The effect of berry abundance and mortality risk on behavior and life history in Scandinavian brown bears

Effekten av bærproduksjon og risiko for dødelighet på atferd og livshistorie til bjørn i Skandinavia

Anne Gabriela Hertel

The effect of berry abundance and mortality risk on behavior and life history in Scandinavian brown bears
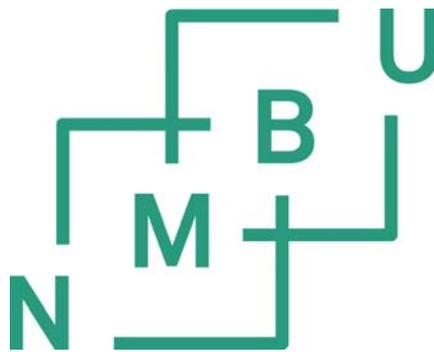
Effekten av bærproduksjon og risiko for dødelighet på atferd og livshistorie til bjørn i Skandinavia

Philosophiae Doctor (PhD) Thesis

Anne Gabriela Hertel

Faculty of Environmental Sciences and Natural Resource Management
Norwegian University of Life Sciences

Ås 2017

PhD supervisors

Professor Jon E. Swenson
Faculty of Environmental Sciences and Natural Resource Management
Norwegian University of Life Sciences
Postbox 5003, 1432 Ås, Norway

Associate Professor Andreas Zedrosser
Department of Environmental and Health Sciences
University of Southeast Norway
3901 Porsgrunn, Norway

Professor Atle Mysterud
Centre for Ecological and Evolutionary Synthesis (CEES)
University of Oslo
Postbox 1066 Blindern, 0316 Oslo, Norway

Dr. Jonas Kindberg
Norwegian Institute for Nature Research
7485 Trondheim, Norway

Dr. Ole-Gunnar Støen
Faculty of Environmental Sciences and Natural Resource Management
Norwegian University of Life Sciences
Postbox 5003, 1432 Ås, Norway

Evaluation committee

Dr. Frank T. van Manen
Department of Forestry, Wildlife and Fisheries
Institute of Agriculture - University of Tennessee
274 Ellington Plant Sciences Building, Knoxville, Tennessee 37996-4563 USA
&
Supervisory Research Wildlife Biologist
Interagency Grizzly Bear Study Team - USGS
2327 University Way, Suite 2, Bozeman, Montana 59715, USA

Dr. Marco Heurich
Chair of Wildlife Ecology and Management
Freiburg University
Fahnenbergplatz, 79085 Freiburg, Germany
&
Bavarian Forest National Park
Department of Conservation and Research
Freyunger Str. 2, 94481 Grafenau, Germany

Professor Leif Egil Loe
Faculty of Environmental Sciences and Natural Resource Management
Norwegian University of Life Sciences
Postbox 5003, 1432 Ås, Norway

Acknowledgements

Thank you Jon for choosing me as your last PhD student, for your fatherly support, open ear and for guiding the development of me and my scientific efforts over the last three years. Andreas, thank you for your guidance and valuable, straight forward advice when I was lost in my own studies. Thanks for lots of creative idea exchange and development, and not least for your companionship and mental support over the years. Atle, thank you for contributing to the development of this thesis with your wealthy knowledge of climate effects research, for your excellent writing skills and unbelievably fast editing support. Jonas for facilitating access to data that were essential for my thesis and Ole-Gunnar for professional advice. Guys – without your support the end product of my efforts, which you currently hold in your hands, would surely have fallen short of its potential, I appreciate all your advice and input! I am grateful that you granted me full access to the bearproject's database and gave me complete intellectual freedom to pursue my research interests.

Jon likes to say that the Scandinavian bear project is like a family. I had a big team with lots of support to start with, but as it happens, this team grew to encompass almost the entire bearproject, with whom I collaborated closely or loosely over the last three years. First, I would like to thank Sam – you were my closest mentor when it came to the day to day little or big questions of science and life as a PhD student. Thank you for the fruitful cooperation and your perpetual open-door policy. Thanks to Richard who helped me improve my coding skills to a new level. Your creative and soundness-driven analytical approaches were inspiring and your career-building advice insightful, it was a pleasure working with you. Martin, you were right when you said that we have a similar "taste" in research - working in tandem with you on that last paper was merging both our ideas, curiosity, and creativity, it was a pleasure that I am happy to repeat at any time! Thanks to Shane, Andrés, and Jack for cooperation, sharpening and supporting my critical view on science, and for insightful discussions, about life, science, politics, and bears. Joanie, Therese, and particularly Gro, my dear office mate, for the girls' chatter and a super fun Alaska trip. Henriette and Hanna, you chaperoned me throughout my PhD period, thanks for a fun fieldwork time and a great collaboration, I wish you all the best for your own future careers. Sven for being the best field station leader there can be, David and the veterinary team for all your efforts marking bears for all of us, Andrea for not getting tired sending me updated tables again and again. I also would like to thank all collaborators from the GLOBE and CAS projects who so readily welcomed me in their project midst.

Thanks to the entire administration staff of our department, who helped me in fighting the paper wars, namely: Kari, Ågot, Mette, Grethe, Ole Wiggo, Gunnar, Stig, and Sjur.

There are many other people who accompanied me during the last three years, at INA, next door, or from Germany. Thanks to all my fellow PhD colleagues at INA, you created a great working and learning environment. I am thankful for our house community in beautiful Norderås, I could not have ended up anywhere better. Caro, Johannes, Frida, Felipe, Karen, and Katinka for your friendship, often expressed in dinners with long, wine-infused conversations. Marte, Sam, Matilda and Vilja for vegetable gardening, building henhouses and turning Norderås into Bullerby with hens, rabbits and Fenre (the dog). Sebastian, you were a fantastic flat mate and friend, always up for a project, always an open ear whether I was in low or high spirits – thank you for the last year in general and for your help with the German translation of my Abstract in particular. Thanks guys for turning Norderås into a home for all

Contents

List of articles

<u>Article I</u>
Hertel, A.G., Steyaert, S.M.J.G., Zedrosser, A., Mysterud, A., Lodberg-Holm, H.K., Gelink, H.W., Kindberg, J. & Swenson, J.E. (2016a) Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. Behavioral Ecology and Sociobiology 70: 831-842. doi: 10.1007/s00265-016-2106-2

<u>Article II</u>
Hertel, A.G., Zedrosser, A., Mysterud, A., Støen, O.-G., Steyaert, S.M.J.G. & Swenson, J.E. (2016b) Temporal effects of hunting on foraging behavior of an apex predator: Do bears forego foraging when risk is high? Oecologia 182: 1019-1029. doi: 10.1007/s00442-016-3729-8

<u>Article III</u>
Lodberg-Holm, H.K.*, Gelink, H.W.*, Hertel, A.G., Swenson, J. E. & Steyaert, S.M.J.G. Brown bears track bilberry fruiting through a landscape of risk. Submitted manuscript. *Authors with equal contribution.

<u>Article IV</u>
Hertel, A.G., Bischof, R., Langvall, O., Mysterud, A., Kindberg, J., Swenson, J.E., Zedrosser, A. Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. Submitted revised manuscript.

<u>Article V</u>
Hertel, A.G., Swenson, J.E., Bischof, R. A case for considering individual variation in diel activity patterns. In revision for invited resubmission.

<u>Article VI</u>
Hertel, A.G.*, Leclerc, M.*, Pelletier, F., Zedrosser, A. Don't poke the bear: Can remote behavior recordings be used to assess personality in elusive wildlife? Submitted manuscript. *Authors with equal contribution.

Abstract

Ecologists who study foraging try to understand how animals decide when and where to forage in order to find enough resources for survival, growth, and reproduction. Hibernators, like the brown bear (Ursus arctos), are especially sensitive to gaining extra mass during the active season, because they are sustained solely by these reserves during hibernation. Bears in Scandinavia use primarily bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum hermaphroditum*) from mid-July until mid-September to increase body mass. This PhD thesis consists of six articles, which all focus on the main objective of understanding how brown bears respond behaviorally to spatial and temporal heterogeneity in resource availability and mortality risk, and how this variation affects their life history parameters.

The first three articles focus on the bears' foraging decisions in relation to spatiotemporal variation in berry abundance and mortality risk. I demonstrate that there is substantial habitat-dependent variation in berry density. Specifically, forestry has transformed the landscape into a matrix of differently aged forest patches, where berries are most abundant in mature, open pine forests and on young clearcuts. In these habitat categories, bears used locations with approximately three times more bilberries, but not lingonberries, than found at random locations. However, bears avoided good foraging locations that coincided with a high mortality risk. This avoidance was stronger for bears that survived the subsequent annual bear hunting season, as compared to bears that were killed during the hunting season. During the hunting season, bears reduced their foraging activity and, when they foraged, they selected locations with fewer bilberries during the hours of highest risk, as compared to before the hunting season. These results demonstrated that bears react to human hunting with antipredation behaviors, similar to those commonly observed in prey animals.

In the fourth article, I explore the effect of fruit masting years on bear life history traits. I show that bilberry and lingonberry production varied in a nonsynchronous fashion over a 10-year period and was affected by climatic events during plant phenology. Bilberry production was negatively impacted by exceptionally cold winters, freezing during flowering, and short and rainy summers. Female bears and their offspring were heavier in years with high bilberry production. Further, female reproductive success was affected by a combination of bilberry production and initial body mass. Initially light-weight females had a lower probability to reproduce than heavier females when bilberry production was low. When bilberry production was high, however, all bears had the same likelihood to reproduce, most likely due to compensatory mass gain by light-weight females.

Lastly, in articles five and six, I elucidate the degree to which individual bears differ behaviorally, and how this may lead to the emergence of different foraging strategies. By investigating six repeatedly measured behaviors – diel activity, degree of diurnality, mean daily travel distance, selection for bogs, clearcuts, and areas close to roads – I found a remarkable degree of variation among individuals and repeatability within individuals. For example, we identified four distinct diel activity strategies within our population, from strictly nocturnal to strictly diurnal. Bears that were followed over more than one year had a higher likelihood of applying the same strategy than any other strategies. From this, I conclude that individuals exhibit different behavioral strategies in our population. With these last two articles, I lay the

foundation for future research into consistent individual variation, e.g., in space-use patterns, and their consequences for life history traits and fitness.

Zusammenfassung

(*loosely translated*)

Ein Teil der Verhaltensökologie beschäftigt sich damit wo und wann Tiere nach Futter suchen um genug Nahrung für Überleben, Wachstum und Reproduktion zu finden. Die Futtersuche von Braunbären muss während der aktiven Zeit besonders effizient sein, da sie während der Winterruhe von den angesammelten Reserven zehren. Braunbären in Skandinavien fressen während der so genannten Hyperphagie im Herbst hauptsächlich Blaubeeren (*Vaccinium myrtillus*), Preiselbeeren (*Vaccinium vitis-idaea*) und Krähenbeeren (*Empetrum hermaphroditum*) um ihre Fettreserven aufzufüllen.

Die vorliegende Dissertation besteht aus sechs Kapiteln welche die Fragestellung behandeln, wie Braunbären ihr Verhalten an zeitliche und räumliche Heterogenität von Nahrungsangebot anpassen und wie diese Heterogenität ihren Lebenszyklus beeinflusst.

Die ersten drei Artikel untersuchen das Nahrungssuchverhalten von Bären unter raumzeitlichen Schwankungen des Beeren - Nahrungsangebots und Sterberisiko. Je nach Habitat gab es beträchtliche Schwankungen in der Dichte von Beeren. Ein Grund dafür ist, dass Forstwirtschaft und Waldpflege das Studiengebiet in Waldstücke unterschiedlichen Alters transformiert haben. Die Beerenproduktion war am höchsten in ausgereiften, offenen Kiefernständen und auf Kahlschlägen. Bären nutzten Stellen mit bis zu dreimal höherer Blaubeerproduktion im Vergleich zu zufälligen Stellen in diesen Habitat Typen. Dies war jedoch nicht der Fall für Preiselbeeren. Bären vermieden während der Nahrungssuche sehr produktive Stellen wenn diese gleichzeitig ein hohen Sterberisiko trugen. Dieses Verhalten war stärker bei Bären welche später die Jagdsaison überlebten, als bei denen die erlegt wurden. Bären reduzierten ihre Futtersuche mit Beginn der Jagdsaison. Wenn sie jedoch in den Morgenstunden wenn der Jagddruck am höchsten war aktiv waren nutzten sie Stellen mit weniger Blaubeeren, im Vergleich zu einer Jagdfreien Periode. Diese Ergebnisse zeigen, dass Bären ähnlich auf menschlichen Jagddruck reagieren wie Beutetiere auf Beutegreifer.

Im vierten Artikel untersuche ich den Effekt von Beeren Mastjahren auf den Lebenszyklus von Bären. Über einen 10 jährigen Zeitraum habe ich analysiert ob Blaubeer- und Preiselbeerproduktion zwischen den Jahren schwanken und wie dies Körpergewicht und Reproduktionserfolg von Bären beeinflusst. Blaubeer- und Preiselbeerproduktion schwankten zwischen den Jahren, jedoch nicht in synchronen Zyklen. Weiblichen Braunbären und ihr Nachwuchs erreichten ein höheres Körpergewicht in Jahren mit hoher Blaubeerproduktion. Der Reproduktionserfolg wurde von einer Kombination von Futterabundanz und Körpergewicht beeinflusst. In Jahren niedriger Blaubeerproduktion hatten weibliche Bären mit geringem Frühjahrsgewicht eine niedrigere Wahrscheinlichkeit zu reproduzieren als solche mit hohem Frühjahrsgewicht. In Mastjahren wurde dieser Effekt jedoch aufgehoben, höchstwahrscheinlich da leichte Bärinnen ihren Gewichtsunterschied im Herbst ausgleichen konnten.

In Artikeln fünf und sechs beleuchte ich inwiefern individuelle Bären sich in ihrem Verhalten unterscheiden und wie dies zu unterschiedlichen Nahrungssuchstrategien führen könnte. Wir untersuchten sechs verschiedene Verhaltensweisen: Aktivitätsrythmus, Ausprägung von Tagaktivität, täglich gewanderte Distanz, Selektion für Moore, Kahlschläge und Gebiete in der Nähe von Straßen. Bären unterschieden sich zwar stark in der Ausprägung

des jeweiligen Verhaltens, die Ausprägung des Verhaltens innerhalb eines Individuen über mehrerer Messungen blieb jedoch konsistent. Zum Beispiel identifizierten wir vier verschiedene Aktivitätsstrategien in unserer Population, welche von ausschließlich nachtaktiv zu ausschließlich tagaktiv reichten. Bären welche in mehreren Jahren gemessen wurden hatten eine höhere Wahrscheinlichkeit dieselbe Strategie anzuwenden als zu einer anderen Strategie zu wechseln. Aufgrund dessen schlussfolgere ich, dass in unserer Population verschiedene Verhaltensstrategien parallel existieren. In einem Versuch die angewandte Aktivitätsstrategie mit der Überlebenswahrscheinlichkeit in der folgenden Jagdsaison zu verbinden, konnten wir jedoch nicht nachweisen dass eine oder mehrere Strategien risikoreicher sind als andere. In diesen beiden letzten Artikeln habe ich den Grundstein für weiterführende Forschung über Verhaltensvariation zwischen Individuen gelegt, zum Beispiel wie sich Individuen in ihren Bewegungsmuster unterscheiden und wie dies ihren Lebenszyklus und ihre Fitness beeinflusst.

Synopsis

Introduction

Energy acquired during food intake is the fundamental currency of all life history. Organisms are driven by the need to find enough food to survive, grow, and reproduce. This primal drive leads to space use geared towards finding those food resources that are most abundant at a given point in time. Ruminants, which are strict herbivores, depend for example on emerging, highly nutritious plants in spring and early summer. In heterogeneous environments, they often migrate along elevational gradients to increase access to emerging plants. The phenomenon has been termed spatio-temporal "green wave surfing" (Bischof et al. 2012). A faster green up shortens the access to emerging plants, which may be so severe that the nutritional disadvantage can be traced in the cohort's fitness later in life. Omnivores are, by definition, more flexible in their diet composition and less dependent on access to one or a few particular food sources than strict herbivores. Many omnivores use highly nutritious food resources, like salmon (Darimont et al. 2008), nuts (Smith and Follmer 1972, Singer et al. 1981), berries (Storch 1993, Welch et al. 1997), fruits (Herrera et al. 1994), or roots (Mitchell et al. 2008), during limited times of the year. In order to exploit these resources optimally, omnivores also track resource availability in a spatio-temporal manner (e.g. the "brown wave" of root phenology Coogan et al. 2012, or the "red wave" of salmon migration Deacy et al. 2016). Adjacent shrubs and trees that produce hard and soft mast (nuts and berries respectively) often synchronize seed production temporally (Silvertown 1980). This phenomenon is termed masting and it leads to years of higher and lower than average food availability for animals. Alternating masting cycles across food species may buffer food shortage when one fails to produce. Recent studies, however, suggest that climatic events could synchronize fruit production failure (Box 1). Spatial heterogeneity in resource availability, together with temporal heterogeneity, both on the intra-annual and interannual scale, present foragers with a cognitive challenge about where and when to search for particular food resources.

To further complicate matters, most animals face predation risk. They are thus not only challenged to optimize foraging time and food intake, but at the same time need to minimize their risk of being killed, the most immediate of all fitness consequences. Prey animals have developed antipredation strategies, tailored to their style of life, living environment, and their predators' hunting tactics. Gregarious animals use group size and cohesion to dilute individual predation risk, increase collective defense ability, and reduce individual vigilance time (Fitzgibbon 1990, Creel and Winnie 2005). Both solitary- and group-living animals decrease encounter probabilities with predators by avoiding habitats that are preferred by their predators or by selecting for denser habitats to reduce detectability (Creel et al. 2005). On the temporal scale, prey animals may shift activity away from time periods when predators are active (Lima and Bednekoff 1999). The disadvantage of antipredator behaviors is, however, although they reduce predation risk, they often impose a cost on food intake. For example, vigilance reduces the time an individual spends foraging (Brown 1999, Fortin et al. 2004), using denser vegetation with increased cover may restrict access to foods growing in more open habitats (Godvik et al. 2009), and temporal displacement can lead to mismatches when food access varies throughout the day (Brook et al. 2012). Indeed, the cost on food intake imposed by antipredation behavior may be as severe as decreased individual fitness (Christianson and Creel 2008, 2010). Because of that, it is expected that animals carefully assess predation risk in order to allocate antipredation behavior to times, places, and circumstances where their benefits outweigh the cost of decreased forage intake (Lima and Bednekoff 1999). Originally, fear

Box 1 Climate effects on berry production in Scandinavia

Bilberry
(*V. myrtillus*)   Lingonberry
(*V. vitis-idaea*)   Crowberry
(*Empetrum sp.*)
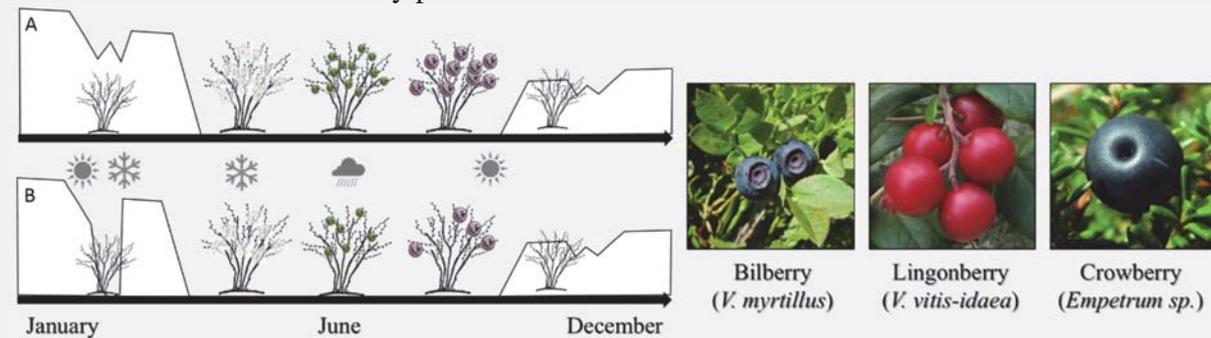
Masting describes the phenomenon of seed production, and thereby the production of fruiting bodies (i.e. fruits, berries, nuts), fluctuating between years in a synchronized fashion across plants in a population (Silvertown 1980). Climate e.g. summer temperature variation, may drive masting cycles (Kelly et al. 2013), and climatic events during plant phenology and flowering may additionally affect fruit production in many masting species (Kelly and Sork 2002). Peak fruit production of bilberry in Scandinavia follows regular cycles of 2-5 years (Selås 2000), which are altered by climatic events during key stages of plant phenology. Bilberry, for example, needs a stable insulating snow cover during winter and berry production is sensitive to cold temperatures during flowering (May), drought stress during fruit ripening (June-July), and high temperatures during bud formation in autumn (August-September) (Selås 2000, Selås et al. 2015). Recent experimental and observational studies from northern Sweden have found consistent evidence that late winter warming events reduce bilberry production by up to 95% (Bokhorst et al. 2008, Bokhorst et al. 2011). During these events, temperatures rise above freezing, causing the snow layer that insulates dormant bilberry plants to melt. Under continuing warm temperatures the soil starts to warm up and plants lose their frost hardiness, causing them to induce phenology. They are vulnerable to severe freezing damage when temperatures return to below zero (Bokhorst et al. 2008). Fewer studies have described the role of climatic events on fruit production of crowberry and lingonberry, probably due to their lower economic value. The effect of winter warming events on berry production in these species is less clear, with no effect on crowberry and a reduction in lingonberry reported after a single warming event (Bokhorst et al. 2008) and no effect on berry production in either species after multiple warming events (Bokhorst et al. 2011).

ecology has described the interactions between prey and their natural predator. Lately however, evidence has accumulated that human presence may elicit similar antipredation behaviors in prey species (Ciuti et al. 2012b, Lone et al. 2015, Lone et al. 2016) and even in apex predators (Ordiz et al. 2011, Wam et al. 2012).

Researchers almost always find food search strategies or behavioral responses to disturbance (like hunting) on the population level. Individual differences are at best controlled for using mixed models with random effects, but are rarely explicitly tested and documented. Differences in an individual's condition (Merrick and Koprowski 2017a), experience (Teitelbaum et al. 2016), or the environmental conditions in its home range (Mysterud and Ims 1998) may lead to substantial inter-individual differences in behavior. When individual differences persist over time and situations (Wolf and Weissing 2012), an animal's personality may explain its reactiveness in a particular situation. Commonly, animal personality is assessed using a suit of five behavioral traits: boldness, exploration, activity, sociability, and

2

aggressiveness (Réale et al. 2007). When behavioral traits are correlated, i.e., when bolder animals are also more exploratory, those suits of traits form a behavioral syndrome (Sih et al. 2004). Personality affects movement and space use (Spiegel et al. 2015), habitat selection (Boon et al. 2008), and stress responses (Raoult et al. 2012). This demonstrates that, ultimately, animal personalities can have profound effects on life history traits and fitness when behavioral traits alter, e.g., food intake, offspring production, or survival (Biro and Stamps 2008, Smith and Blumstein 2008). It may also skew the risk of being killed by a predator or hunter towards certain behavioral types in the population (Ciuti et al. 2012a, Leclerc et al. 2017). Therefore, personality traits are now increasingly recognized as important in conservation studies and efforts (Merrick and Koprowski 2017b), where personality traits may, for example, affect survival in reintroduced or translocated animals (May et al. 2016). Behavioral traits have been investigated mostly in established test situations, like a novel object test or open field test (Réale et al. 2007). A limitation of established personality tests is that animals need to be captured multiple times to assess behavioral repeatability. For obvious reasons, the animal needs to be manageable while being conscious in order to subject it to the test situation. Conducting these tests in the wild is therefore only possible with small-bodied and/or non-predatory, or habituated animals, which can be easily recaptured and handled in an awake state (Bell et al. 2009). Alternatively, behavioral observations have been used to infer behavioral types (Réale and Festa-Bianchet 2003). For elusive species or those that live in inaccessible habitats, neither of these approaches is possible, creating the need for new methodological approaches to assess personality in the wild.

In this thesis, I used the brown bear, an omnivorous hibernator, as a model species to link nutritional constraints, fear ecology, and individual behavioral differences. The brown bear is a particularly interesting study species for my research objectives, because of its crucial dependence on foraging efficiency during hyperphagia to provide sufficient body condition for denning, which in turn affects key life history traits (Box 2). Food abundance and successful foraging in autumn prior to hibernation are vital for a bear's fitness. Although an apex predator at the top of the food chain, bears have been persecuted throughout their range by humans and studies suggest that they respond to human presence with antipredation behaviors, like prey to a natural predator (e.g. Ordiz et al. 2011, Ordiz et al. 2012, Ordiz et al. 2013). Lastly, bears are long-lived, highly cognitive animals, supporting the assumption that pronounced individual variation in behavioral responses may exist.

The Scandinavian brown bear

The brown bear (*Ursus arctos*) has a circumpolar distribution range in the Northern Hemisphere. Brown bears occur from the coastal, arctic regions of Alaska to the deserts of Mongolia, their distribution being strongly limited by human presence. In Europe, the brown bear underwent a slow but constant persecution history over centuries (Frank and Woodroffe 2001). In Sweden, the brown bear was nearly driven to extinction by the beginning of the 20[h] century (Swenson et al. 1999). Population recovery was slow until the mid-1990s, when officials estimated the Scandinavian bear population to encompass approximately 600 individuals. Subsequently the population underwent a phase of strong population growth and reached its peak in 2012, with an estimated 3300 individuals (Swenson et al. 2017). Hunting was reintroduced in 1943 and hunting quotas increased steadily since the 1880s. With a growing population, also hunting quotas increased strongly between 2010 and 2013, with an all-time high quota of 319 bears in 2012. The current (2015) population estimate is 2800 individuals, distributed over three high-density core areas (Fig. 1A).
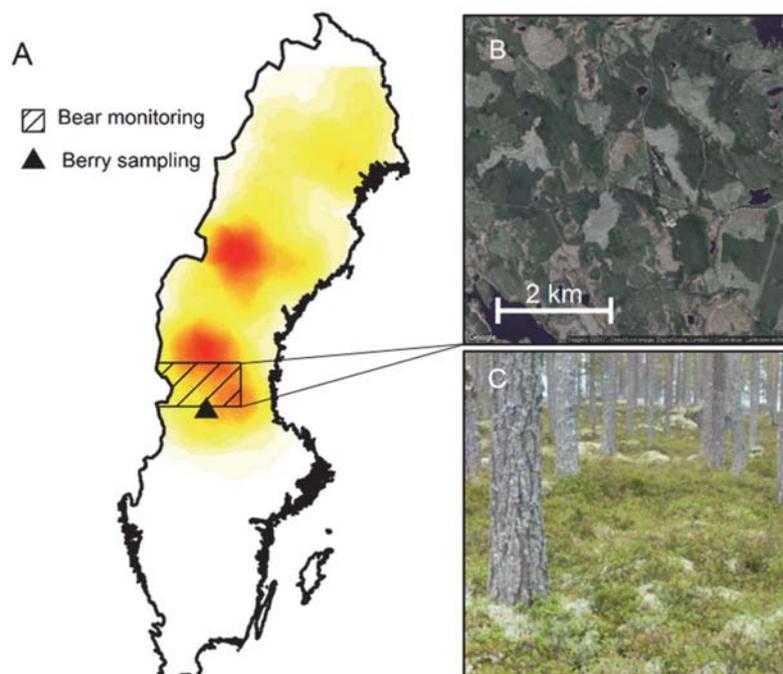

Figure 1. Distribution of the brown bear in Sweden (A). High population density areas are shown in red, lower densities is yellow. The study area of intense bear monitoring is indicated by the hatched rectangle (~13,000 km^2). Berries were sampled in permanent plots at the Siljansfors Experimental Forest (black triangle) during 2006-2015. A satellite imagery extract of the study area is shown in panel B. Bogs and recent clearcuts appear in brown, young forest plantations in light green, and mature forests in dark green. Bilberry plants (*Vaccinium myrtillus*) dominate the field layer of mature forests (C).

The articles in this thesis are based on research in the southern core area (~61° N, 15° E) in the counties of Dalarna and Gävleborg. Bears in this area inhabit an intensely managed boreal forest, interspersed by lakes and bogs (Moe et al. 2007) with little elevation differences (Dahle and Swenson 2003c). Scots pine (*Pinus sylvestris*) is the dominating tree species, followed by Norway spruce (*Picea abies*). Forestry practices, in particular final cutting, have created a matrix of small (median patch size ~2.25 ha, Moe et al. 2007), differently aged forest patches (Fig. 1B), which drive the spatial heterogeneity of resources, like ant galleries (Frank et al. 2015), bedding sites (Ordiz et al. 2011), and berry production (Kardell 1979). The field

layer of open, mature forests is dominated by bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum hermaphroditum*) (Fig 1C, Box 1, Kardell 1979). During final cutting and replantation, berry plants are physically destroyed, creating a patchy plant occurrence on clearcuts (Atlegrim and Sjöberg 1996), with high local berry production due to improved light incidence (Kardell and Eriksson 2011). Berry production ceases during early successional stages, when the forest starts to close; berry plant cover requires approximately 55 years to recover from final cutting (Kardell and Eriksson 2011). Forestry practices can therefore be regarded as the single most important cause of spatial heterogeneity in autumn forage abundance. Human population density in the study area is low (4-7 inhabitants/km^2: (Ordiz et al. 2014)) and mainly concentrated in six settlements (Nellemann et al. 2007). An intense network of forest roads (0.7 km/km^2: (Martin et al. 2010)) however, facilitates easy access into the remotest corners of the study area. Recreational activities, like moose and bear hunting and berry and mushroom picking, are popular with Swedes and mainly concentrated in the summer and autumn months (Box 2, Ordiz et al. 2011).

Bears in the study area have been studied by the Scandinavian Brown Bear Research Project (SBBRP) since the mid-1980s. The aim of the project is to document the basic ecology of the brown bear in Sweden and to inform and advise the Swedish and Norwegian wildlife management agencies. Bears within the study area are followed throughout life and over generations. The majority of the data comes from female bears and their female offspring, because subadult males often disperse over large distances out of the study area (Støen et al. 2006). The reproductive success of adult females that are expected to be pregnant is determined after den emergence from sign of cubs in the hibernaculum, activity data of the female during hibernation (Friebe et al. 2013), and observations from a helicopter. The presence, survival, and number of cubs is thereafter determined from helicopter surveys after the mating season and prior to the hunting season. Family groups are first captured when cubs are one year of age (Box 2). All bears are immobilized via darting from a helicopter, mostly in April or May after den emergence. Early on the project equipped bears with VHF radio transmitters (Telonics ®, Model 500), but since 2003, bears have been instrumented with a GPS collar (Vectronic Aerospace GmbH). Bears over 20 kg also carry an intraperitoneal transmitter (Telonics ®, Model IMP/400/L HC), to facilitate the recapture of bears after collar loss or failure. Bears are weighed in a sling scale and a set of standardized morphological measures (e.g. head and chest circumference) are taken. For bears that are not followed from birth, the first premolar is extracted for age determination by counting the tooth cementum annuli (Mattson's Inc., Milltown, MT). Please refer to Arnemo and Fahlman (2011) for more details on capture and handling procedures.

There are three additional monitoring tools that complement this research: The Swedish National Veterinary Institute (SVA; http://www.sva.se/en) obtains morphometric measurements, sex, and age (again determined from an extracted tooth, see above) from all hunter killed bears. Specifics about the exact date, time, and location of the kill must be reported by the hunters (Bischof et al. 2008). Scats are collected within each county on a ca. five-year rotation to estimate its bear population size. All sightings of large carnivores made by moose hunters are recorded in the first week of moose hunting by the Swedish Association for Hunting and Wildlife Management, from which an effort-corrected large carnivore observation index (LCOI) is derived (Kindberg et al. 2009). The articles in this thesis used bear monitoring data from the last decade (2006-2016).

Box 2 The brown bear annual cycle
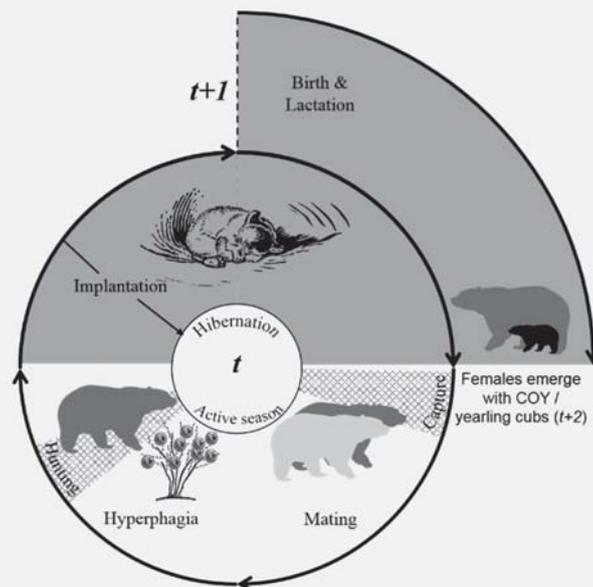
Brown bears are hibernators and thus their annual cycle can be categorized into an active and a passive season. Bears in south-central Sweden spend on average 161 – 196 days, about half of the year, in hibernation. They emerge from their winter den in April-early May (Friebe et al. 2001, Manchi and Swenson 2005). Adult males are the first to leave the den, followed by solitary females, and females with one- or two-year-old cubs. Females with cubs-of-the-year (COY) emerge last from hibernation (Friebe et al. 2001). Solitary, adult bears mate in May and early June (Steyaert et al. 2012). Because bears have a delayed implantation, the fertilized egg stays dormant until females go into hibernation (Hissa 1997). For the Scandinavian population, there is evidence that about 22% of females with cubs-of-the-year lose their litters to infanticide by males (Steyaert et al. 2014). Litter loss triggers estrus in the victimized females, which then sire a new litter, often with the infanticidal male. June is also the predominant period of predation on newborn moose calves (Rauset et al. 2012). In summer, the bears' diet is dominated by forbs, graminoids, and ants (Stenset et al. 2016). In the second half of July, the fruits of bilberry plants. which dominate the ground vegetation in Swedish forests, begin to ripen. This is the beginning of the bears' hyperphagia, during which bears drastically increase their daily energy intake and thereby also their body mass by 35 - 65% as compared to their spring mass (Swenson et al. 2007). The hyperphagia period overlaps with the annual bear hunting season, which starts in Sweden on the 21 August (Swenson et al. 2017). Harvest quotas are neither sex nor age specific, but females accompanied by cubs and their cubs are protected (Bischof et al. 2008). Bears in Sweden are mainly hunted with dogs and quotas fill quickly, usually within the first two weeks. In south-central Sweden, bears enter the den in the end of October (Friebe et al. 2001). During hibernation bears are solely sustained by their stored energy reserves, they do not eat, drink, or defecate. Pregnant female bears, however, implant the fertilized egg at the beginning of December and give birth in the den around end of January (Friebe et al. 2014). Only females in good condition can sustain the elevated energetic costs of lactation (Robbins et al. 2012), which is why mass gain in autumn during hyperphagia is particularly important for reproduction. Females with cubs-of-the-year will den with their offspring for at least one, sometimes two, more winters (Dahle and Swenson 2003a, b). Radio-marked females with yearling cubs are captured, marked, and weighed in the spring after den emergence.

Objectives

My research focused on the period of hyperphagia, when bears in Sweden increase their body mass for the upcoming hibernation by foraging almost exclusively on bilberry, lingonberry, and crowberry, which are distributed patchily in space and vary in berry production among years. Because hyperphagia coincides with the annual bear hunting season in Sweden (Box 2), bears are inevitably faced with trade-offs between foraging and risk avoidance. Like resource abundance, risk is not static, but varies within the course of a day, between weeks due to hunting regimes, and with the spatial accessibility for hunters.

The overarching objective of my thesis was to understand how brown bears respond behaviorally to spatial and temporal heterogeneity in resource availability and risk, and how this variation affects life history parameters. Here are my major objectives:

How do bears cope with resource heterogeneity at different temporal scales?
(Articles I, II, III, IV)
Quantify berry abundance and their use by brown bears at different temporal scales – from daily use (Article II), to weekly variation driven by berry phenology (Articles I and III), to interannual variation driven by climatic events and masting cycles (Article IV, Box 1).

Do bears adjust space use patterns to spatial variation in resource availability?
(Articles I, III)
Quantify berry abundance at random and used locations within differently aged forest patches to evaluate habitat-specific selective foraging (Article I). Spatially predict berry abundance across the study area to contrast use by bears with berry availability (Article III).

How do bears balance foraging and risk avoidance?
(Article II, III, V)
Analyze if bears behave according to the risk allocation hypothesis by actively foraging at times (Article II) and locations (Article III) of lower predation risk. Evaluate whether bears that are active during more risky times of the day face higher mortality (Article V).

Does berry production drive variation in bear life history traits?
(Article IV)
Evaluate the effects of interannual variation in berry production on female body mass in autumn, reproductive success during the subsequent winter, and body mass of yearling cubs in spring (Article IV).

Do we find consistent behavioral variation among bears?
Article (V, VI)
Analyze degree of individual behavioral variation in diel activity patterns (Article V), travel distance, selection of bogs, selection of clearcuts, selection of roads, and diurnality (Article VI) among bears during the berry season. Determine whether these behaviors are repeatable within individuals. Determine whether behaviors are correlated and thus form a behavioral syndrome.

Study design & methods

Over the course of six articles, I have used a great amount of different methodology and I would like to refer the reader to the respective articles for detailed information on model specification and covariates. In order to fully comprehend the results I am synthesizing below, I will however explain the main data sources, sampling designs, and methods used in the different articles here. All statistical analyses were carried out in the software R (R Core Team 2016) and associated packages, which are listed in the respective articles.

Berry sampling design and bear relocations

(Articles I, II,III)

In 2014, we sampled berry abundance at random locations and locations used by bears across the study area. Random locations were sampled continuously from the beginning of the berry-ripening season in mid-July until its end in mid-September. To decrease driving distance between plots and increase sample size, random locations were clustered within three core areas (Fig. 4). The locations of seven GPS-collared adult bears, whose home ranges overlapped with the random core areas, were sampled between 7 August and 4 September (Article I Supplementary material I). To target locations at which bears supposedly had been foraging, we sampled locations where bears had walked between 25 and 300 m for at least 1.5 hrs. Locations were identified in the field by using a handheld GPS device. From this position, a random sampling location was determined by walking 0–9 m (depending on the last number of the plot's Y coordinate) in a randomly assigned direction (north, east, south, west, depending on the last digit of the plot's X coordinate) to avoid any observer bias. A 1-m^2 sampling quadrate was placed at this location. As our aim was to determine berry availability, we relocated the sample plot to the opposite direction from the original GPS location, if the plot contained obvious sign of foraging. Within the sampling quadrate the presence, percentage of plant cover, and number of ripe berries was determined for bilberry, lingonberry, and crowberry. We also measured sugar content (%Brix) in a subsample of 5 ripe berries using a digital wine refractometer (MA885, Milwaukee Instruments, Inc., Rocky Mount, NC, USA). We noted the habitat type as bog, clearcut, young forest, or mature forest. We also extracted elevation, slope, and aspect from a digital elevation model and NDVI from a reclassified satellite image for all locations. For bear locations, we noted the time of day when the bear had been foraging at the location, foraging sign in the area, and the bear's ID.

In Article I, I compared bilberry, lingonberry, and crowberry occurrence (presence/absence), abundance (number of ripe berries per m^2), and sugar content at random and bear locations between 7 August and 4 September. Specifically, I modelled forage availability over the 4-week period in different habitat types. I then determined how selectively bears foraged in the different habitats.

In Article II we estimated the bears' foraging efficiency with regard to berry abundance and quality (sugar content). We calculated how many more berries we found at bear foraging locations as compared to how many berries we would have expected to find at this location on this day, inferred from predictive abundance modelling at random locations presented in Article I. This provided a measure of how much better the foraging location was than a random

location. We compared how efficiently bears selected for good foraging locations in the two weeks before and the first two weeks of the annual bear hunting season. Owing to the generally bimodal activity pattern of bears and the fact that hunting mortality is highest in the morning hours, we also analyzed whether their efficiency in the morning and afternoon bouts were affected differentially by the onset of hunting. Besides the field-observed foraging efficiency, we also estimated when during the day bears were actively foraging in the two periods.

In Article III we used all random locations to map the predicted probability of high density foraging locations, based on logistic regression models. We used a cutoff of 40 berries per m^2 to categorize sampled random locations as high-density (1) or low-density locations (0). The cutoff represented the upper 10% of the densest random sampling plots and was similar to berry densities needed for bears to have a high foraging efficiency (Pelchat and Ruff 1986, Welch et al. 1997). Owing to the phenological ripening of berries across the sampling period (mid-July until mid-September) we created maps for five overlapping periods. We then extracted the probability values at the relocations of 35 bears and at random locations within each bear's home range to compare whether bears use locations with higher predicted probabilities of being a dense berry location.

Berry sampling design, climate variables, & bear life history traits

(Article IV)

For Article IV we obtained berry and climate monitoring data from the Siljansfors Experimental Forest (Fig 1) recorded between 2006 and 2015. To account for site effects on berry production, the number of berries observed in a given year and location was centered by substracting the mean number of berries observed over the entire study period at this location. We formulated candidate models with climate covariates that previously had been found to affect berry production (Box 2) and a year effect only model to identify drivers of interannual variation in berry abundance. From the best model we predicted an annual berry abundance index, which was scaled between 0 and 1 (the worst and best of the 10 berry monitoring years, respectively). Berry abundance indices were constructed for bilberry and lingonberry, but interannual monitoring of crowberry was not available. The berry abundance indices were used to evaluate the effects of variation in species-specific food abundance on three bear life history traits; autumn body mass of hunter-killed female bears, spring body mass of yearling bears captured by the SBBRP, and reproductive success of adult female bears recorded during spring helicopter surveys by the SBBRP.

Behavioral measures

(Articles V & VI)

Long-term GPS tracking and dual motion sensor data were used to infer between-individual differences and within-individual repeatability in five behavioral measures. In article V we described differential diel activity strategies during the berry season. We used 30-min relocation intervals recorded between 1 – 20 August in 2007-2013. We categorized bear behavior between 30-min relocation intervals as either active or passive, depending on whether the bear moved more or less than 25 m during the time interval. We quantified activity during

the day over a three-week period and fitted a Kernel density estimator through the 24-hour cycle, reflecting the probability of activity at any given time of day. From the activity curves, we extracted seven quantitative measures; time of minimum and maximum activity, variability of activity over the three weeks, time active during light hours, time active during risky hours, and proportion of overall activity that coincided with high risk times. We used ordination and cluster analysis to described different diel activity strategies in our population. For bears that were monitored in multiple years, we further evaluated whether they were more likely than randomly expected to apply the same strategy multiple times.

In article VI we calculated mean daily travel distance, the selection ratio for bogs, the selection ratio for clearcuts, and the selection ratio for distance to roads from hourly relocation data and quantified a diurnality index from dual motion sensors. We repeatedly measured individuals during three 10-day periods in summer (P1: 01-10 July, P2: 20-29 July, P3: 10-19 Aug) in 2007-2015. We fitted mixed effects models for each of the four behaviors with BearID and Year as random intercepts, controlling for period (1-3) and age as fixed effects. In addition, we controlled for a functional response in habitat selection by adding the fixed effects of the proportion of bog and clearcut within a home range for bog and clearcut selection, respectively and a quadratic effect of road density for road selection. . We log-transformed daily travel distance and road selection and we square root transformed bog and clearcut selection to fulfil all statistical assumption. We calculated the amount of within-individual repeatability of each behavioral measure by dividing the variance between individuals with the variance between plus the variance within individuals (Nakagawa and Schielzeth 2010). We explored whether the five observed behaviors were correlated and thus formed a behavioral syndrome. If that would be the case, individuals with higher values in one behavior, e.g. travelling farther daily distances, also would have higher values in the other behaviors (being more diurnal, using open areas more, and avoiding areas close to roads less).

Summary of results & discussion

How do bears cope with resource heterogeneity on different temporal scales?

(Articles I, II, III, IV)

Fruit productivity of the berry species prevalent in south-central Scandinavia varies among years and has been previously associated to masting cycles and the weather during critical phenological periods (Selås 2000, Bokhorst et al. 2010). When fruit production cycles are asynchronous among berry species, bears may concentrate search efforts on the species that is most abundant in a given year. Within the course of a year, fruit ripening phenology restricts the availability of berries to limited time periods. The temporal peak of ripening therefor varies among species, with bilberries ripening first, followed by crowberry and lingonberry (Eriksson and Ehrlén 1991). Bears, which rely on berries for mass acquisition, should concentrate their search efforts on the berry species that is most abundant at a given time.

On an intra-annual scale we show that bears respond to the onset of bilberry fruit ripening by increasingly using areas with high expected densities of bilberry, as compared to a period when most berries are still unripe (Article III, see also Fig. 4). Bilberry ripening formed a temporal wave of high resource abundance from the beginning to the end of August. During the peak of this bilberry wave, bears used areas with up to three times more bilberries than found at random locations (Fig 2, Article I). In the beginning of September, however, densities of bilberries generally dropped below 44 berries per square meter, which according to previous studies (Pelchat and Ruff 1986, Welch et al. 1997) should decrease their intake rate, therefore effectively making bilberry a less efficient food resource to forage on. I demonstrate a temporal resource wave to which bears responded as predicted (Fig. 4, Article III). However, contrary to my expectations, I did not find evidence that bears shifted foraging efforts towards lingonberries, once bilberries become less available, even though lingonberry numbers increased to a level allowing efficient foraging by the beginning of September (Fig. 2, Article I). Ripe crowberries occurred rarely on the study area (<10% of sampling plots), both at random and foraging sites, and were thus considered to be of minor importance for foraging bears.
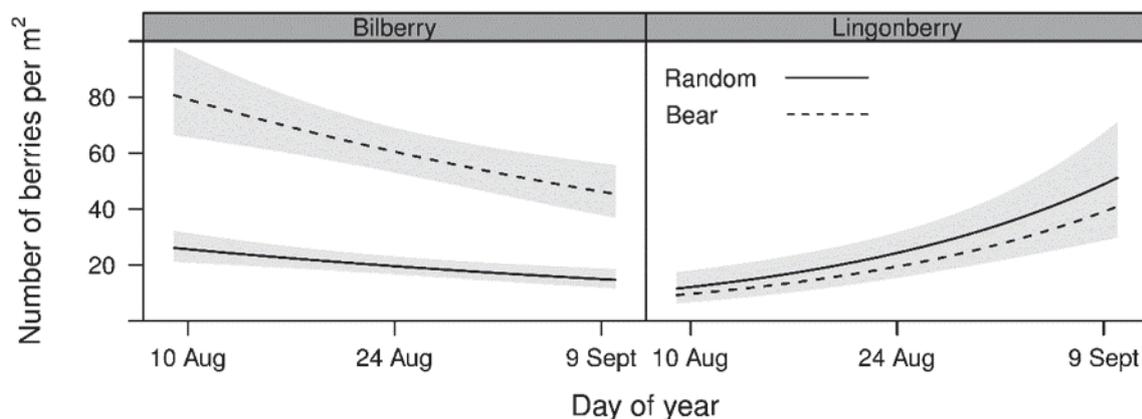

Figure 2. Predicted bilberry (left) and lingonberry (right) abundance per square meter at brown bear foraging and random sites in mature forests in south-central Sweden along a gradient of 32 days. Bears used locations with significantly more bilberries, but not lingonberries, than found at random locations.

On an interannual scale, berry abundance of both bilberry and lingonberry fluctuated between years, as expected (Fig. 3). I further found that climatic events during key stages of

plant phenology significantly affected berry production, as had been found previously (Box 1). For bilberry, berry production was higher when January temperatures were warmer, but lower when minimum temperatures during flowering were lower and amounts of precipitation during summer were higher. A longer growing season had a positive effect on bilberry production. Identifying the right temporal scale at which to measure climatic covariates was crucial for finding some of these effects. Specifically, minimum temperatures measured in May did not produce informative effects, however refining the measurement period to the annually explicit time of flowering did elucidate a negative effect of freezing on berry production. Timing of phenological stages may vary substantially with geographic location. For example, the studies we used to inform our candidate models were conducted in the tundra of northern Sweden (Bokhorst et al. 2011), in central Norway (Selås et al. 2015), and the Suisse Alps (Rixen et al. 2012). My findings highlight that readily accepting effects of climatic events on plant phenology may lead to biased conclusions when these results come from locations with very different environmental conditions. I created berry abundance indices for bilberry and lingonberry from observed counts in the different years and correlated these indices to bear life history traits. I found that bilberry, but not lingonberry, abundance affected autumn bear body mass, spring mass of yearlings, and female reproductive success (see below *Autumn food abundance effects on life history traits* for a detailed description of results), corroborating a strong reliance on bilberry as a food resource (article I).
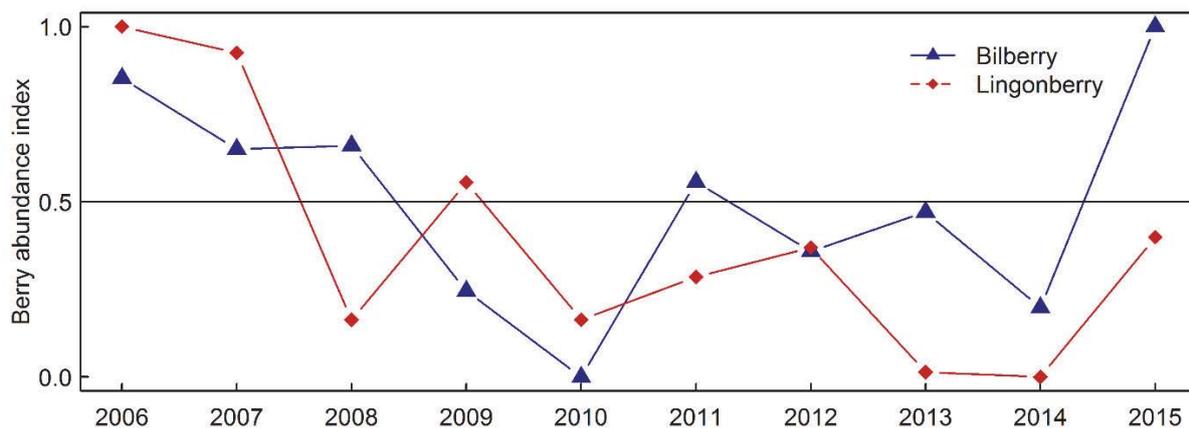

Figure 3. Predicted annual bilberry (blue) and lingonberry (red) abundance index from 2006 until 2015. Indices were modeled from berry abundance at permanent sampling locations (n=54 for bilberry and lingonberry, respectively). Higher values indicate higher relative berry abundance.

A third temporal scale I explored was not associated to temporal variation in forage availability, but rather to temporal heterogeneity in forage use by brown bears. Specifically, brown bears in Sweden are generally described as foraging actively in the morning and afternoon hours (Moe et al. 2007). Ordiz et al. (2012) has shown that bears become more night active at the onset of the hunting season, which I could confirm in article II by showing that bears reduced foraging activity in the morning during the hunting season. I was further able to show that bears not only reduced activity in the morning, but when active, also used less productive foraging locations with fewer berries and berries of lower sugar content (see Fig. 5 and *How do bears balance foraging and risk avoidance?* for a detailed description of results).

I conclude that bears in Sweden have a surprisingly limited ability to react to temporal resource heterogeneity by using other food resources. When bilberry production was low, they did not exploit alternative food resources, which was evident based on the interannual scale in

the body mass of bears (article IV) and on the intra-annual scale by examining the number of alternative berries at foraging locations (article I). On the other hand, bears correctly tracked resource phenology of their main food resource and started allocating search efforts when ripe bilberries occurred in adequate densities for efficient foraging (article III). On a daily scale, however, other factors, such as mortality risk, constrained bears in their exploitation of food resources (article II).

Do bears adjust space use patterns to spatial variation in resource availability?

(Articles I, III)

Bilberry phenology formed a temporal wave of resource abundance, but we did not find evidence of a spatial wave, i.e., temporal heterogeneity in ripening and availability of ripe berries across the landscape. Resource abundance differed among habitat types in a uniform manner over time. The reason for a lack of spatial heterogeneity probably lies in the nature of the terrain in our study area. The study area is situated in central Sweden, does not encompass any major elevational gradients, nor does climate differ substantially across the study area. The largest source of landscape heterogeneity is forestry, which has transformed the landscape into a matrix of differently aged forest patches, interspersed by unproductive bogs. This habitat patchwork drove the spatial variation in food abundance described in articles I and III (Fig 4). I found that bilberries thrive best in mature and old-growth forests, where they form a continuous carpet on the forest floor with a dependable food supply. Clearcutting destroys berry plants during the harvesting process, leading to a patchy plant distribution, but the surviving plants produce berries in high abundance, due to the improved light conditions on clearcuts. When forest succession progresses and clearcuts are colonized by bushes, berry plants are outcompeted and shift their investment from berry production to plant growth. Overall, it has been suggested that the berry layer in forests needs up to 50 years to regenerate after clearcutting (Atlegrim and Sjöberg 1996).
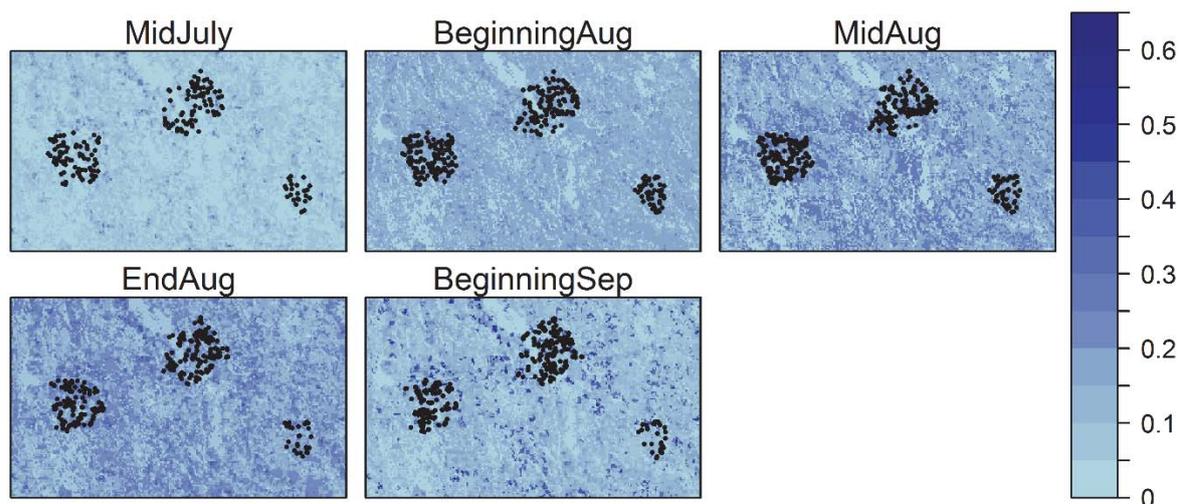

Figure 4. Probability of high bilberry density modeled from random berry sampling locations (n = 821) and predicted across the study area in south-central Sweden between mid-July and beginning of September 2014.

For bears, this means that good foraging areas occur patchily in the landscape, driven by harvesting regimes, creating the need to allocate foraging efforts to locations with high

relative food abundance. Selecting areas for foraging was important, because random locations rarely featured enough (> 44 berries/m2: Pelchat and Ruff 1986) berries to ensure high intake rates (Fig. 2). From bear locations in the field, we found that bears used locations with a) a higher probability of berry occurrence and b) more berries, than randomly found in the landscape in mature forests and clearcuts, but not in young forests or bogs (article I). These results were corroborated in article III, where we compared the predicted probability of high-density bilberry areas between bear and random locations within the bears' home ranges (Fig 4). Based on GPS relocations of 35 bears during 2012-2015, we found that bears used locations with a higher predicted probability of being a dense berry location than randomly available in their home range. They did so, however, only as long as those location did not carry a high mortality risk (see *How do bears balance foraging and risk avoidance?* for a detailed description of results).

How do bears balance foraging and risk avoidance?

(Articles II, III, V)

I found evidence that bears avoided mortality risk, both on a temporal (article II) and on a spatial scale (article III). However, I did not find that they increased their avoidance of risky locations during the hunting season, as compared to a period without hunting (article III). Evidence on whether this avoidance was adaptive and in fact reduced mortality was ambiguous. Bears that avoided high-risk, high-forage areas had a higher survival probability than bears that did not avoid high-risk, high-forage areas in the two weeks before the onset of the hunting season (article III). On the other hand, with an increasing proportion of high-quality berry foraging habitat within a bear's home range, bears also became more diurnal (article V, Fig. 8), suggesting that they were also more exposed to hunters on a temporal scale (red line Fig. 5 left). Our analysis did not produce evidence that more diurnal bears were killed more often, however (Fig. 6).
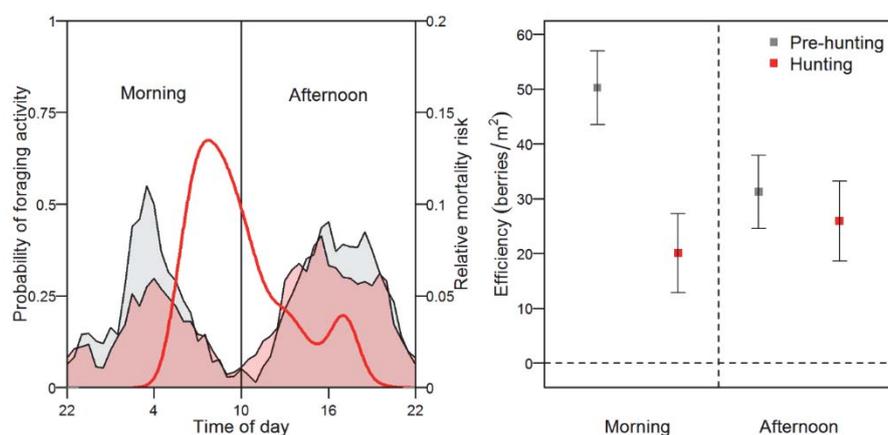

Figure 5. Left: Diel foraging activity in the two weeks prior to the hunting season (gray shaded) and first two weeks of the hunting season (red shaded). The red line indicates the density distribution of mortality risk modeled from time of death of 680 bears killed during the first two week of the annual bear hunting season during 2006-2014. Bears significantly reduced their foraging activity during the morning hours, but not during the afternoon hours. Right: Efficiency of foraging locations in the morning and afternoon foraging bouts, prehunting and during the first two weeks of the hunting season. Efficiency was defined as the observed number of berries at a foraging location minus the expected number of berries on this day and in the specific foraging habitat, based on predictions from random samples (article I, Fig. 2). Bears used locations with more berries than randomly expected at all times (zero line).

Even though our results were not entirely consistent over all spatial and temporal scales we examined, I still conclude that bears seem to be sensitive towards risk detection. I suggest, however, that bears do not sense mortality risk specifically, but react to human disturbance in the forest per se, which increases markedly with the start of the bear hunting season, also because dogs are allowed to be off-leash in the forest from this day on. Our findings in article II are in support of the risk allocation hypothesis (Lima and Bednekoff 1999) in that bears allocated antipredation behavior (i.e. reducing foraging activity) to times of highest risk. The behavioral response occurred in fact slightly before the peak of mortality risk, which can be explained by hunters and dogs being active in the forest in the early morning hours before the bears actually are shot. Importantly, even when active, bears paid a foraging cost by using locations with fewer berries, a result we did not find with a different study design in article III. My explanation is that in article III, we did not control for circadian differences in locations selected by bears prehunting and during the hunting season. It remains unknown whether the cumulative effect of reduced foraging time and reduced forage intake during the morning hours is great enough to impact mass gain of bears during hyperphagia. The start of the hunting season coincides with the peak of the bilberry season (article III) and because bears seem to be dependent on bilberry as primary food resource, I would assume that in years of overall low berry availability, antipredation behavior becomes more costly. The berry sampling took place in 2014, which according to our bilberry index from article IV had the second lowest berry abundance in a ten-year period. Reanalyzing foraging activity during the high-risk hours from GPS locations recorded in other years may elucidate whether the strength of bears' antipredation behavior is also dependent on overall food abundance in a given year.

Does variation in food abundance drive variation in life history traits?

(Article IV)

For my first objective, I have shown that food abundance indeed varied between years. The goal in article IV was to link this variation in food abundance to bear life history traits. We selected three traits that we expected to be affected by food abundance; autumn female body mass, spring yearling body mass, and observed reproductive success of females after den emergence in spring. Indeed, we found female body mass to increase with increasing bilberry index, but not lingonberry index (Fig. 6 left). This is reasonable, given that bears were harvested at the beginning of the hunting season during the peak of bilberry ripening, and quotas were usually filled before lingonberry abundance peaked. The body mass of yearling bears weighed in spring depends entirely on one growing season, weight loss during one hibernation, and maternal effects. It has been used before as an index for food abundance in the previous autumn (Zedrosser et al. 2006). While controlling for maternal body mass, we found that spring weight of yearlings increased with increasing bilberry, but again not lingonberry abundance in the previous autumn (Fig. 6 right). Winter severity also did not affect yearling body mass. These results confirm that the yearling weight index developed in Zedrosser et al. (2006) indeed reflects food abundance in the preceding autumn. We did not find that yearling bears could compensate for low bilberry abundance in years of higher lingonberry abundance (see also *How do bears cope with resource heterogeneity on different temporal scales?*).
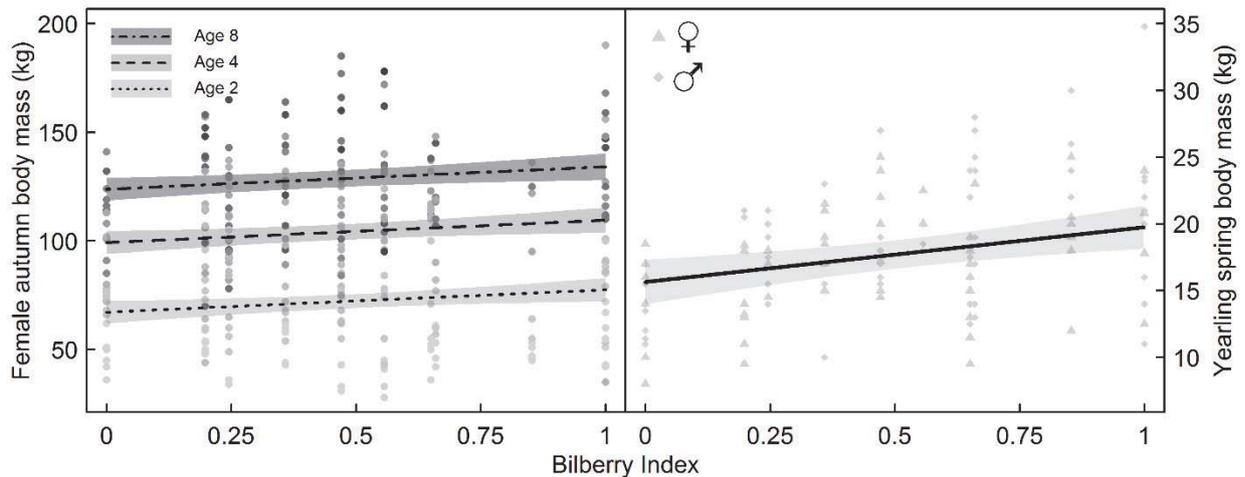
15

Figure 6. Autumn body mass of female bears killed during the hunting season during 2006-2015 (left) and spring body mass of yearlings monitored by the Bear Project during 2007–2016 (right). Body mass increased with increasing autumn forage availability, expressed as the scaled bilberry abundance index. We controlled for the effect of age on body mass with a third order polynomial term. Raw measurements are shown in points, for autumn body mass coloring represents age of a bear with younger bears in lighter colors. Model predictions and 95% confidence intervals are given in lines and shaded areas. For autumn body mass, we chose three representative ages, for yearling spring body mass, we show estimates for a male yearling.

Interestingly, female reproductive success was affected differentially by bilberry abundance, depending on the initial weight when a female entered hyperphagia (Fig. 7). Specifically, in years of low bilberry abundance, bears that entered hyperphagia with a low body mass had a significantly lower probability to reproduce than females that started hyperphagia in average or higher than average body mass. However, with increasing autumn bilberry abundance, the chances for low body mass females to reproduce increased, probably because of compensatory weight gain. At a food abundance index higher than 0.6, there was no significant difference in the probability to reproduce among light or heavy females anymore. Confidence intervals were wide at higher food abundances, however, indicating that other factors than food abundance and initial body mass may determine whether a female reproduces.
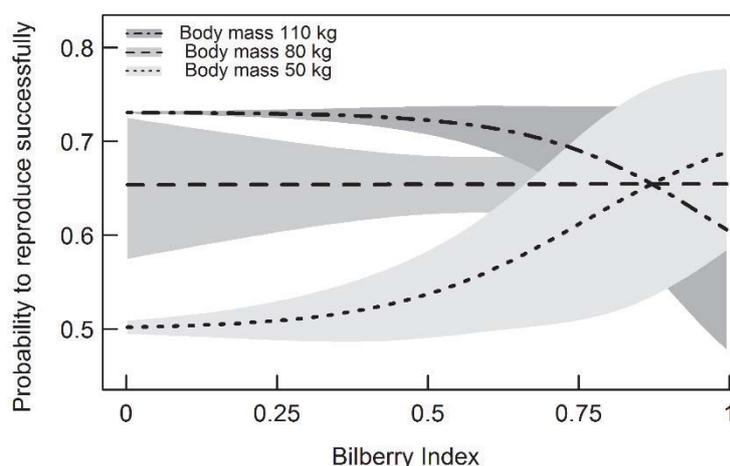

Figure 7. Female reproductive success observed in spring, along a gradient of food abundance during hyperphagia in the previous autumn. The effect of autumn food abundance on reproductive success was modulated by initial body mass prior to hyperphagia. Initial body mass was determined during captures in spring the year before reproductive success was observed. Estimates are shown for a female with a light initial body mass (50 kg), average initial body mass (80 kg) and high initial body mass (110 kg).

16

Do we find consistent behavioral variation among bears?

(Articles V, VI)

The strength of behaviors may differ among individuals within a population. A standard procedure to control for interindividual variation is to fit a random intercept, or less commonly, a random intercept and slope on animal identity. By doing so, we acknowledge that individuals differ in the strength of their behavioral response (random intercept) or in their reactiveness towards the explanatory variable (random slope). For example, in article II I found that bears reduce their foraging activity during the morning hours of the hunting season, but a random effect improved the model fit, indicating that some individuals reacted more strongly than others. These interindividual differences, although controlled for, are rarely explicitly considered when drawing conclusions from modeling results.

In article V, I tested whether bears differ in their distribution of activity over the day, which on the population level is considered to peak in the morning and afternoon. I quantified diel activity in 98 bears monitored over 196 bear-years. I indeed found much stronger variation in diel activity distribution then I initially expected. Using k-means clustering, diel activity curves could be categorized into four activity tactics; diurnal, bimodal with preferred night rest, bimodal with preferred day rest, and nocturnal (Fig. 8).
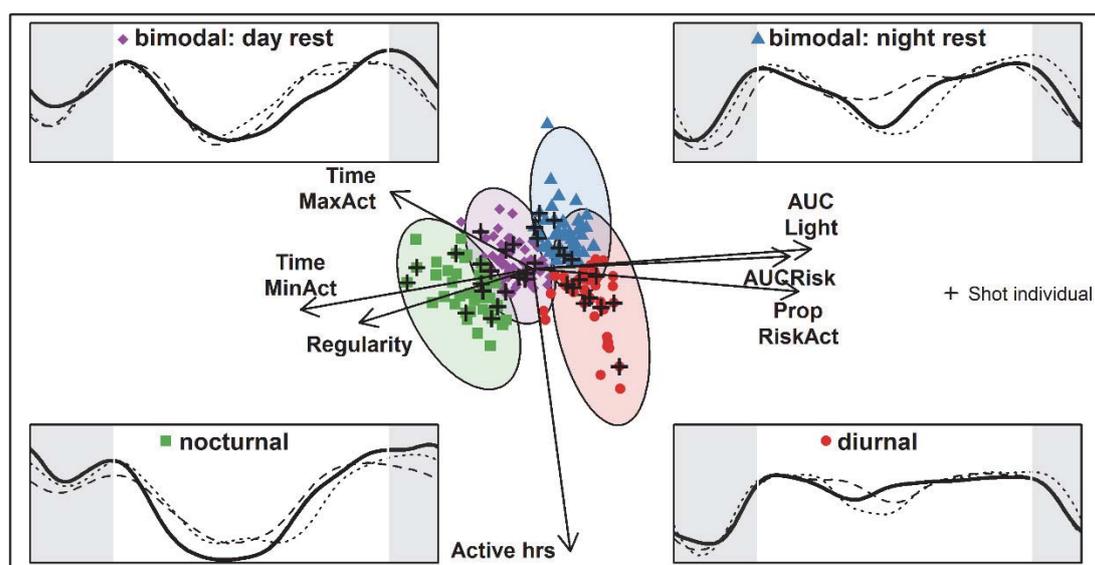

Figure 8. Diel activity strategies of 98 bears monitored over 196 bear-years during the first three weeks of August, which is during the peak of the berry season but before onset of the hunting season. Principal component analysis revealed that the seven measures we used to describe the unique activity curve of a bear could categorize the strategies into four clusters; diurnal, bimodal with preferred night rest, bimodal with preferred day rest, and nocturnal. Individuals that were killed during the upcoming hunting season are indicated with a cross and applied all of the four activity tactics.

Expression of an activity tactic was affected by external factors. Older bears were more diurnal and rested primarily during the night and increased diurnal activity was associated with an increasing proportion of berry habitat within a bear's home range. High bear density was associated with the nocturnal activity tactic and higher road densities with preferred day resting and activity during night. Despite having a significant effect, total explained variance by the covariates was low (7.6%). Against our expectations, the more diurnal individuals did not face a higher mortality risk during the upcoming hunting season. Bears that were killed had been

17

assigned to all of the four activity tactics during the three weeks prior of the onset of the hunting season. Given the low explained variance, we turned our focus towards individual effects. For 50 individuals, activity tactics were obtained for multiple years (148 bear-years, range of individual monitoring years 2-6). We found that bears were significantly more likely to apply the same tactic than expected by chance, and 60% of bears had a prevalence towards one particular tactic. This study provided evidence that individuals differ consistently in their diel activity tactic, similar to a study showing that brown bears on my study area differ consistently in their use of open areas, i.e. clearcuts and bogs (Leclerc et al. 2016). This individual variation is meaningful when timing of activity or space use affect population level processes, because it means that different individuals in a population contribute differentially to these processes. To give one example, diel activity affects predator-prey interactions (Brook et al. 2012) and intraguild temporal niche partitioning (Swanson et al. 2016). When predation success is temporally structured throughout the day and individuals in a population of predators vary in their diel activity tactic, this means that temporal access to prey, foraging strategy, and diet composition may vary among individuals (Araújo et al. 2011). When individual activity tactic has consequences for overall food intake, it may explain individual variation in reproductive success, the intrinsic currency of fitness (Biro & Stamps 2008).
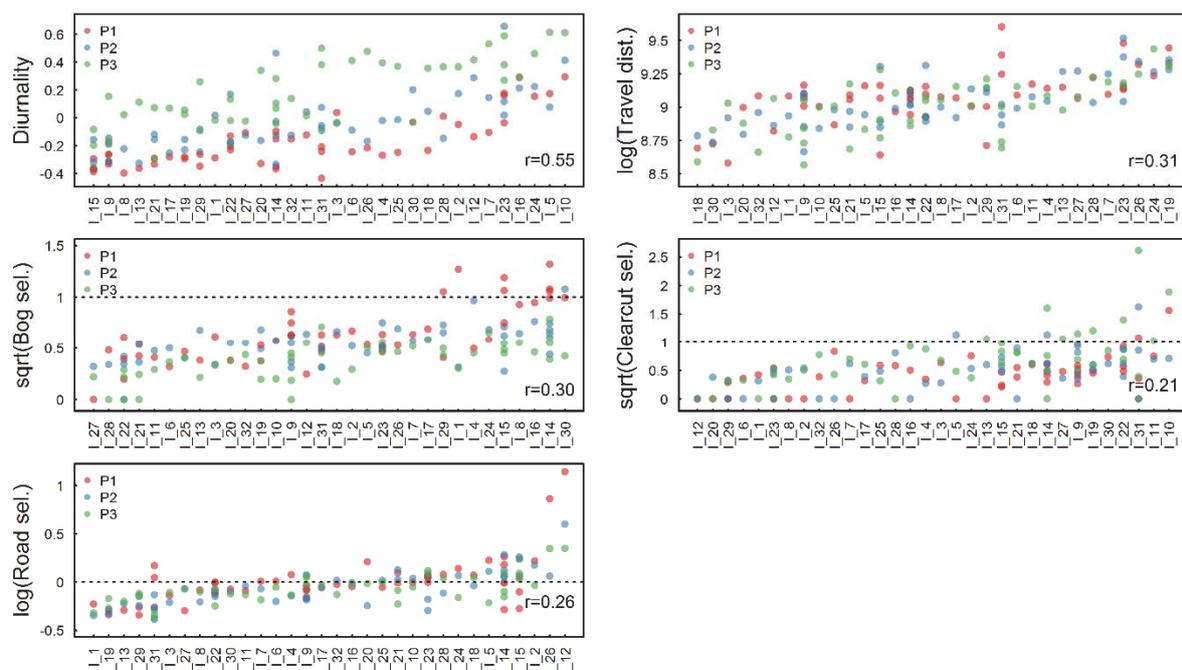

Figure 9. Values of focal behaviors measured in 32 adult female brown bears over 49 bear-years in three periods (P1-P3) between early July and mid-August. Behaviors were repeatable within individuals, confirming that bears showed moderate to pronounced consistency in the five behaviors. Repeatability was calculated from the covariance explained by the random effect of bear ID in a mixed model for each behavioral measure. Values below the dotted lines indicate selection against, values above selection for the respective habitat feature.

The combined results from apparent individual consistency in diel activity (article V) and space use (Leclerc et al. 2016) lead us to investigate whether we could identify several behaviors in bears that are repeatable and therefore good candidates of representing personality traits, and whether these behaviors would be correlated and thus form a behavioral syndrome. Behavioral syndromes lead to co-evolution of behavioral traits and thereby offer an explanation for the persistence of behaviors that, in isolation, seem non-adaptive. The most prominent example of such correlation of behaviors is the bold-shy syndrome (Wilson et al. 1994). In

18

article VI, Leclerc and I selected five distinct behaviors to test our idea; selection ratio of areas close to roads, bogs and clearcuts, diurnality index, and mean daily travel distance. We found moderate to high repeatability values for all five behaviors (Fig. 9), indicating that 21-55% of the variation in behaviors could be explained by consistent variation among individuals. This means that a given bear expressed consistently lower or higher values for a specific behavior over all three measurement periods, compared to other individuals. Using ordination analysis, Bear ID explained 33% of the variation among all measurement points, while environmental covariates (period, age, the proportion of bogs and clearcuts, and a quadratic effect of road density within the home range) explained 27%, leaving 40% of the variation unexplained. This means that individual bears are consistent in their behavior when considering values of multiple behaviors. What we did not find, however, was a clear one-dimensional behavioral syndrome. Our original hypothesis was that some bears would be more diurnal, travel farther distances, select more for areas close to roads, and select more for both open habitat categories. We were prepared to argue that these individuals would be of a generally bolder personality type than individuals which expressed lower values for all five behaviors, because the five behaviors were all expected to increase the risk of encounters with humans. However, we only found that three of the behaviors were correlated - bears that used areas closer to roads were also more diurnal, but they travelled shorter distances. These results highlight that in the wild, bears may face behavioral trade-offs causing them to balance behaviors that would be expected to be positively correlated. Selection for bogs and clearcuts were reflected along the second and third ordination axis, respectively, and were therefore unrelated to the identified behavioral syndrome, and unrelated to each other. There is currently much discussion about how to measure and interpret personality traits in animals. Even when using established behavioral assays, ecologists do not always agree on methodology or how to interpret results (Carter et al. 2013). Essentially, the bears internal motivation behind behaviors may differ from an ecologists anthropomorphic expectations.

Animal personality and particularly the bold-shy axis, may have implications for the adaptability and persistence of animals in human dominated environments. Bolder individuals seem to be more tolerant towards human encroachment and move more easily through human-modified landscapes (Lowry et al. 2013, Sol et al. 2013), they therefore generally may be more resilient towards anthropogenic disturbances than shyer individuals (Sih 2013).
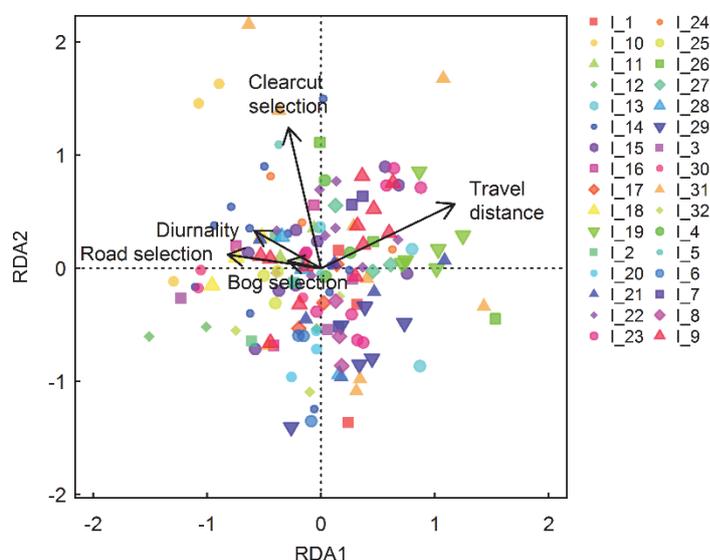

Figure 10. PCA results for five behaviors measured in 32 female brown bears in central Sweden. Arrows represent eigenvectors for behavioral measures. Unique color and character combinations indicate suits of behavioral measures observed from the same individual displayed along the first two PCA axes.

Reflections & future perspectives

A PhD thesis is three years of work in progress. When reflecting on these last three years, I think there were many moments where things could have taken a different turn. In every study there is room for improvement or, for that matter, a different way of interpretation and telling your story. This means that one has the flexibility to develop and pursue one's own ideas, including those that may not have been part of the original outline. I would like to highlight two main ideas that arose during my PhD project, because I believe they have merit for future research.

Modeling berries - Scale issues and how to overcome them

During my studies, I have particularly come to appreciate the challenges of data availability, sample sizes, and both temporal and spatial scales. What surprised me was that this challenge did not include the bear relocation or life history data. Capturing, collaring, and monitoring wildlife in meaningful sample sizes is expensive and is therefore the main bottleneck for many wildlife studies, particularly for financially and time-limited PhD projects. Few funding agencies invest into long-term monitoring programs, despite the fact that research on evolution and life history in long-lived species requires multigenerational monitoring (Clutton-Brock and Sheldon 2010). The SBBRP is in the unique position to have received funding for more than 30 years and the project has done a great job in collecting data in a consistent fashion so they can be used to answer many different research questions. My biggest challenge indeed were the berry data. In the absence of meaningful elevational gradients, which limit berry distribution elsewhere (Roberts et al. 2014, Barber et al. 2016), bilberry is the most common field shrub covering the forest floor in our entire study area (Kardell 1979). Thus, rather than simply modeling presence and absence of berry bushes, we attempted to model fine-scale variation in how many berries these bushes would produce on a very local scale, depending on site characteristics. Such fine-scale food resource maps may help us to better understand animal space use in heterogeneous environments (Nielsen et al. 2010). However, I encountered strong variation in the number of berries per m^2 even among similar locations. Using remotely sensed variables like elevation, habitat category, or NDVI fell short in explaining much of this variation, as did climatic variables. The prime reason for this was a mismatch in the spatial scale of explanatory variables describing a location, and the much more local drivers that influence berry abundance. For example, temperature was measured in 5x5 km grid cells, but there are local temperature differences between different habitat categories (see Article IV Supplementary material Fig. A10), which, given the large spatial scale, are not accounted for in the climate maps. We know that the structure of a forest is the most important driver for berry production (Bergstedt and Milberg 2001) and we know that bilberry produces best in open, mature pine forests (Miina et al. 2009). Using a general habitat category of "mature forest" encompasses every forest patch that is older than some threshold age, but it is not specific for tree species composition or stand density. We therefore a) fell short of explaining much of the spatial variation in berry abundance and b) were limited to a relatively course spatial scale in our berry prediction maps. I have two approaches on how to improve the explanatory power of our statistical models and thereby the accuracy of our predictive maps:

First, we need to improve the information content and spatial scale of explanatory covariates. The most promising tool to do so is airborne laser scanning (ALS). ALS is an emerging technology, in which a high-resolution LiDAR scanner (short for light detection and ranging) is mounted on an airplane to scan the landscape from the air, producing a 3D image of landscape structure. All of Sweden had been scanned with LiDAR by 2014. The Swedish Forest Agency (http://www.skogsstyrelsen.se/en/) has processed the raw data into freely available maps of, e.g., tree height, at a very high spatial resolution of 12.5 m. Further, the raw LiDAR point cloud data are accessible for scientific purposes and, for example, can be used to derive forest metrics like vegetation density at lower height classes, provided the point density in these height classes is sufficient. This means that essentially, one can extract information about forest density at a given height above the ground, e.g. 0.15-1.37 m, for each 12.5 x 12.5 m quadrate in the landscape. Results from Canada (Barber et al. 2016) show that refining berry models by including variables accounting for forest structure at lower height classes improved the overall explained variation by up to 16%.

Second: Finding an appropriate model structure to explain berry abundance was not an easy task. The berry data were generally zero inflated (excess amount of plots with no berries at all), many of the explanatory variables were collinear, we found unforeseen interactions, some of the explanatory variables had nonlinear effects on berry abundance, and I faced problems with heteroscedacity, where the variability of berry abundance was greater at certain levels of the explanatory variable than at others. The sum of these factors indeed made it challenging not to validate parametric model assumptions. Using supervised machine learning algorithms, i.e., decision trees, we can overcome some of these problems. Decision tree techniques are especially suitable for making predictions, as they often increase predictive accuracy compared to parametric models, also because they inherently allow for nonlinear relationships. Further, decision trees can handle both numeric and binary or multinomial classes as input data. For low sample sizes, random forest is a suitable and user-friendly technique and is relatively robust to overfitting. A random forest model tries out different combinations of explanatory variables in parallel and averages the best results into one final model. In the process, the user thus loses control over the model structure, wherefore these models are less suitable for hypothesis testing. Latifi et al. (2017) have shown that using random forest models to predict forest shrub cover from LiDAR-derived forest metrics can yield high explanatory power paired with high predictive accuracies.

In summary, I believe that wildlife ecologists may gain new insights from integrating finer-scale measures of the habitat structure their study animals are inhabiting (Nijland et al. 2015). Habitat structure can indirectly aid in improving forage maps (Barber et al. 2016, Latifi et al. 2017). Habitat structure in height classes that are perceived by the animal as cover from risk may also be used directly in explaining animal space use (Lone et al. 2015).

Same-same, but different? Individual differences in movement patterns

In the last two articles of my PhD, I demonstrate that individual bears in our population vary substantially and consistently in behavioral traits, a sign that these can be used to identify animal personality types. A recent integration of animal personality research into movement ecology may explain the emergence of differential movement patterns among individuals in a population (Spiegel et al. 2017). For example, one proposed movement-based measure of boldness is the strength of area-restricted search behavior (Spiegel et al. 2017). Area-restricted

search is a foraging strategy where animals decelerate speed and frequently turn after they have encountered a food patch, resulting in a locally intense search pattern. Using simulations, Spiegel et al. (2017) have demonstrated that strength of area-restricted search patterns likely differ among personality types. Area-restricted search behavior should be especially prevalent when foraging on resources that are distributed spatially in patches, such as berries (see Article I). However, additional drivers, other than personality, may explain individual differences in space use. Social learning could explain why space use by some individuals is more similar than for others (e.g. Mueller et al. 2013). In solitary species like bears, social learning is limited to the period of maternal rearing. For bears, habitat selection preferences have been shown to be more strongly correlated among related bears (Shafer et al. 2014), which has been suggested to be the result of maternal learning (Nielsen et al. 2013). Also so-called problem bears, i.e. individuals that lose their wariness towards people and seek food close to human settlements, may acquire and learn this behavior from their mother (Morehouse et al. 2016). Another factor that may alter individual space use patterns is experience (Mueller et al. 2013, Teitelbaum et al. 2016). Experience relies on the acquisition of long-term memory of past resource distribution (i.e. number of migration trips, home range tenure, etc.), thereby improving the efficacy of movement paths by making them shorter and more target oriented. Experience may be particularly advantageous in patchy environments, where spatial learning and memory will shorten search time (Fagan et al. 2013). Bison (*Bison bison*), for example, use memory to navigate in a matrix of resource-poor and resource-rich habitat patches (Merkle et al. 2014). Their study system is reminiscent of the distribution of berries in our study system, where forestry creates patches of higher or lower resource abundance. Because bears inhabit home ranges that are relatively stable over time (Leclerc et al. In Press), the navigational capacity of an individual within its home range should benefit from spatial learning and memory and increase with residence time.

Provided that we succeed to produce a more detailed map of berry abundance, we should be able to study some of previously rarely examined relationships that I have proposed here for bears in Scandinavia. The SBBRP's unique dataset of multigenerational, lifelong monitoring data of bears would allow disentangling the effects of maternal learning, experience, and personality on movement patterns. To my knowledge, such an empirical study would be the first of its kind.

Bibliography

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology letters **14**:948-958.

Arnemo, J. M., and Å. Fahlman. 2011. Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Hedmark University College. Evenstad, Norway.

Atlegrim, O., and K. Sjöberg. 1996. Response of bilberry (Vaccinium myrtillus) to clear-cutting and single-tree selection harvests in uneven-aged boreal Picea abies forests. Forest Ecology and Management **86**:39-50.

Barber, Q. E., C. W. Bater, A. C. R. Braid, N. C. Coops, P. Tompalski, and S. E. Nielsen. 2016. Airborne laser scanning for modelling understory shrub abundance and productivity. Forest Ecology and Management **377**:46-54.

Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. Animal Behaviour **77**:771-783.

Bergstedt, J., and P. Milberg. 2001. The impact of logging intensity on field-layer vegetation in Swedish boreal forests. Forest Ecology and Management **154**:105-115.

Biro, P. A., and J. A. Stamps. 2008. Are animal personality traits linked to life-history productivity? Trends in Ecology & Evolution **23**:361-368.

Bischof, R., R. Fujita, A. Zedrosser, A. Söderberg, and J. E. Swenson. 2008. Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. The Journal of Wildlife Management **72**:79-88.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? The American Naturalist **180**:407-424.

Bokhorst, S., J. Bjerke, F. Bowles, J. Melillo, T. Callaghan, and G. Phoenix. 2008. Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. Global Change Biology **14**:2603-2612.

Bokhorst, S., J. Bjerke, L. Street, T. Callaghan, and G. Phoenix. 2011. Impacts of multiple extreme winter warming events on sub-Arctic heathland: phenology, reproduction, growth, and CO_2 flux responses. Global Change Biology **17**:2817-2830.

Bokhorst, S., J. W. Bjerke, M. P. Davey, K. Taulavuori, E. Taulavuori, K. Laine, T. V. Callaghan, and G. K. Phoenix. 2010. Impacts of extreme winter warming events on plant physiology in a sub-Arctic heath community. Physiologia plantarum **140**:128-140.

Boon, A. K., D. Réale, and S. Boutin. 2008. Personality, habitat use, and their consequences for survival in North American red squirrels Tamiasciurus hudsonicus. Oikos **117**:1321-1328.

Brook, L. A., C. N. Johnson, and E. G. Ritchie. 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. Journal of Applied Ecology **49**:1278-1286.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research **1**:49-71.

Carter, A. J., W. E. Feeney, H. H. Marshall, G. Cowlishaw, and R. Heinsohn. 2013. Animal personality: what are behavioural ecologists measuring? Biological Reviews **88**:465-475.

Christianson, D., and S. Creel. 2008. Risk effects in elk: sex-specific responses in grazing and browsing due to predation risk from wolves. Behavioral Ecology **19**:1258-1266.

Christianson, D., and S. Creel. 2010. A nutritionally mediated risk effect of wolves on elk. Ecology **91**:1184-1191.

Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce. 2012a. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society B: biological sciences **279**:4407-4416.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012b. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. Plos One **7**:e50611.

Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution **25**:562-573.

Coogan, S. C., S. E. Nielsen, and G. B. Stenhouse. 2012. Spatial and temporal heterogeneity creates a "brown tide" in root phenology and nutrition. ISRN Ecology **2012**.

Creel, S., and J. A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour **69**:1181-1189.

Creel, S., J. A. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology **86**:3387-3397.

Dahle, B., and J. E. Swenson. 2003a. Factors influencing length of maternal care in brown bears (Ursus arctos) and its effect on offspring. Behavioral Ecology and Sociobiology **54**:352-358.

Dahle, B., and J. E. Swenson. 2003b. Family Breakup in Brown Bears: Are Young Forced to Leave? Journal of Mammalogy **84**:536-540.

Dahle, B., and J. E. Swenson. 2003c. Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. Journal of Zoology **260**:329-335.

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2008. Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. BMC Ecology **8**:14.

Deacy, W., W. Leacock, J. B. Armstrong, and J. A. Stanford. 2016. Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. Ecology **97**:1091-1098.

Eriksson, O., and J. Ehrlén. 1991. Phenological variation in fruit characteristics in vertebrate-dispersed plants. Oecologia **86**:463-470.

Fagan, W. F., M. A. Lewis, M. Auger-Methe, T. Avgar, S. Benhamou, G. Breed, L. LaDage, U. E. Schlagel, W. W. Tang, Y. P. Papastamatiou, J. Forester, and T. Mueller. 2013. Spatial memory and animal movement. Ecology letters **16**:1316-1329.

Fitzgibbon, C. D. 1990. Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. Animal Behaviour **39**:1116-1126.

Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos **107**:172-180.

Frank, L., and R. Woodroffe. 2001. Behaviour of carnivores in exploited and controlled populations. Pages 419-442 *in* J. Gittleman, S. Funk, D. MacDonald, and R. Wayne, editors. Carnivore Conservation. Cambridge University Press, Cambridge.

Frank, S. C., S. M. Steyaert, J. E. Swenson, I. Storch, J. Kindberg, H. Barck, and A. Zedrosser. 2015. A "clearcut" case? Brown bear selection of coarse woody debris and carpenter ants on clearcuts. Forest Ecology and Management **348**:164-173.

Friebe, A., A. L. Evans, J. M. Arnemo, S. Blanc, S. Brunberg, G. Fleissner, J. E. Swenson, and A. Zedrosser. 2014. Factors affecting date of implantation, parturition, and den entry estimated from activity and body temperature in free-ranging brown bears. Plos One **9**:e101410.

Friebe, A., E. S. Jon, and F. Sandegren. 2001. Denning chronology of female brown bears in central Sweden. Ursus **12**:37-45.

Friebe, A., A. Zedrosser, and J. E. Swenson. 2013. Detection of pregnancy in a hibernator based on activity data. European Journal of Wildlife Research **59**:731-741.

Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology **90**:699-710.

Herrera, C. M., P. Jordano, L. Lopez-Soria, and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs **64**:315-344.

Hissa, R. 1997. Physiology of the European brown bear (Ursus arctos arctos). Annales Zoologici Fennici **34**:267-287.

Kardell, L. 1979. Occurrence and production of bilberry, lingonberry and raspberry in Sweden's forests. Forest Ecology and Management **2**:285-298.

Kardell, L., and L. Eriksson. 2011. Blåbärs-och lingonrisets återhämtning 30 år efter kalavverkning och markberedning 1977-2010.

Kelly, D., A. Geldenhuis, A. James, E. P. Holland, M. J. Plank, R. E. Brockie, P. E. Cowan, G. A. Harper, W. G. Lee, M. J. Maitland, A. F. Mark, J. A. Mills, P. R. Wilson, and A. E. Byrom. 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. Ecology letters **16**:90-98.

Kelly, D., and V. L. Sork. 2002. Mast Seeding in Perennial Plants: Why, How, Where? Annual Review of Ecology and Systematics **33**:427-447.

Kindberg, J., G. Ericsson, and J. E. Swenson. 2009. Monitoring rare or elusive large mammals using effort-corrected voluntary observers. Biological Conservation **142**:159-165.

Latifi, H., S. Hill, B. Schumann, M. Heurich, and S. Dech. 2017. Multi-model estimation of understorey shrub, herb and moss cover in temperate forest stands by laser scanner data. Forestry:1-19.

Leclerc, M., S. Frank, A. Zedrosser, S. J.E., and F. Pelletier. In Press. Hunting promotes spatial reorganization and sexually selected infanticide.

Leclerc, M., E. Vander Wal, A. Zedrosser, J. E. Swenson, J. Kindberg, and F. Pelletier. 2016. Quantifying consistent individual differences in habitat selection. Oecologia **180**:697-705.

Leclerc, M., A. Zedrosser, and F. Pelletier. 2017. Harvesting as a potential selective pressure on behavioural traits. Journal of Applied Ecology:n/a-n/a.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. The American Naturalist **153**:649-659.

Lone, K., L. E. Loe, E. L. Meisingset, I. Stamnes, and A. Mysterud. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. Animal Behaviour **102**:127-138.

Lone, K., A. Mysterud, T. Gobakken, J. Odden, J. Linnell, and L. E. Loe. 2016. Temporal variation in habitat selection breaks the catch-22 of spatially contrasting predation risk from multiple predators. Oikos.

Lowry, H., A. Lill, and B. B. M. Wong. 2013. Behavioural responses of wildlife to urban environments. Biological Reviews **88**:537-549.

Manchi, S., and J. E. Swenson. 2005. Denning behaviour of Scandinavian brown bears Ursus arctos. Wildlife Biology **11**:123-132.

Martin, J., M. Basille, B. Van Moorter, J. Kindberg, D. Allaine, and J. E. Swenson. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (Ursus arctos). Canadian Journal of Zoology **88**:875-883.

May, T. M., M. J. Page, and P. A. Fleming. 2016. Predicting survivors: animal temperament and translocation. Behavioral Ecology **27**:969-977.

Merkle, J., D. Fortin, and J. Morales. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. Ecology letters **17**:924-931.

Merrick, M. J., and J. L. Koprowski. 2017a. Altered natal dispersal at the range periphery: The role of behavior, resources, and maternal condition. Ecology and evolution **7**:58-72.

Merrick, M. J., and J. L. Koprowski. 2017b. Should we consider individual behavior differences in applied wildlife conservation studies? Biological Conservation **209**:34-44.

Miina, J., J.-P. Hotanen, and K. Salo. 2009. Modelling the abundance and temporal variation in the production of bilberry (Vaccinium myrtillus L.) in Finnish mineral soil forests. Silva Fennica **43**:577-593.

Mitchell, J., W. Dorney, R. Mayer, and J. McIlroy. 2008. Ecological impacts of feral pig diggings in north Queensland rainforests. Wildlife Research **34**:603-608.

Moe, T., J. Kindberg, I. Jansson, and J. Swenson. 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos). Canadian Journal of Zoology **85**:518-525.

Morehouse, A. T., T. A. Graves, N. Mikle, and M. S. Boyce. 2016. Nature vs. Nurture: Evidence for Social Learning of Conflict Behaviour in Grizzly Bears. Plos One **11**:e0165425.

Mueller, T., R. B. O'Hara, S. J. Converse, R. P. Urbanek, and W. F. Fagan. 2013. Social Learning of Migratory Performance. Science **341**:999-1002.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: Availability influences realtive use in trade-off situations. Ecology **79**:1435-1441.

Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biological Reviews **85**:935-956.

Nellemann, C., O.-G. Støen, J. Kindberg, J. E. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. P. Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. Biological Conservation **138**:157-165.

Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation **143**:1623-1634.

Nielsen, S. E., A. B. A. Shafer, M. S. Boyce, and G. B. Stenhouse. 2013. Does Learning or Instinct Shape Habitat Selection? Plos One **8**:e53721.

Nijland, W., N. C. Coops, S. E. Nielsen, and G. Stenhouse. 2015. Integrating optical satellite data and airborne laser scanning in habitat classification for wildlife management. International Journal of Applied Earth Observation and Geoinformation **38**:242-250.

Ordiz, A., J. Kindberg, S. Sæbø, J. E. Swenson, and O.-G. Støen. 2014. Brown bear circadian behavior reveals human environmental encroachment. Biological Conservation **173**:1-9.

Ordiz, A., O.-G. Stoen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia **166**:59-67.

Ordiz, A., O.-G. Støen, S. Sæbø, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? Biological Conservation **152**:21-28.

Ordiz, A., O. G. Støen, S. Sæbø, V. Sahlen, B. E. Pedersen, J. Kindberg, and J. E. Swenson. 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. Journal of Applied Ecology **50**:306-314.

Pelchat, B. O., and R. L. Ruff. 1986. Habitat and spatial relationships of black bears in boreal mixedwood forest of Alberta. Bears: Their Biology and Management:81-92.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Raoult, V., C. Brown, A. Zuberi, and J. E. Williamson. 2012. Blood cortisol concentrations predict boldness in juvenile mulloway (Argyosomus japonicus). Journal of Ethology **30**:225-232.

Rauset, G. R., J. Kindberg, and J. E. Swenson. 2012. Modeling female brown bear kill rates on moose calves using global positioning satellite data. The Journal of Wildlife Management **76**:1597-1606.

Réale, D., and M. Festa-Bianchet. 2003. Predator-induced natural selection on temperament in bighorn ewes. Animal Behaviour **65**:463-470.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews **82**:291-318.

Rixen, C., M. A. Dawes, S. Wipf, and F. Hagedorn. 2012. Evidence of enhanced freezing damage in treeline plants during six years of CO_2 enrichment and soil warming. Oikos **121**:1532-1543.

Robbins, C. T., M. Ben-David, J. K. Fortin, and O. L. Nelson. 2012. Maternal condition determines birth date and growth of newborn bear cubs. Journal of Mammalogy **93**:540-546.

Roberts, D. R., S. E. Nielsen, and G. B. Stenhouse. 2014. Idiosyncratic responses of grizzly bear habitat to climate change based on projected food resource changes. Ecological Applications **24**:1144-1154.

Selås, V. 2000. Seed production of a masting dwarf shrub, Vaccinium myrtillus, in relation to previous reproduction and weather. Canadian Journal of Botany **78**:423-429.

Selås, V., A. Sønsteby, O. M. Heide, and N. Opstad. 2015. Climatic and seasonal control of annual growth rhythm and flower formation in Vaccinium myrtillus (Ericaceae), and the impact on annual variation in berry production. Plant Ecology and Evolution **148**:350-360.

Shafer, A. B. A., S. E. Nielsen, J. M. Northrup, and G. B. Stenhouse. 2014. Linking genotype, ecotype, and phenotype in an intensively managed large carnivore. Evolutionary Applications **7**:301-312.

Sih, A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Animal Behaviour **85**:1077-1088.

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution **19**:372-378.

Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society **14**:235-250.

Singer, F. J., D. K. Otto, A. R. Tipton, and C. P. Hable. 1981. Home Ranges, Movements, and Habitat Use of European Wild Boar in Tennessee. The Journal of Wildlife Management **45**:343-353.

Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. Behavioral Ecology **19**:448-455.

Smith, C. C., and D. Follmer. 1972. Food preferences of squirrels. Ecology **53**:82-91.

Sol, D., O. Lapiedra, and C. González-Lagos. 2013. Behavioural adjustments for a life in the city. Animal Behaviour **85**:1101-1112.

Spiegel, O., S. T. Leu, C. M. Bull, and A. Sih. 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecology letters **20**:3-18.

Spiegel, O., S. T. Leu, A. Sih, S. S. Godfrey, and C. M. Bull. 2015. When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries. Proceedings of the Royal Society B: biological sciences **282**.

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

Steyaert, S. M., A. Endrestøl, K. Hacklaender, J. E. Swenson, and A. Zedrosser. 2012. The mating system of the brown bear Ursus arctos. Mammal Review **42**:12-34.

Steyaert, S. M., J. E. Swenson, and A. Zedrosser. 2014. Litter loss triggers estrus in a nonsocial seasonal breeder. Ecology and evolution **4**:300-310.

Storch, I. 1993. Habitat selection by capercaillie in summer and autumn: Is bilberry important? Oecologia **95**:257-265.

Støen, O.-G., A. Zedrosser, S. Sæbø, and J. E. Swenson. 2006. Inversely density-dependent natal dispersal in brown bears Ursus arctos. Oecologia **148**:356-364.

Swanson, A., T. Arnold, M. Kosmala, J. Forester, and C. Packer. 2016. In the absence of a "landscape of fear": How lions, hyenas, and cheetahs coexist. Ecology and evolution **6**:8534-8545.

Swenson, J. E., M. Adamič, D. Huber, and S. Stokke. 2007. Brown bear body mass and growth in northern and southern Europe. Oecologia **153**:37-47.

Swenson, J. E., F. Sandegren, A. Söderberg, M. Heim, O. Sørensen, A. Bjärvall, R. Franzén, S. Wikan, and P. Wabakken. 1999. Interactions between brown bears and humans in Scandinavia. Biosphere Conservation **2**:1-9.

Swenson, J. E., M. Schneider, A. Zedrosser, A. Söderberg, R. Franzén, and J. Kindberg. 2017. Challenges of managing a European brown bear population; lessons from Sweden, 1943-2013. Wildlife Biology.

Teitelbaum, C. S., S. J. Converse, W. F. Fagan, K. Böhning-Gaese, R. B. O'Hara, A. E. Lacy, and T. Mueller. 2016. Experience drives innovation of new migration patterns of whooping cranes in response to global change. Nature Communications **7**:12793.

Wam, H. K., K. Eldegard, and O. Hjeljord. 2012. From overlooking to concealed: predator avoidance in an apex carnivore. European Journal of Wildlife Research **58**:1001-1003.

Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. Ecology **78**:1105-1119.

Wilson, D. S., A. B. Clark, K. Coleman, and T. Dearstyne. 1994. Shyness and boldness in humans and other animals. Trends in Ecology & Evolution **9**:442-446.

Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology & Evolution **27**:452-461.

Zedrosser, A., B. Dahle, and J. E. Swenson. 2006. Population density and food conditions determine adult female body size in brown bears. Journal of Mammalogy **87**:510-518.

Paper I
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. - Behavioral Ecology and Sociobiology 70: 831-8423.
DOI: [10.1007/s00265-016-2106-2](10.1007/s00265-016-2106-2)

Paper II
Hertel, A.G., Zedrosser, A., Mysterud, A., Støen, O.-G., Steyaert, S.M.J.G. & Swenson, J.E. 2016. Temporal effects of hunting on foraging behavior of an apex predator: Do bears forego foraging when risk is high? - Oecologia 182: 1019-1029.
DOI: [10.1007/s00442-016-3729-8](10.1007/s00442-016-3729-8)

Paper III
Lodberg-Holm, H.K., Gelink, H.W., Hertel, A.G., Swenson, J.E. & Steyaert, S.M.J.G. Brown bears track bilberry fruiting through a landscape of risk.
(Submitted)

Paper IV
Hertel, A.G., Bischof, R., Langvall, O., Mysterud, A., Kindberg, J., Swenson, J.E. & Zedrosser, A. Berry production drives bottom-up effects on body mass and reproductive success in an omnivore.
(Submitted)

Paper V
Hertel, A.G., Swenson, J.E. & Bischof, R. A case for considering individual variation in diel activity patterns.
(Submitted)

Paper VI
Hertel, A.G., Leclerc, M., Pelletier, F. & Zedrosser, A. Don't poke the bear: Can remote behavior recordings be used to assess personality in elusive wildlife?
(Submitted)