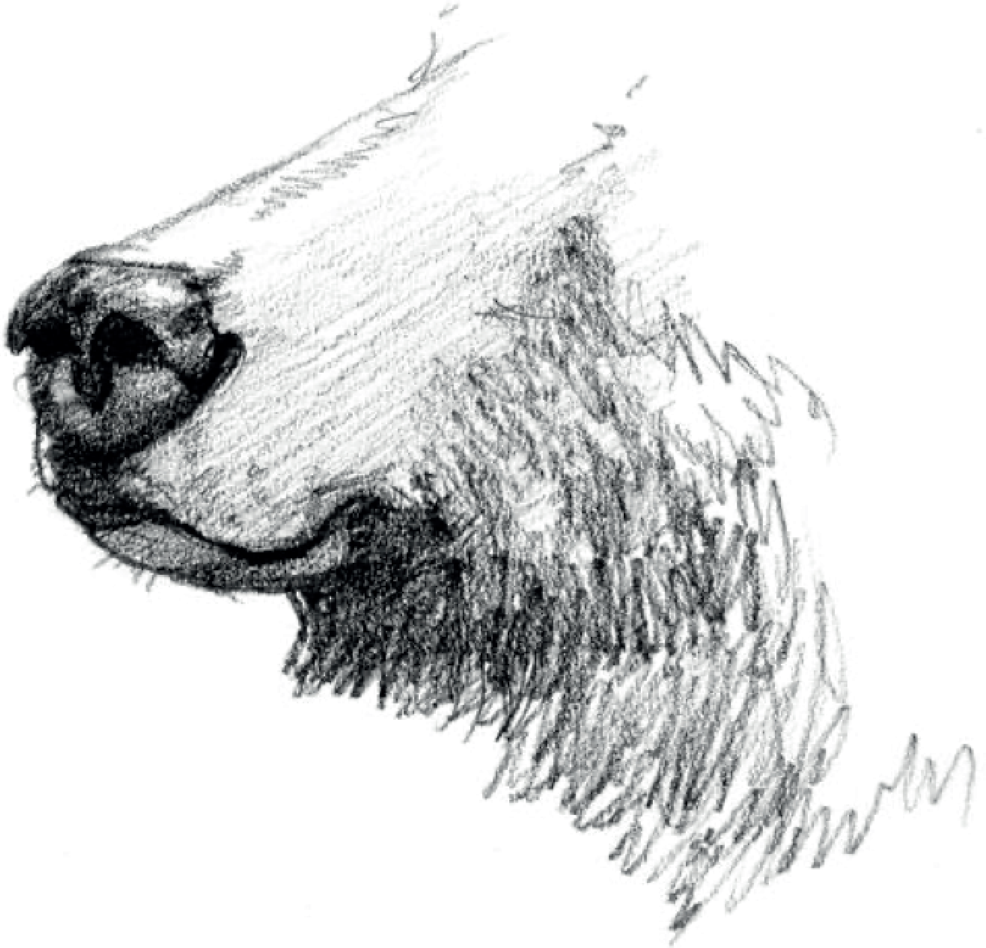
LIÈGE université
Gembloux
Agro-Bio Tech

Factors affecting brown bears *(Ursus arctos)* movement behaviour

Cindy Lamamy



COMMUNAUTÉ FRANÇAISE DE BELGIQUE
UNIVERSITÉ DE LIÈGE – GEMBLOUX AGRO-BIO TECH

Factors affecting brown bears *(Ursus arctos)* movement behaviour

Cindy LAMAMY

Dissertation originale présentée en vue de l'obtention du grade de docteur en sciences agronomiques et ingénierie biologique.

Promoteurs : Cédric VERMEULEN et Vincenzo PENTERIANI
Année civile : 2024

Copyright

This work was supported from by the Project bearMOVE (PID2020-114181GB-I00) and the Excellence Project (CGL2017-82782) financed by the Spanish Ministry of Science and Innovation, the Agencia Estatal de Investigacion (AEI) and the Fondo Europeo de Desarrollo Regional (FEDER, EU).

It also benefitted from a GRUPIN research grant from the Regional Government of Asturias (Ref.: IDI/2018/000151) and from the CSIC/mncn (Consejo Superior de Investigaciones Científicas/ Museo Nacional de Ciencias Naturales).

MINISTERIO
DE CIENCIA
E INNOVACIÓN

AGENCIA
ESTATAL DE
INVESTIGACIÓN

Unión Europea
Fondo Europeo
de Desarrollo Regional
“Una manera de hacer Europa”

GOBIERNO DEL
PRINCIPADO DE ASTURIAS

CSIC
CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS

mncn
museonacionaldecienciasnaturales

Abstract

Most living beings move throughout their lives to meet all their needs and maximize their survival and the survival of their species. These movements take place on highly contrasting spatio-temporal scales, from the foraging of butterflies to the spectacular migration of Arctic terns *(Sterna paradisaea)*. One of the major challenges of this thesis is to better understand the relationships between physiology and movement, which are often governed by the environment in which individuals evolve. We have attempted to assess the main components of movement dynamics in the brown bear (*Ursus arctos)* population of Finland and Russian Karelia. These individuals are subject to external environmental factors, a combination of biotic and abiotic factors, as well as their physiological state, or internal state. We used the movement ecology paradigm of Nathan et al. (2008) to analyze the components that influence movement patterns within the home range, or during dispersal for subadults, for example. The factors behind movement can be multiple, such as the concentration of food for feeding-related movements, the search for a partner for reproductive movements, or escape from a predator (in this case, human). This thesis uses telemetry data to analyze the movements of brown bears in their home ranges.

The brown bear is an interesting case study for two reasons. Firstly, although it has all the physical characteristics of a large carnivore (sharp canines, claws and a carnivorous digestive tract), it is an opportunistic omnivore. Their travel patterns and the study of their movements therefore merit attention. Secondly, brown bears can be extremely flexible in their primary diurnal activity patterns. They can be diurnal as well as crepuscular or nocturnal, depending on the conditions of their environment. In other words, habitat resources, human pressure and population density.

In this thesis, we focused on three themes that may impact on movement patterns. Firstly, we studied the behavior of this facultative carnivore through the prism of moonlight (variation in light intensity), **(chapter 2)**. Indeed, when the moon is full, many strict carnivores such as cheetahs and ocelots see their hunting success increase. Their activity rates therefore increase with light intensity. Brown bears have a fruit-rich diet and, consequently, the prey-predator relationships that drive carnivore dependence on moonlight appear to be weaker than in obligate carnivores.

Secondly, we studied feeding-related movements, and in particular movements in the vicinity of artificial feeding sites **(chapter 3)**. This practice is frequently used for species conservation, to regulate human-wildlife conflicts or for tourism (ecotourism or hunting).

Finally, we investigated age-related differences in movement behavior and, more specifically, potential inter- and intra-individual variations between adult and subadult bears **(chapter 4)**. The contribution of age to movement patterns seems irrelevant, as most observed movement patterns are mainly explained by season and body weight. We hypothesize that two mechanisms may lead subadults and adults to move in similar ways. Firstly, both need to hibernate and therefore need to store energy du-

ring hyperphagia. Secondly, although triggered by different factors, they both make erratic/long movements after hibernation, for dispersal (subadults) or mating (adults), which could help shape similar movement patterns. Different motivations could therefore be expressed by the same behavioral patterns, and equifinality (i.e. similarity of behavior) could be reinforced.

More generally, this study demonstrates the relevance of an ecophysiological approach to the study of movement.

Chapter 5 closes the thesis with a general discussion of the factors influencing brown bear movements.

Résumé

Une grande majorité des êtres vivants se déplacent au cours de leur vie pour rencontrer tous leurs besoins afin de maximiser leur survie et la pérennité de l'espèce. Ces déplacements se font à des échelles spatio-temporelles très contrastées, du butinage des papillons à la migration spectaculaire des sternes arctiques *(Sterna paradisaea)*. L'un des grands défis de cette thèse est de mieux comprendre les relations entre physiologie et déplacements qui sont souvent gouvernés par l'environnement dans lequel évoluent les individus. Nous avons essayé d'évaluer les principales composantes de la dynamique de mouvement de la population d'ours bruns *(Ursus arctos)* de Finlande et de Carélie russe. Ces individus sont soumis à des facteurs environnementaux extérieurs, une combinaison de facteurs biotiques et abiotiques, ainsi qu'à leur état physiologique, ou état interne. Nous nous sommes basés sur le paradigme de l'écologie du mouvement de Nathan et al. (2008) pour analyser les composantes qui influent sur les schémas de déplacements au sein du domaine vital ou lors de leur dispersion pour les subadultes par exemple. Les facteurs à l'origine du mouvement peuvent être multiples, comme la concentration en nourriture en ce qui concerne les mouvements liés à l'alimentation, la recherche d'un partenaire pour les mouvements liés à la reproduction ou encore pour échapper à un prédateur (ici l'homme). Cette thèse s'appuie sur des données de télémétrie pour analyser les mouvements des ours bruns dans leur domaine vital.

L'ours brun est un cas d'étude intéressant pour deux raisons. Bien qu'il présente toutes les caractéristiques physiques d'un grand carnivore (des canines pointues, des griffes et un tube digestif de carnivore), c'est un omnivore opportuniste. Son schéma de déplacements et l'étude de ses mouvements méritent donc de s'y attarder. L'ours brun peut se montrer extrêmement flexible dans son patron d'activité diurne primaire. L'activité diurne est très variable. En fonction du milieu/ de l'habitat, l'ours peut passer d'une activité diurne importante à une activité plutôt crépusculaire ou nocturne. La référence pour dire si un animal est diurne ou nocture, c'est la quantité d'activité diurne qui sert de témoin. C'est-à-dire les ressources présentes dans l'habitat, la pression humaine ou encore la densité de la population.

Dans cette thèse, nous nous sommes focalisés sur trois thématiques qui peuvent impacter les schémas de déplacement. Premièrement, nous avons étudié le comportement de ce carnivore facultatif à travers le prisme du clair de lune (variation de l'intensité lumineuse), **(chapitre 2)**. En effet, à la pleine lune, de nombreux carnivores stricts comme le guépard ou l'ocelot voient leurs succès de chasse augmenter. Les taux d'activité de ces derniers augmentent donc avec l'intensité lumineuse. Les ours bruns ont un régime alimentaire riche en fruits et, par conséquent, les relations proie-prédateur qui sont à l'origine de la dépendance des carnivores au clair de lune semblent être plus faibles chez l'ours que chez les carnivores obligatoires. En d'autres termes, l'ours est peu sensible aux cycles lunaires.

Dans un deuxième temps, nous avons étudié les mouvements liés à l'alimentation et surtout les déplacements aux abords de sites de nourrissage artificiel **(chapitre 3)**. Cette pratique est fréquemment utilisée pour la conservation des espèces, la régulation des conflits Homme-faune ou encore pour le tourisme (écotourisme ou chasse).

Enfin, nous avons testé les différences de comportement de déplacement liées à l'âge et, plus spécifiquement, les variations inter- et intra-individuelles potentielles entre les ours adultes et les ours subadultes **(chapitre 4)**. La contribution de l'âge aux schémas de déplacement ne semble pas pertinente, la plupart des schémas de déplacement observés étant principalement expliqués par la saison et le poids corporel. Nous émettons l'hypothèse que deux mécanismes peuvent conduire les subadultes et les adultes à se déplacer de manière similaire. Tout d'abord, les deux doivent hiberner et, par conséquent, doivent stocker de l'énergie pendant l'hyperphagie. Deuxièmement, bien que déclenchés par des facteurs différents, ils effectuent tous deux des mouvements erratiques/longs après l'hibernation, pour la dispersion (subadultes) ou l'accouplement (adultes), ce qui pourrait contribuer à façonner des schémas de déplacement similaires. Des motivations différentes pourraient donc être exprimées par les mêmes schémas comportementaux, et l'équifinalité (c.-à-d. la similitude des comportements) pourrait s'en trouver renforcée.

Plus généralement, cette étude démontre la pertinence d'une approche d'écophysiologie pour l'étude des mouvements.

Le **chapitre 5** clôt la thèse par une discussion générale portant sur les facteurs influençant les déplacements de l'ours brun.

Remerciements

Une aventure s’achève et voici venue l’heure de remercier les personnes qui m’ont accompagnée et soutenue dans la réalisation de ma thèse de doctorat. Ces dernières années ont été riches en doutes, joies et rencontres. La thèse est pour moi aussi bien un accomplissement professionnel que personnel et je souhaiterais remercier toutes les personnes qui m’ont permis de mener cette thèse à terme.

Je tiens tout d’abord à remercier mes deux promoteurs, **Cédric Vermeulen et Vincenzo Penteriani**, sans qui rien n’aurait été possible. Ils m’ont fait confiance et m’ont encouragée à me lancer dans l’aventure.

Vincenzo, tu m’as fait découvrir le monde un peu obscur de la recherche. J’ai adoré nos « brainstormings » à l’UMIB qui permettent aux jeunes d’échanger librement sur les sujets de recherches en cours. Ton soutien et tes conseils tout au long de ces années m’ont permis d’évoluer et de développer mon esprit critique. Par ailleurs, tu sais nous rappeler qu’une thèse n’est pas que des analyses statistiques et qu’il est bon de sortir sur le terrain. Tu as su me communiquer ton amour pour l’ours brun et me transmettre qu’il était bon de prendre du temps pour observer votre « objet » de recherche. Merci d’encadrer tes étudiants comme des pairs en qui tu as confiance. Merci d’avoir su me sortir de mon ordinateur et de m’avoir rappelé qu’une thèse c’était aussi une belle aventure.

Cédric, un peu perdue après une année de confinement, tu as su être rassurant et m’a convaincue de l’intérêt d’une thèse au vu du travail déjà effectué. Je te remercie pour tout le soutien que tu m’as apporté et de toujours faire passer l’humain en priorité. Tu as été à l’écoute et très conciliant avec ma « double vie » qui a souvent retardé les échéances que l’on se fixait. Tu as été un vrai pilier et mon repère pour continuer d’avancer quand la motivation n’était plus forcément au rendez-vous.

María Del Mar Delgado, although you’re not listed as my promoter, you’re just like the same to me. You’re a person worth knowing. You were the person I took the longest to appreciate, but today, as you put it so well, we’re family. Statistics are just a pretext for exchanging ideas and catching up on our lives. You made me «whirl» my brain with all the R codes, but today I’m really grateful to you. Now I’m looking forward to an expedition to the mountains to radio-tag some snowfinches.

A big thanks to **Ilpo Kojola** and his team who collected the data I worked on. I thank you for your trust and help.

Je tiens également à remercier l’ensemble du comité **(Cédric Vermeulen, Vincenzo Penteriani, María Del Mar Delgado, Philippe Lejeune et Alain Liccope)** qui a suivi mon parcours. Nos échanges annuels ont fait évoluer la thèse et lui ont donné un rythme. Une pensée particulière à **Hugues Claessens** qui m’a offert mon premier job dans les vieux murs de Gembloux et m’a orientée vers Cédric pour la thèse. Merci à **Alain** et **Jean-Yves** pour leur aide dans les démarches administratives.

J’ai rencontré de très belles personnes qui ont apporté de la gaieté dans le quotidien de la thèse. En Espagne ou en Belgique, je remercie les doctorants, post-docs et collègues pour les pauses café, les sorties extra-pro, les conseils et autres : **Alejandra, Carlotta, Chiara, Daniele, Giulia, Jo, Justine, Marie-Pierre, Enrique, Riccardo, Sergey, Simon**. Merci aussi à mes collègues de travail, passés et actuels, qui m’ont encouragée à poursuivre mes efforts malgré un emploi du temps très chargé entre un poste d’ingénieur à plein temps, une vie de maman et de doctorante. Je pense tout particulièrement à **Pauline, Franck, Julien et Pascal.**

Une thèse en « alternance » demande à nos proches une certaine flexibilité comme accepter que des congés se terminent en rédaction de thèse… Mes parents m’ont toujours encouragée à suivre mes rêves. Ils ont été les premiers à croire que je pouvais réussir et on peut dire que mes études n’ont pas été un long fleuve tranquille comme peut en attester **Hugues Claessens** avec mes 75 crédits en BAC2. Je souhaite également remercier ma sœur, **Natasha Bourdette**, actuellement en école d’art qui a réalisé mes illustrations de chapitres ainsi que **Cécile Coulet-Quélin** qui m’a soutenue et aidée dans la mise en page de ce manuscrit.

Dorian, mes derniers remerciements te reviennent.

Merci d’être un papa en or qui m’épaule au quotidien même quand tu es absent. Tu sais trouver les mots pour que je garde le cap et mes objectifs en tête.
Merci d’avoir été à l’écoute lors des moments de doutes et pour tes nombreux encouragements.

Table of content

Chapter 1 : General introduction 1

1 An over view of the situation 3

1.1 Context of the situation 3

1.2 Consequences of the Human Footprint on the wildlife 4

1.3 A brief highlight on the movement ecology paradigm 5

1.4 A focus on the case of bears 8

2 Development and objectives of the thesis 10

2.1 The study area 10

2.2 A brief history of brown bear in Finland 12

2.3 Data collection 14

2.4 Structure of the thesis 15

Chapter 2 : Brown bears do not mind that the moon exists 17

Preamble 19

1 Introduction 21

2 Materials and methods 23

2.1 Study area 23

2.2 Data collection 24

2.3 Movement patterns 25

2.4 Moon phases 25

2.5 Internal and external factors 27

2.6 Statistical analyses 27

3 Results 29

4 Discussion 33

Chapter 3 : Human's impact 39
Preamble 41
1 Introduction 43
2 Materials and methods 45
2.1 Study area 45
2.2 Data collection bear capture and artificial feeding sites 47
2.3 Variable extraction 48
2.4 Statistical analyses 48
3 Results 50
3.1 Probability and intensity of use of artificial feeding sites 50
3.2 The use of artificial feeding sites influences movement patterns 56
4 Discussion 58

Chapter 4 : Movement patterns of subadult bears during the dispersal process 63
Preamble 65
1 Introduction 67
2 Methods 68
2.1 Data collection 68
2.2 Ethical Note 71
2.3 Statistical Analyses 71
3 Results 72
4. Discussion 76

Chapter 5 : General conclusion 79
1 Main results 82
2 Ethical note 87
3 Management and conservational measures 88

Conclusion 90

List of publications 91

References 93

List of figures

Chapter 1: General introduction

Figure 1.1 Estimated total number of protected area visits for each country. Totals (which are transformed into log10) were obtained by applying the appropriate regional GLM to all terrestrial protected areas in a country (excluding those under 10 ha, marine areas and IUCN category I protected areas). Asterisks indicate countries for which observations on visit rates are available. Figure extracted from (Balmford et al. 2015), Source: https://doi.org/10.1371/journal.pbio.1002074.g001 **4**

Figure 1.2 Relationship between the movement capacity of various species and their access to the resource from the local to the landscape scale, adapted from Smith et al. (2014) **6**

Figure 1.3 Components of the movement ecology framework. Drivers of movement (A): an animal is pushed to move because of its physiological state and by its close environment. Regulation of movement (B): the trajectory followed by an individual is influenced by a complex interaction between the physiological state and proximate external cues, as well as by the motion and the navigation capacity. Adapted from Nathan et al. (2008) **7**

Figure 1.4 Evolution of the number of active artificial feeding sites (blue line is private feeding sites, green line is feeding sites for tourism purposes and black dots are feeding sites used for research) between 1978 and 2015s – unpublished data from I.Kojola (Luke – Natural Resources Institute Finland). **11**

Figure 1.5 Bear distribution over Europe (a) and the expansion of the Karelian brown bear population between 2002, 2015 and 2019 (b, c and d). Adapted from the European Commission (Kaczensky et al. 2021) and from Riistahavainnot (http://riistahavainnot.fi/suurpedot/suurpetotutkimus/havaintokartat, Luke, Finland). **13**

Chapter 2 : Brown bears do not mind that the moon exists

Figure 2.1 Distribution of GPS locations of 42 brown bear males (n = 15 subadults, black movement paths) and 29 females (n = 12 subadults, grey movement paths) spread across south-eastern Finland and Russian Karelia (2002—2014). **23**

Figure 2.2 Moon phase estimated effect (smoothed grey lines) on daily home range, daily speed, turning angle, daily distance and net distance as estimated by linear mixed models for total and net distances, and generalized linear mixed models for speed and turning angle (with Gamma distribution as a link function and Poisson distribution, respectively) **(Table 1)**. The moon cycle is represented by a continuous transition from 0 to 2π radians; that is, 0 and 2π radians correspond to the full moon and π radians are the new moon. In order to represent the entire lunar cycle, the fraction of the moon disc illuminated expressed in radians was introduced as an explanatory variable in the statistical model in the form of cos(θ), sin(θ), cos(2θ)and sin(2θ), which corresponds to 1 to 6 in the x-labels. (Brown bear picture: V. Penteriani). **32**

Chapter 3 : Human’s impact

Figure 3.1. Distribution of GPS locations (2002—2015) of 42 brown bear males (green), 24 females (orange) and artificial feeding sites (red diamonds) across south-eastern Finland and Russian Karelia. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.) **46**

Figure 3.2. All bear classes, i.e. adults, subadults and females with cubs, visited the feeding sites with the same crepuscular and nocturnal patterns, with visits during the day being rare (brown bear picture: V. Penteriani). **54**

Figure 3.3. Spatial overlaps of the different classes of radio-collared bears (n = 71 individuals) at feeding sites. Radio-collared females with cubs and adult males do not overlap. Light blue triangles represent feeding sites. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.) **55**

Figure 3.4. Effects of the intensity of use of artificial feeding sites on daily net distance, speed and home range sizes. **57**

Chapter 4 : Movement patterns of subadult bears during the dispersal process

Figure 4.1. Adult (blue bars) versus subadult (orange bars) brown bear daily movement behaviours (Nsubadults ¼ 2275 localizations, Nadults ¼ 2560 localizations): (a) speed (m/s); (b) mean net distance (m); (c) total distance (m); and (d) home range size (km2). The edges of the box plots represent the interquartile range (IQR), the internal line is the median, the whiskers are the maximum (third quartile þ 1.5IQR) and the minimum (first quartile - 1.5xIQR) and the circles are outliers. For each movement parameter interindividual repeatability values (R), standard errors (SE), 95% confidence intervals (CI) and statistical significance of repeatability (P) are given. The icons were downloaded from 123RF royaltyfree stock photos, http://www.123rf.com; speed: ID 89448738 vastard; mean net distance and total distance: ID36170731 Dejan Jovanovic; home range size: ID24965219 Khoon Lay Gan. **75**

Figure 4.2. Different animal motivations may engender similar movement patterns which can lead to equifinality. In this summarized representation, from den exit after hibernation to den entry in order to hibernate, the main subadult and adult brown bear behaviours are shown: subadult dispersal and adult mating, which overlap temporally, and hyperphagia, which both adult and subadult bears experience. Long-distance movements occur during the subadults' explorations of new areas in which to settle (dispersal) and the mating period when adult bears search for mates. This is an example of equifinalistic behaviour, i.e. similar ecological patterns emerge from different initial conditions, which is represented here by the need for long displacements determined by both subadult dispersal and adult mating. See text for further details. Photo credit: V. Penteriani. **78**

Chapter 5 : General conclusion

Figure 5.1. Schematic overview of thesis' results, chapter by chapter. **81**

Figure 5.2. The illuminated fraction of the moon is transformed into radians to differentiate between waning and waxing moons. **83**

Figure 5.3 : Movement – Management framework adapted from (Allen and Singh 2016) for incorporating movement ecology into decision-making processes. First, the framework concerns the type of movement (dispersal, established individuals…). The second step is to identify ecosystem impacts that will drive the decision-making process and determine potential management actions (in space and time). Next, managers take into account the implementation of the proposed actions and their effectiveness. The result is a cyclical process of adaptive management in which the results of the assessment guide management objectives and future actions. **86**

List of tables

Chapter 1 : General introduction

Table 1.1 Comparison of home range sizers (km^2) between brown bear population extracted from (Kojola et al. 2021) **14**

Chapter 2 : Brown bears do not mind that the moon exists

Table 2.1 Values of AICc, ΔAICc and Weighted AICc of the best (ΔAICc < 2) linear mixed or generalized linear models (see text for more details), summary of the null model considered for each movement parameter and the analysis of variance (ANOVA with R2c (i.e. conditional R squared)) showing that the moon did not affect brown bear movement patterns. **30**

Table 2.2 Values (mean ± SD, range) of movement parameters across moon phases **31**

Chapter 3 : Human's impact

Table 3.1. Model-averaged coefficients, AICc, ΔAICc, weighted AICc and RIV values for the probability (at yearly, seasonal and daily scales) and intensity (at yearly and seasonal scales) of use of artificial feeding sites against age and sex, and characteristics of the feeding sites (i.e. number of active feeding sites: Nfeed_site; and time (i.e. years) the feeding sites were active: Time_open), depending on the model. Competitive models are ordered from the highest to the lowest AICc value (best model). Panels A–C are graphical examples of some variables influencing the probability and intensity of use of feeding sites. **51**

Chapter 4 : Movement patterns of subadult bears during the dispersal process

Table 4.1. Characteristics of daily movement patterns of subadult (13 males and 9 females) and adult (25 males and 10 females) brown bears. **70**

Table 4.2. Model selection table and model-averaged coefficients for movement patterns of subadult (13 males and 9 females) and adult (25 males and 10 females) brown bears. **73**

List of supplementary materials

Chapter 2 : Brown bears do not mind that the moon exists

Supplementary Material 1 : Distribution of days over the period and the lunar cycle. **35**

Supplementary Material 2
Values of AICc, ΔAICc and Weighted AICc of all the models built for the five movement parameters where internal and external factors were analysed. **37**

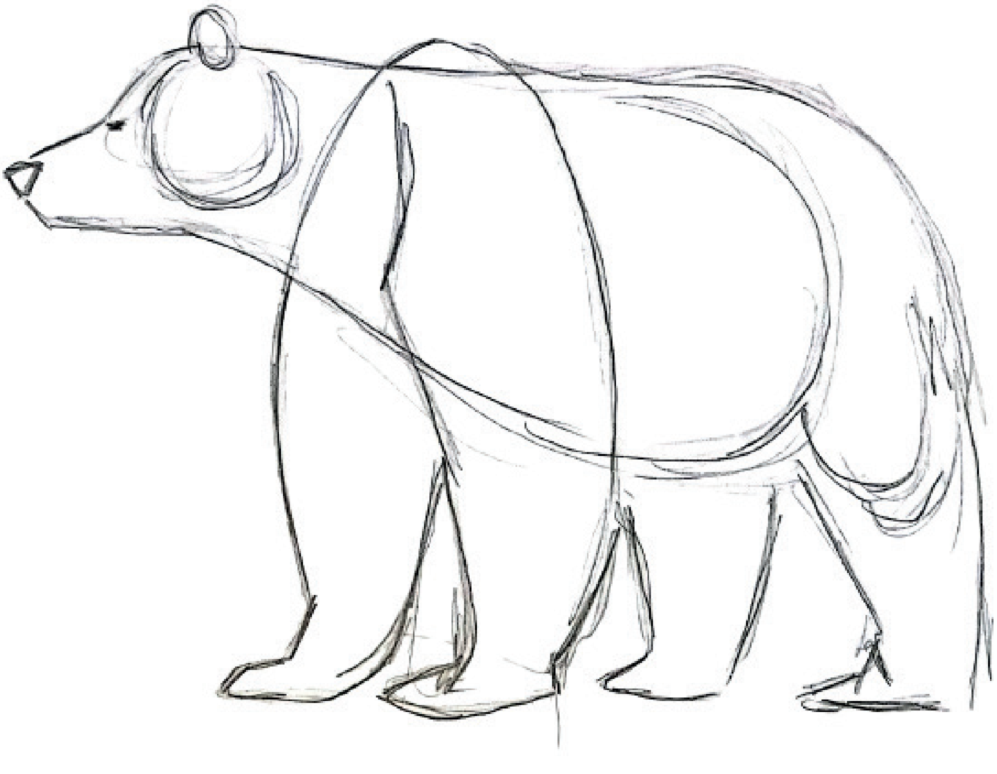
Supplementary Material 3
Values of the variance and standard deviation of all the models built for the five movement parameters where internal and external factors were analysed. **38**

Abbreviations

AICc: Akaike information criterion
ANOVA: ANalysis Of VAriance
CI: Confidence Interval
ID: IDentity of individuals
IUCN: International Union for the Conservation of Nature (IUCN)
GLM: General Linear Model
GLMM: Generalized Linear Mixed Models
GPS: Global Positioning System
HR: Home Range
LoCoH: LOcal COnvex Hull nonparametric kernel method
LMM: Linear Mixed Model
MAFF: Ministry of Agriculture and Forestry
MCP: Minimum Convex Polygon
P: Statistical significance of repeatability
PDOP: Positional Dilution of Precision
RIV: Relative importance value
R2c: conditional R squared
SD: Standard Deviation
SE: Standard Error
VHF: Very High Frequency

1

General introduction



1 An over view of the situation

1.1 Context of the situation

The pressure exerted by humans on natural systems is diverse and one of the main causes of the decline in biological diversity (Barnosky et al. 2011). Human societies have been modifying the Earth's biosphere for at least 12,000 years (Ellis et al. 2021). Successive extinctions of late Quaternary megafauna and the expansion of humans in many parts of the world seem to suggest a much earlier influence (Koch and Barnosky 2006; Prates and Perez 2021). The history of the Earth and that of the human species have now converged. This collision of two histories marks a break in the relationship between humans and the Earth. For the first time, its inhabitants have become the main drivers of the changes that affect it. A new geological epoch in which humans have become the central actor, the Anthropocene, has begun (Steffen et al. 2007; McKenzie et al. 2009). Indeed, the scientists who theorise about this concept consider that the footprint that the human species has left on the planet would be such that it would result in a significant geological influence on the environment, the biosphere and the Earth system as a whole. Human activities - intensive agriculture, deforestation, energy, industries, transport, etc. - have caused a breakdown in the natural balance (Chu and Karr 2017) and a large-scale extinction of biodiversity, especially of plant and animal species on land and in the oceans. These abrupt changes are associated with major factors of decline: deforestation, overfishing, pollution, climate change, and the introduction of invasive species. This epoch characterises the increasing extent and intensity of human activities, which have already profoundly altered the functioning of the Earth system and are responsible for most contemporary environmental changes. Both the distribution of animals and their abundance have been largely influenced by humans over the centuries (Ehrlén and Morris 2015; Cepic et al. 2022). Indeed, human activities have a substantial impact on the environment, from climate change and habitat destruction to leisure activities in natural habitats that have the potential to have a high impact on wildlife (Dubois and Fraser 2013). Species are now facing what is commonly called the human footprint (Wong and Candolin 2015). The concept of the human footprint refers to obvious changes in natural ecosystems, such as landscape fragmentation and climate change, that have an immediate impact on animal species. Over the past 500 years, species are disappearing at an alarming rate. The International Union for Conservation of Nature (IUCN) reports the extinction of about 900 species (www.iucnredlist.org) and more than 500 vertebrate species are on the immediate brink of extinction, i.e., less than 1,000 individuals recorded in the wild (Ceballos et al. 2020, **figure 1.1**). The rate of species extinction could be 100 times higher than in previous mass extinctions - and even then, only those species we know about are included. Our planet's oceans and forests hide an unknown number of species, most of which will be gone before we even hear about them. The picture is likely to be much more critical as the IUCN estimate only covers 5.6% of the global diversity of animals and plants (estimated at ~2.14 million species) (Cowie et al. 2022).

In response to human pressure, animals often show a change in behaviour. Human activities can shape animal movement strategies and can have serious and unexpected consequences for wildlife. While some behavioural responses can be beneficial, others can disrupt benchmarks and thus lead to a decrease in survival, reproductive success and fitness (Rodewald et al. 2011).

1.2 Consequences of the Human Footprint on the wildlife

Enjoyments of nature and leisure activities, such as wildlife watching and hunting, are recognised as the most important ecosystem service (McGinlay et al. 2018). Leisure activities including ecotourism and hunting of charismatic species are rapidly growing as a commercial activity and are currently considered one of the world's largest industries (Blangy and Mehta 2006; Knight 2009). However, there is not yet a good understanding of the magnitude of the impact of leisure activity on targeted species (Balmford et al. 2015). For example, in Europe, the number of annual visits to protected areas has been estimated at 3.8 billion **(figure 1.1)**.

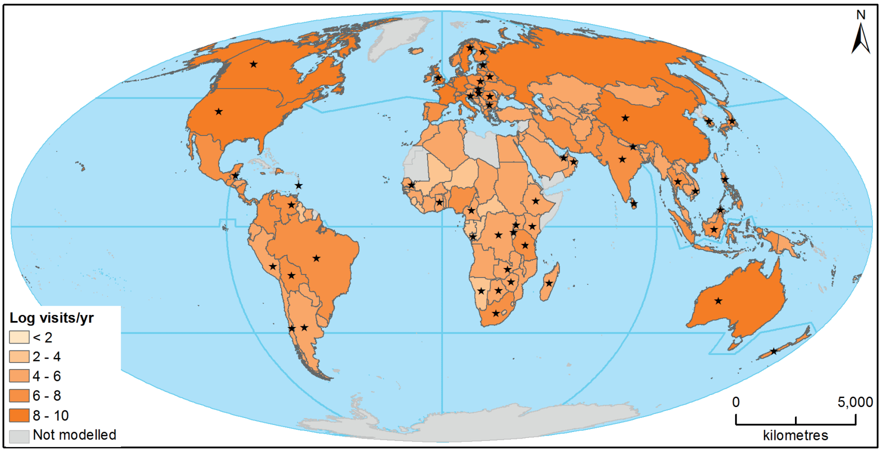


Figure 1.1 Estimated total number of protected area visits for each country. Totals (which are transformed into log10) were obtained by applying the appropriate regional GLM to all terrestrial protected areas in a country (excluding those under 10 ha, marine areas and IUCN category I protected areas). Asterisks indicate countries for which observations on visit rates are available. Figure extracted from (Balmford et al. 2015),
Source: https://doi.org/10.1371/journal.pbio.1002074.g001

In an increasingly urbanised world, where opportunities to be in contact with nature are diminishing, the need to reconnect with nature is increasing. As a result, roads and hiking trails have multiplied in wildlife territory in many countries adding further pressure (Kays et al. 2017). In addition, there is a growing demand from people to interact with wild animals. In particular, unusual, charismatic and/or endangered animals are targeted (Shackley 1996). The observation of wildlife for recreational purposes, as well as hunting them for sport, has recently increased in many European countries (Yost and Wright 2001; Sweanor et al. 2008). As a direct consequence of the growing trend towards seeking direct interactions with wildlife, the establishment of artificial feeding points is commonly used in several European countries (Finland among them). This is used as a strategy to promote both tourism and hunting. More fundamentally, there are still only a small number of comprehensive sources that consider the impacts of feeding wildlife (Orams 2002; Kojola and Heikkinen 2012; Dubois and Fraser 2013). However, the available literature shows that wildlife feeding may produce significant problems, e.g. alteration of natural behaviour patterns, dependency on artificial food and human habituation, an increase of aggressive behaviours towards humans, as well as health problems and increase in conspecific injury rates. As a result, a scientific evaluation of the effects of artificial feeding on wildlife is crucial for species protection and management (Dubois and Fraser 2013; Penteriani et al. 2017).

1.3 A brief highlight on the movement ecology paradigm

Movement of an organism is defined as a change in the spatial location of the individual over time, which is driven by processes that act on multiple spatial and temporal scales (Nathan et al. 2008; Hansson and Åkesson 2014). It is a fundamental characteristic of life because it allows to find food, a partner to mate or to escape predators. Movement mechanisms are diverse according to the species from few meters to several thousand kilometres (Figure 1.3), e.g. the seasonal migration of the Sooty shearwater Ardenna grisea (Cooper et al. 1991) or the Arctic terns *Sterna paradise* (Egevang et al. 2010). Movement mechanisms can be study among others thanks to GPS data collection. Data collection allow us to find where the animal was and its activities. One of the main ecological themes related to GPS data is the spatio-temporal dynamics of home ranges (Kie et al. 2010). A home range is related to the concept of an animal's area where its vital resources are provided (e.g., food, cover or bedding sites). So it is the probability of encountering an animal in a given location given the available data (Kie et al. 2010). An associated concept is the utilization distribution (probability of finding an animal in a defined area within the home range), (Powell 2000; Demšar et al. 2015). Construct the smallest convex polygon around the data is the simplest way of calculating the home range. But this method overestimates the range (Burgman and Fox 2003). Home range estimation methods are various and depend on the data collection (LoCoH, Brownian Bridge, Line based kernel; Powell 2000; Boyle et al. 2008). Therefore, animal mobility is very heterogeneous and allow to access the heterogeneity of the environment they can perceive at various scales (from local to landscape context, **Figure 1.2**).

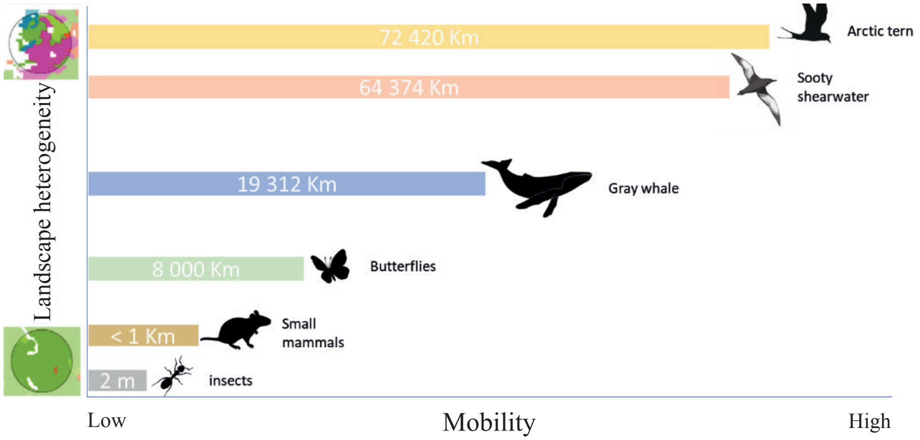


Figure 1.2 Relationship between the movement capacity of various species and their access to the resource from the local to the landscape scale, adapted from Smith et al. (2014)

Over the years, thanks to the development of telemetry technologies (from VHF to GPS technology), we have the possibility to explore spatio-temporal patterns. We can look for various patterns such as patterns within individuals or groups over time or between individuals or groups. Most of the time, we are searching for routines in movement data like reproduction patterns or migration behaviour. Finally, animal movement correspond to behavioural responses. GPS technology allows classification of behaviour such as search of prey, escaping predators, and foraging (Nathan et al. 2012; Shamoun-Baranes et al. 2012; de Weerd et al. 2015). Different types of behaviour are generally extracted from trajectories. The speed parameter extracted from trajectories is crucial to classify behaviour types (Teimouri et al. 2018). Movement is often linked to environmental context. Movement drivers are often motivated by fundamental life-history requirements or intrinsic needs (Scott-Phillips et al., 2011; Shaw, 2016), such as energy (foraging) acquisition, reproduction, predator avoidance and maintenance within physiological optima (Shaw, 2016). However, these needs on their own are not sufficient to explain intraspecific variability and the existence of multiple movement strategies within a species. Indeed, different movement strategies are used to satisfy the same need. Consequently, animal movement also appears to be context-dependent (Bradley et al., 2019; Humphries et al., 2010). The animal's navigation and mobility capabilities determine how an individual will move in response to external factors and internal states (Figure 1.4) (Nathan et al. 2008). It is well-known that a large number of intrinsic factors may affect animal movements. Animals continuously make decisions on how, when and where to move to find suitable areas to meet their vital requirements (Estes et al. 1982; Nathan et al. 2008; Van Moorter et al. 2013). However, animal movements can also be affected by other factors, set of biotic and abiotic environmental factors, such as the availability of food and shelter, landscape structure, weather conditions, and anthropogenic activities (Martin et al. 2008, 2013; Nathan et al. 2008). Therefore, movement data can be complemented by environmental parameters. This mechanistic vision of animal movement lays the foundation for the movement ecology paradigm, which makes it possible to analyze the spatial behavior of all moving animals (Nathan et al. 2008).

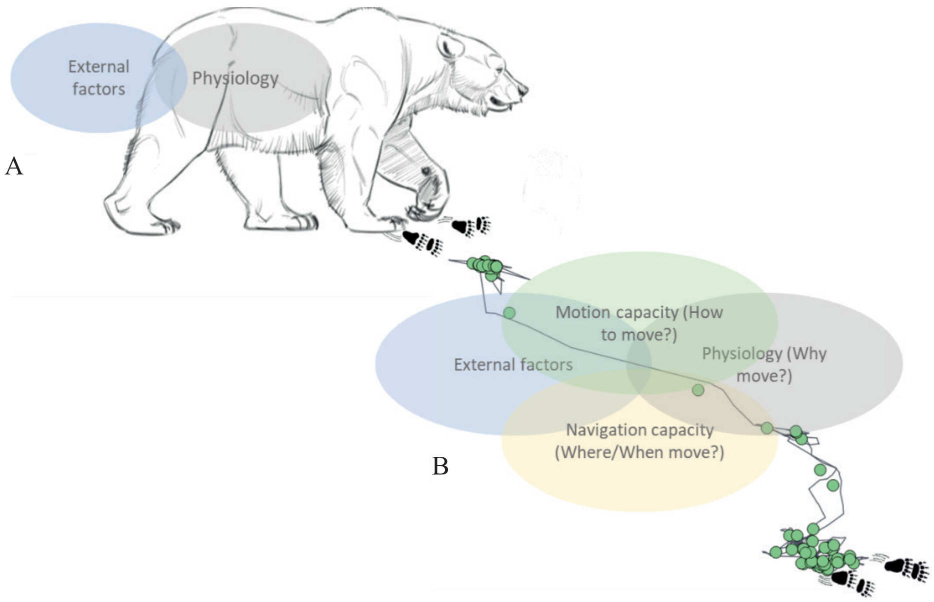


Figure 1.3 Components of the movement ecology framework. Drivers of movement (A): an animal is pushed to move because of its physiological state and by its close environment. Regulation of movement (B): the trajectory followed by an individual is influenced by a complex interaction between the physiological state and proximate external cues, as well as by the motion and the navigation capacity.

Adapted from Nathan et al. (2008)

1.4 A focus on the case of bears

Wildlife movements are usually dependent on different parameters such as photoperiod (Nielsen 1984), temperature (Seryodkin et al. 2013; Pigeon et al. 2016; Delgado et al. 2018), food availability (Heurich et al. 2014), inter- and intraspecific interactions (Monterroso et al. 2013), as well as predation risk. Wildlife, and in particular mammals, usually concentrate their movements at dusk, dawn, and during the night to avoid humans. Large carnivores, such as brown bears *Ursus arctos*, often show great flexibility in their diurnal movements throughout their range depending on human population density. Furthermore, the movement pattern may vary within the population and by reproductive class, suggesting a temporal sharing of niches between the different reproductive classes. In a human-dominated landscape, the probability of encounters with wildlife increases considerably (Gaynor et al., 2018; Zarzo-Arias et al., 2018). Therefore, for obvious reasons, many animals shift their movements to times when human activity is low (Brook et al., 2012; Gaynor et al., 2018; Ordiz et al., 2014). For carnivores, there is a significant shift in diurnal activity towards the dark and crepuscular hours of the day as a response to the local increase of human density (Gaynor et al., 2018; Wu et al., 2018), which can be considered a consequence of anthropogenic stress (Seryodkin et al., 2013).

In Europe, the landscape is dominated by humans and brown bears have to deal with anthropogenic habitat encroachment (Chapron et al., 2014; Swenson et al., 1999; Zedrosser et al., 2001). The yearly movements of brown bears are driven by their life cycle, namely mating, hyperphagia and winter hibernation (Swenson et al., 2000). In addition, intraspecific interactions shape bear behaviour, leading to variation between different reproductive classes (Kaczensky et al., 2006; Lewis & Rachlow, 2011). During the mating season, which usually takes place in late spring or early summer, the movements of bears may vary according to social class and age. Adults are mainly motivated by reproductive behaviour, i.e., finding a mate to reproduce (Dahle & Swenson, 2003; Steyaert et al., 2012). Adult females with cubs try to avoid adult males to reduce the risk of infanticide (Steyaert et al., 2013, 2014; Swenson et al., 2003). Subadults tend to modify their behaviour to avoid potential conflicts with adult males roaming for mates during natal dispersal (Zedrosser et al., 2007). During the hyperphagic season (late summer and autumn), the movements of all breeding classes are mainly motivated by foraging to increase body fat in preparation for winter hibernation. However, how brown bears at different life stages move (daily distance, tortuosity of the path…) during those two seasons remains little documented. Although natural food supplies are often widely dispersed (Hertel, Steyaert, et al., 2016), artificial feeding sites can provide high-caloric, aggregated food sources, which have the potential to alter the movement patterns of bears (Kavčič et al., 2013; Selva et al., 2017; Ziegltrum & Nolte, 1997). However, the impact of artificial feeding on brown bear movements remains largely unknown. In addition to seasonality (reproduction, hyperphagia and hibernation) and circadian rhythms (danger avoidance, hunting success), bear movements and rhythms of activity might also be influenced by lunar cycles. Although seasonal and circadian rhythms have been fairly well described, little is known about the effects of the lunar cycle on the behaviour and physiology of bears. Therefore, sustainable bear conservation and management must take into account the natural movement patterns of bears as well as behavioural responses to human disturbance (Hertel et al., 2017; Tuomainen & Candolin, 2011; Zarzo-Arias et al., 2018.

The brown bear is one of the most targeted species by ecotourism and hunting in Europe and North America (DeBruyn et al. 2004; Penteriani et al. 2017). European brown bears are distributed currently into 10 populations that vary widely in size. Given the large variability in population size (from less than 100 individuals in the French Pyrenees to over 1 000 individuals in Slovakia or Romania for instance), (Figure 1.1), it is not surprising that management regimes vary widely. While the small remanent populations in western Europe are under strict protection, brown bears are a game species in large populations in Eastern or Northern Europe. Over the past several years, Europe has a booming tourism industry that encourages bear watching, as well as hunting to manage the population or for trophies (Linnell et al. 2002). The increasing human encroachment on the bear habitat has contributed significantly to the escalation of conflicts between humans and bears. Human presence shapes the behaviour of bears and therefore their movement strategies. The habituation process is very complex and can vary from one population to another (Majić Skrbinšek and Krofel 2014). The use of artificial feeding sites is a common practice in tourism at the Finnish-Russian border (Kojola and Heikkinen 2012; Penteriani et al. 2017), where about 4,000 visitors come to watch bears every year. Bear feeding sites are also used here for hunting practices. Specific potential negative side-effects of brown bear feeding for hunting purposes include: (a) disruption of denning behaviour and movement strategies; (b) changes in reproductive behaviour and reproductive success; (c) increased population density above the local carrying capacity; (d) natural sex ratio alteration of populations; (e) possible exposure to bio-accumulative contaminants in supplemental food; (f) increased intra- and inter-specific aggressive encounters; (g) changes to the network of scavengers; and (h) reduced ecosystem services, such as seed dispersal (Kavčič et al. 2015). Alternatively, and particularly in brown bears, supplementary feeding may allow males to have access to a larger number of females, as they may overlap into similar area. The population fertility rate could thus remain high and hunting could be sustainable at a higher quota level (Knott et al. 2014). However, in general, the impact of hunting on wildlife has been most pronounced in relation to aspects such as species management, specific removal of sex and age classes of individuals, the percentage of the population allocated to commercial trophy hunting, hunting effects on wild populations and resource selection, both targeted species and predators of game species, biological sustainability of the quotas, the economic sustainability of the hunting organisations and behavioural effects of hunting (Bischof et al. 2008; Ordiz et al. 2012; Gosselin et al. 2014; Knott et al. 2014). As a result, little is known about the side effects of hunting activities on brown bear behaviours and rhythms of activity. In particular, there is a lack of scientific knowledge on the effects of bait hunting on bear behaviour (Jerina et al. 2012). Moreover, hunting may force bears to be more vigilant and can influence habitat distribution and use even more than natural predators affect the behaviour of prey (McCarthy and Fletcher 2015).

2 Development and objectives of the thesis

Studying the mechanisms that shape the brown bear movement strategies at the individual level forms the general framework of this thesis. The work will be mainly aimed to understand patterns of movements, rhythms of activity and the reasons behind them in the Karelian population of brown bears via telemetry. The three main topics that I explored during my thesis are:

1. Influence of external (e.g., moon phases, bear seasons –mating and hyperphagia) and internal (e.g., age, sex, body condition) factors on animal movements;
2. Potential effects of artificial feeding (for both hunting and bear viewing purposes) on behaviour;
3. Age constraints (e.g., juvenile dispersal vs. mating) on movement ecology, i.e. movement patters of subadult vs. adult individuals;

I expect that the results of this thesis will improve our understanding of large carnivore movement strategies, which is crucial for species conservation and management, as well as to reduce human-wildlife conflicts and develop scientifically informed policies.

2.1 The study area

The study area covered most of the southern and central Finland and also involved a part of Russian Karelia, and ranged from 61.69°N to 66.56°N. About 86% of the land area is covered by productive boreal forests. The study area is also characterized by the presence of lakes and peat bogs. The topography is relatively smooth and lies at an altitude of 100 to 576 m above sea level (from our data). Finland and Russian Karelia have a predominantly subarctic climate with a mean annual temperature of 4-5°C to 0-1°C from the south to the north of the study area and the mean annual rainfall is 650 mm (Irannezhad 2015). In central and northern Lapland, winter lasts for about seven months, and snow remains on the ground for more than six months every year (Irannezhad 2015). The number of days with snow cover progressively decreases towards the south and southwest. On the southwestern coast, the ground is covered with snow for an average of 3 to 4 months a year. In addition of the snow cover, at these latitudes, the duration of the night varies significantly between seasons from 4 hours to 17 hours.

Human settlements and high-traffic roads are scarce, but isolated houses and low-traffic roads are widespread in the study area. Nature-based tourism is an example of non-timber forest services that is playing an increasing part as a livelihood in forest-rich rural areas (Lemky 2006). Considering only 40 national parks and national hiking areas, in 2020, the total length of paths was approximately 102,000 kilometres and the total length of trails that could also be used by al-terrain vehicles was around 157,000 kilometres (Lankia et al. 2020). Hiking trails create additional human pressure on wildlife and landscapes.

The demand for wildlife viewing tourism or sport hunting has also risen sharply, which has directly resulted in an increase in the number of artificial feeding sites **(Figure 1.4).**

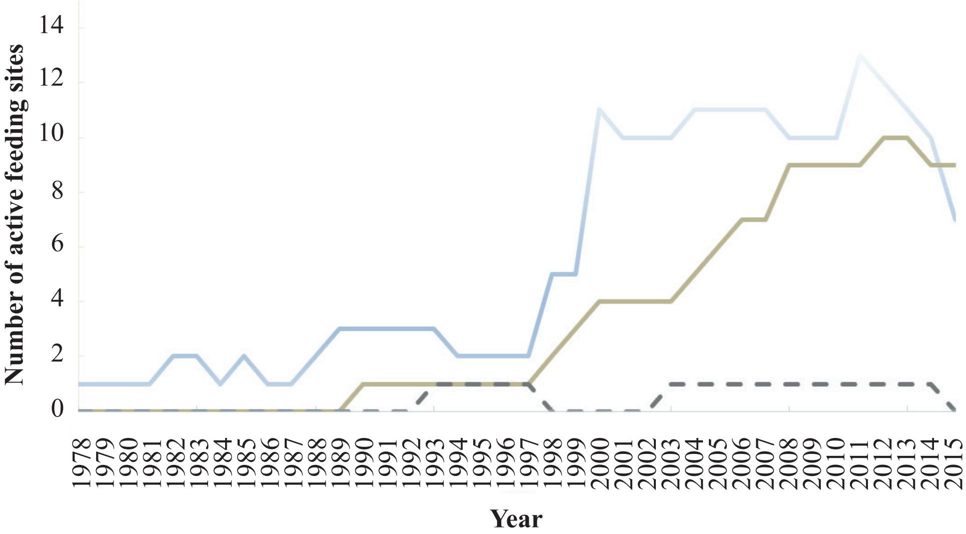


Figure 1.4 Evolution of the number of active artificial feeding sites (blue line is private feeding sites, green line is feeding sites for tourism purposes and black dots are feeding sites used for research) between 1978 and 2015s
unpublished data from I.Kojola (Luke – Natural Resources Institute Finland).

2.2 A brief history of brown bear in Finland

The brown bear, the country's totem animal, the wolverine *(Gulo gulo)*, a small -but dreadful- carnivore, the lynx (*lynx lynx*) and the wolf are the large predators that populate the Finnish territory. These predators came close to extinction in the 19th and early 20th centuries as they were killed for damages they caused to reindeer herds and crops, but also, in the case of the bear, for trophies and their meat (Ermala 2003). As a result, at that time, large carnivores disappeared from many areas of their original range. The brown bear was exterminated from the southern, western, and central parts of the country. Starting in the 1970s, the brown bear population slowly stabilized and started to increase in the southeast thanks to improved protection and continuous dispersal from the core areas in Russian Karelia (Kojola et al. 2006, Figure 1.2). The brown bear is protected by the European Union's Habitats Directive. The Finnish bear population is managed as a game species for which an annual quota is set. Females with cubs are protected and cannot be hunted. In recent years, Finland has allowed an increase in hunting, stating that the population is large enough to be regulated. The hunting rate for brown bears is over 10% (I. Kojola, unpublished data), while on the Russian side of the border, the hunting rate has been estimated at around 5-7% (K. Tirronen, unpublished data). Carnivores can adapt their habitat selection and movements in response to hunting pressure, which can have an impact on the size of their home ranges (Basille et al. 2013; Stillfried et al. 2015; Lodberg-Holm et al. 2019). Here, apart from North America, where home ranges appear to be similar in size, Central Finnish brown bears have one of the largest home ranges of any population in the world (Kojola et al. 2021) (Table 1.1). Apart from Russia, which has the largest brown bear population in the world, Finland has the largest population together with Romania and Sweden. Females' home range size differs between eastern and central Finland, with smaller home ranges in eastern Finland. The bear density in eastern Finland is three times higher than in central Finland (Kojola et al. 2021). That could explain the difference in home range size between the two regions. In the eastern part, females have higher risk of encountering infanticidal males, and a greater danger of being hunted in the region (Kojola et al. 2021). Apart from Russia, which has the largest brown bear population in the world, Finland has the largest population together with Romania and Sweden. The estimate of the Finnish bear population in 2012 was 1600-1800. The winter population is much smaller (about 1,000 to 1,200 bears). Indeed, many males that travel in summer to the easternmost part of Finland spend the winter on the Russian side (Kaczensky et al. 2012). In 2007, the Ministry of Agriculture and Forestry published the management plan for Finland's bears (http://www.mmm.fi/en/index/frontpage/Fishing,_game_reindeer/hunting_game_management/managem entplans/managementplanforthebearpopulation.html) to reduce human-wildlife conflicts. The primary conflict is still depredation on reindeer herds, they might also damage beehives, cattle silage or kill livestock (Kaczensky et al. 2012). The

Ministry of Agriculture recently updated the Management Plan (July 2022, https://mmm.fi/en/-/main-objectives-of-management-plan-for-bear-population-are-to-preserve-favourable-conservation-status-of-bear-population-and-ensure-that-bears-will-not-lose-fear-of-humans) and has included food baits to create harmonised practices.

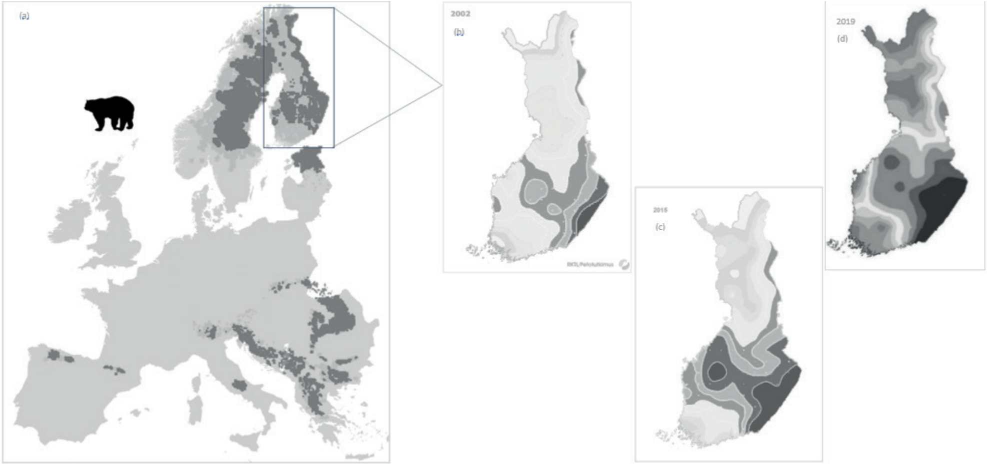


Figure 1.5 Bear distribution over Europe (a) and the expansion of the Karelian brown bear population between 2002, 2015 and 2019 (b, c and d). Adapted from the European Commission (Kaczensky et al. 2021) and from Riistahavainnot (http://riistahavainnot.fi/suurpedot/suurpetotutkimus/havaintokartat, Luke, Finland).

Table 1.1 Comparison of home range sizers (km^2) between brown bear population extracted from (Kojola et al. 2021)

Population	n	Home Range (km2)	Reference
North America	35	2577	[80]
North America (Alaska)	20	356	[82]
North America (Yellwstone)	21	884	[83]
Japan (Hokkaido)	3	43	[84]
Croatia	5	58	[85]
Slovenia	5	53	[86]
Spain	1	28	[87]
Scandinavia	37	437	[21]
Scandinavia (South)	34	217	[34]
Scandinavia (North)	18	280	[34]
Finland (Eastern)	25	127	This study
Finland (Central)	56	862	This study

The increased presence of brown bears in regions where human activities dominate challenges current knowledge about the ecology of the species and its ability to adapt to a highly dynamic ecosystem. Consequently, the ecology of brown bear movements and the consequences of human pressure on their behaviour have yet to be studied in order to improve their management.

2.3 Data collection

From 2002 to 2013, 71 brown bears were captured, usually in spring, after left their winter dens. Of the 71 collared brown bears, 27 were subadults. Brown bears were classified as subadults when they were four years old or younger. Brown bears were tagged from the time they left their dens until October, shortly before they entered hibernation. Sedative doses were adjusted according to the capture period, to take account of physiological changes and body fat levels. They were darted from blinds on temporary baits. Immobilization drugs and dosages followed the protocol of Jalanka and Roeken (1990). The doses injected to immobilize the bears contained medetomidine (50 µg/kg) and ketamine (2.0 mg/kg) (Jalanka and Roeken 1990). Bears were sexed, weighed and aged (Craighead et al. 1970). Individuals were fitted with 1.5 kg GPS (Global Positioning System) collars (Televilt, Lindesberg, Sweden; Vectronic Airspace, Berlin, Germany). The collars were fitted with a pre-programmed drop mechanism, with an average battery life of one year. Some locations were excluded from the database due to poor satellite reception.

2.4 Structure of the thesis

The thesis deals with the spatial behaviour of brown bears across scales, for both individual and population-scale movement. The movement ecology framework is a major theoretical part of this work.

After this introduction (**Chapter 1**), the thesis will be structured as follows in four chapters.:

Chapter 2 will focus on the influence of the moon on the movements of brown bears. The brightness of moonlight can indeed be used as a reference for predators such as the Iberian lynx, hyenas or even cheetahs. At full moon, due to high visibility, predators may increase their activity rate. In general, hunting is more lethal. But what happens with facultative carnivores that are not strictly dependent on their prey?

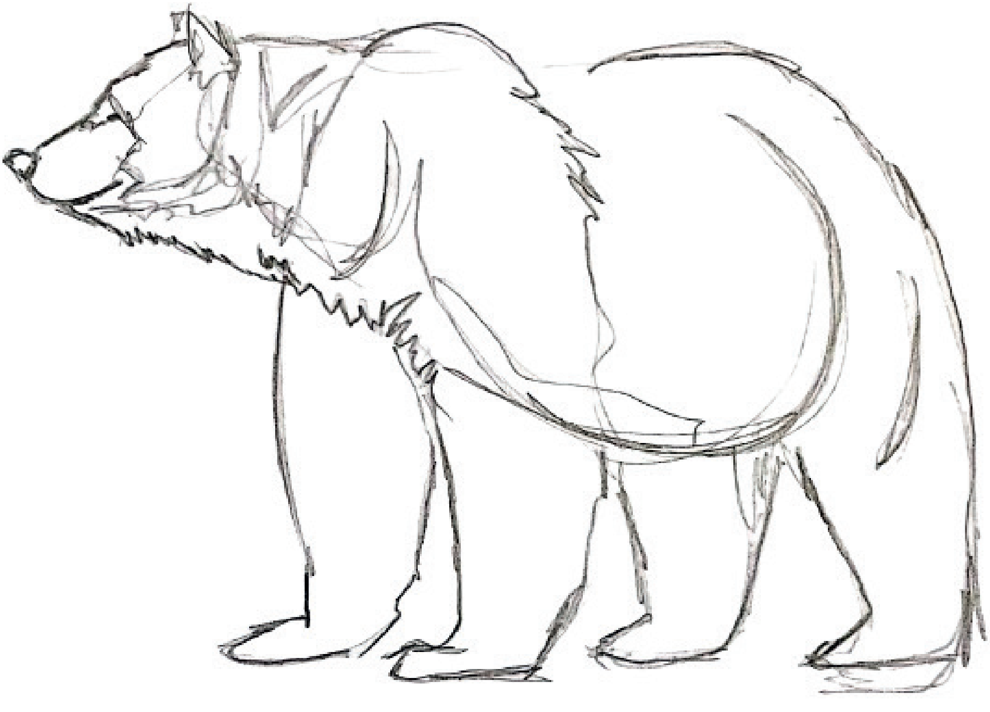
Brown bears have the typical morphological characteristics of carnivores (teeth, claws and defined digestive tract). However, it is omnivorous and very fond of berries. Mo- reover, the brown bear can be extremely flexible in its primary diel activity, from twilight to night activity in order to avoid encounters with humans (hikers, hunters...). Therefore, the objective of this chapter is to describe the main characteristics and circumstances of the influence of moonlight on the brown bear and provide information that could contribute to improve our knowledge on how moonlight can modify the behaviour of such a group of species.

Chapter 3 will provide a better understanding of «why» and «how» brown bears move. Indeed, movements are governed by intrinsic factors such as age, sex, size and reproductive status, as well as by the environment in which the individual is living. In this chapter, in particular, we aim to give a general description of the brown bear's movements in a human-modified landscape. One would expect to find a relationship between the use of feeding sites and changes in brown bear behaviour.

Finally, by delineating the various spatial strategies performed by brown bears at the home range scale (**Chapter 4**), we examine the motion capacity (how to move?) of the species. We decided to focus on an intrinsic factor: age, which is one of the main causes of movement in species with natal dispersal. The requirements and experience of animals change over a lifetime, and movement patterns should reflect these age-specific variations. For this reason, we investigate whether and how the movement patterns of dispersing bears differ from those of adults, which should have a more stable and known territory. In addition, we explore whether there are interindividual differences in movement patterns. The thesis will end with a general discussion on our main findings on brown bears movement strategies and a conclusion proposing research perspectives.

2

Brown bears do not mind that the moon exists



Preamble

In this chapter, we attempt to explore the first parameters influencing brown bear movements. Indeed, species move to meet their primary needs, whether in terms of reproduction or resting and feeding habitats. Although the brown bear is classified as a large carnivore, it is actually a facultative carnivore. In this respect, it represents a special case study. Sometimes they may have predatory patterns, sometimes they are opportunistic omnivores with a diet rich in fruit and, as a result, prey-predator relationships may be weaker compared to obligate carnivores. Through the prism of the amount of night light (lunar phases), we have studied the first patterns of brown bear movement. This first chapter attempts to define the internal and external factors (age, sex, time of year...) that influence movement.

Paper 1: published -

Does moonlight affect movement patterns of a non-obligate carnivore? Brown bears do not mind that the moon exists.

Cindy Lamamy, Maria Del Mar Delgado, Ilpo Kojola, Samueli Heikkinen and Vincenzo Penteriani

This paper has been published in Journal of Zoology in November 2021.

DOI : 10.1111/jzo.12938

Abstract

Moonlight plays a significant role in prey-predator relationships. At full moon, predators' hunting success and activity rates generally increase. Even though the analysis of facultative carnivore movement patterns can improve our knowledge of how moonlight can change the behaviour of such a group of species with diverse ecological needs, few studies have been conducted with facultative carnivores and none with telemetric data. Here, we studied whether moonlight influences brown bear, *Ursus arctos*, movement behaviours. By analysing data collected from 2002 to 2014 for 71 collared individuals inhabiting Finland and Russian Karelia, we found that some internal and external factors are influencing brown bear movement patterns. In particular, this facultative carnivore moves slowly and over short distances during human bear-hunting and hyperphagia periods. However, moonlight does not affect brown bear movements. Although brown bears are large carnivores, they are opportunistic omnivores with a high fruit diet and, therefore, the prey-predator relationships that are behind the dependence of carnivores on moonlight seem to be weaker than in obligate carnivores.

Keywords: animal movements; large carnivore; lunar brightness; moon phase; *Ursus arctos*

1 Introduction

The moon orbits the earth and, in this way, the positions of the sun, moon and earth reflect different illuminations of the moon called lunar phases. The lunar cycle (from new moon to new moon) has an average duration of 29.5 days. It can lead to several environmental modifications, such as changes in the nocturnal atmosphere, e.g., on full moon nights, the amount of light is 250 times greater than on moonless nights (Foster and Roenneberg 2008). These changes are used as benchmarks by some animals to synchronize the reproduction period (e.g., breeding, spawning) (Kronfeld-Schor et al. 2013), adjust the activity rate of finding food (Grant et al. 2012), and for communication (Penteriani et al. 2011). It is therefore not surprising that there is growing evidence that moon phases influence the behaviour of many animal species, including humans (Sjödin et al. 2015).

Night light plays a notable role in nocturnal vision and prey-predator relationships (Dacke et al. 2003; Penteriani et al. 2013; San-Jose et al. 2019). When the moon is close to full, cheetahs, *Acinonyx jubatus*, and wild dogs, *Lycaon pictus*, are more active in order to maximise hunting success as their chase patterns require high visible conditions (Cozzi et al. 2012; Rasmussen and MacDonald 2012). Therefore, their prey are more likely to remain in refuges, limiting their activity and becoming more vigilant (Lima and Dill 1990; Daly et al. 1992; Brown and Kotler 2004; Griffin et al. 2005), feeding back on the activity rhythms of their predators. The activity patterns of Iberian lynx, *Lynx pardinus*, mirror the activity of their main prey, the rabbit, *Oryctolagus cuniculus*. In particular, rabbits move furthest from their dens and are more active around the new moon, and consequently, lynxes reduce their travelling distances and concentrate their movements in the core areas of their home ranges, which generally match those areas with a high density of rabbits (Penteriani et al. 2013). In addition, as behavioural decisions made at one step can have an impact on the behavioural choices at the next step, it has been demonstrated that some carnivores that increase their hunting success on clear nights generally decrease their activity the following day (Cozzi et al. 2012; Rasmussen and MacDonald 2012). Therefore, bright, moonlit nights may create a fitness trade-off by increasing carnivores' hunting success probability (Clarke 1983; Kotler et al. 1988, 2002), but reducing their energy reserve through increased activity to search for hidden prey (but see (Sábato et al. 2006). These behavioural changes can be costly because they take time and energy away from others activities linked to fitness, such as parenting or mating (Lima and Dill 1990).

The animal's navigation and mobility capabilities determine how an individual will move in response to external factors and internal states (Nathan et al. 2008). Animals continuously make decisions on how, when and where to move to find suitable areas to meet their vital requirements (Estes et al. 1982; Nathan et al. 2008; Van Moorter et al. 2013). However, animal movements can also be affected by other factors, such as the availability of food and shelter, landscape structure, weather conditions, and anthropogenic activities (Martin et al. 2008, 2013; Nathan et al. 2008). In this context, the analysis of the movement patterns of carnivores can improve our current knowledge on how moonlight may alter the behaviours of a group of well-differentiated species with diverse ecological needs such as carnivores (Wilson and Mittermeier 2009). The ecological and evolutionary consequences that the moon may have at the individual, population and community levels are numerous; however, there is still a lack of information available on the effect of the different moon phases and the associated moonlight on carnivore movement patterns (but see, e.g., (Grassman et al. 2005; Di Bitetti et al. 2006; Mukherjee et al. 2009; Cozzi et al. 2012; Penteriani et al. 2014).

Of the group of large carnivores, the potential effects of moonlight on movement patterns of brown bears, *Ursus arcto*s, have not yet been studied. The brown bear is an intriguing large carnivore for two reasons. First, even though brown bears have the typical morphological features of carnivores (defined canine teeth, claws and a carnivore digestive tract), they are facultative, or non-obligate, carnivores. That is, they do not exclusively depend on the movements and rhythms of activities of given prey. Second, brown bears can be extremely flexible in their primary diel activity pattern, from diurnal to crepuscular to nocturnal (Rode and Robbins 2000; Gende and Quinn 2004; T. Robbins et al. 2007), and their diel activity can be affected by human encroachment, hunting, bear population density and latitude (Theuerkauf et al. 2003; Ordiz et al. 2012, 2013; Hertel et al. 2017). Thus, even if moonlight has some effect on brown bear movement patterns, omnivory and flexibility in rhythms of activity may weaken moon-dependence, as earlier suggested by Richardson (2017) in a camera trap study.

To our knowledge, previous studies on the effect of moonlight on carnivores have only been carried out on obligate species. Therefore, the distinctive brown bear dietary preferences may provide a different perspective on the potential influence of the moon on the movement strategies of facultative carnivores. To determine whether the lunar phases influence brown bear movements, we studied the daily movement behaviours of 71 brown bears (42 males and 29 females) in Finland and Russian Karelia from 2002 to 2014 **(Figure 2.1)**. On the basis of the main characteristics of brown bears, i.e., being a facultative carnivore with mainly diurnal activity, we hypothesise that movement patterns will not show a clear and strong dependence of bears on moonlight, even though they might have some preference for darker nights as a response to human avoidance and occasional predation events.

2 Materials and methods

2.1 Study area

The movements of our radio-collared brown bears covered most of southern and central Finland (220,000 km2) and also involved a part of Russian Karelia (160,000 km2), and ranged from 61.69°N to 66.56°N. At these latitudes, the length of the night varies significantly between seasons. The topography is relatively smooth with elevation ranging from 100 to 576 m a.s.l. Both regions are largely dominated by highly managed productive boreal forest (Ahti, Hämet-Ahti & Jalas, 1968; Hagen et al., 2015). About 86% of the land area is covered by forests, where the main tree species are the Scots pine *Pinus sylvestris*, the Norway spruce *Picea abies* and various birches *(Betula spp)*. The terrain is also characterized by the presence of lakes and peat bogs. Human settlements and high-traffic roads are scarce, but isolated houses and low-traffic roads are widespread in the study area.

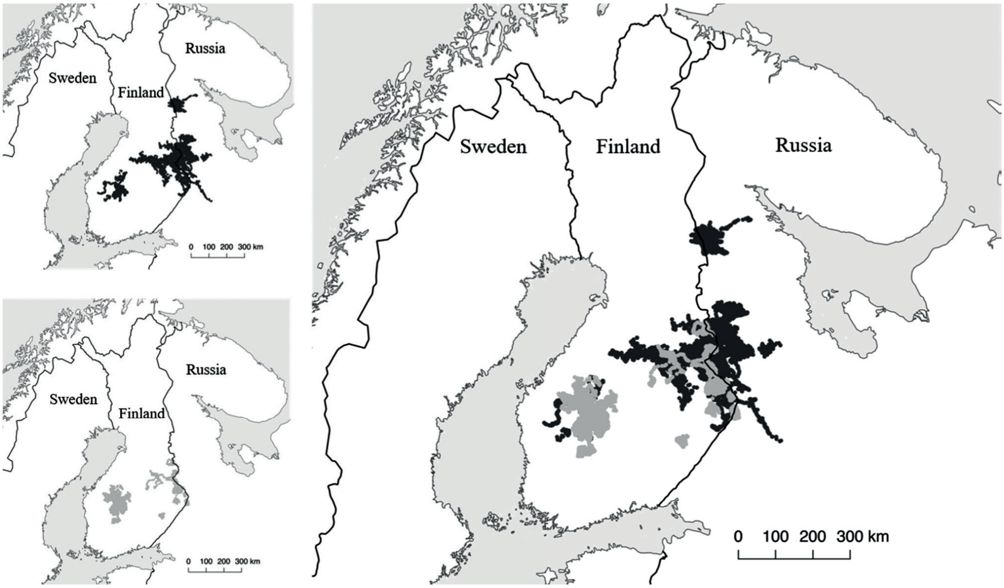


Figure 2.1 Distribution of GPS locations of 42 brown bear males (n = 15 subadults, black movement paths) and 29 females (n = 12 subadults, grey movement paths) spread across south-eastern Finland and Russian Karelia (2002—2014).

2.2 Data collection

From 2002 to 2013, 71 brown bears (i.e., 115 captures as some individuals were captured several times; 2002: 9 individuals among which a subadult male, 7 adults male and an adult female; 2003: 6 individuals among which 3 subadults male and 3 adults male ; 2004: 13 individuals among which 4 subadults male, 8 adults male and an adult female; 2005: 7 individuals among which 5 adults male= 5 and 2 adults female; 2006: 6 individuals among which 5 adults male, and an adult female; 2007: 7 individuals among which 2 subadults male, 4 adults male, and an adult female; 2008: 7 individuals among which 5 adults male, a subadult female and an adult female ; 2009: 9 individuals among which a subadult male, 2 adults male, a subadult female and 5 adults female; 2010: 17 individuals among which 2 subadults male, an adult male, 4 subadults female and 10 adults female; 2011: 16 individuals among which 2 subadults male, an adult male, 5 subadults female, and 8 adults female; 2012: 15 individuals among which 4 subadults male, 4 subadults female and 7 adults female; 2013: 3 individuals among which an adult male, a subadult female and an adult female) were captured generally in spring after they left their winter dens. Brown bears were tagged until October shortly before entering dens, for which higher doses of sedative were necessary due to changes in physiology and body fat levels because of seasonality. They were darted from blinds at temporary baits. Immobilisation drugs and dosages followed the protocol by Jalanka & Roeken, (1990). The injected doses used to immobilize bears contained medetomidine (50 µg/kg) and ketamine (2.0 mg/kg) (Jalanka & Roeken, 1990). To dart bears in late summer or autumn, the spring dose was increased 25-50%, and longer needles were used because of body fat (Arnemo et al., 2007). Bears were sexed, weighed, and aged (on the basis of cementum annuli counts of a first premolar removed at time of capture) (Craighead, Craighead & McCutchen, 1970). Permission to capture and manipulate bears was issued by the County Veterinarian of Oulu and by the Regional State Administrative Agency of Lahti (Finland). Individuals were fitted with a collar that carried 1.5 Kg global positioning system (GPS) transmitters (Televilt, Lindesberg, Sweden; Vectronic Airspace, Berlin, Germany). The weight of the collars was less than 1.0-2.0 % of the bodyweight of adult females (mean (Kg) ± SD = 124.6 ± 27.5) and 0.5-1.0 % of adult males (mean (Kg) ± SD = 212 ± 61.4). Out of the 71 collared brown bears, 27 were subadults. As they might still grow, collars were adjusted so that they could expand and allow for increased body size. Brown bears were categorized as subadults when they were four years old and younger. Bears older than four years were categorized as adults. Collars had a pre-programmed drop off mechanism with an average battery life of one year. Whenever the drop off did not work by the scheduled time owing to technical flaws, the bear was re-captured and the collar was removed. All collars were removed before the end of the project in 2014.

The GPS collars were calibrated to continuously track brown bears, always collecting one location every four hours (n = 173301 total number of locations excluding winter hibernation; mean number of locations per individual ± SD = 2440.9 ±2396.6). Radiotracking sessions (n = 4158 days) started at 2:00 and ended at 22:00. Therefore, data comprised locations collected during the day and the night (hereafter, daily scale). Signals from the satellite transmitters were recorded by the ARGOS satellite system (www.cls.fr). The data provided sufficient days (number of collared individuals per day ± SD = 5.97 ± 4.01, range = 1 to 20) among the different moon phases, which should allow the detection of even a slight lunar effect on brown bear movement patterns if such an effect exists (**Supp. Mat. 1**). We recorded the positional dilution of precision (PDOP) value for all 3-D fixes and the horizontal dilution of precision for 2-D fixes. Following the method developed by D'Eon et al., (2002), we excluded all 2-D fixes. Although this data screening method reduces the data set, it allows a high percentage of detection of large location errors (Bjørneraas et al., 2010)

2.3 Movement patterns

Daily brown bear trajectories were obtained by using the adehabitat package version 0.4.15 for R software (Calenge, 2006).

We estimated the following movement parameters at a daily scale (i.e., we considered both day and night locations): (1) total distance, which is the cumulative sum of the distance between successive relocations on the same daily trajectory; (2) net distance, i.e., distance travelled between the initial position and the final position on a daily scale; (3) average daily speed, which is the mean of the step distance (distance between two relocations) divided by the time interval between consecutive locations; and (4) mean turning angle, where angles between 0 to 90 degrees correspond to directional persistence and angles above 90 degrees indicate that the individual returns towards the previous location. Even though the resolution of the data might seem coarse to estimate the real tortuosity and total daily distance, the fact that all individuals were followed at the same resolution makes the comparison between parameter estimation feasible and reliable. Finally, we estimated (5) the size of the home range at a daily scale per individual (n = 11424 daily home ranges) using the minimum convex polygon (MCP) method (Mohr, 1947; Dahle & Swenson, 2003a). MCP was chosen over the kernel estimator because it is applicable with fewer than 30 locations (Seaman et al., 1999). To set the limits of the home range, we used isopleth values of 95% density. We removed every day with less than five locations to get a better estimate of daily movements.

2.4 Moon phases

(6) Daily moon phases for the study area were obtained from the Naval Oceanography Portal (https://aa.usno.navy.mil/data/docs/MoonFraction.php) and expressed in terms of the fraction of the moon disk illuminated and whether the moon was waxing or waning. The different phases of the moon were calculated as in Penteriani et al., 2011. The fraction of the moon disk illuminated was transformed into radians to give each day an angular equivalent (θ), based on the periodic regression method (De-

Bruyn & Meeuwig, 2001). As a result, the moon cycle is represented by a continuous transition from 0 to 2π radians, i.e., 0 and 2π radians correspond to the full moon and π radians is the new moon. In order to represent the entire lunar cycle, the fraction of the moon disk illuminated expressed in radians was introduced as an explanatory variable in the statistical model in the form of cos(θ), sin(θ), cos(2θ) and sin(2θ) (DeBruyn & Meeuwig, 2001). A semi-lunar cycle (two peaks in a lunar month) can be studied using the terms cos(2θ) and sin(2θ). Peaks are not necessarily of equal amplitude, so all terms are useful for analysing the lunar effect. A significant cos(θ) regression coefficient reflects a peak emerging at the full moon or new moon, e.g., a positive regression coefficient corresponds to a greater distance travelled at the time of the full moon and a shorter distance at the time of the new moon. A significant sin(θ) regression included in the model reflects a peak emerging at first or last quarter, e.g., a positive regression coefficient corresponds to a greater distance travelled at the time of the last quarter and a shorter distance at the time of the first quarter. A significant cos(2θ) regression coefficient reflects two peaks one appearing between the first and last quarter and one between the full and new moon, e.g., a positive regression coefficient corresponds to a greater distance travelled at the time of the new and full moon and a smaller distance at the time of the first and last quarter. A significant sin(2θ) regression coefficient reflects two peaks appearing between the new moon and the first quarter and between the full moon and the last quarter, or between the last quarter and the new moon and between the last quarter and the full moon, e.g., a positive regression coefficient corresponds to a greater distance travelled between full moon and the last quarter or between the new moon and the first quarter. The combination of significant coefficients for both θ and 2θ makes it possible to precisely determine when peaks occur and at what level. Prior research has shown variations in moonlight as a function of cloud cover and suggested that illumination could be increased with high and thin clouds around villages (i.e. light pollution) (Kyba, Ruhtz, Fischer, & Hölker, 2011) or decreased with thick clouds in areas without light pollution. In addition, the level of cloud varies within and between nights. We cannot therefore take the average cloud cover per day without introducing a bias into the analyses. Finally, our study area is very vast in space and time (i.e. thirteen years over more than 350,000 km^2) and we hypothesize that the probability to have a cloudy night is equally distributed over the study period and, therefore, across all lunar phases. The absence of cloud cover variable could only weaken the relationships between the lunar phases and bear movements if there was any moon influence on them rather than creating systematic biases.

2.5 Internal and external factors

In order to take into account other factors that may affect movement patterns, we also considered: (1) age class (i.e., subadults vs. adults); (2) sex; (3) period (i.e., mating vs. hyperphagia season); (4) bear hunting period; and (5) vegetation types. The mating season lasts for about three months from den exit to the 31st of July (Dahle & Swenson, 2003b; Spady, Lindburg & Durrant, 2007), and the period of hyperphagia begins the 1st of August and ends at the end of October when bears enter the den (Ordiz et al., 2017). According to the Finnish Wildlife Agency, the hunting season starts on the 20th of August and closes on the 31st of October. Hunting pressure is not linear over the entire opening season, but due to a lack of data, we were not able to address the variation in hunting pressure. The landscape GIS layer extracted from Earth Data - ORNL DAAC (https://webmap.ornl.gov/ogcdown/dataset.jsp?dg_id=10004_31), resolution 500 meters, was reclassified into five vegetation types: (1) forest (i.e., hardwood and mixed forests); (2) softwood forest (i.e., conifer forests); (3) grasslands; (4) wetland areas; and (5) human settlements. The Intersect tool was used to extract information from each bear's daily home range and then it was transformed into a percentage of land use. Finally, we obtained the duration of darkness for the study area from the Naval Oceanography Portal (https://aa.usno.navy.mil/data/docs/MoonFraction.php).

2.6 Statistical analyses

Statistical analyses only covered vegetation parameters that were well represented in the area, i.e., those with less than 20% of zeros in all the daily home ranges under consideration. The variable 'softwood forest' and 'forest' were highly correlated ($r = 0.88$), and we consequently excluded the variable 'forest', which is less characteristic of Finnish landscapes (Ahti et al., 1968).

For each movement parameter estimated at a daily scale (see Data Collection for more details), we first built models including all explanatory variables except the moon phase variable, i.e., age class, sex, period, hunting and vegetation types. While the residuals of the total and net distances were normally distributed, the ones for speed did not follow a normal distribution. Therefore, we built linear mixed models for total and net distances, and generalised linear mixed models for speed and turning angle (with Gamma distribution as a link function and Poisson distribution, respectively). Finally, as the duration of the night (which might influence the effect of the moon) varies significantly in our study area, we included night length as an offset. We created a set of competing models that included all potential combinations of predictors, and selected the most parsimonious model according to Akaike's information criterion (AICc) (Burnham & Anderson, 2002). Parameter coefficients and the relative importance value (RIV) for the respective explanatory variables were calculated using model averaging on the 95% confidence set (Burnham & Anderson, 2002). We considered this to be our null model. On the top of the effects of the factors included in the null model, the effect of the moon on each of the considered response variables was estimated at the daily scale. The moon (see section Moon phases) was introduced in the form of cos(θ), sin(θ), cos(2θ) and sin(2θ) as continuous explanatory variables. We compared our null model with the one containing the moon phase using maximum likelihood (Myung, 2003). We assumed that the moon had an effect on movement parameters when the p-value between the two models was less than 0.03 (Zuur et al., 2009). As each brown bear was followed for several days (hereafter, sessions) and years, we considered the individual, the session (a session corresponds to one day, i.e., the first location until the last location of the day) and the year as nested random effects. We used the statistical software R v. 3.5.1 (R Foundation for Statistical Computing, 2018) with the lme4 package (Bates et al., 2015), and MuMIn package (Bartoń, 2013) for model generation and model averaging.

3 Results

We found that internal and external factors influenced brown bear movements, which otherwise were not influenced by lunar brightness (Table 1 and Supp. Mat. 2 and 3). That is, models containing the moon phases never performed better than our null models **(Tables 2.1** and **2.2, Figure 2.2)**.

Our null models always included the variable hunting, with brown bears moving slowly, over short distances with more tortuous trajectories during the period in which they could be hunted. In addition, during the hyperphagia period, brown bears moved less (i.e., slower average speed and shorter net distance) and displayed more tortuous trajectories than during the mating period **(Table 2.1)**. Furthermore, brown bears generally moved long distances and showed extensive home ranges when moving in habitats dominated by conifers **(Table 2.1)**. Finally, adult brown bears moved faster and demonstrated more tortuous trajectories within larger home range areas than did subadult individuals, especially during the mating period **(Table 2.1)**. No differences were found between male and female movement patterns **(Table 2.1)**, independent of age class.

Table 2.1 Values of AICc, ΔAICc and Weighted AICc of the best (ΔAICc < 2) linear mixed or generalized linear models (see text for more details), summary of the null model considered for each movement parameter and the analysis of variance (ANOVA with R2c (i.e. conditional R squared)) showing that the moon did not affect brown bear movement patterns.

	Competing models		**AICc**	**ΔAICc**	**Weighted AICc**
Total distance	Conifer+period		39 897	0.00	0.50
		β[a]	**SE[a]**	**p[a]**	**RIV[b]**
	Intercept	6.54	0.14	<0.001	
	Period	-1.75	0.08	<0.001	1.00
	Conifer	0.08	0.06	0.16	0.67
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**R2c**
	Conifer+period	7	39 886		0.88
	Conifer+period + *Moon phase*	11	39 245	0.02	0.88
Net distance	Conifer+period		47 850	0.00	0.64
		β[a]	**SE[a]**	**p[a]**	**RIV[b]**
	Intercept	4.26	0.13	<0.001	
	Period	-1.98	0.07	<0.001	1.00
	Conifer	0.13	0.04	<0.001	1.00
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**R2c**
	Conifer+period	7	47 839		0.90
	Conifer+period + *Moon phase*	11	47 913	0.02	0.90
Home range	Period+conifer		29 557	0.00	0.65
		β[a]	**SE[a]**	**p[a]**	**RIV[b]**
	Intercept	1.52	0.10	<0.001	
	Period	-1.58	0.03	<0.001	1.00
	Conifer	0.04	0.02	0.07	0.59
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**R2c**
	Period+conifer	7	29 592		0.89
	Period+conifer + *Moon phase*	11	29 624	0.41	0.89
Speed	Period+conifer		39 897	0.00	0.50
		β[a]	**SE[a]**	**p[a]**	**RIV[b]**
	Intercept	-2.19	0.70	0.002	
	Period	0.04	0.01	<0.001	1.00
	Conifer	0.09	0.03	0.002	1.00
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**Deviance**
	Period+conifer	7	-225 590		-225 606
	Period+conifer + *Moon phase*	11	-225 325	1.00	-225 349
Tuning angle	Conifer+age		19 169	0.00	0.27
		β[a]	**SE[a]**	**p[a]**	**RIV[b]**
	Intercept	-0.22	0.08	0.006	
	Period	-1.69	0.03	<0.001	1.00
	Age	0.05	0.07	0.44	0.58
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**R2c**
	Period+age	5	19 206		0.39
	+ *Moon phase*	9	19239	0.52	0.39

Table 2.2 Values (mean ± SD, range) of movement parameters across moon phases (🌕 Full moon; 🌗 Last Quarter; 🌑 New Moon; 🌓 First Quarter;).

	Total distance (km)	Net distance (km)	Home range (km^2)	Speed (km/h)
	7.7 ± 6.6, 0-66.2	4.0 ± 4.6, 0-37.8	2.7 ± 7.0, 0-136	0.4 ± 0.7, 0-16.0
	7.5 ± 7.0, 0-50.2	3.7 ± 4.8, 0-47.1	2.8 ± 8.1, 0-131.4	0.4 ± 0.8, 0-15.8
	7.9 ± 7.1, 0-54.5	4.1 ± 4.7, 0-34.6	2.9 ± 7.4, 0-109.7	0.4 ± 0.9, 0-16.0
	8.0 ± 7.1, 0-66.0	4.0 ± 4.7, 0-40.9	3.1 ± 8.8, 0-168	0.4 ± 0.9, 0-15.3

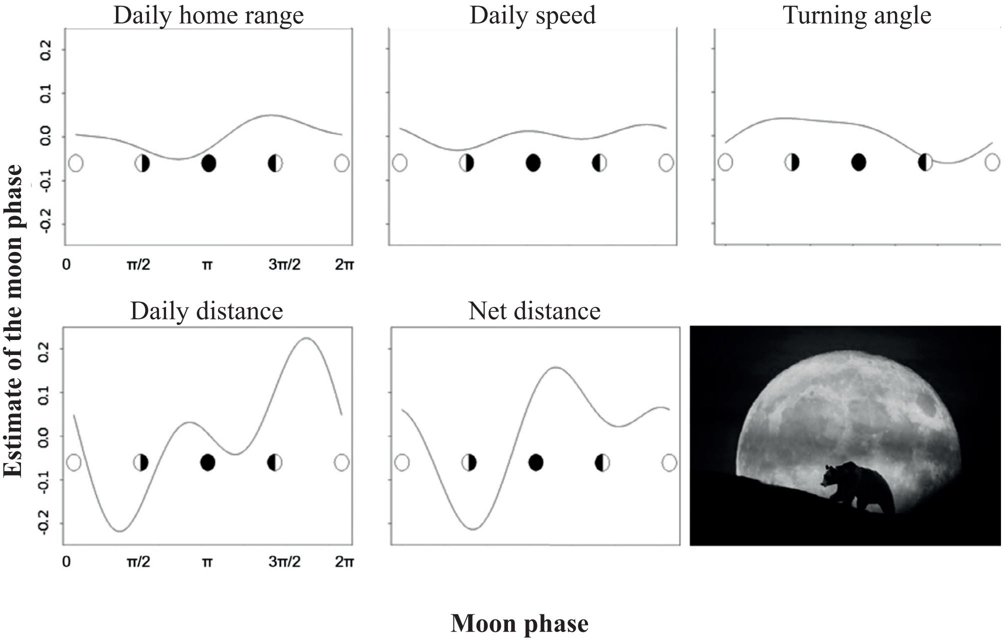


Figure 2.2 Moon phase estimated effect (smoothed grey lines) on daily home range, daily speed, turning angle, daily distance and net distance as estimated by linear mixed models for total and net distances, and generalized linear mixed models for speed and turning angle (with Gamma distribution as a link function and Poisson distribution, respectively) (Table 1). The moon cycle is represented by a continuous transition from 0 to 2π radians; that is, 0 and 2π radians correspond to the full moon and π radians are the new moon. In order to represent the entire lunar cycle, the fraction of the moon disc illuminated expressed in radians was introduced as an explanatory variable in the statistical model in the form of cos(θ), sin(θ), cos(2θ) and sin(2θ), which corresponds to 1 to 6 in the x-labels. (Brown bear picture: V. Penteriani).

4 Discussion

The hunting variable seems to be the parameter influencing all motion parameters. Brown bears move slowly, over short distances and follow more tortuous paths when the hunting season is open. When human pressure is high, factors, such as fear, drive animals to adjust their behaviour to reduce risk. That is, they can allocate most of their time to vigilance at the expense of other vital needs, such as searching for food, to avoid threatening encounters with humans (Loveridge et al., 2007; Ordiz et al., 2011, 2012, 2013; Gosselin et al., 2014).

Changes in movement patterns between the different periods may be related to different biological needs across the breeding season. During the hyperphagic period, brown bears generally moved less and demonstrated torturous trajectories, probably restricting their activity around abundant local food resources (McLoughlin, Ferguson & Messier, 2000; Selva et al., 2017). In contrast, during the mating period, brown bears moved greater distances, most likely with the aim of increasing the probability of finding a potential partner (Steyaert et al., 2012; Graham & Stenhouse, 2014). These results are in line with previous studies showing that, during the mating season, oestrus females might increase their movements to maximize reproductive success and the survival of future cubs (Hrdy, 1979; Ebensperger, 1998; Soltis et al., 2000). Also, brown bears typically travelled long distances and showed extensive home ranges when moving in habitats dominated by conifers. Habitat quality and characteristics may engender diverse costs and benefits, and consequently noticeable differences in movement behaviours (Delgado et al., 2010). In our study area, conifer forest may represent a vegetation type where the costs of movements are low, e.g., increased visibility resulting in less need for vigilance, food source types and availability and/or fewer landscape obstacles. Lastly, adult brown bears moved faster and demonstrated more tortuous trajectories within larger home ranges than subadult individuals, especially during the mating season (Table 2.1). Subadult individuals frequently travel across unfamiliar areas. Uncertainty regarding the location of conspecifics, predators and resources may pose significant problems (Delgado et al., 2009). Because the home ranges of subadult individuals are generally not defended, straight trajectories may allow subadults to disperse among different foraging areas more easily than adults. Limitations, such as intricate social organization and territoriality among neighbours, could force subadults to limit the size of their home range to avoid the high cost of intrusions into neighbouring territories. Although our data does not indicate any differences in movement patterns between males and females, this might be an area of focus for future studies. While we did not consider the reproductive status of females, previous evidence shows that females with cubs of the year may move less and in a more constricted area than other individuals (Ordiz et al., 2017).

Contrary to many other carnivores that have been shown to follow the rhythm of moonlight patterns, brown bear movement patterns were not influenced by the moon phases (see also Richardson, 2017). Models containing the moon phases never performed better than our null models. Notably, even though brown bears have the typical morphological features of carnivores, they are opportunistic omnivores with a diversified diet (Bojarska & Selva, 2012). Although brown bears may show carnivore habits and feed on small mammals as well as large ungulates (Bojarska & Selva, 2012; Niedziałkowska et al., 2019), the brown bear diet is composed of more than 50% vegetal materials (e.g., grass, leaves and roots) and also rich fleshy fruits (e.g., bilberry Vaccinium myrtillus) (Rode & Robbins, 2000; Persson et al., 2001; Rode, Robbins & Shipley, 2001; Cronin, 2005; Stenset et al., 2016). As a result, the prey-predator relationships that are behind the dependence of carnivores on lunar light (Brown & Kotler, 2004b; Berger-Tal et al., 2010; Penteriani et al., 2013; Bhatt et al., 2018) are weaker in brown bears than in other obligate carnivores. In addition, two other factors may have further played a role in reducing the potential effect of the moon on brown bears in our study area. First, bear feeding patterns on natural food might be disrupted by the continuous supply of anthropogenic foods at artificial feeding points established for hunting and bear viewing purposes (Penteriani, Delgado & Melletti, 2010; Penteriani et al., 2017; Kojola & Heikkinen, 2012). In fact, this practice can further modify the bears' non-dependence on prey (Steyaert et al., 2014) and, therefore, the potential influence of moonlight. Second, we should also take into account that this Finnish-Russian bear population is managed through hunting. In line with previous studies (Ordiz et al., 2011), we found that bears under hunting pressure alter their normal activity rhythms and movements.

The lunar cycle is a major factor in activity changes, and many nocturnal and diurnal animals can alter their activity in response to moonlight variations. Animals can adapt their schedules throughout the moon cycle to improve their fitness. The relationship between predators and prey also depends on these adaptations. Although prey are more difficult to find around the full moon as they remain in refuge areas, brighter nights allow carnivores to increase their hunting success through better vision. Thus, it is essential to study the effect of the moon on carnivores as increased hunting success may influence their behavior in the following days. In the case of the brown bear, however, the lunar cycle does not influence their movement patterns. The results of this study suggest that predator-prey interactions and carnivore behaviour still merit further investigation that takes into account (a) the intrinsic characteristics of carnivores (e.g., facultative vs. obligate carnivores), (b) the physical environment in which they move (e.g., vegetation types and nocturnal light), as well as (c) the potential interference of human activities (e.g., hunting and artificial feeding sites). In fact, the effects of some of the external pressures acting on predators, such as moonlight, might be hidden and/or greatly reduced by stronger forces like the needs of carnivores during specific periods of the year (e.g., mating), individual age, human avoidance and/or interference with feeding activity. A more global approach to the study of carnivore behaviours, which takes into account both obligate and facultative carnivores, might change the way we think about their interactions with the environment and humans, and bring to light more complex behavioural patterns than previously thought.

Supplementary Material 1

Distribution of days over the period and the lunar cycle (🌕 Full moon; 🌗 Last Quarter; 🌑 New Moon; 🌓 First Quarter;) according to the sex and age of brown bears and the distribution of the number of individuals radio-tagged by year.

Total number of days by category; mean per individual ± SD; range

	♂		♀	
Lunar phases	Adult	Subadult	Adult	Subadult
🌕	1002;95.4±47.6;13-190	630; 78.3±45.4; 35-215	1758; 73±78.9; 7-318	769; 72.4±53.7; 21-222
🌗	291; 6.6 ± 5.6; 5-26	261; 4.9 ± 4.5; 4-27	652; 30.1±28.4; 23-154	360; 16.6 ± 7.2; 4-30
🌑	720; 73.9±62.4; 34-231	630; 63.7±58.4; 40-180	1762;112.0±68.4;30-317	1010; 93.4±57.7;19-175
🌓	265; 5.0 ± 4.4; 3-21	227; 4.8 ± 4.4; 3-27	623; 31.1±28.2; 23-133	371; 6.7 ± 4.6; 3-41

	♂		♀	
Biological stage	Adult	Subadult	Adult	Subadult
Hyperphagia	1503, 70.0±62.7, 2-244	960, 67.9±62,5, 9-229	2314, 128.5±101,5, 13-360	984, 101.4±26.0, 73-152
Mating	1519, 73±78.9, 5-318	833, 80.5±58,4, 39-225	2503, 125±96,6, 11-388	1066, 100.4±57,7, 13-210

Total number of individuals radio-tagged by year

	♂		♀	
Years	**Adult**	**Subadult**	**Adult**	**Subadult**
2002	7	9	1	0
2003	3	3	0	0
2004	8	4	1	0
2005	5	0	2	0
2006	5	0	1	0
2007	4	2	1	0
2008	5	0	1	1
2009	2	1	5	1
2010	1	2	10	4
2011	1	2	8	5
2012	0	4	7	4
2013	1	0	1	1

Supplementary Material 2

Values of AICc, ΔAICc and Weighted AICc of all the models built for the five movement parameters where internal and external factors were analysed.

	Selected models*	AICc	ΔAICc	Weighte d ΔAICc
Daily distance	**Period/conifer**	**39897.0**	**0**	**0.50**
	Period	39899.1	2.1	0.18
	Period/conifer/sex	39900.0	3.0	0.11
Net distance	**Period/conifer**	**47850.0**	**0**	**0.64**
	Period/conifer/sex	47852.6	2.6	0.18
	Age/period/conifer	47853.3	3.2	0.13
	Age/period/conifer/sex	47855.8	5.8	0.04
Daily speed	**Period/conifer**	**39897.0**	**0**	**0.5**
	Age/period/conifer	39899.1	2.1	0.18
Daily home range	**Period/conifer**	**29557.2**	**0**	**0.65**
	Period	29560.3	3.2	0.13
	Age/period/conifer	29561.2	4.0	0.09
Daily turning angle	**Age/period**	**19169.3**	**0**	**0.27**
	period	**19169.4**	**0.23**	**0.24**
	Age/period/conifer	**19171.0**	**1.29**	**0.11**
	Age/period/conifer	**19171.2**	**1.82**	**0.1**

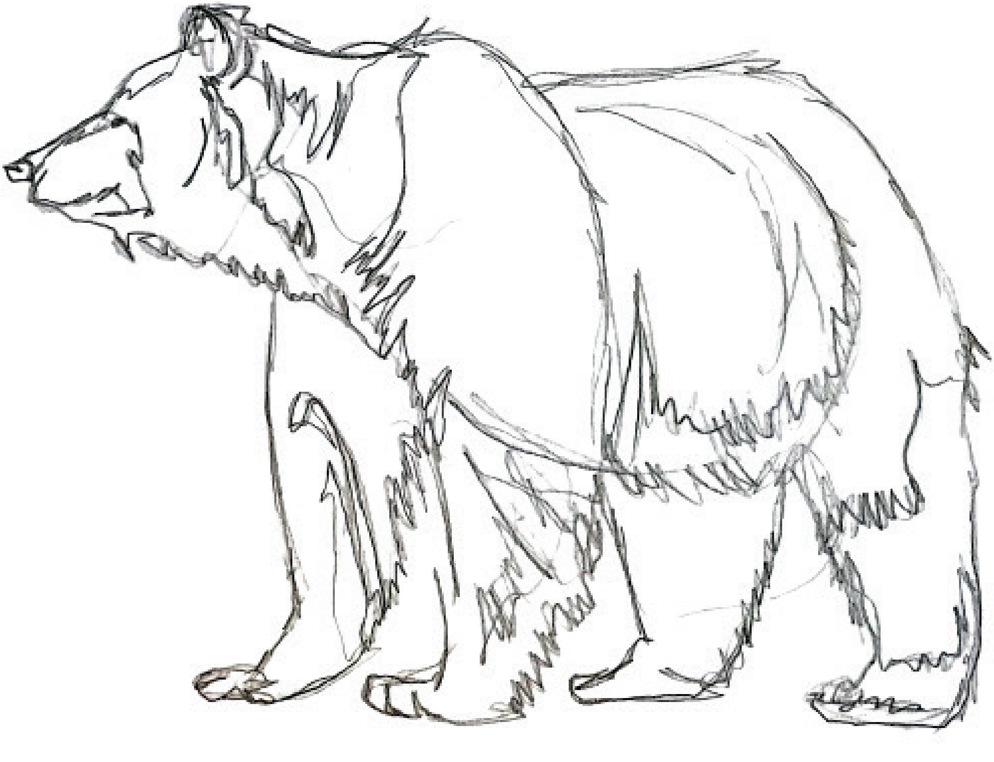
Supplementary Material 3

Values of the variance and standard deviation of all the models built for the five movement parameters where internal and external factors were analysed.

	Randon factors	ϭ2	ϭ
Daily distance	Session:(ID:year)	7.66	2.66
	ID:year	1.42	1.19
	year	0.00	0.00
	Residual	1.39	1.17
Net distance	Session:(ID:year)	7.90	2.80
	ID:year	1.02	1.01
	year	0.00	0.00
	Residual	1.05	1.04
Daily speed	Session:(ID:year)	0.90	0.95
	ID:year	154	1.24
	year	0.02	0.14
	Residual	0.00	0.00
Daily home range	Session:(ID:year)	1.43	1.20
	ID:year	0.39	0.62
	year	0.06	0.23
	Residual	0.30	0.55
Daily turning angle	Session:(ID:year)	0.00	0.00
	ID:year	0.08	0.28
	year	0.03	0.18

3

Human’s impact



Preamble

In chapter 2, I showed that brown bears did not change their movement patterns across the different moon phases. Meanwhile, human activities seem to influence the bear's habits, especially when hunting is open. GPS collars and associated data represent a rich and reliable source of detailed documentation of species behaviour. However, it is very difficult to assess hunting pressure over such a wide area, so in this chapter, we decided to focus on feeding sites dedicated to hunting, research or tourism. We specifically investigated how artificial food supplementation can impact brown bears' movement and rhythms of activity.

Paper 2 : published -

Does artificial feeding affect large carnivore behaviours? The case study of brown bears in a hunted and tourist exploited subpopulation.

Vincenzo Penteriani[1], Cindy Lamamy[1], Ilpo Kojola, Samueli Heikkinen and Maria Del Mar Delgado.

This paper has been published in Biological Conservation in January 2021.

DOI: 10.1016/j.biocon.2021.108949

[1] *These authors contributed equally to this work.*

Abstract

Artificial food supplementation of wildlife is an increasing practice for species conservation, as well as for hunting and viewing tourism. Yet, our understanding of the implications of wildlife supplementary feeding is still very limited. Concerns have been raised over the potential negative impact of artificial feeding, but the effects of this practice on animal movements and rhythms of activity are just beginning to be investigated. Here, with the aim of studying whether the artificial feeding of brown bears may affect their behaviour, we analysed (1) the probability and intensity of feeding site use at different temporal scales, (2) how the use of artificial feeding sites is related to the bear's age and sex, main periods of the bear's annual cycle (i.e. mating and hyperphagia) and characteristics of the feeding sites, and (3) how the use of artificial feeding may be affecting bear movement patterns. We analysed the movements of 71 radio-collared brown bears in southern-central Finland and western Russian Karelia. Artificial feeding sites had several effects on brown bears in boreal habitats. The probability of a feeding site being used was positively correlated to the stability of this food resource over time, whereas sexes and bear classes (subadults, adults and females with cubs) did not show significant differences in the use of feeding sites, which were visited predominantly at night and slightly more during hyperphagia. The probability of using an artificial feeding site affected the daily net distance only (bears using feeding sites: 3.5 ± 4.5 km, range: 0–29 km; bears not using feeding sites: 4.4 ± 4.9 km, range: 0–47 km). Those brown bears using artificial feeding more intensively moved shorter distances at a lower speed within smaller home ranges compared to bears that used this food sources less. Highly predictable and continuously available anthropogenic food may therefore have substantial impacts on brown bear movement patterns, ecology and health. The recorded changes in movement patterns support the evidence that artificial feeding may have important implications for bear ecology and conservation.

Keywords: Artificial feeding, Feeding sites, Food subsidies, Food supplementation, Movement patterns, Supplementary food, *Ursus arctos*

1 Introduction

Food supplementation of wildlife, i.e. the intentional provision of natural and/or non-natural foods to animals, is an increasing practice in species management and conservation, which is broadly applied and affects a wide range of species (Dubois and Fraser, 2013; Ewen et al., 2014; Murray et al., 2016; Selva et al., 2014; Steyaert et al., 2014; Tryjanowski et al., 2017; van Beeck Calkoen et al., 2020; Walpole, 2001). For example, supplementary feeding has been considered necessary because: (a) the distribution and availability of natural food might limit threatened populations (Ewen et al., 2014; Thierry et al., 2020); (b) there is a hypothesised benefit to providing safe food sources, free of veterinary drugs or poisons (Oro et al., 2013); (c) it might aid recovery of hunted populations (Delibes-Mateos et al., 2009) or (d) it may prevent damages in forestry and agriculture (Arnold et al., 2018; Borowski et al., 2019; Selva et al., 2014). But artificial feeding is also widely used to support human leisure activities, by both the hunting and ecotourism industries (Orams, 2002; Penteriani et al., 2017; Prinz et al., 2020; Steyaert et al., 2014), e.g.: (a) to maintain a high quality of trophy animals and a high density of animals for hunting, as well as to attract them to shooting spots (Selva et al., 2014); and (b) to increase the likelihood of wildlife observations as a touristic attraction (Orams, 2002; Penteriani et al., 2017; Prinz et al., 2020; Selva et al., 2014).

However, despite the ubiquity and magnitude of artificial feeding practices, our understanding of the ecological, behavioural, physiological and conservation implications of wildlife supplementary feeding is still very limited (Dubois and Fraser, 2013; Penteriani et al., 2017; Selva et al., 2014), and the range of potential motivations justifying the use or non-use of supplementary feeding is creating divergent opinions among managers (Ewen et al., 2014; Mysterud et al., 2019; Tryjanowski et al., 2017; van Beeck Calkoen et al., 2020; Walpole, 2001). The expected benefits of providing supplementary food is often not carefully evaluated and previous studies have demonstrated that artificial feeding may negatively affect both the population it is intended to help (Dunkley and Cattet, 2003; Ewen et al., 2014; Felton et al., 2017; Milner et al., 2014) and animal communities surrounding feeding spots. Indeed, food subsidies may redistribute and aggregate local predators, increasing the top-down effect of predation on alternative prey (Candler et al., 2019; Oja et al., 2015; Selva et al., 2014), and/or affect many non-target species, which could have several ecological and management-relevant effects, together with potentially undesired consequences such as disruption of animal cycles, e.g. hibernation (Bojarska et al., 2019; Candler et al., 2019; Fležar et al., 2019; Krofel et al., 2017; Krofel and Jerina, 2016; Manning and Baltzer, 2011). Additionally, supplemental feeding may (Candler et al., 2019; Dunkley and Cattet, 2003; Felton et al., 2017; Milner et al., 2014; Murray et al., 2016): (a) increase the risk of pathogen transmission by increasing contact rates between hosts and promoting pathogen accumulation at and around feeding sites; (b) be a source of immunosuppressive contaminants; and (c) increase wildlife stress, rates of injury and/or malnutrition. Actually, human-provided food has the potential to alter the overall dietary quality and hormonal patterns linked to seasonal nutritional requirements (Sergiel et al., 2020). Artificial feeding in forest ecosystems also has the potential to favour the expansion of non-native plant species (Jaroszewicz et al., 2017). Together with health effects, there is also a wide variety of negative impacts on wildlife that can occur as a result of artificial feeding for touristic purposes, e.g. alteration of natural behaviour patterns, dependency on anthropogenic food resources and habituation to humans, and an increase in animal aggression towards humans (Dubois and Fraser, 2013; Dunkley and Cattet, 2003; Orams, 2002; Penteriani et al., 2017; Steyaert et al., 2014; Walpole, 2001).

Among the species targeted by artificial feeding, bears are among the most common in the world, especially brown bears *Ursus arctos* (Penteriani et al., 2017; Penteriani and Melletti, 2020). Bears are generally fed to move individuals away from undesired locations (e.g. diversionary feeding; Garshelis et al., 2017; Ziegltrum, 2004), bait them for hunting and/or attract them close to bear viewing sites (e.g. Kirby et al., 2017; Massé et al., 2014). Brown bears are omnivorous opportunists that feed on a variety of food sources, including anthropogenic foods (Bojarska and Selva, 2012), and artificial feeding is commonly used to bait them for hunting (Bischof et al., 2008; Kavčič et al., 2015; Steyaert et al., 2014) and diversionary feeding purposes (Elfström et al., 2014; Garshelis et al., 2017; Kavčič et al., 2015), as well as for bear viewing (Penteriani et al., 2018, Penteriani et al., 2017). Since the beginning of the last decade, concerns have been raised over the potential impact of brown bear artificial feeding in Europe (Kojola and Heikkinen, 2012; Morales-González et al., 2020; Penteriani et al., 2018, Penteriani et al., 2017, Penteriani et al., 2010; Steyaert et al., 2014; Štofík et al., 2016). However, despite the ubiquity and magnitude of this practice (artificial feeding is practiced in at least 57% of European bear viewing sites; Penteriani et al., 2017), the effects of artificial feeding on bear movements and rhythms of activity are just beginning to be investigated (Bojarska et al., 2019; Selva et al., 2017; Todorov et al., 2020), as is also occurring in other artificially fed species (Ossi et al., 2017). Because how, why and where animals move may have important consequences at the individual and population levels (Nathan et al., 2008), alterations in movements due to anthropogenic sources of food may be associated with changes in food habits, reproduction, intra- and interspecific interactions and space use (Cozzi et al., 2016; Newsome et al., 2015; Penteriani et al., 2018; Selva et al., 2017).

Here, we aim to study whether brown bear artificial feeding for leisure purposes, mainly bear viewing, are affecting individual behaviours. Food at Karelian feeding sites for brown bears is delivered every evening, in the front of the blinds that are in use by people in the following night (author's personal data). Before mad cow syndrome dead cows were commonly used as bait, but nowadays the most important baits are dog food pellets and remnants from the salmon fillet factories, which require daily refills. Nowadays, the replenishing of feeding site cannot occur before evening, otherwise seagulls and ravens would consume pellets and salmon before bears start to be active.

First, we studied temporal patterns of artificial feeding use, i.e. the probability and intensity of feeding site use at different temporal scales (yearly, seasonal and daily temporal scales), and whether the use of artificial feedings is influenced by the internal features of individuals (i.e. age and sex), the main periods of the bear's annual cycle (i.e. mating and hyperphagia) and the characteristics of the feeding sites (i.e. number of available artificial feedings and time they remained opened). Second, we studied whether the use of artificial feeding may affect brown bear movement patterns. Because human activities can impact environmental predictability and, therefore, animal movement (Riotte-Lambert and Matthiopoulos, 2020), prolonged and stable sources of food, such as feeding sites, have the potential to determine the emergence of movement patterns other than those related to the use of natural resources only. One of the most significant properties of anthropogenic food maintained consistently over time is its fairly high predictability, more reliable for feeding individuals than intermittent natural food resources (Tryjanowski et al., 2017).

2 Materials and methods

2.1 Study area

The movements of our radio-collared brown bears covered most of southern and central Finland (220,000 km^2) and also encompassed a part of Russian Karelia (160,000 km2; **Figure 3.1**), and ranged from 61.69°N to 66.56°N. The topography is relatively smooth with elevation ranging from 100 to 576 m a.s.l. Both regions are largely dominated by highly managed boreal forest (Ahti et al., 1968; Hagen et al., 2015). About 86% of the land area is covered by forests, where the main tree species are Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and various birches *(Betula spp.)*. The terrain is also characterized by the presence of lakes and peat bogs. Human settlements and high-traffic roads are scarce, but isolated houses and low-traffic roads are widespread in the study area. Tourism around wildlife, especially brown bear and other large carnivores, has developed in the 2010–2020 decade in eastern Finland (Kojola and Heikkinen, 2012; Penteriani et al., 2017, Penteriani et al., 2010), where (a) bear-watching tourism is expected to increase, mainly by means of present enterprises expanding their activities (Eskelinen, 2009; Penteriani et al., 2017), and (b) ca. 4000 visitors arrived annually to observe bears at the Finnish-Russian border at the beginning of the last decade (Kojola and Heikkinen, 2012). However, intensity and patterns of artificial feeding were similar during the whole study period (author's unpublished data) and, thus, we are confident that artificial feeding did not influence results and how the data from before 2010 relate to the situation after the development of tourism.

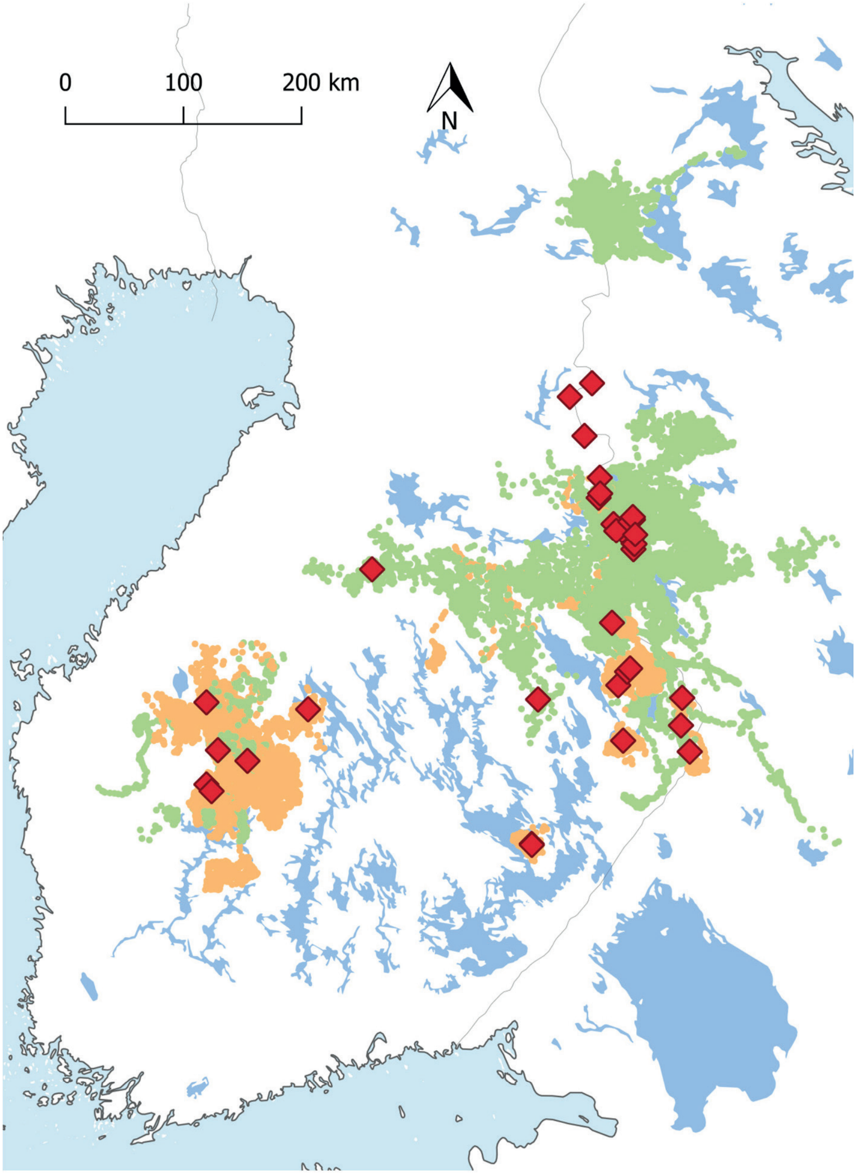


Figure 3.1. Distribution of GPS locations (2002—2015) of 42 brown bear males (green), 24 females (orange) and artificial feeding sites (red diamonds) across south-eastern Finland and Russian Karelia. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2 Data collection, bear capture and artificial feeding sites.

From 2002 to 2013, 71 brown bears (i.e. 115 total captures as some individuals were captured several times; 2002: n = 9; 2003: n = 6; 2004: n = 13; 2005: n = 7; 2006: n = 6; 2007: n = 7; 2008: n = 7; 2009: n = 9; 2010: n = 17; 2011: n = 16; 2012: n = 15; 2013: n = 3) were captured from spring until they entered the winter den. Due to changes in bear physiology and body fat levels, sedative doses were adjusted according to the season of capture, and bears were darted from blinds built at temporary baits. Immobilisation drugs and dosages followed the protocol by Jalanka and Roeken (1990). The tranquilizer contained a mix of medetomidine (50 μg/kg) and ketamine (2 mg/kg), with their proportion adjusted according to the size of the bear (Jalanka and Roeken, 1990). Usually in late summer–early autumn, the spring dosage is increased by 25–50%, and longer needles are used due to increased body fat (Arnemo et al., 2007). Bears were sexed, weighed and a first premolar removed for age determination via cementum annuli counts (Craighead et al., 1970). Permission to capture and handle bears was issued by the County Veterinarian of Oulu, and by the Regional State Administrative Agency of Lahti (Finland). Individuals were fitted with a collar that carried a single 1.5 kg global positioning system (GPS) transmitter (Televilt, Lindesberg, Sweden; Vectronic Airspace, Berlin, Germany). The weight of the collars was less than 1.0–2.0% of the bodyweight of adult females (mean ± SD = 124.6 ± 27.5 kg) and 0.5–1.0% of adult males (mean ± SD = 212 ± 61.4 kg). For subadults, the collars were adjusted to allow individuals to grow and increase in body size, and we used cotton belt so that collars would drop-off before a subadult bear would grow too much to start having problems. Brown bears were categorized as subadult when they were <4 years old. Collars had a pre-programmed drop off mechanism with an average battery life of one year. The drop-off worked well for 40% of collars. When the mechanism did not work due to technical defects, the bear was recaptured and the collar was removed. All collars were removed before the end of the project in 2014. The GPS collars were calibrated to continuously track brown bears, collecting one location every 2 h (n = 74,723 locations, denning period excluded; mean number of locations per individual ± SD = 1966.6 ± 1833.3; mean number of tracking days per individual ± SD = 696 ± 670 days, range = 68–3562 days). Signals from the satellite transmitters were recorded by the ARGOS satellite system (www.cls.fr). We recorded the positional dilution of precision (PDOP) value for all 3-D fixes and the horizontal dilution of precision for 2-D fixes. Following the method developed by D'Eon et al. (2002), we excluded all 2-D fixes. Although this data screening method reduces the data set (i.e. n = 68,943 locations), it allows removing large location errors (Bjørneraas et al., 2010). Thirty known artificial feeding sites of our study area were included in the analyses. On average, 11.1 ± 1.8 feeding sites (range = 7–13) were active per year (until bears started hibernating), and they were rather equally supplied in the mating and hyperphagia periods. Average distance between active artificial feeding sites was 187.6 ± 116.4 km, ranging from less than 1 km to 415.2 km.

2.3 Variable extraction.

We considered the following nine parameters: (1) age (i.e. subadults, single adults and females with cubs); (2) sex; (3) season (i.e. mating vs. hyperphagia seasons); (4) year; (5) number of active artificial feeding sites per year; (6) number of years that the feeding site nearest to the bear's location was active; (7) influence of a feeding site, i.e., a binomial variable showing if the bear visited or not a feeding site (one location within 500 m of a feeding site) at least once per day; (8) the percentage of bear locations within 500 m of a feeding site in a day, which is the sum of the locations inside a 500 m buffer zone around feeding sites divided by the total number of locations recorded on a daily scale, and (9) the time of day (i.e. dawn from 1 h before to 1 h after sunrise; daylight from 1 h after sunrise to 1 h before sunset; dusk from 1 h before to 1 h after sunset; and night from 1 h after sunset to 1 h before sunrise). The sex and age descriptions specified above allow the internal state of the individual to be assessed. The mating season lasts for about three months from den exit to the 31st of July (Dahle and Swenson, 2003a; Spady et al., 2007), and the period of hyperphagia begins the 1st of August and terminates at the end of October when bears enter the den (Ordiz et al., 2017). Lastly, we obtained daily brown bear trajectories by using the adehabitat package (version 0.4.15) for R software (Calenge, 2006). We estimated the following two movement parameters at a daily scale: (1) net distance, i.e. distance travelled between initial position and final position each day; and (2) average daily speed, which is the mean of the step distance (distance between two relocations) divided by the time interval between consecutive locations. To deal with missing fixes we took 4-hour interval and assumed that bears moved in a straight line (but we allowed only 1 missing value per day). Finally, we also estimated the size of the home range at a daily scale per individual (n = 4244 daily home ranges, after removing individuals with less than 15 days of data) using the minimum convex polygon (MCP) method (Dahle and Swenson, 2003b; Mohr, 1947). MCP was chosen over the kernel estimator because it is applicable with less than 30 locations (Seaman et al., 1999). To set the limits of the home range, we used isopleths values of 95% density.

2.4 Statistical analyses.

Probability of use of artificial feeding sites

We built two sets of Generalized Linear Mixed Models (GLMMs), both including the probability that a bear visited a feeding site at least once in a day as a binomial response variable (i.e. 1 = when the percentage of locations within 500 m of the feeding site is higher or equal to 1, or 0 = when the percentage of locations within 500 m of the feeding site is equal to 0). In the first set of models, we included year, season, age, sex and characteristics of the feeding site as explanatory variables. In the second set of models, we included time of day together with age and sex as explanatory variables.

Intensity of use of artificial feeding sites

To explore the intensity of use of artificial feeding sites for those bears that visited a feeding site at least once in a day, we built a set of models which included the number of locations within 500 m of the feeding site as the response variable, i.e. [(number of bear locations within 500 m around a feeding site / total number of locations per day) *100]. Specifically, we used GLMMs with Poisson distribution, and included year, season, internal features of individuals and characteristics of the artificial feedings as explanatory variables. Because the total number of locations recorded varied across days and bears, we included the total number of locations per bear per day as an offset in the models following Ferrari and Comelli (2016) and Wagenius et al. (2012).

Does the use of artificial feeding sites influence movement patterns?

To assess whether movement patterns are influenced by the use of artificial feeding sites, we first built a set of GLMMs with Gamma distribution for each movement parameter (i.e. daily net distance, daily mean speed and daily home range size). Each set of models included one of the above-mentioned variables as a response variable, and the probability of using artificial feeding sites as an explanatory variable. Second, by considering only those bears that visited a feeding site at least once a day, we built a second set of GLMMs with Gamma distribution for each movement parameter, and the intensity of use of artificial feeding sites as an explanatory variable. Whereas the aim of the first set of models is to assess whether movements are affected by the probability of using a feeding site (i.e. if a bear uses or not feeding sites), the second one aims to assess if and how movements are affected by the intensity with which bears use feeding sites (excluding those bears that never use feeding sites).

In all sets of models, to take into account the differences in behaviour between brown bears, we included the individual as a random factor. For analysis of the probability and intensity of use of artificial feeding sites, we constructed a set of competing models that included all possible combinations of predictor variables, from the simplest null model (intercept model only) to a complete model that included all landscape parameters. The best competing model or set of models was chosen based on Akaike's information criterion (AICc). Models with a ΔAICc below 2 were considered as equally competitive. Values of ΔAICc and weighted AICc, indicating the probability that the model selected was the best among the competing candidates (Table 3.1), were calculated as well. Parameter coefficients and the relative importance value (RIV) of each explanatory variable were generated by employing model averaging on the 95% confidence set (Burnham and Anderson, 2002). Models were run in R v. 3.5.1 statistical software (R Foundation for Statistical Computing, 2018) using the lme4 package (Bates et al., 2015). Model generation and model averaging were performed using the MuMIn package (Barton, 2018).

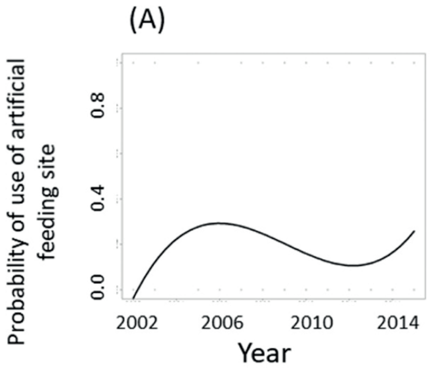
3 Results

Out of a total of 1210 days of male tracking, males visited a feeding site at least once 218 days (18.0%), whereas females visited feeding sites 443 days (13.7%, n = 3223 days of tracking). The frequency of days spent at feeding stations was almost the same for subadults (16.3% of days, n = 1505 days of tracking) and adults (15.3% of days, n = 1826 days of tracking), and slightly less for females with cubs (12.3% of days, n = 1102 days of tracking; Fig. 2). Finally, for all bears, feeding sites were visited a total of 325 days during the mating period (13.8%, n = 2362 days of tracking) compared to 336 days during hyperphagia (16.2%, n = 2071 days of tracking).

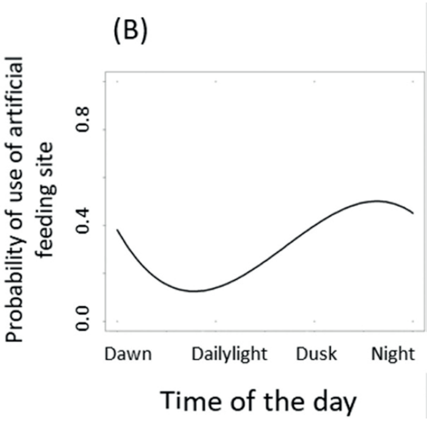
3.1 Probability and intensity of use of artificial feeding sites.

We found that the probability of a brown bear visiting a feeding site was influenced by some external factors, but not by any of the internal factors that we took into account in our analyses. The most parsimonious model included the year and season, as well as the time that the feeding site nearest to the bear's location was active. Specifically, the probability that brown bears visited feeding sites increased **(Table 3.1)**: (1) over the years **(Table 3.1; panel A)**, with the probability of a brown bear visiting a feeding site being higher when the latter was opened for several years in a row; and (2) during the hyperphagia period. The probability of a brown bear visiting a feeding site increased from 0.14 to 0.18 depending on the time the feeding site was active (from 1 to 25 years); that is, the longer the duration of feeding site activity over the years, the higher the probability of receiving a visit from a bear. We also found that the probability of a brown bear visiting a feeding site was influenced by the time of day, being higher at night (**Table 3.1; panel B**) for all bear classes **(Figure 3.2)**. However, no spatial overlap occurred between the radio-collared females with cubs and adult males, which used different feeding sites **(Figure 3.3)**. In addition, we also found that the intensity of use of feeding sites was higher when the feeding site was open several years in a row **(Table 3.1; panel C)**.

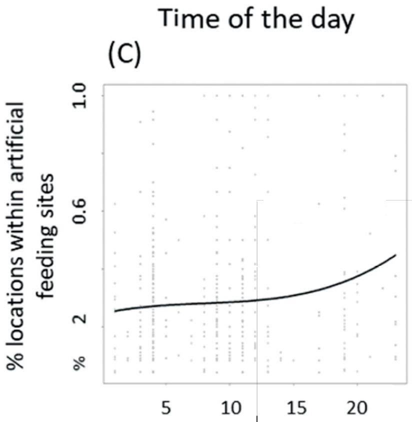
Table 3.1. Model-averaged coefficients, AICc, ΔAICc, weighted AICc and RIV values for the probability (at yearly, seasonal and daily scales) and intensity (at yearly and seasonal scales) of use of artificial feeding sites against age and sex, and characteristics of the feeding sites (i.e. number of active feeding sites: Nfeed_site; and time (i.e. years) the feeding sites were active: Time_open), depending on the model. Competitive models are ordered from the highest to the lowest AICc value (best model). Panels A–C are graphical examples of some variables influencing the probability and intensity of use of feeding sites.



Dependent variable	Competing models		AICc	ΔAICc	Weight AICc
	Age+NFeed_site+Time_open +Year + Season		2836.34	1.81	0.12
	Age+ Time_open+Year + Season		**2834.53**	**0.00**	**0.28**
Probability of use of the artificial feeding sites (yearly and seasonal temporal scales)	Explanatory variables	Model-averaged coefficients and relative importance values			
		β	SE	Cl	RIV
	Intercept	-3,30	0.67	-4.61;-1.98	
	Time_open	**0,25**	**0.08**	**0.09;0.40**	**0.99**
	Year	**0.37**	**0.15**	**0.08;0.66**	**0.91**
	Season	**0.22**	**0.11**	**0.00;0.43**	**0.74**
	NFeed_site	0.08	0.12	-0.15;0.33	0.34
	Adults	-0.44	0.47	-1.35;0.48	0.79
	Females w/clubs	-0.75	0.45	-1.62;0.12	0.79
	Sex	-0.03	0.98	-1.96;1.90	0.25



Dependent variable	Competing models		AICc	ΔAICc	Weight AICc
	Age+Sex+Time of the day		12063.77	1.95	0.27
	Age+ Time of the day		**12061.82**	**0.00**	**0.73**
Probability of use of the artificial feeding sites (daily and temporal scales)	Explanatory variables	Model-averaged coefficients and relative importance values			
		β	SE	Cl	RIV
	Intercept	-0,33	0.67	-4.61;-1.98	
	Adults	**-0.81**	**0.08**	**0.09;0.40**	**0.99**
	Females w/cubs	**-0.30**	**0.15**	**0.08;0.66**	**0.91**
	Daylight/Night	**-1.43**	**0.11**	**0.00;0.43**	**0.74**
	Night/Dusk	0.10	0.12	-0.15;0.33	0.34
	Night/Night	0.43	0.47	-1.35;0.48	0.79
	Sex	0.08	0.45	-1.62;0.12	0.79



	Competing models		AICc	ΔAICc	Weight AICc
Probability of use of the artificial feeding sites (daily and temporal scales)	Age+Time _open + Season		12063.77	1.95	0.27
	Age+Time _open + Year		**12061.82**	**0.00**	**0.73**
	Age+NFeed_site+Time_open +Year+Season				
	Age+Time _open + Year+Season				
	Age+NFeed_site+Time_open				
	Age+NFeed_site+Time_open+-Season				
	Explanatory variables	Model-averaged coefficients and relative importance values β	SE	Cl	RIV
	Intercept	-1,18	0.15	-1.58;-1.15	
	Time_open	**0.08**	0.04	0.01;0.16	**0.80**
	Year	-0.06	0.06	-0.17;0.06	**0.37**
	Season	0.08	0.05	-0.01;0.16	**0.61**
	NFeed_site	-0.05	0.03	-0.12;0.01	**0.58**
	Adults	-0.26	0.16	-0.58;0.06	**0.83**
	Females w/cubs	-0.10	0.16	-0.41;0.21	**0.83**
	Sex	0.04	0.15	-0.32;0.34	**0.25**

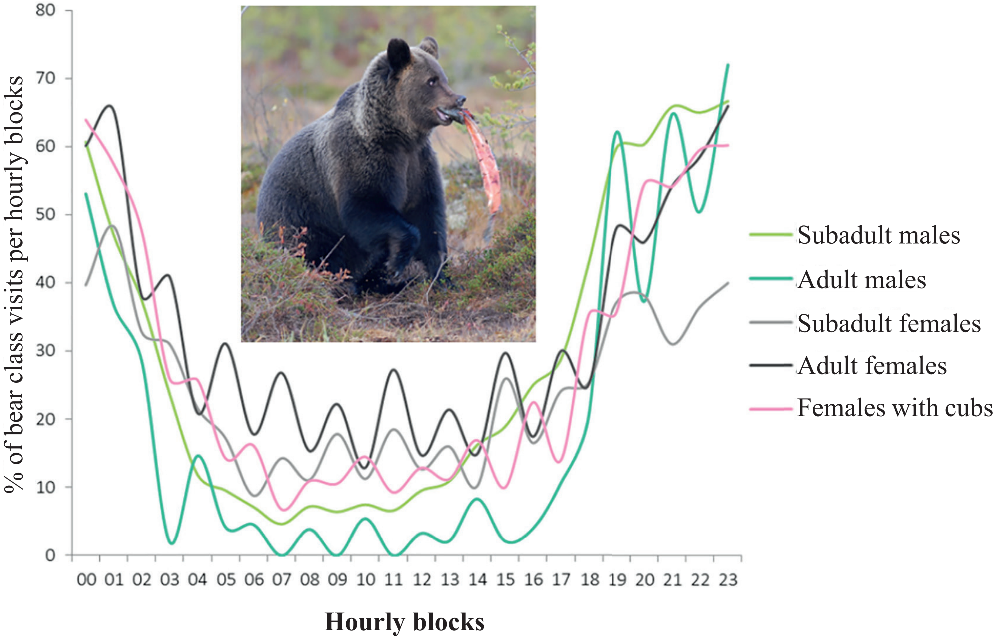


Figure 3.2. All bear classes, i.e. adults, subadults and females with cubs, visited the feeding sites with the same crepuscular and nocturnal patterns, with visits during the day being rare (brown bear picture: V. Penteriani).

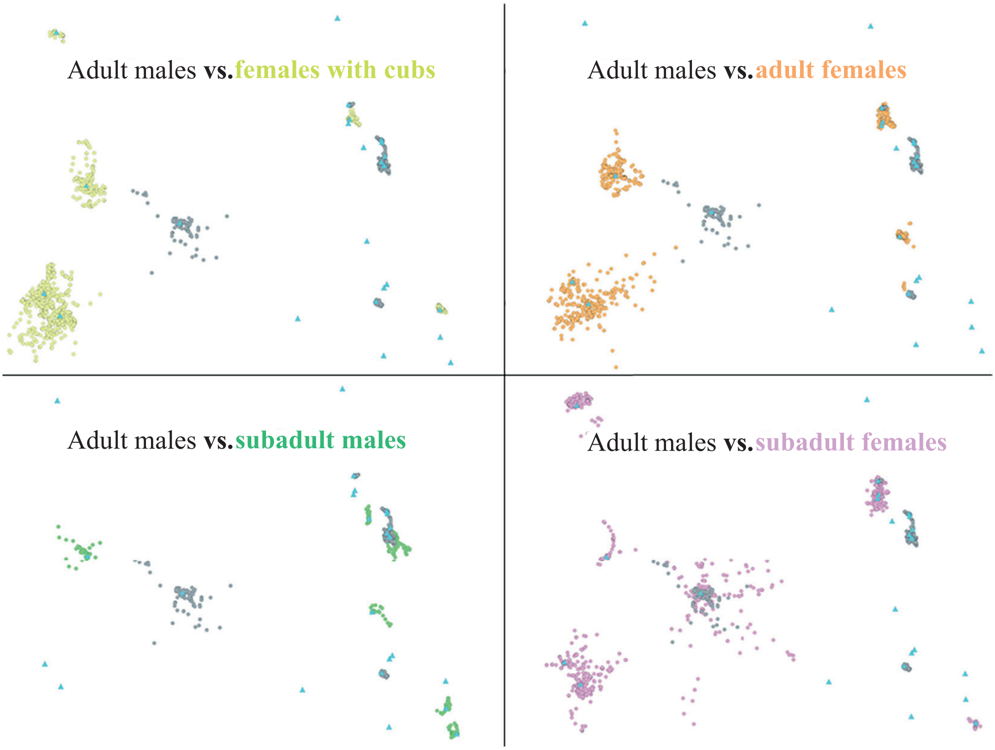


Figure 3.3. Spatial overlaps of the different classes of radio-collared bears (n = 71 individuals) at feeding sites. Radio-collared females with cubs and adult males do not overlap. Light blue triangles represent feeding sites. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2 The use of artificial feeding sites influences movement patterns.

The use of artificial feedings influenced some movement patterns. On one hand, the probability of using an artificial feeding site affected the daily net distance only (bears using feeding sites: 3.5 ± 4.5 km, range: 0–29 km; bears not using feeding sites: 4.4 ± 4.9 km, range: 0–47 km). Specifically, bears moved shorter daily net distances when the probability of visiting artificial feeding sites was high ($\beta = -0.22$, CI = −0.332; −0.113). On the other hand, the intensity of use of feeding sites influenced net distance ($\beta = -0.01$, CI = −0.024; −0.016; **Figure 3.4A**), average daily speed ($\beta = -0.01$, CI = −0.013; −0.010; **Figure 3.4B**) and daily home range size ($\beta = -0.02$, CI = −0.029; −0.020; **Figure 3.4C**). That is, bears moved shorter distances, at a lower speed, and within smaller home ranges when the intensity of use of feeding sites increased.

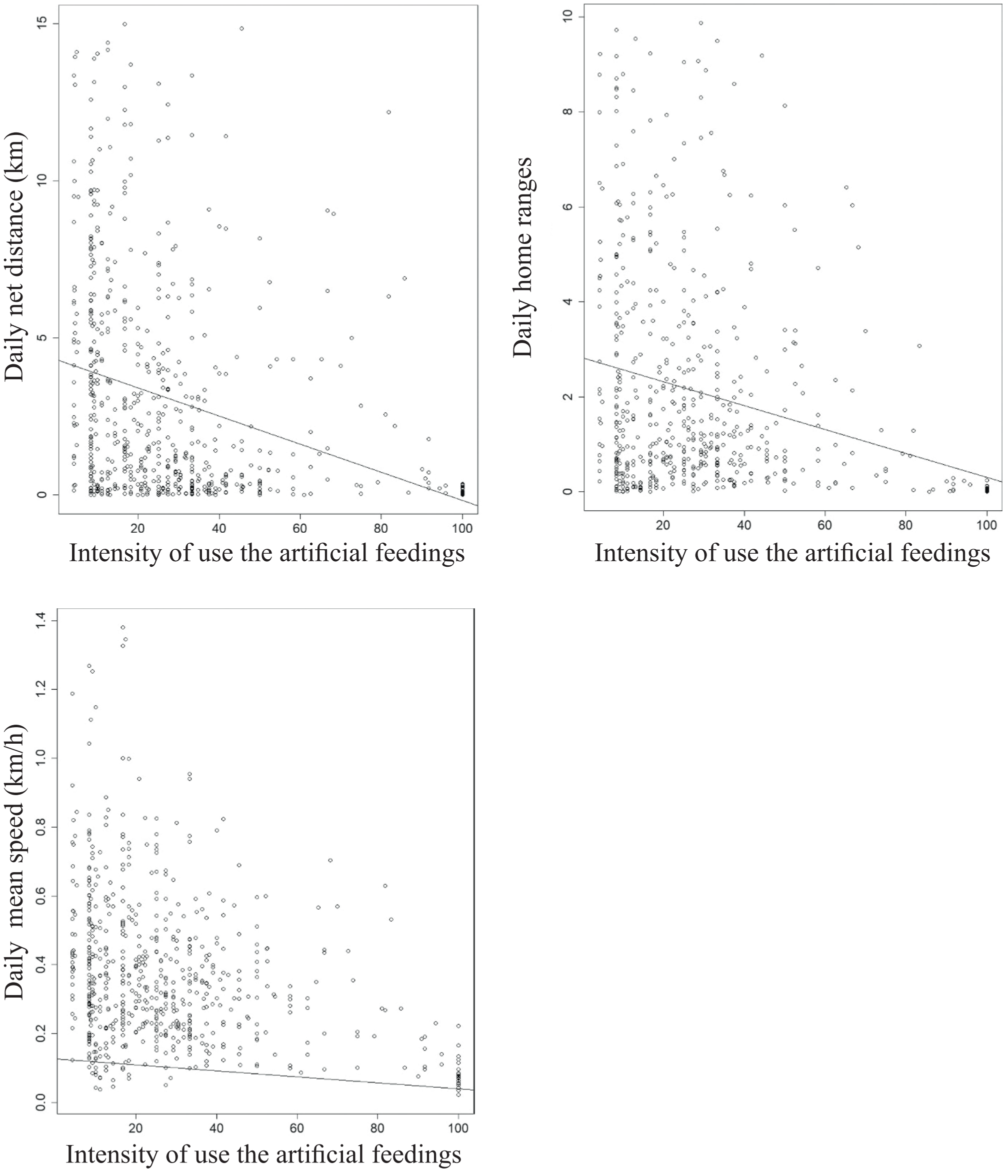


Figure 3.4. Effects of the intensity of use of artificial feeding sites on daily net distance, speed and home range sizes.

4 Discussion

Brown bears in boreal habitats are sensitive to the presence of artificial feeding sites within their home ranges. On one hand, both the probability of a particular feeding site being used and the intensity of its use were positively correlated to the stability of this food resource over time. This is probably due to individual spatial memory and learning, which are advantageous in environments with a relatively high level of resource predictability (Fagan et al., 2013; Mery, 2013; Riotte-Lambert and Matthiopoulos, 2020), as artificial feeding sites are. On the other hand, the use of feeding sites was not clearly related to sex, age class or reproductive status (subadults, adults and females with cubs). Feeding sites were visited predominately at night (twilight included) and slightly more during hyperphagia.

Brown bears using garbage dumps in northeast Turkey were also observed to increase visitation rates during hyperphagia (Cozzi et al., 2016). Given the importance of storing fat during hyperphagia, foraging is the main activity of brown bears during this season (González-Bernardo et al., 2020; Swenson et al., 2020). This may contribute to explaining the more intense use of feeding sites during the brown bears' hyperphagia period, when the nutritional impact of feeding sites should be higher than in other periods. During hyperphagia, bears must consume large amounts of food and they may need to make large displacements in order to find sufficient high-energy foods to build up large fat reserves before hibernation (Swenson et al., 2020). By staying close to the feeding sites, fed bears in our study area should not need to travel long distances or move quickly in order to find food, probably indicating that they are meeting a relevant part of their energetic demands at the feeding sites during hyperphagia (Massé et al., 2014). Yet, the relatively low visitation rates throughout the year, i.e. feeding sites were visited 13.8% and 16.2% of the days during the mating and hyperphagia periods, respectively, might reveal that Karelian brown bears are not strictly dependent on artificial feeding, probably due to abundant local natural food resources (e.g. wild berries are available onwards late July, author's unpublished data). If during hyperphagia, which is crucial for successful bear hibernation and cub production (Farley and Robbins, 1995; González-Bernardo et al., 2020; López-Alfaro et al., 2013), brown bears invest a large proportion of time in security (primarily nocturnal foraging to avoid humans and conspecific aggression), this might reduce time for foraging and imply high foraging costs (Brown and Kotler, 2004). However, we cannot discard the possibility that intraspecific competition might have also contributed to reduce bear visitation rates to artificial feeding sites. Compared to the densities reported in other parts of Europe (e.g. 14 artificial feeding sites/100 km2 in Bieszczady Mountains in Poland; Bojarska et al., 2019), it seems that artificial feeding site density in our study area is low. This would increase chances that intraspecific competition for food at these sites could be an important factor contributing to low visitation rates at the individual level.

Artificial feeding caused brown bears to move short distances at a low speed within small home ranges when they increased the intensity of use of feeding sites. Generally, individuals that travel quickly and over long distances may exploit local resources less thoroughly and need more energy for movement, but they can potentially encounter higher quality resource patches by moving more. In fact, individuals with greater displacements may encounter and cross more habitat patches per day than individuals with shorter displacement distances (Hertel et al., 2019). But this possibility, which can occur in animals depending on natural resources only, is probably less important when part of the diet is composed of predictable and continuously renewed resources, as in the case of artificial feeding sites. Actually, at a within-resource-patch scale, as a response to environmental predictability (i.e. continuous resource availability at given spatial localities), many animals use an area-restricted search (also called 'intensive search') strategy by adopting a more tortuous path or reducing speed when moving in a profitable area (Benhamou, 1994). These restricted patterns of movements are typical of moving organisms faced with constancy over time and space, which involves fixed, nondepletable (or immediately renewable) and nonmoving resources (Riotte-Lambert and Matthiopoulos, 2020). This tendency of artificially fed brown bears to restrict their movements (as also observed in North American brown bears Ursus arctos horribilis; Blanchard and Knight, 1991) might be revealing an increase in fidelity to places with supplementary foods that, as an end result, may provoke changes in bear behaviour through 'domestication', reduce population range expansion and diminish long-distance displacements (Cozzi et al., 2016; Selva et al., 2017).

Large carnivores, such as brown bears, have shown to alter their behaviour to reduce encounters with humans by becoming more nocturnal (Ordiz et al., 2014, Ordiz et al., 2011). Legal hunting, which takes place during the day, is the most important cause of mortality for brown bears in Scandinavia, e.g. >80% of bear deaths in Sweden between 1984 and 2006 (Bischof et al., 2009). Thus, nocturnal habits help bears to avoid encounters with people in general and, more specifically, to reduce mortality risk in areas where human activities like hunting are practiced. This might help explain the prevalently nocturnal patterns of feeding site visitations and the influence of artificial feeding on space use and movements of bears recorded for the Karelian subpopulation, an explanation that has been proposed for brown bears moving in landscapes characterized by high densities of artificial feeding sites for hunting purposes in both Slovenia (Jerina et al., 2012) and Sweden (Zedrosser et al., 2013). Indeed, the distribution of visits within a 24-hour period showed a clear bimodal pattern, with most visits registered during the early morning and evening hours, and the fewest visits being registered during the middle of the day. But, since brown bear general activity patterns frequently show bimodal activity with peaks around evening and morning, and lowest activity in midday (Swenson et al., 2020), this behaviour cannot be entirely attributed to the presence of artificial feeding sites and risk of hunting mortality.

In contrast to previous studies, we also observed that subadults, adults and females with cubs visited artificial feeding sites predominantly between sunset and sunrise (**Figure 3.2**). Thus, there was no apparent temporal avoidance to reduce intraspecific conflicts between, for example, adult males and subadults or females with cubs to avoid the risks of infanticide, and no avoidance of risky dominance hierarchies among different bear classes (Jerina, 2012; Penteriani et al., 2018, Penteriani et al., 2017; Steyaert et al., 2012; Zedrosser et al., 2013). To our knowledge, this is the first record of the apparent lack of avoidance mechanisms of females with cubs and subadults towards potentially aggressive adult males at feeding sites and, more generally, at sources of anthropogenic food. We suggest that this might be due to the schedule of daily food replenishing of Karelian artificial feeding sites, i.e. primarily in late afternoon (author's unpublished data). This means that most of the food is available from sunset to sunrise only, whereas the amount of food is irrelevant during the day. Thus, if bear classes at risk of adult male aggression want to find food there, they need to run the risk of visiting artificial feeding sites at a decreasing rate from sunset to sunrise, as Karelian radio-collared bears effectively did (**Figure 3.2**). Such a human-induced pattern of largely nocturnal bear visits to artificial feeding sites has the potential to trap females with cubs and subadults in a possibly highly risky time bracket when feeding. An effective way to avoid such a problem would be to require the people/companies that manage artificial feeding sites for bears: (a) to include in their feeding schedule at least one replenishment of feeding sites a little after sunrise, thus offering subadults and females with cubs the opportunity to choose a safer visitation time, as reported in other areas (Jerina et al., 2012; Zedrosser et al., 2013); (b) use foods that cannot be quickly reduced by seagulls and ravens coming to exploit these resources after sunrise; and/or (c) placing food in boxes with heavy lids or/and on raised platforms could further prevent birds or ungulates feeding (Fležar et al., 2019).

Even if we cannot radio-collar all the bears using each feeding site, the absence of any spatial overlap between marked females with cubs and adult males might indicate that females with cubs may use a mechanism of spatial avoidance (Steyaert et al., 2012) by predominantly using those feeding sites that are not used by adult males (**Figure 3.3**). This possibility is also consistent with the patterns of spatial overlap recorded for subadults (both males and females), which largely overlap with adult males (**Figure 3.3**). However, we cannot discard the influence of an additional, not mutually exclusive effect on artificial feeding site visitation patterns, i.e. the relatively low bear densities in Finland compared to other parts of Europe where artificial feeding is practiced, which might enable bears to easily avoid dangerous conspecifics spatially.

Highly predictable and continuously available anthropogenic food has substantial ecological impacts on movement patterns in another ursid, the American black bear Ursus americanus, for which the practice of baiting for hunting purposes is widespread in North America. In fact, as we detected in brown bears, fed bears showed reduced annual and seasonal home ranges and decrease movement rates, especially in autumn and during the daytime in all seasons (Massé et al., 2014). But artificial feeding does not only affect bear species. For example, analogous home range contractions have been reported for the red deer Cervus elaphus, potentially leading to increased disease transmission and intra- and interspecific (sympatric wild and domestic ungulates, respectively) competition due to the high deer densities around feeding sites. And this collateral effect of artificial feeding can result in the exact opposite of what was intended by managers, i.e. increase deer trophy value to hunters and reduce forest damages (Jerina, 2012).

Because frequenting artificial feeding sites modifies individual behaviour, thus affecting the overall energy budget of bears, and artificial feeding has the potential to produce several collateral negative effects on bear ecology, behaviour and health (Kavčič et al., 2015; Penteriani et al., 2018, Penteriani et al., 2017; Skuban et al., 2016), the recorded changes in movement patterns add more weight to the evidence that artificial feeding may have important but overlooked implications for bear ecology and management. Thus, managers should focus on minimizing human-induced behaviours in large carnivores that might cause fitness disadvantages for the affected individuals and as a result have the potential to distress the ecosystems in which large carnivores play key ecological roles (Ordiz et al., 2014). Though some displacements of bears due to the presence of feeding sites can occur with minimal nutritional effects, when estimating the impacts of artificial feeding on local bear populations we should always consider local factors such as the carrying capacity of the area relative to the existing bear population, annual availability and distance of alternative food resources, as well as the distance and energy needed to move to alternative food sources. Indeed, potential detrimental effects on fed bears may be strictly dependent on local conditions and change as a function of the bear population and landscape features. Thus, every area should be regarded as a separate case and the suitability and location of brown bear feeding should be evaluated on the basis of the conservation status of the bear population, bear behaviour and local density, year-to-year availability of food resources and their use, as well as anthropogenic activities that may interact with bears (Morales-González et al., 2020).

4

Movement patterns of subadult bears during the dispersal process

Preamble

Relying on the results of **Chapters 2** and **3**, we aimed to acquire direct and precise information on the routes and modes of movement of subadult bears throughout the dispersal process. To understand the rhythms of subadult bear activity during dispersal as a function of habitat and the different periods that characterize the bear's life cycle, namely:

(a) when bears emerge from the den after hibernation (early spring);

(b) during the adult mating season (spring to early summer);

(c) during the hyperphagia period (late summer to autumn) and

(d) during the weeks preceding hibernation (winter).

Paper 3 : published -

Age Ain’t Nothing But a Number: factors other than age shape brown bear movement patterns

Vincenzo Penteriani[1], Cindy Lamamy[1], Ilpo Kojola, Samueli Heikkinen, Cédric Vermeulen and Maria Del Mar Delgado

This paper has been published in Animal Behaviour in January 2022.

DOI: 10.1016/j.anbehav.2021.10.020

[1] *These authors contributed equally to this work.*

Abstract

Movement patterns may reflect individual age-specific variation. For example, individuals that sample novel areas (e.g. natal dispersal) may show different movements from those of adults settling in more stable areas and moving around local environments to procure food and shelter. The long-term study of a solitary large carnivore, the brown bear, *Ursus arctos*, allowed us to test for age-related differences in movement behaviour and, more specifically, for potential inter- versus intraindividual variation among adult versus subadult bears. In addition to age, we also explored factors other than individual characteristics that have the potential to determine movement patterns: sex, season (mating versus hyperphagia) and body weight. The contribution of age to movement patterns seemed to be irrelevant, most of the observed movement patterns being primarily explained by season and body weight. Moreover, intraindividual movements within a home range were more marked among subadult brown bears. We hypothesize that two mechanisms may lead to subadults and adults moving similarly. First, both must hibernate and, consequently, need to store energy during hyperphagia. Second, although triggered by different factors, both make erratic/long movements after hibernation, for dispersal (subadults) or mating (adults), which might contribute to shaping similar movement patterns. Different motivations could thus be expressed through the same behavioural patterns, and equifinality (i.e. similar ecological patterns emerge from different initial conditions) might be considered an intrinsic property of animal behaviours.

Keywords: Equifinality, Home range, Hyperphagia, Mating, Movement ecology, Net distance, Speed, *Ursus arctos*.

1 Introduction

Animals differ in their expression of a variety of behaviours, and this can be due to a multitude of intrinsic factors, such as age, sex, size and internal state. In addition to differences in behaviour attributable to such factors, animals also exhibit consistent individual differences in behaviour for a wide range of traits, across time and contexts (Nilsson et al., 2014). Movement is a central population process, and some important population phenomena depend on individual movement behaviour (Abrahms et al., 2020; Jingxuan & Jiang, 2020; Patterson et al., 2008). The needs and experience of animals change throughout life, and movement patterns should reflect this age-specific variation (Delgado et al., 2009; Delgado et al., 2010; Graf et al., 2016). For example, subadult individuals that actively sample novel areas for short periods, for example during natal dispersal, should show different movement behaviours from adults, which settle more permanently in an area (Delgado et al., 2009). The dispersal of juveniles is inherently riskier than remaining in a well-known area (Fletcher et al., 2019), which is typical of adults that generally move around local environments to procure food, find shelter and seek mating opportunities (Abrahms et al., 2020; Fletcher et al., 2019). Longer residence times than those that characterize areas crossed during dispersal and, consequently, more accurate spatial information allow an individual to reduce uncertainty about its position with respect to given locations and resources (Fagan et al., 2013). For example, individual differences in movement patterns related to age have been found in moose, *Alces alces*, with older males having larger home ranges than younger individuals (Cederlund & Sand, 1994), wild boars, *Sus scrofa* (Keuling et al., 2008), and Eurasian beavers, *Castor fiber* (Graf et al., 2016). Different extents of extraterritorial movement have also been observed between adult and yearling wolves, *Canis lupus* (Messier, 1985). Dispersing individuals have a high risk of mortality (e.g. humaninduced causes, resource deprivation, unfavourable environmental conditions; Bonte et al., 2012). Moreover, dispersing through some environments is more challenging than moving through others, leading to differences in movement patterns (Fletcher et al., 2019). Thus, analyses of animal movements that include the different stages that individuals go through over their lifetime, that is, from natal dispersal to adulthood and mating when individuals shift from a wandering to a more sedentary phase characterized by settlement in fairly fixed areas of activity (Delgado & Penteriani, 2008; Delgado et al., 2009), represent a unique opportunity to explore possible age-specific variation in movement patterns, one of the notable gaps in movement ecology (Nathan et al., 2008). Although many facets of animal movements have been extensively studied for a long time (Fagan et al., 2013; Fletcher et al., 2019; Nilsson et al., 2014), how important age is in driving animal movement is still an open question in movement ecology. We studied a solitary large carnivore, the brown bear, Ursus arctos, a species with overlapping home ranges (Dahle & Swenson, 2003b). Individuals disperse from their natal home range as subadults (1e4 years old; Støen et al., 2006; Zedrosser et al., 2007). Although both females and males may disperse long distances (Shirane et al., 2019), females usually tend to disperse less often or over shorter distances than males (Støen et al., 2006). We examined a data series from a long-term study (12 years) of brown bears in southern and central Finland and Russian Karelia. Our main aim was to characterize and compare the movement behaviour of subadults versus adults. We further investigated the extent of individual variation with the aim of understanding whether inter-and intraindividual differences in movement behaviours depend on individual age. In particular, because adult brown bears tend to move short distances within well-established home ranges (e.g. for mating, Støen et al., 2006; Zedrosser et al., 2007), we predicted their interindividual variation would be higher than their intraindividual variation. Similarly, we also predicted that subadult individuals, which usually move across largely unknown surroundings and over large distances, might have higher intrathan interindividual variation. In addition to age, we predicted that other individual characteristics, such as sex, seasonal requirements (i.e. mating and hyperphagia) and/or physical characteristics (e.g. body weight) might also affect movements in (1) a nonmutually exclusive way or (2) in a more prevalent way than age, thus hindering the effect of age on movement patterns. We hypothesized that three distinct scenarios are possible. First, owing to the diverse needs of individuals of different ages, movement patterns of subadult and adult bears may differ, with, for example, longer movements of subadults (Pop et al., 2018), as they are mainly influenced by natal dispersal. In the second scenario, age has less effect because of the requirements of a given season, for example longer movements over large areas during the mating season (Dahle & Swenson, 2003a, 2003b) or an increase in searching for food during the hyperphagia season (Penteriani & Melletti, 2021) because of physiological constraints during hibernation (Gonzalez- Bernardo et al., 2020). Consequently, movement patterns will be mostly the result of different seasonal requirements rather than age. Finally, movement behaviour may be affected by interactions between intrinsic (e.g. age, sex, body size) and extrinsic (seasonal requirements of bears) factors (Kay et al., 2017).

2 Methods

2.1 Data Collection

From 2002 to 2013, we captured and radio-collared 57 brown bears (**Table 4.1**) inhabiting southern and central Finland and Russian Karelia (for more details on the study area, see Penteriani et al., 2021). When captured (for more details on the capture protocol followed, see Penteriani et al., 2021), bears were sexed and weighed. Additionally, they were classified as subadults (1-4 years old) or adults (> 5 years old; Craighead et al., 1970, Støen et al., 2006; Zedrosser et al., 2007). Bears were fitted with GPS transmitters (Televilt, Lindesberg, Sweden; Vectronic Airspace, Berlin, Germany; for more information see Penteriani et al., 2021) that collected one location every 2 h (N = 74 724 locations excluding the denning period), corresponding to 28 789 locations for subadults and 45 935 locations for adults (mean number of locations per individual ± SD = 978.2 ± 957.2). The weight of the collars (ca. 600 g) was less than 1.0-2.0% of the body weight of adult females (mean ± SD = 124.6 ± 27.5 kg) and 0.5-1.0% of adult males (mean ± SD = 212 ± 61.4 kg). We recorded the positional dilution of precision value for all 3-D fixes and the horizontal dilution of precision for 2-D fixes. Because 2-D fixes have higher location error, we removed them following the method developed by D'Eon et al., (2002) to increase the accuracy of the data and therefore of the movement metrics. Although this datascreening method reduces the data set, it allows us to detect a high percentage of large location errors (Bjørneraas et al., 2010). By using the package adehabitat, version 0.4.15, for R software (Calenge, 2006), we estimated the following movement parameters for each daily trajectory: (1) average daily speed; (2) mean net distance, i.e. mean distance travelled between the initial position and the final position on a daily scale; (3) total distance, which is the sum of the distance between successive relocations on the same daily trajectory; and (4) the size of the home range (km2) at a daily scale per individual using the local convex hull (LoCoH) method (Getz et al., 2007; Getz & Wilmers, 2004). To construct the daily LoCoH, we used the fixed number of points procedure, such that we first subsampled those days with at least eight locations, and then selected k = 7 as the optimum value parameter for constructing the LoCoH with our data set (for more details of this method, see Getz et al., 2007). We considered the following explanatory variables: (1) age (excluding females with cubs; Gardner et al., 2014); (2) sex; (3) season, i.e. mating (Dahle & Swenson, 2003b; Spady et al., 2007) versus hyperphagia (Ordiz et al., 2017); and (4) body weight (kg)

Table 4.1. Characteristics of daily movement patterns of subadult (13 males and 9 females) and adult (25 males and 10 females) brown bears.

	Subadults	**Adults**
Speed (m/s)	0.01 ± 0.08 (0.0-0,6;2275)	0.1 ± 0.09 (0.0-1.0; 2560)
Mean net distance (m)	14 637 ± 13 338 (84-81 474;2275	33 645 ± 36 640 (241-155 548; 2560)
Total distance (m)	9049 ± 7640 (20-136 851; 2275	9819 ± 9830 (38-98 315; 2560)
Home range size (km^2)	4.5 ± 7.4 (0.02-85.9; 718)	5.1 ± 10.3 (0.02-133.3; 767)
	Subadults males	**Subadults females**
Speed (m/s)	0.1 ± 0.1 (0.0-0.6; 882)	0.1 ± 0.1 (0.0-0.6; 1369)
Mean net distance (m)	17 442 ± 15 710 (84-81 474; 882)	12 145 ± 9621 (157- 56 354;1369)
Total distance (m)	9715 ± 8796 (20-136 851; 882)	8544 ± 6630 (20-73 902; 1369)
Home range size (km^2)	3.8 ± 6.7 (0.02-85.9; 436)	5.7 ± 8.3 (0.02-41.0; 327)
	Adults males	**Adults females**
Speed (m/s)	0.1 ± 0.1 (0.0-1.0; 1829)	0.1 ± 0.1 (0.0-0.5; 755)
Mean net distance (m)	38 266 ± 39 718 (314- 155 548;1829)	23 087 ± 24 334 (241- 88 588;755)
Total distance (m)	10 625 ± 11 108 (29-98 315; 1829)	7978 ± 5346 (38-40 907; 755)
Home range size (km^2)	3.5 ± 4.6 (0.02-133.3; 440)	6.4 ± 12.9 (0.02-133.3; 440)

Means are given ± SD, with range and number of locations per bear group in parentheses. N = 55 756 locations for the total of 57 individuals.

2.2 Ethical Note

For subadults, collars had a preprogrammed drop-off mechanism with an average battery life of 1 year. Whenever the drop-off did not occur by the scheduled time owing to technical flaws, the bear was recaptured, and the collar was removed manually. All collars were removed before the end of the project in 2014. Permission to capture and manipulate bears was issued by the County Veterinarian of Oulu and the Regional State Administrative Agency of Lahti (Finland). This research adheres to the ASAB/ABS Guidelines for the use of animals in research. The capturing of bears met the guidelines issued by the Animal Care and Use Committee at the University of Oulu (OYEKT-6e99), and permits were provided by the provincial government of Oulu (OLH-01951/Ym-23). During bear captures and tracking no adverse effects of manipulations were observed.

2.3 Statistical Analyses

We studied whether and how subadult and adult brown bears differ in their movement behaviours taking sex, body weight and season into account. As the effect of sex may not necessarily be additive with body weight and age, we also included their interaction terms. We fitted linear mixed models (LMMs) with the four calculated movement parameters as response variables. Visual inspection of the data and model residuals was performed for all models to check for model assumptions and the presence of outliers. After we log-transformed the speed and home range variables, the residuals for all response variables were normally distributed and we therefore fitted the models using a normal distribution. In each model, we included the autoregressive correlation structure AR(1) to take the fact that daily movement parameters were temporally autocorrelated into account. To account for repeated but unbalanced measurements within individuals, we included the individual as a random factor. The set of competing models was generated with all subsets of explanatory variables in the full model and then we employed model averaging on the 95% confidence set to derive values of the Akaike information criterion corrected for small sample size (AICc), ΔAICc, weighted AICc (w) and parameter coefficients of each explanatory variable using the full-model averaging approach. Following standard procedures, we calculated the weighted AICc for each candidate model (wi) as the probability of model i being the best-approximating model from the set of candidate models. We considered models with ΔAICc values lower than 2 as equally competitive. When there might be high model selection uncertainty, model averaging allows formal inference based on the entire set of models considered (Grueber et al., 2011; Symonds & Moussalli, 2011). LMMs were run using the lme4 package (Bates & Maechler, 2009), while multimodel inference and model averaging were run using the MuMIn package (Barton, 2018). Finally, to assess interindividual variation in movement behaviours for both subadult and adult bears, we rebuilt the most parsimonious models selected above. We estimated the proportion of the variance explained by the random intercept effect, by accounting for the variance explained by the fixed effects (i.e. adjusted interindividual repeatability). We used the rptR package in R (Nakagawa & Schielzeth, 2013; Stoffel et al., 2017) to calculate interindividual repeatability values (R), standard errors, 95% confidence intervals (CI) and statistical significance of repeatability. All analyses were performed using R 3.5.0 (R Development Core Team, 2018).

3 Results

Age was never included as an explanatory variable in the most parsimonious models analysing daily brown bear movement behaviour (Table 4.2), indicating that movement patterns and the area prospected by individuals did not differ between age classes (Figure 4.1). Factors other than age did influence bear movement patterns, even if only slightly (see R2 in Table 4.2). Season, sex and bodyweight affected daily movement parameters more than age (Table 4.2), supporting our third hypothesis. In particular, at the daily scale (see Table 4.2 for parameter estimates of the models): (1) individuals moved slightly faster, over larger distances and had larger home ranges during the mating season (speed: mean ± SD = 0.1 ± 0.06 m/s; total distance = 8.8 ± 6.4 km; home range = 6.0 ± 11.4 km2) than during the hyperphagia season (speed = 0.08 ± 0.07m/s; total distance = 7.3 ± 5.4 km; home range = 3.5 ± 5.7 km2); (2) males moved slightly shorter net distances (4.1 ± 2.9 km) but travelled over larger total distances (8.1 ± 5.2 km) within a smaller home range (3.6 ± 5.9 km2) than females (daily net distance = 5.5 ± 2.7 km; total distance = 7.8 ± 6.6 km; home range = 6.1 ± 11.4 km2); and (3) the heaviest bears had the smallest daily home ranges (Table 4.2). Interindividual variation in movement behaviours was moderate (R; Figure 4.1), indicating that individuals mostly adopted flexible movement behaviour. For interindividual differences adjusted Rs ranged from 12% to 33% of the variation in the movement parameters considered (Figure 4.1). Notably, interindividual variation was very similar for both subadult and adult bears for all movement parameters, except home range. Variation among home ranges was substantially higher among subadults than adults **(Figure 4.1).**

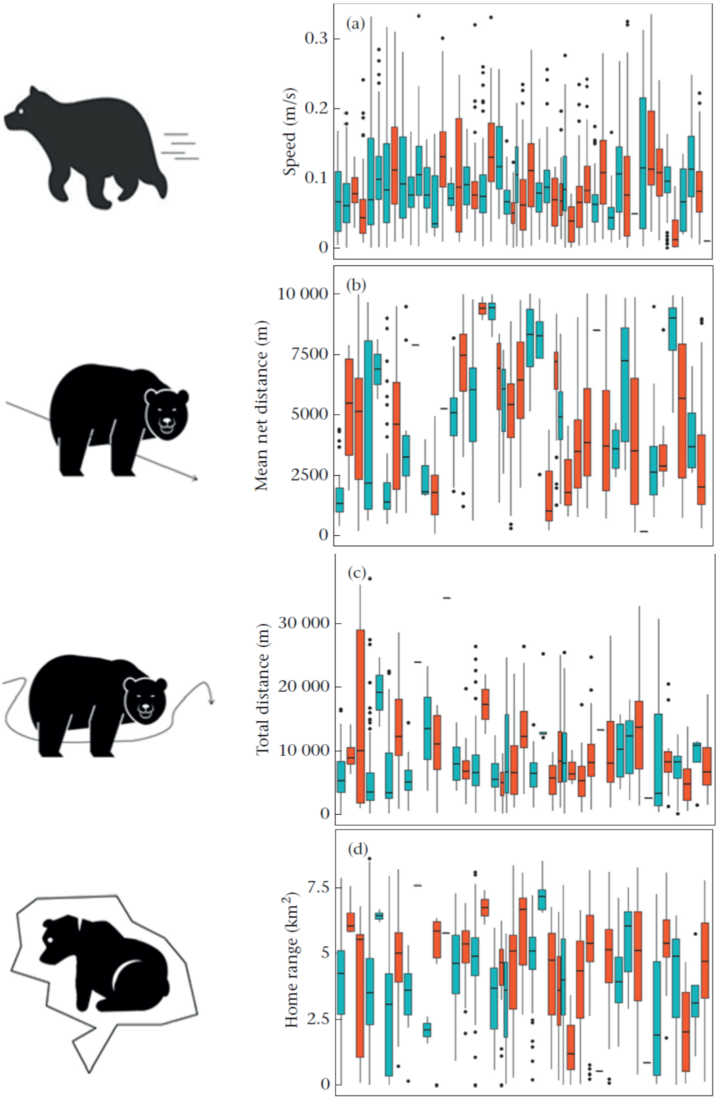
Table 4.2. Model selection table and model-averaged coefficients for movement patterns of subadult (13 males and 9 females) and adult (25 males and 10 females) brown bears.

Dependent variable	Explanatory variables	Model averaged coefficients			Cl
		β	SE	z	
Speed (N=2619, R^2m=0.05; R^2c=0.09),competing model =season, *df*=5, AICc = 7925.53, ΔAICc = 0.00, weight=0,97					
	Intercept	1.06e-01	0.77e-03	28.30	(7690.53; 12,05.04)
	Season(hyperphagia)	2.79e-0.2	3.82-03	7.29	(1744.07; 268.95)
	Sex(male)	-2.66e-04	1.88e-03	0.14	(-7047,20.1612.17)
	Body weight	5.61e07	1.66e-04	0.003	(-2691.73; 308.94)
	Age (adult)	3.09e-06	4.25e-04	0.007	(-2940.05; 4595.09)
	Body weight*sex(male)	-2.93e-08	2.96e-05	0.001	(-7439.56; 3586.62)
	Age(adult)*sex(male)	1.15e-08	1.73e-05	0.001	(-4735.38; 4486.88)
Mean net distance (N=1045, R^2m=0.11; R^2c=0.37), competing model=Age*sex + Body weight*sex + Season, *df*=10, AICc=18 891.08, Δ AICc=0.00, weight=1.00					
	Intercept	4459.7	582.7	7.65	(3316.23; 5603.24)
	Body weight	-925.6	390.4	-2.37	(-1691.63; -159.55)
	Sex (male)	-253.4	1084.4	0.23	(2450.62; 1943.90)
	Season(hyperphagia)	251.7	246.00	1.02	(-230.31; 735.16)
	Body weight*sex(male)	-936.2	1428.7	0.65	(3740.95; 1867.35)
	Age(adult)	515.6	959.6	0.54	(-1367.41; 2398.69)
	Age(adult)*sex(male)	515.1	1184.7	0.43	(-1809.98; 2841.14)

N = 55 756 locations for the total of 57 individuals. For the explanatory variables, i.e. age, sex, body weight and season, we report the estimate (b), SE, z-value and confidence interval (CI) obtained from model-averaging coefficients on the 95% confidence set of models. Only the models with ΔAICc < 2 are shown.

Dependent variable	Explanatory variables	Model averaged coefficients			Cl
		β	SE	z	
Total distance (N=1044, R^2m=0.02; R^2c=0.23), competing model=Age*sex + Body weight*sex + Season, *df*=10, AICc=120 805.11, Δ AICc=0.00, weight=1.00					
	Intercept	9947.8	1150.3	8.64	(7690.54; 12 205.04)
	Season(hyperphagia)	-737.0	513.1	1.43.40	(-1744.07; 268.95)
	Body weight	-1191.4	764.6	1.55	(_2691.73; 308.94)
	Sex (male)	-2717.5	2136.9	1.23	(-7047.20; 1612.17)
	Age(adult)	827.5	1919.9	0.43	(-2940.05; 4595.09)
	Body weight*sex(male)	-1925.9	2809.2	0.68	(-7439.57; 3586.62)
	Age(adult)*sex(male)	-124.2	2349.3	0.05	(-4735.38; 4486.88)
Home range (N=1485, R^2m=0.04; R^2c=0.16), competing model=Season+Body weight, *df*-6, AICc=5258.95, Δ AICc=1.31, weight=0.14					
	Intercept	0.75	0.18	4.16	(0.40;1.11)
	Season(hyperphagia)	-0.32	0.16	1.96	(-0.61; -0.12)
	Body weight	-0.22	0.16	1.37	(-0.53; -0.06)
	Sex (male)	-0.11	0.23	0.44	(-0.88; 0.36)
	Age(adult)	0.05	0.17	0.27	(-0.41: 0.76)
	Body weight*sex(male)	0.04	0.19	0.19	(-0.64; 1.21)
	Age(adult)*sex(male)	-0.0008	0.11	0.008	(-1.01; 0.97)

N = 55 756 locations for the total of 57 individuals. For the explanatory variables, i.e. age, sex, body weight and season, we report the estimate (b), SE, z-value and confidence interval (CI) obtained from model-averaging coefficients on the 95% confidence set of models. Only the models with ΔAICc < 2 are shown.



Adults
R (±SE) = 0.33 ± 0.09
Cl = [0.134, 0.502]
P = 0.003

Subadults
R (±SE) = 0.32 ± 0.09
Cl = [0.137, 0.473]
P =<0.0001

Adults
R (±SE) = 0.32 ± 0.09
Cl = [0.119, 0.487]
P < 0.0001

Subadults
R (±SE) = 0.26 ± 0.08
Cl = [0.093, 0.422]
P =<0.0001

Adults
R (±SE) = 0.26 ± 0.08
Cl = [0.097, 0.432]
P < 0.0001

Subadults
R (±SE) = 0.20 ± 0.07
Cl = [0.061, 0.35]
P =<0.0001

Adults
R (±SE) = 0.12 ± 0.06
Cl = [0.013, 0.251]
P < 0.0267

Subadults
R (±SE) = 0.30 ± 0.09
Cl = [0.114, 0.468]
P =<0.0001

Figure 4.1. Adult (blue bars) versus subadult (orange bars) brown bear daily movement behaviours (Nsubadults ¼ 2275 localizations, Nadults ¼ 2560 localizations): (a) speed (m/s); (b) mean net distance (m); (c) total distance (m); and (d) home range size (km2). The edges of the box plots represent the interquartile range (IQR), the internal line is the median, the whiskers are the maximum (third quartile þ 1.5IQR) and the minimum (first quartile - 1.5xIQR) and the circles are outliers. For each movement parameter interindividual repeatability values (R), standard errors (SE), 95% confidence intervals (CI) and statistical significance of repeatability (P) are given. The icons were downloaded from 123RF royaltyfree stock photos, http://www.123rf.com; speed: ID 89448738 vastard; mean net distance and total distance: ID36170731 Dejan Jovanovic; home range size: ID24965219 Khoon Lay Gan.

4 Discussion

Age contributed little to the daily patterns of the four movement parameters of brown bears (i.e. average daily speed, mean net distance, total distance and home range size) that we analysed here. Conversely, season, sex and body weight explained most of the observed daily movement patterns. Moreover, interindividual movement variation within a home range was more marked among subadults.

Little information exists on the effect of age on animal movements and, more specifically, on brown bear movement patterns; however, in accordance with our results, Ballard et al. (1982) did not find any differences associated with age in the daily movements of southcentral Alaskan grizzly bears, *Ursus arctos horribilis*. Dahle and Swenson (2003a, 2003b) found that both male and oestrous female brown bears moved further in the mating season, probably because both sexes roamed to find mates; their movement patterns could not be explained by seasonal changes in food availability or increased foraging movements of oestrous females to replenish body reserves after cub rearing. Similarly, movement behaviour and home range size of brown bears differed between seasons in Pop et al.'s (2018) study, with males having larger territories during the hyperphagia season. Body size influences an individual's physiology and imposes morphological and ecological constraints (Swihart et al.,1988). Despite the scarce information available on the relationship between body mass and animal movements and home range size (Haskell et al., 2002; Swihart et al., 1988), body mass has already been shown to affect, for example, movement tortuosity in forest-dwelling didelphid marsupials (Vinı & Prevedello, 2010) and, more generally, the size of mammal home ranges (Swihart et al., 1988). This is the case for our larger brown bears, which had smaller home ranges than smaller individuals. Finally, even though we did not find any age-related difference in speed, as reported by Hernando et al. (2020) for a human-modified landscape in Greece, we detected similar patterns for the influence of the mating season on movement peaks. The activity rates and high home range variation recorded for subadult males in Greece (Hernando et al., 2020) has been considered the result of a mix of subadult inexperience in resource use and tolerance for humans, as well as an attempt to avoid intraspecific agonistic interactions. Because large home ranges for subadult males have also been recorded in other human modified landscapes in Europe (Hernando et al., 2020), bear movement patterns might be a consequence of local differences in habitat quality or the perception of local risks, together with features of the landscape in which bears move.

Increases in distance moved and home range size may be the result of several nonmutually exclusive factors, for example (1) increased movement of males during the mating season to increase their rate of encounter with females (Dahle & Swenson, 2003b; Steyaert et al., 2012); (2) sexual size dimorphism (and, more generally, body size), which increases metabolic demands in males compared to females (or in larger individuals compared to smaller ones; Dahle & Swenson, 2003b); and (3) physiological needs during certain periods, such as the hyperphagia season, during which bears search for food in order to store fat reserves (González-Bernardo et al., 2020; Swenson et al., 2021). Note that although season was always included in the most parsimonious models for both individual movements and home ranges in our study, it generally had a weak effect. This may be because we assumed fixed dates for the seasons. As there may be interindividual and interannual variability in the dates, breaking the movement data into two discrete periods common to all individuals may have weakened the effect of season.

Our results might suggest that differences in age-related needs are not able to explain differences in movement patterns and home range size between subadults and adults (the first and third scenarios that we hypothesized). Thus, factors other than age might determine patterns of brown bear movement. For example, based on the parameters we analysed here, we can hypothesize that two mechanisms may lead to subadults and adults moving similarly. First, both must hibernate and, consequently, need to store energy during hyperphagia. As they have the same requirements, both adults and subadults may show similar food-oriented patterns of movement, that is, the common search for food determines the emergence of similar patterns of movement. Second, both adults and subadults move long distances after hibernation, but for different reasons. Both yearlings recently exited from winter dens with their mothers and older subadults are predicted to make erratic and long movements during their juvenile dispersal (Bonte et al., 2012; Clobert et al., 2001; Clobert et al., 2004; Zedrosser et al., 2007). The exploration of new areas in which to settle during dispersal might be one of the causes of the observed higher interindividual variation in subadult movements. Because dispersal movements may occur anywhere during the exploration of new areas (Clobert et al., 2001; Delgado et al., 2009), subadults may cross diverse areas depending on their starting point after leaving the natal area. Interindividual variation in movement behaviour may be the result of individuals varying movement patterns and space use across gradients of, for example, food availability (Hertel, Niemelä et al., 2020; Hertel, Royauté et al., 2020; Webber et al., 2020). In contrast to subadults, adult brown bears move long distances to find mates (Dahle & Swenson, 2003b; Steyaert et al., 2012). Thus, after the spring den exit, both subadults and adults need to travel long distances, for dispersal and mating, respectively, and thus their movement patterns converge. That is, all individuals end up behaving (i.e. moving) similarly, regardless of the initial state or movement aims that drive convergence in behaviour (Luttbeg & Sih, 2010).

Equifinality occurs when similar ecological patterns emerge from different initial conditions (Penteriani, 2008). Thus, different motivations (subadult dispersal versus adult mating in our case) could be expressed through the same individual behaviour (Aspden et al., 2010) and equifinality (sensu von Bertalanffy, 1950) might be considered an intrinsic property of certain animal behaviours. The concept of equifinality can help explain why similar patterns have different origins: they can be the result of different causes, factors or pressures, such as the need for long movements determined by both subadult dispersal and adult mating **(Figure 4.2)**. That is, independent of their causes or stimuli, similar movement patterns may result from different behaviours (Popescu & Rymer, 2000). To our knowledge, this is the first time that equifinality has been detected in the movement patterns of a large carnivore and, more generally, in movement ecology. Our study shows how careful we need to be when examining behavioural patterns in animal populations, as equifinality may lead to mistakes in our understanding of the mechanisms behind observed patterns (von Bertalanffy, 1950)

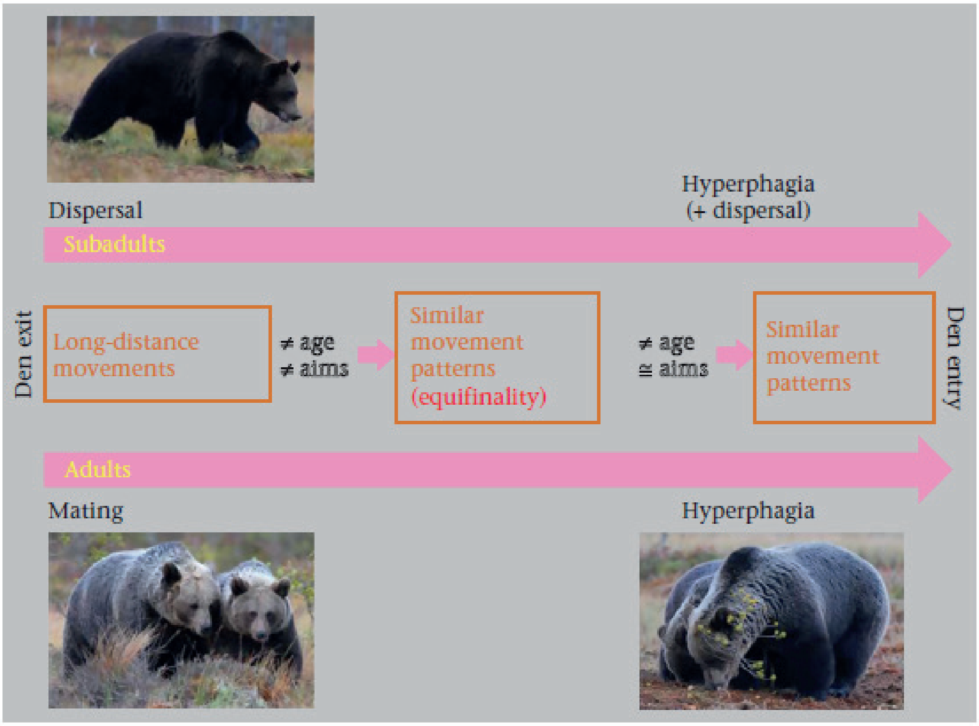
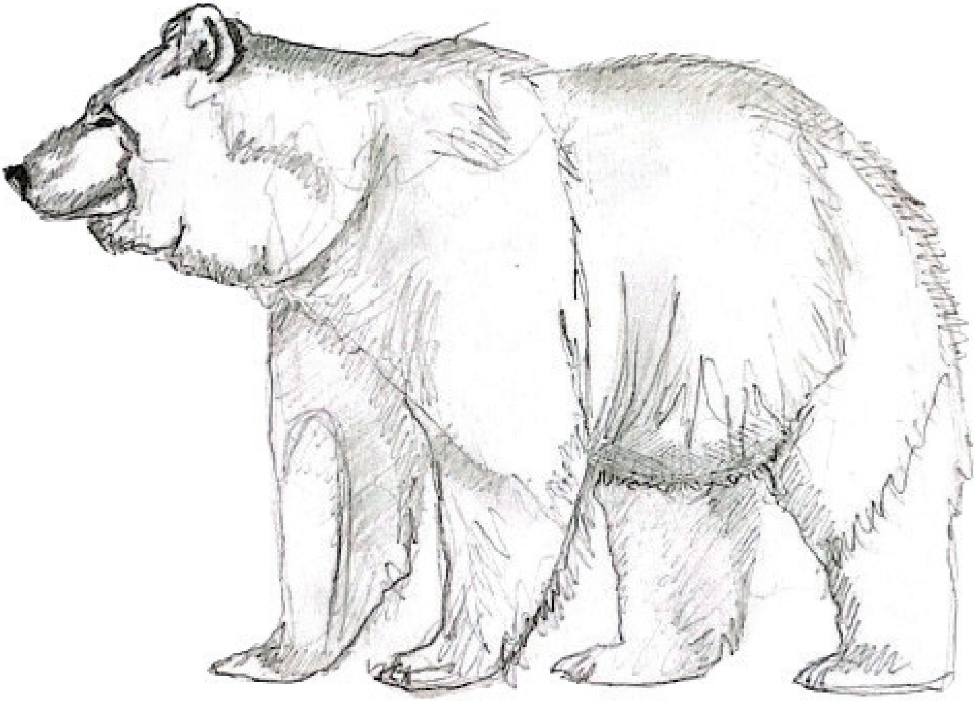


Figure 4.2. Different animal motivations may engender similar movement patterns which can lead to equifinality. In this summarized representation, from den exit after hibernation to den entry in order to hibernate, the main subadult and adult brown bear behaviours are shown: subadult dispersal and adult mating, which overlap temporally, and hyperphagia, which both adult and subadult bears experience. Long-distance movements occur during the subadults' explorations of new areas in which to settle (dispersal) and the mating period when adult bears search for mates. This is an example of equifinalistic behaviour, i.e. similar ecological patterns emerge from different initial conditions, which is represented here by the need for long displacements determined by both subadult dispersal and adult mating. See text for further details. Photo credit: V. Penteriani.

5

General conclusion



In this thesis, I investigated some of the factors that can shape brown bear movement strategies at the individual level. The thesis uses telemetry to identify patterns of movement, rhythms of activity and the factors behind them in the Karelian brown bear population. An overview of the results, chapter by chapter, is presented in Figure 5.1.

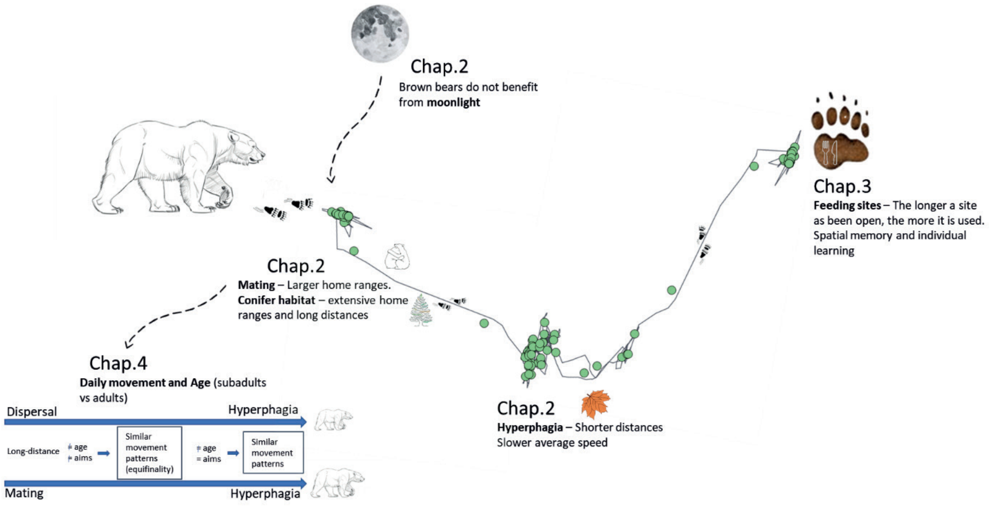


Figure 5.1. Schematic overview of thesis' results, chapter by chapter.

The three main topics that I explored during my thesis are:

1. Influence of external (e.g., moon phases, bear seasons–mating and hyperphagia) and internal (e.g., age, sex, body condition) factors on animal movements;

2. Potential effects of artificial feeding (for both hunting and bear viewing purposes) on movement behaviour;

3. Age constraints (e.g., juvenile dispersal vs. mating) on movement ecology, i.e. movement patters of subadult vs. adult individuals;

1 Main results

Using the illuminated fraction of the moon **(chapter 2, figure 5.2)**, I was able to study the rhythm of the brown bear according to the moon phases. We did not include the potential effects of actual local cloud cover because it is recorded on a spatio-temporal scale that does not make this information useful for telemetry analyses of species that move widely. In fact, cloud cover can vary considerably over the course of a single night and in areas that are very close together. This means that, during long journeys over their large home ranges or over several linear kilometres, brown bears can be confronted with different cloud cover conditions during the same night. But above all, the spatial resolution of the weather station recording the meteorological data is not as fine as the bears' movements require. Thus, the inclusion of very general cloud cover values risks distorting the behavioural analyses because they do not really indicate the local cloud cover, i.e. where the bears are actually moving. In addition, the long-term duration of our telemetric study would have made it possible to detect a lunar effect on bear behaviour even though, on certain nights or parts of nights, clouds could have partially covered the brightness of the moon. In this respect, we must not forget that even under cloudy skies, the nocturnal luminosity of full moon nights is higher than that of new moon nights, and the way in which these variations in luminosity can influence the animals' movements is likely to be rather speculative if taken into account at all. Similarly, we did not consider light pollution, given that it is negligible due to the low rate of human settlements and high-traffic roads (https://www.lightpollutionmap.info). However, isolated houses and low-traffic roads are widespread in the study area.

Unlike other carnivores that have been shown to follow the rhythm of moonlight, brown bear movement patterns were not influenced by moon phases (see also Richardson, 2017). Although brown bears have the morphological characteristics typical of carnivores, they are opportunistic omnivores with a diverse diet (Bojarska and Selva 2012; Coogan et al. 2018). Consequently, the prey-predator relationships that drive carnivore dependence on moonlight (Brown & Kotler, 2004b; Berger-Tal et al., 2010; Penteriani et al., 2013; Bhatt et al., 2018) may be weaker in brown bears than in other obligate carnivores. In addition, two other factors may have played a role in reducing the potential effect of the moon on brown bears in our study area. Firstly, we must take into account that this Finnish-Russian bear population is managed by hunting. Consistent with previous studies (Ordiz et al. 2011; Gosselin et al. 2015), we found that bears under hunting pressure alter their normal activity rhythms and movements. Secondly, the presence of artificial feeding points may have reduced the potential influence of moonlight (Penteriani, Delgado & Melletti, 2010; Penteriani et al., 2017; Kojola & Heikkinen, 2012). This practice may alter bears' non-dependence on prey (Steyaert et al., 2014) and, consequently, the potential influence of moonlight. Ideally, a study on the influence of the moon should take place in an area where this practice does not exist.

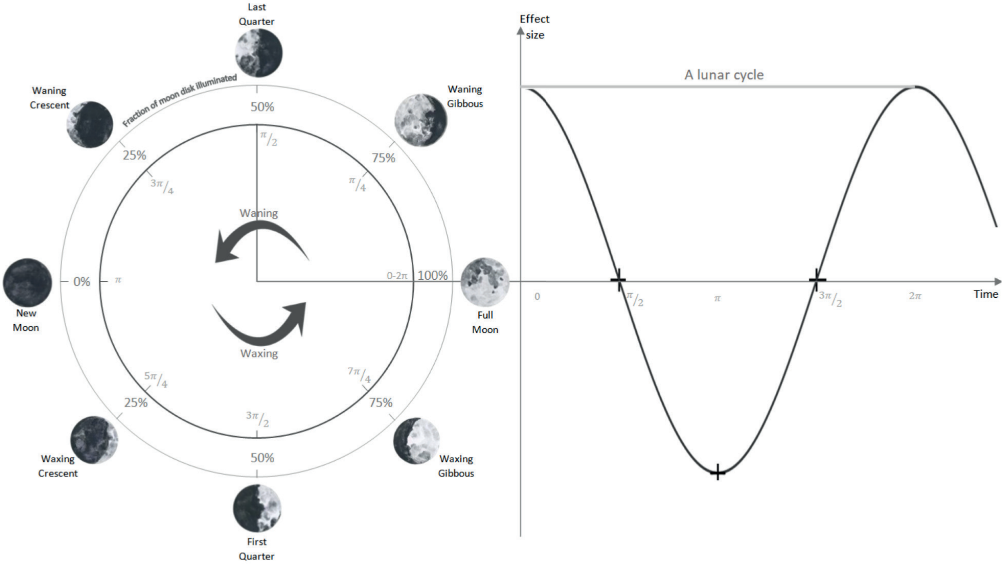


Figure 5.2. The illuminated fraction of the moon is transformed into radians to differentiate between waning and waxing moons.

The brown bear is a hibernating omnivore with a diet that varies geographically and seasonally throughout its range (Dahle et al. 1998; Bojarska and Selva 2012). Bears eat mainly plants (Mowat and Heard 2006; Štofik et al. 2013). Bears also follow seasonal or inter-annual pulses of calorie-rich resources (Munro et al. 2006; Naves et al. 2006). The availability of high-fat foods, necessary to maintain a balanced energy intake, coincides with the hyperphagic prehibernation period in bears in late summer and autumn (Coogan et al. 2018), and the time allocated to forage leads to a reduction in daily distances (chapter 2). The increase in human feeding in ecosystems is changing these patterns and is causing increasing concern (Oro et al. 2013). Recent studies have shown that artificial feeding modifies the spatial and temporal availability of natural foods and have highlighted changes in the diet composition and seasonality of brown bears (Kavčič et al. 2015; Sergiel et al. 2020). We have also observed changes in energy-related activities such as wintering (Krofel et al. 2017) and movements (chapter 3) (Selva et al. 2017a). Movement is a fundamental part of any animal's life. How, why and where animals move can have far-reaching consequences at individual, population and ecosystem levels (Nathan et al. 2008). Changes in movement are asso- ciated with a cascade of subsequent changes to population dynamics that are closely linked to individual performance, and which can greatly vary with the diet quality (Hertel et al. 2017). Given the worldwide extent of wildlife supplemental feeding, it is important to better understand the impact of this practice on movement ecology and the resulting consequences for species and ecosystems (Bojarska and Selva 2012; Oro et al. 2013). In addition, artificial feeding can lead to changes in the nutritional ecology and physiology of wildlife, which are generally negative and have a signifi- cant impact on foraging behaviour and food availability (Birnie-Gauvin et al. 2017). In addition to modifying the composition of the diet, may alter hibernation patterns as well as movements of bears (Selva et al. 2017b; Sergiel et al. 2020). Poor quality an- thropogenic food can also jeopardise the health and immune function of wild animals (Strandin et al. 2018). As foraging occurs in many different contexts around the world (Oro et al. 2013), it can have significant consequences for species of conservation concern.

The availability and quality of food varies greatly from one site to another. In our area of distribution, this can range from 200kg/week to 10,000kg/week (meat, fish, cookies or even dog food, depending on the site (field observations). Ecotourism for bear watching and photography is likely to remain an important part of tourism in the oriental regions of Finland. However, if Finnish legislators continue to accept the practice of feeding bears, police officers and game managers should have a common plan of action for those times when bears lose their distrust of humans. Feeding for tourism purposes is different from other reasons behind artificial feeding of wildlife, e.g., avoidance of human-bear conflicts by displacing bears far from human settlements, because in this case the bears are baited to feed a few meters from wooden hides that protect humans from bears (I. Kojola, pers. obs.). It is likely that the bears that visit these places smell humans in the caches and become accustomed to their presence, which could have long-term consequences. The starting points differ markedly from the usual conflicts between humans and large carnivores because, in this case, the beneficiaries of bear tourism are private companies that do not have the right to eliminate habituated bears prone to generate conflicts, as this role is reserved for public game management. In any case, it is important to specify responsibilities and practices to help solving bear problems.

On top of all this, feeding can disrupt an individual's very ecology. By simply observing our data, we found that there were active bears in winter. This has also been the subject of further study (Selva et al. 2017a). Supplementary feeding has been shown to reduce home range size and to alter migration patterns (chapter 3). Both the probability of a feeding site being used and the intensity of its use were positively correlated to the stability of this food resource over time. This is probably due to individual spatial memory and learning, which are advantageous in environments with a relatively high level of resource predictability as artificial feeding sites are (Fagan et al. 2013; Riotte-Lambert and Matthiopoulos 2020). Feeding sites seemed to be visited predominately at night (twilight included) and more during hyperphagia (chapter 3) (Cozzi et al. 2016). During hyperphagia, foraging is the main activity of brown bears (González-Bernardo et al. 2020). Bears must consume large amounts of food and they may need to make large displacements in order to find sufficient high-energy foods to build up large fat reserves before hibernation (Swenson et al. 2020). Karelian brown bears are not strictly dependent on artificial feeding, probably due to abundant local natural food resources, e.g., wild berries are available onwards late July (author's unpublished data).

Brown bears move short distances and at low speeds within small home ranges as the intensity of use of feeding sites increases. Individuals that move more are more likely to encounter and traverse more resource-rich areas per day than individuals that move less (Hertel et al. 2019). This pattern is probably less pronounced when part of the diet consists of predictable and continuously renewed resources, as in the case of artificial feeding sites. This tendency of artificially fed brown bears to restrict their movements (as also observed in North American brown bears Ursus arctos horribilis; (Blanchard and Knight 1991)) could be indicative of increased fidelity to complementary food sites, which could ultimately lead to changes in bear behavior through «domestication», reducing population range expansion and decreasing long-distance movements (Cozzi et al. 2016; Selva et al. 2017a).

Given that food supplementation alters individual behavior, thus affecting the bears' overall energy budget, and that artificial feeding is likely to produce several negative collateral effects on bear ecology, behavior and health (Kavčič et al. 2015; Skuban et al. 2016; Penteriani et al. 2017, 2018), the changes recorded in movement patterns lend further weight to the evidence that artificial feeding may have important implications for bear ecology and management (Ordiz et al. 2014). Artificial feeding has been shown to impact the spatio-temporal availability of natural foods, leading to changes in brown bear diet composition, seasonality, and energy-related activities (Krofel et al. 2017). Diet quality is crucial for individual performance, influencing population dynamics, density, and life history. Human provisioning of food negatively affects wildlife's nutritional ecology and physiology, impacting foraging behavior and food availability (Hertel et al. 2018). The consequences on organism fitness remain unclear and require diverse approaches (Murray et al. 2016). For example, Iberian lynx (Lynx pardinus) respond positively to artificial feeding ((López-Bao et al. 2008). Also, the practice was recognized as an efficient long-term conservation measure for the population of the Swedish arctic fox (Alopex lagopus) (Angerbjörn et al. 2002). Even if the purpose of feeding is clearly defined, its real effects cannot be always strictly controlled, and may have some effects on non-target species. For example, birds including species of a high conservation importance are known to use artificial feeding sites (Fležar et al. 2019). Species diversity at the feeding sites depend of the season and according to the type of artificial food (with or without carrion), (Fležar et al. 2019). When estimating the impacts of artificial feeding on species and especially on local bear populations, we should always take into account local factors such as the carrying capacity of the area in relation to the existing bear population, the annual availability at feeding sites and the distance to alternative food resources, as well as the energy required to travel to these food sources. Thus, each area must be considered as a special case, and the suitability and location of brown bear feeding must be assessed on the basis of the conservation status of the bear population, bear behavior and local density, annual availability of food resources and their utilization, as well as anthropogenic activities likely to interact with bears (Figure 7), (Morales-González et al. 2020).

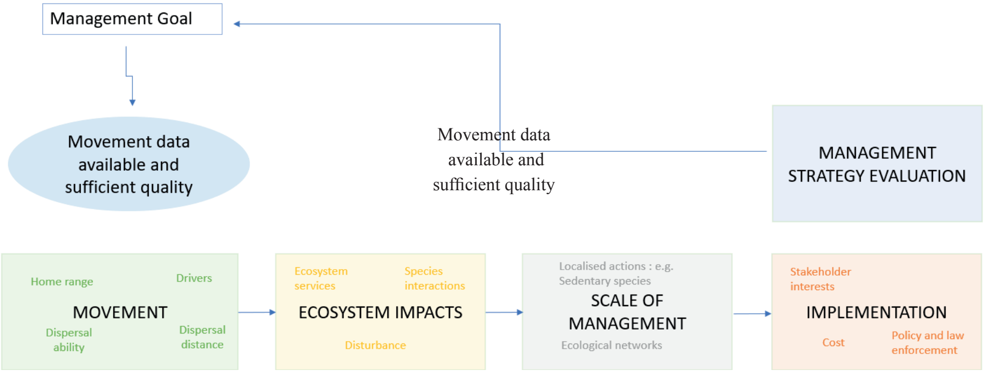


Figure 5.3 : Movement – Management framework adapted from (Allen and Singh 2016) for incorporating movement ecology into decision-making processes. First, the framework concerns the type of movement (dispersal, established individuals…). The second step is to identify ecosystem impacts that will drive the decision-making process and determine potential management actions (in space and time). Next, managers take into account the implementation of the proposed actions and their effectiveness. The result is a cyclical process of adaptive management in which the results of the assessment guide management objectives and future actions.

Brown bears have large home range sizes and travel long distances to meet their needs. Their movement patterns are mainly driven by seasonality (mating and hyperphagia) that plays an important role in their habitats' selection (Pop et al. 2018b). Alongside the availability of food, other factors such as age, the availability of dens or avoidance of congeners can influence the movements of individuals. All these parameters make it even more difficult to understand patterns of space use (Nathan et al. 2008). Our studies showed that age contributed little to the daily patterns of brown bears and this is supported by (Pop et al. 2018a). Conversely, season, sex and body weight explained most of the observed daily movement patterns. Moreover, interindividual movement variation within a home range was more marked among subadults. Body size influences an individual's physiology and imposes morphological and ecological constraints (Swihart et al. 1988). In other countries where the landscape is dominated by humans, extensive home ranges for subadult males have also been recorded (Hernando et al., 2020). Bear movement patterns could therefore be the consequence of local differences in habitat quality. Furthermore, we have shown that two different purposes can lead to subadults and adults moving in a similar way. Firstly, during hyperphagia, both need to hibernate and therefore need to store energy. Since they have the same needs, adults and subadults may show similar foraging patterns. This goal induces the emergence of similar movement patterns. Secondly, adults and subadults move long distances after hibernation, but for different reasons. Yearlings and older subadults are thought to make erratic, long-distance movements during their dispersal (Zedrosser et al. 2007; Bonte et al. 2012). The exploration of new areas in which to settle during dispersal might be one of the causes of the observed higher interindividual variation in subadult movements. In contrast to subadults, adult brown bears move long distances to find mates (Dahle and Swenson 2003; Steyaert et al. 2012). Thus, after the spring den exit, both subadults and adults need to travel long distances, for dispersal and mating, respectively, and thus their movement patterns converge. That is, all individuals end up behaving similarly, regardless of the initial state or movement aims that drive convergence in behaviour (Luttbeg and Sih 2010). Equifinality occurs when similar ecological patterns emerge from different initial conditions (Penteriani 2008). Thus, different motivations (subadult dispersal vs. adult mating in our case) could be expressed through the same individual behavior (Aspden et al. 2010) and equifinality might be considered an intrinsic property of certain animal behaviors. The concept of equifinality can help explain why similar patterns have different origins. Actually, similar behavioral patterns can be the result of different causes, factors or pressures, such as the need for long movements determined by both subadult dispersal and adult mating. That is, independent of their causes or stimuli, similar movement patterns may result from different behaviors (Popescu and Rymer 2000).

2 Ethical note

Animal models are a key element in understanding their needs. A fundamental principle of research ethics is to balance the benefits of research against the burden imposed on animals. The use of wild animals for research requires an assessment of the effects of capture and invasive sampling. Determining the severity and duration of these interventions on the animal's physiology and behaviour enables the study methodology to be refined if needed. Thiel et al. (2023) showed that capture may alter the behaviour and physiology of bears.

For our study, bears were captured and collared at bait sites. The weight of the collars was less than 1.0-2.0% of the body weight of adult females and 0.5-1.0% of adult males. For subadults, collars had a preprogrammed drop-off mechanism with an average battery life of 1 year. Whenever the drop-off did not occur by the scheduled time owing to technical flaws, the bear was recaptured, and the collar was removed manually. All collars were removed before the end of the project in 2014. Age is an essential trait for understanding the ecology and management of wildlife. In our case, bears were aged with the cementum annuli method (Craighead, Craighead & McCutchen, 1970). It's one of the most common and ubiquitous methods to age mammals. This method has been used in bears despite some disadvantages, such as high invasiveness, expensive, time-consuming and the requirement for experienced observers (Gable, Johnson-Bice & Windels, 2023; Nakamura et al., 2023). Today, due to the high invasiveness of the study, researches try to establish a novel age estimation method. Nakamura *et al*. (2023)

Today, due to the high invasiveness of the study, researches try to establish a novel age estimation method. Nakamura et al. (2023) draw a protocol based on an epigenetic method to age brown bears, which provides benefits over tooth-based methods, including high accuracy, less invasiveness, and a simple procedure.

Permission to capture and manipulate bears was issued by the County Veterinarian of Oulu and the Regional State Administrative Agency of Lahti (Finland). This research adheres to the ASAB/ABS Guidelines for the use of animals in research. The capturing of bears met the guidelines issued by the Animal Care and Use Committee at the University of Oulu and permits were provided by the provincial government of Oulu. During bear captures and tracking no adverse effects of manipulations were observed.

3 Management and conservational measures

Man has always been attracted to large carnivores, not only because of the threat they pose to livestock and sometimes to man, but also because their strength, agility and beauty fascinate and inspire the human imagination. Once threatened in Finland, the bear is now strictly protected under the Habitats Directive. They are a highly valued part of Finland's wildlife. The bear is also a valuable game animal that is hunted every year for population management purposes. Hunting has not been an obstacle to maintaining a favourable conservation status, which the bear has had since 2000.

Unlike Norway and Sweden, Finland manages the brown bear at national level. The measures set out in the bear population management plan aim to maintain its favourable conservation status and ensure that bears do not lose their fear of humans, while meeting the needs of people living in areas inhabited by bears. The main objective of Finland's brown bear management plan is to pursue ecologically, economically and socially sustainable management of the population. The brown bear is considered a game species under Finnish law, and the Finnish Ministry of Agriculture and Forestry (MAFF) is responsible for its management. The measures in the management plan concern population monitoring, population management measures, damage prevention and conflict management, official assistance to the police by the game management associations (SRVA), cooperation and communication with stakeholders. The management plan is essentially based on two studies. One aims to develop an additional method based on the genetic identification of individuals for monitoring the bear population (Finnish Institute of Natural Resources) and the other on the provision of food in the natural environment (chapter 3). According to the management plan, a vast project led by the Ministry of Agriculture and Forestry will be launched to study the use of feeding sites for observation purposes and the possible need to create harmonised practices with the various stakeholders. The Ministry of Agriculture and Forestry organised a stakeholder event in June 2022 to discuss the finalised draft for the Management Plan. The previous Management Plan for the Bear Population dates back to 2007. One part of the conservation of large carnivores depends on the socio-political and administrative situation (Treves & Karanth, 2003). The legal establishment of conservation measures often requires a long administrative process. Administrative and legal frameworks can limit the effectiveness of these measures when they are not adapted to natural dynamics (Rayfield et al., 2008, Hermoso et al., 2019). Therefore, to achieve effective conservation, the application of management measures must be implemented by monitoring population dynamics with up-to-date information (Hill et al., 2017).

From around 200 bears in the 1970s, the population size has risen sharply to around 2,400 individuals today (Kojola and Laitala 2000; Heikkinen et al. 2021). Finland is divided into four management areas: the reindeer husbandry area in the north, the stable population area in the east, the bear dispersal area in central Finland and the population growth area in western Finland. MAFF sets annual harvest quotas for each management areas, based on population size and harvest scenarios provided by the Finnish Institute of Natural Resources (LUKE), also taking into account the damage caused by bears. The data on which the population size estimates are based are collected by a network of ~2,000 volunteers, most of whom are hunters (Heikkinen et al. 2021). Volunteers are trained and the collected data are uploaded via a link to the online observation database «Tassu» («Paw» in English; Kojola et al. 2018).

Damage and compensation

Approximately 13% of Finland's bear population lives in the area of domestic reindeer (Heikkinen et al. 2021) and most of the damage caused by bears occurs in this area. Compensation is only paid for reindeer over one year old. There are also few reported cases each year of bears damaging beehives, hay bales or feeding on agricultural crops, particularly oats or fruit such as strawberries. All these types of damage are fully compensated by the Finnish government.

The brown bear is a well-studied species. Nevertheless, there is no reason to reduce research on the brown bear and there are many reasons for this:

- Different combinations of both natural and anthropogenic dynamics can lead to the reduction or expansion of the range of a large carnivore population ((Naves et al., 2003; Martínez Cano et al., 2016).
- Expanding populations often come into conflict with human interests, mainly because of the damage they cause (Woodroffe et al., 2003).
- A higher density of brown bears could change their social structure
- Develop management measures to better meet the needs of bears

The protection and concern that can be achieved through bear research would not only help to improve the situation of brown bears in Finland and make it more secure for the long-term, but would also benefit a number of other species that share the bear population's ecosystem.

Conclusion

Movement ecology is an important field of study for understanding how brown bears use their habitat and has been developed in recent years thanks to animal tracking technologies (Tomkiewicz et al. 2010). The information extracted from telemetry is essential for developing effective conservation and management strategies that promote the long-term survival of animal populations. Research in movement ecology generates knowledge that enables managers to implement flexible actions in space and time (Allen and Singh 2016). Knowing where and when a species is a prerequisite for the successful implementation of spatial-temporal approaches to wildlife conservation and management, which allow managers to develop compromise scenarios that balance conservation needs with anthropogenic activities (O'Neal et al. 2008; Shillinger et al. 2008; Redpath et al. 2013).

Brown bears are known to be highly mobile animals, capable of traveling long distances in a variety of habitats. This mobility is influenced by a variety of factors, including food availability, reproductive status, sex and human activity. For example, foraging brown bears may travel long distances in search of quality feeding sites.

This thesis provides a glimpse into the strategy of the brown bear movements, which I hope may contribute to future changes in management policies. To limit the effect of additional food, we can imagine a renewal (position or close the feeding site after couple of years) of feeding sites to reduce habituation. The study area is vast, and we can create zones without artificial feeding and prevent some side effects of feeding like diseases due to a non-appropriate diet. Future research should focus on sociality in bear populations because social interactions between conspecifics are important even in solitary species. Ignorance of social interactions can lead to a poor understanding of animal ecology and, consequently, to unsuccessful species management.

List of publications

Paper 1 -

Does moonlight affect movement patterns of a non-obligate carnivore? Brown bears do not mind that the moon exists.

Cindy Lamamy, Maria Del Mar Delgado, Ilpo Kojola, Samueli Heikkinen and Vincenzo Penteriani

This paper has been published in Journal of Zoology in November 2021.

Paper 2 -

Does artificial feeding affect large carnivore behaviours? The case study of brown bears in a hunted and tourist exploited subpopulation.

Vincenzo Penteriani[1], Cindy Lamamy[1], Ilpo Kojola, Samueli Heikkinen and Maria Del Mar Delgado.

[1] *These authors contributed equally to this work.*

This paper has been published in Biological Conservation in January 2021.

Paper 3 -

Age Ain't Nothing But a Number: factors other than age shape brown bear movement patterns

Vincenzo Penteriani[1], Cindy Lamamy[1], Ilpo Kojola, Samueli Heikkinen, Cédric Vermeulen and Maria Del Mar Delgado

[1] *These authors contributed equally to this work.*

This paper has been published in Animal Behaviour 183(2022)61e67.

Paper 4-

Submitted - Brown bear use of anthropogenic areas helps explain their movement rate and distance travelled during the mating season

Daniele Falcinelli, Maria Del Mar Delgado, Cindy Lamamy, Ilpo Kojola, Samueli Heikkinen and Vincenzo Penteriani

Paper 5-

Can landscape characteristics help explain the different trends of Cantabrian brown bear subpopulations?

Cindy Lamamy, Giulia Bombieri, Alejandra Zarzo-Arias, Enrique González-Bernardo and Vincenzo Penteriani

This paper has been published in Mammal Research 64, 559–567 (2019)

Paper 6-

Rubbing behaviour of brown bears: Factors affecting rub tree selectivity and density.

Enrique González-Bernardo, Carlotta Bagnasco, Giulia Bombieri, Alejandra Zarzo-Arias, Hector Ruiz-Villar, Anna Morales-González, Cindy Lamamy, Andres Ordiz, David Cañedo, J. Díaz García, Daniel Chamberlain and Vincenzo Penteriani

This paper has been published in Journal of Mammalogy Volume 102, Issue 2, April 2021, Pages 468–480

References

Abrahms, B., Aikens, E.O., Armstrong, J.B., Deacy, W.W., Kauffman, M.J. & Merkle, J.A. (2020). Emerging Perspectives on Resource Tracking and Animal Movement Ecology. Trends Ecol. Evol. 2777, 1–13.

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their actions in North Western Europe. Ann. Bot. Fenn. 5, 169–211.

Allen, A.M. & Singh, N.J. (2016). Linking Movement Ecology with Wildlife Management and Conservation. Front. Ecol. Evol. 3.

Angerbjörn, A., Tannerfeldt, M. & Elmhagen, B. (2002). Presentation av SEFALO-projektet: Vilka chanser har fjällräven att överleva i Sverige?

Arnemo, J.M., Fahlman, Å., Ahlqvist, P., Brunberg, S., Segerström, P. & Swenson, J.E. (2007). Biomedical protocol for free-ranging brown bears (Ursus arctos) in Scandinavia.

Arnold, J.M., Gerhardt, P., Steyaert, S.M.J.G., Hochbichler, E. & Hackländer, K. (2018). Diversionary feeding can reduce red deer habitat selection pressure on vulnerable forest stands, but is not a panacea for red deer damage. For. Ecol. Manage. 407, 166–173.

Aspden, T., Ingledew, D. & Parkinson, J. (2010). Motives and Health-related Behaviours An Investigation of Equipotentiality and Equifinality. J. Health Psychol. 15, 467–479.

Ballard, W.B., Miller, S.D. & Spraker, T.H. (1982). Home Range, Daily Movements, and Reproductive Biology of Brown Bears in Southcentral Alaska. Can. Field-Naturalist 96, 1–5.

Balmford, A., Green, J.M.H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M. & Manica, A. (2015). Walk on the Wild Side: Estimating the Global Magnitude of Visits to Protected Areas. PLOS Biol. 13, e1002074.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011). Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57.

Bartoń, K. (2013). Model selection and model averaging based on information criteria (AICc and alike). Compr. R Arch. Netw. 1, 13.

Barton, K. (2018). Package 'MuMIn': Multi-model inference. Available at: http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Bates, D. & Maechler, M. (2009). lme4: Linear Mixed-Effects Models using S4 Classes. Version 0.999375-31.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48.

Benhamou, S. (1994). Spatial memory and searching efficiency. Anim. Behav. 47, 1423–1433.

Berger-Tal, O., Mukherjee, S., Kotler, B.P. & Brown, J.S. (2010). Complex state-dependent games between owls and gerbils. Ecol. Lett. 13, 302–310.

Bhatt, U.M., Habib, B., Sarma, H.K. & Lyngdoh, S.L. (2018). Catch me if you can: Species interactions and moon illumination effect on mammals of tropical semi-evergreen forest of Manas National Park, Assam, India. bioRxiv.

Birnie-Gauvin, K., Peiman, K.S., Raubenheimer, D. & Cooke, S.J. (2017). Nutritional physiology and ecology of wildlife in a changing world. Conserv. Physiol. 5.

Bischof, R., Fujita, R., Zedrosser, A., Söderberg, A. & Swenson, J.E. (2008). Hunting Patterns, Ban on Baiting, and Harvest Demographics of Brown Bears in Sweden. J. Wildl. Manage. 72, 79–88.

Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A. & Gimenez, O. (2009). The Magnitude and Selectivity of Natural and Multiple Anthropogenic Mortality Causes in Hunted Brown Bears. J. Anim. Ecol. 78, 656–665.

Bjørneraas, K., Van Moorter, B., Rolandsen, C.M. & Herfindal, I. (2010). Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. J. Wildl. Manage. 74, 1361–1366.

Blanchard, B.M. & Knight, R.R. (1991). Movements of yellowstone grizzly bears. Biol. Conserv. 58, 41–67.

Blangy, S. & Mehta, H. (2006). Ecotourism and ecological restoration. J. Nat. Conserv. 14, 233–236.

Bojarska, K. & Selva, N. (2012). Spatial patterns in brown bear Ursus arctos diet: the role of geographical and environmental factors. Mamm. Rev. 42, 120–143.

Bojarska, K., Drobniak, S., Jakubiec, Z. & Zyśk-Gorczyńska, E. (2019). Winter insomnia: How weather conditions and supplementary feeding affect the brown bear activity in a long-term study. Glob. Ecol. Conserv. 16, e00523 Contents.

Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V.M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T.G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier, C.M., Palmer, S.C.F., Turlure, C. & Travis, J.M.J. (2012). Costs of dispersal. Biol. Rev. 87, 290–312.

Borowski, Z., Bałazy, R., Ciesielski, M. & Korzeniewski, K. (2019). Does winter supplementary feeding affect deer damage in a forest ecosystem? A field test in areas with different levels of deer pressure. Pest Manag. Sci. 75, 893–899.

Boyle, S.A., Lourenço, W.C., da Silva, L.R. & Smith, A.T. (2008). Home Range Estimates Vary with Sample Size and Methods. Folia Primatol. 80, 33–42.

Bridges, A.S., Vaughan, M.R. & Klenzendorf, S. (2004). Seasonal variation in American black bear Ursus americanus activity patterns: quantification via remote photography. Wildlife Biol. 10, 277–284.

Brown, J.S. & Kotler, B.P. (2004). Hazardous duty pay and the foraging cost of predation. Ecol. Lett. 7, 999–1014.

Burgman, M.A. & Fox, J.C. (2003). Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. Anim. Conserv. 6, 19–28.

Burnham, K.P. & Anderson, D.R. (2002). Model selection and multimodel inference: A practical information-theoretic approach. Springer.

Ceballos, G., Ehrlich, P.R. & Raven, P.H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. Proc. Natl. Acad. Sci. 117, 13596–13602.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecol. Modell. 197, 516–519.

Candler, E.M., Severud, W.J. & Bump, J.K. (2019). Who takes the bait? Nontarget species use of bear hunter bait sites. Human-Wildlife Interact. 13, 98–110.

Cederlund, G. & Sand, H. (1994). Home-range size in relation to age and sex in moose. J. Mammal. 75, 1005–1012.

Cepic, M., Bechtold, U. & Wilfing, H. (2022). Modelling human influences on biodiversity at a global scale–A human ecology perspective. Ecol. Modell. 465, 109854.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D. & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. Science (80-.). 346, 1517–1519.

Chu, E.W. & Karr, J.R. (2017). Environmental Impact: Concept, Consequences, Measurement ☆. In Reference Module in Life Sciences. Elsevier.

Clarke, J.A. (1983). Moonlight's influence on predator/prey interactions between short-eared owls (Asio tlammeus) and deermice (Peromyscus maniculatus). Behav. Ecol. Sociobiol. 13, 205–209.

Clobert, J., Danchin, E., Dhondt, A. & Nichols, J. (2001). Dispersal. Oxford: Oxford University Press.

Clobert, J., Ims, R. & Rousset, F. (2004). Causes, mechanisms and consequences of dispersal. In Ecology, genetics, and evolution of metapopulations: 307–335. Hanski, I. & Gaggiotti, O. (Eds.). Academic Press.

Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Coops, N.C. & Nielsen, S.E. (2018). Functional macronutritional generalism in a large omnivore, the brown bear. Ecol. Evol. 8, 2365–2376.

Cooper, J., Underhill, L.G. & Avery, G. (1991). PRIMARY AND TRANSEQUATORIAL THE SOOTY SHEARWATEr. Condor 93, 724–730.

Cowie, R.H., Bouchet, P. & Fontaine, B. (2022). The Sixth Mass Extinction: fact, fiction or speculation? Biol. Rev. 97, 640–663.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W. & Schmid, B. (2012). Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. Ecology 93, 2590–2599.

Cozzi, G., Chynoweth, M., Kusak, J., Coban, E., Çoban, A., Ozgul, A. & Sekercioglu, C. (2016). Anthropogenic food resources foster the coexistence of distinct life history strategies: Year-round sedentary and migratory brown bears. J. Zool. 300, 142–150.

Craighead, J.J., Craighead, F.C. & McCutchen, H.E. (1970). Age Determination of Grizzly Bears from Fourth Premolar Tooth Sections. J. Wildl. Manage. 34, 353.

Cronin, T. (2005). The Visual Ecology of Predator-Prey Interactions. Ecol. Predator-Prey Interact.

D'Eon, R.G., Serrouya, R., Smith, G. & Kochanny, C.O. (2002). GPS Radiotelemetry Error and Bias in Mountainous Terrain. Wildl. Soc. Bull. 30, 430–439.

Dacke, M., Nilsson, D.-E., Scholtz, C.H., Byrne, M. & Warrant, E.J. (2003). Insect orientation to polarized moonlight. Nature 424, 33–33.

Dahle, B. & Swenson, J.E. (2003a). Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. J. Zool. 260, 329–335.

Dahle, B. & Swenson, J.E. (2003b). Seasonal range size in relation to reproductive strategies in brown bears Ursus arctos. J. Anim. Ecol. 72, 660–667.

Dahle, B., Sandegren, F., Swenson, J.E., Wedule, E.H. & Sorensen, O.J. (1998). The Diet of brown bears, Ursus arctos in central Scandinavia: effect of access to free ranging domestic sheep Ovis aries. Wildlife Biol. 64, 147–158.

Daly, M., Behrends, P.R., Wilson, M.I. & Jacobs, L.F. (1992). Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, Dipodomys merriami. Anim. Behav. 44, 1–9.

de Weerd, N., van Langevelde, F., van Oeveren, H., Nolet, B.A., Kölzsch, A., Prins, H.H.T. & de Boer, W.F. (2015). Deriving Animal Behaviour from High-Frequency GPS: Tracking Cows in Open and Forested Habitat. PLoS One 10, e0129030.

DeBruyn, A.M.H. & Meeuwig, J.J. (2001). Detecting lunar cycles in marine ecology: periodic regression versus categorical ANOVA 214, 307–310.

DeBruyn, T.D., Smith, T.S., Proffitt, K., Partridge, S. & Drummer, T.D. (2004). Brown Bear Response to Elevated Viewing Structures at Brooks River, Alaska. Wildl. Soc. Bull. 32, 1132–1140.

Delgado, M. del M., Penteriani, V., Nams, V.O. & Campioni, L. (2009). Changes of movement patterns from early dispersal to settlement. Behav. Ecol. Sociobiol. 64, 35–43.

Delgado, M. del M., Penteriani, V., Revilla, E. & Nams, V.O. (2010). The effect of phenotypic traits and external cues on natal dispersal movements. J. Anim. Ecol. 79, 620–632.

Delgado, M.D.M. & Penteriani, V. (2008). Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. Am. Nat. 172.

Delgado, M.M., Tikhonov, G., Meyke, E., Babushkin, M., Bespalova, T., Bondarchuk, S., Esengeldenova, A., Fedchenko, I., Kalinkin, Y., Knorre, A., Kosenkov, G., Kozsheechkin, V., Kuznetsov, A., Larin, E., Mirsaitov, D., Prokosheva, I., Rozhkov, Y., Rykov, A., Seryodkin, I. V., Shubin, S., Sibgatullin, R., Sikkila, N., Sitnikova, E., Sultangareeva, L., Vasin, A., Yarushina, L., Kurhinen, J. & Penteriani, V. (2018). The seasonal sensitivity of brown bear denning phenology in response to climatic variability. Front. Zool. 15, 41.

Delibes-Mateos, M., Ferreras, P. & Villafuerte, R. (2009). European rabbit population trends and associated factors: a review of the situation in the Iberian Peninsula. Mamm. Rev. 39, 124–140.

Demšar, U., Buchin, K., Cagnacci, F., Safi, K., Speckmann, B., Weghe, N. de, Weiskopf, D. & Weibel, R. (2015). Analysis and visualisation of movement: An interdisciplinary review. Mov. Ecol. 3, 1–24.

Di Bitetti, M.S., Paviolo, A. & De Angelo, C. (2006). Density, habitat use and activity patterns of ocelots (Leopardus pardalis) in the Atlantic Forest of Misiones, Argentina. J. Zool. 270.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carr, G., Garc, J.R., Gruber, B., Lafourcade, B., Leit, P.J., Tamara, M., Mcclean, C., Osborne, P.E., Der, B.S., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2012). Collinearity : a review of methods to deal with it and a simulation study evaluating their performance Collinearity : a review of methods to deal with it and a simulation study evaluating their performance.

Dubois, S. & Fraser, D. (2013). A Framework to Evaluate Wildlife Feeding in Research, Wildlife Management, Tourism and Recreation. Animals 3, 978–994.

Dunkley, L. & Cattet, M.R.L. (2003). A comprehensive review of the ecological and human social effects of artificial feeding and baiting of wildlife. Can. Coop. Wildl. Heal. Cent. Newsletters Publ.

Ebensperger, L.A. (1998). Strategies and counterstrategies to infanticide in mammals. Biol. Rev. 73, 321–346.

Egevang, C., Stenhouse, I.J., Phillips, R.A., Petersen, A., Fox, J.W. & Silk, J.R.D. (2010). Tracking of Arctic terns Sterna paradisaea reveals longest animal migration. Proc. Natl. Acad. Sci. 107, 2078–2081.

Ehrlén, J. & Morris, W.F. (2015). Predicting changes in the distribution and abundance of species under environmental change. Ecol. Lett. 18, 303–314.

Elfström, M., Zedrosser, A., Støen, O.G. & Swenson, J.E. (2014). Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: Review and management implications. Mamm. Rev. 44, 5–18.

Ellis, E.C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D.Q., Gill, J.L., Kaplan, J.O., Kingston, N., Locke, H., McMichael, C.N.H., Ranco, D., Rick, T.C., Shaw, M.R., Stephens, L., Svenning, J.-C. & Watson, J.E.M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. Proc. Natl. Acad. Sci. 118.

Ermala, A. (2003). A Survey of Large Predators in Finland during the 19 th –20 th Centuries. Acta Zool. Litu. 13, 15–20.

Eskelinen, P. (2009). Finnish brown bear watching tourism entrepreneurship in numbers (in Finnish). Riista- ja kalatalous – Selvityksiä 15, Helsinki.

Estes, J.A., Jameson, R.J. & Rhode, E.B. (1982). Activity and Prey Election in the Sea Otter: Influence of Population Status on Community Structure. Am. Nat. 120, 242–258.

Ewen, J.G., Walker, L., Canessa, S. & Groombridge, J.J. (2014). Improving supplementary feeding in species conservation. Conserv. Biol. 29, 341–349.

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W., Papastamatiou, Y.P., Forester, J. & Mueller, T. (2013). Spatial memory and animal movement. Ecol. Lett. 16, 1316–1329.

Farley, S.D. & Robbins, C.T. (1995). Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can. J. Zool. 73, 2216–2222.

Felton, A.M., Felton, A., Cromsigt, J.P.G.M., Edenius, L., Malmsten, J. & Wam, H.K. (2017). Interactions between ungulates, forests, and supplementary feeding: the role of nutritional balancing in determining outcomes. Mammal Res. 62, 1–7.

Ferrari, A. & Comelli, M. (2016). A comparison of methods for the analysis of binomial clustered outcomes in behavioral research. J. Neurosci. Methods 274, 131–140.

Fletcher, R.J., Sefair, J., Wang, C., Poli, C.L., Smith, T.A.H., Bruna, E.M., Holt, R., Barfield, M., Marx, A.J. & Acevedo, M. (2019). Towards a unified framework for connectivity that disentangles movement and mortality in space and time. Ecol. Lett. 22, 1680–1689.

Fležar, U., Costa, B., Bordjan, D., Jerina, K. & Krofel, M. (2019). Free food for everyone: artificial feeding of brown bears provides food for many non-target species. Eur. J. Wildl. Res. 65, 1.

Foster, R.G. & Roenneberg, T. (2008). Human Responses to the Geophysical Daily, Annual and Lunar Cycles. Curr. Biol. 18, R784–R794.

Gable, T.D., Johnson-Bice, S.M. & Windels, S.K. (2023). A simple, low-cost method to age mammals? An alternative to cementum annuli analysis. Ecol. Evol. 13, e9710.

Gardner, C.L., Pamperin, N.J., Benson, J.F., Gardner, C.L., Pamperin, N.J. & Benson, J.F. (2014). Movement patterns and space use of maternal grizzly bears influence cub survival in Interior Alaska. Ursus 25, 121–138.

Garshelis, D.L., Baruch-Mordo, S., Bryant, A., Gunther, K.A. & Jerina, K. (2017). Is diversionary feeding an effective tool for reducing human–bear conflicts? Case studies from North America and Europe. Ursus 28, 31–55.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. (2018). The influence of human disturbance on wildlife nocturnality. Science (80-.). 360, 1232–1235.

Gende, S.M. & Quinn, T.P. (2004). The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. Can. J. Zool. 82, 75–85.

González-Bernardo, E., Russo, L.F., Valderrábano, E., Fernández, Á. & Penteriani, V. (2020). Denning in brown bears. Ecol. Evol. 10, 6844–6862.

Gosselin, J., Zedrosser, A., Swenson, J.E. & Pelletier, F. (2015). The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. Proc. R. Soc. B Biol. Sci. 282, 20141840.

Graf, P.M., Mayer, M., Zedrosser, A., Hackländer, K. & Rosell, F. (2016). Territory size and age explain movement patterns in the Eurasian beaver. Mamm. Biol. 81, 587–594.

Graham, K. & Stenhouse, G.B. (2014). Home range, movements, and denning chronology of the Grizzly Bear (Ursus arctos) in west-central Alberta. Can. Field-Naturalist 128, 223.

Grant, R., Halliday, T. & Chadwick, E. (2012). Amphibians' response to the lunar synodic cycle-a review of current knowledge, recommendations, and implications for conservation. Behav. Ecol. 24, 53–62.

Grassman, L., Tewes, M. & Silvy, N. (2005). Ranging, habitat use and activity patterns of binturong Arctictis binturongand yellow-throated marten Martes flavigulain north-central Thailand. Wildlife Biol. 11, 49–57.

Griffin, P.C., Griffin, S.C., Waroquiers, C. & Mills, L.S. (2005). Mortality by moonlight: Predation risk and the snowshoe hare. Behav. Ecol. 16, 938–944.

Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. J. Evol. Biol. 24, 699–711.

Hagen, S.B., Kopatz, A., Aspi, J., Kojola, I. & Geir Eiken, H. (2015). Evidence of rapid change in genetic structure and diversity during range expansion in a recovering large terrestrial carnivore. Proc. R. Soc. B Biol. Sci. 282, 13–16.

Hansson, L.-A. & Åkesson, S. (2014). Animal Movement Across Scales. Oxford Univ. Press. OXford, UK.

Haskell, J.P., Ritchie, M.E. & Olff, H. (2002). Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418, 527–530.

Heikkinen, S., Kojola I. & Mantyniemi, S., Karhukanta Suomessa 2020 [Bear population in Finland 2020]. Luonnonvara- ja biotalouden tutkimus 20/2021. Luonnonvarakeskus (Helsinki 2021).

Hernando, M.D.G., Karamanlidis, A.A., Papakostas, G. & Beecham, J. (2020). Reduced movement of wildlife in Mediterranean landscapes : a case study of brown bears in Greece. J. Zool.

Hertel, A.G., Bischof, R., Langval, O., Mysterud, A., Kindberg, J., Swenson, J.E. & Zedrosser, A. (2018). Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. Oikos 127, 197–207.

Hertel, A.G., Hertel, A.G., Niemelä, P.T., Dingemanse, N.J., Mueller, T. & Mueller, T. (2020a). A guide for studying among-individual behavioral variation from movement data in the wild. Mov. Ecol. 8, 30.

Hertel, A.G., Leclerc, M., Warren, D., Pelletier, F., Zedrosser, A. & Mueller, T. (2019). Don’t poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. Anim. Behav. 147, 91–104.

Hertel, A.G., Royauté, R., Zedrosser, A. & Mueller, T. (2020b). Biologging reveals individual variation in behavioural predictability in the wild. J. Anim. Ecol.

Hertel, A.G., Swenson, J.E. & Bischof, R. (2017). A case for considering individual variation in diel activity patterns. Behav. Ecol. 28, 1524–1531.

Hertel, A.G., Steyaert, S.M.J.G., Zedrosser, A., Mysterud, A., Lodberg-Holm, H.K., Gelink, H.W., Kindberg, J. & Swenson, J.E. (2016). Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. Behav. Ecol. Sociobiol. 70, 831–842.

Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattisson, J., Odden, J., Persson, J., Rauset, G.R., Schmidt, K. & Linnell, J.D.C. (2014). Activity Patterns of Eurasian Lynx Are Modulated by Light Regime and Individual Traits over a Wide Latitudinal Range. PLoS One 9, e114143.

Hrdy, S.B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. Ethol. Sociobiol. 1, 13–40.

Irannezhad, M. (2015). Spatio-temporal Climate Variability and Snow Resource Changes in Finland.

Jalanka, H.H. & Roeken, B.O. (1990). The Use of Medetomidine, Medetomidine-Ketamine Combinations, and Atipamezole in Nondomestic Mammals: A Review. J. Zoo Wildl. Med. 21, 259–282.

Jaroszewicz, B., Kwiecień, K., Czortek, P., Olech, W. & Pirożnikow, E. (2017). Winter supplementary feeding influences forest soil seed banks and vegetation. Appl. Veg. Sci. 20, 683–691.

Jerina, K. (2012). Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. J. Mammal. 93, 1139–1148.

Jerina, K., Krofel, M., Stergar, M. & VIDEMŠEK, U. (2012). Final report: Factors Affecting Brown Bear Habituation To Humans : a Gps Telemetry Study.

Jerina, K., Krofel, M., Stergar, M. & VIDEMŠEK, U. (2012). Final report: Factors Affecting Brown Bear Habituation To Humans : a Gps Telemetry Study.

Jingxuan, W. & Jiang, G. (2020). Advances in Terrestrial Mammal Movement Ecology: An Overview. J. Zool. Res. 1, 28–35.

Kaczensky, P., Huber, D., Knauer, F., Roth, H., Wagner, A. & Kusak, J. (2006). Activity patterns of brown bears (Ursus arctos) in Slovenia and Croatia. J. Zool. 269, 474–485.

Kaczensky, P., Chapron, G., Arx, M. von, Huber, D., Andrén, H. & Linnell, J. (2012). Status, management and distribution of large carnivores – bear, lynx, wolf & wolverine – in Europe. Eur. Comm. 1–200.

Kaczensky, P., Linnell, J.D.C., Huber, D., Von Arx, M., Andren, H., Breitenmoser, U. & Boitani, L. (2021). Distribution of large carnivores in Europe 2012 - 2016: Distribution maps for Brown bear, Eurasian lynx, Grey wolf, and Wolverine. Dryad, Dataset.

Kavčič, I., Adamič, M., Kaczensky, P., Krofel, M., Kobal, M. & Jerina, K. (2015). Fast food bears: brown bear diet in a human-dominated landscape with intensive supplemental feeding. Wildlife Biol. 21, 1–8.

Kay, S.L., Fischer, J.W., Monaghan, A.J., Beasley, J.C., Boughton, R., Campbell, T.A., Cooper, S.M., Ditchkoff, S.S., Hartley, S.B., Kilgo, J.C., Wisely, S.M., Wyckoff, A.C., VerCauteren, K.C. & Pepin, K.M. (2017). Quantifying drivers of wild pig movement across multiple spatial and temporal scales. Mov. Ecol. 5, 14.

Kays, R., Parsons, A.W., Baker, M.C., Kalies, E.L., Forrester, T., Costello, R., Rota, C.T., Millspaugh, J.J. & McShea, W.J. (2017). Does hunting or hiking affect wildlife communities in protected areas? J. Appl. Ecol. 54, 242–252.

Keuling, O., Stier, N. & Roth, M. (2008). Annual and seasonal space use of different age classes of female wild boar Sus scrofa L. Eur. J. Wildl. Res. 54, 403–412.

Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S., Gaillard, J.-M. & Moorcroft, P.R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philos. Trans. R. Soc. B Biol. Sci. 365, 2221–2231.

Kirby, R., Macfarland, D.M. & Pauli, J.N. (2017). Consumption of intentional food subsidies by a hunted carnivore. J. Wildl. Manage. 81, 1161–1169.

Knight, J. (2009). Making wildlife viewable: Habituation and attraction. Soc. Anim. 17, 167–184.

Knott, E.J., Bunnefeld, N., Huber, D., Reljić, S., Kereži, V. & Milner-Gulland, E.J. (2014). The potential impacts of changes in bear hunting policy for hunting organisations in Croatia. Eur. J. Wildl. Res. 60, 85–97.

Koch, P.L. & Barnosky, A.D. (2006). Late quaternary extinctions: State of the debate. Annu. Rev. Ecol. Evol. Syst. 37, 215–250.

Kojola, I. & Heikkinen, S. (2012). Problem brown bears Ursus arctos in Finland in relation to bear feeding for tourism purposes and the density of bears and humans . Wildlife Biol. 18, 258–263.

Kojola, I., Hallikainen, V., Heikkinen, S. & Nivala, V. (2021). Inadvertent shooting of brown bear cubs in Finland: what can managers do to reduce it? Wildlife Biol. 2021.

Kojola, I., Hallikainen, V., Nygren, T., Pesonen, M. & Ruusila, V. (2006). Recent trends and harvest in Finland's brown bear population. Ursus 17, 159–164.

Kotler, B.P., Brown, J.S., Dall, S.R.X., Gresser, S., Ganey, D. & Bouskila, A. (2002). Foraging games between gerbils and their predators: Temporal dynamics of resource depletion and apprehension in gerbils. Evol. Ecol. Res. 4, 495–518.

Kotler, B.P., Brown, J.S., Smith, R.J. & Wirtz, W.O. (1988). The Effects of Morphology and Body Size on Rates of Owl Predation on Desert Rodents. Oikos 53, 145.

Krofel, M. & Jerina, K. (2016). Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. Biol. Conserv. 197, 40–46.

Krofel, M., Špacapan, M. & Jerina, K. (2017). Winter sleep with room service: denning behaviour of brown bears with access to anthropogenic food. J. Zool. 302, 8–14.

Kronfeld-Schor, N., Dominoni, D., de la Iglesia, H., Levy, O., Herzog, E.D., Dayan, T. & Helfrich-Forster, C. (2013). Chronobiology by moonlight. Proc. R. Soc. B Biol. Sci. 280, 1765.

Lamamy, C., Bombieri, G., Zarzo-arias, A., González-bernardo, E. & Penteriani, V. (2019). Can landscape characteristics help explain the different trends of Cantabrian brown bear subpopulations ? Mammal Res.

Lankia, T., Neuvonen, M., Pouta, E., Sievänen, T. & Torvelainen, J. (2020). Outdoor recreation in ecosystem service accounting: pilot accounts from Finland. Scand. J. For. Res. 35, 186–197.

Lemky, K. (2006). Nature-based Tourism in Peripheral Areas: Development or Disaster? edited by C. MichaelHall and StephenBoyd, Channel View Publications, Toronto, 2005, x + 281 pp., paper $US44.95 (ISBN 1845410009). Can. Geogr. / Le Géographe Can. 50, 411–412.

Lewis, J.S. & Rachlow, J.L. (2011). Activity Patterns of Black Bears in Relation to Sex, Season, and Daily Movement Rates. West. North Am. Nat. 71, 388–395.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Linnell, J.D.C., Steuer, D., Odden, J., Kaczensky, P. & Swenson, J.E. (2002). European Brown Bear Compendium. Safari Club Int. Found. Wildl. Conserv. Issues - Tech. Ser. 1–131.

López-Bao, J. V., Rodríguez, A. & Palomares, F. (2008). Behavioural response of a trophic specialist, the Iberian lynx, to supplementary food: Patterns of food use and implications for conservation. Biol. Conserv. 141, 1857–1867.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biol. Conserv. 134, 548–558.

Luttbeg, B. & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. Philos. Trans. R. Soc. B Biol. Sci. 365, 3977–3990.

Majić Skrbinšek, A. & Krofel, M. (2014). Defining, preventing, and reacting to problem bear behaviour in Europe. Eur. Comm.

Manning, J.L. & Baltzer, J.L. (2011). Impacts of black bear baiting on Acadian forest dynamics - An indirect edge effect? For. Ecol. Manage. 262, 838–844.

Martin, J., Calenge, C., Quenette, P.Y. & Allainé, D. (2008). Importance of movement constraints in habitat selection studies. Ecol. Modell. 213, 257–262.

Martin, J., van Moorter, B., Revilla, E., Blanchard, P., Dray, S., Quenette, P.-Y., Allainé, D. & Swenson, J.E. (2013). Reciprocal modulation of internal and external factors determines individual movements. J. Anim. Ecol. 82, 290–300.

Martínez Cano, I., Taboada, F.G., Naves, J., Fernández-Gil, A. & Wiegand, T. (2016). Decline and recovery of a large carnivore: environmental change and long-term trends in an endangered brown bear population. Proc. R. Soc. B Biol. Sci. 283, 20161832.Massé, S., Dussault, C., Dussault, C. & Ibarzabal, J. (2014). How artificial feeding for tourism-watching modifies black bear space use and habitat selection. J. Wildl. Manage. 78, 1228–1238.

McCarthy, K.P. & Fletcher, R.J. (2015). Does hunting activity for game species have indirect effects on resource selection by the endangered Florida panther? Anim. Conserv. 18, 138–145.

McGinlay, J., Parsons, D.J., Morris, J., Graves, A., Hubatova, M., Bradbury, R.B. & Bullock, J.M. (2018). Leisure activities and social factors influence the generation of cultural ecosystem service benefits. Ecosyst. Serv. 31, 468–480.

McKenzie, H.W., Lewis, M.A. & Merrill, E.H. (2009). First passage time analysis of animal movement and insights into the functional response. Bull. Math. Biol. 71, 107–129.

McLoughlin, P.D., Ferguson, S.H. & Messier, F. (2000). Intraspecic variation in home range overlap with habitat quality: a comparison among brown bear populations. Entomol. Exp. Appl. 14, 39–60.

Mery, F. (2013). Natural variation in learning and memory. Curr. Opin. Neurobiol. 23, 52–56.

Messier, F. (1985). Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Can. J. Zool. 63, 239–245.

Milner, J.M., Van Beest, F.M., Schmidt, K.T., Brook, R.K. & Storaas, T. (2014). To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. J. Wildl. Manage. 78, 1322–1334.

Mohr, C.O. (1947). Table of Equivalent Populations of North American Small Mammals. Am. Midl. Nat. 37, 223–249.

Monterroso, P., Alves, P.C. & Ferreras, P. (2013). Catch Me If You Can: Diel Activity Patterns of Mammalian Prey and Predators. Ethology 119, 1044–1056.

Morales-González, A., Ruiz-Villar, H., Ordiz, A. & Penteriani, V. (2020). Large carnivores living alongside humans: Brown bears in human-modified landscapes. Glob. Ecol. Conserv. 22, e00937.

Mowat, G. & Heard, D.C. (2006). Major components of grizzly bear diet across North America. Can. J. Zool. 84, 473–489.

Mukherjee, S., Zelcer, M. & Kotler, B.P. (2009). Patch use in time and space for a meso-predator in a risky world. Oecologia 159, 661–668.

Munro, R.H.M., Nielsen, S.E., Price, M.H., Stenhouse, G.B. & Boyce, M.S. (2006). SEASONAL AND DIEL PATTERNS OF GRIZZLY BEAR DIET AND ACTIVITY IN WEST-CENTRAL ALBERTA. J. Mammal. 87, 1112–1121.

Murray, M.H., Becker, D.J., Hall, R.J. & Hernandez, S.M. (2016). Wildlife health and supplemental feeding: A review and management recommendations. Biol. Conserv. 204, 163–174.

Mysterud, A., Viljugrein, H., Solberg, E.J. & Rolandsen, C.M. (2019). Legal regulation of supplementary cervid feeding facing chronic wasting disease. J. Wildl. Manage. 83, 1667–1675.

Myung, I.J. (2003). Tutorial on maximum likelihood estimation. J. Math. Psychol. 47, 90–100.

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142.

Nakamura, S., Yamazaki, J., Matsumoto, N., Inoue-Murayama, M., Qi, H., Yamanaka, M., Nakanishi, M., Yanagawa, Y., Sashika, M., Tsubota, T., Ito, H. & Shimozuru, M. (2023). Age estimation based on blood DNA methylation levels in brown bears. Mol. Ecol. Resour. 23, 1211–1225.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008). A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. 105, 19052–19059.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. & Getz, W.M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. J. Exp. Biol. 215, 986–996.

Naves, J., T. Wiegand, E. Revilla, and M. Delibes. 2003. Endangered Species Constrained by Natural and Human Factors: the Case of Brown Bears in Northern Spain. Conservation Biology 17:1276–1289.

Naves, J., Fernández-Gil, A., Rodríguez, C. & Delibes, M. (2006). BROWN BEAR FOOD HABITS AT THE BORDER OF ITS RANGE: A LONG-TERM STUDY. J. Mammal. 87, 899–908.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. & Dickman, C.R. (2015). The ecological effects of providing resource subsidies to predators. Glob. Ecol. Biogeogr. 24, 1–11.

Niedziałkowska, M., Hayward, M.W., Borowik, T., Jędrzejewski, W. & Jędrzejewska, B. (2019). A meta-analysis of ungulate predation and prey selection by the brown bear Ursus arctos in Eurasia. Mammal Res. 64, 1–9.

Nielsen, E.T. (1984). Relation of Behavioural Activity Rhythms To the Changes of Day and Night. a Revision of Views. Behaviour 89, 147–173.

Nilsson, J.-åke, Brönmark, C., Hansson, L. & Chapman, B.B. (2014). Individuality in movement : the role of animal personality. In Animal Movement Across Scales: 90–109. Hansson, L.-A. & Åkesson, S. (Eds.). Oxford, UK: Oxford University Press.

O'Neal, B.J., Heske, E.J. & Stafford, J.D. (2008). Waterbird Response to Wetlands Restored Through the Conservation Reserve Enhancement Program. J. Wildl. Manage. 72, 654–664.

Oja, R., Zilmer, K. & Valdmann, H. (2015). Spatiotemporal effects of supplementary feeding of wild boar (Sus scrofa) on artificial ground nest depredation. PLoS One 10, 1–11.

Orams, M.B. (2002). Feeding wildlife as a tourism atraction: a review of issues and impacts. Tour. Manag. 23, 281–293.

Ordiz, A., Kindberg, J., Sæbø, S., Swenson, J.E. & Støen, O.-G. (2014). Brown bear circadian behavior reveals human environmental encroachment. Biol. Conserv. 173, 1–9.

Ordiz, A., Saebø, S., Kindberg, J., Swenson, J.E. & Støen, O.-G. (2017). Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? Anim. Conserv. 20, 51–60.

Ordiz, A., Støen, O.-G., Delibes, M. & Swenson, J.E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166, 59–67.

Ordiz, A., Støen, O.-G., Sæbø, S., Kindberg, J., Delibes, M. & Swenson, J.E. (2012). Do bears know they are being hunted? Biol. Conserv. 152, 21–28.

Ordiz, A., Støen, O.-G., Saebø, S., Sahlén, V., Pedersen, B.E., Kindberg, J. & Swenson, J.E. (2013). Lasting behavioural responses of brown bears to experimental encounters with humans. J. Appl. Ecol. 50, 306–314.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. & Martínez-Abraín, A. (2013). Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514.

Ossi, F., Gaillard, J.M., Hebblewhite, M., Morellet, N., Ranc, N., Sandfort, R., Kroeschel, M., Kjellander, P., Mysterud, A., Linnell, J.D.C., Heurich, M., Soennichsen, L., Sustr, P., Berger, A., Rocca, M., Urbano, F. & Cagnacci, F. (2017). Plastic response by a small cervid to supplemental feeding in winter across a wide environmental gradient. Ecosphere 8, e01629.

Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008). State – space models of individual animal movement. Trends Ecol. Evol. 23, 87–94.

Penteriani, V. & Melletti, M. (Eds.). (2020). Bears of the World: Ecology, Conservation and Management. Cambridge University Press, UK.

Penteriani, V. (2008). When similar ecological patterns in time emerge from different initial conditions: equifinality in the breeding performance of animal populations. Ecol. Complex. 5, 66–68.

Penteriani, V., del Mar Delgado, M., Kuparinen, A., Saurola, P., Valkama, J., Salo, E., Toivola, J., Aebischer, A. & Arlettaz, R. (2014). Bright moonlight triggers natal dispersal departures. Behav. Ecol. Sociobiol. 68, 743–747.

Penteriani, V., Delgado, M. del M. & Melletti, M. (2010). Don't feed the bears! Oryx 44, 169–170.

Penteriani, V., Delgado, M.D.M., Krofel, M., Jerina, K., Ordiz, A., Dalerum, F., Zarzo-Arias, A. & Bombieri, G. (2018). Evolutionary and ecological traps for brown bears Ursus arctos in human-modified landscapes. Mamm. Rev. 48, 180–193.

Penteriani, V., Delgado, M.M. & Melletti, M. (2010). Don't feed the bears! Oryx 44, 169–170.

Penteriani, V., Kuparinen, A., del Mar Delgado, M., Palomares, F., López-Bao, J.V., Fedriani, J.M., Calzada, J., Moreno, S., Villafuerte, R., Campioni, L. & Lourenço, R. (2013). Responses of a top and a meso predator and their prey to moon phases. Oecologia 173, 753–766.

Penteriani, V., Kuparinen, A., Delgado, M. del M., Lourenço, R. & Campioni, L. (2011). Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. Anim. Behav. 82, 413–420.

Penteriani, V., López-Bao, J.V., Bettega, C., Dalerum, F., Delgado, M. del M., Jerina, K., Kojola, I., Krofel, M. & Ordiz, A. (2017). Consequences of brown bear viewing tourism: A review. Biol. Conserv. 206, 169–180.

Persson, I.-L., Wikan, S., Swenson, J.E. & Mysterud, I. (2001). The diet of the brown bear Ursus arctos in the Pasvik Valley, northeastern Norway. Wildlife Biol. 7, 27–37.

Pigeon, K.E., Stenhouse, G. & Côté, S.D. (2016). Drivers of hibernation: linking food and weather to denning behaviour of grizzly bears. Behav. Ecol. Sociobiol. 70, 1745–1754.

Pop, I.M., Bereczky, L., Chiriac, S., Iosif, R., Nita, A., Popescu, V.D. & Rozylowicz, L. (2018a). Movement ecology of brown bears (Ursus arctos) in the Romanian Eastern Carpathians. Nat. Conserv. 26, 15–31.

Pop, M.I., Iosif, R., Miu, I. V., Rozylowicz, L. & Popescu, V.D. (2018b). Combining resource selection functions and home-range data to identify habitat conservation priorities for brown bears. Anim. Conserv. 21, 352–362.

Popescu, F.C. & Rymer, W.Z. (2000). End Points of Planar Reaching Movements Are Disrupted by Small Force Pulses: An Evaluation of the Hypothesis of Equifinality. J. Neurophysiol. 84, 2670–2679.

Powell, R. (2000). Animal Home Ranges and Territories and Home Range Estimators. In Research techniques in animal ecology: controversies and consequences: 64–110.

Prates, L. & Perez, S.I. (2021). Late Pleistocene South American megafaunal extinctions associated with rise of Fishtail points and human population. Nat. Commun. 12, 2175.

Prinz, N., Story, R., Lyon, S., Ferse, S.C.A. & Bejarano, S. (2020). To Feed or Not to Feed? Coral Reef Fish Responses to Artificial Feeding and Stakeholder Perceptions in the Aitutaki Lagoon, Cook Islands. Front. Mar. Sci. 7, 1–16.

R Development Core Team. (2016). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.r-project.org.

R Foundation for Statistical Computing. (2018). R: A Language and Environment for Statistical Computing.

Rasmussen, G.S.A. & MacDonald, D.W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. J. Zool. 286, 232–242.

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D.C., Watt, A. & Gutiérrez, R.J. (2013). Understanding and managing conservation conflicts. Trends Ecol. Evol. 28, 100–109.

Richardson, M.L. (2017). Daily and Monthly Activity of Brown Bears (Ursus arctos) Near a Proposed Industrial Project in Coastal British Columbia . West. North Am. Nat. 77, 118–123.

Riotte-Lambert, L. & Matthiopoulos, J. (2020). Environmental Predictability as a Cause and Consequence of Animal Movement. Trends Ecol. Evol. 35, 163–174.

Rode, K.D. & Robbins, C.T. (2000). Why bears consume mixed diets during fruit abundance. Can. J. Zool. 78, 1640–1645.

Rode, K.D., Robbins, C.T. & Shipley, L.A. (2001). Constraints on herbivory by grizzly bears. Oecologia 128, 62–71.

Rodewald, A.D., Kearns, L.J. & Shustack, D.P. (2011). Ecological Society of America Anthropogenic resource subsidies decouple predator — prey relationships. Ecol. Appl. 21, 936–943.

Sábato, M.A.L., Melo, L.F.B. de, Magni, E.M.V., Young, R.J. & Coelho, C.M. (2006). A note on the effect of the full moon on the activity of wild maned wolves, Chrysocyon brachyurus. Behav. Processes 73, 228–230.

San-Jose, L.M., Séchaud, R., Schalcher, K., Judes, C., Questiaux, A., Oliveira-Xavier, A., Gémard, C., Almasi, B., Béziers, P., Kelber, A., Amar, A. & Roulin, A. (2019). Differential fitness effects of moonlight on plumage colour morphs in barn owls. Nat. Ecol. Evol. 3, 1331–1340.

Seaman, D.E., Millspaugh, Joshua J. Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999). Effects of sample size on kernel home range estimates. J. Wildl. Manage. 63, 739–747.

Selva, N., Berezowska-Cnota, T. & Elguero-Claramunt, I. (2014). Unforeseen Effects of Supplementary Feeding : Ungulate Baiting Sites as Hotspots for Ground-Nest Predation. PLoS One 9, e90740.

Selva, N., Teitelbaum, C.S., Sergiel, A., Zwijacz-Kozica, T., Zięba, F., Bojarska, K. & Mueller, T. (2017). Supplementary ungulate feeding affects movement behavior of brown bears. Basic Appl. Ecol. 24, 68–76.

Sergiel, A., Barja, I., Navarro-Castilla, Á., Zwijacz-Kozica, T. & Selva, N. (2020). Losing seasonal patterns in a hibernating omnivore? Diet quality proxies and faecal cortisol metabolites in brown bears in areas with and without artificial feeding. PLoS One 15, e0242341.

Seryodkin, I. V, Kostyria, A. V, Goodrich, J.M. & Miquelle, D.G. (2013). Daily activity patterns of brown bear (Ursus arctos) of the Sikhote-Alin mountain range (Primorskiy Krai, Russia). Russ. J. Ecol. 44, 50–55.

Shackley, M. (1996). Wildlife Tourism. Int. Thomson Bus. Press. London.

Shamoun-Baranes, J., Bom, R., van Loon, E.E., Ens, B.J., Oosterbeek, K. & Bouten, W. (2012). From Sensor Data to Animal Behaviour: An Oystercatcher Example. PLoS One 7, e37997.

Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P., Wallace, B.P., Spotila, J.R., Paladino, F. V, Piedra, R., Eckert, S.A. & Block, B.A. (2008). Persistent Leatherback Turtle Migrations Present Opportunities for Conservation. PLoS Biol. 6, e171.

Shirane, Y., Shimozuru, M., Yamanaka, M., Tsuruga, H., Nakanishi, M., Ishinazaka, T., Nose, T., Kasai, S., Shirayanagi, M. & Masuda, Y. (2019). Sex-biased dispersal and inbreeding avoidance in Hokkaido brown bears. J. Mammal. 100, 1317–1326.

Sjödin, A., Hjorth, M.F., Damsgaard, C.T., Ritz, C., Astrup, A. & Michaelsen, K.F. (2015). Physical activity, sleep duration and metabolic health in children fluctuate with the lunar cycle: science behind the myth. Clin. Obes. 5, 60–66.

Skuban, M., Finďo, S. & Kajba, M. (2016). Human impacts on bear feeding habits and habitat selection in the Poľana Mountains, Slovakia. Eur. J. Wildl. Res. 62, 353–364.

Soltis, J., Thomsen, R., Matsubayashi, K. & Takenaka, O. (2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (Macaca fuscata). Behav. Ecol. Sociobiol. 48, 195–202.

Spady, T.J., Lindburg, D.G. & Durrant, B.S. (2007). Evolution of reproductive seasonality in bears. Mamm. Rev. 37, 21–53.

Steffen, W., Crutzen, P.J. & McNeill, J.R. (2007). The anthropocene: Are humans now overwhelming the great forces of nature? Ambio 36, 614–621.

Stenset, N.E., Lutnæs, P.N., Bjarnadóttir, V., Dahle, B., Fossum, K.H., Jigsved, P., Johansen, T., Neumann, W., Opseth, O., Rønning, O., Steyaert, S.M.J.G., Zedrosser, A., Brunberg, S. & Swenson, J.E. (2016). Seasonal and annual variation in the diet of brown bears Ursus arctos in the boreal forest of southcentral Sweden. Wildlife Biol. 22, 107–116.

Steyaert, S.M.J.G., Endrestøl, A., Hackländer, K., Swenson, J.E. & Zedrosser, A. (2012). The mating system of the brown bear Ursus arctos. Mamm. Rev. 42, 12–34.

Steyaert, S.M.J.G., Kindberg, J., Jerina, K., Krofel, M., Stergar, M., Swenson, J.E. & Zedrosser, A. (2014). Behavioral correlates of supplementary feeding of wildlife: Can general conclusions be drawn? Basic Appl. Ecol. 15, 669–676.

Støen, O.-G., Zedrosser, A., Sæbø, S. & Swenson, J.E. (2006). Inversely density-dependent natal dispersal in brown bears Ursus arctos. Oecologia 148, 356e364.

Stoffel, M.A., Nakagawa, S. & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol. Evol. 8, 1639–1644.

Štofik, J., Merganič, J., Merganičová, K. & Saniga, M. (2013). Seasonal Changes in Food Composition of the Brown Bear (Ursus arctos) from the Edge of Its Occurrence — Eastern Carpathians (Slovakia). Folia Zool. 62, 222–231.

Štofík, J., Merganič, J., Merganičová, K., Bučko, J. & Saniga, M. (2016). Brown bear winter feeding ecology in the area with supplementary feeding - Eastern Carpathians (Slovakia). Polish J. Ecol. 64, 277–288.

Strandin, T., Babayan, S.A. & Forbes, K.M. (2018). Reviewing the effects of food provisioning on wildlife immunity. Philos. Trans. R. Soc. B Biol. Sci. 373, 20170088.

Sweanor, L.L., Logan, K.A., Bauer, J.W., Millsap, B. & Boyce, W.M. (2008). Puma and Human Spatial and Temporal Use of a Popular California State Park. J. Wildl. Manage. 72, 1076–1084.

Swenson, J.E., Adamič, M., Huber, D. & Stokke, S. (2007). Brown bear body mass and growth in northern and southern Europe. Oecologia 153, 37–47.

Swenson, J.E., Ambarlı, H., Arnemo, J.M., Baskin, L., Ciucci, P., Danilov, P.I., Delibes, M., Elfström, M., Evans, A.L., Groff, C., Hertel, A.G., Huber, D., Jerina, K., Karamanlidis, A.A., Kindberg, J., Kojola, I., Krofel, M., Kusak, J., Mano, T., Melletti, M., Mertzanis, Y., Ordiz, A., Palazón, S., Parchizadeh, J., Penteriani, V., Quenette, P.-Y., Sergiel, A., Selva, N., Seryodkin, I., Skuban, M., Steyaert, S.M.J.G., Støen, O.-G., Tirronen, K.F. & Zedrosser, A. (2020). Brown Bear (Ursus arctos; Eurasia). In Bears of the World: Ecology, Conservation and Management: 139–161. Melletti, M. & Penteriani, V. (Eds.). Cambridge: Cambridge University Press.

Swihart, R.K., Slade, N.A. & Bergstrom, B.J. (1988). Relating Body Size to the Rate of Home Range Use in Mammals. Ecology 69, 393–399.

Symonds, M.R.E. & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65, 13–21.

T. Robbins, C., K. Fortin, J., D. Rode, K., D. Farley, S., A. Shipley, L. & A. Felicetti, L. (2007). Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 116, 1675–1682.

Teimouri, M., Indahl, U., Sickel, H. & Tveite, H. (2018). Deriving Animal Movement Behaviors Using Movement Parameters Extracted from Location Data. ISPRS Int. J. Geo-Information 7, 78.

Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Okarma, H., Ruczyński, I., Śniezko, S. & Gula, R. (2003). Daily Patterns and Duration of Wolf Activity in the Białowieza Forest, Poland. J. Mammal. 84, 243–253.

Thierry, A.M., De Bouillane De Lacoste, N., Ulvund, K., Andersen, R., MeÅs, R., Eide, N.E. & Landa, A. (2020). Use of Supplementary Feeding Dispensers by Arctic Foxes in Norway. J. Wildl. Manage. 84, 622–635.

Tomkiewicz, S.M., Fuller, M.R., Kie, J.G. & Bates, K.K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. Philos. Trans. R. Soc. B Biol. Sci. 365, 2163–2176.

Treves, A. & Karanth, K.U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. Conserv. Biol. 17, 1491–1499.

Tryjanowski, P., Panek, M., Karg, J., Szumacher-Strabel, M., Cieślak, A. & Ciach, M. (2017). Long-term changes in the quantity and quality of supplementary feeding of wildlife: Are influenced by game managers? Folia Zool. 66, 248–253.

Tuomainen, U. & Candolin, U. (2011). Behavioural responses to human-induced environmental change. Biol. Rev. 86, 640–657.

Van Beeck Calkoen, S.T.S., Mühlbauer, L., Andrén, H., Apollonio, M., Balčiauskas, L., Belotti, E., Carranza, J., Cottam, J., Filli, F., Gatiso, T.T., Hetherington, D., Karamanlidis, A.A., Krofel, M., Kuehl, H.S., Linnell, J.D.C., Müller, J., Ozolins, J., Premier, J., Ranc, N., Schmidt, K., Zlatanova, D., Bachmann, M., Fonseca, C., Lonescu, O., Nyman, M., Šprem, N., Sunde, P., Tannik, M. & Heurich, M. (2020). Ungulate management in European national parks: Why a more integrated European policy is needed. J. Environ. Manage. 260, 110068.

Van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C.M., Solberg, E.J. & Sæther, B.E. (2013). Understanding scales of movement: Animals ride waves and ripples of environmental change. J. Anim. Ecol. 82, 770–780.

Vieira, M.V., M. & Prevedello, J.A. (2010). Movement behaviour within and beyond perceptual ranges in three small mammals : effects of matrix type and body mass. J. Anim. Ecol. 79, 1315–1323.

Von Bertalanffy, L. (1950). The Theory of Open Systems in Physics and Biology. Scence (80-.). 111, 23–29.

Wagenius, S., Dykstra, A.B., Ridley, C.E. & Shaw, R.G. (2012). Seedling Recruitment in the Long-Lived Perennial, Echinacea angustifolia: A 10-Year Experiment. Restor. Ecol. 20, 352–359.

Walpole, M.J. (2001). Feeding dragons in Komodo National Park: A tourism tool with conservation complications. Anim. Conserv. 4, 67–73.

Webber, Q.M.R., Laforge, M.P., Bonar, M., Robitaille, A.L., Hart, C., Zabihi-Seissan, S. & Wal, E. Vander. (2020). The ecology of individual differences empirically applied to space-use and movement tactics. Am. Nat. 196, E1–E15.

Wilson, D.E. & Mittermeier, R.A. (Eds.). (2009). Handbook of the Mammals of the World – Volume 1, Carnivores. Lynx Edicions in association with Conservation International and IUCN.

Wong, B.B.M. & Candolin, U. (2015). Behavioral responses to changing environments. Behav. Ecol. 26, 665–673.

Woodroffe R, Thirgood S, Rabinowitz A, eds. (2005). People and Wildlife, Conflict or Co-existence? , Conservation Biology. Cambridge University Press.

Wu, Y., Wang, H., Wang, H. & Feng, J. (2018). Arms race of temporal partitioning between carnivorous and herbivorous mammals. Sci. Rep. 8, 1713.

Yost, A.C. & Wright, R.G. (2001). Moose, Caribou, and Grizzly Bear Distribution in Relation to Road Traffic in Denali National Park, Alaska. ARCTIC 54.

Zarzo-Arias, A., Delgado, M., Ordiz, A., García, J., Cañedo, D., González, M., Romo, C., Vázquez, P., Bombieri, G., Bettega, C., Russo, L.F., Cabral, P., García-González, R., Martinez-Padilla, J. & Penteriani, V. (2018). Brown bear behaviour in human-modified landscapes: The case of the endangered Cantabrian population, NW Spain. Glob. Ecol. Conserv. 16, e00499.

Zedrosser, A., Dahle, B., Swenson, J.E. & Gerstl, N. (2001). Status and Management of the Brown Bear in Europe. Ursus 12, 9–20.

Zedrosser, A., Steyaert, S.M.J.G., Brunberg, S., Swenson, J. & Kindberg, J. (2013). The effects of baiting for hunting purposes on brown bears and their behaviour. Skandinaviska Björnprojektet.

Zedrosser, A., Støen, O.-G., Sæbø, S. & Swenson, J.E. (2007). Should I stay or should I go? Natal dispersal in the brown bear. Anim. Behav. 74, 369–376.

Ziegltrum, G. (2004). Efficacy of Black Bear Supplemental Feeding To Reduce Conifer Damage in Western Washington. J. Wildl. Manage. 68, 470–474.

Ziegltrum, G. & Nolte, D. (1997). Black bear damage and management in Washington state. Proc. Seventh East. Wildl. Damage Manag. Conf. 7, 104–107.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). Mixed Effects Models and Extensions in Ecology with R. New-York: Springer.