patterns of Plant Phenology Determine Ungulate Movement Tactics." In: *Current Biology* 30.17, 3444–3449.e4.
- Alados, C. L. (1986). "Aggressive behaviour, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenaica*)." In: *Behavioural Processes* 12.2, pp. 145–158.
- Aldridge, C. L. and Boyce, M. S. (2008). "Accounting for Fitness: Combining Survival and Selection when Assessing Wildlife-Habitat Relationships." In: *Israel Journal of Ecology and Evolution* 54.3-4, pp. 389–419.
- Allen, A. M. and Singh, N. J. (2016). "Linking Movement Ecology with Wildlife Management and Conservation." In: *Frontiers in Ecology and Evolution* 3, p. 155.
- Allen, T. F. H. and Starr, T. B. (1982). *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press.

- Anderson, A. E., Medin, D. E., and Bowden, D. C. (1974). "Growth and Morphometry of the Carcass, Selected Bones, Organs, and Glands of Mule Deer." In: *Wildlife Monographs* 39, pp. 3–122.
- Anderson, A. E. and Wallmo, O. C. (1984). "Odocoileus hemionus." In: *Mammalian Species* 219, pp. 1–9.
- Anderson, D. P. et al. (2005). "Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes." In: *Landscape Ecology* 20.3, pp. 257–271.
- Andrzejewski, R. and Mazurkiewicz, M. (1976). "Abundance of food supply and size of the bank vole's home range." In: *Acta theriol* 21.12, pp. 237–253.
- Apollonio, M., Andersen, R., and Putman, R. (2010). *European ungulates and their management in the 21st century*. Cambridge University Press.
- Archie, E. A., Moss, C. J., and Alberts, S. C. (2006). "The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants." In: *Proceedings of the Royal Society B: Biological Sciences* 273.1586, pp. 513–522.
- Atwood, T. C., Gese, E. M., and Kunkel, K. E. (2009). "Spatial Partitioning of Predation Risk in a Multiple Predator-Multiple Prey System." In: *The Journal of Wildlife Management* 73.6, pp. 876–884.
- Aureli, F. et al. (2008). "Fission-Fusion Dynamics: New Research Frameworks." In: *Current Anthropology* 49.4, pp. 627–654.
- Azad, M., Hossain, M., and Bhuiyan, A. (2005). "Feeding and management of spotted deer at Dhaka zoo." In: *International Journal of Zoological Research* 1.1, pp. 48–52.
- Baguette, M. and Van Dyck, H. (2007). "Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal." In: *Landscape Ecology* 22.8, pp. 1117–1129.
- Baharav, D. (1983). "Reproductive strategies in female Mountain and Dorcas gazelles (*Gazella gazella gazella* and *Gazella dorcas*)." In: *Journal of Zoology* 200.4, pp. 445–453.
- Barrett, M. W. (1981). "Environmental Characteristics and Functional Significance of Pronghorn Fawn Bedding Sites in Alberta." In: *The Journal of Wildlife Management* 45.1, pp. 120–131.
- Barrette, C. (2009a). "Antler eating and antler growth in wild Axis deer." In: *Mammalia* 49.4, pp. 491–500.
- (2009b). "The size of Axis deer fluid groups in Wilpattu national park, Sri Lanka." In: *Mammalia* 55.2, pp. 207–220.

- Bartlam-Brooks, H. L. A., Bonyongo, M. C., and Harris, S. (2013). "How landscape scale changes affect ecological processes in conservation areas: external factors influence land use by zebra (*Equus burchelli*) in the Okavango Delta." In: *Ecology and Evolution* 3.9, pp. 2795–2805.
- Barton, K. (2020). *MuMIn: Multi-Model Inference*.
- Basille, M. et al. (2013). "Selecting Habitat to Survive: The Impact of Road Density on Survival in a Large Carnivore." In: *PLOS ONE* 8.7, e65493.
- Baskin, L. and Danell, K. (2003). *Ecology of ungulates: a handbook of species in Eastern Europe and Northern and Central Asia*. Springer Science & Business Media.
- Bastille-Rousseau, G., Yackulic, C. B., Gibbs, J. P., Frair, J. L., Cabrera, F., and Blake, S. (2019). "Migration triggers in a large herbivore: Galápagos giant tortoises navigating resource gradients on volcanoes." In: *Ecology* 100.6, e02658.
- Bates, L. A., Sayialel, K. N., Njiraini, N. W., Poole, J. H., Moss, C. J., and Byrne, R. W. (2008). "African elephants have expectations about the locations of out-of-sight family members." In: *Biology Letters* 4.1, pp. 34–36.
- Beauchamp, G. and Ruxton, G. D. (2008). "Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks." In: *Animal Behaviour* 75.6, pp. 1837–1842.
- Beekman, J. H. and Prins, H. H. T. (1989). "Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo, *Syncerus coffer*." In: *African Journal of Ecology* 27.2, pp. 129–147.
- Bell, R. H. V. (1971). "A Grazing Ecosystem in the Serengeti." In: *Scientific American* 225.1, pp. 86–93.
- Bender, L. C., Lomas, L. A., and Kamienski, T. (2007). "Habitat Effects on Condition of Doe Mule Deer in Arid Mixed Woodland-grassland." In: *Rangeland Ecology & Management* 60.3, pp. 277–284.
- Benoit, L. et al. (2020). "Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore." In: *Journal of Animal Ecology* 89.1, pp. 173–185.
- Berg, J. E., Reimer, J., Smolko, P., Bohm, H., Hebblewhite, M., and Merrill, E. H. (2021). "Mothers' Movements: Shifts in Calving Area Selection by Partially Migratory Elk." In: *The Journal of Wildlife Management* 85.7, pp. 1476–1489.
- Berg, J. E. (2019). "Shifts in strategy: Calving and calf survival in a partially migratory elk population." In.
- Berger-Tal, O. and Saltz, D. (2019). "Invisible barriers: anthropogenic impacts on inter- and intra-specific interactions as drivers of landscape-independent fragmentation." In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 374.1781, p. 20180049.

- Bergerud, A. T., Butler, H. E., and Miller, D. R. (1984). "Antipredator tactics of calving caribou: dispersion in mountains." In: *Canadian Journal of Zoology* 62.8, pp. 1566–1575.
- Bevanda, M., Fronhofer, E. A., Heurich, M., Müller, J., and Reineking, B. (2015). "Landscape configuration is a major determinant of home range size variation." In: *Ecosphere* 6.10, art195.
- Beyer, H. L. et al. (2016). "'You shall not pass!': quantifying barrier permeability and proximity avoidance by animals." In: *Journal of Animal Ecology* 85.1, pp. 43–53.
- Bhat, U., Kempes, C. P., and Yeakel, J. D. (2020). "Scaling the risk landscape drives optimal life-history strategies and the evolution of grazing." In: *Proceedings of the National Academy of Sciences* 117.3, pp. 1580–1586.
- Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., and Mysterud, A. (2012). "A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave?" In: *The American Naturalist* 180.4, pp. 407–424.
- Bissonette, J. A. (1997). "Scale-Sensitive Ecological Properties: Historical Context, Current Meaning." In: *Wildlife and Landscape Ecology: Effects of Pattern and Scale*. Ed. by Bissonette, J. A. New York, NY: Springer, pp. 3–31.
- Bjørneraas, K., Herfindal, I., Solberg, E. J., Sæther, B.-E., van Moorter, B., and Rolandsen, C. M. (2012). "Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore." In: *Oecologia* 168.1, pp. 231–243.
- Bjørneraas, K., Moorter, B. V., Rolandsen, C. M., and Herfindal, I. (2010). "Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics." In: *The Journal of Wildlife Management* 74.6, pp. 1361–1366.
- Blackwell, P. G. (1997). "Random diffusion models for animal movement." In: *Ecological Modelling* 100.1, pp. 87–102.
- Blanc, J. J. (2007). *African elephant status report 2007: an update from the African elephant database*. 33. Iucn.
- Blancou, L. (1935). "Buffles de l'Oubangui-Chari-Tchad." In: *La Terre et la vie*.
- Boldt, A. and Ingold, P. (2005). "Effects of air traffic, snow cover and weather on altitudinal short-term and medium-term movements of female Alpine chamois *Rupicapra rupicapra* in winter." In: *Wildlife Biology* 11.4, pp. 351–362.
- Bon, R., Gonzalez, G., Bosch, M. D., and Cugnasse, J. M. (1992). "Ram rut-involvement in a hunted population of mouflons." In: *Acta Theriologica* 37.1-2, pp. 63–71.
- Bon, R., Dardaillon, M., and Estevez, I. (1993). "Mating and Lambing Periods as Related to Age of Female Mouflon." In: *Journal of Mammalogy* 74.3, pp. 752–757.

- Bonnot, N. et al. (2013). "Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer." In: *European Journal of Wildlife Research* 59.2, pp. 185–193.
- Börger, L., Dalziel, B. D., and Fryxell, J. M. (2008). "Are there general mechanisms of animal home range behaviour? A review and prospects for future research: Home range modelling." In: *Ecology Letters* 11.6, pp. 637–650.
- Börger, L. and Fryxell, J. (2012). "Quantifying individual differences in dispersal using net squared displacement." In: *Dispersal Ecology and Evolution*. Ed. by Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M. Oxford University Press, pp. 222–230.
- Börger, L. et al. (2006a). "An Integrated Approach to Identify Spatiotemporal and Individual-Level Determinants of Animal Home Range Size." In: *The American Naturalist* 168.4, pp. 471–485.
- Börger, L. et al. (2006b). "Effects of sampling regime on the mean and variance of home range size estimates." In: *Journal of Animal Ecology* 75.6, pp. 1393–1405.
- Borowik, T., Pettorelli, N., Sönnichsen, L., and Jędrzejewska, B. (2013). "Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats." In: *European Journal of Wildlife Research* 59.5, pp. 675–682.
- Boschetti, M., Bocchi, S., and Brivio, P. A. (2007). "Assessment of pasture production in the Italian Alps using spectrometric and remote sensing information." In: *Agriculture, Ecosystems & Environment* 118.1, pp. 267–272.
- Bourgoin, G., Marchand, P., Hewison, A. J. M., Ruckstuhl, K. E., and Garel, M. (2018). "Social behaviour as a predominant driver of sexual, age-dependent and reproductive segregation in Mediterranean mouflon." In: *Animal Behaviour* 136, pp. 87–100.
- Bowyer, R. T. (2004). "Sexual Segregation in Ruminants: Definitions, Hypotheses, and Implications for Conservation and Management." In: *Journal of Mammalogy* 85.6, pp. 1039–1052.
- Bowyer, R. T., McCullough, D. R., Rachlow, J. L., Ciuti, S., and Whiting, J. C. (2020). "Evolution of ungulate mating systems: Integrating social and environmental factors." In: *Ecology and Evolution* 10.11, pp. 5160–5178.
- Brambilla, P., Bocci, A., Ferrari, C., and Lovari, S. (2006). "Food patch distribution determines home range size of adult male chamois only in rich habitats." In: *Ethology Ecology & Evolution* 18.3, pp. 185–193.
- Brashares, J. S. and Arcese, P. (2002). "Role of forage, habitat and predation in the behavioural plasticity of a small African antelope." In: *Journal of Animal Ecology* 71.4, pp. 626–638.
- Breheny, P. and Burchett, W. (2017). "Visualization of Regression Models Using visreg." In: *The R Journal* 9.2, pp. 56–71.

Bro-Jørgensen, J. (2007). "The Intensity of Sexual Selection Predicts Weapon Size in Male Bovids." In: *Evolution* 61.6, pp. 1316–1326.

— (2008). "Dense habitats selecting for small body size: a comparative study on bovids." In: *Oikos* 117.5, pp. 729–737.

Brody, S. (1945). "Bioenergetics and Growth, Reinhold Publ." In: *Co., New York*, pp. 265–266.

Brook, R. K. (2010). "Habitat selection by parturient elk (*Cervus elaphus*) in agricultural and forested landscapes." In: *Canadian Journal of Zoology* 88.10, pp. 968–976.

Brooks, M. E. et al. (2017). "glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling." In: *The R Journal* 9.2, pp. 378–400.

Brown, J. S. (1988). "Patch use as an indicator of habitat preference, predation risk, and competition." In: *Behavioral Ecology and Sociobiology* 22.1, pp. 37–47.

— (1999). "Vigilance, patch use and habitat selection: Foraging under predation risk." In: *Evolutionary Ecology Research* 1.1, pp. 49–71.

Bubenik, G. A., Schams, D., White, R. J., Rowell, J., Blake, J., and Bartos, L. (1997). "Seasonal Levels of Reproductive Hormones and Their Relationship to the Antler Cycle of Male and Female Reindeer (*Rangifer tarandus*)." In: *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 116.2, pp. 269–277.

Buchmann, C. M., Schurr, F. M., Nathan, R., and Jeltsch, F. (2013). "Habitat loss and fragmentation affecting mammal and bird communities—The role of interspecific competition and individual space use." In: *Ecological Informatics. The analysis and application of spatial ecological data to support the conservation of biodiversity* 14, pp. 90–98.

Bunnefeld, N. et al. (2011). "A model-driven approach to quantify migration patterns: individual, regional and yearly differences." In: *Journal of Animal Ecology* 80.2, pp. 466–476.

Burnham, K. P. and Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. New York: Springer-Verlag.

Burt, W. H. (1943). "Territoriality and Home Range Concepts as Applied to Mammals." In: *Journal of Mammalogy* 24.3, pp. 346–352.

Bustnes, J. O. (1996). "Is Parental Care a Constraint on the Habitat Use of Common Eider Females?" In: *The Condor* 98.1, pp. 22–26.

Buuveibaatar, B. et al. (2013). "Factors affecting survival and cause-specific mortality of saiga calves in Mongolia." In: *Journal of Mammalogy* 94.1, pp. 127–136.

- Cagnacci, F., Boitani, L., Powell, R. A., and Boyce, M. S. (2010). "Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges." In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1550, pp. 2157–2162.
- Calabrese, J. M., Fleming, C. H., and Gurarie, E. (2016). "ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process." In: *Methods in Ecology and Evolution* 7.9, pp. 1124–1132.
- Calabrese, J. M. et al. (2018). "Disentangling social interactions and environmental drivers in multi-individual wildlife tracking data." In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 373.1746, p. 20170007.
- Calenge, C. (2006). "The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals." In: *Ecological Modelling* 197.3, pp. 516–519.
- Camp, M. J., Rachlow, J. L., Woods, B. A., Johnson, T. R., and Shipley, L. A. (2012). "When to Run and When to Hide: The Influence of Concealment, Visibility, and Proximity to Refugia on Perceptions of Risk." In: *Ethology* 118.10, pp. 1010–1017.
- Camp, M., Rachlow, J., Woods, B., Johnson, T., and Shipley, L. (2013). "Examining functional components of cover: the relationship between concealment and visibility in shrub-steppe habitat." In: *Ecosphere* 4.2, pp. 1–14.
- Campioni, L., Delgado, M. d. M., Lourenço, R., Bastianelli, G., Fernández, N., and Penteriani, V. (2013). "Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species." In: *Oecologia* 172.2, pp. 371–385.
- Carl, G. R. and Robbins, C. T. (1988). "The energetic cost of predator avoidance in neonatal ungulates: hiding versus following." In: *Canadian Journal of Zoology*.
- Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press.
- Carranza, J., Garcia-Muñoz, A. J., and de Dios Vargas, J. (1995). "Experimental shifting from harem defence to territoriality in rutting red deer." In: *Animal Behaviour* 49.2, pp. 551–554.
- Carroll, G. et al. (2021). "Flexible use of a dynamic energy landscape buffers a marine predator against extreme climate variability." In: *Proceedings of the Royal Society B: Biological Sciences* 288.1956, p. 20210671.
- Case, T. J. (1978). "On the Evolution and Adaptive Significance of Postnatal Growth Rates in the Terrestrial Vertebrates." In: *The Quarterly Review of Biology*.
- Catusse, M. (1996). *La grande faune de montagne*. Dubray.
- Caughley, G. (1976). "The elephant problem—an alternative hypothesis." In: *African Journal of Ecology* 14.4, pp. 265–283.

Cederlund, G. and Sand, H. (1994). "Home-Range Size in Relation to Age and Sex in Moose." In: *Journal of Mammalogy* 75.4, pp. 1005–1012.

Cerling, T. E., Wittemyer, G., Ehleringer, J. R., Remien, C. H., and Douglas-Hamilton, I. (2009). "History of Animals using Isotope Records (HAIR): A 6-year dietary history of one family of African elephants." In: *Proceedings of the National Academy of Sciences of the United States of America* 106.20, pp. 8093–8100.

Chapman, C. A. (1990). "Ecological Constraints on Group Size in Three Species of Neotropical Primates." In: *Folia Primatologica* 55.1, pp. 1–9.

Chapple, R. S., English, A. W., and Mulley, R. C. (1993). "Characteristics of the oestrous cycle and duration of gestation in chital hinds (*Axis axis*)." In: *Reproduction* 98.1, pp. 23–26.

Charnov, E. L. (1976a). "Optimal foraging, the marginal value theorem." In: *Theoretical Population Biology* 9.2, pp. 129–136.

— (1976b). "Optimal Foraging: Attack Strategy of a Mantid." In: *The American Naturalist* 110.971, pp. 141–151.

Chassagneux, A., Calenge, C., Siat, V., Mortz, P., Baubet, E., and Saïd, S. (2019). "Proximity to the risk and landscape features modulate female red deer movement patterns over several days after drive hunts." In: *Wildlife Biology* 2019.1, pp. 1–10.

Chassagneux, A. et al. (2020). "Should I stay or should I go? Determinants of immediate and delayed movement responses of female red deer (*Cervus elaphus*) to drive hunts." In: *PLOS ONE* 15.3, e0228865.

Ciuti, S., Bongi, P., Vassale, S., and Apollonio, M. (2006). "Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation." In: *Journal of Zoology* 268.1, pp. 97–107.

Ciuti, S. et al. (2012). "Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear." In: *PLoS ONE* 7.11.

Clark, K., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J., and Sayers, E. W. (2016). "GenBank." In: *Nucleic Acids Research* 44.Database issue, pp. D67–D72.

Clauss, M., Lechner-Doll, M., and Streich, W. J. (2003). "Ruminant diversification as an adaptation to the physicommechanical characteristics of forage." In: *Oikos* 102.2, pp. 253–262.

Clutton-Brock, T. H. (1988). *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press.

Clutton-Brock, T. H., Albon, S. D., and Guinness, F. E. (1989). "Fitness costs of gestation and lactation in wild mammals." In: *Nature* 337.6204, pp. 260–262.

- Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red deer: behavior and ecology of two sexes*. University of Chicago press.
- Clutton-Brock, T. H. (1989). "Review Lecture: Mammalian mating systems." In: *Proceedings of the Royal Society of London. B. Biological Sciences* 236.1285, pp. 339–372.
- Clutton-Brock, T. H., Iason G. R., Albon S. D., and Guinness F. E. (2009). "Effects of lactation on feeding behaviour and habitat use in wild Red deer hinds." In: *Journal of Zoology* 198.2, pp. 227–236.
- Codron, D. and Clauss, M. (2010). "Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species." In: *Canadian Journal of Zoology* 88.11, pp. 1129–1138.
- Conner, M. M. and Miller, M. W. (2004). "Movement Patterns and Spatial Epidemiology of a Prion Disease in Mule Deer Population Units." In: *Ecological Applications* 14.6, pp. 1870–1881.
- Corlatti, L., Béthaz, S., von Hardenberg, A., Bassano, B., Palme, R., and Lovari, S. (2012). "Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs." In: *Animal Behaviour* 84.4, pp. 1061–1070.
- Corlatti, L., Caroli, M., Pietrocini, V., and Lovari, S. (2013). "Rutting behaviour of territorial and nonterritorial male chamois: Is there a home advantage?" In: *Behavioural Processes* 92, pp. 118–124.
- Corlatti, L., Cotza, A., and Nelli, L. (2021). "Linking alternative reproductive tactics and habitat selection in Northern chamois." In: *Ecology and Evolution* 11.11, pp. 7057–7068.
- Côté, S. D. and Festa-Bianchet, M. (2001). "Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality." In: *Oecologia* 127.2, pp. 230–238.
- Coulson, T., Benton, T., Lundberg, P., Dall, S., Kendall, B., and Gaillard, J.-M. (2006). "Estimating individual contributions to population growth: evolutionary fitness in ecological time." In: *Proceedings of the Royal Society B: Biological Sciences* 273.1586, pp. 547–555.
- Courbin, N. et al. (2016). "Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale." In: *Oikos* 125.6, pp. 829–838.
- Courbin, N. et al. (2019). "Zebra diel migrations reduce encounter risk with lions at night." In: *Journal of Animal Ecology* 88.1, pp. 92–101.
- Courriot, O. et al. (2018). "Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore." In: *Oecologia* 187.1, pp. 47–60.

- Couturier, M. A. (1961). "Ecologie et protection du bouquetin (*Capra aegagrus ibex ibex* L.) et du chamois (*Rupicapra rupicapra rupicapra* (L.) dans les Alpes." In: *La Terre et la vie*.
- Crane, M., Silva, I., Marshall, B. M., and Strine, C. T. (2021). "Lots of movement, little progress: a review of reptile home range literature." In: *PeerJ* 9, e11742.
- Creel, S. (2018). "The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response." In: *Ecology Letters* 21.7, pp. 947–956.
- Creel, S., Christianson, D., Liley, S., and Winnie, J. A. (2007). "Predation Risk Affects Reproductive Physiology and Demography of Elk." In: *Science* 315.5814, pp. 960–960.
- Creel, S., Christianson, D. A., and Winnie, J. A. (2011). "A survey of the effects of wolf predation risk on pregnancy rates and calf recruitment in elk." In: *Ecological Applications* 21.8, pp. 2847–2853.
- Creel, S., Schuette, P., and Christianson, D. (2014). "Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community." In: *Behavioral Ecology* 25.4, pp. 773–784.
- Creel, S., Winnie Jr., J., Maxwell, B., Hamlin, K., and Creel, M. (2005). "Elk Alter Habitat Selection as an Antipredator Response to Wolves." In: *Ecology* 86.12, pp. 3387–3397.
- Crete, M. and Daigle, C. (1999). "Management of indigenous North American deer at the end of the 20th century in relation to large predators and primary production." In: *Acta Veterinaria Hungarica* 47.1, pp. 1–16.
- Cronin, M. A., MacNeil, M. D., and Patton, J. C. (2005). "Variation in Mitochondrial DNA and Microsatellite DNA in Caribou (*Rangifer tarandus*) in North America." In: *Journal of Mammalogy* 86.3, pp. 495–505.
- Cushman, S. A. and McGarigal, K. (2004). "Patterns in the species–environment relationship depend on both scale and choice of response variables." In: *Oikos* 105.1, pp. 117–124.
- Daleszczyk, K., Krasińska, M., Krasiński, Z., and Bunevich, A. (2007). "Habitat structure, climatic factors, and habitat use by European bison (*Bison bonasus*) in Polish and Belarusian parts of the Białowieża Forest, Poland." In: *Canadian Journal of Zoology* 85.2, pp. 261–272.
- Damuth, J. (1981). "Home range, home range overlap, and species energy use among herbivorous mammals." In: *Biological Journal of the Linnean Society* 15.3, pp. 185–193.
- Danchin, É., Giraldeau, L.-A., Valone, T. J., and Wagner, R. H. (2004). "Public Information: From Nosy Neighbors to Cultural Evolution." In: *Science* 305.5683, pp. 487–491.

- Darracq, A. K. and Tandy, J. (2019). "Misuse of Habitat Terminology by Wildlife Educators, Scientists, and Organizations." In: *The Journal of Wildlife Management* 83.4, pp. 782–789.
- De Magalhães, J. P. and Costa, J. (2009). "A database of vertebrate longevity records and their relation to other life-history traits." In: *Journal of Evolutionary Biology* 22.8, pp. 1770–1774.
- De Beer, Y. and van Aarde, R. J. (2008). "Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas?" In: *Journal of Arid Environments* 72.11, pp. 2017–2025.
- Debeffe, L. et al. (2014). "A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic." In: *Oecologia* 176.2, pp. 431–443.
- Dechen Quinn, A. C., Williams, D. M., and Porter, W. F. (2013). "Landscape structure influences space use by white-tailed deer." In: *Journal of Mammalogy* 94.2, pp. 398–407.
- Decristophoris, P. M. A., Hardenberg, A. v., and McElligott, A. G. (2007). "Testosterone is positively related to the output of nematode eggs in male Alpine ibex (*Capra ibex*) faeces." In: *Evolutionary Ecology Research* 9.8, pp. 1277–1292.
- Demment, M. W. and Van Soest, P. J. (1985). "A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores." In: *The American Naturalist* 125.5, pp. 641–672.
- Demšar, U. et al. (2015). "Analysis and visualisation of movement: an interdisciplinary review." In: *Movement Ecology* 3.1, p. 5.
- Desy, E. A., Batzli, G. O., and Liu, J. (1990). "Effects of Food and Predation on Behaviour of Prairie Voles: A Field Experiment." In: *Oikos* 58.2, pp. 159–168.
- Diefenbach, D. R., Alt, G. L., Wallingford, B. D., Rosenberry, C. S., and Long, E. S. (2019). "Effect of male age structure on reproduction in white-tailed deer." In: *The Journal of Wildlife Management* 83.6, pp. 1368–1376.
- Djaković, N., Holand, Ø., Hovland, A., Weladji, R., Røed, K., and Nieminen, M. (2015). "Effects of males' presence on female behaviour during the rut." In: *Ethology Ecology & Evolution* 27.2, pp. 148–160.
- Dobson, F. S. (2007). "A lifestyle view of life-history evolution." In: *Proceedings of the National Academy of Sciences* 104.45, pp. 17565–17566.
- Dominoni, D. M. et al. (2020). "Why conservation biology can benefit from sensory ecology." In: *Nature Ecology & Evolution* 4.4, pp. 502–511.
- Doran-Sheehy, D. M., Greer, D., Mongo, P., and Schwindt, D. (2004). "Impact of ecological and social factors on ranging in western gorillas." In: *American Journal of Primatology* 64.2, pp. 207–222.

- Drent, R., Ebbinge, B., and Weijand, B. (1978). "Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report." In: *Verh Orn Ges Bayern* 23, pp. 239–264.
- Ducros, D. et al. (2020). "Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape." In: *Oikos* 129.1, pp. 81–92.
- Dunn, J. E. and Gipson, P. S. (1977). "Analysis of Radio Telemetry Data in Studies of Home Range." In: *Biometrics* 33.1, pp. 85–101.
- Dunning, J. B., Danielson, B. J., and Pulliam, H. R. (1992). "Ecological Processes That Affect Populations in Complex Landscapes." In: *Oikos* 65.1, pp. 169–175.
- Duparc, A. (2016). "Dynamiques spatio-temporelles des ressources alimentaires et des activités humaines : impacts sur la sélection d'habitat d'un grand herbivore de montagne." PhD thesis. Université Grenoble Alpes.
- Duparc, A., Garel, M., Marchand, P., Dubray, D., Maillard, D., and Loison, A. (2019). "Revisiting the functional response in habitat selection for large herbivores: a matter of spatial variation in resource distribution?" In: *Behavioral Ecology* 30.6, pp. 1725–1733.
- (2020). "Through the taste buds of a large herbivore: foodscape modeling contributes to an understanding of forage selection processes." In: *Oikos* 129.2, pp. 170–183.
- Dussault, C., Courtois, R., Ouellet, J.-P., and Girard, I. (2005a). "Space use of moose in relation to food availability." In: *Canadian Journal of Zoology* 83.11, pp. 1431–1437.
- Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L., and Jolicoeur, H. (2005b). "Linking moose habitat selection to limiting factors." In: *Ecography* 28.5, pp. 619–628.
- Du Toit, J. T. and Olff, H. (2014). "Generalities in grazing and browsing ecology: using across-guild comparisons to control contingencies." In: *Oecologia* 174.4, pp. 1075–1083.
- Emlen, J. M. (1966). "The Role of Time and Energy in Food Preference." In: *The American Naturalist* 100.916, pp. 611–617.
- Emlen, S. T. and Oring, L. W. (1977). "Ecology, Sexual Selection, and the Evolution of Mating Systems." In: *Science* 197.4300, pp. 215–223.
- English, A. K., Chauvenet, A. L. M., Safi, K., and Pettorelli, N. (2012). "Reassessing the Determinants of Breeding Synchrony in Ungulates." In: *PLOS ONE* 7.7, e41444.
- Espmark, Y. (1964). "Rutting behaviour in reindeer (*Rangifer tarandus* L.)" In: *Animal Behaviour* 12.1, pp. 159–163.
- Estes, R. (1991). *The behavior guide to African mammals*. Vol. 64. University of California Press Berkeley.
- Estes, R. D. (1974). "Social organization of the African Bovidae." In: *The behaviour of ungulates and its relation to management* 1, pp. 166–205.

- Estes, R. D. and Estes, R. K. (1979). "The Birth and Survival of Wildebeest Calves." In: *Zeitschrift für Tierpsychologie* 50.1, pp. 45–95.
- Fagan, W. F., Lutscher, F., and Schneider, K. (2007). "Population and Community Consequences of Spatial Subsidies Derived from Central-Place Foraging." In: *The American Naturalist* 170.6, pp. 902–915.
- Fagan, W. F. et al. (2013). "Spatial memory and animal movement." In: *Ecology Letters* 16.10, pp. 1316–1329.
- Fandos, P., Vigal, C., and Fernandez-Lopez, J. (1989). "Weight estimation of Spanish ibex, *Capra pyrenaica*, and chamois, *Rupicapra rupicapra* (Mammalia, Bovidae)." In: *Z. Sugetierkunde* 54, pp. 239–242.
- Fauchald, P. (1999). "Foraging in a Hierarchical Patch System." In: *The American Naturalist* 153.6, pp. 603–613.
- Festa-Bianchet, M. (1988). "Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance." In: *Oecologia* 75.4, pp. 580–586.
- Festa-Bianchet, M. (1988). "Birthdate and survival in bighorn lambs (*Ovis canadensis*)." In: *Journal of Zoology* 214.4, pp. 653–661.
- Fieberg, J. and Börger, L. (2012). "Could you please phrase "home range" as a question?" In: *Journal of Mammalogy* 93.4, pp. 890–902.
- Fisher, D. O., Blomberg, S. P., and Owens, I. P. F. (2002). "Convergent Maternal Care Strategies in Ungulates and Macropods." In: *Evolution* 56.1, pp. 167–176.
- Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., and Calabrese, J. M. (2015). "Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator." In: *Ecology* 96.5, pp. 1182–1188.
- (2016). "Estimating where and how animals travel: an optimal framework for path reconstruction from autocorrelated tracking data." In: *Ecology* 97.3, pp. 576–582.
- Fleming, C. H., Calabrese, J. M., Mueller, T., Olson, K. A., Leimgruber, P., and Fagan, W. F. (2014). "From Fine-Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement Modes across Spatiotemporal Scales." In: *The American Naturalist* 183.5, E154–E167.
- Fleming, C. H., Subaşı, Y., and Calabrese, J. M. (2015). "Maximum-entropy description of animal movement." In: *Physical Review E* 91.3, p. 032107.
- Fleming, C. H. and Calabrese, J. M. (2020). *ctmm: Continuous-Time Movement Modeling*.
- Flombaum, P. and Sala, O. E. (2007). "A non-destructive and rapid method to estimate biomass and aboveground net primary production in arid environments." In: *Journal of Arid Environments* 69.2, pp. 352–358.

- Fortin, D., Boyce, M. S., Merrill, E. H., and Fryxell, J. M. (2004). "Foraging costs of vigilance in large mammalian herbivores." In: *Oikos* 107.1, pp. 172–180.
- Frafjord, K. (2016). "Influence of Reproductive Status: Home Range Size in Water Voles (*Arvicola amphibius*)." In: *PLOS ONE* 11.4, e0154338.
- Fretwell, S. D. and Lucas, H. L. (1969). "On territorial behavior and other factors influencing habitat distribution in birds." In: *Acta Biotheoretica* 19.1, pp. 16–36.
- Frid, A. and Dill, L. (2002). "Human-caused Disturbance Stimuli as a Form of Predation Risk." In: *Conservation Ecology* 6.1.
- Fritz, H. and Loison, A. (2006). "Large herbivores across biomes." In: *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Ed. by Danell, K., Bergström, R., Duncan, P., and Pastor, J. Conservation Biology. Cambridge University Press, pp. 19–49.
- Froy, H. et al. (2018). "Declining home range area predicts reduced late-life survival in two wild ungulate populations." In: *Ecology Letters* 21.7, pp. 1001–1009.
- Fryxell, J. M. and Sinclair, A. R. E. (1988). "Causes and consequences of migration by large herbivores." In: *Trends in Ecology & Evolution* 3.9, pp. 237–241.
- Fryxell, J. M. (1991). "Forage Quality and Aggregation by Large Herbivores." In: *The American Naturalist* 138.2, pp. 478–498.
- Fryxell, J. M., Greever, J., and Sinclair, A. R. E. (1988). "Why are Migratory Ungulates So Abundant?" In: *The American Naturalist* 131.6, pp. 781–798.
- Fryxell, J. M. et al. (2008). "Multiple movement modes by large herbivores at multiple spatiotemporal scales." In: *Proceedings of the National Academy of Sciences* 105.49, pp. 19114–19119.
- Fuller, J. A., Garrott, R. A., White, P. J., Aune, K. E., Roffe, T. J., and Rhyan, J. C. (2007). "Reproduction and Survival of Yellowstone Bison." In: *The Journal of Wildlife Management* 71.7, pp. 2365–2372.
- Gaillard, J.-M., Delorme, D., Jean-Marie, B., Van Laere, G., Boisaubert, B., and Pradel, R. (1993). "Roe Deer Survival Patterns: A Comparative Analysis of Contrasting Populations." In: *Journal of Animal Ecology* 62.4, pp. 778–791.
- Gaillard, J.-M., Festa-Bianchet, M., Delorme, D., and Jorgenson, J. (2000). "Body mass and individual fitness in female ungulates: bigger is not always better." In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267.1442, pp. 471–477.
- Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N. G. (1998). "Population dynamics of large herbivores: variable recruitment with constant adult survival." In: *Trends in Ecology & Evolution* 13.2, pp. 58–63.

- Gaillard, J.-M., Pontier, D., Allaine, D., Loison, A., Herve, J.-C., and Heizman, A. (1997). "Variation in growth form and precocity at birth in eutherian mammals." In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 264.1383, pp. 859–868.
- Gaillard, J.-M. et al. (2010). "Habitat–performance relationships: finding the right metric at a given spatial scale." In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1550, pp. 2255–2265.
- Gallagher, A. J., Creel, S., Wilson, R. P., and Cooke, S. J. (2017). "Energy Landscapes and the Landscape of Fear." In: *Trends in Ecology & Evolution* 32.2, pp. 88–96.
- Garfelt-Paulsen, I. M. et al. (2021). "Don't go chasing the ghosts of the past: habitat selection and site fidelity during calving in an Arctic ungulate." In: *Wildlife Biology* 2021.2, wlb.00740.
- Garrouste, E. L., Hansen, A. J., and Lawrence, R. L. (2016). "Using NDVI and EVI to Map Spatiotemporal Variation in the Biomass and Quality of Forage for Migratory Elk in the Greater Yellowstone Ecosystem." In: *Remote Sensing* 8.5, p. 404.
- Gautestad, A. O. and Mysterud, I. (2005). "Intrinsic Scaling Complexity in Animal Dispersion and Abundance." In: *The American Naturalist* 165.1, pp. 44–55.
- Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., and Brashares, J. S. (2019). "Landscapes of Fear: Spatial Patterns of Risk Perception and Response." In: *Trends in Ecology & Evolution* 34.4, pp. 355–368.
- Gebert, C. and Verheyden-Tixier, H. (2001). "Variations of diet composition of Red Deer (*Cervus elaphus* L.) in Europe." In: *Mammal Review* 31.3-4, pp. 189–201.
- Geist, V. (1974). "On the Relationship of Social Evolution and Ecology in Ungulates." In: *Integrative and Comparative Biology* 14.1, pp. 205–220.
- (1998). *Deer of the world: their evolution, behaviour, and ecology*. Stackpole books.
- Gelman, A. and Rubin, D. B. (1992). "Inference from Iterative Simulation Using Multiple Sequences." In: *Statistical Science* 7.4, pp. 457–472.
- Geremia, C. et al. (2019). "Migrating bison engineer the green wave." In: *Proceedings of the National Academy of Sciences* 116.51, pp. 25707–25713.
- Gittleman, J. L. and Harvey, P. H. (1982). "Carnivore home-range size, metabolic needs and ecology." In: *Behavioral Ecology and Sociobiology* 10.1, pp. 57–63.
- Gordon, I. J. (2003). "Browsing and grazing ruminants: are they different beasts?" In: *Forest Ecology and Management* 181.1-2, pp. 13–21.
- Gordon, I. J. and Illius, A. W. (1994). "The functional significance of the browser-grazer dichotomy in African ruminants." In: *Oecologia* 98.2, pp. 167–175.

- Gouy, M., Guindon, S., and Gascuel, O. (2010). "SeaView Version 4: A Multiplatform Graphical User Interface for Sequence Alignment and Phylogenetic Tree Building." In: *Molecular Biology and Evolution* 27.2, pp. 221–224.
- Grainger, M., Aarde, R. v., and Whyte, I. (2005). "Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa." In: *African Journal of Ecology* 43.4, pp. 369–375.
- Grange, S. et al. (2015). "Demography of plains zebras (*Equus quagga*) under heavy predation." In: *Population Ecology* 57.1, pp. 201–214.
- Grant, J., Chapman, C., and Richardson, K. (1992). "Defended versus undefended home range size of carnivores, ungulates and primates." In: *Behavioral Ecology and Sociobiology* 31.3, pp. 149–161.
- Green, W. C. H. (1992). "The development of independence in bison: pre-weaning spatial relations between mothers and calves." In: *Animal Behaviour* 43.5, pp. 759–773.
- Greenwood, P. J. (1980). "Mating systems, philopatry and dispersal in birds and mammals." In: *Animal Behaviour* 28.4, pp. 1140–1162.
- Grignolio, S., Parrini, F., Bassano, B., Luccarini, S., and Apollonio, M. (2003). "Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*." In: *FOLIA ZOOLOGICA-PRAHA*- 52.2, pp. 113–120.
- Grignolio, S., Rossi, I., Bertolotto, E., Bassano, B., and Apollonio, M. (2007). "Influence of the Kid on Space Use and Habitat Selection of Female Alpine Ibex." In: *Journal of Wildlife Management* 71.3, pp. 713–719.
- Groves, C. and Grubb, P. (2011). *Ungulate Taxonomy*. JHU Press.
- Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W., and Gascuel, O. (2010). "New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0." In: *Systematic Biology* 59.3, pp. 307–321.
- Guinness, F. E., Clutton-Brock, T. H., and Albon, S. D. (1978). "Factors Affecting Calf Mortality in Red Deer (*Cervus elaphus*)." In: *Journal of Animal Ecology* 47.3, pp. 817–832.
- Gurarie, E., Bracis, C., Delgado, M., Meckley, T. D., Kojola, I., and Wagner, C. M. (2016). "What is the animal doing? Tools for exploring behavioural structure in animal movements." In: *Journal of Animal Ecology* 85.1, pp. 69–84.
- Hadfield, J. D. (2010). "MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package." In: *Journal of statistical software* 33.2, pp. 1–22.
- Hall, L. S., Krausman, P. R., and Morrison, M. L. (1997). "The Habitat Concept and a Plea for Standard Terminology." In: *Wildlife Society Bulletin (1973-2006)* 25.1, pp. 173–182.

- Halsey, L. G. (2016). "Terrestrial movement energetics: current knowledge and its application to the optimising animal." In: *Journal of Experimental Biology* 219.10, pp. 1424–1431.
- Hansen, B. B., Aanes, R., Herfindal, I., Sæther, B.-E., and Henriksen, S. (2009a). "Winter habitat–space use in a large arctic herbivore facing contrasting forage abundance." In: *Polar Biology* 32.7, pp. 971–984.
- Hansen, B. B., Herfindal, I., Aanes, R., Sæther, B.-E., and Henriksen, S. (2009b). "Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore." In: *Oikos* 118.6, pp. 859–872.
- Harestad, A. S. and Bunnell, F. L. (1979). "Home Range and Body Weight—A Reevaluation." In: *Ecology* 60.2, pp. 389–402.
- Hart, E. E., Fennessy, J., Wells, E., and Ciuti, S. (2021). "Seasonal shifts in sociosexual behaviour and reproductive phenology in giraffe." In: *Behavioral Ecology and Sociobiology* 75.1, p. 15.
- Haskell, J. P., Ritchie, M. E., and Olf, H. (2002). "Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges." In: *Nature* 418.6897, pp. 527–530.
- Hebblewhite, M., Merrill, E., and McDermid, G. (2008). "A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population." In: *Ecological Monographs* 78.2, pp. 141–166.
- Hebblewhite, M. and Merrill, E. H. (2007). "Multiscale wolf predation risk for elk: does migration reduce risk?" In: *Oecologia* 152.2, pp. 377–387.
- (2009). "Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate." In: *Ecology* 90.12, pp. 3445–3454.
- Heit, D. R., Ortiz-Calo, W., and Montgomery, R. A. (2021). "Landscape complexity persists as a critical source of bias in terrestrial animal home range estimation." In: *Ecology* 102.8, e03427.
- Heithaus, M. R. and Dill, L. M. (2002). "Food Availability and Tiger Shark Predation Risk Influence Bottlenose Dolphin Habitat Use." In: *Ecology* 83.2, pp. 480–491.
- Hernández, L. and Laundré, J. W. (2005). "Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*." In: *Wildlife Biology* 11.3, pp. 215–220.
- Hoem, S. A., Melis, C., Linnell, J. D. C., and Andersen, R. (2007). "Fighting behaviour in territorial male roe deer *Capreolus capreolus*: the effects of antler size and residence." In: *European Journal of Wildlife Research* 53.1, pp. 1–8.

- Hofmann, R. R. (1989). "Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system." In: *Oecologia* 78.4, pp. 443–457.
- Hogg, J. T., Dunn, S. J., Poissant, J., Pelletier, F., and Byers, J. A. (2017). "Capital vs. income-dependent optimal birth date in two North American ungulates." In: *Ecosphere* 8.4, e01766.
- Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., and Spiegel, O. (2008). "Trends and missing parts in the study of movement ecology." In: *Proceedings of the National Academy of Sciences* 105.49, pp. 19060–19065.
- Hopcraft, J. G. C., Olf, H., and Sinclair, A. R. E. (2010). "Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas." In: *Trends in Ecology & Evolution* 25.2, pp. 119–128.
- Hopcraft, J. G. C. (2010). *Ecological implications of food and predation risk for herbivores in the Serengeti*. University Library Groningen][Host].
- Hutchinson, G. E. (1957). "Population studies: Animal ecology and demography." In: *Bulletin of Mathematical Biology* 53.1, pp. 193–213.
- Hutto, R. L. (1985). "Habitat selection by nonbreeding, migratory land." In: *Habitat selection in birds*. Vol. 455.
- Ims, R. A. (1988). "The potential for sexual selection in males: Effect of sex ratio and spatiotemporal distribution of receptive females." In: *Evolutionary Ecology* 2.4, pp. 338–352.
- Janis, C. (2008). "An Evolutionary History of Browsing and Grazing Ungulates." In: *The Ecology of Browsing and Grazing*. Ed. by Gordon, I. J. and Prins, H. H. T. Ecological Studies. Berlin, Heidelberg: Springer, pp. 21–45.
- Jarman, P. J. (1974). "The Social Organisation of Antelope in Relation To Their Ecology." In: *Behaviour* 48.1-4, pp. 215–267.
- Jarnemo, A. (2004). *Neonatal mortality in Roe Deer*. Acta Universitatis Agriculturae Sueciae Silvestria 321. Uppsala: Swedish University of Agricultural Sciences.
- Jetz, W., Carbone, C., Fulford, J., and Brown, J. H. (2004). "The Scaling of Animal Space Use." In: *Science* 306.5694, pp. 266–268.
- Johansson, A. (1996). "Territory Establishment and Antler Cycle in Male Roe Deer." In: *Ethology* 102.4, pp. 549–559.
- Johnson, C., Piel, A. K., Forman, D., Stewart, F. A., and King, A. J. (2015). "The ecological determinants of baboon troop movements at local and continental scales." In: *Movement Ecology* 3.1, pp. 1–13.

- Johnson, D. H. (1980). "The Comparison of Usage and Availability Measurements for Evaluating Resource Preference." In: *Ecology* 61.1, pp. 65–71.
- Jönsson, K. I. (1997). "Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction." In: *Oikos* 78.1, pp. 57–66.
- Joo, R. et al. (2020). "A decade of movement ecology." In: *arXiv:2006.00110 [q-bio]*.
- Kauffman, M. J. et al. (2021a). "Causes, Consequences, and Conservation of Ungulate Migration." In: *Annual Review of Ecology, Evolution, and Systematics* 52.1, pp. 453–478.
- Kauffman, M. J. et al. (2021b). "Mapping out a future for ungulate migrations." In: *Science* 372.6542, pp. 566–569.
- Kays, R., Crofoot, M. C., Jetz, W., and Wikelski, M. (2015). "Terrestrial animal tracking as an eye on life and planet." In: *Science* 348.6240.
- Kelt, D. A. and Vuren, D. V. (1999). "Energetic Constraints and the Relationship between Body Size and Home Range Area in Mammals." In: *Ecology* 80.1, p. 337.
- Kie, J. G. and Czech, B. (2000). "Mule and black-tailed deer." In: *Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA*, pp. 629–657.
- Kie, J. G. (1999). "Optimal Foraging and Risk of Predation: Effects on Behavior and Social Structure in Ungulates." In: *Journal of Mammalogy* 80.4, pp. 1114–1129.
- Kie, J. G., Bowyer, R. T., Nicholson, M. C., Boroski, B. B., and Loft, E. R. (2002). "Landscape Heterogeneity at Differing Scales: Effects on Spatial Distribution of Mule Deer." In: *Ecology* 83.2, pp. 530–544.
- Kie, J. G. et al. (2010). "The home-range concept: are traditional estimators still relevant with modern telemetry technology?" In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1550, pp. 2221–2231.
- Kilpatrick, H. J., Labonte, A. M., and Barclay, J. S. (2011). "Effects of landscape and land-ownership patterns on deer movements in a suburban community." In: *Wildlife Society Bulletin* 35.3, pp. 227–234.
- Kirk, D. A. et al. (2018). "Our use, misuse, and abandonment of a concept: Whither habitat?" In: *Ecology and Evolution* 8.8, pp. 4197–4208.
- Kittle, A. M., Fryxell, J. M., Desy, G. E., and Hamr, J. (2008). "The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates." In: *Oecologia* 157.1, pp. 163–175.
- Kjellander, P., Hewison, A. J. M., Liberg, O., Angibault, J.-M., Bideau, E., and Cargnelutti, B. (2004). "Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies." In: *Oecologia* 139.3, pp. 478–485.

- Kojola, I. (1986). "Rutting behaviour in an enclosed group of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.)" In: *Rangifer*, pp. 173–179.
- Krasińska, M., Krasiński, Z. A., Bunevich, A. N., et al. (2000). "Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Bia\lowieża Forest." In: *Acta Theriologica* 45.3, pp. 321–334.
- Krasińska, M. and Krasiński, Z. A. (1995). "Composition, group size, and spatial distribution of European bison bulls in Białowieża Forest." In: *Acta Theriologica* 40, pp. 1–21.
- Krebs, J. R. (1971). "Territory and Breeding Density in the Great Tit, *Parus Major* L." In: *Ecology* 52.1, pp. 2–22.
- Kuijper, D. P. J. et al. (2014). "What Cues Do Ungulates Use to Assess Predation Risk in Dense Temperate Forests?" In: *PLOS ONE* 9.1, e84607.
- Lack, D. L. (1968). "Ecological adaptations for breeding in birds." In.
- Laforge, M. P., Bonar, M., and Wal, E. V. (2021). "Tracking snowmelt to jump the green wave: phenological drivers of migration in a northern ungulate." In: *Ecology* 102.3, e03268.
- LaManna, J. A. and Martin, T. E. (2016). "Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species." In: *Ecology Letters* 19.4, pp. 403–413.
- Lambert, R. T. (1999). "Conceptus-endometrial interactions and reproductive hormone profiles during embryonic diapause and reactivation of the blastocyst in the European roe deer (*Capreolus capreolus*)." In: *Rangifer* 19.1, pp. 41–49.
- Lamberti, P., Mauri, L., Merli, E., Dusi, S., and Apollonio, M. (2006). "Use of space and habitat selection by roe deer *Capreolus capreolus* in a Mediterranean coastal area: how does woods landscape affect home range?" In: *Journal of Ethology* 24.2, pp. 181–188.
- Lariviere, S. and Messier, F. (1997). "Seasonal and daily activity patterns of striped skunks (*Mephitis mephitis*) in the Canadian prairies." In: *Journal of Zoology* 243.2, pp. 255–262.
- Lassmann, T. and Sonnhammer, E. L. (2005). "Kalign – an accurate and fast multiple sequence alignment algorithm." In: *BMC Bioinformatics* 6.1, p. 298.
- Laundré, J. W., Hernández, L., and Altendorf, K. B. (2001). "Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A." In: *Canadian Journal of Zoology* 79.8, pp. 1401–1409.
- Laundré, J. W., Hernandez, L., and Ripple, W. J. (2010). "The Landscape of Fear: Ecological Implications of Being Afraid." In: *The Open Ecology Journal* 3.1.

- Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M., and Breton, L. (2008). "Behavioral Adaptations of Moose to Roadside Salt Pools." In: *Journal of Wildlife Management* 72.5, pp. 1094–1100.
- Laver, P. N. and Kelly, M. J. (2008). "A Critical Review of Home Range Studies." In: *Journal of Wildlife Management* 72.1, pp. 290–298.
- Leach, R. and Edge, W. (1994). "Summer Home-Range and Habitat Selection by White-Tailed Deer in the Swan-Valley, Montana." In: *Northwest Science* 68.1, pp. 31–36.
- Leblond, M., Dussault, C., Ouellet, J.-P., and St-Laurent, M.-H. (2016). "Caribou avoiding wolves face increased predation by bears – Caught between Scylla and Charybdis." In: *Journal of Applied Ecology* 53.4, pp. 1078–1087.
- Lefort, V., Longueville, J.-E., and Gascuel, O. (2017). "SMS: Smart Model Selection in PhyML." In: *Molecular Biology and Evolution* 34.9, pp. 2422–2424.
- Lendrum, P. E., Anderson, C. R., Monteith, K. L., Jenks, J. A., and Bowyer, R. T. (2014). "Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality." In: *Mammalian Biology* 79.6, pp. 369–375.
- Lent, P. C. (1965). "Rutting behaviour in a barren-ground caribou population." In: *Animal Behaviour* 13.2, pp. 259–264.
- (1974). "Mother-infant relationships in ungulates." In: *The behaviour of ungulates and its relation to management* 1, pp. 14–55.
- Li, H. and Reynolds, J. F. (1994). "A Simulation Experiment to Quantify Spatial Heterogeneity in Categorical Maps." In: *Ecology* 75.8, pp. 2446–2455.
- Liberati, A. et al. (2009). "The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate health care interventions: explanation and elaboration." In: *PLoS medicine* 6.7, e1000100.
- Liberg, O., Johansson, A., Andersen, R., and Linnell, J. D. C. (1998). "Mating system, mating tactics and the function of male territoriality in roe deer." In: *The European roe deer: the biology of success. Scandinavian University Press, Oslo*, pp. 221–256.
- Lima, S. L. and Bednekoff, P. A. (1999). "Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis." In: *The American Naturalist* 153.6, pp. 649–659.
- Lima, S. L. and Dill, L. M. (1990). "Behavioral decisions made under the risk of predation: a review and prospectus." In: *Canadian Journal of Zoology* 68.4, pp. 619–640.
- Lincoln, G. A. (1998). "Reproductive seasonality and maturation throughout the complete life-cycle in the mouflon ram (*Ovis musimon*)." In: *Animal Reproduction Science* 53.1, pp. 87–105.

- Lincoln, G. A. and Guinness, F. E. (1973). "The sexual significance of the rut in red deer." In: *Journal of Reproduction and Fertility. Supplement* 19, pp. 475–489.
- Lincoln, G. A. and Tyler, N. J. C. (1994). "Role of gonadal hormones in the regulation of the seasonal antler cycle in female reindeer, *Rangifer tarandus*." In: *Reproduction* 101.1, pp. 129–138.
- Lindstedt, S. L., Miller, B. J., and Buskirk, S. W. (1986). "Home Range, Time, and Body Size in Mammals." In: *Ecology* 67.2, pp. 413–418.
- Lindström, J. (1999). "Early development and fitness in birds and mammals." In: *Trends in Ecology & Evolution* 14.9, pp. 343–348.
- Linnell, J. D. C. and Andersen, R. (1998a). "Timing and synchrony of birth in a hider species, the roe deer *Capreolus capreolus*." In: *Journal of Zoology* 244.4, pp. 497–504.
- Linnell, J. D. C., Aanes, R., and Andersen, R. (1995). "Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates." In: *Wildlife Biology* 1.1, pp. 209–223.
- Linnell, J. D. C., Nijhuis, P., Teurlings, I., and Andersen, R. (1999). "Selection of bed-sites by roe deer *Capreolus capreolus* fawns in a boreal forest landscape." In: *Wildlife Biology* 5.1, pp. 225–231.
- Linnell, J. D. and Andersen, R. (1998b). "Territorial fidelity and tenure in roe deer bucks." In: *Acta Theriologica* 43.1, pp. 67–75.
- Loe, L. E. et al. (2005). "Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France." In: *Journal of Animal Ecology* 74.4, pp. 579–588.
- Loe, L. E. et al. (2007). "Activity pattern of arctic reindeer in a predator-free environment: no need to keep a daily rhythm." In: *Oecologia* 152.4, pp. 617–624.
- Loison, A. (1995). "Approches intra-et inter-spécifiques de la dynamique des populations: l'exemple du chamois." PhD thesis. Lyon 1.
- Loison, A., Gaillard, J.-M., Pélabon, C., and Yoccoz, N. G. (1999). "What factors shape sexual size dimorphism in ungulates?" In: *Evolutionary Ecology Research* 1.5, pp. 611–633.
- Long, R. A., Kie, J. G., Bowyer, R. T., and Hurley, M. A. (2009). "Resource Selection and Movements by Female Mule Deer *Odocoileus hemionus*: Effects of Reproductive Stage." In: *Wildlife Biology* 15.3, pp. 288–298.
- Lovari, S., Sacconi, F., and Trivellini, G. (2006). "Do alternative strategies of space use occur in male Alpine chamois?" In: *Ethology Ecology & Evolution* 18.3, pp. 221–231.
- Lüdecke, D. (2019). "sjstats: Statistical functions for regression models (version 0.17.4)." In: *R package*: <https://www.cran.r-project.org/package=sjstats>. doi 10.

- Lummaa, V. and Clutton-Brock, T. (2002). "Early development, survival and reproduction in humans." In: *Trends in Ecology & Evolution* 17.3, pp. 141–147.
- Lynch, M. (1991). "Methods for the Analysis of Comparative Data in Evolutionary Biology." In: *Evolution* 45.5, pp. 1065–1080.
- MacArthur, R. H. and Pianka, E. R. (1966). "On Optimal Use of a Patchy Environment." In: *The American Naturalist* 100.916, pp. 603–609.
- Mahaney, W. C. (1987). "Behaviour of the African buffalo on Mount Kenya." In: *African Journal of Ecology* 25.3, pp. 199–202.
- Mainguy, J., Côté, S. D., Cardinal, E., and Houle, M. (2008). "Mating Tactics and Mate Choice in Relation to Age and Social Rank in Male Mountain Goats." In: *Journal of Mammalogy* 89.3, pp. 626–635.
- Malagnino, A. et al. (2021). "Do reproductive constraints or experience drive age-dependent space use in two large herbivores?" In: *Animal Behaviour* 172, pp. 121–133.
- Marchand, P., Garel, M., Bourgoin, G., Dubray, D., Maillard, D., and Loison, A. (2014). "Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area." In: *Biological Conservation* 177, pp. 1–11.
- Marchand, P. et al. (2017). "Sociospatial structure explains marked variation in brucellosis seroprevalence in an Alpine ibex population." In: *Scientific Reports* 7.1, p. 15592.
- Marchand, P. et al. (2021). "A standardised biologging approach to infer parturition: An application in large herbivores across the hider-follower continuum." In: *Methods in Ecology and Evolution* 12.6, pp. 1017–1030.
- Martin, R. D. and MacLarnon, A. M. (1985). "Gestation period, neonatal size and maternal investment in placental mammals." In: *Nature* 313.5999, pp. 220–223.
- Massé, A. and Côté, S. D. (2012). "Linking habitat heterogeneity to space use by large herbivores at multiple scales: From habitat mosaics to forest canopy openings." In: *Forest Ecology and Management* 285, pp. 67–76.
- Mattioli, S., Fico, R., Lorenzini, R., and Nobili, G. (2003). "Mesola red deer: physical characteristics, population dynamics and conservation perspectives." In: *Hystrix, the Italian Journal of Mammalogy* 14.1-2.
- Mautz, W. W. (1978). "Sledding on a Bushy Hillside: The Fat Cycle in Deer." In: *Wildlife Society Bulletin (1973-2006)* 6.2, pp. 88–90.
- Mayr, E. (1961). "Cause and Effect in Biology." In: *Science* 134.3489, pp. 1501–1506.
- Mazerolle, M. J. (2020). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*.

- McDonald, J. E. and Fuller, T. K. (2005). "Effects of Spring Acorn Availability on Black Bear Diet, Milk Composition, and Cub Survival." In: *Journal of Mammalogy* 86.5, pp. 1022–1028.
- McLoughlin, P. D. et al. (2007). "Lifetime Reproductive Success and Composition of the Home Range in a Large Herbivore." In: *Ecology* 88.12, pp. 3192–3201.
- McLoughlin, P. D., Case, R. L., Gau, R. J., Cluff, D. H., Mulders, R., and Messier, F. (2002). "Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic." In: *Oecologia* 132.1, pp. 102–108.
- McLoughlin, P. D. and Ferguson, S. H. (2000). "A hierarchical pattern of limiting factors helps explain variation in home range size." In: *Écoscience* 7.2, pp. 123–130.
- McLoughlin, P. D., Ferguson, S. H., and Messier, F. (2000). "Intraspecific Variation in Home Range Overlap with Habitat Quality: A Comparison among Brown Bear Populations." In: *Evolutionary Ecology* 14.1, pp. 39–60.
- McNab, B. K. (1963). "Bioenergetics and the Determination of Home Range Size." In: *The American Naturalist* 97.894, pp. 133–140.
- McNamara, J. M. and Houston, A. I. (1987). "Memory and the efficient use of information." In: *Journal of Theoretical Biology* 125.4, pp. 385–395.
- McNaughton, S. J. and Georgiadis, N. J. (1986). "Ecology of African Grazing and Browsing Mammals." In: *Annual Review of Ecology and Systematics* 17, pp. 39–65.
- Meagher, M. (1986). "Bison bison." In: *Mammalian Species* 266, pp. 1–8.
- Middleton, A. D. et al. (2018). "Green-wave surfing increases fat gain in a migratory ungulate." In: *Oikos* 127.7, pp. 1060–1068.
- Miller, F. (2003). "Caribou–Rangifer tarandus. Wild Mammals of North America: Biology, Management, and Conservation." In: *The Johns Hopkins University Press, Baltimore, MD. G. Samelius et al. Ostfeld, RS & Keesing, F.(2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution* 15, pp. 232–237.
- Mishra, H. and Wemmer, C. (1987). "The comparative breeding ecology of four cervids in Royal Chitwan National Park. Biology and management of the Cervida." In: *Research symposia of the National Zoological Park. Smithsonian Institution Press, Washington DC.*
- Mitchell, M. S. and Powell, R. A. (2004). "A mechanistic home range model for optimal use of spatially distributed resources." In: *Ecological Modelling* 177.1, pp. 209–232.
- (2008). "Estimated home ranges can misrepresent habitat relationships on patchy landscapes." In: *Ecological Modelling* 216.3, pp. 409–414.
- Mitchell, S. C. (2005). "How useful is the concept of habitat? – a critique." In: *Oikos* 110.3, pp. 634–638.

- Miura, S. (1981). "Social behaviour of the axis deer during the dry season in Guindy Sanctuary, Madras." In.
- Moe, S. R. and Wegge, P. (1994). "Spacing behaviour and habitat use of axis deer (*Axis axis*) in lowland Nepal." In: *Canadian Journal of Zoology* 72.10, pp. 1735–1744.
- (1997). "The effects of cutting and burning on grass quality and axis deer (*Axis axis*) use of grassland in lowland Nepal." In: *Journal of Tropical Ecology* 13.2, pp. 279–292.
- Moll, R. J. et al. (2017). "The many faces of fear: a synthesis of the methodological variation in characterizing predation risk." In: *Journal of Animal Ecology* 86.4, pp. 749–765.
- Montgomery, R. A., Moll, R. J., Say-Sallaz, E., Valeix, M., and Prugh, L. R. (2019). "A tendency to simplify complex systems." In: *Biological Conservation* 233, pp. 1–11.
- Moorcroft, P. R., Lewis, M. A., and Crabtree, R. L. (1999). "Home Range Analysis Using a Mechanistic Home Range Model." In: *Ecology* 80.5, pp. 1656–1665.
- Moorcroft, P. R., Lewis, M. A., and Crabtree, R. L. (2006). "Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone." In: *Proceedings of the Royal Society B: Biological Sciences* 273.1594, pp. 1651–1659.
- Moorcroft, P. R. (2012). "Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions." In: *Journal of Mammalogy* 93.4, pp. 903–916.
- Morales, J. M. et al. (2010). "Building the bridge between animal movement and population dynamics." In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1550, pp. 2289–2301.
- Morellet, N. et al. (2013). "Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe." In: *Journal of Animal Ecology* 82.6, pp. 1326–1339.
- Mueller, T. and Fagan, W. F. (2008). "Search and navigation in dynamic environments – from individual behaviors to population distributions." In: *Oikos* 117.5, pp. 654–664.
- Mueller, T., Olson, K. A., Fuller, T. K., Schaller, G. B., Murray, M. G., and Leimgruber, P. (2008). "In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity." In: *Journal of Applied Ecology* 45.2, pp. 649–658.
- Mueller, T. et al. (2011). "How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data." In: *Global Ecology and Biogeography* 20.5, pp. 683–694.
- Murray, M. G. (1982). "The Rut of Impala: Aspects of Seasonal Mating under Tropical Conditions." In: *Zeitschrift für Tierpsychologie* 59.4, pp. 319–337.

Murwira, A. (2003). *Scale matters!: a new approach to quantify spatial heterogeneity for predicting the distribution of wildlife*. Wageningen Universiteit.

Mysterud, A., Bonenfant, C., Loe, L. E., Langvatn, R., Yoccoz, N. G., and Stenseth, N. C. (2008). "The timing of male reproductive effort relative to female ovulation in a capital breeder." In: *Journal of Animal Ecology* 77.3, pp. 469–477.

Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. (2011). "Partial migration in expanding red deer populations at northern latitudes – a role for density dependence?" In: *Oikos* 120.12, pp. 1817–1825.

Mysterud, A., Pérez-Barbería, F. J., and Gordon, I. J. (2001). "The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants." In: *Oecologia* 127.1, pp. 30–39.

Naidoo, R., Preez, P. D., Stuart-Hill, G., Chris Weaver, L., Jago, M., and Wegmann, M. (2012). "Factors affecting intraspecific variation in home range size of a large African herbivore." In: *Landscape Ecology* 27.10, pp. 1523–1534.

Nakagawa, S. and Poulin, R. (2012). "Meta-analytic insights into evolutionary ecology: an introduction and synthesis." In: *Evolutionary Ecology* 26.5, pp. 1085–1099.

Nakagawa, S. and Santos, E. S. A. (2012). "Methodological issues and advances in biological meta-analysis." In: *Evolutionary Ecology* 26.5, pp. 1253–1274.

Nandintsetseg, D., Kaczensky, P., Ganbaatar, O., Leimgruber, P., and Mueller, T. (2016). "Spatiotemporal habitat dynamics of ungulates in unpredictable environments: The khulan (*Equus hemionus*) in the Mongolian Gobi desert as a case study." In: *Biological Conservation* 204, pp. 313–321.

Nandintsetseg, D. et al. (2019). "Variability in nomadism: environmental gradients modulate the movement behaviors of dryland ungulates." In: *Ecosphere* 10.11, e02924.

Nathan, R. et al. (2008). "A movement ecology paradigm for unifying organismal movement research." In: *Proceedings of the National Academy of Sciences* 105.49, pp. 19052–19059.

Nicholson, M. C., Bowyer, R. T., and Kie, J. G. (1997). "Habitat Selection and Survival of Mule Deer: Tradeoffs Associated with Migration." In: *Journal of Mammalogy* 78.2, pp. 483–504.

Nilsen, E. B., Herfindal, I., and Linnell, J. D. C. (2005). "Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity?" In: *Écoscience* 12.1, pp. 68–75.

Nilsen, E. B., Linnell, J. D. C., and Andersen, R. (2004). "Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*." In: *Journal of Animal Ecology* 73.1, pp. 44–50.

- Nilsen, E. B., Pedersen, S., and Linnell, J. D. C. (2008). "Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions?" In: *Ecological Research* 23.3, pp. 635–639.
- Noonan, M. J. et al. (2019). "A comprehensive analysis of autocorrelation and bias in home range estimation." In: *Ecological Monographs* 89.2, e01344.
- Noonan, M. J. et al. (2020). "Effects of body size on estimation of mammalian area requirements." In: *Conservation Biology* 34.4, pp. 1017–1028.
- Odum, E. P. (1971). *Fundamentals of ecology*. Vol. 3. Saunders Philadelphia.
- Ofstad, E. G., Herfindal, I., Solberg, E. J., and Sæther, B.-E. (2016). "Home ranges, habitat and body mass: simple correlates of home range size in ungulates." In: *Proceedings of the Royal Society B: Biological Sciences* 283.1845, p. 20161234.
- Oftedal, O. T., Boness, D. J., and Tedman, R. A. (1987). "The Behavior, Physiology, and Anatomy of Lactation in the Pinnipedia." In: *Current Mammalogy*. Ed. by Genoways, H. H. Boston, MA: Springer US, pp. 175–245.
- Ogutu, J. O., Piepho, H.-P., and Dublin, H. T. (2014). "Reproductive seasonality in African ungulates in relation to rainfall." In: *Wildlife Research* 41.4, pp. 323–342.
- Olson, J. M. (1992). "Growth, the Development of Endothermy, and the Allocation of Energy in Red-Winged Blackbirds (*Agelaius phoeniceus*) during the Nestling Period." In: *Physiological Zoology* 65.1, pp. 124–152.
- Olson, K. A., Fuller, T. K., Schaller, G. B., Lhagvasuren, B., and Odonkhuu, D. (2005). "Reproduction, neonatal weights, and first-year survival of Mongolian gazelles (*Procapra gutturosa*)." In: *Journal of Zoology* 265.3, pp. 227–233.
- Ouithavon, K., Bhumpakphan, N., Denduangboripant, J., Siriaroonrat, B., Trakulnaleamsai, S., et al. (2009). "An Analysis of the Phylogenetic Relationship of Thai Cervids Inferred from Nucleotide Sequences of Protein Kinase C Iota (PRKCI) Intron." In: *Kasetsart Journal, Natural Sciences* 43.4, pp. 709–719.
- Owen, .-. N. (1996). "Ecological guidelines for waterpoints in extensive protected areas." In: *South African Journal of Wildlife Research - 24-month delayed open access* 26.4, pp. 107–112.
- Owen-Smith, N. (1977). "On Territoriality in Ungulates and an Evolutionary Model." In: *The Quarterly Review of Biology* 52.1, pp. 1–38.
- (2008). "Changing vulnerability to predation related to season and sex in an African ungulate assemblage." In: *Oikos* 117.4, pp. 602–610.
- Owen-Smith, N. and Cain, J. W. (2007). "Indicators of Adaptive Responses in Home Range Utilization and Movement Patterns by a Large Mammalian Herbivore." In: *Israel Journal of Ecology and Evolution* 53.3-4, pp. 423–438.

Owen-Smith, R. N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge university press.

Pagel, M. (1999). "Inferring the historical patterns of biological evolution." In: *Nature* 401.6756, pp. 877–884.

Panting, B. (2018). "Influence of Environmental Variables on Survival Rates of Pronghorn (*Antilocapra americana*) Neonates Across Idaho." In: *All Graduate Theses and Dissertations*.

Panzacchi, M., Herfindal, I., Linnell, J. D. C., Odden, M., Odden, J., and Andersen, R. (2010). "Trade-offs between maternal foraging and fawn predation risk in an income breeder." In: *Behavioral Ecology and Sociobiology* 64.8, pp. 1267–1278.

Pavitt, A. T., Walling, C. A., Möstl, E., Pemberton, J. M., and Kruuk, L. E. B. (2015). "Cortisol but not testosterone is repeatable and varies with reproductive effort in wild red deer stags." In: *General and Comparative Endocrinology* 222, pp. 62–68.

Pays, O., Fortin, D., Gassani, J., and Duchesne, J. (2012). "Group Dynamics and Landscape Features Constrain the Exploration of Herds in Fusion-Fission Societies: The Case of European Roe Deer." In: *PLOS ONE* 7.3, e34678.

Pays, O., Renaud, P.-C., Loisel, P., Petit, M., Gerard, J.-F., and Jarman, P. J. (2007). "Prey synchronize their vigilant behaviour with other group members." In: *Proceedings of the Royal Society B: Biological Sciences* 274.1615, pp. 1287–1291.

Pellerin, M., Saïd, S., and Gaillard, J.-M. (2008). "Roe deer *Capreolus capreolus* home-range sizes estimated from VHF and GPS data." In: *Wildlife Biology* 14.1, pp. 101–110.

Pérez-Barbería, F. J., Gordon, I. J., and Pagel, M. (2002). "The Origins of Sexual Dimorphism in Body Size in Ungulates." In: *Evolution* 56.6, pp. 1276–1285.

Pérez-Barbería, F. J. and Gordon, I. J. (1999). "The relative roles of phylogeny, body size and feeding style on the activity time of temperate ruminants: a reanalysis." In: *Oecologia* 120.2, pp. 193–197.

— (2000). "Differences in body mass and oral morphology between the sexes in the Artiodactyla: evolutionary relationships with sexual segregation." In: *Evolutionary Ecology Research* 2.5, pp. 667–684.

Péron, G. (2019). "The time frame of home-range studies: from function to utilization." In: *Biological Reviews* 94.6, pp. 1974–1982.

Péron, G. et al. (2017). "Periodic continuous-time movement models uncover behavioral changes of wild canids along anthropization gradients." In: *Ecological Monographs* 87.3, pp. 442–456.

Péron, G. et al. (2018). "Circadian periodicity in space use by ungulates of temperate regions: How much, when and why?" In: *Journal of Animal Ecology* 87.5, pp. 1299–1308.

- Pettorelli, N. (2013). *The Normalized Difference Vegetation Index*. OUP Oxford.
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., and Stenseth, N. C. (2005). "Using the satellite-derived NDVI to assess ecological responses to environmental change." In: *Trends in Ecology & Evolution* 20.9, pp. 503–510.
- Pettorelli, N. et al. (2006). "Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer." In: *Oikos* 112.3, pp. 565–572.
- Pierce, G. J. and Ollason, J. G. (1987). "Eight Reasons Why Optimal Foraging Theory Is a Complete Waste of Time." In: *Oikos* 49.1, pp. 111–118.
- Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D., and Courtois, R. (2012). "Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape." In: *The Journal of Wildlife Management* 76.1, pp. 189–199.
- Plard, F., Bonenfant, C., and Gaillard, J.-M. (2011). "Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver." In: *Oikos* 120.4, pp. 601–606.
- Plummer, M., Best, N., Cowles, K., and Vines, K. (2006). "CODA: convergence diagnosis and output analysis for MCMC." In: *R news* 6.1, pp. 7–11.
- Pojar, T. M. and Bowden, D. C. (2004). "Neonatal Mule Deer Fawn Survival in West-Central Colorado." In: *The Journal of Wildlife Management* 68.3, pp. 550–560.
- Portanier, E. et al. (2018). "Landscape genetics matches with behavioral ecology and brings new insight on the functional connectivity in Mediterranean mouflon." In: *Landscape Ecology* 33.7, pp. 1069–1085.
- Powell, R. A., Zimmerman, J. W., Seaman, D. E., and Powell, C. (1996). *Ecology and Behaviour of North American Black Bears: Home Ranges, Habitat and Social Organization*. Chapman & Hall Wildlife Ecology and Behaviour Series. Springer Netherlands.
- Powell, R. A. and Mitchell, M. S. (2012). "What is a home range?" In: *Journal of Mammalogy* 93.4, pp. 948–958.
- Powell, R. A., Powell, R. A., Zimmerman, J. W., and Seaman, D. E. (1997). *Ecology and behaviour of North American black bears: home ranges, habitat, and social organization*. Vol. 4. Springer Science & Business Media.
- Preisser, E. L., Bolnick, D. I., and Benard, M. F. (2005). "Scared to Death? The Effects of Intimidation and Consumption in Predator–Prey Interactions." In: *Ecology* 86.2, pp. 501–509.
- Prins, H. (1996). *Ecology and behaviour of the African buffalo: social inequality and decision making*. Vol. 1. Springer Science & Business Media.

- Proffitt, K. M., Cunningham, J. A., Hamlin, K. L., and Garrott, R. A. (2014). "Bottom-up and top-down influences on pregnancy rates and recruitment of northern Yellowstone elk." In: *The Journal of Wildlife Management* 78.8, pp. 1383–1393.
- Prox, L. and Farine, D. (2020). "A framework for conceptualizing dimensions of social organization in mammals." In: *Ecology and Evolution* 10.2, pp. 791–807.
- Prugh, L. R. et al. (2019). "Designing studies of predation risk for improved inference in carnivore-ungulate systems." In: *Biological Conservation* 232, pp. 194–207.
- Pulliam, H. R. (1973). "On the advantages of flocking." In: *Journal of Theoretical Biology* 38, pp. 419–422.
- (1988). "Sources, Sinks, and Population Regulation." In: *The American Naturalist* 132.5, pp. 652–661.
- Pyke, G. H. (1984). "Optimal Foraging Theory: A Critical Review." In: *Annual Review of Ecology and Systematics* 15.1, pp. 523–575.
- R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Radeloff, V. C. et al. (2019). "The Dynamic Habitat Indices (DHIs) from MODIS and global biodiversity." In: *Remote Sensing of Environment* 222, pp. 204–214.
- Ralls, K., Kranz, K., and Lundrigan, B. (1986). "Mother-young relationships in captive ungulates: variability and clustering." In: *Animal Behaviour* 34, pp. 134–145.
- Raman, T. R. S. (1997). "Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India." In: *Journal of Biosciences* 22.2, pp. 203–218.
- Ramanzin, M., Sturaro, E., and Zanon, D. (2007). "Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps." In: *Canadian Journal of Zoology* 85.2, pp. 280–289.
- Redfern, J. V., Grant, R., Biggs, H., and Getz, W. M. (2003). "Surface-Water Constraints on Herbivore Foraging in the Kruger National Park, South Africa." In: *Ecology* 84.8, pp. 2092–2107.
- Redjadj, C. et al. (2012). "Estimating herbaceous plant biomass in mountain grasslands: a comparative study using three different methods." In: *Alpine Botany* 122.1, pp. 57–63.
- Rettie, W. J. and Messier, F. (2000). "Hierarchical habitat selection by woodland caribou: its relationship to limiting factors." In: *Ecography* 23.4, pp. 466–478.
- Ribeiro Jr, P. J., Diggle, P. J., Ribeiro Jr, M. P. J., and Suggs, M. (2007). "The geoR package." In: *R news* 1.2, pp. 14–18.
- Ripple, W. J. et al. (2015). "Collapse of the world's largest herbivores." In: *Science Advances* 1.4, e1400103.

- Rivrud, I. M., Loe, L. E., and Mysterud, A. (2010). "How does local weather predict red deer home range size at different temporal scales?" In: *Journal of Animal Ecology* 79.6, pp. 1280–1295.
- Rivrud, I. M., Sivertsen, T. R., Mysterud, A., Åhman, B., Støen, O.-G., and Skarin, A. (2018). "Reindeer green-wave surfing constrained by predators." In: *Ecosphere* 9.5, e02210.
- Robinson, W. R., Peters, R. H., and Zimmermann, J. (1983). "The effects of body size and temperature on metabolic rate of organisms." In: *Canadian Journal of Zoology* 61.2, pp. 281–288.
- Rocchini, D., Metz, M., Ricotta, C., Landa, M., Frigeri, A., and Neteler, M. (2013). "Fourier transforms for detecting multitemporal landscape fragmentation by remote sensing." In: *International Journal of Remote Sensing* 34.24, pp. 8907–8916.
- Roelants, H., Schneider, F., Göritz, F., Streich, J., and Blottner, S. (2002). "Seasonal Changes of Spermatogonial Proliferation in Roe Deer, Demonstrated by Flow Cytometric Analysis of c-kit Receptor, in Relation to Follicle-Stimulating Hormone, Luteinizing Hormone, and Testosterone1." In: *Biology of Reproduction* 66.2, pp. 305–312.
- Ruckstuhl, K. E. (2007). "Sexual segregation in vertebrates: proximate and ultimate causes." In: *Integrative and Comparative Biology* 47.2, pp. 245–257.
- Rutberg, A. T. (1987). "Adaptive Hypotheses of Birth Synchrony in Ruminants: An Interspecific Test." In: *The American Naturalist* 130.5, pp. 692–710.
- Sabal, M. C. et al. (2021). "Predation landscapes influence migratory prey ecology and evolution." In: *Trends in Ecology & Evolution* 36.8, pp. 737–749.
- Sacher, G. A. and Staffeldt, E. F. (1974). "Relation of Gestation Time to Brain Weight for Placental Mammals: Implications for the Theory of Vertebrate Growth." In: *The American Naturalist* 108.963, pp. 593–615.
- Säid, S. and Servanty, S. (2005). "The Influence of Landscape Structure on Female Roe Deer Home-range Size." In: *Landscape Ecology* 20.8, pp. 1003–1012.
- Säid, S. et al. (2005). "Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland." In: *Journal of Zoology* 267.3, pp. 301–308.
- Säid, S. et al. (2009). "What shapes intra-specific variation in home range size? A case study of female roe deer." In: *Oikos* 118.9, pp. 1299–1306.
- Saito, M. and Idani, G. (2018). "Giraffe Mother-Calf Relationships in the Miombo Woodland of Katavi National Park, Tanzania." In: *Mammal Study* 43.1, pp. 11–17.

- San José, C., Braza, F., and Aragón, S. (1999). "The effect of age and experience on the reproductive performance and prenatal expenditure of resources in female fallow deer (*Dama dama*).” In: *Canadian Journal of Zoology* 77.11, pp. 1717–1722.
- Sankar, K. and Acharya, B. (2004). "Spotted Deer or Chital.(K. Sankar, & SP Goyal, Eds.)” In: *ENVIS Bulletin: Wildlife and Protected Areas* 7.1, pp. 171–180.
- Santiago-Moreno, J., Gómez-Brunet, A., González-Bulnes, A., Toledano-Díaz, A., Malpaux, B., and López-Sebastián, A. (2005). "Differences in reproductive pattern between wild and domestic rams are not associated with inter-specific annual variations in plasma prolactin and melatonin concentrations.” In: *Domestic Animal Endocrinology* 28.4, pp. 416–429.
- Santiago-Moreno, J., Toledano-Díaz, A., Pulido-Pastor, A., Gómez-Brunet, A., and López-Sebastián, A. (2007). "Horn quality and postmortem sperm parameters in Spanish ibex (*Capra pyrenaica hispanica*).” In: *Animal Reproduction Science* 99.3, pp. 354–362.
- Santin-Janin, H., Garel, M., Chapuis, J.-L., and Pontier, D. (2009). "Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: a case study on the Kerguelen archipelago.” In: *Polar Biology* 32.6, pp. 861–871.
- Sawyer, H. and Kauffman, M. J. (2011). "Stopover ecology of a migratory ungulate.” In: *Journal of Animal Ecology* 80.5, pp. 1078–1087.
- Sawyer, H., Kauffman, M. J., Middleton, A. D., Morrison, T. A., Nielson, R. M., and Wyckoff, T. B. (2013). "A framework for understanding semi-permeable barrier effects on migratory ungulates.” In: *Journal of Applied Ecology* 50.1, pp. 68–78.
- Say-Sallaz, E., Chamaillé-Jammes, S., Fritz, H., and Valeix, M. (2019). "Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg.” In: *Biological Conservation* 235, pp. 36–52.
- Scacco, M., Flack, A., Duriez, O., Wikelski, M., and Safi, K. (2019). "Static landscape features predict uplift locations for soaring birds across Europe.” In: *Royal Society Open Science* 6.1, p. 181440.
- Schmitt, M. H., Stears, K., and Shrader, A. M. (2016). "Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe.” In: *Behavioral Ecology* 27.4, pp. 1073–1077.
- Schmitt, M. H., Stears, K., Wilmers, C. C., and Shrader, A. M. (2014). "Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds.” In: *Animal Behaviour* 96, pp. 151–158.
- Schmitz, O. J., Beckerman, A. P., and O’Brien, K. M. (1997). "Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions.” In: *Ecology* 78.5, pp. 1388–1399.

- Schoener, T. W. (1971). "Theory of Feeding Strategies." In: *Annual Review of Ecology and Systematics* 2.1, pp. 369–404.
- Schofield, G. et al. (2010). "Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management." In: *Biological Conservation* 143.3, pp. 722–730.
- Scillitani, L., Sturaro, E., Monaco, A., Rossi, L., and Ramanzin, M. (2012). "Factors affecting home range size of male Alpine ibex (*Capra ibex ibex*) in the Marmolada massif." In: *Hystrix, the Italian Journal of Mammalogy* 23.2, pp. 19–27.
- Scillitani, L. et al. (2013). "Habitat selection in translocated gregarious ungulate species: An interplay between sociality and ecological requirements." In: *The Journal of Wildlife Management* 77.4, pp. 761–769.
- Searle, K. R., Hobbs, N. T., and Gordon, I. J. (2007). "It's the "Foodscape", not the Landscape: Using Foraging Behavior to Make Functional Assessments of Landscape Condition." In: *Israel Journal of Ecology and Evolution* 53.3-4, pp. 297–316.
- Searle, K. R. and Shipley, L. A. (2008). "The Comparative Feeding Behaviour of Large Browsing and Grazing Herbivores." In: *The Ecology of Browsing and Grazing*. Ed. by Gordon, I. J. and Prins, H. H. T. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 117–148.
- Seigle-Ferrand, J. et al. (2021). "A Systematic Review of Within-Population Variation in the Size of Home Range Across Ungulates: What Do We Know After 50 Years of Telemetry Studies?" In: *Frontiers in Ecology and Evolution* 8.
- Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., and Swift, D. M. (1987). "Large Herbivore Foraging and Ecological Hierarchies." In: *BioScience* 37.11, pp. 789–799.
- Serrano, E. et al. (2015). "Border Disease Virus: An Exceptional Driver of Chamois Populations Among Other Threats." In: *Frontiers in Microbiology* 6, p. 1307.
- Service, C. N. et al. (2019). "Salmonid species diversity predicts salmon consumption by terrestrial wildlife." In: *Journal of Animal Ecology* 88.3, pp. 392–404.
- Shakeri, Y. N., White, K. S., and Waite, J. N. (2021). "Staying close to home: Ecological constraints on space use and range fidelity in a mountain ungulate." In: *Ecology and Evolution* 11.16, pp. 11051–11064.
- Shepard, E. L. C., Williamson, C., and Windsor, S. P. (2016). "Fine-scale flight strategies of gulls in urban airflows indicate risk and reward in city living." In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1704, p. 20150394.
- Shepard, E. L. C. et al. (2013). "Energy Landscapes Shape Animal Movement Ecology." In: *The American Naturalist* 182.3, pp. 298–312.

- Shiple, L. A. (1999). "Grazers and browsers: how digestive morphology affects diet selection." In: *Grazing behavior of livestock and wildlife* 70, pp. 20–27.
- Sigouin, D., Ouellet, J. .-, and Courtois, R. (1997). "Geographical variation in the mating and calving periods of moose." In: *Alces* 33.January 1997, pp. 85–95.
- Sinclair, A. R. E. (1977). "The African buffalo; a study of resource limitation of populations." In.
- Sinclair, A. R. E., Mduma, S., and Brashares, J. S. (2003). "Patterns of predation in a diverse predator–prey system." In: *Nature* 425.6955, pp. 288–290.
- Sinclair, A. R. E., Mduma, S. A. R., and Arcese, P. (2000). "What Determines Phenology and Synchrony of Ungulate Breeding in Serengeti?" In: *Ecology* 81.8, pp. 2100–2111.
- Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., and Ericsson, G. (2012). "From migration to nomadism: movement variability in a northern ungulate across its latitudinal range." In: *Ecological Applications* 22.7, pp. 2007–2020.
- Skinner, J. D. and Chimimba, C. T. (2005). *The mammals of the southern African sub-region*. Cambridge University Press.
- Soberón, J. (2007). "Grinnellian and Eltonian niches and geographic distributions of species." In: *Ecology Letters* 10.12, pp. 1115–1123.
- Solberg, E. J., Rolandsen, C. M., Heim, M., Linnell, J. D. C., Herfindal, I., and Sæther, B.-E. (2010). "Age and sex-specific variation in detectability of moose (*Alces alces*) during the hunting season: implications for population monitoring." In: *European Journal of Wildlife Research* 56.6, pp. 871–881.
- Sommer, R. S., Zachos, F. E., Street, M., Jöris, O., Skog, A., and Benecke, N. (2008). "Late Quaternary distribution dynamics and phylogeography of the red deer (*Cervus elaphus*) in Europe." In: *Quaternary Science Reviews* 27.7, pp. 714–733.
- Spiegel, O. and Crofoot, M. C. (2016). "The feedback between where we go and what we know—information shapes movement, but movement also impacts information acquisition." In: *Current Opinion in Behavioral Sciences*. Behavioral ecology 12, pp. 90–96.
- Steidl, R. J., Hayes, J. P., and Schaubert, E. (1997). "Statistical Power Analysis in Wildlife Research." In: *The Journal of Wildlife Management* 61.2, pp. 270–279.
- Stephens, P. A., Boyd, I. L., McNamara, J. M., and Houston, A. I. (2009). "Capital breeding and income breeding: their meaning, measurement, and worth." In: *Ecology* 90.8, pp. 2057–2067.
- Stephenson, T. R. et al. (2020). "Linking population performance to nutritional condition in an alpine ungulate." In: *Journal of Mammalogy*. Ed. by Barboza, P., gya091.
- Streiner, D. L. and Norman, G. R. (2011). "Correction for Multiple Testing: Is There a Resolution?" In: *Chest* 140.1, pp. 16–18.

- Sundell-Turner, N. M. and Rodewald, A. D. (2008). "A comparison of landscape metrics for conservation planning." In: *Landscape and Urban Planning* 86.3, pp. 219–225.
- Tamburello, N., Côté, I. M., and Dulvy, N. K. (2015). "Energy and the Scaling of Animal Space Use." In: *The American Naturalist* 186.2, pp. 196–211.
- Tao, Y., Börger, L., and Hastings, A. (2016). "Dynamic Range Size Analysis of Territorial Animals: An Optimality Approach." In: *The American Naturalist* 188.4, pp. 460–474.
- Taylor, R. D. (1988). "Age determination of the African buffalo, *Syncerus coffer* (Sparman) in Zimbabwe." In: *African Journal of Ecology* 26.3, pp. 207–220.
- Team, R. D. C. (2017). "R development core team." In: *RA Lang Environ Stat Comput* 55, pp. 275–286.
- Teitelbaum, C. S. and Mueller, T. (2019). "Beyond Migration: Causes and Consequences of Nomadic Animal Movements." In: *Trends in Ecology & Evolution* 34.6, pp. 569–581.
- Teitelbaum, C. S. et al. (2015). "How far to go? Determinants of migration distance in land mammals." In: *Ecology Letters* 18.6, pp. 545–552.
- Thel, L., Bonenfant, C., and Chamaillé-Jammes, S. (2021). "Does timing of birth affect juvenile and mare survival in wild plains zebra?" In: *bioRxiv*.
- Thel, L., Chamaillé-Jammes, S., and Bonenfant, C. (2021). "How to describe and measure phenology? An investigation on the diversity of metrics using phenology of births in large herbivores." In: *bioRxiv*.
- Thing, H., Klein, D. R., Jingfors, K., and Holt, S. (1987). "Ecology of muskoxen in Jameson Land, northeast Greenland." In: *Ecography* 10.2, pp. 95–103.
- Thorup, K. et al. (2017). "Resource tracking within and across continents in long-distance bird migrants." In: *Science Advances* 3.1, e1601360.
- Toïgo, C. and Gaillard, J.-M. (2003). "Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness?" In: *Oikos* 101.2, pp. 376–384.
- "Parental Investment and Sexual Selection" (1972). In: *Sexual Selection and the Descent of Man*. Ed. by Trivers, R. L. Routledge.
- Trivers, R. L. (1974). "Parent-Offspring Conflict." In: *American Zoologist* 14.1, pp. 249–264.
- Tucker, M. A., Ord, T. J., and Rogers, T. L. (2014). "Evolutionary predictors of mammalian home range size: body mass, diet and the environment." In: *Global Ecology and Biogeography* 23.10, pp. 1105–1114.
- Tucker, M. A. et al. (2018). "Moving in the Anthropocene: Global reductions in terrestrial mammalian movements." In: *Science* 359.6374, pp. 466–469.

- Tufto, J., Andersen, R., and Linnell, J. (1996). "Habitat Use and Ecological Correlates of Home Range Size in a Small Cervid: The Roe Deer." In: *Journal of Animal Ecology* 65.6, pp. 715–724.
- Turchin, P. (1991). "Translating Foraging Movements in Heterogeneous Environments into the Spatial Distribution of Foragers." In: *Ecology* 72.4, pp. 1253–1266.
- Turner, M. G. (2005). "Landscape Ecology: What Is the State of the Science?" In: *Annual Review of Ecology, Evolution, and Systematics* 36.1, pp. 319–344.
- Turner, W. C., Jolles, A. E., and Owen-Smith, N. (2005). "Alternating sexual segregation during the mating season by male African buffalo (*Syncerus caffer*)." In: *Journal of Zoology* 267.3, pp. 291–299.
- Van Dyke, F. (2007). "Colonization of non-traditional range in dispersing elk, *Cervus elaphus nelsoni*, populations." In: *The Canadian field-naturalist* 121.2, pp. 133–141.
- Van Hooft, P. et al. (2010). "Rainfall-driven sex-ratio genes in African buffalo suggested by correlations between Y-chromosomal haplotype frequencies and foetal sex ratio." In: *BMC Evolutionary Biology* 10.1, p. 106.
- Van Hooft, W. F., Groen, A. E., and Prins, H. H. T. (2000). "Microsatellite analysis of genetic diversity in African buffalo (*Syncerus caffer*) populations throughout Africa." In: *Molecular Ecology* 9.12, pp. 2017–2025.
- (2002). "Phylogeography of the African buffalo based on mitochondrial and Y-chromosomal loci: Pleistocene origin and population expansion of the Cape buffalo subspecies." In: *Molecular Ecology* 11.2, pp. 267–279.
- Van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J., and Sæther, B.-E. (2013). "Understanding scales of movement: animals ride waves and ripples of environmental change." In: *Journal of Animal Ecology* 82.4, pp. 770–780.
- Van Moorter, B., Gaillard, J.-M., McLoughlin, P. D., Delorme, D., Klein, F., and Boyce, M. S. (2009a). "Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales." In: *Oecologia* 159.3, pp. 669–678.
- Van Moorter, B., Rolandsen, C. M., Basille, M., and Gaillard, J.-M. (2016). "Movement is the glue connecting home ranges and habitat selection." In: *Journal of Animal Ecology* 85.1, pp. 21–31.
- Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S., and Gaillard, J.-M. (2009b). "Memory keeps you at home: a mechanistic model for home range emergence." In: *Oikos* 118.5, pp. 641–652.
- Van Teylingen, K. E. and Kerley, G. I. H. (1995). *Habitat characteristics of increasing and decreasing oribi subpopulations in Eastern Cape Province, South Africa*. Text.

- Van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M., and Mysterud, A. (2011). "What determines variation in home range size across spatiotemporal scales in a large browsing herbivore?" In: *Journal of Animal Ecology* 80.4, pp. 771–785.
- Vanpé, C., Morellet, N., Kjellander, P., Goulard, M., Liberg, O., and Hewison, A. M. (2009). "Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality." In: *Journal of Animal Ecology* 78.1, pp. 42–51.
- Van Wieren, S. E. (1996). "Do large herbivores select a diet that maximizes short-term energy intake rate?" In: *Forest Ecology and Management. Ungulates in Temperate Forest Ecosystems* 88.1, pp. 149–156.
- Vercauteren, K. C. and Hygnstrom, S. E. (1998). "Effects of Agricultural Activities and Hunting on Home Ranges of Female White-Tailed Deer." In: *The Journal of Wildlife Management* 62.1, pp. 280–285.
- Viana, D. S. et al. (2018). "Linking seasonal home range size with habitat selection and movement in a mountain ungulate." In: *Movement Ecology* 6.1, pp. 1–11.
- Volampeno, M. S. N., Masters, J. C., and Downs, C. T. (2011). "Home range size in the blue-eyed black lemur (*Eulemur flavifrons*): A comparison between dry and wet seasons." In: *Mammalian Biology* 76.2, pp. 157–164.
- Von Hardenberg, A., Bassano, B., Peracino, A., and Lovari, S. (2000). "Male Alpine Chamois Occupy Territories at Hotspots Before the Mating Season." In: *Ethology* 106.7, pp. 617–630.
- Wallmo, O. C. (1981). "Mule and black-tailed deer in North America. A Wildlife Management Institute book." In.
- Walter, W. D. et al. (2009). "Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer." In: *Landscape Ecology* 24.10, pp. 1405–1420.
- Webb, S. L., Gee, K. L., Strickland, B. K., Demarais, S., and DeYoung, R. W. (2010). "Measuring Fine-Scale White-Tailed Deer Movements and Environmental Influences Using GPS Collars." In: *International Journal of Ecology* 2010, e459610.
- Whitehead, P. E. and McEwan, E. H. (1973). "Seasonal variation in the plasma testosterone concentration of reindeer and caribou." In: *Canadian Journal of Zoology* 51.6, pp. 651–658.
- Whittaker, R. H., Levin, S. A., and Root, R. B. (1973). "Niche, Habitat, and Ecotope." In: *The American Naturalist*.
- Widmer, O., Saïd, S., Miroir, J., Duncan, P., Gaillard, J.-M., and Klein, F. (2004). "The effects of hurricane Lothar on habitat use of roe deer." In: *Forest Ecology and Management* 195.1, pp. 237–242.

- Wiens, J. A. (1989). "Spatial Scaling in Ecology." In: *Functional Ecology* 3.4, pp. 385–397.
- Wiens, J. A. (1976). "Population responses to patchy environments." In: *Annual Review of Ecology and Systematics* 7.1, pp. 81–120.
- Wiens, J. A., Crawford, C. S., and Gosz, J. R. (1985). "Boundary Dynamics: A Conceptual Framework for Studying Landscape Ecosystems." In: *Oikos* 45.3, pp. 421–427.
- Williams, H. J. and Safi, K. (2021). "Certainty and integration of options in animal movement." In: *Trends in Ecology & Evolution*.
- Willisch, C. S. and Ingold, P. (2007). "Feeding or Resting? The Strategy of Rutting Male Alpine Chamois." In: *Ethology* 113.1, pp. 97–104.
- Willisch, C. S. and Neuhaus, P. (2009). "Alternative Mating Tactics and Their Impact on Survival in Adult Male Alpine Ibex (*Capra ibex ibex*)." In: *Journal of Mammalogy* 90.6, pp. 1421–1430.
- Wilson, R. P., Shepard, E. L. C., and Liebsch, N. (2008). "Prying into the intimate details of animal lives: use of a daily diary on animals." In: *Endangered Species Research* 4.1-2, pp. 123–137.
- Winterbach, H. E. K. (1998). *Research review : The status and distribution of Cape buffalo Syncerus caffer caffer in southern Africa*. Text.
- Wolf, M., Frair, J., Merrill, E., and Turchin, P. (2009). "The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*." In: *Ecography* 32.3, pp. 401–410.
- Zeale, M. R. K., Davidson-Watts, I., and Jones, G. (2012). "Home range use and habitat selection by barbastelle bats (*Barbastella barbastellus*): implications for conservation." In: *Journal of Mammalogy* 93.4, pp. 1110–1118.
- Zeveloff, S. I. and Boyce, M. S. (1980). "Parental Investment and Mating Systems in Mammals." In: *Evolution* 34.5, pp. 973–982.
- (1986). "Maternal investment in mammals." In: *Nature* 321.6069, pp. 537–538.

APPENDICES





Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape

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Abstract

Although inter-individual heterogeneity in many aspects of dispersal behaviour is widely reported, this key life-history trait is predominantly modelled as a dichotomous state of philopatry versus dispersal. The increasing body of evidence for dispersal syndromes (i.e. a suite of correlated morphological, behavioural and life-history traits associated with dispersal) implies substantial but, to date, undocumented individual heterogeneity in behavioural tactics during dispersal. Using a large sample ($n = 154$) of GPS monitored juvenile roe deer *Capreolus capreolus*, we evaluated among-individual behavioural heterogeneity in dispersal tactics, and the individual and environmental drivers of these alternative tactics. We developed a sequential three-stage decision tree based on space use stability, exploration events and the directionality of movement. We identified six discrete alternative behavioural tactics during the dispersal period which were characterised by different timing, amplitude and duration in movement: slightly less than half of the deer were sedentary, either 'strictly philopatric' or 'explorers', which subsequently settled on their natal range; around 40% dispersed ('classic dispersal'), of which, one in six subsequently aborted, moving back to their natal range ('aborted dispersal'); finally, around 15% expressed either a 'progressive dispersal' tactic, gradually moving away from their natal area to settle elsewhere, or a 'multi-range' tactic. The propensity to express an alternative dispersal tactic was strongly influenced by an individual's local environment. In particular, when landscape heterogeneity, resource quality and human-related disturbance in the natal range were low, individuals were 1) more likely to adopt the alternative tactics of either progressive dispersal or multi-ranging, but 2) also more likely to abort their dispersal attempt. Our work indicates that natal dispersal is likely not a single uniform behaviour, but that individuals may adopt a variety of alternative movement tactics which are likely governed by different selection pressures, with potentially important impacts for population dynamics and functioning.

Keywords: directionality, exploration, GPS, movement ecology, natal range, ungulate.

DISPERSAL describes any movement of an organism which may impact gene flow through space (Ronce, 2007), with far-reaching consequences for many biological processes such as population structuring, biological invasions and species adaptation (Clobert et al., 2012; Ronce, 2007). However, while there is now a solid theoretical and empirical underpinning to current knowledge on dispersal (Clobert et al., 2012; Fronhofer et al., 2018; Gibbs et al., 2010; Holyoak et al., 2008), empirical studies describing the diversity of dispersal-related movement behaviours in the wild remain relatively scarce (but see Debeffe et al., 2012; Mayer, Zedrosser, and Rosell, 2017 for recent examples). In particular, over the last two decades, a growing body of literature has demonstrated that dispersal is a highly heterogeneous process (Bowler and Benton, 2005; Fronhofer et al., 2018), comprising three phases, emigration, transience and settlement. Experimental and empirical approaches have demonstrated marked heterogeneity among individuals in, for example, the propensity (Bonte et al., 2003) and timing (Mayer, Zedrosser, and Rosell, 2017) of emigration, the duration of dispersal transience (Rémy et al., 2011) and habitat selection during settlement (Haughland and Larsen, 2004). Indeed, individuals may adjust their dispersal decisions plastically in relation to a variety of environmental factors (Bonte, Bossuyt, and Lens, 2007; Bonte et al., 2008; Jacob et al., 2016). For instance, the quality of the natal environment may impact the ability of an individual to establish its post-dispersal range (Stamps, 2006) and should therefore influence its decision whether or not to disperse. Indeed, informed dispersal in relation to seasonality and environmental conditions is likely widespread in animals (Clobert et al., 2009).

In some species, development of specific morphological and/or physiological specializations is required to successfully disperse, generating discrete disperser and non-disperser phenotypes (Braendle et al., 2006; Martorell and Martínez-López, 2014). Because dispersal syndromes (covariation among morphological and/or behavioural traits) appear to be widespread (Clobert et al., 2009; Ronce and Clobert, 2012), individuals may also express discrete alternative behavioural tactics during dispersal (Clobert et al., 2009; Doerr and Doerr, 2005). By alternative tactics, we mean the set of alternative behaviours an individual may potentially express in response to a given environmental context. For example, Bonte et al. (2008) showed that individual spiders can disperse through either ballooning or rappelling depending on thermal conditions during development, while alternative amphidromous and non-amphidromous dispersal tactics were identified in the goby *Awaous stamineus* (Hogan et al., 2014). These alternative tactics likely incur different costs: for example, increasing dispersal distance can increase mortality costs (Stamps, Krishnan, and Reid, 2005), while energy costs

are likely higher for dispersing individuals that do not successfully settle in their post-dispersal range and must return to their natal range (Maag et al., 2019). However, despite the potential impact of these costs for the evolution of dispersal, no study has yet investigated alternative behavioural tactics across the phases of the dispersal process. This is, without doubt, in part due to the logistical challenge of recording detailed behaviour in the wild. Indeed, dispersing individuals may move rapidly through the landscape, often cryptically and potentially at night, so that direct observation is impossible. For sufficiently large species, remote monitoring by, for example, animal borne GPS devices provides the opportunity to track dispersal movements and behaviours in a precise way (Kays et al., 2015). However, there are, as yet, very few studies that have amassed sufficient data to address this question in a natural setting and, hence, dispersal is still invariably modelled as a dichotomous state of philopatry versus dispersal (Torrents-Ticó et al., 2018).

Here, we exploited a long-term dataset on a wild population of roe deer *Capreolus capreolus* inhabiting a heterogeneous landscape in the south of France to investigate 1) inter-individual heterogeneity in dispersal behaviour and 2) the individual and environmental drivers of these alternative tactics. We collected precise information on the spatial behaviour of a large sample ($n = 154$) of juvenile roe deer using intensive GPS tracking during the period of dispersal and coupled it with detailed data on landscape structure and individual phenotype. Dispersal in roe deer occurs at around 1 year of age, between the end of March and May (Debeffe et al., 2012), and is equally prevalent in both sexes (Coulon et al., 2006; Gaillard et al., 2008). Subsequently, most individuals remain faithful to their settlement range for their entire life (Hewison, Vincent, and Reby, 1998; Linnell and Andersen, 1998). Although there is substantial published baseline information in this species (Coulon et al., 2004; Vanpé et al., 2016; Wahlström and Liberg, 1995), as elsewhere, dispersal and philopatry were considered as the sole alternative behavioural states (but see Debeffe et al., 2013; Van Moorter et al., 2008 on pre-dispersal exploration behaviour). Thus, in a first step, we developed a method to classify individuals in terms of alternative dispersal tactics based on the spatial distribution, directionality and duration of their movements in relation to their presumed natal range. Subsequently, we investigated how individuals that were assigned to these novel alternative behavioural tactics differed in terms of their phenotype and their natal environment. In particular, we expected that the propensity of an individual to express a given tactic would depend on the characteristics of its natal range in terms of the availability of crops and meadows for feeding, the level of anthropogenic disturbance and landscape heterogeneity.

A.2 Material and Methods

A.2.1 Study area

The roe deer population inhabits a heterogeneous landscape of ca 19,000 ha in southwest France (43°13'N, 0°52'E) composed of 36% crops (e.g. alfalfa, wheat, barley, sunflower,

corn, soya, sorghum and rape), 31% meadows, 18% small oak-dominated (*Quercus spp.*) woodland patches and hedges, and two large forests of 672 and 515 ha (see Martin et al., 2018 for more details). Human presence is high, with villages, isolated houses and farms, and an extensive (2.15 km.km⁻²) secondary road network all widely distributed. Drive hunts with dogs occur on a regular basis from September to February and stalking from June to August. Roe deer density was estimated using a capture-mark-resighting approach at ca 10 deer per 100 ha in the more open areas of the landscape, and two to three times higher in the forest massifs (Hewison et al., 2007). The climate is oceanic, with an average temperature of 11–12°C and 800 mm precipitation per year, mostly rain.

A.2.2 Roe deer monitoring

Capture events occurred during winter from 2002 to 2017, on 11 different sites, using net drives with about 30–100 beaters and catchers placed regularly along a 4 km net line. When caught, roe deer were tranquilised using an intramuscular injection of acepromazine (0.075 mg.kg⁻¹), and placed in a wooden retention box to prevent stress and injury prior to marking (for more details of the capture procedure, see Morellet et al., 2009). For each animal, we recorded sex, body mass and age class. Juveniles (8–10 months old) were distinguished from older deer based on the presence of a tricuspid third pre-molar milk tooth (Ratcliffe and Mayle, 1992). To record their natal dispersal behaviour, juveniles were then equipped with a GPS collar, some of which also provided remote data transmission. Collars were programmed to record a GPS location every 4 h for the first two years of the study, and every 6 h subsequently, over a period of approximately 11 months. In total, we obtained GPS records for 170 juveniles since 2002. We removed the first seven days of monitoring, when behavioural alterations due to capture and handling may be pronounced (Morellet et al., 2009), prior to analyses. We then performed differential correction to improve fix accuracy (Adrados et al., 2003) and eliminated obviously erroneous locations (0.0003% of the total dataset). Once we had removed individuals that experienced collar dysfunction or mortality events during the first seven days of monitoring, we obtained a final sample of 154 juveniles for analysis.

A.2.3 Classification method and criteria

Our central objective was to analyse inter-individual variation in movement behaviour in order to characterise alternative movement tactics during the process of natal dispersal. Based on current knowledge of dispersal ecology, we identified home range stability, exploration movements and directionality as informative criteria that are generally used to characterise dispersal (Elliot et al., 2014; Haughland and Larsen, 2004; VanderWaal, Mosser, and Packer, 2009). To classify individuals, we first investigated clustering methods such as the K-nearest neighbours method (Mucherino, Papajorgji, and Pardalos, 2009) and random forest analysis (Breiman, 2001). However, the order in which these criteria are implemented is critical to differentiate alternative tactics, such that the value taken by one criterion depends on the value of the criterion implemented at the

previous step. This involves a step-by-step calculation of variables, which is difficult to implement in a classic clustering approach. We hence elaborated a biologically-informed and unsupervised classification method based on current knowledge with respect to home range stability, exploration events and movement directionality. First, to distinguish small-scale, within-range movements linked to foraging activity from larger-scale movements outside of the usual home range, we segmented the time-series of GPS locations (x- and y-coordinates) for each individual using Lavielle's method (1999) originally developed for a one-dimensional variable, but recently adapted by Patin et al. (2020) to handle bi-dimensional data (R package *segclust2d*). This approach detects significant change points in a time series (here, the geographical coordinates of locations of an individual) which we used to identify spatio-temporal units corresponding to distinct ranges occupied successively by that individual, and linked by inter-range transitional movements. To provide enough flexibility for identifying alternative movement behaviours, we set the maximum number of segments to 15 and the minimum duration of each segment to 42 h (i.e. 7 inter-fix intervals of 6 h). However, in practice, we considered that a given segment corresponded to a distinct range when the individual's residence time in that segment lasted at least seven days (i.e. a minimum of 28 locations, see Couriot et al., 2018). Residence time (i.e. the total time spent by an individual in a given area, Barraquand and Benhamou, 2008) for a given segment was estimated as the average time spent within a radius of 500 m (the average size of a roe deer home range at a monthly scale in this study area, Morellet et al., 2013) over all locations of that segment (using the R package *recurse*, Bracis, Bildstein, and Mueller, 2018). Because juvenile roe deer which were caught and monitored from their first winter are very unlikely to have already dispersed (Debeffe et al., 2012), and since migratory behaviour is negligible in our study population, the first segment of the time series that corresponded to a range was considered to be the natal range of that individual. Similarly, as GPS monitoring ceased in late autumn, we assumed that the last range identified from the time series represented the settlement range, since roe deer have been widely reported to occupy a stable adult range from 15 months of age onwards (Debeffe et al., 2012), with a very high level of site fidelity thereafter (Hewison, Vincent, and Reby, 1998). To illustrate this high spatial fidelity in our study system, we quantified the degree of overlap in locations of those individuals for which we had spatial information that covered several years. For individuals that were VHF- or GPS-monitored over at least two years during their lifetime, we measured range overlap using 50% fixed kernels between the post-dispersal range and the adult range, or between two subsequent adult ranges (libraries *adehabitatHR*, Calenge, 2006 and *rgeos*, Bivand and Rundel, 2017). For those that were monitored for one year only, but were subsequently recovered when they died, we compared their location at death to their locations during the monitoring period. When location at death or the adult range overlapped with the post-settlement range or the adult range in a previous year, we considered the animal to be faithful to its home range. Firstly, of the 58 adults that were monitored during two or more years, 54 (~ 93%) were faithful to their core home range. Second, of the 30 juveniles that

were monitored by GPS during the post-dispersal phase, 28 (~ 93%) were subsequently located within their settlement range during adulthood (see Supplementary Information I for more details). Thus, the vast majority of individuals remained where they settled after the dispersal phase, irrespective of whether they dispersed or not, and hence most likely reproduced on their settlement range. Note, however, that some roe deer females may perform reproductive excursions during the rut, outside of their usual home range, presumably to mate with unrelated males (Debeffe et al., 2014). Finally, to identify alternative movement tactics during the dispersal period, we analysed the time series of ranges and inter-range movements for each individual using a sequential three-stage decision tree (Figure A.1).

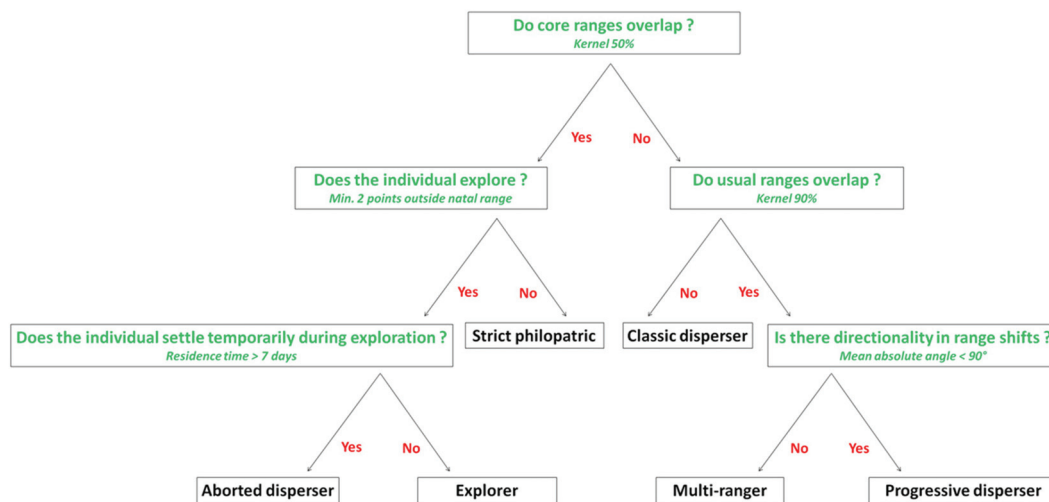


FIGURE A.1: Classification steps to discriminate between alternative movement tactics of juvenile roe deer during the dispersal phase. The classification criteria are given in green, the dichotomous alternatives are in red and the six behavioural tactics identified with this decision tree are in black.

A.2.4 Step 1. Did the individual use spatially-separate ranges?

By definition, dispersal occurs when an individual leaves its natal range and moves away to settle in a post-dispersal settlement range which is spatially distinct from the natal range and where reproduction potentially occurs (Kenward et al., 2002; Ronce, 2007). Therefore, as a first step, we measured the degree of overlap between the natal and settlement ranges. Ranges were estimated using fixed-kernel methods and an ad hoc approach to select the optimal smoothing parameter with the `adehabitatHR` package (Calenge, 2006) for R. We measured the overlap at two spatial scales with the `rgeos` package (Bivand and Rundel, 2017): using the 50% fixed-kernel, which corresponds to the core area of the home range, and the 90% fixed-kernel, which corresponds to the estimated usual home range, hereafter named usual range (Börger et al., 2006; Wornton, 1989). When core areas of the natal and settlement ranges overlapped, the individual was assigned to one of the philopatric categories (see Step 2), whereas when both the core areas and usual ranges did not overlap, the individual was assigned to the ‘classic

disperser' tactic. When the core areas did not overlap, but the usual ranges did, we considered that these individuals were unusually mobile to conform to a strict definition of philopatry and, hence, required further investigation (see [Step 3](#)).

A.2.5 Step 2. Did the individual explore?

Because exploration is a common behaviour which may allow juveniles to assess the potential costs and benefits of dispersing (Clobert et al., 2009), in a second step, we investigated whether those individuals considered as philopatric above were, indeed, strictly sedentary ('strict philopatric' tactic) or whether they had explored the surrounding environment prior to settling on their natal range. To avoid confounding exploration with GPS error (Börger et al., 2006), we considered that an exploration event occurred if at least two successive fixes (i.e. incorporating an inter-fix interval of 6 h) were situated outside an individual's usual range (Debeffe et al., 2013). Then, to distinguish between individuals that performed short term movements to explore their surrounding environment ('explorer' tactic), but that were essentially philopatric, from those that actually left their natal range to settle temporarily in a new range, before aborting the dispersal attempt and returning to their natal range ('aborted disperser' tactic), we calculated the residence time associated with the exploration event. Because pre-dispersal exploration events in juvenile roe deer typically last around 24 h and never more than six days (Debeffe et al., 2013), we considered that a residence time of seven days or more indicated temporary settlement and, hence, the individual was classified as an aborted disperser.

A.2.6 Step 3. Did the individual shift its range in a consistent direction?

Although dispersal is often envisaged as an abrupt shift in spatial location (Greenwood, 1980), it may not always include a clearly defined transience stage. Thus, in the third step of our classification, for individuals that were identified as unusually mobile above (see [Step 1](#)), we distinguished individuals that gradually moved away from their natal area in a consistent direction during a protracted dispersal transience phase ('progressive disperser' tactic) from individuals that moved periodically among different seasonal sub-ranges ('multirange' tactic *sensu* Courriot et al., 2018). To do so, for all mobile individuals whose trajectory included at least three segments, we analysed directionality in their movement paths; that is, we measured the successive relative angles between the centroid of each segment using the package *adehabitatLT* (Calenge, 2006) and calculated the mean of the absolute angle values for each individual. With respect to the straight line that connected the centroids of the first two segments, we considered that the individual expressed directional persistence when the mean angle was less than 90°, so that the Euclidian distance from the natal area sequentially increased ('progressive disperser' tactic). Alternatively, a mean angle greater than 90° indicated that the animal moved back towards its initial location (i.e. the natal area), and therefore expressed a 'multi-range' tactic. Note that we could not evaluate directionality for individuals that only occupied two ranges. Because the multi-range tactic is a way to track seasonal

fluctuations in resource distribution, and hence generally encompasses more than two sub-ranges within a given season (Courriot et al., 2018), we considered that these individuals were also ‘progressive dispersers’ (50% of the progressive dispersal class).

A.2.7 Drivers of alternative dispersal tactics

To identify the potential individual and environmental drivers of the alternative dispersal tactics identified above, we analysed the propensity for a juvenile roe deer to adopt a given tactic in relation to its sex, its body mass at capture and the habitat characteristics of its natal range. More precisely, we generated three landscape descriptors that were shown to affect dispersal behaviour in previous studies (Fey, Hämäläinen, and Selonen, 2016; Matthysen, 2012): 1) we used the proportion of crops and meadows in the natal range to index nutritional quality of that range, as these habitats provide high quality resources for roe deer (Hewison et al., 2009); 2) to index landscape heterogeneity, we calculated the Shannon index based on the proportions of different habitat types within the natal range; 3) to index human-related disturbance, we calculated the distance to the nearest anthropogenic feature (road or building) in the natal range. In order to control for inter-individual variation in natal range size, we estimated these landscape descriptors for each individual within a standardised buffer of 98 ha (which corresponds to the average size of a natal range in our dataset) centred on the geometric centroid of the individual’s natal range. We calculated the three landscape descriptors based on 10,000 randomly sampled locations within each buffer. We characterised local landscape composition in terms of land cover types with ArcGIS 10 (ESRI, 2018) using a geographical information system in which all land cover polygons were manually digitized, based on aerial photographs, and described each summer using 41 land cover categories through field observation (for more details, see Morellet et al., 2011). For each random location, we recorded land use information for the year during which the individual was monitored, and we averaged all land use information obtained for the 10,000 locations in order to extract individual mean values for each landscape descriptor. Given the high level of co-linearity among the landscape descriptors, we first performed a principal component analysis (PCA) with varimax rotation to generate two or more independent (orthogonal) variables that described among-individual variation in landscape structure of the natal range (library `ade4`, Bougeard and Dray, 2018). The three descriptors were scaled and centred prior to the PCA. We then used the principal components of the PCA that explained the most variation to analyse the relationship between landscape structure in the natal range and the propensity to adopt a given movement tactic.

We analysed alternative dispersal tactics one by one (relative to a reference dispersal tactic) as separate binary response variables and used generalized linear models with a logit link function (library `stats`, <http://www.r-project.org>) to analyse the propensity of an individual to adopt a specific movement tactic. More precisely, compared to classical dispersal, we evaluated the hypotheses that 1) the propensity to adopt an alternative dispersal tactic and 2) the propensity to abort a dispersal attempt would

depend on the characteristics of an individual's natal range in terms of availability of crops and meadows, level of anthropogenic disturbance and landscape heterogeneity. To evaluate the above hypotheses, we first built a reference model including body mass (one individual was removed from this analysis because we had no body mass data for it), sex, their interaction (because the drivers of condition-dependent dispersal are likely sex-specific (Hewison et al. unpubl.) and the principal components of the landscape descriptors. Then, we compared a set of candidate models which comprised our reference model and all simpler nested models, including the constant model. Initially, we investigated both linear and non-linear effects of body mass using sex-specific thin plate regression splines. However, because in all cases linear models provided better fit to the data, we present only these results. We based our model selection on Akaike's information criterion corrected for small sample size (AICc, Burnham and Anderson, 2002) and performed model averaging on all models within a Δ AICc of 2 of the best model (library MuMIn, barton_mumin_2018). For each model, we calculated Cook's distances to evaluate whether any observations might have a disproportionate influence on our results (library base). Replicating the analyses after removing two such influential observations showed that model selection was robust to the inclusion of these points (results not shown). We used a binomial approach because it was better aligned with the structure of our hypotheses, but note that we obtained very similar results using multinomial models to evaluate the effect of landscape structure and phenotype on the six dispersal tactics simultaneously (library nnet, Venables and Ripley, 2002; see Supplementary Information II Tables SA.6, SA.7). Statistical analyses were performed using the R software ver.3.3.2 (<http://www.r-project.org>).

A.2.8 Data availability

The dataset analysed in this study is available from EURODEER (<https://eurodeer.org/>) upon request, and from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3s41j61> (Ducros et al., 2019).

A.3 Results

A.3.1 Identifying alternative movement tactics

Using our classification decision tree, we assigned 147 (68 males, 79 females) of the 154 juvenile roe deer to one of the six alternative movement tactics during the period of dispersal (Figure A.2; see Supplementary Information Figure SA.2 for more examples of individual trajectories). The remaining seven individuals could not be assigned to any behavioural tactic, either because we obtained too few GPS locations after initial data processing ($n = 3$), or because the animal moved erratically immediately after the capture event so that we were unable to identify the natal range ($n = 4$). Most individuals were either classified as classic dispersers, with a clear and well-defined transience stage ($n = 49$; 30 females and 19 males), or explorers, which only left their initial range for short periods of time and subsequently settled on their natal range ($n = 62$; 32 females

and 30 males). Otherwise, 14 individuals were classified as progressive dispersers which gradually moved away from their natal area to settle elsewhere (5 females and 9 males), whereas 9 were classified as aborted dispersers which temporarily settled in a novel range, but moved back to settle in their natal range (5 females and 4 males). Finally, 9 individuals were assigned to the multirange tactic (4 females and 5 males), while only 4 were strictly philopatric, never leaving their natal range (3 females and 1 male). For subsequent analyses, we therefore pooled these strictly philopatric individuals with the explorers as a single ‘philopatric’ class.

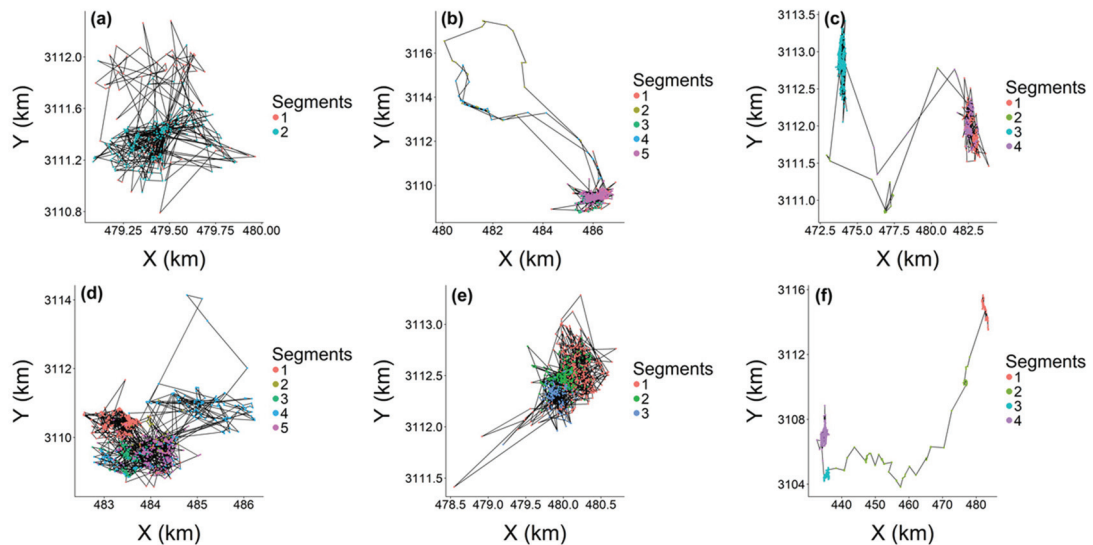


FIGURE A.2: Examples of the six alternative movement tactics exhibited by juvenile roe deer during the dispersal phase: (a) strict philopatric; (b) explorer; (c) aborted disperser; (d) multi-ranger; (e) progressive disperser; (f) classic disperser. Each dot represents a GPS location, successive locations are linked by a straight line. Successive segments identified by the segmentation approach are coded in different colours and numbered chronologically. Latitude and longitude are expressed in kilometres.

Using the bi-dimensional adaptation of Lavielle’s segmentation approach, the movement paths comprised, on average, 2.3 (SD±1.2) segments (range 1–7 segments) per individual, lasting between 2 and 320 days. Except for the first segment which lasted, on average, 76.2±38.9 days, there was pronounced variation in segment duration, both among segments and among classes (Supplementary Information Table SA.8 for details). Mean departure date from the natal area ranged from the 1 April for multi-rangers to the 14 May for progressive dispersers, while classic dispersers and aborted dispersers initiated dispersal, on average, the 20 April and the 2 May, respectively. However, there was also marked intra-class variation in departure date, especially for progressive dispersers (Supplementary Information III Table SA.9). Finally, the straight line distance between the initial and final segment centroids also varied both between and within classes, ranging from 0.2±0.1 km for strictly philopatric individuals to 12.9±2.0 km for classic dispersers (±SD). In comparison to classic dispersers, aborted dispersers moved shorter distances from their natal range to their temporary settlement range (4.9±2.6 km), while the distance between their natal and final settlement ranges (0.4±0.1

km) was equivalent to that of strictly philopatric individuals. Progressive dispersers, multi-rangers and explorers moved the centroid of their range, on average, 1.0 ± 0.2 , 0.7 ± 0.1 and 0.3 ± 0.03 km, respectively, between their initial and final ranges.

A.3.2 Drivers of alternative dispersal tactics

Based on the eigenvalues and PC scores (Supplementary Information IV Figure SA.3, Table SA.10), for subsequent analyses we retained only the first axis of the PCA (PC1), explaining 85% of variation in landscape structure. Positive values of the PC1 indicated a low availability of crops and meadows in the home range, a low value of the Shannon index (low habitat heterogeneity) and a high distance to the nearest anthropogenic feature. PC1, thus, described a composite gradient of the availability of crops and meadows for feeding, landscape heterogeneity and disturbance.

Contrasting the environmental and phenotypic drivers of progressive dispersal versus classic dispersal

The set of retained models describing the propensity to adopt the progressive dispersal tactic rather than a classic dispersal tactic contained the PC1 of the landscape descriptors (all models within a $\Delta AICc$ of 2) and the two-way interaction between body mass and sex (Supplementary Information II Table SA.3). The interaction indicated a negative relationship between the propensity to progressively disperse and body mass for females, but a positive one for males, however, these effects were weak (Table A.1). In contrast,

TABLE A.1: Summary statistics from the model averaging procedure based on generalized linear models (within a $\Delta AICc$ of 2 from the best model), describing individual propensity to adopt a progressive dispersal tactic (versus a classic dispersal tactic) in relation to body mass, sex and landscape structure in the natal range. Landscape structure was indexed as the coordinates along the first axis of the PCA performed on three landscape descriptors (availability of crops and meadows, levels of habitat heterogeneity and anthropogenic disturbance in the natal range). We report parameter estimates ($\pm SE$) for each variable that featured in the retained models, z-values, confidence intervals at 2.5 and 97.5% (CI). The proportion of deviance explained by the model, calculated as the ratio between the residual (54.39) and null (66.74) deviances, was 0.815.

Variables	Estimates	SE	z-value	CI 2.5%	CI 97.5%
Intercept	1.34	4.93	0.27	-8.40	11.09
Landscape	0.66	0.31	2.08	0.04	1.29
Sex (male)	-1.32	6.15	0.21	-13.48	10.85
Body mass	-0.44	0.37	1.17	-1.18	0.30
Body mass \times sex (male)	0.68	0.49	1.36	-0.30	1.65

we found strong support for the hypothesis that the propensity to adopt a progressive dispersal rather than a classic dispersal tactic was linked to landscape structure in the natal range. The propensity to be a progressive disperser increased as the scores on the PC1 of landscape descriptors increased (estimate of 0.66 ± 0.31 (SE), $n = 63$, Table A.1), indicating that individuals living in the more homogeneous local landscapes, with lower resource quality, but subject to less anthropogenic disturbance, were more than twice as

likely to adopt a progressive disperser tactic ($P_{\text{progressive disperser}} = 0.31$) than those living in the more heterogeneous open landscapes ($P_{\text{progressive disperser}} = 0.13$; [Figure A.3a](#)).

Contrasting the environmental and phenotypic drivers of multi-ranging versus classic dispersal

The set of retained models describing the propensity of an individual to adopt the multi-range tactic rather than a classic dispersal tactic contained the PC1 of the landscape descriptors (almost all models within a ΔAICc of 2) and the two-way interaction between body mass and sex ([Supplementary Information II Table SA.4](#)). The interaction indicated that the propensity to adopt the multi-range tactic increased as body mass decreased for males, but not for females ([Table A.2](#)), but the effect was weak again. However, we found strong support for the hypothesis that the propensity of a juvenile roe deer to adopt a multi-range tactic rather than a classic dispersal tactic was linked to the landscape structure in its natal range. The propensity to adopt a multi-range tactic increased as the scores on the PC1 of landscape descriptors increased (estimate of 0.76 ± 0.36 (SE), $n = 58$, [Table A.2](#)), indicating that individuals living in the more homogeneous local landscapes, with lower resource quality, but subject to less anthropogenic disturbance, were more than nine times more likely to adopt a multi-range tactic ($P_{\text{multi-ranger}} = 0.28$) than those living in the more heterogeneous open landscapes ($P_{\text{multi-ranger}} = 0.03$; [Figure A.3b](#)).

TABLE A.2: Summary statistics from the model averaging procedure based on generalized linear models (within a ΔAICc of 2 from the best model), describing individual propensity to adopt a multi-range tactic (versus a classic dispersal tactic) in relation to body mass, sex and landscape structure in the natal range. Landscape structure was indexed as the coordinates along the first axis of the PCA performed on three landscape descriptors (availability of crops and meadows, levels of habitat heterogeneity and anthropogenic disturbance in the natal range). We report parameter estimates ($\pm\text{SE}$) for each variable that featured in the retained models, z-values, confidence intervals at 2.5 and 97.5% (CI). The proportion of deviance explained by the model, calculated as the ratio between the residual (33.95) and null (50.06) deviances, was 0.678.

Variables	Estimates	SE	z-value	CI 2.5%	CI 97.5%
Intercept	-1.06	4.48	0.23	-10.01	7.89
Landscape	0.76	0.36	2.08	0.04	1.47
Body mass	-0.06	0.33	0.17	-0.71	0.60
Sex (male)	23.02	12.76	1.76	-2.56	48.60
Body mass \times Sex (male)	-1.35	0.78	1.69	-2.91	0.22

Contrasting the environmental and phenotypic drivers of aborted dispersal versus classic dispersal

The set of retained models describing the propensity to abort the dispersal attempt (i.e. aborted dispersal versus classic dispersal) contained the additive effects of the PC1 of the landscape descriptors (all models within a ΔAICc of 2), body mass and sex ([Supplementary Information II Table SA.5](#)). Once again, the influence of body mass and sex on the propensity to abort dispersal were only weakly supported ([Table A.3](#)). In contrast, we found strong support for the hypothesis that the probability that a

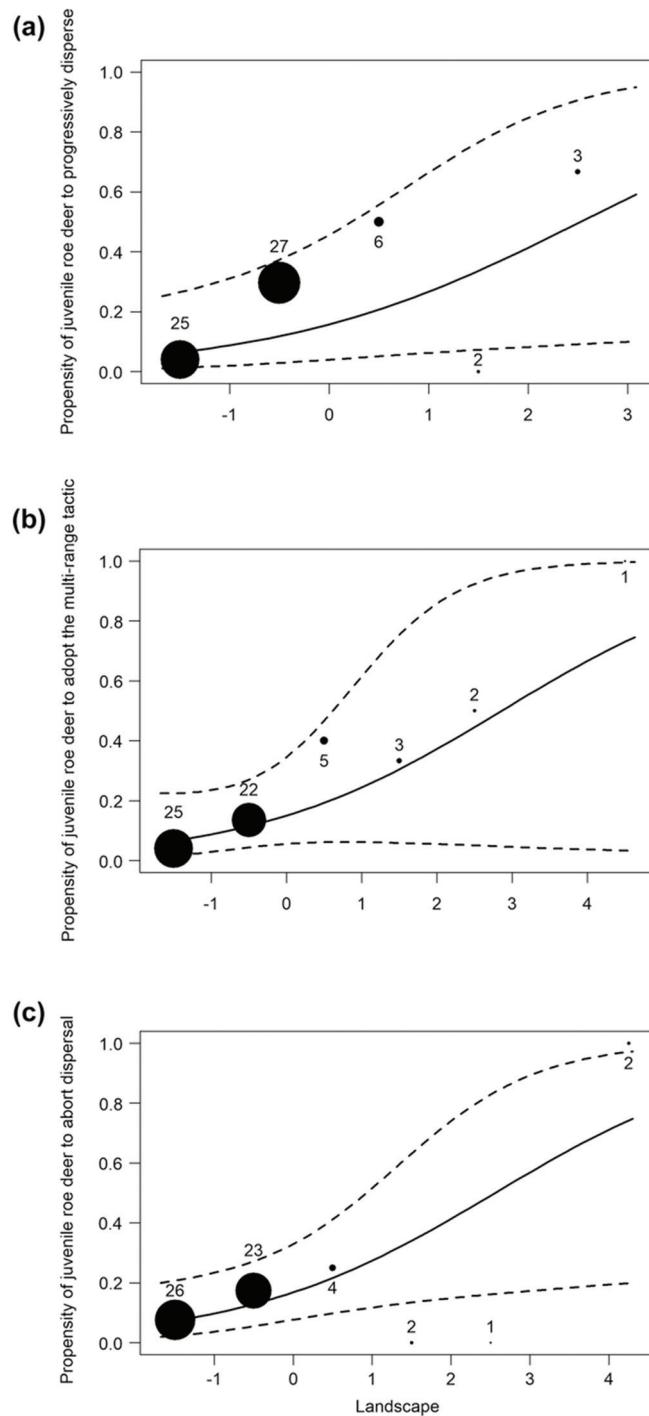


FIGURE A.3: Variation in the propensity of juvenile roe deer to (a) progressively disperse, (b) adopt the multi-range tactic, (c) abort their dispersal attempt (versus classically disperse) as a function of increasing landscape heterogeneity, availability of crops and meadows and anthropogenic disturbance (described by the PC1 of these three descriptors; low scores of the PC1 indicate a highly heterogeneous local landscape with both high levels of crops and meadows and high levels of anthropogenic disturbance). The line (and dotted lines) represents the model predictions (and the associated 95% confidence intervals). Points (proportional to sample size and centred for intervals of 1 unit of PC1) represent the observed propensity to adopt the given tactic for a given level of landscape heterogeneity, crop/meadow availability and disturbance.

TABLE A.3: Summary statistics from the model averaging procedure based on generalized linear models (within a ΔAICc of 2 from the best model), describing individual propensity to adopt an aborted dispersal tactic (versus a classic dispersal tactic) in relation to body mass, sex and landscape structure in the natal range. Landscape structure was indexed as the coordinates along the first axis of the PCA performed on three landscape descriptors (availability of crops and meadows, levels of habitat heterogeneity and anthropogenic disturbance in the natal range). We report parameter estimates ($\pm\text{SE}$) for each variable that featured in the retained models, z-values, confidence intervals at 2.5 and 97.5% (CI). The proportion of deviance explained by the model, calculated as the ratio between the residual (43.67) and null (50.06) deviances, was 0.872.

Variables	Estimates	SE	z-value	CI 2.5%	CI 97.5%
Intercept	-2.06	2.14	0.94	-6.33	2.22
Landscape	0.62	0.27	2.23	0.08	1.17
Sex (male)	0.70	0.82	0.83	-0.95	2.34
Body mass	0.13	0.25	0.52	-0.37	0.63

juvenile roe deer aborted its dispersal attempt was linked to landscape structure in the natal range. The propensity to abort a dispersal attempt increased as the scores on the PC1 of landscape descriptors increased (estimate of 0.62 ± 0.27 (SE), $n = 58$, $DF = 2$, Table A.3), such that individuals living in the more homogeneous landscapes, of poorer resource quality and with less anthropogenic disturbance in their natal range, were more than three times more likely to abort their dispersal attempt ($P_{\text{aborted disperser}} = 0.24$) than those living in the more heterogeneous open habitats ($P_{\text{aborted disperser}} = 0.07$; Figure A.3c).

A.4 Discussion

Marked heterogeneity among individuals in dispersal-related traits has been widely documented in recent times (Bowler and Benton, 2005; Clobert et al., 2009), for example, in terms of propensity to disperse (Bonte et al., 2003) or distance travelled (Brown and Crone, 2016). Here, using an exceptionally large and detailed data set on juvenile roe deer, we developed a novel methodology to identify six discrete alternative behavioural tactics during dispersal. These tactics were characterised by different timing, amplitude and directionality in movement behaviour. A post hoc analysis based on movement parameters revealing inter- and intra-individual variation in movement behaviour (Supplementary Information V) indicated that our classification was moderately robust, allowing us to classify individuals into ecologically meaningful groups and suggesting that our methodology could be informative for other study systems. We also demonstrated that the expression of these alternative tactics was overwhelmingly influenced by the individual's natal environment. Our work indicates that individuals may adopt a variety of alternative movement tactics during natal dispersal in response to particular proximal drivers, with potentially important impacts for population dynamics (Clobert et al., 2009).

Natal dispersal promotes gene flow and influences population structure, in particular, by determining the geographical distance between close relatives and, thereby, limiting

inbreeding (Bohonak, 1999). Because roe deer adults have very high site fidelity to their post-dispersal range (Linnell and Andersen, 1998), with about 93.5% of individuals remaining faithful to their settlement range (Material and methods, Supplementary Information I), they most likely reproduce where they settle at the end of dispersal transience. The six alternative dispersal tactics that we identified are, hence, likely to have contrasting implications for gene flow and population structure. Classic dispersers should contribute most to gene flow as they dispersed, on average, more than 10 kilometres (equivalent to around 10 home range diameters), well beyond any spatial structure in relatedness (Bonnot et al., 2010). In contrast, the role of aborted dispersal for gene flow may differ between the sexes, because females (Hewison, 1996), but not males (Vanpé et al., 2009), are sexually active at 15 months of age in roe deer. Therefore, although all but two (both males) of the nine aborted dispersers spent at least part of that summer rut on their aborted dispersal range prior to returning to their natal range (mean aborted dispersal duration = 84.8 ± 59.6 days (SD)), only the five females actually likely copulated there. This behaviour would appear to be the reproductive equivalent of the rut excursion behaviour that has been widely reported in female roe deer adults (Debeffe et al., 2014), generating female-mediated gene flow of the male genome over intermediate distances, contrary to classic dispersal, which generates gene flow of both male and female genomes. In contrast, progressive dispersal and multi-ranging tactics result in settlement in an immediately neighbouring range, with little potential impact on gene flow at the landscape scale, but likely facilitating avoidance of incestuous mating with parents.

Phenotype-dependence in the propensity of an individual to disperse is widespread across organisms (Clobert et al., 2009). For example, heavier individuals have been shown to disperse more often and further compared to lighter individuals in a variety of species (Barbraud, Johnson, and Bertault, 2003; Searcy et al., 2018), including roe deer (Debeffe et al., 2012). Heavier individuals are likely better able to offset the costs of dispersal (Bonte et al., 2012) and may be able to settle more easily in a novel range (Stamps, 2006). Our results support previous work showing that heavy individuals have a greater propensity to disperse long distances (i.e. 'classic dispersal' in our study, results not shown; see Debeffe et al., 2012), but indicate that body condition is not a determinant of whether an individual successfully settles or, rather, aborts its dispersal attempt. Furthermore, there was only a weak evidence for sex-specific influence of body mass on the propensity of an individual to use the multi-range or progressive dispersal tactics. Thus, because these two alternative tactics require no real increase in overall mobility compared to philopatry, we suggest that the role of body mass in determining dispersal tactics is likely related to the capacity of an individual to offset the associated costs of dispersal in relation to its sex. Our results might also suggest that the ultimate drivers of dispersal tactics are sex-specific, as classic dispersal was slightly female-biased (61.2% female), while slightly more males were progressive dispersers or multi-rangers (60.9% male). Because this contrasts with previous findings (Coulon

et al., 2006; Gaillard et al., 2008), additional data will be required to explore whether dispersal tactics do really differ between the sexes.

If dispersal is a response to density-dependent scramble competition for resources (Bowler and Benton, 2005; Clobert et al., 2012), individuals should base their dispersal decisions on the quality of their natal habitat (Stamps, 2006) relative to the surrounding alternative habitat (Matthysen, 2012). Here, we demonstrated that dispersing individuals that were born on a higher quality and heterogeneous natal range almost exclusively adopted a classic dispersal tactic, whereas around half of all dispersers that were born in lower quality homogeneous forest habitat adopted either a progressive dispersal tactic (Figure A.3a) or a multi-range tactic (Figure A.3b). There are at least two non-mutually exclusive interpretations of these results. First, high availability of crops and meadows in the natal range promotes rapid growth so that juveniles born in the most open sectors of the landscape are around 20% heavier than those in pure forest habitat (Hewison et al., 2009). Hence, these individuals may be better able to offset the costs of classic long-range dispersal (Bonte et al., 2012) compared to individuals living in poorer habitat which may be forced to adopt the alternative, short-range, and presumably less costly, movement tactics. Alternatively, juveniles born in the open agricultural landscapes are likely habituated to a high level of habitat patchiness and baseline anthropogenic disturbance. As a consequence, they may be less reluctant to cross habitat boundaries (Wiens, 1976) and better able to deal with the alien landscape of fear through which they must navigate during classic dispersal transience and settlement. This interpretation is supported by the observation that individuals which subsequently aborted their dispersal attempt were also predominantly born in the more homogeneous and less disturbed forest habitats (Figure A.3b, Supplementary Information IV Table SA.11). Detailed comparison of the habitat characteristics of natal and settlement ranges should provide a better understanding of why around 15% of dispersers abandon their settlement range after only a few months residence and return to their natal site.

Our work provides further evidence of the huge complexity in dispersal behaviour. Within the theoretical framework developed by Baguette and Van Dyck (2007), it seems likely that the alternative dispersal tactics we identified are responses to different selective pressures. For example, short dispersal distances may suffice to avoid kin competition and inbreeding (Baguette and Van Dyck, 2007), in particular between parents and offspring, which might generate a progressive dispersal or multi-range tactic linked to the spatial structure of relatedness. In contrast, density-dependent conspecific competition for resources is likely to select for long distance dispersal (i.e. 'classic dispersal'), notably in response to environmental heterogeneity, driving emigration from the population (Baguette and Van Dyck, 2007). The next step will be to quantify the link between dispersal behaviour and individual performance so as to better understand the ultimate drivers of different dispersal tactics and their consequences for gene flow and population structure.

Permits

All capture and marking procedures were done in accordance with French and European laws for animal welfare (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection).

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Author contributions

A. Coulon and A. J. M. Hewison contributed equally to this paper. AC, AJMH and NM conceived the original idea for this manuscript; DD, AC, AJMH, NM, LD, BC, BL and YC participated in data collection; DD, AC, AJMH and NM designed the methodology and analysed the data; RP and KA assisted with the analytical approach; DD, AC, AJMH and NM led the writing of the manuscript, with inputs from all contributing authors. All authors gave final approval for publication.

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Conflict of interest

The authors declare that they have no conflict of interest.

References

- Adrados, C., Verheyden-Tixier, H., Cargnelutti, B., Pépin, D., and Janeau, G. (2003). "GPS approach to study fine-scale site use by wild red deer during active and inactive behaviors." In: *Wildlife Society Bulletin (1973-2006)* 31.2, pp. 544–552.
- Baguette, M. and Van Dyck, H. (2007). "Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal." In: *Landscape Ecology* 22.8, pp. 1117–1129.

- Barbraud, C., Johnson, A. R., and Bertault, G. (2003). "Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition." In: *Journal of Animal Ecology* 72.2, pp. 246–257.
- Barraquand, F. and Benhamou, S. (2008). "Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts." In: *Ecology* 89.12, pp. 3336–3348.
- Bivand, R. and Rundel, C. (2017). *rgeos: interface to geometry engine - Open Source ('GEOS')*.
- Bohonak, A. J. (1999). "Dispersal, gene flow, and population structure." In: *The Quarterly Review of Biology* 74.1, pp. 21–45.
- Bonnot, N. et al. (2010). "No difference between the sexes in fine-scale spatial genetic structure of roe deer." In: *PLOS ONE* 5.12, e14436.
- Bonte, D., Bossuyt, B., and Lens, L. (2007). "Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider." In: *Behavioral Ecology* 18.2, pp. 438–443.
- Bonte, D., Travis, J. M. J., Clercq, N. D., Zwertvaegher, I., and Lens, L. (2008). "Thermal conditions during juvenile development affect adult dispersal in a spider." In: *Proceedings of the National Academy of Sciences* 105.44, pp. 17000–17005.
- Bonte, D., Vandenbroecke, N., Lens, L., and Maelfait, J.-P. (2003). "Low propensity for aerial dispersal in specialist spiders from fragmented landscapes." In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270.1524, pp. 1601–1607.
- Bonte, D. et al. (2012). "Costs of dispersal." In: *Biological Reviews* 87.2, pp. 290–312.
- Börger, L. et al. (2006). "Effects of sampling regime on the mean and variance of home range size estimates." In: *Journal of Animal Ecology* 75.6, pp. 1393–1405.
- Bougeard, S. and Dray, S. (2018). "Supervised multiblock analysis in R with the ade4 package." In: *Journal of Statistical Software* 86.1, pp. 1–17.
- Bowler, D. E. and Benton, T. G. (2005). "Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics." In: *Biological Reviews* 80.2, pp. 205–225.
- Bracis, C., Bildstein, K. L., and Mueller, T. (2018). "Revisitation analysis uncovers spatio-temporal patterns in animal movement data." In: *Ecography* 41.11, pp. 1801–1811.
- Braendle, C., Davis, G. K., Brisson, J. A., and Stern, D. L. (2006). "Wing dimorphism in aphids." In: *Heredity* 97.3, pp. 192–199.
- Breiman, L. (2001). "Random forests." In: *Machine Learning* 45.1, pp. 5–32.
- Brown, L. M. and Crone, E. E. (2016). "Individual variation changes dispersal distance and area requirements of a checkerspot butterfly." In: *Ecology* 97.1, pp. 106–115.

Burnham, K. P. and Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. New York: Springer-Verlag.

Calenge, C. (2006). “The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals.” In: *Ecological Modelling* 197.3, pp. 516–519.

Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M., eds. (2012). *Dispersal ecology and evolution*. Oxford: Oxford University Press.

Clobert, J., Galliard, J.-F. L., Cote, J., Meylan, S., and Massot, M. (2009). “Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations.” In: *Ecology Letters* 12.3, pp. 197–209.

Coulon, A. et al. (2006). “Dispersal is not female biased in a resource-defence mating ungulate, the European roe deer.” In: *Proceedings of the Royal Society B: Biological Sciences* 273.1584, pp. 341–348.

Coulon, A. et al. (2004). “Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach.” In: *Molecular Ecology* 13.9, pp. 2841–2850.

Couriot, O. et al. (2018). “Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore.” In: *Oecologia* 187.1, pp. 47–60.

Debeffe, L. et al. (2013). “Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer.” In: *Animal Behaviour* 86.1, pp. 143–151.

Debeffe, L. et al. (2012). “Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further.” In: *Journal of Animal Ecology* 81.6, pp. 1327–1327.

Debeffe, L. et al. (2014). “A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic.” In: *Oecologia* 176.2, pp. 431–443.

Doerr, E. D. and Doerr, V. A. J. (2005). “Dispersal range analysis: quantifying individual variation in dispersal behaviour.” In: *Oecologia* 142.1, pp. 1–10.

Ducros, D. et al. (2019). “Data from: Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape.” In: *Dryad*.

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., and Macdonald, D. W. (2014). “Movements vary according to dispersal stage, group size, and rainfall: the case of the African lion.” In: *Ecology* 95.10, pp. 2860–2869.

ESRI, E. S. R. I. (2018). *ArcGIS release 10.6.1*. Redlands, CA.

Fey, K., Hämäläinen, S., and Selonen, V. (2016). “Roads are no barrier for dispersing red squirrels in an urban environment.” In: *Behavioral Ecology* 27.3, pp. 741–747.

- Fronhofer, E. A. et al. (2018). "Bottom-up and top-down control of dispersal across major organismal groups." In: *Nature Ecology & Evolution* 2.12, pp. 1859–1863.
- Gaillard, J.-M. et al. (2008). "Population density and sex do not influence fine-scale natal dispersal in roe deer." In: *Proceedings of the Royal Society B: Biological Sciences* 275.1646, pp. 2025–2030.
- Gibbs, M., Saastamoinen, M., Coulon, A., and Stevens, V. M. (2010). "Organisms on the move: ecology and evolution of dispersal." In: *Biology Letters* 6.2, pp. 146–148.
- Greenwood, P. J. (1980). "Mating systems, philopatry and dispersal in birds and mammals." In: *Animal Behaviour* 28.4, pp. 1140–1162.
- Haughland, D. L. and Larsen, K. W. (2004). "Exploration correlates with settlement: red squirrel dispersal in contrasting habitats." In: *Journal of Animal Ecology* 73.6, pp. 1024–1034.
- Hewison, A. J. M. et al. (2007). "Using radio-tracking and direct observation to estimate roe deer *Capreolus Capreolus* density in a fragmented landscape: a pilot study." In: *Wildlife Biology* 13.3, pp. 313–320.
- Hewison, A. J. M. et al. (2009). "Landscape fragmentation influences winter body mass of roe deer." In: *Ecography* 32.6, pp. 1062–1070.
- Hewison, A., Vincent, J., and Reby, D. (1998). "Social organisation of European roe deer." In: *The European roe deer : The biology of success*. Oslo: Scandinavian University Press, pp. 189–219.
- Hewison, A. M. (1996). "Variation in the fecundity of roe deer in Britain: effects of age and body weight." In: *Acta theriologica* 41.2, pp. 187–198.
- Hogan, J. D., Blum, M. J., Gilliam, J. F., Bickford, N., and McIntyre, P. B. (2014). "Consequences of alternative dispersal strategies in a putatively amphidromous fish." In: *Ecology* 95.9, pp. 2397–2408.
- Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., and Spiegel, O. (2008). "Trends and missing parts in the study of movement ecology." In: *Proceedings of the National Academy of Sciences* 105.49, pp. 19060–19065.
- Jacob, S. et al. (2016). "Cooperation-mediated plasticity in dispersal and colonization." In: *Evolution* 70.10, pp. 2336–2345.
- Kays, R., Crofoot, M. C., Jetz, W., and Wikelski, M. (2015). "Terrestrial animal tracking as an eye on life and planet." In: *Science* 348.6240.
- Kenward, R. E., Rushton, S. P., Perrins, C. M., Macdonald, D. W., and South, A. B. (2002). "From marking to modelling: dispersal study techniques for land vertebrates." In: *Dispersal ecology*. Blackwell Publishing, pp. 50–71.

Lavielle, M. (1999). "Detection of multiple changes in a sequence of dependent variables." In: *Stochastic Processes and their Applications* 83.1, pp. 79–102.

Linnell, J. D. and Andersen, R. (1998). "Territorial fidelity and tenure in roe deer bucks." In: *Acta Theriologica* 43.1, pp. 67–75.

Maag, N. et al. (2019). "Cost of dispersal in a social mammal: body mass loss and increased stress." In: *Proceedings of the Royal Society B: Biological Sciences* 286.1896, p. 20190033.

Martin, J. et al. (2018). "Temporal shifts in landscape connectivity for an ecosystem engineer, the roe deer, across a multiple-use landscape." In: *Landscape Ecology* 33.6, pp. 937–954.

Martorell, C. and Martínez-López, M. (2014). "Informed dispersal in plants: *Heterosperma pinnatum* (Asteraceae) adjusts its dispersal mode to escape from competition and water stress." In: *Oikos* 123.2, pp. 225–231.

Matthysen, E. (2012). "Multicausality of dispersal: a review." In: *Dispersal Ecology and Evolution*. Oxford: Oxford University Press.

Mayer, M., Zedrosser, A., and Rosell, F. (2017). "When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver." In: *Animal Behaviour* 123, pp. 375–382.

Morellet, N., Verheyden, H., Angibault, J.-M., Cargnelutti, B., Lourtet, B., and Hewison, M. A. J. (2009). "The effect of capture on ranging behaviour and activity of the European roe deer *Capreolus capreolus*." In: *Wildlife Biology* 15.3, pp. 278–287.

Morellet, N. et al. (2011). "Landscape composition influences roe deer habitat selection at both home range and landscape scales." In: *Landscape Ecology* 26.7, pp. 999–1010.

Morellet, N. et al. (2013). "Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe." In: *Journal of Animal Ecology* 82.6, pp. 1326–1339.

Mucherino, A., Papajorgji, P. J., and Pardalos, P. M. (2009). "K-nearest neighbor classification." In: *Data Mining in Agriculture*. Ed. by Mucherino, A., Papajorgji, P. J., and Pardalos, P. M. Springer Optimization and Its Applications. New York, NY: Springer, pp. 83–106.

Patin, R., Etienne, M.-P., Lebarbier, E., Chamaillé-Jammes, S., and Benhamou, S. (2020). "Identifying stationary phases in multivariate time series for highlighting behavioural modes and home range settlements." In: *Journal of Animal Ecology* 89.1, pp. 44–56.

Ratcliffe, P. R. and Mayle, B. A. (1992). *Roe deer biology and management*. Forestry Commission.

- Rémy, A., Galliard, J.-F. L., Gundersen, G., Steen, H., and Andreassen, H. P. (2011). "Effects of individual condition and habitat quality on natal dispersal behaviour in a small rodent." In: *Journal of Animal Ecology* 80.5, pp. 929–937.
- Ronce, O. (2007). "How Does It Feel to Be Like a Rolling Stone? Ten Questions About Dispersal Evolution." In: *Annual Review of Ecology, Evolution, and Systematics* 38.1, pp. 231–253.
- Ronce, O. and Clobert, J. (2012). "Dispersal syndromes." In: *Dispersal Ecology and Evolution*. Oxford: Oxford University Press.
- Searcy, C., *, Gilbert, B., Krkošek, M., Rowe, L., and McCauley, S. (2018). "Positive correlation between dispersal and body size in Green Frogs (*Rana clamitans*) naturally colonizing an experimental landscape." In: *Canadian Journal of Zoology* 96.12, pp. 1378–1384.
- Stamps, J. A. (2006). "The silver spoon effect and habitat selection by natal dispersers." In: *Ecology Letters* 9.11, pp. 1179–1185.
- Stamps, J. A., Krishnan, V. V., and Reid, M. L. (2005). "Search costs and habitat selection by dispersers." In: *Ecology* 86.2, pp. 510–518.
- Torrents-Ticó, M., Bennett, N. C., Jarvis, J. U. M., and Zöttl, M. (2018). "Growth affects dispersal success in social mole-rats, but not the duration of philopatry." In: *Biology Letters* 14.2, p. 20180005.
- Van Moorter, B. et al. (2008). "Evidence for exploration behaviour in young roe deer (*Capreolus capreolus*) prior to dispersal." In: *Ethology Ecology & Evolution* 20.1, pp. 1–15.
- VanderWaal, K. L., Mosser, A., and Packer, C. (2009). "Optimal group size, dispersal decisions and postdispersal relationships in female African lions." In: *Animal Behaviour* 77.4, pp. 949–954.
- Vanpé, C. et al. (2009). "Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer." In: *Journal of Mammalogy* 90.3, pp. 661–665.
- Vanpé, C. et al. (2016). "Immune gene variability influences roe deer natal dispersal." In: *Oikos* 125.12, pp. 1790–1801.
- Venables, W. N. and Ripley, B. D. (2002). *Modern applied statistics with S*. 4th ed. Statistics and Computing. New York: Springer-Verlag.
- Wahlström, L. K. and Liberg, O. (1995). "Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*)." In: *Journal of Zoology* 235.3, pp. 455–467.
- Wiens, J. A. (1976). "Population responses to patchy environments." In: *Annual Review of Ecology and Systematics* 7.1, pp. 81–120.
- Worton, B. J. (1989). "Kernel methods for estimating the utilization distribution in home-range studies." In: *Ecology* 70.1, pp. 164–168.

Supplementary Information

I. Spatial fidelity in roe deer

To estimate spatial fidelity in our study population, we quantified the degree of overlap in locations of those individuals for which we had spatial information that covered several years. For individuals that were VHF- or GPS- monitored over at least two years during their lifetime, we measured range overlap using 50% fixed kernels between the post-dispersal range and the adult range, or between two subsequent adult ranges (see Tables S1 and S2) (libraries `adehabitatHR`, Calenge, 2006 and `rgeos`, Bivand and Rundel, 2017). In addition, for those that were monitored only one year, but were subsequently recovered when they died, we compared their location at death to the locations during the monitoring period, using graphs (`plot` function in R) (see Figure SA.1). When location at death or the adult range overlapped with the post-settlement range or the adult range in a previous year, we considered the animal to be faithful to its home range.

Firstly, of the 58 adults that were monitored during two or more years, 54 (~ 93%) were faithful to their core home range. Second, of the 30 juveniles that were monitored by GPS during the post-dispersal phase, 28 (~ 93%) were subsequently located within their settlement range during adulthood.

TABLE SA.1: Overlap between the post-dispersal range and the adult range for 15 individuals monitored both as a juvenile and an adult – Overlap was measured using a 50 % kernel – ID : individual identity ; a value of 0 indicates the ranges did not overlap.

ID	Overlap (%)
378	76.97
412	0
444	80.25
486	31.35
504	73.28
516	85.52
722	59.11
738	99.04
858	79.67
900	7.021
931	35.75
955	66.32
984	30.38
F1213	0.4541
F1347	75.17

TABLE SA.2: Overlap between successive adult annual ranges for GPS-tracked adult roe deer – Overlap was measured using a 50 % kernel – ID : individual identity ; a value of 0 indicates the ranges did not overlap

ID	Overlap (%)
252	99
260	0
426	44.54
328	63.04
504	54.76
746	66.56
806	70.96
820	89.86
542	69.27
818	69.41
F572	84.43
104	0
202	77.31
212	46.06
390	92.23
484	0
572	99.92
672	90.9
7	81.15
778	92.26
838	75.01
916	51.68
932	92.07
968	0
47	84.83

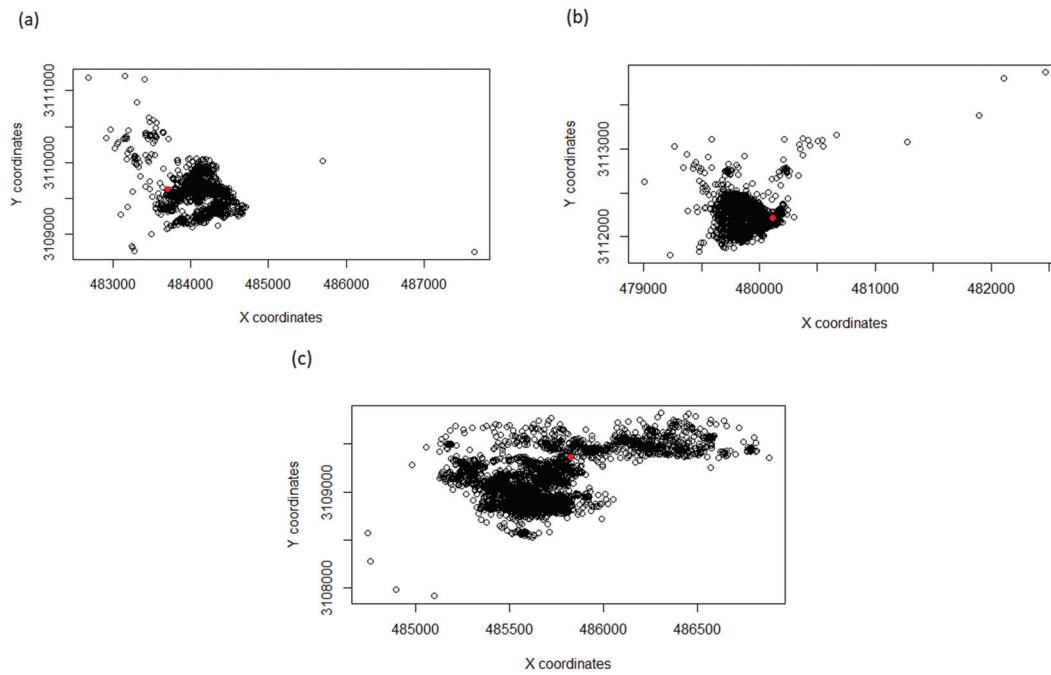


FIGURE SA.1: Examples of overlap between the location at death and locations from GPS devices for three individuals (a, b and c). Individual 'a' died five years after the monitoring period, and individuals 'b' and 'c' died two years after the monitoring period. The location at death is represented by a red point on each figure. All locations at death were clearly within the previous home range.

II. Generalised Linear Models and Multinomial Models to investigate drivers of alternative dispersal tactics

TABLE SA.3: Candidate generalised linear models in a $\Delta AICc$ of 2 describing individual propensity to adopt a progressive dispersal tactic (vs. a classic dispersal tactic) in relation to body mass, sex and landscape structure. We also report the results for the null model. The landscape variable was calculated as the coordinates along the first axis of the PCA performed on the landscape descriptors (availability of crops and meadows, levels of landscape heterogeneity and anthropogenic disturbance). The reference class is classic dispersal and the reference sex is female. Models are ranked by order of increasing AICc; we report the $\Delta AICc$ (difference in AICc values between a given model and the model with the lowest AICc), the number of estimated parameters (df), AICc weights, null and residual deviances, as well as the percentage of deviance explained (ratio).

Model	df	AICc	$\Delta AICc$	AICc Weight	Null deviance	Residual deviance	Ratio
Landscape + sex	3	64.1	0.0	0.35	66.74	57.73	86.50
Landscape	2	65.0	0.9	0.23		60.78	91.07
Landscape + body mass + sex	4	65.2	1.1	0.20		56.48	84.63
Landscape + body mass*sex	5	65.4	1.3	0.18		54.39	81.50
Null model	1	68.8	4.7	0.03		66.74	100

TABLE SA.4: Candidate generalised linear models in a $\Delta AICc$ of 2 describing individual propensity to adopt a multi-range tactic (vs. a classic dispersal tactic) in relation to body mass, sex and landscape structure. We also report the results for the null model. The landscape variable was calculated as the coordinates along the first axis of the PCA performed on the landscape descriptors (availability of crops and meadows, levels of landscape heterogeneity and anthropogenic disturbance). The reference class is classic dispersal and the reference sex is female. Models are ranked by order of increasing AICc; we report the $\Delta AICc$ (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df), AICc weights, null and residual deviances, as well as the percentage of deviance explained (ratio).

Model	df	AICc	$\Delta AICc$	AICc Weight	Null deviance	Residual deviance	Ratio
Landscape + body mass*sex	5	45.1	0.0	0.33	50.06	33.95	67.82
Landscape	2	45.4	0.3	0.23		41.14	82.18
Body mass*sex	4	46.1	1.0	0.20		37.39	74.69
Landscape + body mass	3	46.5	1.4	0.17		40.03	79.96
Null model	1	52.1	7.0	0.01		50.06	100

TABLE SA.5: Candidate generalised linear models in a ΔAICc of 2 describing individual propensity to adopt an aborted dispersal tactic (vs. a classic dispersal tactic) in relation to body mass, sex and landscape structure. We also report the results for the null model. The landscape variable was calculated as the coordinates along the first axis of the PCA performed on the landscape descriptors (availability of crops and meadows, levels of landscape heterogeneity and anthropogenic disturbance). The reference class is classic dispersal and the reference sex is female. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df), AICc weights, null and residual deviances, as well as the percentage of deviance explained (ratio).

Model	df	AICc	ΔAICc	AICc Weight	Null deviance	Residual deviance	Ratio
Landscape	2	48.6	0.0	0.50	50.06	44.41	88.71
Landscape + sex	3	50.1	1.5	0.24		43.69	87.28
Landscape + body mass	3	50.6	2.0	0.1		44.13	88.15
Null model	1	52.1	3.5	0.09		50.06	100

TABLE SA.6: Candidate multinomial models describing individual propensity to adopt one of the four alternative tactics (vs. a classic dispersal tactic) in relation to body mass, sex and landscape structure within a ΔAICc of 10. We also report the results for the null model. Philopatric individuals were combined with explorers. The landscape variable was calculated as the coordinates along the first axis of the PCA performed on the landscape descriptors (availability of crops and meadows, levels of landscape heterogeneity and anthropogenic disturbance). The reference class is classic dispersal and the reference sex is female. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df).

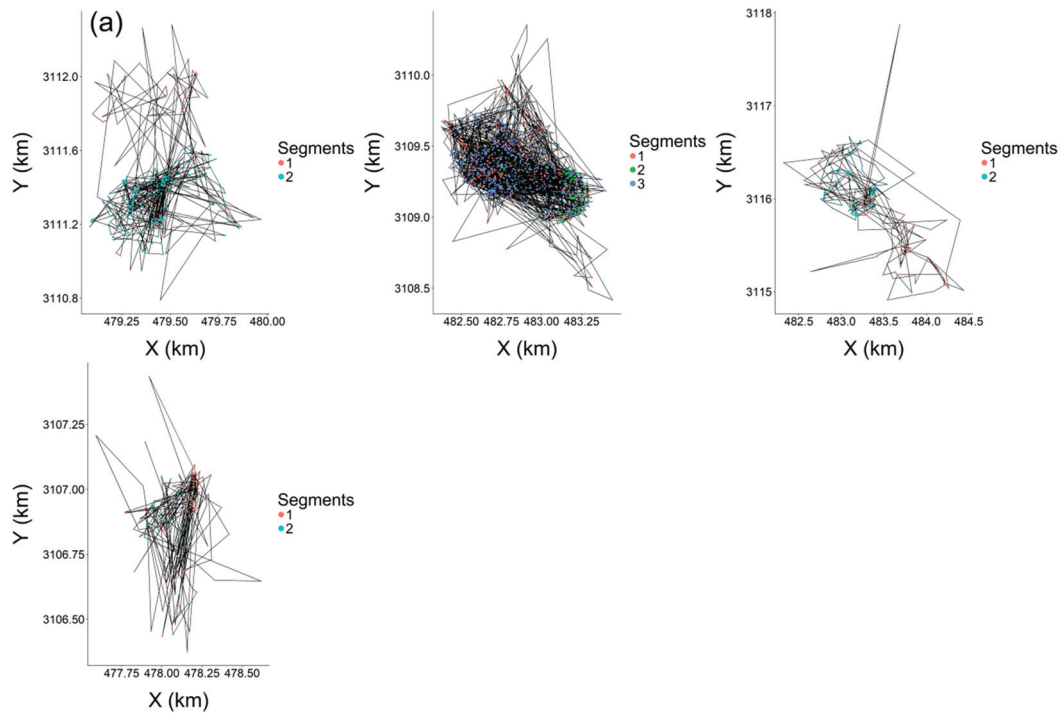
Model	df	AICc	ΔAICc
Landscape	8	374.69	0.0
Landscape + sex	12	380.44	5.7
Landscape + body mass	12	382.13	7.4
Null model	4	386.43	11.7

TABLE SA.7: Summary statistics from the model averaging procedure based on multinomial models discriminating all dispersal tactics (classic dispersers, aborting dispersers, progressive dispersers, multi-rangers and philopatric individuals, i.e. a combination of strict philopatric individuals and explorers) based on landscape, sex and body mass – classic dispersers constitute the reference class and the reference sex is female. Models were run using the function `multinom` from the library (`mgcv`, Wood, 2011). We report estimates, standard errors, null and residual deviances, as well as the percentage of deviance explained (Ratio).

	Coefficients				Null deviance	Residual deviance	Ratio
	Intercept	SE (Intercept)	Landscape	SE (Landscape)			
Progressive dispersers	-1.00	0.33	0.62	0.26	378.15	357.65	94.58
Multi-rangers	-1.52	0.41	0.82	0.27			
Philopatric individuals	0.52	0.24	0.71	0.22			
Aborted dispersers	-1.47	0.40	0.75	0.27			

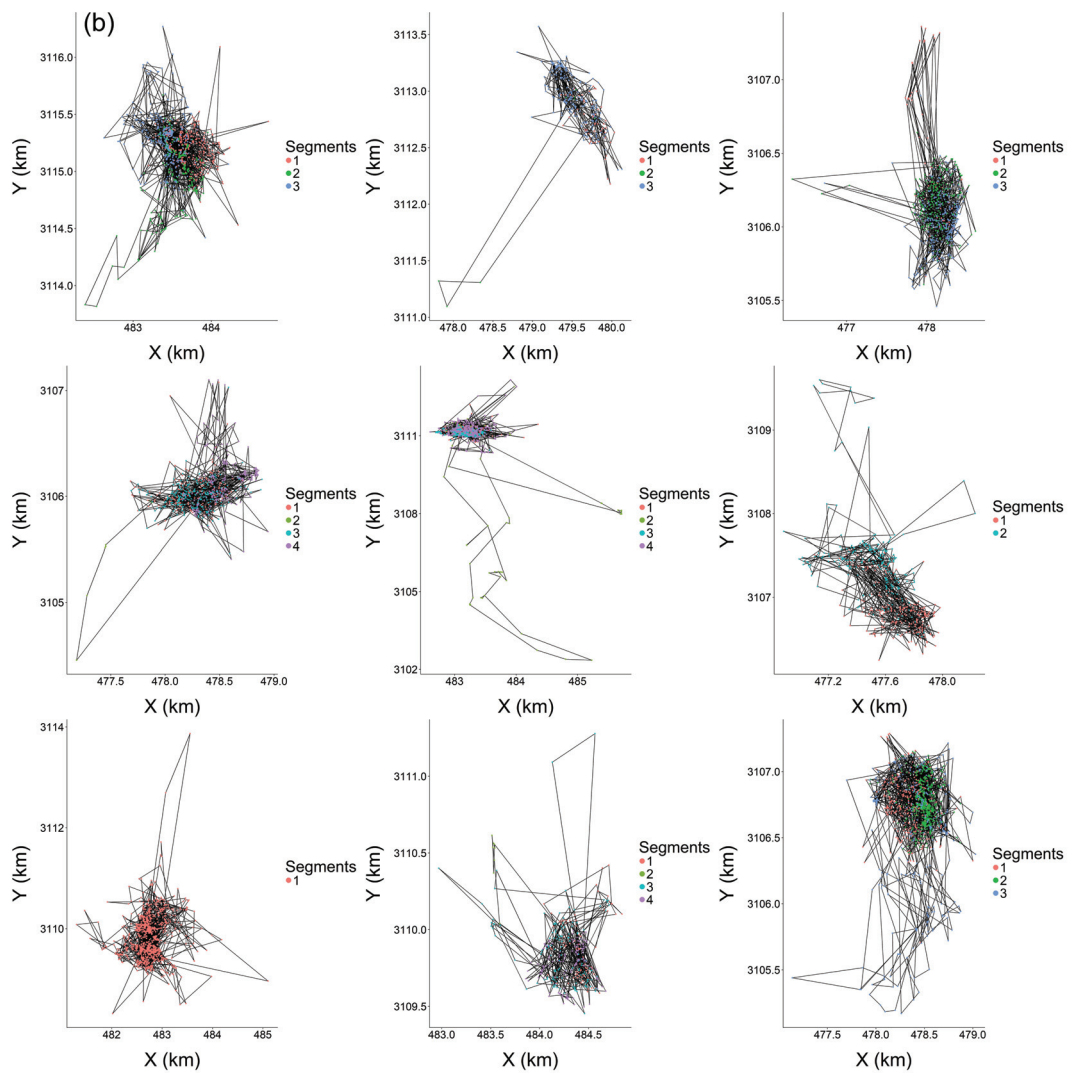
III. Classification results - Descriptive approach

FIGURE SA.2: Additional examples of individual trajectories for each movement tactic exhibited by roe deer, as assigned by our classification: a. Strict philopatric; b. Explorer; c. Aborted disperser; d. Multi-ranger; e. Progressive disperser; f. Classic disperser. Each dot represents a GPS location, and successive locations are linked by a straight line. Successive segments identified by the segmentation approach are coded in different colours and numbered chronologically. X and Y coordinates are expressed in kilometres.



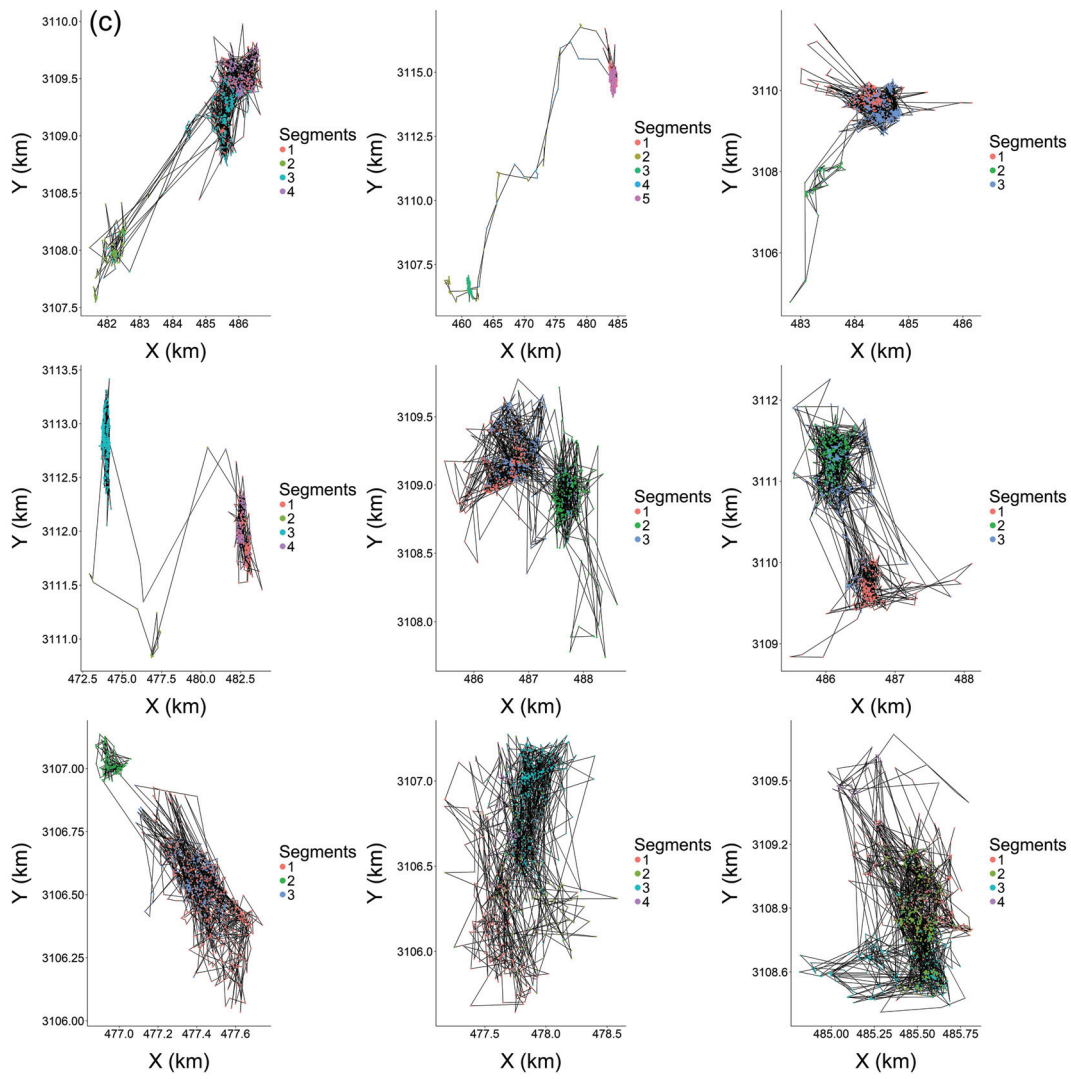
(A) Strict philopatric

FIGURE SA.2: (Continued)



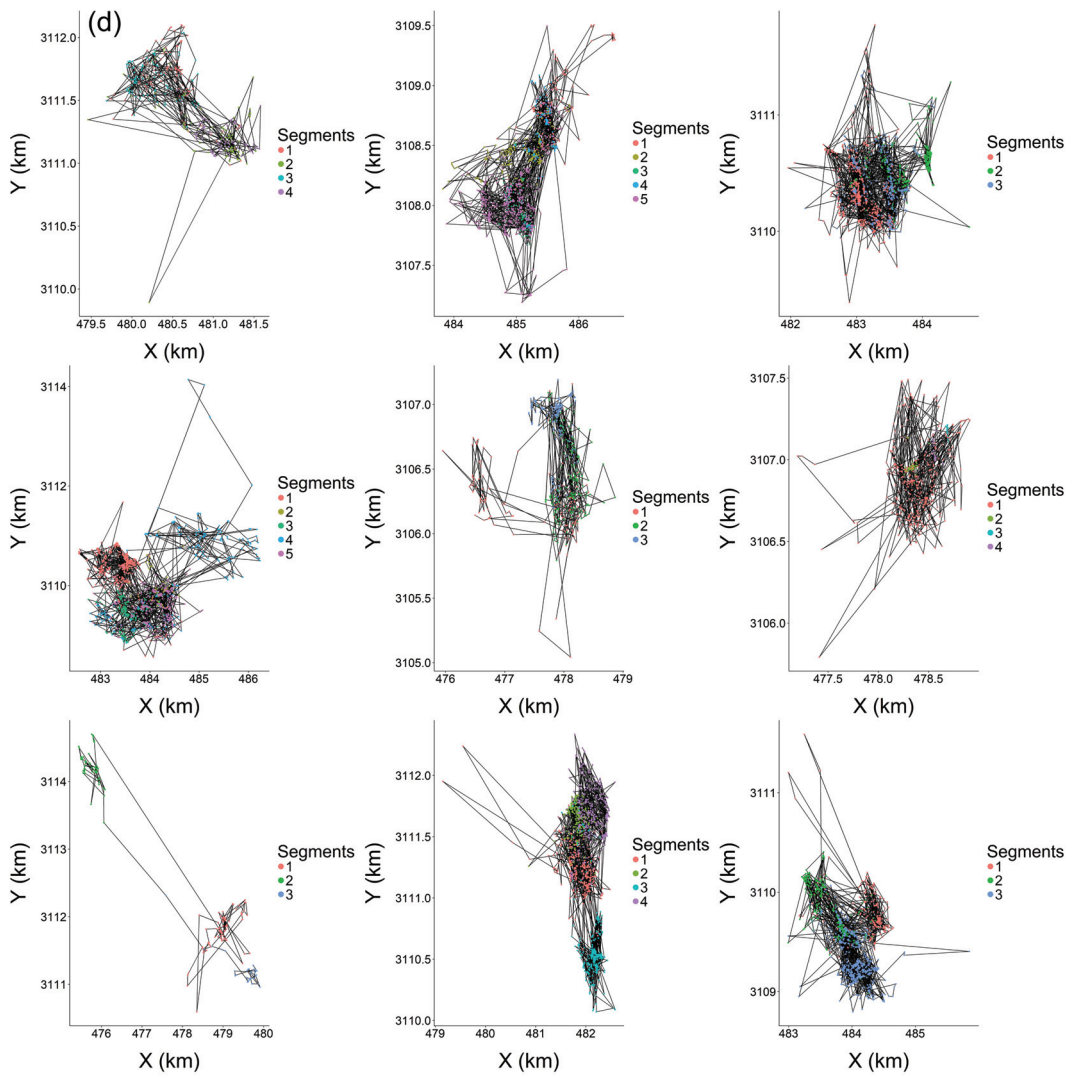
(B) Explorer

FIGURE SA.2: (Continued)



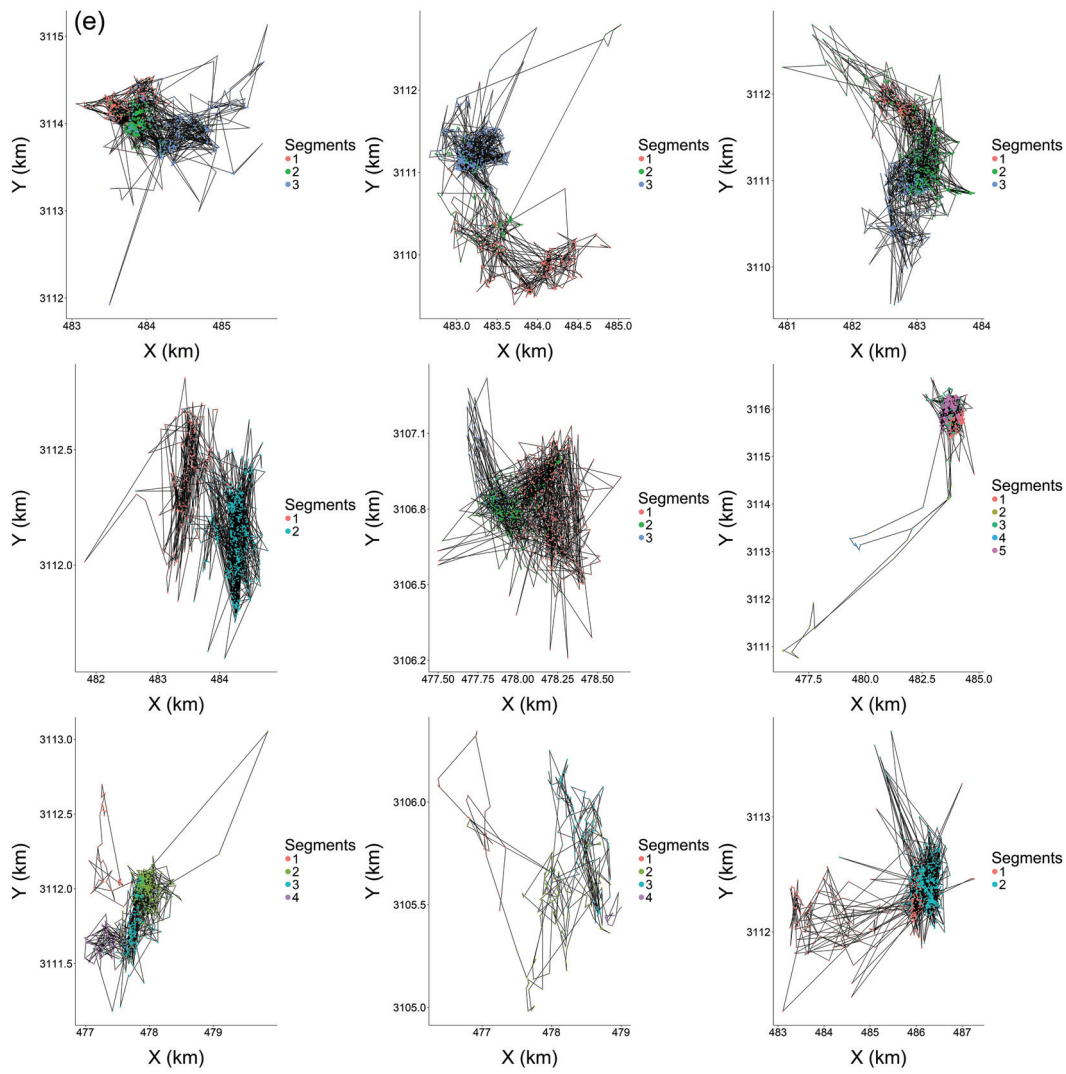
(c) Aborted disperser

FIGURE SA.2: (Continued)



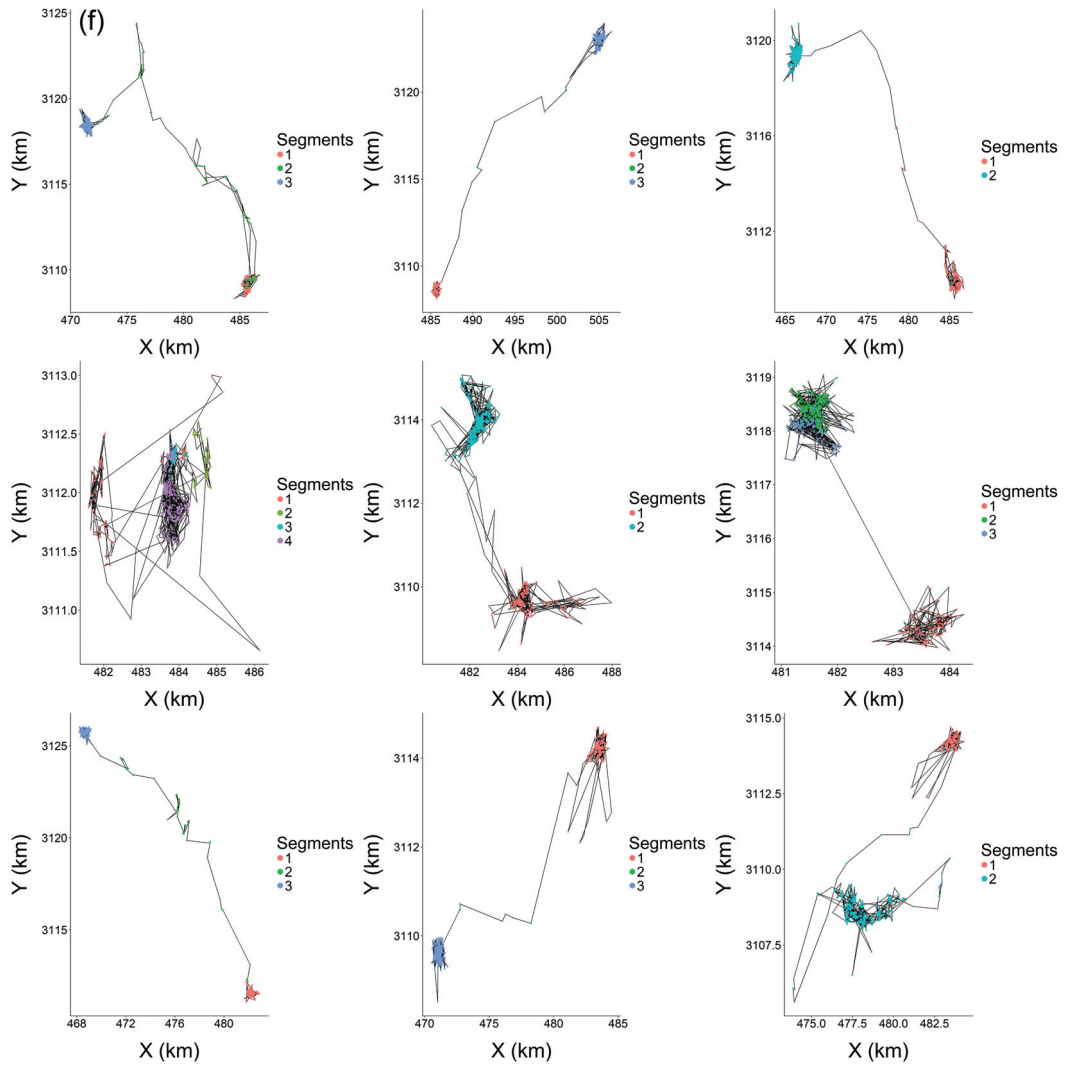
(d) Multi-ranger

FIGURE SA.2: (Continued)



(E) Progressive disperser

FIGURE SA.2: (Continued)



(F) Classic disperser

TABLE SA.8: Mean duration (\pm sd) of segments for each dispersal tactic identified (N classic dispersers = 49; N progressive dispersers = 14; N explorers = 62; N multi-ranger = 9; N strict philopatrics = 4; N aborted dispersers = 9) – N (sample size) is the number of individuals used to calculate the mean durations for each dispersal tactic and segment.

Dispersal tactic	Segment	Mean duration (days)	Standard deviation	N (sample size)
Classic disperser	1	75.7	33.4	49
	2	92.5	92.1	49
	3	134.5	86.9	33
	4	95.8	85.5	5
	5	17.0	NA	1
	6	15.0	NA	1
Progressive disperser	1	76.4	45.4	14
	2	133.1	76.8	14
	3	105.1	75.1	8
	4	13.0	17.3	2
	5	101.0	NA	1
Explorer	1	87.9	49.4	62
	2	60.7	51.4	59
	3	81.5	55.4	50
	4	42.5	32.8	27
	5	70.1	52.3	14
	6	22.0	8.5	2
	7	37.0	NA	1
Multi-ranger	1	71.1	39.4	9
	2	48.2	28.3	9
	3	61.6	50.9	9
	4	45.6	30.8	6
	5	106.5	46.0	3
Strict philopatric	1	66.8	36.3	4
	2	60.5	57.1	4
	3	169.8	NA	1
Aborted disperser	1	79.3	29.6	9
	2	58.0	50.2	9
	3	114.0	40.8	9
	4	33.2	28.6	5
	5	118.0	NA	1

TABLE SA.9: Mean departure date (\pm sd) from each segment for each dispersal tactic identified (N classic dispersers = 49; N progressive dispersers = 14; N explorers = 62; N multi-ranger = 9; N strict philopatrics = 4; N aborted dispersers = 9) – N (sample size) is the number of individuals used to calculate the mean durations for each dispersal tactic and segment.

Dispersal tactic	Departed segment	Mean date	Standard deviation (in days)	N (sample size)
Classic disperser	1	20th April	28.3	49
	2	25th May	57.8	33
	3	8th June	44.5	5
	4	7th November	NA	1
	5	24th November	NA	1
Progressive disperser	1	14th May	76.1	14
	2	25th June	69.6	8
	3	14th July	78.0	2
	4	30th July	NA	1
Explorer	1	2nd May	59.0	59
	2	9th June	66.7	50
	3	15th July	57.7	27
	4	12th August	48.3	14
	5	20th July	16.8	2
	6	6th August	NA	1
Multi-ranger	1	1st April	42.9	9
	2	20th May	56.6	9
	3	4th July	58.3	5
	4	23rd September	8.0	2
Aborted disperser	1	2nd May	25.1	9
	2	29th June	63.5	9
	3	26th September	46.5	5
	4	25th August	NA	1

IV. Environmental variables and their representation in each dispersal tactic

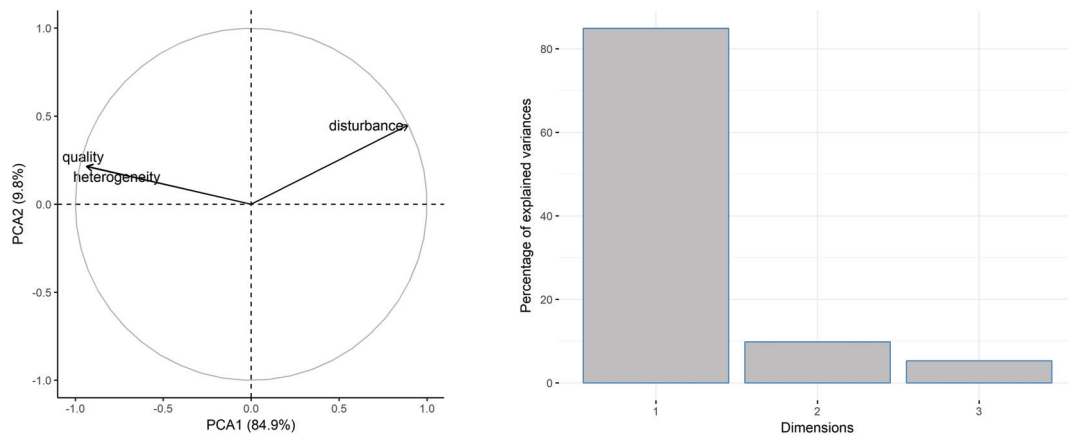


FIGURE SA.3: Plot of the first and second principal components and the proportion of the total variance explained from the PCA of landscape structure in the natal range. The PCA contains three centred and scaled landscape descriptors: nutritional quality indexed as the proportion of crops and meadows in the natal range; level of landscape heterogeneity indexed as the mean Shannon index value in the natal range; and level of human-related disturbance indexed as the mean distance to the nearest anthropogenic feature (road or building) within the natal range (high values of the descriptor 'disturbance' indicate a high distance to roads or buildings).

TABLE SA.10: Principal Component Analysis scores and proportion of variance explained by the three axes of the PCA on landscape characteristics of the natal range for 146 monitored juvenile roe deer.

Variable	Axis 1	Axis 2	Axis 3
Shannon index	34.4	15.5	50.1
Crop and meadow proportion	34.3	15.8	49.9
Distance to nearest anthropogenic feature	31.3	68.7	3.95×10^{-4}
Eigenvalues	2.55	0.29	0.16
Cumulative Explained Variance (%)	84.9	94.7	100

TABLE SA.11: Mean phenotypic and landscape descriptors in the natal range (with their standard deviations) for each behavioural tactic identified during the dispersal phase – Classes: CD: Classic dispersers; PD: Progressive dispersers; E: Explorers; MR: Multi-rangers; P: strict Philopatrics; AD: Aborted dispersers. Descriptors: Bd_mass: body mass; Crop: Proportion of crops and meadows in the natal range; Shannon: mean Shannon index value based on the proportions of different habitat types in the natal range; Anthro_dist: mean distance to the nearest anthropogenic feature in the natal range (road or building); sd_x : standard deviation associated with a given descriptor, x. Female proportion = Proportion of females in a given class.

Class	Bd_mass (bm)	sd_bm	Crop (c)	sd_c	Shannon (s)	sd_s	Anthro_dist (ad)	sd_ad	Female proportion (%)
CD	17.02	1.70	0.90	0.23	1.75	0.31	183.21	71.10	61.20
PD	16.67	2.33	0.75	0.31	1.46	0.44	232.32	97.71	35.70
E	16.28	2.12	0.72	0.36	1.42	0.54	270.03	156.43	51.60
MR	15.56	2.33	0.61	0.37	1.30	0.67	277.14	145.11	44.40
P	14.78	2.13	0.57	0.32	1.45	0.52	237.03	127.10	75.00
AD	16.72	1.96	0.72	0.43	1.39	0.68	287.32	155.96	55.50

V. Assessing the robustness of our classification

To evaluate the relevance of our classification, we conducted an exploratory post hoc analysis of inter- and intra-individual variation in movement behaviour across tactics using continuous-time stochastic movement models (CTSMM, see Calabrese, Fleming, and Gurarie, 2016). The objective was to assess whether individuals were consistent in their spatial behaviour over time within and across tactics. First, using the *ctmm* package developed by Calabrese, Fleming, and Gurarie (2016), we fitted Ornstein-Uhlenbeck models to individual monthly tracks and extracted three movement parameters: τ_p measures the position autocorrelation time and is interpreted as the home range crossing time (or the inverse of the attraction force) and D is a diffusion coefficient representing the rate of increase of the mean squared displacement over time. σ^2 measures the movement variance (scaling to home range size, see Calabrese, Fleming, and Gurarie, 2016 for more details) and is estimated using the values of τ_p and D through the following formula:

$$\sigma^2 = \frac{D^2 \tau_p}{2}$$

Then, to evaluate the degree to which individuals were consistent in their spatial behaviour over time for a given tactic, we estimated individual repeatability of these parameters for each of the dispersal tactics (package *rptR* in R – Stoffel, Nakagawa, and Schielzeth, 2017). The repeatability models included month as a fixed effect as well as the identity of the individual as a random effect on the intercept in order to measure the adjusted individual repeatability (Stoffel, Nakagawa, and Schielzeth, 2017). Movement behaviour was significantly repeatable for most of the 15 parameter-tactic (5 tactics \times 3 parameters) combinations (12 out of 15), with repeatability values that ranged from 0.10 to 0.56 (Table SA.12). Although these repeatability values are moderate, averaging around 0.3, they are consistent with previous estimates for repeatability of movement and, more generally, most behavioural traits (Bell, Hankison, and Laskowski, 2009; Garamszegi et al., 2009; Hertel et al., 2019). Note that temporal repeatability was much lower for classic dispersers (0.02 to 0.10) due to the short-lived and abrupt modification of movement behaviour during long-range dispersal transience. These results, hence, indicate that, for a given tactic, individuals are consistent in their movement behaviour over time.

Second, we assessed whether our classification reliably discriminated between alternative dispersal tactics by evaluating inter- and intra-tactic variation in these three movement parameters. For each individual monthly track, we computed a measure of heterogeneity for each parameter. In other words, we wanted to see if there was any consistency in among-tactic differences of each parameter across the monitored months. We used a *z-value* measure for this purpose by applying the following formula:

$$z.mvtpar = \frac{(\max(mvtpar) - \text{mean}(mvtpar))}{sd(mvtpar)}$$

(where *mvtpar* is τ_p , σ^2 or D , $\max(mvtpar)$ is the maximum value of the parameter reached during the individual monthly track, $\text{mean}(mvtpar)$ is the mean value of

the parameter across the same track and $sd(mvtpar)$ is the standard deviation of the parameter across the track). Hence, a low $z.mvtpar$ means that there is no significant fluctuation (or peaks) in parameter values (homogeneity) across the monitored months, and a high $z.mvtpar$ means that there are some high fluctuations of values (heterogeneity). We then tested whether these z – values were repeatable within a given tactic. Repeatability models contained the assigned tactic as a random effect and considered individuals as repetitions (package rptR in R – Stoffel, Nakagawa, and Schielzeth, 2017). We found moderate but significant values of repeatability for σ^2 and τ_p (0.24 ± 0.13 , $p < 0.0001$ and 0.36 ± 0.16 , $p < 0.0001$ respectively), but not for D (0 ± 0.024 , $p = 1$). Indeed, D represents the mean squared displacement which does not encompass any notion of home range, but rather is based on distance travelled and hence likely poorly discriminates between alternative dispersal tactics (several alternative tactics had very similar straight line distances between the initial and final segment centroids – see Results section). On the contrary, τ_p and σ^2 are related to home range size and stability, and thus might better reflect behavioural changes in space use. Thus, according to these statistics, the tactics we identified appear moderately robust (with respect to two mechanistic movement parameters) and individuals are classified into ecologically meaningful groups.

TABLE SA.12: Repeatability models for each class and each movement parameter (τ_p , σ^2 and D). Strictly philopatric individuals and explorers were pooled in these analyses. Each model includes month as a fixed effect as well as the identity of the individual as a random effect on the intercept. Repeatability values above 0.2 are highlighted in bold.

Dispersal tactic	Parameter	R±SE	p-value
Classic dispersers	τ_p	0.03±0.026	$p = 0.11$
	σ^2	0.02±0.025	$p = 0.248$
	D	0.10±0.037	$p = 0.000663$
Explorers	τ_p	0.17±0.036	$p = 4.06e-09$
	σ^2	0.32±0.057	$p = 5.12e-25$
	D	0.14±0.038	$p = 6.05e-07$
Progressive dispersers	τ_p	0.23±0.096	$p = 0.000485$
	σ^2	0.35±0.1	$p = 8.04e-08$
	D	0.29±0.09	$p = 2.12e-05$
Multi-rangers	τ_p	0.33±0.155	$p = 0.00445$
	σ^2	0.56±0.162	$p = 4.18e-07$
	D	0.25±0.136	$p = 0.00911$
Aborted dispersers	τ_p	0.04±0.054	$p = 0.335$
	σ^2	0.13±0.107	$p = 0.0421$
	D	0.27±0.118	$p = 0.000552$

References in Supplementary Information

- Bell, A. M., Hankison, S. J., and Laskowski, K. L. (2009). "The repeatability of behaviour: a meta-analysis." In: *Animal Behaviour* 77.4, pp. 771–783.
- Bivand, R. and Rundel, C. (2017). *rgeos: interface to geometry engine - Open Source ('GEOS')*.
- Calabrese, J. M., Fleming, C. H., and Gurarie, E. (2016). "ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process." In: *Methods in Ecology and Evolution* 7.9, pp. 1124–1132.
- Calenge, C. (2006). "The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals." In: *Ecological Modelling* 197.3, pp. 516–519.
- Garamszegi, L. Z. et al. (2009). "Changing philosophies and tools for statistical inferences in behavioral ecology." In: *Behavioral Ecology* 20.6, pp. 1363–1375.
- Hertel, A. G., Leclerc, M., Warren, D., Pelletier, F., Zedrosser, A., and Mueller, T. (2019). "Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife." In: *Animal Behaviour* 147, pp. 91–104.
- Stoffel, M. A., Nakagawa, S., and Schielzeth, H. (2017). "rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models." In: *Methods in Ecology and Evolution* 8.11, 1639–1644.
- Wood, S. N. (2011). "Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models." In: *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73.1, pp. 3–36.

