University of South-Eastern Norway
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Norwegian Beaver Project

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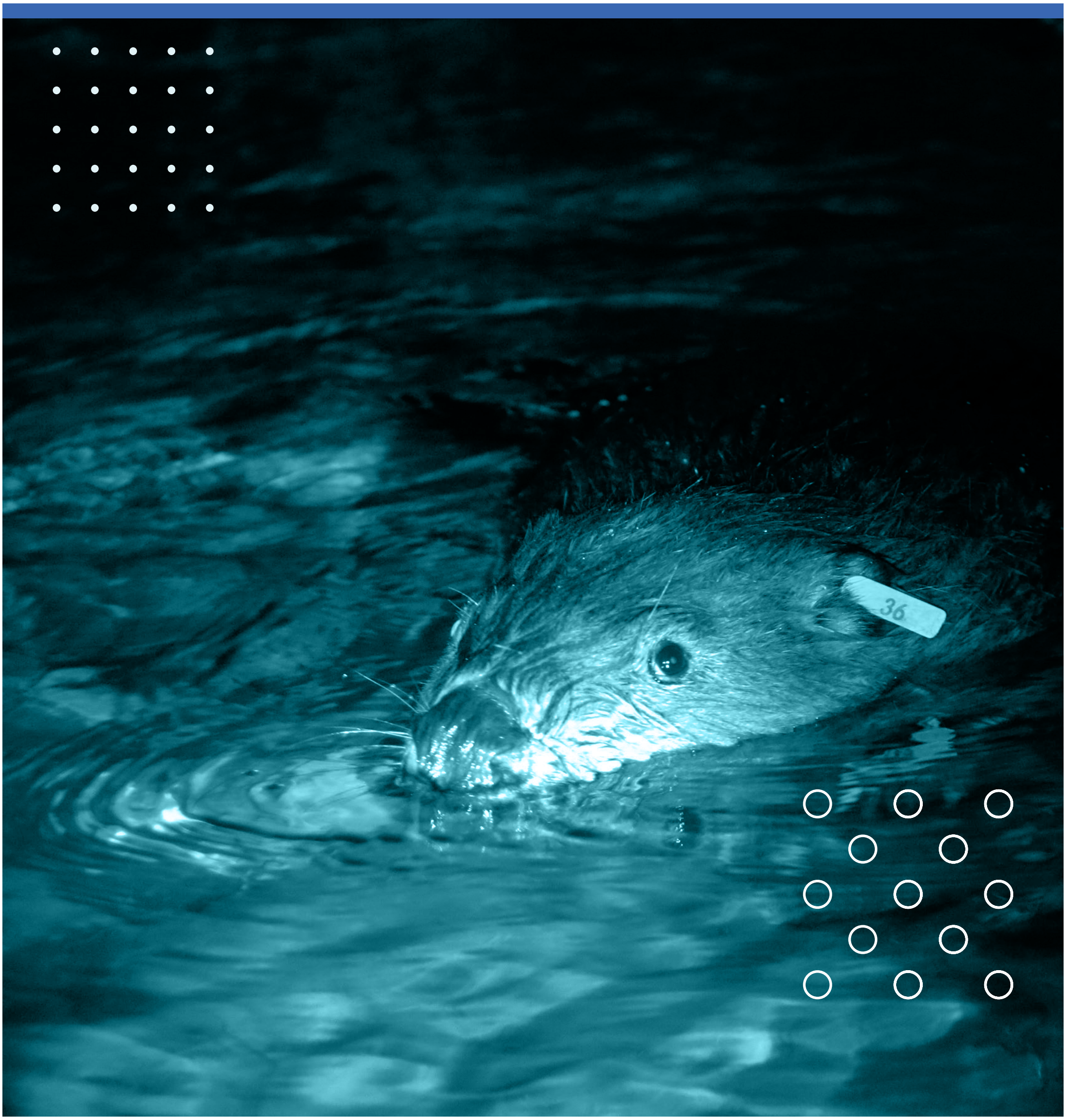
Hanna Kavli Lodberg- Holm

Spatio-temporal foraging behavior, habitat selection and impacts of bio-logging on Eurasian beavers, *Castor fiber*



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Preface

Throughout my PhD many people have asked me why I am studying something as peculiar as beavers. The question "What will do you do with a PhD on beavers?" has been asked more than once. My interest in wildlife and animal behavior did not start with a fascination for beavers. Growing up in Telemark, beavers were just a natural part of the landscape and occasionally a source of annoyance when they swam over my fishing line. I was, however, fascinated by large carnivores, especially wolves, from an early age. This passion lingered over the years and steered me in the direction of behavioral ecology. Through my masters and working with wolves and brown bears, I realized that my fascination with these species was to a large degree based around their impacts on the ecosystem and the trophic cascades this might create. It turned out that large carnivores were not the only species worth mentioning in that regard.

The beaver's role as an ecosystem engineer is fundamental for why beavers deserve our research attention, in my opinion. Few species have such a large impact on ecosystems. Beavers can transform small creeks and forests into connected wetlands teaming with biodiversity (Hood and Larson 2015, Law et al. 2017a, Law et al. 2019), while cleaning polluted waters, preventing floods, fires, and droughts, and storing carbon with potential implications for climate change (Rosell et al. 2005, Wohl 2021). Beavers have exposed to human eradication campaigns for centuries as hunters pursued their furs and castoreum sacks, but they persisted and are now recovering through large parts of their prior range (Nolet and Rosell 1998, Halley et al. 2021). Despite increased recognition of their role as an keystone species and ecosystem engineer, conflicts often arise with human communities (Parker and Rosell 2012, Campbell-Palmer et al. 2016). Research can hopefully contribute to mitigate some of these conflicts through insights into beaver behavior.

Beavers are not one homogenous group but consisting of families made up of individuals with different ages, social responsibilities, and energetic needs. Behavioral ecology is increasingly acknowledging the complexities of wildlife behavior and interactions with the ecosystem. Beavers provide a perfect model species to study some of these complexities by inhabiting both the aquatic and terrestrial sphere, being generalists and opportunistic foragers and with intricate social systems. They are also unique by being among the few monogamous and monomorphic mammals (Kleiman 1977).

Beaver habitats consists of varying resources and threats that are dynamic in both space and time. Large parts of their historic range have been converted into an anthropogenic landscape, which means beavers must adapt their spatial and temporal activities, foraging and habitat selection to human disturbances and novel food sources. At the same time, beavers are affected by our efforts to study them, which calls for investigations of the impact of our research methods. In this thesis I have investigated temporal trends in beaver behavior, while exploring drivers of individual differences, as well as the impact of bio-logging methods used to study these mechanisms. As I have so often explained to people wondering why I am doing this PhD, these topics not only provides insight into an important ecosystem engineer but may also provide knowledge relevant for wider topics within ecology. I hope that increased knowledge of temporal dynamics and individual differences may contribute to give wildlife more space and encourage the conservation of more diverse landscapes, while also encouraging co-existence with human communities.

A beaver splashes its tail as the sun sets during fieldwork in the Gvarv river. Photo: Frank Rosell

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everyday life, providing constructive solutions on everything from statistics to beaver trapping, and made sure that I maintained a balance through it all. I am eternally grateful!

Abstract

Wild animals deal with a dynamic landscape consisting of both food resources and threats that vary across space and time. This thesis investigated spatio-temporal foraging behavior and habitat selection of Eurasian beavers (*Castor fiber*), while also exploring potential negative impacts of the methods used to study their behavior. We explored how sex, age, reproductive status, body condition, and density impacted beaver behavior. Through tagging beavers with VHF transmitters and GPS loggers, we could track beaver movements and behavior across the landscape, seasons, and the night. We found that reproductively active females displayed similar foraging patterns as males, but differed in seasonal activity patterns, habitat selection, and diet during certain times of the year. The socio-reproductive groups also differed in circadian habitat selection patterns, revealing potentially different strategies in balancing foraging and risk. These differences indicate that even monogamous and monomorphic species may display sex-specific behavioral differences and differences related to age and other physiological and demographic characteristics. We found that beavers foraged extensively on cereals during late summer, which may play an important role in beaver foraging ecology and body condition. Beavers tagged with bio-loggers displayed lower weight gain during the tagging period, but the difference was small and there was much individual variability. There was also considerable individual variability in beaver habitat selection, some influenced by age and other beaver-specific characteristics, but much remained unexplained and raised new research questions. We concluded that beaver behavior is highly dynamic and variable across time and among individuals, which highlights the complexity of wildlife behavior and interactions within the ecosystem.

List of papers

Article I

Lodberg-Holm, H. K., Steyaert, S. M. J. G., Reinhardt, S., & Rosell, F. (2021). Size is not everything: differing activity and foraging patterns between the sexes in a monomorphic mammal. Behavioral Ecology and Sociobiology, 75(4), 1-14.

Article II

Lodberg-Holm, H. K., Garvik, E. S., Fountain, M. S. Reinhardt, S., & Rosell, F. Crop circles revealed? Spatio-temporal patterns of beaver selection for agriculture and foraging on cereals. Second revision submitted to: Agriculture, Ecosystems & Environment.

Article III

Lodberg-Holm, H. K., Wang, G., Reinhardt, S., & Rosell, F. Individual variation and spatio-temporal trends in terrestrial habitat selection of Eurasian beavers. Submitted to: Ecological Monographs.

Article IV

Robstad, C. A., Lodberg-Holm, H. K., Mayer, M., & Rosell, F. (2021). The impact of bio-logging on body weight change of the Eurasian beaver. PLOS ONE, 16(12), e0261453.

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1 Introduction

A species survival is closely related to its behavior, which enables animals to find food, mates, reproduce and protect themselves from predators and conspecifics (Drickamer et al. 2002). Habitat selection and foraging behavior are key to how animals interact with their environments and often display clear spatial and temporal patterns. Habitat selection occurs on different levels, which refers to the hierarchical organization of the habitat. The first-order refers to the physical or geographical range of a species, second-order to the selection of a home range, third-order is selection of habitat patches within the home range, and fourth-order represents selection of specific resources within these habitat patches (Johnson 1980, McGarigal et al. 2016). Scale of habitat selection on the other hand refers to the grain of observation on a spatial or temporal scale, which are the units in which animal selection is explored (Mayor et al. 2009, McGarigal et al. 2016). Habitat selection and foraging patterns may both be highly variable across time, which requires attention not only on the spatial scales but also temporal.

1.1 Temporal trends in foraging and habitat selection

Animals respond to spatial and temporal environmental variation through habitat selection while balancing the need to obtain resources and avoid predators (Milligan et al. 2020). Especially in temperate and polar regions, seasonal changes in food availability, nutritional content and energetic demands of certain life-history events may impact these patterns (Owen-Smith et al. 2010, Merems et al. 2020). When food availability differs in both space and time, it impacts foraging behavior and habitat selection, but such temporal trends generally receive less research attention (Dupke et al. 2017, Northrup et al. 2021). Seasonal and diurnal activity patterns are often complex and affected by factors such as weather, disturbance, predation, and access to forage (Dupke et al. 2017). Animals also engage in different activities throughout the day, that spans from resting to foraging, and the resources and habitats used for these activities may vary (Northrup et al. 2021). This again leads to different habitat selection patterns that also vary spatially between geographic regions and across time influenced by factors such as predation risk and human disturbances (Mayor et al. 2009, Richter et al. 2020).

1.2 Human disturbances and predation risk

Human disturbances or predation risk may drive temporal and spatial adaptions such as selection of areas with higher vegetation cover during daytime and more open areas during night (Bjørneraas et al. 2011, Dupke et al. 2017), or adopting a completely nocturnal lifestyle with physiological adaptions to support this (Hut et al. 2012). However, temporal switches may also occur within shorter time frames in response to environmental cues, predation or social interactions (Hut et al. 2012). Diurnal patterns reflect activity budgets as well as the balance between obtaining food resources and avoiding predators, including humans that tend to be more active during the day (Richter et al. 2020, de Gabriel Hernando et al. 2021). Brown bears (*Ursus arctos*) in Greece for example displayed clear diurnal patterns by being closer to human settlements at night and moving to remote natural habitats during daytime (de Gabriel Hernando et al. 2021), while in Sweden bears became more nocturnal as a response to the onset of the bear hunting season (Ordiz et al. 2012). Diel patterns may be more pronounced in certain seasons than others (Roberts et al. 2017). Red deer (*Cervus elaphus*) for example selected for more vegetation cover in summer and fall compared to other seasons, probably due to higher levels of human activity as well as climatic factors (Richter et al. 2020). Such switches are also often linked to food availability and nutritional content of food items.

1.3 Temporal variation in food availability

Animal movement patterns may change in response to seasonal foraging opportunities and some species expand their home range or even become nomadic when food resources are seasonally variable or less abundant (Owen-Smith et al. 2010). Wildlife often switch between different food items according to availability, but may also reduce foraging activity during times of high availability (Bertolino et al. 2004). Certain food items may also offer attractive nutrients leading to increased foraging, shift in diet, or spatial movement, such as moose

(*Alces alces*) foraging on aquatic vegetation in spring and early summer to obtain sodium (Fraser et al. 1982), or red deer jumping the green wave by moving to higher elevation during spring to access more palatable young plants (Bischof et al. 2012). Brown bears on the other hand switch to strong selection for berries when these become available in late summer, but selection is weakened at the onset of the hunting season (Hertel et al. 2016, Lodberg-Holm et al. 2019). Another such seasonally abundant food item, crops, may provide wildlife with extra nutrients, but also pose a risk of human encounters.

Agriculture is expanding globally and has contributed to large-scale global biodiversity loss (Sánchez-Bayo and Wyckhuys 2019), but also provides supplementary food for many generalist and omnivorous species (Oro et al. 2013). Availability of nutritious crops may induce wildlife to shift foraging towards these abundant food resources, and is not necessarily linked to declines in natural forage (Chiyo et al. 2005). Energy maximizing species such as black bears (*U. americanus*) opportunistically forage on crops to supplement their natural diet as these food sources have a high calorie content (Ditmer et al. 2018). Crops and especially cereals are a good source of both proteins and carbohydrates (Remonti et al. 2011). By being spatially clustered and temporally predictable, access to crops may decrease foraging time and increase fitness for a wide range of species (Oro et al. 2013, Ditmer et al. 2015b). Seasonal timing of crop depredation depends on both species and growth stage of the crop plant in question. Badgers (*Meles meles*) for example forage extensively on cereals when these are available during fall to build up fat reserves (Roper et al. 1995). Crop-raiding behavior often also display clear diurnal patterns such as African elephants (*Loxodonta africana*) foraging in crop fields at nigh to reduce the risk of encountering humans (Troup et al. 2020, Vogel et al. 2020), but such diurnal patterns may differ in relation to sex and reproductive status for many species (Bjørneraas et al. 2011, Ditmer et al. 2018, Vogel et al. 2020). Demographic and physiological characteristics may also impact general habitat selection patterns and act as drivers of individual variability.

1.4 Drivers of individual variability

Individual variation in habitat selection may be extensive and make it challenging to conclude on population-level trends (Milligan et al. 2020). However, these differences are also interesting to explore rather than treat them as a nuisance (Hertel et al. 2020, Northrup et al. 2021). A wide range of factors may impact this variability including behavioral syndromes linked to personality (Hertel et al. 2019, Aliperti et al. 2021), a reflection of beneficial environmental conditions (William et al. 2018), physiological variables such as sex and reproductive status (Bjørneraas et al. 2011, Ditmer et al. 2015a), as well as age and body condition (Hertel et al. 2017, Hata et al. 2021). Habitat selection and foraging commonly differ between males and females, especially in size dimorphic species, driven by different energetic needs associated with body size, mating systems and vulnerability to predation (Oehlers et al. 2011, Ditmer et al. 2015b, Pecorella et al. 2019). In African elephants for example, females are often more risk aversive and mostly foraged on crops during nighttime and displayed different diurnal habitat selection and activity patterns compared to males (Vogel et al. 2020). However, in red deer, females are more willing to risk crossing roads compared to males, indicating that females are not always more risk aversive than males (Meisingset et al. 2013). Sexual segregation have a wide range of causes and most likely a combination is the best reflection of the truth, as one main theory has not yet been able to account for all differences in various species (Ruckstuhl 2007). Still, in habitat selection studies, sex-specific patterns are often ignored, which may cause overestimation or underestimation of the importance of certain habitat types (Oliveira et al. 2018). Differences between the sexes may also be seasonally specific such as female Mediterranean mouflons (*Ovis gmelini musimon*) selecting for better foraging locations during gestation and after weaning, while shifting to safer habitats when accompanied by dependent lambs, but displaying similar habitat selection as males in autumn and winter (Marchand et al. 2015). During reproductive periods, differences may even occur between males and females in monogamous and monomorphic species where fewer such differences are expected and investigated (Lewis et al. 2002).

Bi-parental care is more common in monogamous species which may cause more similar habitat selection and foraging patterns (Kleiman 1977, Burke et al. 2015). However, females may still have higher energy requirements during gestation and lactation, which may lead to increased foraging or selection of habitats with higher food quality (Clutton-Brock et al. 1982, Logan and Sanson 2003, Pipia et al. 2008). Female red ruffed lemurs (*Varecia rubra*) for example foraged more than males during lactation, even though they both rested less and travelled more during the same time (Vasey 2005). In several monomorphic sea birds, females travelled further or dived deeper to access better quality food compared to males especially prior to reproduction (Lewis et al. 2002, Hedd et al. 2014). However, in monomorphic African oryx (*Oryx beisa*), males spent the longest time foraging, but females still took more bites per time unit (Ruckstuhl and Neuhaus 2009).

Reproductive cycles not only impact foraging and habitat selection, but reproductive success may be the best measure of true habitat quality and fitness consequences of differing strategies (McLoughlin et al. 2007, Gaillard et al. 2010). In roe deer (*Capreolus capreolus*) in France, lifetime reproductive success could be explained by several habitat features within individual territories (McLoughlin et al. 2007). While in young sika deer (*Cervus nippon*), individuals foraging on crops had larger body size and also a higher reproductive rate than those that did not exploit this food source (Hata et al. 2021), and adult male elephants that foraged on crops became larger for their age with possible implications for the length of musth episodes and increased reproduction (Chiyo et al. 2011). In black bears in Minnesota, cereal consumption increased body condition of males and body mass of females, but there was no evidence that this impacted reproduction (Ditmer et al. 2015b). Foraging and habitat selection may differ among individuals and offer the possibility to link different strategies to its consequences in terms of body condition, reproduction, survival, and ultimately fitness (McLoughlin et al. 2007, Merems et al. 2020, Ofstad et al. 2020, Northrup et al. 2021). However, investigating these differences require tools to monitor spatial movements and behavior of individuals as well as long-term monitoring of populations.

1.5 Methods to study animal behavior

Observations of wild animals can be challenging due to the environment the animal moves through (Ropert-Coudert and Wilson 2005). In recent decades, new technology to track animals using bio-loggers are creating opportunities to explore animal behavior and movements (Wilson et al. 2008, Wilmers et al. 2015). Bio-loggers enables researchers to monitor animals as they move through widely different environments spanning from terrestrial, avian and aquatic ecosystems (Cooke et al. 2004, Hussey et al. 2015, Kays et al. 2015), and explore how animals move through a complex landscape consisting of unevenly spread food resources, predation risk, environmental conditions and anthropogenic disturbances (Hays et al. 2016). Bio-loggers such as GPS and Daily Diaries containing both tri-axial accelerometers and magnetometers can study animal behavior and spatial movement in great detail, and shed light on both foraging behavior and habitat selection (Wilmers et al. 2015). Many of these devices were developed to monitor marine species that are difficult to observe while moving across vast ocean distances (Wilson et al. 2007, Hussey et al. 2015), but are increasingly being used to study also terrestrial species (Kays et al. 2015). Through technological development these devices are becoming increasingly smaller, enabling attachment on a wider range of species (Portugal and White 2018).

However, as new species are targeted and new attachment mechanisms developed, a wide range of negative impacts may arise, which should be carefully investigated and considered (Hawkins 2004). Negative impacts maybe associated with capture stress (Jordan 2005, Baylis et al. 2015), increased drag (Bodey et al. 2018, Rosen et al. 2018) and adding weight to an animal amongst many others (Portugal and White 2018). These impacts are often species-specific, dependent on animal lifestyles (Wilson et al. 2021) and may vary among individuals (Lear et al. 2018). Impacts may include energy expenditure related to movement (Rosen et al. 2018), survival or reproduction (Barron et al. 2010, Bodey et al. 2018). A main challenge with studying potential negative effects of bio-logging is the need for a control group of untagged animals to compare the tagged animals with (Authier et al. 2013). Without direct comparisons with a control group, subtle differences in behavior or body condition may be missed.

Negative impacts may have important consequences for both data validity and animal welfare (Soulsbury et al. 2020, Cleasby et al. 2021), but bio-logging still opens unique opportunities to study interesting aspects of animal ecology.

Data from bio-loggers may inform us about temporal trends in foraging behavior and habitat selection, which can be matched with information about reproduction and physiology to explore both the drivers and consequences of different foraging and habitat selection strategies (Ropert-Coudert and Wilson 2005, Northrup et al. 2021). In some species these patterns are not only important to understand the ecology of the species and to inform management and conservation (Milligan et al. 2020, Northrup et al. 2021), but may also have wide scale consequences for the very structure of the ecosystem. One such species, the Eurasian beaver (*Castor fiber*), is known as an ecosystem engineer, together with its close relative the North American beaver (*C. canadensis*) (Rosell et al. 2005, Hood and Larson 2014).

2 Study species

2.1 The beaver – an ecosystem engineer on the rebound

Eurasian and North American beavers appear similar, and despite the eight chromosomes separating them, their behavior and ecological niche are almost identical (Parker et al. 2012), and both species are therefore discussed interchangeably throughout this thesis. Eurasian beavers used to be distributed from British Isles to Eastern Siberia, but by the 19th century they were almost eliminated with only 1200 individuals in eight isolated populations remaining (Nolet and Rosell 1998). In North America, there is great uncertainty concerning population sizes prior to European arrival, but probably beavers populated close to half the continent playing an important role in maintaining large wetland areas (Wohl 2021). In recent decades, both beaver species have been reintroduced within their previous ranges in Europe and North America motivated by an effort to recover the species and/or to restore their ecological functions (Gibson and Olden 2014, Halley et al. 2021). Beavers have in some places settled into areas with a very high human density, which illustrate that they do not require untouched wilderness to persist (Halley and Rosell 2002, Halley et al. 2021), even though they prefer to settle outside highly anthropogenic areas (Zwolicki et al. 2019).

Beavers are known as ecosystem engineers through their foraging and building activities, which changes the structure of ecosystems and creates habitats for other species, with implications for biodiversity (Hood and Larson 2014, Law et al. 2017b, Law et al. 2019). They play a key role in ecosystem processes such as species composition, vegetation structure, hydrology, and water chemistry (Rosell et al. 2005, Parker et al. 2007, Gibson and Olden 2014). Beavers mostly impact the relatively undisturbed forest zone located around waterways where they may contribute to transform forested areas into wetlands (Nummi and Kuuluvainen 2013, Wohl 2021), and connect these through beaver constructed channels (Hood and Larson 2015). Beaver foraging can also cause shifts in the composition of herbaceous plant species and biomass due to selective felling and browsing on certain species (Jones et al. 2009, Law et al. 2014b), and reduce biomass of invasive species (Parker et al., 2007). The beaver is also unique by being semi-aquatic that inhabits both the aquatic and terrestrial spheres, which may contribute to energy fluxes between these zones (Johnston 2017). As beavers contribute to shape ecosystems, it is especially important to understand their foraging strategies (Gallant et al. 2016) and habitat selection patterns.

2.2 Diet and foraging behavior

Beavers focus their foraging close to the water and are characterized as central place foragers, even though there is conflicting evidence on whether they are more selective (Raffel et al. 2009, Gerwing et al. 2013), or prefer larger or smaller food items with increasing distance from water (Belovsky 1984, Haarberg and Rosell 2006, Raffel et al. 2009). Beavers are also energy-maximizers, which implies that they cut more vegetation than they need in high quality habitats (Gallant et al. 2016). In autumn, beavers increase felling rates of trees in order to construct a winter food cache consisting of sticks and branches, which they subsequently forage on during the winter season in ice-covered areas (Svendsen 1980, Busher et al. 2020). After relying mostly on the bark of trees as their main food source in winter, beavers tend to switch towards a more diverse diet in summer.

The beaver summer diet includes twigs, leaves and roots (Nolet et al. 1995), as well as aquatic plants that are more digestible, nutritious, less costly to transport, and may provide safer foraging habitats in relation to predators (Cebrian and Lartigue 2004, Law et al. 2014a, Bergman et al. 2018). Aquatic vegetation provides an important food source for beavers especially during summer (Svendsen 1980, Milligan and Humphries 2010, Mortensen et al. 2021). Beavers may also forage on crops, which has occasionally been found in their diet (Roberts and Arner 1984, Bełżecki et al. 2018), even though extensive conflicts with farmers due to foraging are rarely mentioned (Campbell et al. 2012a, Ulicsni et al. 2020). A study from the Czech Republic showed that beavers preferred wheat (*Triticum aestivum*) and barley (*Hordeum sativum*), but also foraged on several other crop species when these were available (Mikulka et al. 2020). The highly variable diet of beavers is both a result of seasonal availability (Krojerová-Prokešová et al. 2010), but also an adaption to obtain a variety of nutrients (Nolet et al. 1995). Beavers deposit fat reserves in autumn, which they then mobilize in winter and spring (Aleksiuk and Cowan 1969). There have been conflicting results on whether the beaver diet differs between the males and females or age groups, with some studies finding no differences (Roberts and Arner 1984, Krojerová-Prokešová et al. 2010), and other studies identifying differences between males and females (Bełżecki et al. 2018).

2.3 Territoriality and activity patterns

Beavers are highly territorial and maintain exclusive territories that they protect year around (Nolet and Rosell 1994). The territories rarely change in size and seem to depend more on colonization history than the quality of habitats (Campbell et al. 2005). Beavers are sexually monomorphic and monogamous (Aleksiuk and Cowan 1969), even though partner changes and extra pair copulations do occur (Nimje et al. 2019, Mayer et al. 2020). They are also nocturnal and mostly active between dusk and dawn (Sharpe and Rosell 2003, Swinnen et al. 2015), while maintaining a 24 hour activity cycle that may expand to 26-28 hour cycles during winter (Potvin and Bovet 1975). Beavers usually emerge from their lodges between 18:00-20:00 and remain active until 04:30-06:00 in the morning (Sharpe and Rosell 2003). They mostly reside within their lodge or burrow during daytime, where sleeping and eating are dominating activities (Mott et al. 2011). Their nocturnal lifestyle is surprising as it requires increased energy use, combined with their poor eyesight, food sources being equally available during daytime, this circadian rhythm is most likely an adaption to avoid human persecutors (Swinnen et al. 2015).

Beavers are often studied as family groups, but differences related to age, reproductive status and sex have also been identified. The territory of male and female beavers have been found to overlap with 81%, they moved similar distances during a night, but males patrolled a slightly larger area and tended to spend more time at the territory borders, while having slightly longer activity periods (Sharpe and Rosell 2003, Herr and Rosell 2004, Rosell and Thomsen 2006). When moving outside the lodge, the pair tends to move independent of each other, which may increase the efficiency of territory defense (McClanahan et al. 2020). All beavers contribute to patrol and scent mark their territory after 5 months (Wilsson 1971, Herr and Rosell 2004). Still, the reproductive pair, and especially the male, contributes the most to scent marking (Rosell and Thomsen 2006, Hohwieler et al. 2018). Scent marking peaks in April and May when most young beavers disperse (Rosell and Nolet 1997, Rosell et al. 1998). Female beavers give birth within the lodge sometime in May-June (Wilsson 1971, Mayer et al. 2017b) whereupon the reproductive female spends most of her time in the lodge during lactation (Żurowski et al. 1974). Young beavers tend to be active for longer periods per day, while older beavers spend more time on land during senescence (Graf et al. 2016b, Cabré et al. 2020). Pregnant female beavers are disproportionally killed during spring hunting in Norway (Parker et al. 2002), but the cause of them being more exposed to hunters have not yet been identified (Mayer et al. 2017b). Studying sex-specific differences in beaver habitat selection may contribute to answer this question and inform wider research topics such as the occurrence of behavioral differences in monogamous and monomorphic mammals and individual differences within group-living species.

2.4 Beaver habitat selection

Beaver habitat selection has received substantial research attention especially following recent beaver reintroductions and recovery efforts (Fustec et al. 2001, Scrafford et al. 2018). Several studies have focused on second-order habitat selection exploring where beavers place their territories in relation to large scale landscape features (Curtis and Jensen 2004, Francis et al. 2017) or third-order selection based on visible signs of beaver use within the territory such as foraging on trees, construction of lodges or dams (Pinto et al. 2009, John et al. 2010, Scrafford et al. 2018). Several studies have shown that beavers reside close to waterways with a low stream gradient, increased sinuosity, and with riverbanks consisting of silt-soil banks (Curtis and Jensen 2004, Pinto et al. 2009, Scrafford et al. 2018). Within territories they prefer open water, wetlands and terrestrial habitats close to water (Steyaert et al. 2015, Wang et al. 2019, Barela et al. 2021). In terms of vegetation, they select for woody areas dominated by shrubs and deciduous trees such as willows (*Salix*) (Fustec et al. 2001, Pinto et al. 2009, Gerwing et al. 2013). A special challenge with beaver habitat selection studies is distinguishing between vegetation types and landscape features that beavers select for, and those that are the result of beaver habitat engineering (Hood and Bayley 2008, Barela et al. 2020). Increased dominance of deciduous trees and shrubs may be the result of beaver foraging, creation of gaps in the forest and regrowth from foraged stumps (Jones et al. 2009, Nummi and Kuuluvainen 2013). Beavers are considered a forest species that either avoids or display no selection patterns in relation to open areas such as agriculture (Curtis and Jensen 2004, Steyaert et al. 2015, Wang et al. 2019), but individual differences, seasonal or circadian habitat selection have not been investigated in beavers to the best of our knowledge.

Only a small selection of studies has investigated beaver habitat selection using spatial locations obtained either from VHF transmitters or GPS loggers but these have not investigated temporal trends (Steyaert et al. 2015, Francis et al. 2017, Wang et al. 2019, Barela et al. 2020). Sex-specific differences in beaver habitat selection has not been identified (Steyaert et al. 2015), but such differences have not been investigated within different time periods to the best of our knowledge. The size of beaver territories have been found to differ between seasons (Korbelová et al. 2016) and core areas may shift (McClintic et al. 2014a), but this trend tend to disappear once beavers get more established and beaver densities increase (Nolet and Rosell 1994). To the best of our knowledge, no previous studies have explored seasonal or diurnal changes in third-order beaver habitat selection, despite foraging studies indicating that diets vary considerably across seasons (Svendsen 1980, Milligan and Humphries 2010, Vorel et al. 2015). Insight into both beaver foraging behavior and habitat selection requires detailed knowledge of how beavers move in the landscape. This may be revealed by tagging beavers using bio-loggers, but this also involves inherent risks that must always be considered when applying such methods.

2.5 Tagging of beavers

The body shape of beavers with thick necks and small heads have made them challenging to tag with conventional methods such as collars (Rothmeyer et al. 2002). Attachment of radio transmitters on the tail (Korbelová et al. 2016, Smith et al. 2016, Barela et al. 2020) or surgically implanted transmitters (Nolet and Rosell 1994, McKinstry and Anderson 2003, Ranheim et al. 2004) are the most common attachment procedures on beavers. However, these methods are invasive and requires full anesthesia in the case of implants with inherent risks (Ranheim et al. 2004). Tail mounts require local anesthesia while drilling of a hole through the beaver tail, which may cause permanent damage and potential weight loss during winter (Smith et al. 2016). Still, equipping beavers with these radio transmitters has facilitated spatial tracking of beavers (Francis et al. 2017, Barela et al. 2020), and behavioral observations by allowing the beaver to be tracked and observed during nighttime (Nolet and Rosell 1994, Sharpe and Rosell 2003). Tracking beavers using radio transmitters is however time consuming and entail a risk of disturbing their behavior.

The Norwegian Beaver Project (NBP) has developed a new method to attach bio-loggers by gluing the tag onto the fur at the lower back of the beaver that allows for the attachment of several devices, including VHF to facilitate radio tracking in the field, GPS to log spatial locations, and Daily Diary to log movement in a three dimensional space, which can later be translated into behaviors (Graf et al. 2015). These bio-loggers have provided extensive data on beaver behavior with topics ranging from territory use and behavior (Graf et al. 2016b, Mayer et al. 2017c, Mayer et al. 2020), movement patterns of the reproductive pair (McClanahan et al. 2020), habitat selection (Steyaert et al. 2015), diving behavior (Graf et al. 2018, Mortensen et al. 2021) and activity periods and movement (Cabré et al. 2020). Several studies have assessed this method and found only short-term changes in activity patterns the day following tagging (Graf et al. 2016a), but no long-term effects of being tagged at least once on body condition, reproduction or survival (Mortensen and Rosell 2020). However, the impact of tagging on beaver body condition during the tagging period has not yet been investigated, nor individual variability in potential impacts or in comparison with a control group. Assessing such impacts should always be given careful consideration, but at the same time bio-logging offers a valuable tool to gain insight into the behavior of this cryptic species.

3 Objectives

The goal of this thesis was to explore spatio-temporal foraging and habitat selection of Eurasian beavers, while also assessing potential negative impacts of attaching bio-logging tags. We investigated potential drivers of individual differences such as age, sex, socio-reproductive status, reproductive effort, beaver density, and body condition, to better understand the mechanisms that drives foraging and habitat selection (Fig. 1).

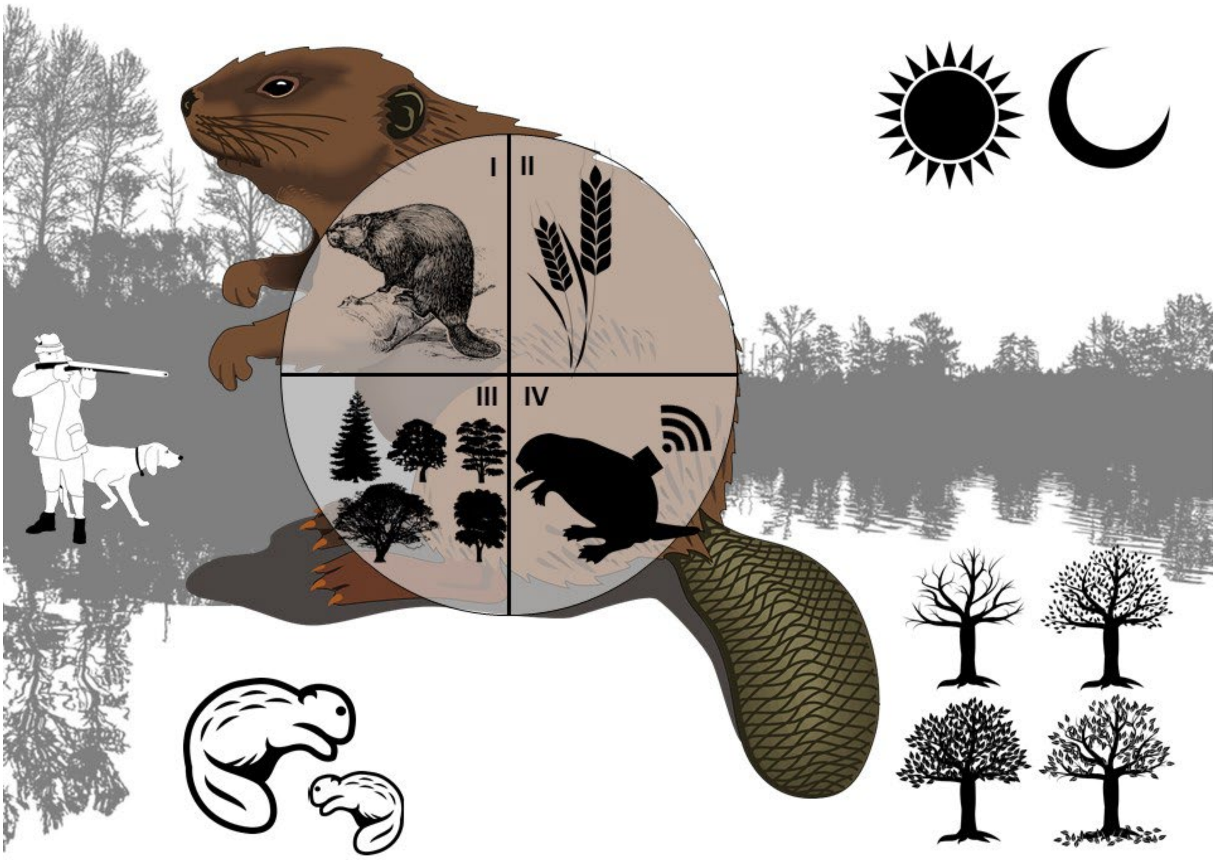

Figure 1: Graphical summary of the content of the four research articles included in this thesis. Article I deal with beaver activity budgets and foraging activity, article II with foraging on cereal fields, article III with beaver habitat selection and article IV with the effects of bio-logging. Habitat, seasonality, circadian patterns, human disturbances, and individual variability are symbolized as common topics across these articles.

3.1 Foraging behavior, diet, and crop depredation (Article I and II)

The first article explored temporal activity patterns of beavers and how they balance foraging against other activities across the seasons and the night. We also investigated sex-specific seasonal use of different food items. We hypothesized that due to the cost of reproduction, females should forage more, travel less, and spend more time in the lodge during the reproductive period and during the night. We also expected females to travel and forage more in summer and forage on nutritious plants such as aquatic vegetation and herbs. In the second article, we focused in on beaver foraging on a novel food source, cereals. We investigated the extent of foraging, spatio-temporal foraging patterns as well as drivers behind beaver use of crop fields. We hypothesized that beavers would forage close to the water with less buffer vegetation, as well as in areas with lower elevational gain from the river and lower slopes and on mature wheat and barley. We hypothesized more extensive foraging within territories with higher coverage of agriculture and individual use of crop fields might differ in relation to age, sex, reproductive status, and body condition.

3.2 Individual and temporal habitat selection (Article III)

In the third article, we explored individual variability and spatio-temporal habitat selection of beavers. The focus was set on terrestrial environments and wetlands as habitat selection has already been investigated in aquatic environments within the study area (Mortensen et al. 2021). We hypothesized that we would find individual differences driven by reproductive effort, age, body condition and beaver density. We also hypothesized distinct temporal trends related to seasonal food availability and human disturbances, and that these might differ according to socio-reproductive status.

3.3 Assessing impacts of tagging (Article IV)

In the fourth article, we investigated potential negative effects of tagging beavers with bio-loggers and compared weight gain in tagged and untagged beavers as a control group. We hypothesized that the glue-on tags used in the NBP would reduce body weight gain in beavers compared to untagged beavers. We predicted that these negative effects would increase during the colder months of the year when beavers spend more energy on thermoregulation and have lower food access. We also hypothesized that beavers would gain less weight with increasing tag weight and duration of tagging and accounted for potential impacts of sex and age.

4 Material and methods

4.1 Study area

The study area of the NBP encompasses three rivers: Gvarv, Sauar and Staumen, located in Midt-Telemark and Nome municipalities in Telemark, southeastern Norway (Fig. 2). These rivers all converge into lake Norsjø, and the sections incorporated in the study area includes 32 km of river, with widths varying between 30 to 150 m. Due to the size of the rivers and the amount of water running through, beavers cannot construct dams in the main rivers, and large stretches of the rivers are usually ice-free during winter (Herr and Rosell 2004). The landscape surrounding the rivers are a patchwork of agricultural land and forested areas with a few smaller villages, roads, and railways. Cereals are the most common crop and was grown on 60% of all fields in 2019-2020 (Landbruksdirektoratet 2021a). Wheat and oats dominate the production followed by barley and rye (Landbruksdirektoratet 2021b). The forested areas surrounding the rivers are dominated by Norway spruce (*Picea abies*), grey alder (*Alnus incana*), Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*), downy birch (*Betula pubescens*), bird cherry (*Prunus padus*), and rowan (*Sorbus aucuparia*) (Haarberg and Rosell 2006). Mean daily temperature is 6.5 °C with a mean precipitation of 2.3 mm (eKlima 2020). Human activity on the rivers is highest during summer when boat traffic increase for recreational purposes (Flemsæter et al. 2020).

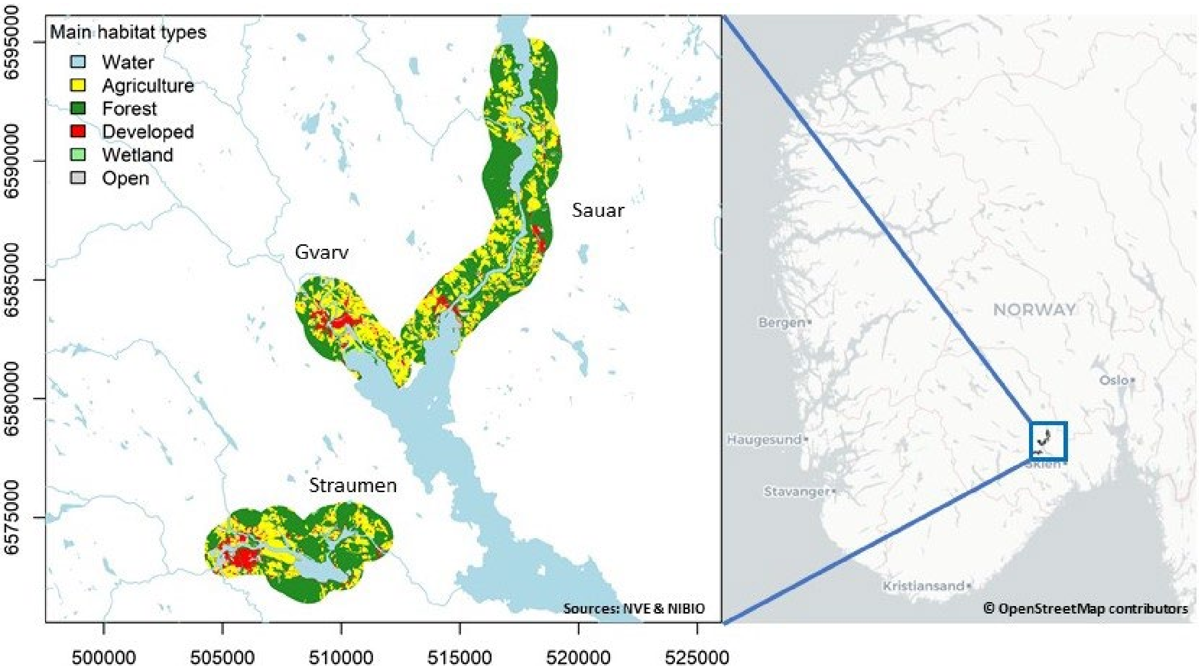

Figure 2: Study area of the Norwegian Beaver Project including the three rivers Straumen, Gvarv and Sauar in Midt-Telemark and Nome municipalities in southeastern Norway.

4.2 Study animals and population

Eurasian beavers have been present in the rivers for approximately 100 years and are believed to be at carrying capacity (Campbell et al. 2012b, Mayer et al. 2020). Monitoring of the resident beaver population has been ongoing as part of the NBP since 1997. From yearly live-captures and observations, all territory owners or reproductive pairs have been identified (Mayer et al. 2017a), as well as any beavers still residing within their parents territories (Mayer et al. 2017d). Beaver kits have been registered after they emerge from the lodge. Genetic testing using hair samples was used to determine parentage of some beavers (Nimje et al. 2021). Average reproductive effort of tagged beavers was estimated by summing all the kits born by that beaver and dividing it with the number of years that beaver was monitored. We found that average yearly reproduction of beavers older than 3 years was 0.52 kits per year. Over the course of the study, around 30 beaver families have been monitored continuously (Mayer et al. 2017a), with some variations as certain territories have dissolved into separate territories and sometimes merged back together in later years. Family sizes within the study area ranges from 2 to 12 beavers with an average of 3.97 ± 1.88 members (Mayer et al. 2020). The beaver density is 1.23 ± 0.32 beavers per km of shoreline, and each beaver territory ranges from 3.5 ±1.59 km and 3.28 ± 1.45 km of river length, as identified in different studies (Graf et al. 2016b, Mayer et al. 2020). The high beaver density is the main limitation for dispersal of young beavers that may remain within their parents territories up to seven years old (Mayer et al. 2017d). There is a low risk of predation for beavers within the study area, as most large carnivores that pose a threat to beavers have been exterminated, but there is a low but stable population of lynx (*Lynx lynx*) (Rovdata 2021). Beaver hunting takes place from 1 October until 30 April (Miljødirektoratet 2022). During 2009-2014, hunters did not harvest more than 5% of the population (Graf et al. 2016b), while 12% of the population were harvested between 1998-2017 (Mayer 2017). However, hunting has not been closely monitored after a change in beaver hunting policy in 2017, when municipalities were no longer required to set quotas giving landowners more opportunity to regulate hunting on their own property (Lovdata 2017). Beavers in the study area tend to focus their foraging on woody vegetation on grey alder, rowan, willow, birch, the prunus family and few conifers (Haarberg and Rosell 2006). The resident beaver population select for habitats in narrow stretches of the river, shallow areas close to the bank, gentle bank slopes and areas with deciduous forest cover (Pinto et al. 2009).

4.3 Beaver captures and monitoring

All the articles included in this thesis depends on live-capturing beavers to tag them with bio-loggers or radio transmitters. A special live-capture method has been developed by the NBP and remained unchanged throughout the study period (Rosell and Hovde 2001). Beavers were captured during hours of darkness using a small motorboat with an outward engine and spotlights to locate beavers along the riverbanks. Captures took place during the ice-free season from March to November. Spotted beavers were tracked to a shallow area and captured using a net either in the water or on land (Rosell and Hovde 2001). Captured beavers were transferred to a cloth sack where they could be handled without the use on anesthesia. Body length and tail measurements were taken and used to calculate tail fat index as an indication of body condition (Rosell et al. 2010, Parker et al. 2017). Each beaver was weighed and aged based on weight during the first capture (Rosell et al. 2010). One additional year was added every year since the initial capture. During most tagging events, we weighed beavers both during tag attachment and after tag removal, which was used to estimate daily percentage weight change used in article IV. Captured beavers were sexed during the first capture by extracting anal gland secretion from the cloaca and determining the color and viscosity. Female secretion is characterized as a thick grey paste, while male is fluid and straw colored (Rosell and Sun 1999). Each beaver was inserted with a passive integrated responder (PIT) used to identify individuals with a scanner during captures and sometimes using a reader installed by the lodge entrance to identify which beavers used the lodge (Briggs et al. 2021). Each beaver was also fitted with a plastic or metal ear tag to facilitate visual identification (Sharpe and Rosell 2003).

4.4 VHF and GPS tagging

Beavers were tagged with two types of telemetry. In article I, we used an older dataset with radio tracking of beavers during 2000, 2001, 2006 and 2007 including 41 beavers from 20 territories. The radio transmitters were either attached to the beaver tail or implanted surgically (Sharpe and Rosell 2003, Ranheim et al. 2004). Tagged beavers were monitored in the field in the immediate days following attachment, and while one beaver died post-operatively, the others were observed moving around normally within their territories following tag attachment (Sharpe and Rosell 2003, Ranheim et al. 2004). One week prior to attachment, two observers started tracking beavers from the same territory on successive nights (on average 7 ± 2.89 SD nights per beaver) from the time they emerged from their lodge in the evening until their returned in the morning while recording their behavior, social interactions and foraging items and recording spatial locations every 15 min (Sharpe and Rosell 2003). In total, we used 5430 15-min observations of beaver behavior and 3312 continuous observations of foraging events to investigate temporal activity patterns and foraging. Direct observations of animals can be used to study behaviors such as foraging, especially when the animals are habituated to human observers (Pelletier and Festa-Bianchet

2004, Masi et al. 2009), or are observed at sufficient distance to limit disruption (White et al. 1998, Ruckstuhl and Neuhaus 2009). According to Sharpe and Rosell (2003) the disturbance to the beavers appeared to be minimal, supported by previous studies that have used similar observation methodology (Nolet and Rosell 1994, Buech 1995).

In the third article, GPS loggers were attached to 74 beavers during 104 tagging events (tagging event = one beaver tagged in a particular year) for periods of 2-22 days during the months March to November in 2009 to 2021. The GPS recorded a spatial location every 15 min from 19:00 until 07:00/08:00 in the morning, but did not track beavers during daytime, which is outside the main activity periods (Sharpe and Rosell 2003), and locations could not be fixed from within beaver lodges or burrows (Justicia et al. 2018). GPS loggers were combined with a VHF and Daily Diary. Data from the Daily Diaries was not used in the research articles included in this thesis. The tag was glued onto the fur of the beaver on the lower back, approximately 15 cm above the tail, using two-component epoxy (Graf et al. 2016a). The position was chosen both to minimize drag and ensure that the tag would stay above water during swimming at the surface and thereby able to connect with the satellites. The tag either fell off by itself after 2-3 weeks and subsequently collected from the water, on land or the beaver lodge, or the beaver was recaptured, and the tag removed from the outer fur using a scalpel. Some of the GPS loggers used for article III were tested for performance on beavers and had a locational error of 15.7 ± 21.9 m and a fix rate of 86%, which is only 8% lower than the fix rate of stationary GPS units (Justicia et al. 2018). We removed all 2-D locations and those with a HDOP >5 from the dataset to increase accuracy (Justicia et al. 2018). As the focus in both article II and III was beaver movement and habitat selection in terrestrial environments, we removed all GPS fixes in the water. Misclassifications of GPS locations in water or on land probably occurs, but this error should be unbiased (Cabré et al. 2020). Beavers may change their behavior during the trapping night by spending more time in the lodge (Graf et al. 2016a), and we therefore removed GPS data collected during capturing nights.

4.5 Ethical statement and animal welfare

Beaver capture and handling was approved by Norwegian Experimental Animal Board (FOTS id 742, id 2170, 2579, 4384, 6282, 8687, 15947, 19557) and the Norwegian Directorate for Nature Management (2008/14367 ART-VI-ID, archive code 444.5, 446.15/3, 14415). All studies also complied with the ASAB/ABS guidelines for treatment of animals in behavioral research (ASAB/ABS 2020) and was carried out according to the ARRIVE guidelines (Percie du Sert et al. 2020). We did not record any significant injuries to beavers caused by our research methods, but one beaver died post-operatively during implanting of a VHF transmitter in 2001. Three tagged beavers died of natural causes or were shot by hunters during this study in 2000-2001, but these deaths were not related to tagging. One female beaver tagged with GPS was found dead in a lodge entrance in 2018 and sent to the Norwegian Veterinary Institute for a necropsy, but the cause of death and whether it was related to tagging could not be determined. Potential long-term effects of capture, handling and tagging of beavers in the project has been investigated by Mortensen and Rosell (2020) who found that the number of capture and handling events negatively affected reproduction during the first years of the project, but this effect subsided in more recent years, possibly due to habituation. Being tagged at least once in a beavers' lifetime did not impact body condition, survival and reproduction (Mortensen and Rosell 2020). However, impacts on body weight have not been investigated during the tagging period, nor has individual impacts been assessed.

4.6 Territory estimates

The estimates of territory size and placement used in article I, II and III were established based on tracking beavers in the field using VHF transmitters, observations of scent marking locations at the territory borders and GPS data. In article I, we identified the main lodge for each beaver-year using spatial locations from when the beaver was observed either in a lodge or burrow and estimated the most intensely used 10% kernel using the adehabitatHR package (Calenge 2006). In article III, we experimented with different territory estimation methods and found that they often exaggerated the size of the beaver territories by including inland areas especially where rivers meander (John et al. 2010, Mayer et al. 2017c). The definition of habitat available within the territory is important for accurate results in habitat selection studies (Northrup et al. 2021, Street et al. 2021). Beavers usually stays within 60-77 m from water but may move further to obtain especially attractive food sources (Donkor and Fryxell 1999, Steyaert et al. 2015). We decided to include areas within 100 m from the river as potentially "available" habitats in article III and searched this zone for beaver foraging in cereal fields in article II. To analyze beaver habitat selection in article III, we also buffered the 95% MCP with 100 m to include areas next to the rivers where beavers swim past while removing areas more than 100 m away from water. In article II that investigated seasonal foraging on cereals, we used a combination of GPS data and scent marking observations to determine the territory extents as we did not have GPS data from all surveyed territories during the relevant study years.

4.7 Field registrations

In article II, we documented beaver foraging on cereals fields during late summer and early autumn 2019 and 2020. We surveyed all cereal fields within 100 m of the river within 17 beaver territories throughout the field season, with an average 11 days between each survey. We also surveyed control plots not foraged by beavers spaced 50 m apart along the edges of the fields to represent available but non-foraged locations. The size of each foraged patch was estimated and in both foraged and control locations, we registered distance to the closest water, percentage cover of trees, shrubs and grass/field layer between the river and the field. In every location we also recorded the species of cereal and the maturity of the cereal plants. Beaver foraging was distinguished based on the presence of a trail going down to the river with cereal plants deposited along the trail and in the water.

4.8 Data preparation

This thesis utilized three main datasets; the first article is based on an old dataset containing behavioral observations of VHF tagged beavers, while article II use both field surveys in cereal fields and GPS data collected between 2010-2021. Article III uses only the GPS dataset, while article IV investigates weight change in some of these GPS tagged beavers during the tagging period. In article I, we grouped beaver activity observations into the same categories as Sharpe and Rosell (2003), and decided to focus on foraging and the other two most common activities, travelling and being in the lodge. Foraging items were classified into three groups: trees/shrubs, aquatic vegetation, and herbs/grass.

GPS locational data was used both in in article II, where we investigated the proportion of GPS fixes that overlapped with crop fields and in article III that investigated spatio-temporal and individual patterns of beaver habitat selection. For both articles we focused on terrestrial GPS locations. In article III, we contrasted GPS locations (used) with random locations (available) within each beaver territory using resource selection functions (Johnson 1980). We created available points randomly within each beavers' yearly territory in a ratio 5:1 in relation to the GPS locations. Habitat data was extracted from various land cover maps both for article II (foraged and control plots and GPS fixes) and article III (GPS and available locations). From a land cover map of Norway (Kartverket 2016), we extracted habitat types both as categorical variables (article II and article III) and continuous proportions within a 15 m buffer around each location (article III). We calculated the Euclidean distance from each location to water (article II and III) and human developed areas (settlements, roads, and railways) (article III). For both article II and III, we obtained elevation data from a digital elevation model (Kartverket 2019), and calculated elevational gain between each location and the closest water. Slope was estimated for each locations using the "terrain" function in the R package raster (Hijmans 2020). For article IV, we obtained estimates of water temperature in the study area from the Norwegian Water Resources and Energy Directorate (NVE).

All the articles deal with temporal trends in some form, and in article I, II and III, we converted date and hour of the night into continuous estimates. Exploring temporal trends by comparing pre-defined time periods may simplify trends and dealing with time as a continuous variable is therefore recommended (Richter et al. 2020). We converted date to Julian day, which we defined as the number of days since 1 January every year. Hour of the night was converted to active hour, which we defined the first hour where most beavers emerge from the lodge (19:00) as active hour 1 and the last active hour at 8:00 when most beavers have already returned to the lodge. When referring to seasons in the discussions, we defined March-May as spring, June-August as summer and September-November as autumn.

4.9 Statistical analysis

For each analysis, we followed similar data exploration procedures using the steps suggested by Zuur et al. (2010). Collinearity between the explanatory variables were investigated using both Pearson correlation test with a cut-off value of 0.7, and variance inflation factors (VIF) with a cutoff value of 10 (Zuur et al. 2010, Harrison et al. 2018). In article I and article III, we investigated temporal trends over longer time periods, which we did not expect to appear as linear effect, and therefore used generalized additive mixed effects models (GAMM). In article I, we used frequentist methods (Wood 2017), while we applied a Bayesian analysis in article III (Zuur et al. 2017). In article II, where we modelled temporal foraging over a relatively short time period while cereals matured, and we therefore treated Julian day as a linear effect using generalized mixed effects models (GLMM) (Zuur et al. 2009), and in article IV where we only had two body weight measurements from each beaver, we used daily percent body weight change as the response using linear mixed models (LMM).

In article I, we investigated seasonal and diurnal activity patterns in beavers and seasonal use of food items. Whether each activity or food item was observed or not was used as the response with a Bernoulli distribution. We included Julian day and active hour as a smoothers interacting with sex to investigate whether males and females displayed different seasonal and diurnal trends. However, we did not investigate circadian trends for food items as we did not hypothesize this as important. We accounted for potential effects of distance to the main lodge interacting with sex (only for the activity analysis) and age, while accounting for year and beaver ID as random intercepts. In article II, we modelled the probability that a location in the cereal fields was foraged by beavers (1=foraged and 0=control plot) using a Bernoulli distribution. Julian day, cereal species, width of the buffer zone covered by trees, bush or grass, slope, elevational gain, and distance to closest river were included as explanatory variables. We also modelled the extent of foraging in each foraged patch using the same explanatory variables but with a gamma distribution. We included plot ID and field

ID as random intercepts in both analyses. Finally, we summarized the extent of foraging on cereals in each territory across the two years and used GLM and a negative binomial distribution to investigate whether territory size or habitat cover within the territories impacted foraging. We also used the proportion of GPS fixes within crop fields in each beaver-year and modelled this in relation to sex, age, female reproduction the current or following year, weight, body condition and year using linear regression.

In article III, we investigated third-order habitat selection using a Bayesian framework and integrated nested Laplace approximations (INLA) (Rue et al. 2009). Bayesian modelling of species occurrence is increasingly being used and INLA is computationally more effective than methods relying on Markov Chain Monte Carlo simulations (Beguin et al. 2012, Sadykova et al. 2017, Lezama-Ochoa et al. 2020). INLA can also account for spatial autocorrelation between locations through stochastic partial differential equations (INLA-SPDE) where locations closer in space are assumed more similar than those located further apart (Beguin et al. 2012, Lezama-Ochoa et al. 2020). We used resource selection functions (RSF) and contrasted GPS with available locations using GLMM and a Bernoulli distribution. RSF and GLM models are the most common methods to study habitat selection and offers a very flexible framework (Gaillard et al. 2010, McLoughlin et al. 2010, McGarigal et al. 2016). Random effects of beaver ID and year were included to account for unbalanced sampling between individuals and autocorrelation between the same individual and year (McLoughlin et al. 2010). We divided the RSF analysis in two parts; first we investigated population-level and individual variation in habitat selection, while in part two, we investigated temporal trends specific to each socio-reproductive group. For the first part, we included both random intercepts and slopes to obtain individual selection estimates (Northrup et al. 2021). We used these as the response in a additional set of models using GLM and a Gaussian distribution with beaver family ID as a random intercept. Average yearly reproduction, age, tail fat index as a measure of body condition and family size as a measure of density were included as potential explanatory variables. For the second part, we again used RSF models, but this time applied GAMM models with interactions between habitat types and both Julian day and active hour, to investigate temporal trends in habitat selection. We compared four types of spatio-temporal models to account for the spatial autocorrelation and conducted the analysis separately for each socio-reproductive beaver group. We distinguished between reproductively active females, reproductively active males, and non-reproductive beavers.

In article IV, we investigated body weight change during the tagging period and compared tagged beavers with an untagged control group. The first analysis contrasted these two groups using daily percent weight change as the response in relation to tagging status (tagged or untagged) as well as age, season, and sex. We then focused in on the tagged individuals and used total percent weight change as the response in relation to season, weight of the tag, water temperature, sex, age, and tagging duration. Beaver ID and year was accounted for as random intercepts in all models.

We followed some common model selection procedures in each analysis. In article I, II and IV we constructed candidate models including a null model and compared these using AICc model selection (Anderson and Burnham 2004), and the model.sel function from the MuMIn package (Barton 2020). For each candidate model set we selected the top models within a ΔAICc <2. In cases with several top models, we selected the most parsimonious (simplest) among these to avoid including variables with limited statistical importance (Arnold 2010). Variables included in the final model where 95% confidence intervals overlapped with zero were considered uninformative. In article III, we used a different model selection procedure as these models were very computationally demanding, making in unpractical to run a long list of candidate models. We instead fitted a full model and compared this with a null model using deviance information criterion (DIC) (Zuur et al. 2017) to observe whether the explanatory variables explained any of the variation in the data. If the full model was most supported, we progressed using a backward selection procedure by variables with credible intervals overlapping with zero until all parameters were considered informative.

5 Results and discussion

5.1 Temporal foraging patterns (article I and II)

Foraging was the most common beaver activity outside the lodge and accounted for 30% of the tracking observations in article I. However, beavers spent the largest part of the night in the lodge (34%) and spent considerable time travelling (28%). Other studies have observed similar activity patterns, but even more time dedicated to foraging (Buech 1995, Gallant et al. 2016). In line with other studies, we found that once foraging, most beavers were mostly alone and only accompanied by another beaver in 6% of observations, which is similar to what has been found in previous studies (McClanahan et al. 2020). Surprisingly, we found no clear seasonal trend in foraging nor any sex-specific trends (Fig. 3). We expected especially females to forage more in response to reproduction. Monomorphic female meerkats (*Suricata suricatta*) for example foraged at a higher intensity than males when they were reproductively active (Doolan and Macdonald 1996). Female raccoon dogs (*Nyctereutes procyonoides*) that usually do not display differences in foraging behavior between the sexes shifted to increased female foraging during reproductive period probably due to increased energetic needs (Zoller and Drygala 2013). However, in other monomorphic species such as lemurs (*Lepilemur ruficaudatus*) no differences in foraging behavior, travel nor nutritious content in foraging items were identified even in the reproductive season (Ganzhorn et al. 2004). Our findings are in line with beavers being income breeders that rely on previously accumulated fat reserves instead of compensating with increased foraging in spring and summer (Rödel et al. 2015, Parker et al. 2017), but an investigation of sex-specific foraging patterns during fall could have revealed larger differences between the sexes.

We did, however, identify some sex-specific activity patterns such as females spending more time in the lodge during spring (Fig. 3), which could be expected if she has dependent kits (Wilsson 1971), while males travelled more in late spring and summer, which could be a response to an increase in dispersing beavers (Rosell et al. 1998). Following reproduction beavers tend to spend more time closer to the lodge in May-June to protect their kits

(McClintic et al. 2014b), but this responsibility may fall more on the females especially in spring (Buech 1995). The beavers also displayed clear circadian patterns in all three activities, but there were no sex-specific differences (Fig. 3). Foraging peaked in the middle of the night, being in the lodge was most common in the beginning and end of the beavers' activity period and travelling occurred throughout the night, but slightly less in the evening and more in the morning (Fig. 3). Foraging also increased further away from the lodge and with increasing age of the beaver.

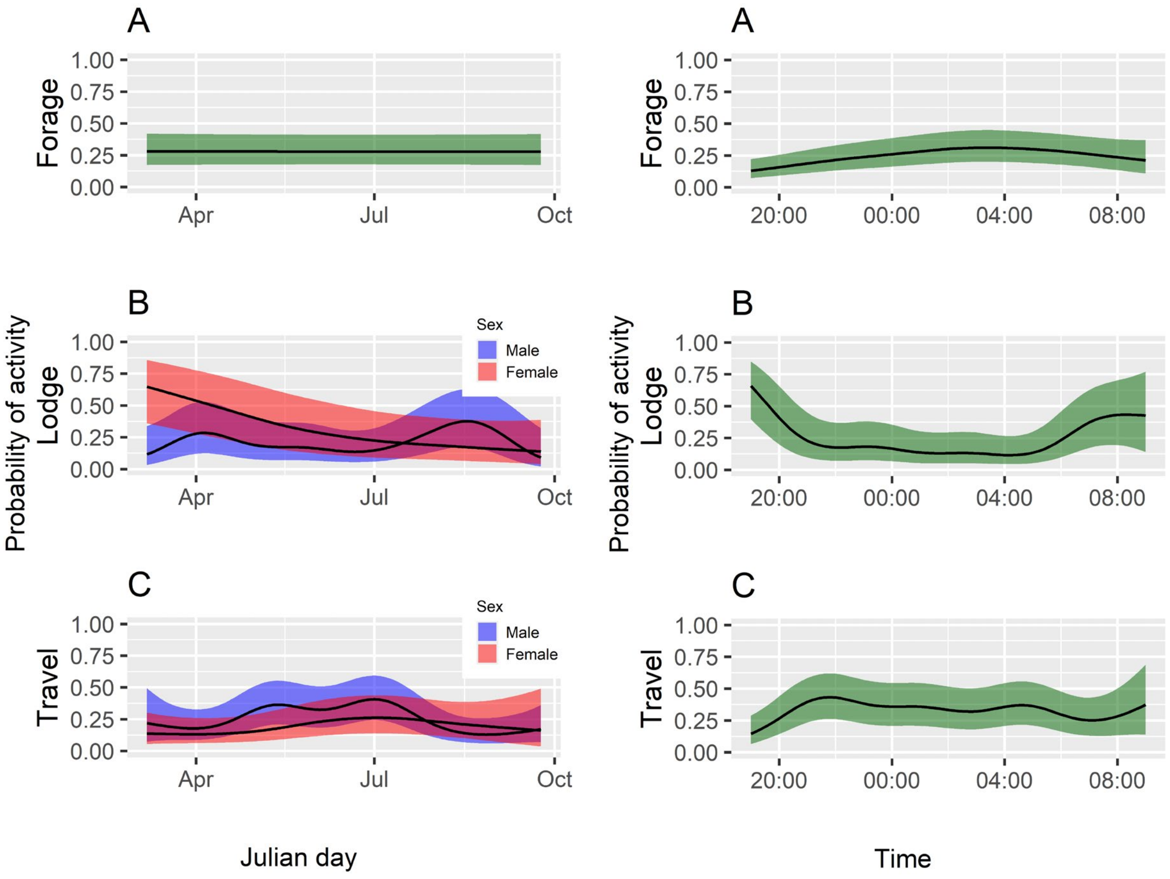

Figure 3: Predicted effect of Julian day and hour of the night on the probability of Eurasian beaver (*Castor fiber*) activities including foraging (A), being in a lodge (B) and travelling (C). The left panel show the smoother for Julian day and the right panel presents the estimated smoother for hour of the night. Red signifies females and the blue males, while the green represents both groups in cases where there were no differences between the sexes. The

model predictions are based on beaver activity observations from spring to late summer during the years 2000, 2001, 2006 and 2007 in southeastern Norway.

We also investigated seasonal shifts in foraging patterns and use of food items in article I. The most common food items were trees and shrubs that made out 73% of foraging items, followed by aquatic vegetation (16%) and herbs/grasses (11%). These proportions are not too dissimilar to a Canadian study showing that beavers spent 18% of their time foraging, in which 48% was spent foraging on trees, 33% on shrubs, 15% on herbs and 7% on aquatic vegetation (Gallant et al. 2016). Not surprisingly deciduous trees were most dominant food item in the beaver diet, but beavers also occasionally foraged on coniferous species in spring. We expected females to forage more on nutritious food sources such as aquatic vegetation and grasses and herbs during spring. This was partly confirmed, as female aquatic foraging peaked in both spring and autumn with a subsequent decline in foraging on trees/shrubs, but there were no sex-specific differences in foraging on herbs/grasses (Fig. 4). Sex-specific foraging on aquatic vegetation and trees/shrubs maybe a result of female selecting for food items with a higher nutritional content (Nolet et al. 1995), but could also represent a risk aversive foraging tactic to reduce predation risk on land where beavers are more vulnerable (Gable et al. 2016). Aquatic vegetation also has high levels of certain nutrients such as nitrogen, phosphorus and sodium that may be useful for female beavers during reproduction as shown for several other species (Blair-West et al. 1968, Cebrian and Lartigue 2004).

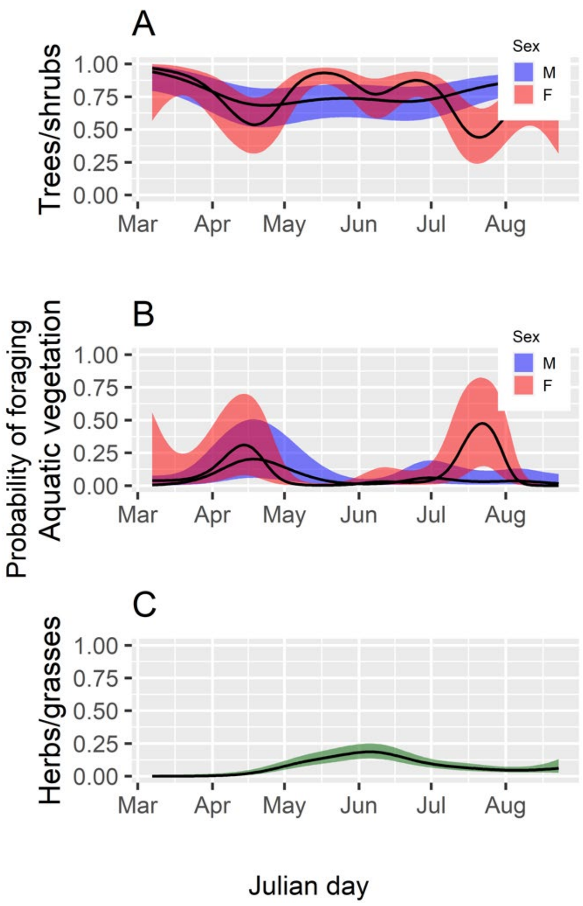

Figure 4: Predicted effects of the probability of Eurasian beaver (*Castor fiber*) use of trees/shrubs (A), aquatic vegetation (B) and herbs/grasses (C) across the study season (5 March–23 September). Red signifies females and the blue males, while the green represents both groups in cases where there were no differences between the sexes. The predictions are based on beaver activity observations from spring to late summer during the years 2000, 2001, 2006 and 2007 in southeastern Norway.

In article II, we focused on another seasonally abundant food source that beavers utilize within our study area, cereals. This food source was included in the herb/grass category explored in article I. However, use of herb/grass was found to peak during June in article I (Fig. 4), which is prior to when cereals in the study area is mature. Very few of the behavioral observations from article I mentioned cereals, possibly suggesting that use of this food item has increased in recent years. While a study from North America found less beaver activity within agricultural areas compared to protected areas (Nelner and Hood 2011), the Eurasian beaver have been found to settle closer to agriculture than North American beavers (Alakoski et al. 2019). We have observed beaver foraging in cereal fields in recent years, leading us to investigate their use of this novel food source. During our two-year survey, we found 172 patches foraged by beavers, composing an area of 3136 m2. By far, beavers preferred wheat that composed 72% of the foraged areas, followed by oat (19%), barley (8%) and rye (2%). Beavers displayed a preference for mature grains, even though barley was foraged to a larger extent when still immature (Fig. 5). Camera trap footage indicated that beavers cut cereal plants close to the ground and transported them down to the river where most of the feeding occurred. Species such as the Svalbard pink-footed geese (*Anser brachyrhynchus*) and Greenland white-fronted geese (*A. albifrons flavirostris*) have in recent years shifted foraging areas to agricultural crops, which have caused them to abandon natural foraging areas and enabled a large scale increase in reproductive output (Fox et al. 2005), which causes conflicts with local farmers in Norway (Simonsen et al. 2016). Beaver foraging on cereals do not occur on the same scale or cause such large scale conflicts and has therefore received less research attention, but cereals may still play an important role in providing beavers with important nutrients (Mikulka et al. 2020).

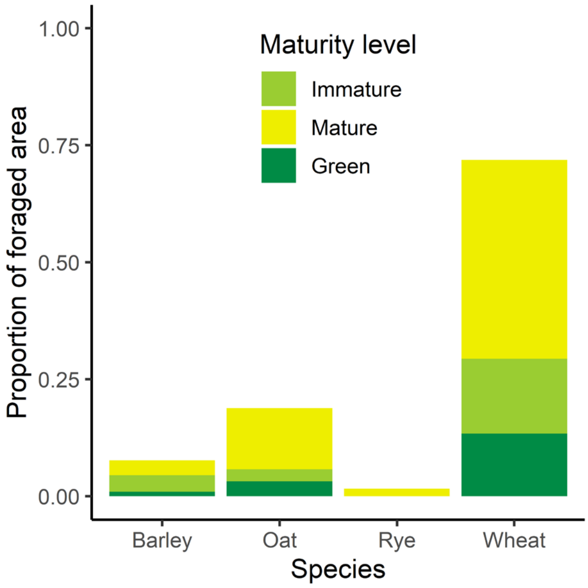

Figure 5: Proportion of barley (*Hordeum sativum*), oat (*Avena sativa*), rye (*Secale cereale*) and wheat (*Triticum aestivum*) foraged by Eurasian beavers (*Castor fiber*) in southeastern Norway 2019 and 2020. The proportion foraged of each maturity level is also shown.

As we expected there were some clear spatial patterns in beaver foraging on cereals and foraging occurred mostly in fields with lower elevational gain and with a smaller vegetated buffer zone between the field and the closest river (Fig. 6). These trends are in line with previous beaver habitat selection studies that concluded that beavers avoid steep climbs and areas far away from water (Pinto et al. 2009, Steyaert et al. 2015). The forest edge or protected areas may represent safety for other crop depredating species (Lemessa et al. 2013, Regmi et al. 2013), and water offers safety for beavers, clearly illustrated by how they transport this food source to the water for consumption. However, when foraging further from water, they surprisingly foraged larger areas, which may reflect their nature as central-place foragers that tend to select larger food items with increasing distance (Haarberg and Rosell 2006). Studies of other central place foragers have also indicated that load sized may increase when foraging further away from their central place (Orians and Pearson 1979, Jackson 2001). We also identified beaver foraging on crops further from water compared to what has been reported in previous studies (Campbell et al. 2012a, Mikulka et al. 2020).

Clear temporal trends were also identified with an increase in the probability of cereal foraging until the end of the season when crops were harvested by the farmers (Fig. 6). Wildlife crop depredation often increases during attractive phenological stages (Putman 1986, Roper et al. 1995, Chiyo et al. 2005). Cereals seemed to become most attractive when the plants changed color from green to yellow. Certain beaver families foraged more within their territories than others, but the drivers of these difference were not clear. There were indications that the extent of foraging increased with higher cover of agricultural fields, suggesting that differences might be related to availability. Some species such as European bison (*Bison bonasus*) are driven to forage on crops due to depleted food sources in winter (Hofman-Kamińska and Kowalczyk 2012). While we did not assess natural food availability for beavers, we found no indication that low availability of natural habitats influenced beaver foraging on cereals. Sex, age, or reproduction did not impact beaver use of crop fields. This is contrary to other crop depredating species that display large increases reproduction due to access to crops (Fox et al. 2005, Becker et al. 2015). We did, however, find that beavers in good body condition used crop fields more, which suggests they do gain some benefits (Fig. 7). There were also tendencies that heavier beavers using crop fields more and an increase in use over years, but this was not statistically important. We concluded that beaver foraging on cereals represent optimistic foraging behavior and while foraging still occurs in low levels, it might represent an increasingly important part of the foraging ecology of beavers within anthropogenic landscapes.

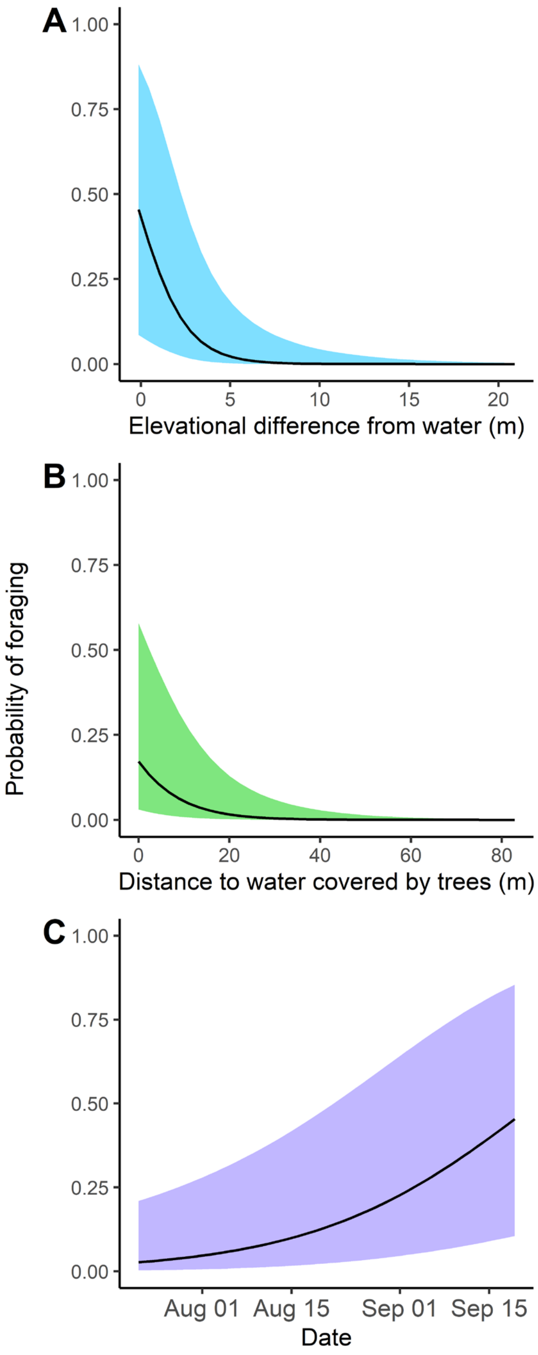

Figure 6: Probability of foraging on cereals within Eurasian beaver (*Castor fiber*) territories in southeastern Norway, 2019 and 2020. Predictions of foraging probability have been predicted in relation to elevational difference from water level in meters (A) and distance to river covered by trees (B) and days since 1 January (Julian day) converted here to date for visualization purposes (C). All predictions are based on a generalized linear mixed effect model

(GLMM) with a Bernoulli distribution contrasting foraged and control plots within cereal fields less than 100 m from water. Model estimates have been converted from the logit scales to probabilities, and the colored area represents the 95% confidence intervals.

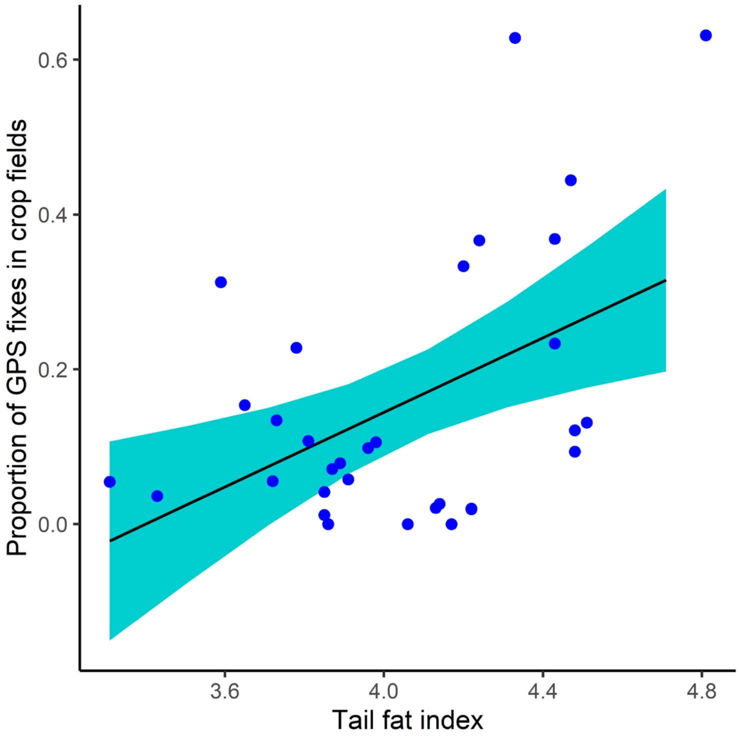

Figure 7: Predicted effect of tail fat index as a measure of body condition on the proportion of GPS fixes within crop fields in each tagging event (beaver-year) for Eurasian beavers (*Castor fiber*) in southeastern Norway, 2010-2021. All predictions are based on a linear regression model with a Gaussian distribution. and the colored area represents the 95% confidence intervals. The blue points represent proportion of GPS fixes within crop fields for each beaver-year.

5.2 Spatio-temporal habitat selection

In article III, we explored habitat selection of beavers and investigated individual variation, seasonal and circadian trends. Habitat selection implies that a resource or a habitat is used disproportionally to its availability, and is calculated based on the relationship between use and availability within a landscape (Gaillard et al. 2010). Underlying habitat selection studies is the theory of ideal free distribution stating that animals select habitats that maximize their fitness until density of animals increases to a level where advantages are no longer gained (Northrup et al. 2021). Different terms are often used in association with habitat selection studies such as probability of use, selection, occupancy and preference, which often leads to confusion (Lele et al. 2013). However, methods that rely on an RSF framework estimates the probability of selection, which does not inform about the probability of use that also depends on the probability that a resource is actually encountered. Habitats can therefore have a high probability of selection because they are especially attractive, but a low probability of use because they represent rare habitat types (Lele et al. 2013, Fieberg et al. 2021).

We found that while beavers used forests the most with 75% of GPS fixes overlapping within this habitat type, they only selected against increasing distance to water and higher elevational gain, as well as against crops, developed- and open areas, while forests, distance to developed areas, slope and wetlands did not impact population-level habitat selection. The beavers revealed the clearest selection patterns in relation to distance to water, with all beavers selecting against, except six that did not display any clear selection patterns. Beavers staying close to water matches well with central place foraging behavior and trends in other semi-aquatic species such as southern water voles (*Arvicola sapidus*) (Cameron et al. 2018) and wood turtles (*Clemmys insculpta*) (Compton et al. 2002) that found safety and food sources in close proximity to water. Habitat types such as crops, developed- and open areas represent typical high-risk habitats of encountering humans and are often avoided by wildlife (Mori et al. 2014, Steyaert et al. 2016, Ofstad et al. 2020). For certain species such as caribou (*Rangifer tarandus caribou*), distance to areas with human disturbances was a key predictor for resource selection (DeCesare et al. 2012). While beavers also avoided developed areas, they showed no population-level avoidance of distance to developed areas, indicating that they do not respond as strongly to these areas as other species, which has also been confirmed in previous beaver studies (Hood 2020). We also found considerable individual variation in beaver selection especially in relation to distance to developed areas and forests (Fig. 8). While some beavers selected strongly against these, others selected for them, which may have caused the lack of clear population-level trend (Newediuk et al. 2022).

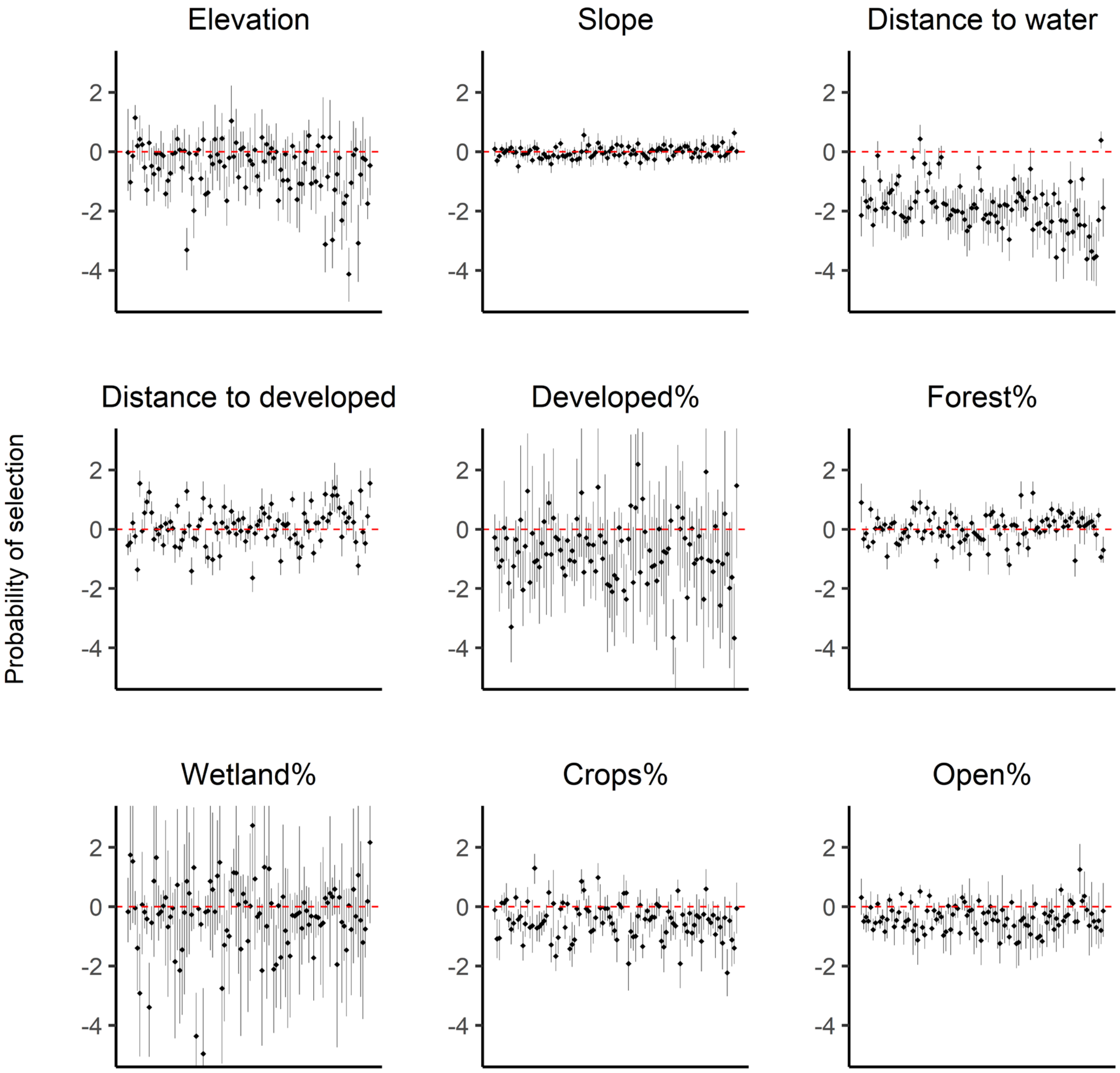

Figure 8: Individual selection estimates for Eurasian beaver (*Castor fiber*) selection of percentage habitat types, elevation, slope, and distance to water and developed areas in southeastern Norway, 2009-2021. Each point represents a specific beaver-year while the vertical lines represent the 95% credible intervals around each estimate. The dashed red line represents zero and individual estimates with credible intervals that overlap with this line means that the beaver does not display selection either for or against the habitat variable in question. Estimates above this line indicates selection for the habitat variable in questions and estimates bellow the lines indicates selection against.

We explored potential drivers of these individual difference but could not identify any demographic or physiological variables that explained a complete shift in selection among beavers. Age of the beaver had the strongest impact on selection estimates and with increasing age, beavers avoid elevational gain more but selected less strongly against crops and open areas and stronger for forests (Fig. 9). This may reflect an age trend where older beavers spend more time on land while increasing foraging (Graf et al. 2016b, Lodberg-Holm et al. 2021), which they may engage in within these habitats. Younger beavers on the other hand were willing to climb further up from water level (Fig. 9), which may give access higher food availability as food items tend to be depleted close to the water's edge within beaver territories (Fryxell 1992). Differences in habitat selection in relation to age have received overall less research attention in habitat selection studies, but examples of such differences have been identified in a wide range of species (Ficetola et al. 2013, Cameron et al. 2018). We also investigated impacts of average reproduction, beaver density and body condition, but these had mostly negligible impacts on individual variation. We did, however, find that individuals with higher average reproduction selected less strongly against elevation and those in good body condition and from larger families less strongly against distance to water. This could suggest that accepting a higher climb and further distance to water might give some benefits in terms of reproduction and body condition, and that beavers from larger families need to walk further to obtain food resources. Beavers in better body condition also avoided crops more strongly, which contradicts findings from other crop depredating species that tended to increase in body size when foraging on crops (Ditmer et al. 2015b, Hata et al. 2021). However, this article explores selection across all seasons, while article II focus in on the cereal season, which indicated that increased crop use may in fact be associated with a better body condition.

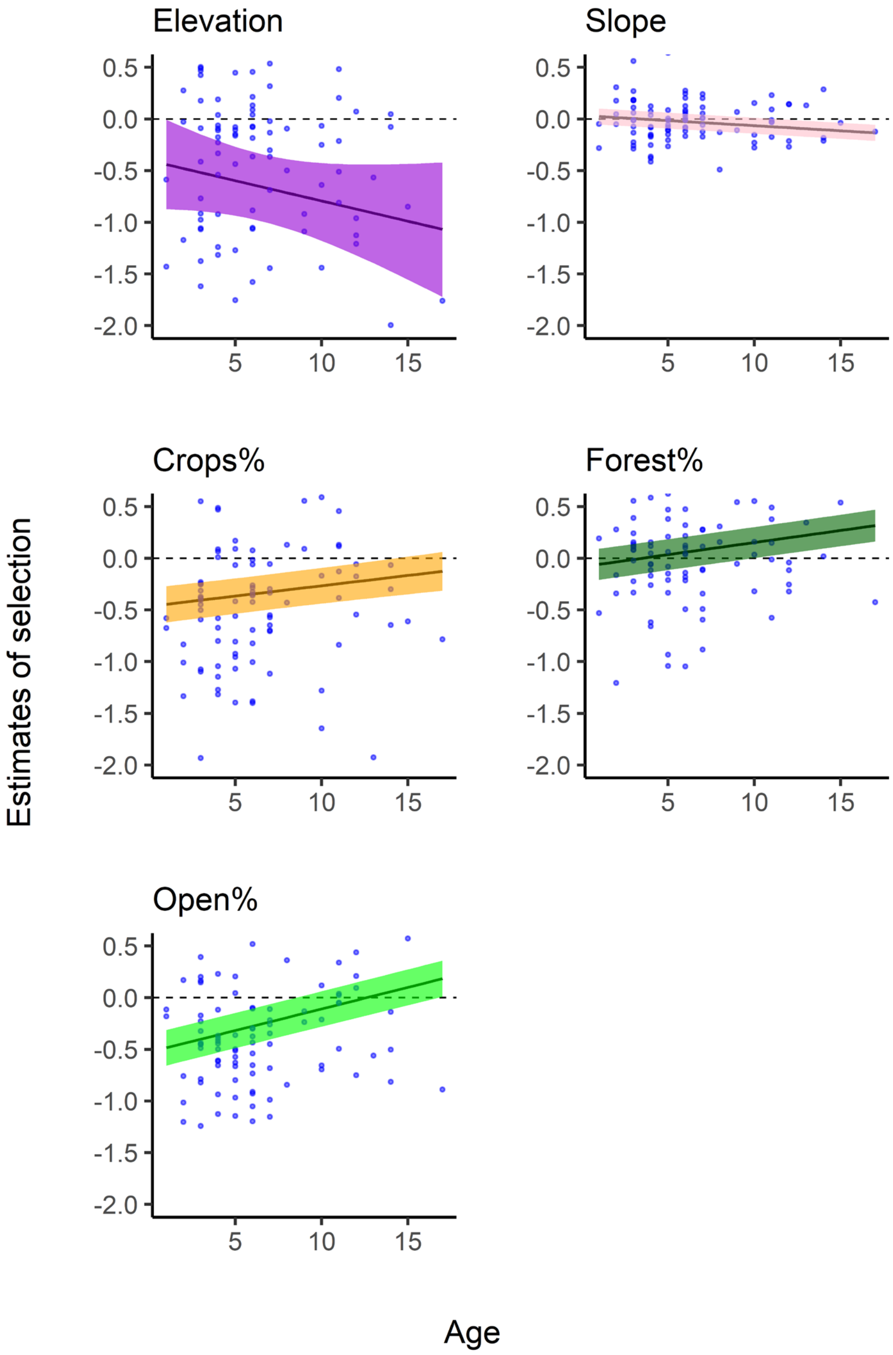

Figure 9: Individual habitat selection estimates of Eurasian beavers (*Castor fiber*) (N=90) in southeastern Norway, 2009-2021. Predicted effect of age is obtained from a linear mixed effect model using integrated nested Laplace approximation (R-INLA) while accounting for beaver family ID as a random effect. Estimates above the stabled line indicates selection for the habitat variable in question and estimates bellow the lines indicates selection against.

Spatial scales have received much research attention in habitat selection studies, but less attention has been directed on temporal scales that may be more important in certain contexts (Mayor et al. 2009). Differences between males and females may for example only become apparent within certain seasons, while they display similar habitat selection patterns at other times of the year (McLoughlin et al. 2002). Especially for monogamous species that usually display low levels of behavioral sexual dimorphism (Kleiman 1977), differences could be restricted to the reproductive period when females experience increased energy use (Elliott et al. 2010, Zoller and Drygala 2013). We therefore investigated temporal habitat selection separately for the different socio-reproductive groups. In terms of seasonal habitat selection trends, the combined group of reproductively active males and non-reproductive beavers displayed different trends than reproductively active females for certain habitat types. All beavers switched to selection for crops in mid-summer, but the reproductive active males and non-reproductive selected against developed areas during late summer and the reproductively active females selected against wetlands in early summer. The reproductively active males and non-reproductive also selected for open areas and wetlands during spring (Fig. 10).

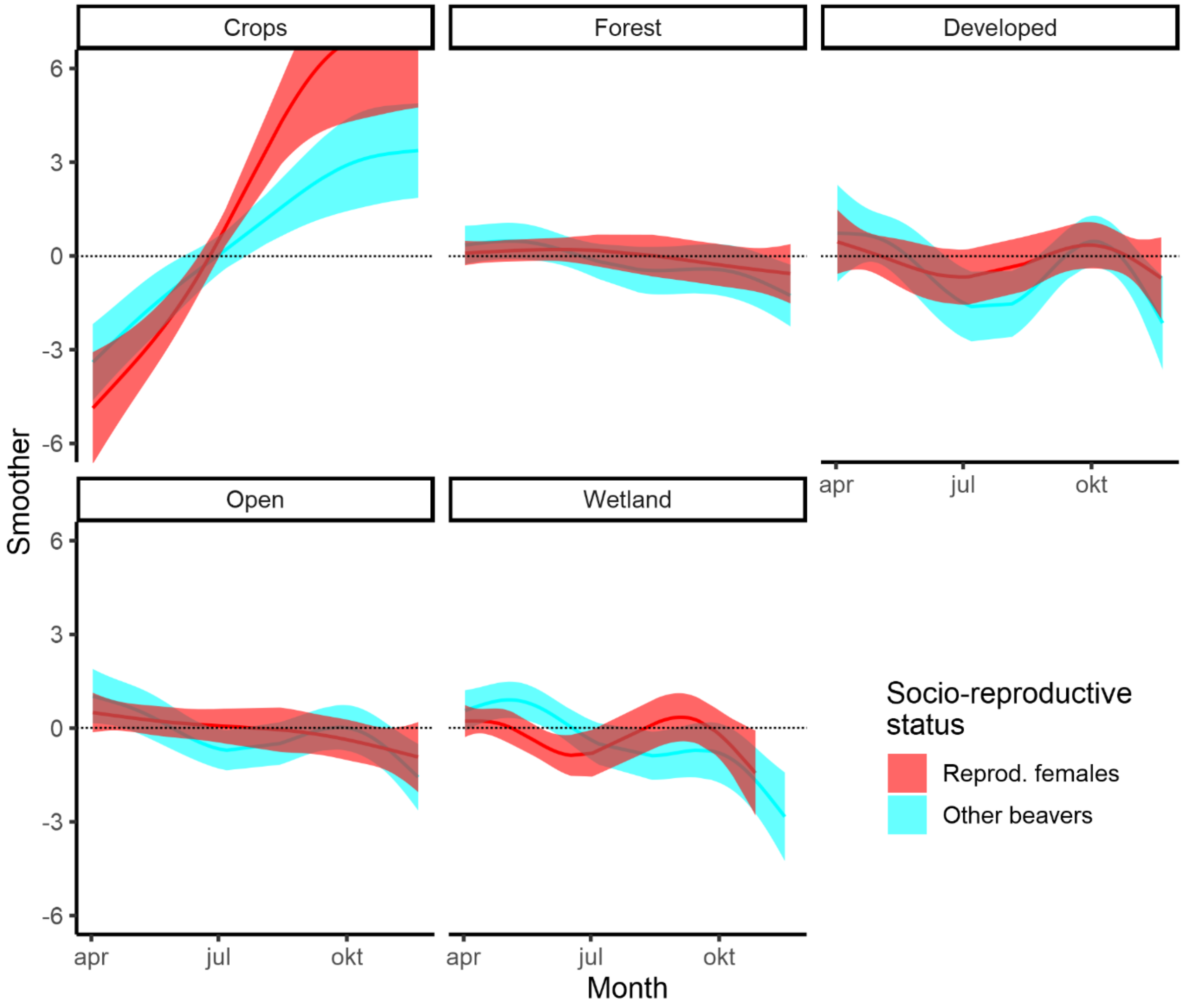

Figure 10: Habitat selection estimate smoothers for Julian day interacting with habitat types for Eurasian beavers (*Castor fiber*) (N=104) in southeastern Norway, 2009-2021. Julian day has been converted to months for visual interpretation. A generalized additive mixed model using integrated nested Laplace approximation and stochastic partial differential equations (INLA-SPDE) was fitted for each socio-reproductive group. This includes reproductively active females (Reprod. females), and combined group of reproductively active males and non-reproductive beavers (Other beavers). The stapled black line represents zero, which means no selection for or against the habitat variable in question. Estimates above the stabled line indicates selection for the habitat variable in question and estimates bellow the lines indicates selection against.

These seasonal patterns most likely reflect both temporal foraging opportunities and varying risk of human encounters. Selection for open areas and wetlands in spring coincides with the emergence of herbs and aquatic vegetation that are important foraging items for beavers during the vegetation season (Svendsen 1980, Nolet et al. 1995, Milligan and Humphries 2010). Open areas are often selected for by other herbivores in spring when they are foraging on palatable young plants (Godvik et al. 2009, Ofstad et al. 2020). Reproductively active females show tendencies towards increased selection for open areas and wetlands during this time also, but this effect was not statistically important (Fig. 8). This may be a result of female beavers spending more time in the lodge with the kits during this period (Wilsson 1971, Sun 2003). In mid-summer cereals mature within our study area, which coincides with the strong switch in selection of all beavers towards crops (Fig. 10). Temporally abundant and highly nutritious crops provides and additional food source for a wide range of wildlife species (Roper et al. 1995, Chiyo et al. 2011, Oro et al. 2013). However, the selection for crops among some beavers suggests that this food source may play a part in beavers foraging ecology especially within agricultural landscapes, which also supports our findings in article II. The lack of population-level selection for forests, that are usually important foraging habitats for beavers (Haarberg and Rosell 2006, Pinto et al. 2009), could be due to these areas being the most common habitat type in the study area. Frequent use by beavers may therefore not be translated to strong selection. However, we also lacked data on vegetation structure within the different forest types, which may play an important role in selection patterns for herbivores (Mysterud et al. 1999, Bjørneraas et al. 2012). The avoidance of developed areas during summer may reflect increased human activity within the study area during this time (Flemsæter et al. 2020). Deer in Germany similarly selected for more vegetation cover due to increased human activity in summer (Dupke et al. 2017, Richter et al. 2020). Reproductively active females did not, however, avoid developed areas during summer (Fig. 8), which may reflect less risk aversion in females (Meisingset et al. 2013). Especially in monogamous species with a high level of co-parenting, females might accept more risks than males to obtain high quality foraging areas to compensate for their increased energy use during reproduction (Lewis et al. 2002, Zoller and Drygala 2013).

Circadian patterns of habitat selection commonly reflects human disturbances and predation risk especially for herbivores (Dupke et al. 2017). The reproductively active pair seemed to display circadian patterns adapted to avoid encounters with humans. They selected for wetlands during morning and evening, which presumably would have lower human disturbances, while they selected for more exposed open areas in the middle of the night (Fig. 11). Open areas entail a high risk of being shot by human hunters for large ungulates (Godvik et al. 2009, Ofstad et al. 2020), and we expect beavers to also perceive a higher risk in these areas. Non-reproductive beavers, however, displayed opposite patterns and selected for open areas mostly in the morning, while selecting for wetlands in the middle of the night (Fig. 11). This might reflect less experience in these individuals or a mechanism among social species to reduce competition for food sources. Platypuses (*Ornithorhynchus anatinus*) for example although not group-living, often share burrows with conspecifics, but avoid each other while foraging to reduce competition (Bethge et al. 2009). Group-living species such as badgers and wild banded mongoose (*Mungos mungo*) also foraged in different locations within their shared territory presumably to reduce competition (Robertson et al. 2014, Sheppard et al. 2018). The varying circadian habitat selection patterns of beavers could also be a mechanism to reduce conflicts or a strategy for effective territory defense (McClanahan et al. 2020).

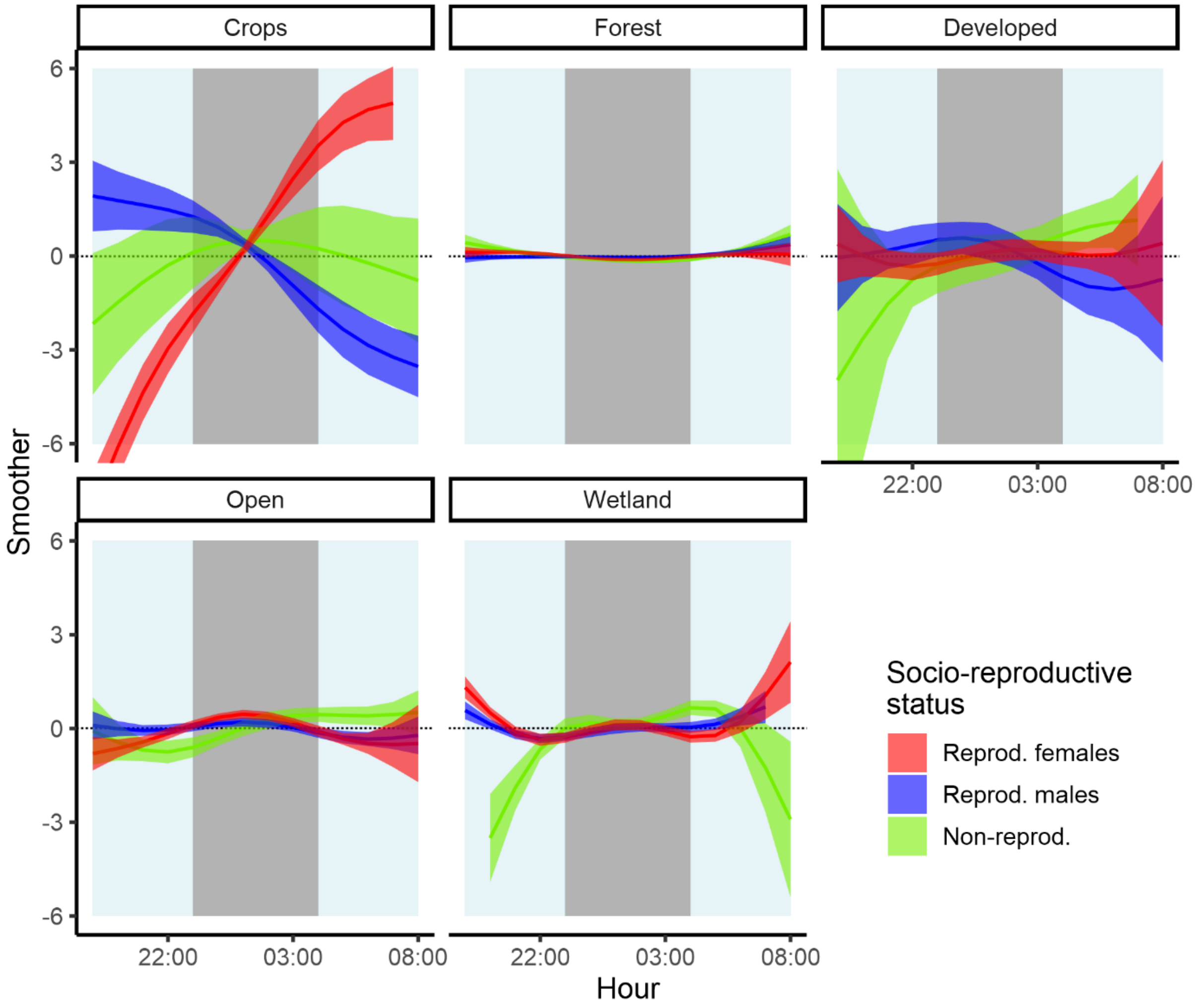

Figure 11: Habitat selection estimate smoothers for active hour interacting with habitat types for Eurasian beavers (*Castor fiber*) (N=104) in southeastern Norway, 2009-2021. Active hour has been converted into a 24-hour format to aid interpretation. A generalized additive mixed model using integrated nested Laplace approximation and stochastic partial differential equations (INLA-SPDE) was fitted for each socio-reproductive group. This includes reproductively active females (Reprod. females), reproductively active males (Reprod. Males) and non-reproductive beavers (Other beavers). The stapled black line represents zero, which means no selection for or against the habitat variable in question. Estimates above the stabled line indicates selection for the habitat variable in question and estimates bellow the lines indicates selection against. The lighter background represents the range of sundown to sunrise times across the study period, while the dark represents the hours of darkness.

5.3 Impacts of tagging on body condition

In article IV, we investigated potential negative impacts of tagging beavers using the same bio-loggers as applied in article III. We found a statistically important difference in daily percent weight change of the untagged versus the tagged beavers. While untagged beavers on average gained 23 g per day between captures, the untagged beavers declined with 14 g per day. The effect of tagging status was also retained in the most supported model showing a difference in percent weight change between the two groups (Fig. 12). These differences were small and differences in the length between capture events for the two groups may have influenced the results, but it still indicates that tagging reduces the ability of beavers to gain weight during the tagging period. It further emphasize the importance of comparing tagging impacts with a control group, which may reveal that even though tagged animals are not losing weight, they may gain weight at a lower rate compared to untagged individuals (Authier et al. 2013).

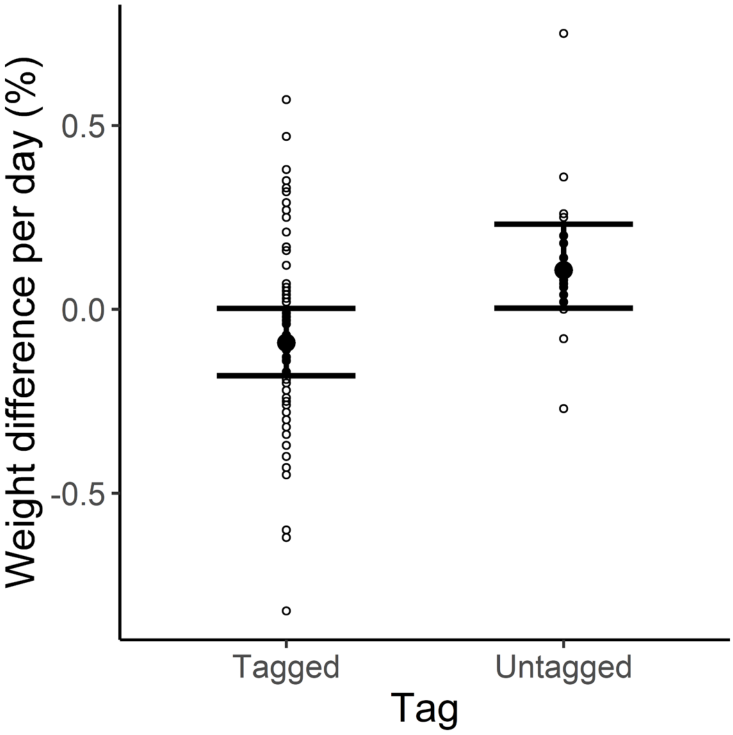

Figure 12: Estimated daily weight change (%) between captures for tagged and untagged Eurasian beavers (*Castor fiber*) in southeastern Norway (2006–2020). The prediction is based

on a linear mixed effects model using percent daily body weight change as the response variable. The horizontal lines represent the 95% confidence intervals around each mean.

We also found considerable variation in weight change between individual beavers where one tagged beaver lost 2,333 g (11.5%) during the tagging period. In total, 57% of the tagged beavers lost weight, while only two of the untagged beavers (7%) lost weight (Fig. 13). Even though some tagged beavers gained weight as well (42%), this was a much lower percentage that the untagged beavers that mostly gained weight (93%) (Fig. 13). This illustrates considerable individual variation in the impact of tagging, which may be ignored when just considering population-level trends. We investigated potential causes of this individual variation in the tagged beavers such as the weight of the tag in relation to the body weight of the beaver, water temperature, sex, age, season, and length of the tagging period, but none of these were statistically important.

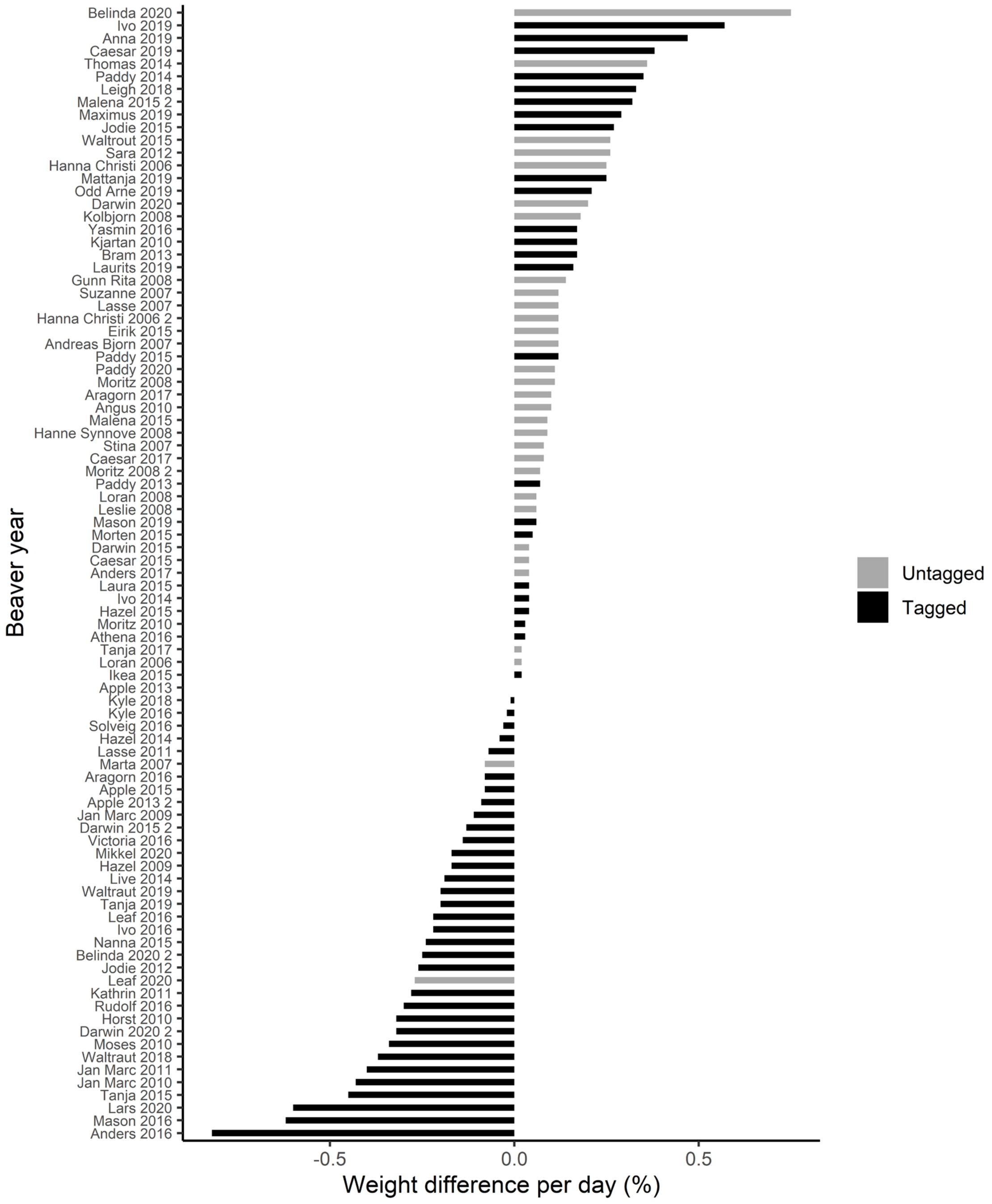

Figure 13: Daily percentage body weight change between captures for Eurasian beavers (*Castor fiber*) in southeastern Norway 2006–2020. Tagged beavers are shown in black while untagged are shown in dark grey.

The weight of the tag relative to total body weight did not affect body weight change in the tagged beavers, which may be due to all tags representing less than 1.3% of the beaver body weight. This is below the threshold suggested by several studies (Portugal and White 2018). The drag effect maybe more important than weight per se for aquatic and semi-aquatic species (Culik and Wilson 1991, Kay et al. 2019), but this was not investigated in the current study. Considering that beavers are relatively slow moving in the water, drag might have less of an impact compared to other species relying on speed to capture fast moving prey (Wilson et al. 2021). Another study tagging beavers using tail mounts found that tagged beavers lost more weight during winter than untagged individuals (Smith et al. 2016). We did not tag beavers during winter, which may have reduced the effect of season and water temperature on body weight change. The length of tagging also had no impact on beaver body weight gain, but since the glue-on tags mostly fall off within 2-3 weeks, we could not compare extensive variation in tagging lengths. Despite previous studies only finding slight behavioral changes in the first two days (Graf et al. 2016a), and no effect of being tagged at least once in a beaver's lifetime (Mortensen and Rosell 2020), we found an impact that may affect individual animal welfare. The question remains how biologically important these findings are, how long it takes beavers to recover following tagging, and to what extent this impacts beaver movement and behavior. Considering that alternative methods such as tail mounts often cause damage and disfigurement to the beaver tail (Smith et al. 2016, Windels and Belant 2016), we still believe that the glue-on method is the best short-term attachment method for beavers per today.

6 Conclusion and future perspectives

This thesis investigated temporal foraging and habitat selection, as well as potential impacts of bio-logging methods applied to study the behavior of Eurasian beavers. We found that neither foraging nor habitat selection were static, but rather dynamic with temporal trends across seasons and the night. Temporal dimensions are sometimes overlooked in animal behavior studies such as habitat selection, which may lead to simplistic understandings of animal ecology (Richter et al. 2020). Investigating temporal trends might also reveal subtle differences in foraging behavior and habitat selection between the sexes and in relation to reproductive status (Elliott et al. 2010, Zoller and Drygala 2013). Monogamy is a rare strategy among mammals (Kleiman 1977, Lukas and Clutton-Brock 2013) and while the sexes in polygamous species often display behavioral differences so profound that they probably should be considered as separate species (Oehlers et al. 2011), fewer differences are expected and explored in monogamous species. Still, time-specific differences can reflect varying energy expenditure and strategies among males and females especially in relation to reproduction (Clutton-Brock et al. 1982, Ruckstuhl 2007). We showed that males and females differed in activity patterns and selection of food items during certain times of year. Beavers also displayed circadian activity patterns and different habitat selection trends among socio-reproductive groups. There were also individual differences and the impacts of physiological and demographic characteristics such as age, body condition and density, where age had the largest impact on beaver activity and habitat selection, while body condition impacted use of crop fields.

Beavers within our study area inhabit a diverse landscape consisting of a patchwork of natural and anthropogenic habitats. They adapt to this landscape both in space and time and regulate their activities, foraging and habitat selection according to both food availability and human activity patterns. In late summer and early autumn, we showed that beavers exploited a rather novel food source, cereals, with clear foraging preferences for certain species and maturity levels, as well as spatial foraging patterns. We could not, however, connect foraging on cereals specifically to most demographic or physiological characteristics that have been identified in other wildlife species (Fox et al. 2005, Hata et al. 2021), except that beavers in good body condition used crop fields more. Animals may also display large individual variation in behavior driven by physiological or social characteristics. It is vital to investigate these differences to provide the full picture of a species requirements and preferences (Pape and Löffler 2015, Merems et al. 2020). Individual differences can also shed light on other topics of interest in behavioral ecology such as personality (Aliperti et al. 2021), nice specialization (Bolnick et al. 2003), and mechanisms to reduce conflict and foster cooperation within group living species (Dall et al. 2012). Animals may also display individual differences in how they respond to our research methods. We investigated both weight change in tagged individuals by comparing them to an untagged control group, but we also investigated individual variability. Comparisons between the two groups indicated that tagged beavers gained less weight during tagging, but the difference was small. However, the individual variability illustrates that certain beavers may be more impacted than others, which would not be recognized by comparing group averages. Despite these negative impacts, glue-on attachment is still a valuable method to investigate behavior and spatio-temporal behavior of beavers. However, constant efforts should be made to monitor impacts and improve methods to obtain the most unbiased understanding of wildlife behavior and interactions with the ecosystem.

6.1 Fine-scale beaver habitat selection

As a continuation of the work in this thesis, habitat selection of beavers could be investigated in more detail by combining GPS data with data from Daily Diaries to reconstruct exact and detailed movement paths of beavers both on land and in the water (Wilson et al. 2007, Bidder et al. 2015). Daily Diary contains both accelerometers that measures the acceleration and speed together with magnetometers that register their heading, which can describe animal movement and behavior in a three-dimensional space (Wilson et al. 2008, Williams et al. 2017). These estimates might give more details on fine scale habitat selection and use of core areas within the territories (Magowan et al. 2022). Step-Selection Functions (SSF) could then be used link consecutive animal locations and contrast these with random steps that represent the available habitat around each location within the movement limitations of the species in question (Thurfjell et al. 2014, Avgar et al. 2017). Integrated step selection analysis (iSSA) can incorporate both movement and habitat selection (Prokopenko et al. 2017) and could offer a more detailed perspective on beaver habitat selection and habitat characteristics that influence beaver movements. Step-selection methods are often complicated to fit with datasets containing several individuals, but this is increasingly being implemented either using random effects or through individual modelling (Thurfjell et al. 2014, Fieberg et al. 2021), which would be interesting to apply to beavers. However, more detailed movement data also requires more detailed habitat information.

Habitat selection was explored on a rather coarse spatial scale in this thesis, using mostly on habitat types, as well as various distance measurement to water and developed areas. In future studies it would be interesting to expand this study with more details of vegetation structure within foraging patches. Habitat selection not only differ between vegetation types, but also within these patches such as roe deer selecting stronger for forest areas with a higher availability of herbs in summer (Mysterud et al. 1999) or bears locating the best berry patches within the forest (Hertel et al. 2016). Higher resolution vegetation data could be obtained using remote sensing methods (Wilmers et al. 2015). Remote sensing either from satellites or drones could provide information on vegetation heigh, density, biomass as well as species surrounding the rivers and temporal variability in vegetation biomass (Atkins et al. 2018, Moeslund et al. 2019). These methods not only offer detailed description of forest composition, but also biomass and harvest patterns within agricultural landscapes such as pastures and cereal fields (Howison et al. 2018). Through utilizing these data sources, we could also dive deeper into how beaver habitat selection is impacted by predation fear and human disturbances.

6.2 Foraging in a landscape of fear

Herbivores and other wildlife species balance optimal foraging to gain food resources and adapt their behavior to avoid predators (Lima 1998, Brown et al. 2001). Both the quality and quantity of food sources as well as predation risk varies in space and time, which requires animals to trade-off safety and access to resources (McArthur et al. 2014). Defenses against predators are separated into primary defenses, which animals maintain independent of temporal and spatial predation risk, and secondary, that are only initiated when animals perceive high predation risk (Apfelbach et al. 2005). As predation risk varies both across time and space it might create a landscape of fear where animals have to adapt spatio-temporal behavior to both food availability and fear of predation (Laundré et al. 2010). Such responses may force animals to forage in areas with lower quality and together with the physical effects of stress, may negatively impact body condition and fitness (Apfelbach et al. 2005, Creel and Christianson 2008, McArthur et al. 2014). Behavioral responses represent indirect effects of predation with potentially large impacts through reduced foraging efficiency and stress (Creel and Christianson 2008). Animals may evaluate predation risk associated with landscape features such as openness and vegetation cover, or by direct cues of predator presence such as scent, smell, or visual observation (Apfelbach et al. 2005, Kuijper et al. 2014).

In addition to humans, wolves (*Canis lupus*) are the main predator of beavers in Europe and North America (Gable and Windels 2018). Wolves hunt beavers by hiding close to high-activity beaver areas and ambushing them in shallow water or on land (Gable et al. 2016, Gable et al. 2018). Experimental studies have shown that beavers respond to odors of predators by either avoiding the tainted food sources (Engelhart and Müller-Schwarze 1995, Rosell and Czech 2000, Salandre et al. 2017), or by not over-marking castoreum from conspecifics when predators scents are present (Rosell and Sanda 2006). However, we lack information on how such scent signals might impact beaver movement, foraging behavior and habitat selection. As beavers are ecosystem engineers with large impacts on ecosystems and biodiversity (Hood and Larson 2015, Wohl 2021), beaver removal through predation impact larger ecological processes such as nutrient cycling, nutrient storage and forest succession (Gable et al. 2020). However, indirect effects of predation of beavers through behavioral changes could potentially also cause wide scale ecological impacts. Tracking beaver movements while exposing them to cues of predator presence could reveal whether risk of predation induces beavers to shift habitat selection and foraging behavior. Using GPS data and Daily Diaries we could track beaver movement before and during scent exposure to investigate potential effects on foraging and habitat selection. These methods could also be expanded to the effects of human disturbances such as increases in boat traffic during summer and disturbances associated with human movement close to beaver lodges. Individual responses to predator scent could also be investigated, and such individual differences could also be studied to explore the ecology of group-living species.

6.3 Individual ecology of a group-living species

Individuals may display differences in habitat selection, foraging behavior, diet and spatio-temporal activity as a reflection of personality, division of labor, or niche specialization (Dall et al. 2012). Most commonly such individual differences represent different habitat availability of individuals that do not overlap in space (Bolnick et al. 2003), but may also occur among those that share territories or home ranges (Robertson et al. 2014, Sheppard et al. 2018, O'Brien et al. 2020). Differences can relate to age, sex or reproductive status due to different energetic needs, experience levels, risk acceptance and phenotypic traits (Araújo et al. 2011), but may also occur independently of demographic characteristics (Zango et al. 2020). Intraspecific competition is often a major driver behind individual specialization (Araújo et al. 2011). Badgers differed in diet within the same family group, suggesting they specialize foraging on different food items, possibly to reduce competition (Robertson et al. 2014). Male alliances of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) foraged in different locations than other alliances sharing the same area (O'Brien et al. 2020), while wild banded mongoose reduced their niche width in larger social groups that experienced higher intraspecific competition (Sheppard et al. 2018). Specialization may contribute to reduce competition and play an important role in the evolution of stable social systems (Dall et al. 2012, Sheppard et al. 2018), which would be very interesting to explore within beaver families that seem to maintain peaceful relations within their family groups (Mott et al. 2011).

The NBP have unique datasets and methods to explore nice portioning and individual specialization within and among beaver families. Both spatial data and dietary information can be used to investigate individual differences such as foraging locations, movement characteristics, site fidelity, and occurrence of food items within diets (Zango et al. 2020). Beaver territories within our study area varies both in size and density influenced by historical settlement patterns (Campbell et al. 2005), reproductive output between different beaver pairs (Nimje et al. 2021), and delayed dispersal of young beavers (Mayer et al. 2017d). This offer opportunities to study niche partitioning related to varying beaver densities that may reflect intraspecific competition. Daily Diaries has previously been used to distinguish different beaver behaviors (Graf et al. 2015) and could be applied to describe individual foraging patterns in more detail (Chakravarty et al. 2020). GPS data and behavioral observations could also contribute with information on individual habitat selection and foraging. Scat samples have also been sampled repeatedly from individuals, families, and across seasons within the study area the last 20 years. Beaver diets have been described in previous studies using various histological approaches either investigating scats or stomach contents (Krojerová-Prokešová et al. 2010, Bełżecki et al. 2018), but DNA methods open up new opportunities to identify plant species, even those that are highly digested (Valenti et al. 2009, Nielsen et al. 2018). This offers opportunities to study diet width within and among beaver families and again relate this to density. Together this data could facilitate an investigation of the individual ecology of beavers and how this relates to social structures. Development of new bio-logging methods could also allow us to track even more beavers and over longer time-periods while also ensuring further improvements in animal welfare.

6.4 Exploring behavior and movement through new bio-logging methods

Tagging beavers with bio-loggers is needed to explore most of these topics and require continued work to improve attachment methods and assess potential negative impacts. New tagging methods could be developed to extend retention time and obtain more data across longer time scales. New attachment mechanism using a rubber band around the tail have already been attempted on one beaver within the study area and showed promising results by remaining attached for over a year. We also want to experiment with new attachment methods inspired by plants seed dispersal methods such as burrs that attach onto the fur of animals. Similar designs are already being developed as prototypes to tag polar bears (*Ursus maritimus*) (personal communication: B. J. Kirschhoffer, 2021). These would probably only function as short-term attachments but could reduce handling time and damage made to the beaver fur. New methods would also require new investigations of animal welfare in terms of behavior, body weight gain during and following tagging, as well as cumulative effects from multiple tagging events during a beaver's lifetime. Daily Diaries could be used to study more subtle behavioral impacts such as impacts on movements following tagging and ventilation rates during captures (Wilson et al. 2019). Improvement and development of these bio-logging methods could help us answer some of the constantly new research questions that emerge when studying this semi-aquatic and ecosystem engineering species.

7 References

Alakoski, R., K. Kauhala, and V. Selonen. 2019. Differences in habitat use between the native Eurasian beaver and the invasive North American beaver in Finland. Biological Invasions **21**:1601–1613.

Aleksiuk, M., and I. M. Cowan. 1969. Aspects of seasonal energy expenditure in the beaver (Castor canadensis Kuhl) at the northern limit of its distribution. Canadian Journal of Zoology **47**:471-481.

Aliperti, J. R., B. E. Davis, N. A. Fangue, A. E. Todgham, and D. H. Van Vuren. 2021. Bridging animal personality with space use and resource use in a free-ranging population of an asocial ground squirrel. Animal Behaviour **180**:291-306.

Anderson, D., and K. Burnham. 2004. Model selection and multi-model inference. Second edition. Springer-Verlag, New York.

Apfelbach, R., C. D. Blanchard, R. J. Blanchard, R. A. Hayes, and I. S. McGregor. 2005. The effects of predator odors in mammalian prey species: A review of field and laboratory studies. Neuroscience & Biobehavioral Reviews **29**:1123-1144.

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

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. The Journal of Wildlife Management **74**:1175-1178.

ASAB/ABS. 2020. Guidelines for the treatment of animals in behavioural research and teaching. Animal Behaviour **159**:I-XI.

Atkins, J. W., G. Bohrer, R. T. Fahey, B. S. Hardiman, T. H. Morin, A. E. L. Stovall, N. Zimmerman, and C. M. Gough. 2018. Quantifying vegetation and canopy structural complexity from terrestrial LiDAR data using the forestr r package. Methods in Ecology and Evolution **9**:2057-2066.

Authier, M., C. Péron, A. Mante, P. Vidal, and D. Grémillet. 2013. Designing observational biologging studies to assess the causal effect of instrumentation. Methods in Ecology and Evolution **4**:802-810.

Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative selection strength: quantifying effect size in habitat- and step-selection inference. Ecology and Evolution **7**:5322-5330.

Barela, I., L. M. Burger, J. Taylor, K. O. Evans, R. Ogawa, L. McClintic, and G. Wang. 2020. Relationships between survival and habitat suitability of semi-aquatic mammals. Ecology and Evolution **10**:4867– 4875.

Barela, I. A., L. M. Burger, G. Wang, K. O. Evans, Q. Meng, and J. D. Taylor. 2021. Spatial transferability of expert opinion models for American beaver habitat. Ecological Informatics **61**:101211.

Barron, D. G., J. D. Brawn, and P. J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods in Ecology and Evolution **1**:180-187.

Barton, K. 2020. MuMIn: Multi-model Inference. R package version 1.43.17.

Baylis, A. M. M., B. Page, I. Staniland, J. P. Y. Arnould, and J. McKenzie. 2015. Taking the sting out of darting: risks, restraint drugs and procedures for the chemical restraint of Southern Hemisphere otariids. Marine Mammal Science **31**:322-344.

Becker, D. J., D. G. Streicker, and S. Altizer. 2015. Linking anthropogenic resources to wildlife–pathogen dynamics: a review and meta-analysis. Ecology Letters **18**:483-495.

Beguin, J., S. Martino, H. Rue, and S. G. Cumming. 2012. Hierarchical analysis of spatially autocorrelated ecological data using integrated nested Laplace approximation. Methods in Ecology and Evolution **3**:921-929.

Belovsky, G. E. 1984. Summer diet optimization by beaver. American Midland Naturalist **111**:209-222.

Bełżecki, G., R. Miltko, B. Kowalik, A. W. Demiaszkiewicz, J. Lachowicz, Z. Giżejewski, A. Obidziński, and N. R. McEwan. 2018. Seasonal variations of the digestive tract of the Eurasian beaver Castor fiber. Mammal Research **63**:21-31.

Bergman, B. G., J. K. Bump, and M. C. Romanski. 2018. Revisiting the role of aquatic plants in beaver habitat selection. The American Midland Naturalist **179**:222-246.

Bertolino, S., P. J. Mazzoglio, M. Vaiana, and I. Currado. 2004. Activity budget and foraging behavior of introduced Callosciurus finlaysonii (Rodentia, Sciuridae) in Italy. Journal of Mammalogy **85**:254-259.

Bethge, P., S. Munks, H. Otley, and S. Nicol. 2009. Activity patterns and sharing of time and space of platypuses, Ornithorhynchus anatinus, in a subalpine Tasmanian lake. Journal of Mammalogy **90**:1350-1356.

Bidder, O. R., J. S. Walker, M. W. Jones, M. D. Holton, P. Urge, D. M. Scantlebury, N. J. Marks, E. A. Magowan, I. E. Maguire, and R. P. Wilson. 2015. Step by step: reconstruction of terrestrial animal movement paths by dead-reckoning. Movement Ecology **3**:23.

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.

Bjørneraas, K., I. Herfindal, E. J. Solberg, B.-E. Sæther, B. van Moorter, and C. M. Rolandsen. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia **168**:231-243.

Bjørneraas, K., E. J. Solberg, I. Herfindal, B. V. Moorter, C. M. Rolandsen, J.-P. Tremblay, C. Skarpe, B.-E. Sæther, R. Eriksen, and R. Astrup. 2011. Moose Alces alces habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology **17**:44-54.

Blair-West, J., J. Coghlan, D. Denton, J. Nelson, E. Orchard, B. Scoggins, R. Wright, K. Myers, and C. Junqueira. 1968. Physiological, morphological and behavioural adaptation to a sodium deficient environment by wild native Australian and introduced species of animals. Nature **217**:922-928.

Bodey, T. W., I. R. Cleasby, F. Bell, N. Parr, A. Schultz, S. C. Votier, and S. Bearhop. 2018. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. Methods in Ecology and Evolution **9**:946-955.

Bolnick, Daniel I., R. Svanbäck, James A. Fordyce, Louie H. Yang, Jeremy M. Davis, C. D. Hulsey, and Matthew L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist **161**:1-28.

Briggs, A. J. A., C. A. Robstad, and F. Rosell. 2021. Using radio-frequency identification technology to monitor Eurasian beavers. Wildlife Society Bulletin **45**:154-161.

Brown, J. S., B. Kotler, and A. Bouskila. 2001. Ecology of fear: foraging games between predators and prey with pulsed resources. Pages 71-87 *in* Annales Zoologici Fennici. Helsinki: Suomen Biologian Seura Vanamo, 1964-.

Buech, R. R. 1995. Sex differences in behavior of beavers living in near-boreal lake habitat. Canadian Journal of Zoology **73**:2133-2143.

Burke, C. M., W. A. Montevecchi, and P. M. Regular. 2015. Seasonal variation in parental care drives sex-specific foraging by a monomorphic seabird. PLOS ONE **10**:e0141190.

Busher, P. E., M. Mayer, A. Ulevičius, A. Samus, G. Hartman, and F. Rosell. 2020. Food caching behavior of the Eurasian beaver in northern Europe. Wildlife Biology **2020**.

Cabré, L. B., M. Mayer, S. Steyaert, and F. Rosell. 2020. Beaver (Castor fiber) activity and spatial movement in response to light and weather conditions. Mammalian Biology **100**:261–271.

Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling **197**:516-519.

Cameron, M. F., K. J. Frost, J. M. Ver Hoef, G. A. Breed, A. V. Whiting, J. Goodwin, and P. L. Boveng. 2018. Habitat selection and seasonal movements of young bearded seals (Erignathus barbatus) in the Bering Sea. PLOS ONE **13**:e0192743.

Campbell-Palmer, R., D. Gow, R. Campbell, H. Dickson, S. Girling, J. Gurnell, D. Halley, S. Jones, S. Lisle, H. Parker, G. Schwab, and F. Rosell. 2016. The Eurasian beaver handbook: ecology and management of *Castor fiber*. Pelagic Publishing, UK, Exeter.

Campbell, R. D., A. Harrington, A. Ross, and L. Harrington. 2012a. Distribution, population assessment and activities of beavers in Tayside. Scottish Natural Heritage Commissioned Report No. 540.

Campbell, R. D., P. Nouvellet, C. Newman, D. W. Macdonald, and F. Rosell. 2012b. The influence of mean climate trends and climate variance on beaver survival and recruitment dynamics. Global Change Biology **18**:2730-2742.

Campbell, R. D., F. Rosell, B. A. Nolet, and V. A. A. Dijkstra. 2005. Territory and group sizes in Eurasian beavers (Castor fiber): echoes of settlement and reproduction? Behavioral Ecology and Sociobiology **58**:597-607.

Cebrian, J., and J. Lartigue. 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecological Monographs **74**:237-259.

Chakravarty, P., G. Cozzi, H. Dejnabadi, P.-A. Léziart, M. Manser, A. Ozgul, and K. Aminian. 2020. Seek and learn: Automated identification of microevents in animal behaviour using envelopes of acceleration data and machine learning. Methods in Ecology and Evolution **11**:1639-1651.

Chiyo, P. I., E. P. Cochrane, L. Naughton, and G. I. Basuta. 2005. Temporal patterns of crop raiding by elephants: a response to changes in forage quality or crop availability? African Journal of Ecology **43**:48-55.

Chiyo, P. I., P. C. Lee, C. J. Moss, E. A. Archie, J. A. Hollister-Smith, and S. C. Alberts. 2011. No risk, no gain: effects of crop raiding and genetic diversity on body size in male elephants. Behavioral Ecology **22**:552-558.

Cleasby, I. R., B. J. Morrissey, M. Bolton, E. Owen, L. Wilson, S. Wischnewski, and S. Nakagawa. 2021. What is our power to detect device effects in animal tracking studies? Methods in Ecology and Evolution **12**:1174-1185.

Clutton-Brock, T. H., G. R. Iason, S. D. Albon, and F. E. Guinness. 1982. Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. Journal of Zoology **198**:227-236.

Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (Clemmys insculpta): an application of paired logistic regression. Ecology **83**:833-843.

Cooke, S. J., S. G. Hinch, M. Wikelski, R. D. Andrews, L. J. Kuchel, T. G. Wolcott, and P. J. Butler. 2004. Biotelemetry: a mechanistic approach to ecology. Trends in Ecology & Evolution **19**:334-343.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology & Evolution **23**:194-201.

Culik, B., and R. P. Wilson. 1991. Swimming energetics and performance of instrumented adélie penguins (Pygoscelis adeliae). Journal of Experimental biology **158**:355-368.

Curtis, P. D., and P. G. Jensen. 2004. Habitat features affecting beaver occupancy along roadsides in New York state. Journal of Wildlife Management **68**:278-287.

Dall, S. R. X., A. M. Bell, D. I. Bolnick, and F. L. W. Ratnieks. 2012. An evolutionary ecology of individual differences. Ecology Letters **15**:1189-1198.

de Gabriel Hernando, M., A. A. Karamanlidis, K. Grivas, L. Krambokoukis, G. Papakostas, and J. Beecham. 2021. Habitat use and selection patterns inform habitat conservation priorities of an endangered large carnivore in southern Europe. Endangered Species Research **44**:203-215.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications **22**:1068-1083.

Ditmer, M. A., T. E. Burk, and D. L. Garshelis. 2015a. Do innate food preferences and learning affect crop raiding by American black bears? Ursus **26**:40-52.

Ditmer, M. A., D. L. Garshelis, K. V. Noyce, A. W. Haveles, and J. R. Fieberg. 2015b. Are American black bears in an agricultural landscape being sustained by crops? Journal of Mammalogy **97**:54-67.

Ditmer, M. A., K. V. Noyce, J. R. Fieberg, and D. L. Garshelis. 2018. Delineating the ecological and geographic edge of an opportunist: The American black bear exploiting an agricultural landscape. Ecological Modelling **387**:205-219.

Donkor, N. T., and J. M. Fryxell. 1999. Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. Forest Ecology and Management **118**:83-92.

Doolan, S. P., and D. W. Macdonald. 1996. Diet and foraging behaviour of group-living meerkats, Suricata suricatta, in the southern Kalahari. Journal of Zoology **239**:697-716.

Drickamer, L. C., S. H. Vessey, and E. M. Jakob. 2002. Animal Behavior Fifth Edition. McGraw-Hill, New York.

Dupke, C., C. Bonenfant, B. Reineking, R. Hable, T. Zeppenfeld, M. Ewald, and M. Heurich. 2017. Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. Ecography **40**:1014-1027.

eKlima. 2020. Gridded values for counties, with trend. Norwegian Meteorological Institute.

Elliott, K. H., A. J. Gaston, and D. Crump. 2010. Sex-specific behavior by a monomorphic seabird represents risk partitioning. Behavioral Ecology **21**:1024-1032.

Engelhart, A., and D. Müller-Schwarze. 1995. Responses of beaver (Castor canadensis Kuhl) to predator chemicals. Journal of Chemical Ecology **21**:1349-1364.

Ficetola, G. F., R. Pennati, and R. Manenti. 2013. Spatial segregation among age classes in cave salamanders: habitat selection or social interactions? Population Ecology **55**:217-226.

Fieberg, J., J. Signer, B. Smith, and T. Avgar. 2021. A 'How to' guide for interpreting parameters in habitat-selection analyses. Journal of Animal Ecology **90**:1027-1043.

Flemsæter, F., P. Stokowski, and S. Frisvoll. 2020. The rhythms of canal tourism: Synchronizing the host-visitor interface. Journal of Rural Studies **78**:199-210.

Fox, A. D., J. Madsen, H. Boyd, E. Kuijken, D. W. Norriss, I. M. Tombre, and D. A. Stroud. 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. Global Change Biology **11**:881-893.

Francis, R. A., J. D. Taylor, E. Dibble, B. Strickland, V. M. Petro, C. Easterwood, and G. Wang. 2017. Restricted cross-scale habitat selection by American beavers. Current Zoology **63**:703-710.

Fraser, D., B. Thompson, and D. Arthur. 1982. Aquatic feeding by moose: seasonal variation in relation to plant chemical composition and use of mineral licks. Canadian Journal of Zoology **60**:3121-3126.

Fryxell, J. M. 1992. Space use by beavers in relation to resource abundance. Oikos **64**:474-478.

Fustec, J., T. Lode, D. Le Jacques, and J. P. Cormier. 2001. Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. Freshwater Biology **46**:1361-1371.

Gable, T. D., S. M. Johnson-Bice, A. T. Homkes, S. K. Windels, and J. K. Bump. 2020. Outsized effect of predation: wolves alter wetland creation and recolonization by killing ecosystem engineers. Science Advances **6**:eabc5439.

Gable, T. D., and S. K. Windels. 2018. Kill rates and predation rates of wolves on beavers. The Journal of Wildlife Management **82**:466-472.

Gable, T. D., S. K. Windels, J. G. Bruggink, and A. T. Homkes. 2016. Where and how wolves (*Canis lupus*) kill beavers (*Castor canadensis*). PLOS ONE **11**:e0165537.

Gable, T. D., S. K. Windels, M. C. Romanski, and F. Rosell. 2018. The forgotten prey of an iconic predator: a review of interactions between grey wolves Canis lupus and beavers Castor spp. Mammal Review **48**:123-138.

Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat–performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2255-2265.

Gallant, D., L. Léger, É. Tremblay, D. Berteaux, N. Lecomte, and L. Vasseur. 2016. Linking time budgets to habitat quality suggests that beavers (Castor canadensis) are energy maximizers. Canadian Journal of Zoology **94**:671-676.

Ganzhorn, J. U., T. Pietsch, J. Fietz, S. Gross, J. Schmid, and N. Steiner. 2004. Selection of food and ranging behaviour in a sexually monomorphic folivorous lemur: Lepilemur ruficaudatus. Journal of Zoology **263**:393-399.

Gerwing, T. G., C. J. Johnson, and C. Alström-Rapaport. 2013. Factors influencing forage selection by the North American beaver (Castor canadensis). Mammalian Biology **78**:79-86.

Gibson, P. P., and J. D. Olden. 2014. Ecology, management, and conservation implications of North American beaver (Castor canadensis) in dryland streams. Aquatic Conservation: Marine and Freshwater Ecosystems **24**:391-409.

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.

Graf, P. M., J. Hochreiter, K. Hackländer, R. P. Wilson, and F. Rosell. 2016a. Short-term effects of tagging on activity and movement patterns of Eurasian beavers (Castor fiber). European Journal of Wildlife Research **62**:725-736.

Graf, P. M., M. Mayer, A. Zedrosser, K. Hackländer, and F. Rosell. 2016b. Territory size and age explain movement patterns in the Eurasian beaver. Mammalian Biology **81**:587-594.

Graf, P. M., R. P. Wilson, L. Qasem, K. Hackländer, and F. Rosell. 2015. The use of acceleration to code for animal behaviours; a case study in free-ranging Eurasian beavers Castor fiber. PLOS ONE **10**:e0136751.

Graf, P. M., R. P. Wilson, L. C. Sanchez, K. Hackländer, and F. Rosell. 2018. Diving behavior in a free-living, semi-aquatic herbivore, the Eurasian beaver Castor fiber. Ecology and Evolution **8**:997-1008.

Halley, D., and F. Rosell. 2002. The beaver's reconquest of Eurasia: status, population development and management of a conservation success. Mammal Review **32**:153-178.

Halley, D. J., A. P. Saveljev, and F. Rosell. 2021. Population and distribution of beavers Castor fiber and Castor canadensis in Eurasia. Mammal Review **51**:1-24.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ **6**:e4794.

Hata, A., R. Nakashita, T. Anezaki, M. Minami, Y. Fukue, N. Higuchi, H. Uno, Y. Nakajima, M. Saeki, and C. Kozakai. 2021. Agricultural crop consumption induces precocious maturity in deer by improving physical and reproductive performance. Ecosphere **12**:e03464.

Hawkins, P. 2004. Bio-logging and animal welfare: practical refinements. Memoirs of the National Institute of Polar Research, Special Issue **58**:58-68.

Hays, G. C., L. C. Ferreira, A. M. Sequeira, M. G. Meekan, C. M. Duarte, H. Bailey, F. Bailleul, W. D. Bowen, M. J. Caley, and D. P. Costa. 2016. Key questions in marine megafauna movement ecology. Trends in Ecology & Evolution **31**:463-475.

Hedd, A., W. A. Montevecchi, R. A. Phillips, and D. A. Fifield. 2014. Seasonal sexual segregation by monomorphic sooty shearwaters Puffinus griseus reflects different reproductive roles during the pre-laying period. PLOS ONE **9**:e85572.

Herr, J., and F. Rosell. 2004. Use of space and movement patterns in monogamous adult Eurasian beavers (Castor fiber). Journal of Zoology **262**:257-264.

Hertel, A. G., M. Leclerc, D. Warren, F. Pelletier, A. Zedrosser, and T. Mueller. 2019. Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. Animal Behaviour **147**:91-104.

Hertel, A. G., P. T. Niemelä, N. J. Dingemanse, and T. Mueller. 2020. A guide for studying among-individual behavioral variation from movement data in the wild. Movement Ecology **8**:30.

Hertel, A. G., S. M. J. G. Steyaert, A. Zedrosser, A. Mysterud, H. K. Lodberg-Holm, H. W. Gelink, J. Kindberg, and J. E. Swenson. 2016. Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. Behavioral Ecology and Sociobiology **70**:831-842.

Hertel, A. G., J. E. Swenson, and R. Bischof. 2017. A case for considering individual variation in diel activity patterns. Behavioral Ecology **28**:1524-1531.

Hijmans, R. J. 2020. raster: geographic data analysis and modeling. R package version 3.3-7.

Hofman-Kamińska, E., and R. Kowalczyk. 2012. Farm crops depredation by European bison (Bison bonasus) in the vicinity of forest habitats in northeastern Poland. Environmental Management **50**:530-541.

Hohwieler, K., F. Rosell, and M. Mayer. 2018. Scent-marking behavior by subordinate Eurasian beavers. Ethology **124**:591-599.

Hood, G., and S. Bayley. 2008. The effects of high ungulate densities on foraging choices by beaver (Castor canadensis) in the mixed-wood boreal forest. Canadian Journal of Zoology **86**:484-496.

Hood, G. A. 2020. Not all ponds are created equal: long-term beaver (Castor canadensis) lodge occupancy in a heterogeneous landscape. Canadian Journal of Zoology **98**:210-218.

Hood, G. A., and D. G. Larson. 2014. Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. Wetlands **34**:19-29.

Hood, G. A., and D. G. Larson. 2015. Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. Freshwater Biology **60**:198-208.

Howison, R. A., T. Piersma, R. Kentie, J. C. E. W. Hooijmeijer, and H. Olff. 2018. Quantifying landscape-level land-use intensity patterns through radar-based remote sensing. Journal of Applied Ecology **55**:1276-1287.

Hussey, N. E., S. T. Kessel, K. Aarestrup, S. J. Cooke, P. D. Cowley, A. T. Fisk, R. G. Harcourt, K. N. Holland, S. J. Iverson, J. F. Kocik, J. E. M. Flemming, and F. G. Whoriskey. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. Science **348**:1255642.

Hut, R. A., N. Kronfeld-Schor, V. van der Vinne, and H. De la Iglesia. 2012. Chapter 17 - In search of a temporal niche: Environmental factors. Pages 281-304 *in* A. Kalsbeek, M. Merrow, T. Roenneberg, and R. G. Foster, editors. Progress in Brain Research. Elsevier.

Haarberg, O., and F. Rosell. 2006. Selective foraging on woody plant species by the Eurasian beaver (Castor fiber) in Telemark, Norway. Journal of Zoology **270**:201-208.

Jackson, T. P. 2001. Factors influencing food collection behaviour of Brants' whistling rat (Parotomys brantsii): a central place forager. Journal of Zoology **255**:15-23.

John, F., S. Baker, and V. Kostkan. 2010. Habitat selection of an expanding beaver (Castor fiber) population in central and upper Morava River basin. European Journal of Wildlife Research **56**:663-671.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61**:65-71.

Johnston, C. A. 2017. Beavers: boreal ecosystem engineers. Springer International Publishing AG Cham, Switzerland.

Jones, K., D. Gilvear, N. Willby, and M. Gaywood. 2009. Willow (Salix spp.) and aspen (Populus tremula) regrowth after felling by the Eurasian beaver (Castor fiber): implications for riparian woodland conservation in Scotland. Aquatic Conservation: Marine and Freshwater Ecosystems **19**:75.

Jordan, B. 2005. Science-based assessment of animal welfare: wild and captive animals. Revue scientifique et technique (International Office of Epizootics) **24**:515-528.

Justicia, L. S., F. Rosell, and M. Mayer. 2018. Performance of GPS units for deployment on semiaquatic animals. PLOS ONE **13**:e0207938.

Kartverket. 2016. FKB-AR5.

Kartverket. 2019. DTM 10.

Kay, W. P., D. S. Naumann, H. J. Bowen, S. J. Withers, B. J. Evans, R. P. Wilson, T. B. Stringell, J. C. Bull, P. W. Hopkins, and L. Börger. 2019. Minimizing the impact of biologging devices: Using computational fluid dynamics for optimizing tag design and positioning. Methods in Ecology and Evolution **10**:1222-1233.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. Terrestrial animal tracking as an eye on life and planet. Science **348**:aaa2478.

Kleiman, D. G. 1977. Monogamy in mammals. The Quarterly Review of Biology **52**:39-69.

Korbelová, J., L. Hamšíková, J. Maloň, L. Válková, and A. Vorel. 2016. Seasonal variation in the home range size of the Eurasian beaver: do patterns vary across habitats? Mammal Research **61**:243-253.

Krojerová-Prokešová, J., M. Barančeková, L. Hamšíková, and A. Vorel. 2010. Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources. Journal of Zoology **281**:183-193.

Kuijper, D. P. J., M. Verwijmeren, M. Churski, A. Zbyryt, K. Schmidt, B. Jędrzejewska, and C. Smit. 2014. What cues do ungulates use to assess predation risk in dense temperate forests? PLOS ONE **9**:e84607.

Landbruksdirektoratet. 2021a. PT-900 Antallstatistikk - per 1.10.

Landbruksdirektoratet. 2021b. PT-912 Antall dekar og søkere med de ulike vekstgruppene.

Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal.

Law, A., N. Bunnefeld, and N. J. Willby. 2014a. Beavers and lilies: selective herbivory and adaptive foraging behaviour. Freshwater Biology **59**:224-232.

Law, A., M. J. Gaywood, K. C. Jones, P. Ramsay, and N. J. Willby. 2017a. Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. Science of The Total Environment **605**:1021-1030.

Law, A., M. J. Gaywood, K. C. Jones, P. Ramsay, and N. J. Willby. 2017b. Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. Science of The Total Environment **605-606**:1021-1030.

Law, A., K. C. Jones, and N. J. Willby. 2014b. Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation. Aquatic Botany **116**:27-34.

Law, A., O. Levanoni, G. Foster, F. Ecke, and N. J. Willby. 2019. Are beavers a solution to the freshwater biodiversity crisis? Diversity and Distributions **25**:1763-1772.

Lear, K. O., A. C. Gleiss, and N. M. Whitney. 2018. Metabolic rates and the energetic cost of external tag attachment in juvenile blacktip sharks Carcharhinus limbatus. Journal of Fish Biology **93**:391-395.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. Journal of Animal Ecology **82**:1183-1191.

Lemessa, D., K. Hylander, and P. Hambäck. 2013. Composition of crops and land-use types in relation to crop raiding pattern at different distances from forests. Agriculture, Ecosystems & Environment **167**:71-78.

Lewis, S., S. Benvenuti, L. Dall–Antonia, R. Griffiths, L. Money, T. N. Sherratt, S. Wanless, and K. C. Hamer. 2002. Sex-specific foraging behaviour in a monomorphic seabird. Proceedings of the Royal Society of London. Series B: Biological Sciences **269**:1687-1693.

Lezama-Ochoa, N., M. G. Pennino, M. A. Hall, J. Lopez, and H. Murua. 2020. Using a Bayesian modelling approach (INLA-SPDE) to predict the occurrence of the spinetail devil ray (Mobular mobular). Scientific Reports **10**:18822.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. Bioscience **48**:25-34.

Lodberg-Holm, H. K., H. W. Gelink, A. G. Hertel, J. E. Swenson, M. Domevscik, and S. M. J. G. Steyaert. 2019. A human-induced landscape of fear influences foraging behavior of brown bears. Basic and Applied Ecology **35**:18-27.

Lodberg-Holm, H. K., S. M. J. G. Steyaert, S. Reinhardt, and F. Rosell. 2021. Size is not everything: differing activity and foraging patterns between the sexes in a monomorphic mammal. Behavioral Ecology and Sociobiology **75**:76.

Logan, M., and G. D. Sanson. 2003. The effects of lactation on the feeding behaviour and activity patterns of free-ranging female koalas (Phascolarctos cinereus Goldfuss). Australian Journal of Zoology **51**:415-428.

Lovdata. 2017. Forskrift om forvaltning av bever. Landbruks- og matdepartementet.

Lukas, D., and T. H. Clutton-Brock. 2013. The evolution of social monogamy in mammals. Science **341**:526-530.

Magowan, E. A., I. E. Maguire, S. Smith, S. Redpath, N. J. Marks, R. P. Wilson, F. Menzies, M. O'Hagan, and D. M. Scantlebury. 2022. Dead-reckoning elucidates fine-scale habitat use by European badgers Meles meles. Animal Biotelemetry **10**:10.

Marchand, P., M. Garel, G. Bourgoin, D. Dubray, D. Maillard, and A. Loison. 2015. Coupling scale-specific habitat selection and activity reveals sex-specific food/cover trade-offs in a large herbivore. Animal Behaviour **102**:169-187.

Masi, S., C. Cipolletta, and M. M. Robbins. 2009. Western lowland gorillas (Gorilla gorilla gorilla) change their activity patterns in response to frugivory. American Journal of Primatology **71**:91-100.

Mayer, M. 2017. Territoriality and life history strategies of the Eurasian beaver. PhD thesis, University of South-Eastern Norway.

Mayer, M., S. C. Frank, A. Zedrosser, and F. Rosell. 2020. Causes and consequences of inverse density-dependent territorial behaviour and aggression in a monogamous mammal. Journal of Animal Ecology **89**:577-588.

Mayer, M., F. Künzel, A. Zedrosser, and F. Rosell. 2017a. The 7-year itch: non-adaptive mate change in the Eurasian beaver. Behavioral Ecology and Sociobiology **71**:32.

Mayer, M., C. Robstad, E. P. Serra, K. Hohwieler, B. Fuchs, A. L. Evans, J. M. Arnemo, A. Zedrosser, and F. Rosell. 2017b. Exposure of the Eurasian beaver (Castor fiber) towards hunters during the spring hunt. Department of Natural Sciences and Environmental Health, University College of Southeast Norway. Bø i Telemark, Norway

Mayer, M., A. Zedrosser, and F. Rosell. 2017c. Extra-territorial movements differ between territory holders and subordinates in a large, monogamous rodent. Scientific Reports **7**:15261.

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

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience **16**:238-247.

McArthur, C., P. B. Banks, R. Boonstra, and J. S. Forbey. 2014. The dilemma of foraging herbivores: dealing with food and fear. Oecologia **176**:677-689.

McClanahan, K., F. Rosell, and M. Mayer. 2020. Minding your own business: low pair cohesion in a territorial, monogamous mammal. Animal Behaviour **166**:119-128.

McClintic, L., J. Taylor, J. Jones, R. Singleton, and G. Wang. 2014a. Effects of spatiotemporal resource heterogeneity on home range size of American beaver. Journal of Zoology **293**:134-141.

McClintic, L. F., G. Wang, J. D. Taylor, and J. C. Jones. 2014b. Movement characteristics of American beavers (Castor canadensis). Behaviour **151**:1249-1265.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology **31**:1161-1175.

McKinstry, M. C., and S. H. Anderson. 2003. Survival, fates, and success of transplanted beavers (Castor canadensis) in Wyoming. Journal of Wildlife Rehabilitation:17-23.

McLoughlin, P. D., R. L. Case, R. J. Gau, D. H. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. Oecologia **132**:102-108.

McLoughlin, P. D., J.-M. Gaillard, M. S. Boyce, C. Bonenfant, F. Messier, P. Duncan, D. Delorme, B. V. Moorter, S. Saïd, and F. Klein. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology **88**:3192-3201.

McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology **79**:4-12.

Meisingset, E. L., L. E. Loe, Ø. Brekkum, B. Van Moorter, and A. Mysterud. 2013. Red deer habitat selection and movements in relation to roads. The Journal of Wildlife Management **77**:181-191.

Merems, J. L., L. A. Shipley, T. Levi, J. Ruprecht, D. A. Clark, M. J. Wisdom, N. J. Jackson, K. M. Stewart, and R. A. Long. 2020. Nutritional-landscape models link habitat use to condition of mule deer (Odocoileus hemionus). Frontiers in Ecology and Evolution **8**.

Mikulka, O., M. Homolka, J. Drimaj, and J. Kamler. 2020. European beaver (Castor fiber) in open agricultural landscapes: crop grazing and the potential for economic damage. European Journal of Wildlife Research **66**:101.

Miljødirektoratet. 2022. Jakttider: Informasjon om jakt- og fangsttider 1. april 2017 – 31. mars 2022.

Milligan, H. E., and M. M. Humphries. 2010. The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic-terrestrial ecosystem linkages in a subarctic environment. Oikos **119**:1877-1886.

Milligan, M. C., L. I. Berkeley, and L. B. McNew. 2020. Habitat selection of female sharp-tailed grouse in grasslands managed for livestock production. PLOS ONE **15**:e0233756.

Moeslund, J. E., A. Zlinszky, R. Ejrnæs, A. K. Brunbjerg, P. K. Bøcher, J.-C. Svenning, and S. Normand. 2019. LIDAR explains diversity of plants, fungi, lichens and bryophytes across multiple habitats and large geographic extent. bioRxiv:509794.

Mori, E., S. Lovari, A. Sforzi, G. Romeo, C. Pisani, A. Massolo, and L. Fattorini. 2014. Patterns of spatial overlap in a monogamous large rodent, the crested porcupine. Behavioural Processes **107**:112-118.

Mortensen, R. M., S. Reinhardt, M. E. Hjønnevåg, R. P. Wilson, and F. Rosell. 2021. Aquatic habitat use in a semi-aquatic mammal: the Eurasian beaver. Animal Biotelemetry **9**:35.

Mortensen, R. M., and F. Rosell. 2020. Long-term capture and handling effects on body condition, reproduction and survival in a semi-aquatic mammal. Scientific Reports **10**:17886.

Mott, C. L., C. K. Bloomquist, and C. K. Nielsen. 2011. Seasonal, diel, and ontogenetic patterns of within-den behavior in beavers (Castor canadensis). Mammalian Biology **76**:436-444.

Mysterud, A., P. K. Larsen, R. A. Ims, and E. Østbye. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Canadian Journal of Zoology **77**:776-783.

Nelner, T. B., and G. A. Hood. 2011. Effect of agriculture and presence of American beaver *Castor canadensis* on winter biodiversity of mammals. Wildlife Biology **17**:326-336.

Newediuk, L., C. M. Prokopenko, and E. Vander Wal. 2022. Individual differences in habitat selection mediate landscape level predictions of a functional response. Oecologia **198**:99-110.

Nielsen, J. M., E. L. Clare, B. Hayden, M. T. Brett, and P. Kratina. 2018. Diet tracing in ecology: method comparison and selection. Methods in Ecology and Evolution **9**:278-291.

Nimje, P., H. V. Tinnesand, C. D. Buesching, M. Sæbø, H. Senn, A. Zedrosser, and F. Rosell. 2019. Almost faithful: SNP markers reveal low levels of extra-pair paternity in the Eurasian beaver. PeerJ Preprints **7**:e27866v27861.

Nimje, P. S., M. Mayer, A. Zedrosser, M. Sæbø, and F. Rosell. 2021. Territory acquisition and mate choice in a monogamous mammal, the Eurasian beaver. Animal Behaviour **178**:165-173.

Nolet, B. A., and F. Rosell. 1994. Territoriality and time budgets in beavers during sequential settlement. Canadian Journal of Zoology **72**:1227-1237.

Nolet, B. A., and F. Rosell. 1998. Comeback of the beaver Castor fiber: an overview of old and new conservation problems. Biological Conservation **83**:165-173.

Nolet, B. A., P. J. Van Der Veer, E. G. J. Evers, and M. M. Ottenheim. 1995. A linear programming model of diet choice of free-living beavers. Netherlands Journal of Zoology **45**:315-337.

Northrup, J. M., E. Vander Wal, M. Bonar, J. Fieberg, M. P. Laforge, M. Leclerc, C. M. Prokopenko, and B. D. Gerber. 2021. Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. Ecological Applications **32**:e02470.

Nummi, P., and T. Kuuluvainen. 2013. Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. Boreal Environmental Research **18**:13–24.

O'Brien, O., S. J. Allen, M. Krützen, and R. C. Connor. 2020. Alliance-specific habitat selection by male Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia. Animal Behaviour **164**:39-49.

Oehlers, S. A., R. T. Bowyer, F. Huettmann, D. K. Person, and W. B. Kessler. 2011. Sex and scale: implications for habitat selection by Alaskan moose Alces alces gigas. Wildlife Biology **17**:67-84, 18.

Ofstad, E. G., S. S. Markussen, B.-E. Sæther, E. J. Solberg, M. Heim, H. Haanes, K. H. Røed, and I. Herfindal. 2020. Opposing fitness consequences of habitat use in a harvested moose population. Journal of Animal Ecology **89**:1701-1710.

Oliveira, T., F. Urra, J. M. López-Martín, E. Ballesteros-Duperón, J. M. Barea-Azcón, M. Moléon, J. M. Gil-Sánchez, P. C. Alves, F. Díaz-Ruíz, P. Ferreras, and P. Monterroso. 2018. Females know better: sex-biased habitat selection by the European wildcat. Ecology and Evolution **8**:9464-9477.

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.

Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155-177 *in* J. Horn, G. R. Stairs, and R. D. Mitchell, editors. Analysis of ecological systems. Ohio State Press, Columbus.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters **16**:1501-1514.

Owen-Smith, N., J. Fryxell, and E. Merrill. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2267-2278.

Pape, R., and J. Löffler. 2015. Ecological dynamics in habitat selection of reindeer: an interplay of spatial scale, time, and individual animal's choice. Polar Biology **38**:1891-1903.

Parker, H., P. Nummi, G. Hartman, and F. Rosell. 2012. Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and a strategy for eradication. Wildlife Biology **18**:354-365.

Parker, H., and F. Rosell. 2012. Beaver management in Norway-A review of recent literature and current problems. HiT Publication no. 4/2012, Telemark University College, Norway.

Parker, H., F. Rosell, T. A. Hermansen, G. Sørløkk, and M. Stærk. 2002. Sex and age composition of spring-hunted Eurasian beaver in Norway. The Journal of Wildlife Management **66**:1164-1170.

Parker, H., A. Zedrosser, and F. Rosell. 2017. Age-specific reproduction in relation to body size and condition in female Eurasian beavers. Journal of Zoology **302**:236-243.

Parker, J. D., C. C. Caudill, and M. E. Hay. 2007. Beaver herbivory on aquatic plants. Oecologia **151**:616-625.

Pecorella, I., N. Fattorini, E. Macchi, and F. Ferretti. 2019. Sex/age differences in foraging, vigilance and alertness in a social herbivore. acta ethologica **22**:1-8.

Pelletier, F., and M. Festa-Bianchet. 2004. Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, Ovis canadensis. Behavioral Ecology and Sociobiology **56**:546-551.

Percie du Sert, N., A. Ahluwalia, S. Alam, M. T. Avey, M. Baker, W. J. Browne, A. Clark, I. C. Cuthill, U. Dirnagl, M. Emerson, P. Garner, S. T. Holgate, D. W. Howells, V. Hurst, N. A. Karp, S. E. Lazic, K. Lidster, C. J. MacCallum, M. Macleod, E. J. Pearl, O. H. Petersen, F. Rawle, P. Reynolds, K. Rooney, E. S. Sena, S. D. Silberberg, T. Steckler, and H. Würbel. 2020. Reporting animal research: Explanation and elaboration for the ARRIVE guidelines 2.0. PLOS Biology **18**:e3000411.

Pinto, B., M. J. Santos, and F. Rosell. 2009. Habitat selection of the Eurasian beaver (Castor fiber) near its carrying capacity: an example from Norway. Canadian Journal of Zoology **87**:317-325.

Pipia, A., S. Ciuti, S. Grignolio, S. Luchetti, R. Madau, and M. Apollonio. 2008. Influence of sex, season, temperature and reproductive status on daily activity patterns in Sardinian mouflon (Ovis orientalis musimon). Behaviour **145**:1723-1745.

Portugal, S. J., and C. R. White. 2018. Miniaturization of biologgers is not alleviating the 5% rule. Methods in Ecology and Evolution **9**:1662-1666.

Potvin, C. L., and J. Bovet. 1975. Annual cycle of patterns of activity rhythms in beaver colonies (Castor canadensis). Journal of Comparative Physiology **98**:243-256.

Prokopenko, C. M., M. S. Boyce, and T. Avgar. 2017. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. Journal of Applied Ecology **54**:470-479.

Putman, R. J. 1986. Foraging by roe deer in agricultural areas and impact on arable crops. Journal of Applied Ecology **23**:91-99.

Raffel, T. R., N. Smith, C. Cortright, and A. J. Gatz. 2009. Central place foraging by beavers (Castor canadensis) in a complex lake habitat. The American Midland Naturalist **162**:62-73.

Ranheim, B., F. Rosell, H. A. Haga, and J. M. Arnemo. 2004. Field anaesthetic and surgical techniques for implantation of intraperitoneal radio transmitters in Eurasian beavers *Castor fiber*. Wildlife Biology **10**:11-15.

Regmi, G. R., K. A.-I. Nekaris, K. Kandel, and V. Nijman. 2013. Crop-raiding macaques: predictions, patterns and perceptions from Langtang National Park, Nepal. Endangered Species Research **20**:217-226.

Remonti, L., A. Balestrieri, and C. Prigioni. 2011. Percentage of protein, lipids, and carbohydrates in the diet of badger (Meles meles) populations across Europe. Ecological Research **26**:487-495.

Richter, L., N. Balkenhol, C. Raab, H. Reinecke, M. Meißner, S. Herzog, J. Isselstein, and J. Signer. 2020. So close and yet so different: The importance of considering temporal dynamics to understand habitat selection. Basic and Applied Ecology **43**:99-109.

Roberts, C. P., J. W. Cain III, and R. D. Cox. 2017. Identifying ecologically relevant scales of habitat selection: diel habitat selection in elk. Ecosphere **8**:e02013.

Roberts, T. H., and D. H. Arner. 1984. Food habits of beaver in East-Central Mississippi. The Journal of Wildlife Management **48**:1414-1419.

Robertson, A., R. A. McDonald, R. J. Delahay, S. D. Kelly, and S. Bearhop. 2014. Individual foraging specialisation in a social mammal: the European badger (Meles meles). Oecologia **176**:409-421.

Roper, T. J., S. R. Findlay, P. Lüps, and D. J. Shepherdson. 1995. Damage by badgers Meles meles to wheat Triticum vulgare and barley Hordeum sativum crops. Journal of Applied Ecology **32**:720-726.

Ropert-Coudert, Y., and R. P. Wilson. 2005. Trends and perspectives in animal-attached remote sensing. Frontiers in Ecology and the Environment **3**:437-444.

Rosell, F., F. Bergan, and H. Parker. 1998. Scent-marking in the Eurasian beaver (*Castor fiber*) as a means of territory defense. Journal of Chemical Ecology **24**:207-219.

Rosell, F., O. Bozsér, P. Collen, and H. Parker. 2005. Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. Mammal Review **35**:248-276.

Rosell, F., and A. Czech. 2000. Responses of foraging Eurasian beavers Castor fiber to predator odours. Wildlife Biology **6**:13-21.

Rosell, F., and B. Hovde. 2001. Methods of aquatic and terrestrial netting to capture Eurasian beavers. Wildlife Society Bulletin **29**:269-274.

Rosell, F., and B. A. Nolet. 1997. Factors affecting scent-marking behavior in Eurasian beaver (*Castor fiber*). Journal of Chemical Ecology **23**:673-689.

Rosell, F., and J. Sanda. 2006. Potential risks of olfactory signaling: the effect of predators on scent marking by beavers. Behavioral Ecology **17**:897-904.

Rosell, F., and L. X. Sun. 1999. Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *Castor fiber*. Wildlife Biology **5**:119-123.

Rosell, F., and L. R. Thomsen. 2006. Sexual dimorphism in territorial scent marking by adult Eurasian beavers (*Castor fiber*). Journal of Chemical Ecology **32**:1301-1315.

Rosell, F., A. Zedrosser, and H. Parker. 2010. Correlates of body measurements and age in Eurasian beaver from Norway. European Journal of Wildlife Research **56**:43-48.

Rosen, D. A. S., C. G. Gerlinsky, and A. W. Trites. 2018. Telemetry tags increase the costs of swimming in northern fur seals, Callorhinus ursinus. Marine Mammal Science **34**:385-402.

Rothmeyer, S. W., M. C. McKinstry, and S. H. Anderson. 2002. Tail attachment of modified ear-tag radio transmitters on beavers. Wildlife Society Bulletin **30**:425-429.

Rovdata. 2021. Bestandsstatus - Gaupe.

Ruckstuhl, K. E. 2007. Sexual segregation in vertebrates: proximate and ultimate causes. Integrative and Comparative Biology **47**:245-257.

Ruckstuhl, K. E., and P. Neuhaus. 2009. Activity budgets and sociality in a monomorphic ungulate: the African oryx (Oryx gazella). Canadian Journal of Zoology **87**:165-174.

Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society: Series B (Statistical Methodology) **71**:319-392.

Rödel, H. G., T. G. Valencak, A. Handrek, and R. Monclús. 2015. Paying the energetic costs of reproduction: reliance on postpartum foraging and stored reserves. Behavioral Ecology **27**:748-756.

Sadykova, D., B. E. Scott, M. De Dominicis, S. L. Wakelin, A. Sadykov, and J. Wolf. 2017. Bayesian joint models with INLA exploring marine mobile predator–prey and competitor species habitat overlap. Ecology and Evolution **7**:5212-5226.

Salandre, J. A., R. Beil, J. A. Loehr, and J. Sundell. 2017. Foraging decisions of North American beaver (Castor canadensis) are shaped by energy constraints and predation risk. Mammal Research **62**:229-239.

Sánchez-Bayo, F., and K. A. G. Wyckhuys. 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation **232**:8-27.

Scrafford, M. A., D. B. Tyers, D. T. Patten, and B. F. Sowell. 2018. Beaver habitat selection for 24 Yr since reintroduction north of Yellowstone National Park. Rangeland Ecology & Management **71**:266-273.

Sharpe, F., and F. Rosell. 2003. Time budgets and sex differences in the Eurasian beaver. Animal Behaviour **66**:1059-1067.

Sheppard, C. E., R. Inger, R. A. McDonald, S. Barker, A. L. Jackson, F. J. Thompson, E. I. K. Vitikainen, M. A. Cant, and H. H. Marshall. 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal. Ecology Letters **21**:665-673.

Simonsen, C. E., J. Madsen, I. M. Tombre, and J. Nabe-Nielsen. 2016. Is it worthwhile scaring geese to alleviate damage to crops? – An experimental study. Journal of Applied Ecology **53**:916-924.

Smith, J. B., S. K. Windels, T. Wolf, R. W. Klaver, and J. L. Belant. 2016. Do transmitters affect survival and body condition of American beavers Castor canadensis? Wildlife Biology **22**:117-123.

Soulsbury, C. D., H. E. Gray, L. M. Smith, V. Braithwaite, S. C. Cotter, R. W. Elwood, A. Wilkinson, and L. M. Collins. 2020. The welfare and ethics of research involving wild animals: A primer. Methods in Ecology and Evolution **11**:1164-1181.

Steyaert, S. M. J. G., A. Zedrosser, M. Elfström, A. Ordiz, M. Leclerc, S. C. Frank, J. Kindberg, O.-G. Støen, S. Brunberg, and J. E. Swenson. 2016. Ecological implications from spatial patterns in human-caused brown bear mortality. Wildlife Biology **22**:144-152, 149.

Steyaert, S. M. J. G., A. Zedrosser, and F. Rosell. 2015. Socio-ecological features other than sex affect habitat selection in the socially obligate monogamous Eurasian beaver. Oecologia **179**:1023-1032.

Street, G. M., J. R. Potts, L. Börger, J. C. Beasley, S. Demarais, J. M. Fryxell, P. D. McLoughlin, K. L. Monteith, C. M. Prokopenko, M. C. Ribeiro, A. R. Rodgers, B. K. Strickland, F. M. van Beest, D. A. Bernasconi, L. T. Beumer, G. Dharmarajan, S. P. Dwinnell, D. A. Keiter, A. Keuroghlian, L. J. Newediuk, J. E. F. Oshima, O. Rhodes Jr., P. E. Schlichting, N. M. Schmidt, and E. Vander Wal. 2021. Solving the sample size problem for resource selection functions. Methods in Ecology and Evolution **12**:2421-2431.

Sun, L. 2003. Monogamy correlates, socioecological factors, and mating systems in beavers. Monogamy: mating strategies and partnerships in birds, humans and other mammals (UH Reichard and C. Boesch, eds.). Cambridge University Press, Cambridge, United Kingdom:138-146.

Svendsen, G. E. 1980. Seasonal change in feeding patterns of beaver in southeastern Ohio. The Journal of Wildlife Management **44**:285-290.

Swinnen, K. R. R., N. K. Hughes, and H. Leirs. 2015. Beaver (Castor fiber) activity patterns in a predator-free landscape. What is keeping them in the dark? Mammalian Biology **80**:477-483.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology **2**:4.

Troup, G., B. Doran, J. Au, L. E. King, I. Douglas-Hamilton, and R. Heinsohn. 2020. Movement tortuosity and speed reveal the trade-offs of crop raiding for African elephants. Animal Behaviour **168**:97-108.

Ulicsni, V., D. Babai, E. Juhász, Z. Molnár, and M. Biró. 2020. Local knowledge about a newly reintroduced, rapidly spreading species (Eurasian beaver) and perception of its impact on ecosystem services. PLOS ONE **15**:e0233506.

Valenti, A., C. Miquel, M. A. Nawaz, E. Bellemain, E. Coissac, F. Pompanon, L. Gielly, C. Cruaud, G. Nascetti, P. Wincker, J. E. Swenson, and P. Taberlet. 2009. New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the trnL approach. Molecular Ecology Resources **9**:51-60.

Vasey, N. 2005. Activity budgets and activity rhythms in red ruffed lemurs (Varecia rubra) on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. American Journal of Primatology **66**:23-44.

Vogel, S. M., B. Lambert, A. C. Songhurst, G. P. McCulloch, A. L. Stronza, and T. Coulson. 2020. Exploring movement decisions: Can Bayesian movement-state models explain crop consumption behaviour in elephants (Loxodonta africana)? Journal of Animal Ecology **89**:1055-1068.

Vorel, A., L. Válková, L. Hamšíková, J. Maloň, and J. Korbelová. 2015. Beaver foraging behaviour: seasonal foraging specialization by a choosy generalist herbivore. Behavioral Ecology and Sociobiology **69**:1221-1235.

Wang, G., L. F. McClintic, and J. D. Taylor. 2019. Habitat selection by American beaver at multiple spatial scales. Animal Biotelemetry **7**:10.

White, D. J., K. C. Kendall, and H. D. Picton. 1998. Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. Canadian Journal of Zoology **76**:221-227.

William, G., G. Jean-Michel, S. Sonia, B. Christophe, M. Atle, M. Nicolas, P. Maryline, and C. Clément. 2018. Same habitat types but different use: evidence of context-dependent habitat selection in roe deer across populations. Scientific Reports **8**:5102.

Williams, H. J., M. D. Holton, E. L. C. Shepard, N. Largey, B. Norman, P. G. Ryan, O. Duriez, M. Scantlebury, F. Quintana, E. A. Magowan, N. J. Marks, A. N. Alagaili, N. C. Bennett, and R. P. Wilson. 2017. Identification of animal movement patterns using tri-axial magnetometry. Movement Ecology **5**:6.

Wilmers, C. C., B. Nickel, C. M. Bryce, J. A. Smith, R. E. Wheat, and V. Yovovich. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology **96**:1741-1753.

Wilson, R. P., M. Holton, V. L. Wilson, R. Gunner, B. Tysse, G. I. Wilson, F. Quintana, C. Duarte, and D. M. Scantlebury. 2019. Towards informed metrics for examining the role of human-induced animal responses in tag studies on wild animals. Integrative Zoology **14**:17-29.

Wilson, R. P., N. Liebsch, I. M. Davies, F. Quintana, H. Weimerskirch, S. Storch, K. Lucke, U. Siebert, S. Zankl, G. Müller, I. Zimmer, A. Scolaro, C. Campagna, J. Plötz, H. Bornemann, J. Teilmann, and C. R. McMahon. 2007. All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. Deep Sea Research Part II: Topical Studies in Oceanography **54**:193-210.

Wilson, R. P., K. A. Rose, R. Gunner, M. D. Holton, N. J. Marks, N. C. Bennett, S. H. Bell, J. P. Twining, J. Hesketh, C. M. Duarte, N. Bezodis, M. Jezek, M. Painter, V. Silovsky, M. C. Crofoot, R. Harel, J. P. Y. Arnould, B. M. Allan, D. A. Whisson, A. Alagaili, and D. M. Scantlebury. 2021. Animal lifestyle changes acceptable mass limits for attached tags. bioRxiv:2021.2004.2027.441641.

Wilson, R. P., E. Shepard, and N. Liebsch. 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. Endangered Species Research **4**:123-137.

Wilsson, L. 1971. Observations and experiments on the ethology of the European beaver (Castor fiber L.). Viltrevy **8**:160-203.

Windels, S. K., and J. L. Belant. 2016. Performance of tail-mounted transmitters on American beavers Castor canadensis in a northern climate. Wildlife Biology **22**:124-129, 126.

Wohl, E. 2021. Legacy effects of loss of beavers in the continental United States. Environmental Research Letters **16**:025010.

Wood, S. N. 2017. Generalized additive models: an introduction with R. Chapman and Hall/CRC, New York.

Zango, L., L. Navarro-Herrero, M. García-Vendrell, K. Safi, and J. González-Solís. 2020. Niche partitioning and individual specialization among age, breeding status and sex classes in a long-lived seabird. Animal Behaviour **170**:1-14.

Zoller, H., and F. Drygala. 2013. Activity patterns of the invasive raccoon dog (Nyctereutes procyonoides) in North East Germany. Folia Zoologica **62**:290-296, 297.

Żurowski, W., J. Kisza, A. Kruk, and A. Roskosz. 1974. Lactation and chemical composition of milk of the European beaver (*Castor fiber* L.). Journal of Mammalogy **55**:847-850.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution **1**:3-14.

Zuur, A. F., E. N. Ieno, and A. A. Saveliev. 2017. Spatial, temporal and spatial–temporal ecological data analysis with R-INLA. Highland Statistics Ltd, Newburgh, United Kingdom.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology. Springer Science and Business Media, New York.

Zwolicki, A., R. Pudełko, K. Moskal, J. Świderska, S. Saath, and A. Weydmann. 2019. The importance of spatial scale in habitat selection by European beaver. Ecography **41**:187-200.

Article 1

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ORIGINAL ARTICLE

Size is not everything: differing activity and foraging patterns between the sexes in a monomorphic mammal

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Abstract

Animals balance foraging with other activities, and activity patterns may differ between sexes due to differing physical requirements and reproductive investments. Sex-specific behavioural differences are common in sexually dimorphic mammals, but have received limited research attention in monomorphic mammals where the sexes are similar in body size. Eurasian beavers (*Castor fiber*) are obligate monogamous and monomorphic mammals and a good model species to study sex-specific differences. As females increase energy expenditure during reproduction, we hypothesized differing seasonal activity budgets, circadian activity rhythms and foraging patterns between male and reproducing female beavers. To test this hypothesis, we equipped adult beavers with VHF transmitters (N=41; 16 female, 25 male) and observed them throughout their active period at night from spring to late summer. Occurrence of their main activities (foraging, travelling and being in lodge) and use of food items (trees/shrubs, aquatic vegetation and herbs/grasses) were modelled to investigate sex-specific seasonal activity budgets and circadian activity rhythms. The sexes did not differ in time spent foraging across the season or night, but during spring, females resided more in the lodge and travelled less. Males and females both foraged on aquatic vegetation during spring, but females used this food source also during late summer, whereas males mostly foraged on trees/shrubs throughout the year. We conclude that seasonal activity budgets and foraging differ subtly between the sexes, which may relate to different energy budgets associated with reproduction and nutritional requirements. Such subtle seasonal behavioural adaptions may be vital for survival and reproduction of monomorphic species.

Significance statement

Activity budgets and foraging patterns of animals are key to their survival and may differ between males and females with different body sizes and physical requirements. In monomorphic species, where males and females have similar body sizes, fewer differences are expected, but may still be pronounced during certain times of the year. We modelled sex-specific seasonal activity budgets and circadian activity rhythms and use of food items in a monomorphic mammal, the Eurasian beaver. By treating season and time of day as a continuous variable rather than modelling differences within distinct predefined periods, we identified subtle sex-specific seasonal trends in activity budgets and use of food items.

Keywords Activity · *Castor fiber* · Foraging · Eurasian beaver · Monomorphic · Sex

Introduction

Foraging is vital for an animal's fitness, and foraging behaviour is optimized in order to maximize intake of resources (Drickamer et al. 2002; Owen-Smith et al. 2010). Animals must balance their energetic needs against the costs of foraging, such as predation risk and thermoregulation (Brown et al. 1999; Zub et al. 2009), and against time spent on other behaviours such as territory defence (Ydenberg and Krebs 1987). The 24-h luminance cycle of night and day usually regulates the circadian rhythm of several species, which may also vary

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seasonally (Hut et al. 2012). Species such as Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Arnold et al. 2018) display very stable activity patterns despite extreme difference in light conditions, while others, such as brown bears (*Ursus arctos*), hibernate during winter and forage intensely during summer (Hertel et al. 2016). Animals may also display strong seasonal foraging patterns linked to plant phenology (Bischof et al. 2012), switching to seasonally abundant food sources (McLellan and Hovey 1995), or building up of food caches in autumn or following masting events (Humphries et al. 2002).

Seasonal activity budgets, circadian activity rhythms and diet may vary in relation to sex, age and reproductive status. Several studies have indicated differences in activity budgets and foraging between the sexes in dimorphic species, with body size as the assumed main driver, but differing investments in reproduction between the sexes may also play a role (Pelletier and Festa-Bianchet 2004; Ruckstuhl 2007). Much of the work on monomorphic species has focused on sea birds in relation to reproductive roles of males and females (Lewis et al. 2002; Shaffer et al. 2003; Hedd et al. 2014; Burke et al. 2015). In mammals, the lactation period increases energetic requirements of females and may cause differences in foraging behaviour and habitat selection between the sexes (Clutton-Brock et al. 1982; Logan and Sanson 2003; Ruckstuhl et al. 2005). Lactation is both energetically costly for females, but also requires additional nutrients, which may increase investments in foraging, decrease time spent on other activities and/or cause dietary changes (Speakman 2008; Rödel et al. 2015). In monomorphic racoon dogs (*Nyctereutes procyonoides*), females increased foraging during lactation (Zoller and Drygala 2013), while female red-tailed sportive lemurs (*Lepilemur ruficaudatus*) selected food items with overall lower fibre content (Ganzhorn et al. 2004). Differences in activity budgets have also been observed in monomorphic mammals outside the reproductive season, such as female red ruffed lemurs (*Varecia rubra*) that fed and rested more than males throughout the year (Vasey 2005). However, in monogamous and monomorphic African oryx (*Oryx gazella*), no differences in activity budgets or foraging intensity of males and females were documented (Ruckstuhl and Neuhaus 2009). Overall, differences in foraging behaviour of males and females in monomorphic species have received less research attention than sex differences in size-dimorphic species (Lewis et al. 2002; Pérez-Barbería et al. 2002). Due to the energetic impact of reproduction on females, such differences may be temporally specific, present only at certain times of the year. Studies commonly use predefined temporal units such as seasons or night/day to statistically compare activity budgets and use of dietary items, which may miss more subtle temporal variations (Lewis et al. 2002; Vasey 2005; Zoller and Drygala 2013). Including time as predefined categories may also simplify more complex trends when exploring animal interactions with the environment (Richter et al. 2020). In this paper, we explore whether males and females in a monogamous and monomorphic mammal display differing temporal trends in activity budgets and circadian activity rhythms and use of food resources, while using time as a continuous variable and the Eurasian beaver (*Castor fiber*) as a model species.

The Eurasian beavers, together with the closely related North American beaver (*Castor canadensis*), are obligate monogamous and monomorphic mammals with similar body mass of males and females (Wilsson 1971; Novak 1999; Sun 2003). Beavers are territorial and typically live in family groups consisting of the dominant reproductive pair and offspring from the current and previous years. The kits are born in May–June, after which the dominant pair display a high degree of biparental care with both parents supplying the kits with food inside the lodge until they forage by themselves in late summer (Wilsson 1971; Novak 1999; Sun 2003). The female is still the primary caregiver for the kits during the first 90 days while lactating, which restricts her movements outside the lodge (Żurowski et al. 1974; Mayer et al. 2017a). Beavers are mostly active between dusk and dawn (Sharpe and Rosell 2003; Mott et al. 2011; Swinnen et al. 2015), but may display regional as well as seasonal variation in circadian activity rhythms (Potvin and Bovet 1975; Nolet and Rosell 1994; Gallant et al. 2004). At night, beavers spend much of their time foraging, but this is balanced with travelling and being in the lodge (Sharpe and Rosell 2003; Mott et al. 2011).

Beavers are central place foragers, which implies that they reduce foraging intensity and become more selective with further distance from their central place, i.e. their lodges and the water (Gallant et al. 2004; Haarberg and Rosell 2006; Gerwing et al. 2013). They are also selective foragers on woody vegetation (Fryxell and Doucet 1993; Nolet et al. 1994), but their diet varies seasonally from relying mostly on the bark of deciduous trees during winter to more nutritionally rich deciduous leaves, aquatic vegetation and herbaceous plants during summer (Svendsen 1980; Roberts and Arner 1984; Milligan and Humphries 2010). Several studies have indicated such seasonal shifts in diet, but few dietary differences between the sexes (Roberts and Arner 1984; Krojerová-Prokešová et al. 2010; Bełżecki et al. 2018). However, most dietary studies rely on histological analysis of beaver scats or stomach content, which may be biased towards less digestible food items (Nielsen et al. 2018).

Previous studies have identified few differences in activity and foraging patterns between male and female beavers, although some differences are related to age. Beaver kits foraged less on land, while older individuals increased time spent away from the water, possibly due to increased boldness with age (Svendsen 1980; Graf et al. 2016). Male beavers also tend to travel more and have longer activity periods than females (Sharpe and Rosell 2003). There have been limited number of studies comparing activity budgets between the sexes and age groups in beavers, and such studies have typically compared occurrences of activity types between seasons or periods of the night (Sharpe and Rosell 2003). Especially in monomorphic and monogamous mammals such as beavers, differences between the sexes may be subtle and limited to specific time periods, requiring in-depth temporal exploration of seasonal and circadian activity budgets and foraging.

Our goal was to model the beavers' seasonal activity budgets, circadian activity rhythms and foraging patterns to test to what extent sex-specific differences in behaviour occur. We hypothesize that females have greater energetic demands during gestation and lactation in late spring. Therefore, we predict that females should forage more, travel less and spend more time in the lodge compared to males during spring and during an average night (a). In summer, we predict that females will spend less time in lodge and travel and forage more than males to compensate for energetic expenditures related to reproduction incurred during the spring (b). Additionally, we predict that in spring and in the summer months following reproduction, females should forage more on nutrient-rich plant groups such as aquatic vegetation, herbs and grasses that require less handling time (c). We also accounted for the age of the beaver and distance to the main lodge as potential explanatory variables.

Methods

Study area

The study area is located in South-Eastern Norway and includes three rivers: Gvarv, Sauar and Straumen (59°23′ N, 09°09′ E) located in Midt-Telemark and Nome municipalities. The mean daily temperature is 6.5°C, and the mean daily precipitation is 2.3 mm (eKlima 2020). Combined, the rivers extend approximately 32 km and are between 30 to 150 m wide. All three rivers empty into Norsjø Lake. The rivers meander through a relatively flat area of boreal forests as well as agricultural fields, pastures and small villages where short sections of the rivers freeze during winter. The Gvarv and Straumen rivers are regulated by hydropower dams upriver from the study area (Haarberg and Rosell 2006). The most common woody vegetations along the river are grey alder (*Alnus incana*), bird cherry (*Prunus padus*), common ash (*Fraxinus excelsior*), rowan (*Sorbus aucuparia*), alder buckthorn (*Frangula alnus*), birch (*Betula* spp.), red elderberry (*Sambucus racemosa*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Haarberg and Rosell 2006). The most common aquatic species in the rivers include bulbous rush (*Juncus bulbosus bulbosus)*, water lobelia (*Lobelia dortmanna*), lake quillwort (*Isoetes lacustris*), shoreweed (*Littorella uniflora*) and water awlwort (*Subularia aquatica*) (Hjønnevåg 2020). The area supports a high-density beaver population with long-term stable territories (Mayer et al. 2019), which has been monitored as part of the Norwegian Beaver Project since 1997 (Halley and Rosell 2002; Campbell et al. 2005). Large carnivores such as wolves (*Canis lupus*) and bears have been extirpated from the area, but lynx (*Lynx lynx*) are in low densities (Rosell and Sanda 2006). Red foxes have been observed preying on beaver kits (Kile et al. 1996) and are common throughout South-Eastern Norway (Pedersen et al. 2016).

Live capture

Beavers were live captured at night using landing nets from boats with outboard engines from March to September during the years 2000, 2001, 2006 and 2007, adhering to vetted methods (Rosell and Hovde 2001). We transferred the captured beaver to a cloth sack, in which it was measured and tagged. Age was estimated based on either previous observations of the beaver as a kit or based on minimum age estimated from body weight (Rosell et al. 2010). Beavers captured for the first time weighing ≥17 kg and ≤19.5 kg were considered at least 2 years old, while those >19.5 kg were at minimum 3 years old (Rosell et al. 2010; Mayer et al. 2017b). An additional year was added to the minimum age every year following the initial capture. The sex of the beaver was established by the colour and viscosity of their anal gland secretion, where females have a greyish thick paste and males a more oily secretion with pale white or yellow colour (Rosell and Sun 1999). Based on long-term monitoring, we established that all tagged females were dominant, which means they are the oldest female in the territory and the only one reproducing. Whether the dominant female reproduced each year was determined by increased nipple size, kits being observed in the territory the following autumn, yearlings observed the following year or observations of adults provisioning food to the lodge in spring and summer (Wilsson 1971).

We tagged the captured beavers with two different types of VHF transmitters to track their movements. Seventeen beavers were tagged with Alterra TX30.3A1 intraperitoneal 30-MHz radio transmitter (63 g) equipped with a temperature sensor and movement sensor (Alterra (IBN/DLO), 6700 AA Wageningen, the Netherlands). These transmitters were implanted into the peritoneal cavity, and for this study, only the radio signal was utilized, while the temperature and movement data were not used. Beavers tagged with these implants were anesthetized immediately after capture using a mixture of medetomidine (0.05 mg/kg), ketamine (5 mg/kg) and butorphanol (0.1 mg/kg) (Ranheim et al. 2004) and released within 5 h after capture (Sharpe and Rosell 2003). One beaver tagged with an internal implant died post-operatively, while all other beavers were successfully released back into their territory following captures (Ranheim et al. 2004). No negative impact on behaviour or movements was observed in the days following surgery other than an increase in time spent in the lodge the following 2 days (Sharpe and Rosell 2003; Ranheim et al. 2004). Long-term monitoring showed that the beavers continued to reside within their territories 17–24 months after tagging (Ranheim et al. 2004). Another 24 beavers were tagged with external tail-mounted transmitters (Advanced Telemetry System, Isanti, Minnesota, USA, Model 16M ear tag for beaver tail, weight 38 g), or proximity loggers with VHF transmitters also mounted on the beaver tail (Sirtrack Ltd., Private Bag 1403, Goddard Lane, Havelock North 4157, New Zealand) (Sharpe and Rosell 2003; Campbell 2010). These beavers were not anesthetized as the tail consists mostly of adipose tissue. A small 5-mm hole was made onto one side of the tail, 10 cm from the base, and the radio transmitter was fitted using a screw, washer and nut through the hole. Each beaver was released within 10 min after capture and most were observed engaging in normal behaviour shortly after release (Sharpe and Rosell 2003).

Data collection

Observations of radio-tracked beavers were conducted between March and August 2000, April and August 2001, May and August 2006 and April and September in 2007. It was not possible to record data blind because our study involved focal animals in the field. Tracking of beavers tagged with internal transmitters started 1 week following surgery, while tracking of beavers with external tail transmitters started no sooner than 3 days following capture. Individual beavers were tracked during randomly selected nights from the time they emerged from their lodge after 19:00 until they returned to the lodge after 08:00, which we define as their active period (Campbell 2010). The behaviour of each focal beaver was continuously monitored by two observers in a motorized boat using binoculars and spotlights (Sharpe and Rosell 2003). Such observations from boats have minimal impact on the beavers' behaviour (Rosell and Hovde 2001). To determine seasonal activity budgets, circadian activity rhythms and diet, we registered the beaver's behaviour every minute if it was clearly visible and noted its location every 15 min. The beaver behaviours were categorized as the following: foraging, travelling, in lodge, diving, defensive, alerted, social/grooming or other (see Table S1 for details). The most common activity types, which were used in the analysis, included foraging, traveling and being in the lodge. Foraging observations included all handling of potential food items in the water or on land, which included observations such as felling trees, eating food items close to the water, diving and foraging on aquatic vegetation. Travelling described all movement, either on land or in the water, independent of distance from the lodge. Being in the lodge included all observations of beavers either sitting on top of or directly next to a lodge or being inside the lodge (Table S1). Food items were classified as trees/shrubs, aquatic vegetation or herb/grasses. When possible to observe, the foraged trees/shrubs were categorized as either deciduous or coniferous.

Data preparation

We used the coordinates of all beaver observations to create a 95% kernel home range for each family in each year with the adehabitatHR package in R version 3.6.1 (Calenge 2006; R Core Team 2019). Beaver observations outside their territory, which are typically explorative trips into other territories, were excluded from the analysis. Beavers often have several lodges and burrows throughout their territory (Żurowski 1992), and several lodge locations were sometimes registered within the same territory during 1 year. To establish which lodge functioned as the beavers' main lodge that year, all observations of a beaver in a lodge or burrow were pooled according to territory and year. We then created a 10% kernel range of these positions to find the lodge that was used most intensely. For each of these kernel polygons, we estimated the geographical centre point and determined this as the location of the main lodge. Regardless, observations of beavers spending time in lodges other than their main lodge were recorded as being in a lodge. We calculated the Euclidean distance from the main lodge to each beaver observation while outside a lodge, within each territory and year. As the rivers in the study area mostly run straight, and beavers rarely move long distances on land, most observations were made down river or upriver from the main lodge and rarely involved long distances moved on land. The date of each beaver observation was transformed to Julian day where each day was assigned a number, starting from one on January 1 and ending with 365 on December 31. The time of each observation was transformed to active hour, which means that the first hour of observations from 19:00 to 20:00 became active hour 1, and the last observations from 07:00 to 08:00 became active hour 13. A few observations of beavers were made outside this principle activity period, but these were subsequently removed from the analysis, as we did not have sufficient observations to model beaver activity during those times. For the first part of the analysis, we modelled the probability of the beavers' main activities (foraging, being in a lodge and travelling), where Julian day and activity hour were used as proxies for seasonal and daily changes. We used a subset of 15-min time point observations for which we had spatial coordinates to factor in the distance to the main lodge. For the second part of the analysis, we explored probability of use of different food items (trees/shrubs, aquatic vegetation and herbs/grasses), using all 1-min time point samples involving foraging.

Statistical analysis

We used generalized additive mixed models (GAMMs) to evaluate the probability of beavers engaging in each activity, and foraging on different food items, using the R package 'gamm4' and maximum likelihood estimation (ML) (Wood et al. 2017). Penalized regression splines and cross-validation were used to find the appropriate level of smoothing (Zuur 2012; Zuur et al. 2014; Wood et al. 2017). We constructed separate sets of candidate models for each activity (foraging, travelling and being in a lodge) and food item (trees/shrubs, aquatic vegetation and herbs/grasses), using the occurrence of that activity or food item as a binomial response variable (exhibiting a focal behaviour or foraging on food item = 1, exhibiting other behaviours or foraging on other items = 0). For modelling the probability that a given activity would occur at any given point in time, we included the following explanatory variables as splines: Julian day and active hour. We considered a potential interaction between sex and Julian day and active hour to explore whether the sexes had different seasonal activity budgets and circadian activity rhythms. We also included distance to lodge interacting with sex to explore whether males moved further from the lodge than females and age as linear fixed effects. To model the probability that the beavers would use different food items, we included a spline on Julian day interacting with sex and age as a linear fixed effect. We included beaver identity (ID) and year as crossed random factors on the intercept in all candidate models. A model with no fixed effects, but only the random factors, was also included in every candidate model set (Table S2). We used Spearman correlation test with a cut-off value of 0.6 and variance inflation factors (VIF) with a cut-off value of >3 as indicators of collinearity between the numerical explanatory variables (Zuur et al. 2009). None of the variables were found to be collinear and they were therefore all retained in the analysis.

For model selection, we used the 'model.sel' function in the MuMIn package (Barton 2011), which compares a priori defined candidate models based on Akaike information criterion (AIC) corrected for a small sample size (AIC_c) (Anderson 2007; Zuur et al. 2009; Arnold 2010). An extension of the MuMIn package using a wrapper function was enabled to allow for model comparison using AIC_c with GAMM models (Barton 2011). If several of the models had a ΔAIC_c value (i.e. the difference between the AIC_c score of any candidate model and the top ranked model) that ranged between 0 and 2, we selected the most parsimonious model to avoid the inclusion of 'pretending variables' (i.e. confounding variables or variables with limited biological importance) (Arnold 2010). We chose to select the most parsimonious model to plot the model effect instead of model averaging due to nested nature of the candidate models with many containing the same variables (Harrison et al. 2018). To validate the models, we plotted the model residuals against each explanatory variable and visually inspected patterns or trends in the residuals (Zuur 2012). All geographical and statistical analyses were conducted using R version 3.6.1 (R Core Team 2019).

Data availability

The datasets analysed during the current study are available from the USN Research Data Achieve at https://doi.org/10.23642/usn.14191427

Results

Activity budgets

We analysed 5430 observations of beaver behaviour at 15-min intervals during 225 observation nights, which included 20 beaver territories and 41 beavers, of which 16 were females (all dominant) and 25 were males (18 dominants and 7 where offspring from previous years). Ages of the beavers varied from 2 to 12 years. Observations were conducted from March to September, and in each month, 211–1459, 15-min observations were recorded. Being in a lodge was the most common activity accounting for 34% of all observations, followed by foraging (30%) and travelling (28%). Beavers usually foraged alone and were only accompanied by another beaver in 6% of all foraging observations, which was either an offspring/parent (51%) or partner (34%). Males and females did not differ in terms of time spent with a kit while outside the lodge.

We found seasonal activity budgets and circadian activity rhythms in time spent foraging, being in a lodge and travelling (Table 1). The models all explored the probability of the beavers engaging in a certain behaviour in relation to the explanatory variables, and not time spent on each activity, but for simplicity, we refer to the model outcomes as increasing foraging, travelling or time spent in lodge. Two candidate models exploring foraging received similar support, and the most parsimonious contained age, distance to main lodge and active hour, as well as Julian day, yet no sex-specific effects (Table S2). Beavers foraged consistently throughout the study period, and we found no seasonal peaks in foraging activity (Fig. 1a, Table 1). We found a weak daily trend in probability of foraging with less foraging in the evening and a slight increase towards 04:00 followed by a slight decrease during morning (Fig. 2a, Table 1). Beavers foraged more with increasing distance from the main lodge (Fig. 3a, Table 1) and with increasing age (Fig. 4a, Table 1).

The most parsimonious model exploring the probability of being in the lodge contained age, active hour and Julian day interacting with sex (Table S2). Males and females displayed different seasonal trends in time spent in the lodge, with females spending more time in the lodge during spring (March–May), while gradually decreasing time spent in the lodge towards late summer. Males also spent more time in the lodge from April to May, and again from August to September, which contrasted with females that were less likely to spend time in the lodge during this time (Fig. 1b, Table 1). Beavers spent most time in the lodge during early evening and late morning (Fig. 2b, Table 1). Distance to lodge was not included as an explanatory variable in the lodge models, but time spent in the lodge increased slightly in older beavers.

The most parsimonious candidate model predicting the probability of travelling contained age, active hour and

Table 1 Summary of most parsimonious model to predict the probability of beaver foraging, travelling and being in a lodge in spring–late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway. Each model was fitted with a GAMM with year and beaver ID as random factors on the intercept. Observations of beaver activity are collected from 41 beavers (*N*=5430). Estimates (β**)** and standard errors (SE) are given for the intercept and linear terms. Each spline variable included in the model is specified with effective degrees of freedom (edf) and test statistics (Ch.sq)

Foraging	β	SE	Smooth terms	edf	Ch.sq
Intercept	−1.7667	0.36746	s(Julian_day)	1.941	1.426
Age	0.0742	0.04197	s(Active_hou)	3.523	73.256
Distance_lodge	0.00108	0.00012			
Travelling	β	SE	Smooth terms	edf	Ch.sq
Intercept	−1.3447	0.42741	s(Julian_day):SexFemale	1	12.27
Age	−0.111	0.03545	s(Julian_day):SexMale	6.71	84.44
Distance_lodge	0.00175	0.00024	s(Active_hou)	6.93	50.88
SexMale	0.77299	0.24097			
Distance_lodge:SexMale	−0.0013	0.00027			
Lodge	β	SE	Smooth terms	edf	Ch.sq
Intercept	−1.1787	0.62497	s(Julian_day):SexFemale	1.923	49.89
Age	0.11615	0.05739	s(Julian_day):SexMale	6.932	69.82
SexMale	−0.4152	0.39969	s(Active_hou)	7.32	261.08

Julian day and distance to the main lodge interacting with sex (Table S2). The sexes differed slightly in travelling with females being less likely to travel during early spring, yet increasing travelling slightly towards late summer. Males travelled the most from May to July (Fig. 1c). The beavers were less likely to travel in early evening, while they travelled stably throughout the rest of the night, and with a slight increase in the morning (Table S2). Both males and females travelled more with increasing distance from the lodge, yet at the farthest distances, females were more likely to travel than males. Travelling also decreased slightly with increasing age of the beavers.

Food items

We used 3312 1-min time point samples from 37 beavers in 18 territories, including 13 females (all dominant) and 24 males (16 dominant and 5 offspring from previous years) for analysing the use of different food items. We could identify food items in 81% of beaver foraging observations. The most common food item were trees/shrubs, which were recorded in 72.8% of observations. Aquatic vegetation was registered in 16.4% of foraging observations and herbs/grasses in 10.8%. When the foraged tree type could be identified, deciduous trees/shrubs were the most common tree type in 90.7% of observations, while 9.2% were coniferous trees, which were mostly foraged during spring. Two models received equal support in predicting probability of beaver use of trees/shrubs and aquatic vegetation. The most parsimonious of these included a spline on Julian day as a sex-specific effect (Table S3). This revealed sex-specific differences in the seasonal use of trees/shrubs and aquatic vegetation (Table 2, Fig. 5a, b, c). Males used trees/shrubs throughout the whole study period, but with a small decrease during late spring and summer (May–July). Females, however, used trees/shrubs less during two periods of the year, first in mid-April, and then in mid-July, while simultaneously increasing their use of aquatic vegetation (Fig. 5a, b). Males also used more aquatic vegetation in spring. Among the candidate models in predicting the use of herbs/grasses, four models received equal support, and the most parsimonious contained only a spline Julian day, but no sex-specific differences (Table S3). Use of herbs/grasses was highest from May to July, but with overall lower probability of use compared to the two other food items (Table 2, Fig. 5c).

Discussion

Beavers displayed variation in both seasonal activity budgets and circadian activity rhythms and seasonal trends in the use of different food items, but we only observed some sex-specific differences. We did not find strong seasonal or daily trends in foraging, and there were no differences between the sexes in terms of foraging. This was contrary to expectations of increased female foraging in spring and during the night (a). As predicted, females spent more time in the lodge and less time travelling during spring (a) and subsequently decreased

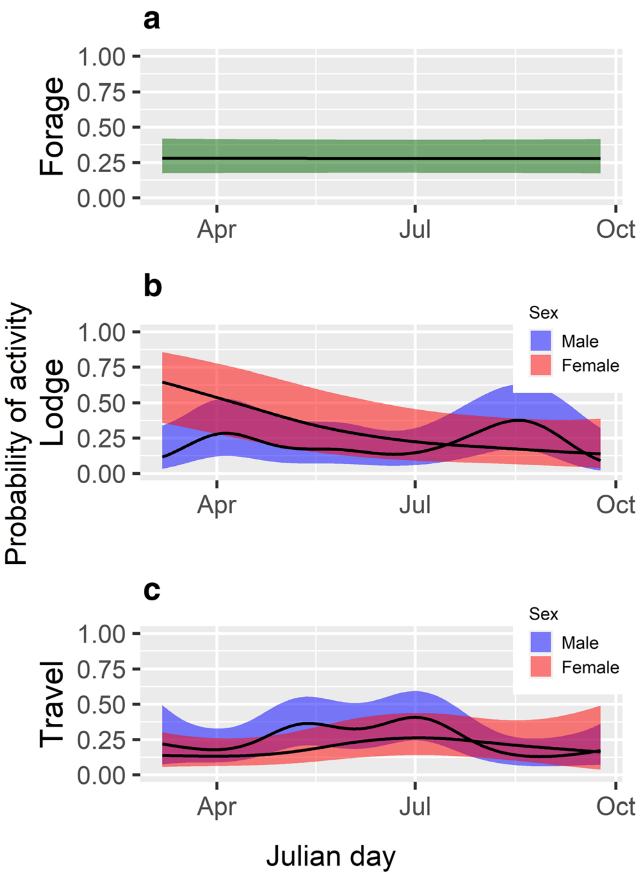

Fig. 1 Predicted effect of Julian day on the probability of Eurasian beaver foraging (**a**), being in a lodge (**b**) and travelling (**c**). Julian day has been converted back to month for plotting purposes. The line represents the estimated smoother produced by a GAMM model, while the polygons represent the 95% confidence interval around the estimate. The red lines represent females and the blue males. There was no difference between males and females for foraging, and both are represented with a green line. The predictions are based on beaver activity observations from spring to late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway

time spent in lodge and slightly increased travelling in late summer (b). However, the differences in seasonal activity budgets between the sexes were very subtle. Males and females did not differ in terms of circadian activity rhythm. Our prediction that females used nutrient-rich food such as aquatic vegetation and less wood during spring and late summer was supported, but we found no difference in the use of herbs/grasses to the sexes contrary to our prediction (c).

Activity budgets in comparative perspective

When beavers were outside the lodge, foraging was their main activity followed by travelling, which reaffirms the general trend found in Eurasian beavers by Sharpe and Rosell (2003), but foraging was an even more important daily activity in North American beavers (Gallant et al. 2016). There are several potential explanations why beavers increase foraging

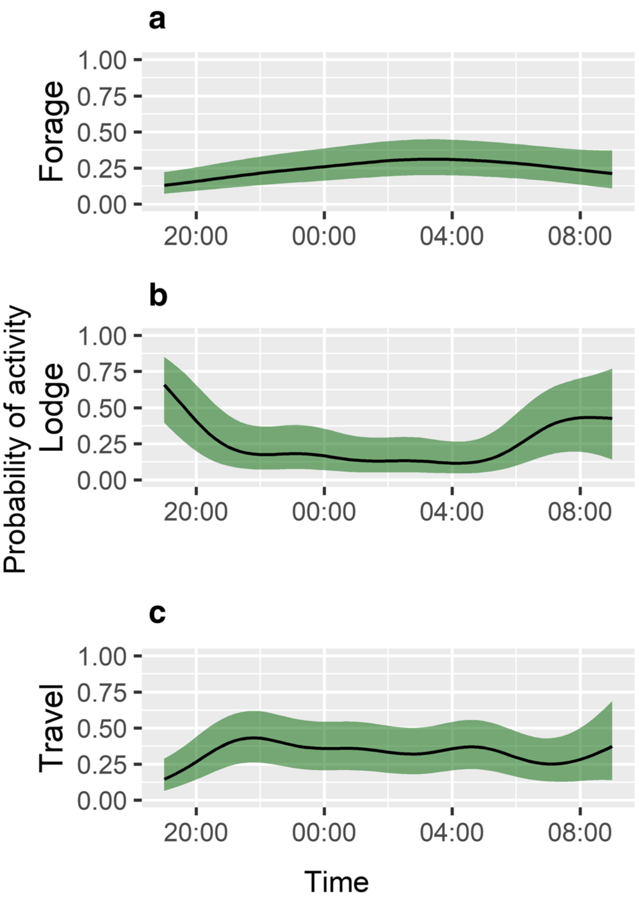

Fig. 2 Predicted effect of active hour on the probability of Eurasian beaver foraging (**a**), being in a lodge (**b**) and travelling (**c**). Active hour represents the beavers' active hours from 19:00 until 08:00 and has been converted back to hour of the day for plotting purposes. The line represents the estimated smoother produced by a GAMM model, while the polygons represent the 95% confidence interval around the estimates. There was no difference between males and females, and both are represented with a green line. The predictions are based on beaver activity observations from spring to late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway

activity with increasing distance from the lodge. Dominant beavers often spend more time close to the border to the neighbouring territory where they patrol for intruders (Graf et al. 2016), and they might simultaneously forage. Depletion of resources in a beaver territory may lead to both foraging further inland or abandonment of the territory (Goryainova et al. 2014; Hood 2020) and together with build-up of plant defences in browsed vegetation (Bryant et al. 1991) might induce foraging further away. As food sources such as aquatic vegetation and herbs/grasses are only seasonally available, we were surprised not to find an overall increase in foraging during summer. Animals may display very different strategies to deal with fluctuations in food availability and quality even within the same species. In monomorphic red ruffed lemurs, males fed most often during seasonal food abundance, whereas female time spent feeding was stable throughout the year (Vasey 2005). Intense foraging during

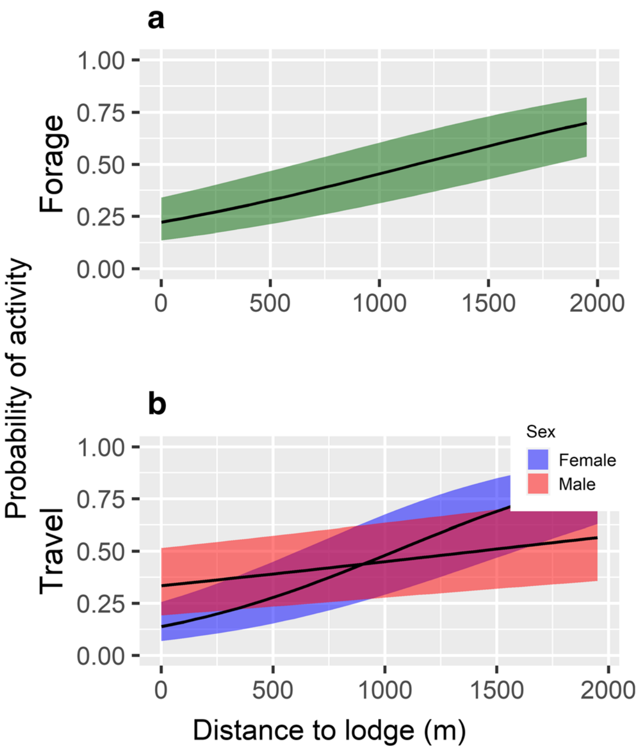

Fig. 3 Predicted effects of distance to the main lodge on the probability of Eurasian beaver foraging (**a**) and travelling (**b**). Distance to main lodge represents the Euclidian distance (m). The lines represent the estimated smoother produced by a GAMM model, while the polygons represent the 95% confidence interval around the estimates. There was no difference between males and females for foraging, and both are represented with a green line. The predictions are based on beaver activity observations from spring to late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway

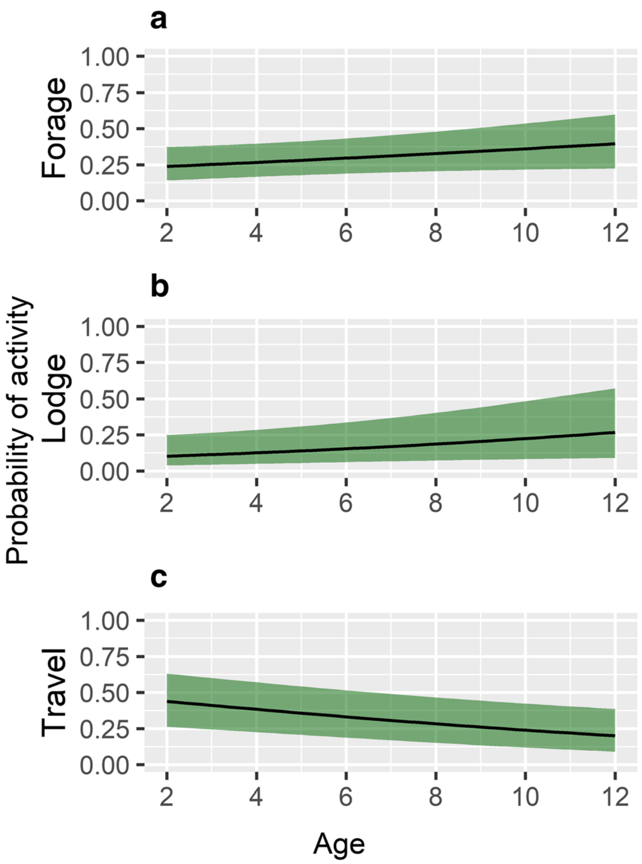

Fig. 4 Predicted effects of age (years) on the probability of Eurasian beaver foraging (**a**), being in lodge (**b**) and travelling (**c**). The line represents the estimated regression line, while the polygons represent the 95% confidence interval around the estimates. There was no difference between males and females, and both are represented with a green line. The predictions are based on beaver activity observations from spring to late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway

autumn is common in species that either hibernate or build food caches to get them through the winter (Welch et al. 1997; Lee 2002). Observations of beavers later in the autumn might have revealed larger increases in foraging activity (Potvin and Bovet 1975).

The beavers also displayed distinct circadian activity rhythms. Being in a lodge was, not surprisingly, most likely to occur in late evening and early morning, while they travelled more in the morning. The morning and early evening represents the start and end of the beaver's active period, which may explain these patterns (Sharpe and Rosell 2003). Circadian activity rhythms of animals may also be impacted by season (Pita et al. 2011; Pagon et al. 2013), which we did not account for. However, the subtle temporal variations that we found contrast with Sharpe and Rosell (2003) who found no significant differences in activity patterns when comparing different parts of the season and night. This illustrates how temporal modelling of activity budgets with Julian day as a continuous variable may reveal more subtle variations in animal behaviour.

Sex-specific temporal activity budgets

Due to the energetic cost of gestation and lactation, a stronger increase in foraging activity among females would be expected during the reproductive period (Clutton-Brock et al. 1982; Logan and Sanson 2003; Vasey 2005). Increased time spent foraging has been observed in reproducing females during the reproductive period in other monomorphic animals such as meerkats (*Suricata suricatta)* (Doolan and Macdonald 1996), tree rats (*Thallomys nigricauda*) (Eccard et al. 2004), and female birds during incubation (Hedd et al. 2014). Female beavers not foraging more than males in spring may indicate that beavers display traits of an income breeder relying on previously stored fat resources (Rödel et al. 2015). Rainfall during the previous autumn has been shown to be inversely related to beaver reproduction the following year, probably due to rain reducing growth rates of the vegetation (Campbell et al. 2013). Females may display increased foraging activity during autumn in the year prior to reproduction, which we did not explore in this study. In

Table 2 Summary of the most parsimonious models to predict the probability of beaver use of trees/shrubs, aquatic vegetation and herbs/grasses in spring–late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway. Observations of beaver activity are collected from 37 beavers (*N*=3312). Each model was fitted with a GAMM with year and beaver ID as random variables on the intercept. Estimates (β**)** and standard errors (SE) are given for the intercept and linear terms. Each spline variable included in the model is specified with effective degrees of freedom (edf) and test statistics (Ch.sq)

Trees/shrubs	β	SE	Splines	edf	Ch.sq
Intercept	1.29913	0.40084	s(Julian_day):SexFemale	8.052	113.14
SexMale	−0.0661	0.4615	s(Julian_day):SexMale	4.818	29.11
Aquatic	β	SE	Splines	edf	Ch.sq
Intercept	−3.4382	0.8064	s(Julian_day):SexFemale	7.981	180.82
SexMale	0.2895	0.8796	s(Julian_day):SexMale	6.997	58.05
Herbs/grasses	β	SE	Splines	edf	Ch.sq
Intercept	−2.5146	0.1795	s(Julian_day)	5.086	77.22

monomorphic plain zebra (*Equus burchelli*) and African oryx (*O. gazella*), the sexes also did not differ in time spent foraging, but rather in bites taken per minute (Neuhaus and Ruckstuhl 2002; Ruckstuhl and Neuhaus 2009), which we could also not account for due to limited visibility of nocturnal observations.

Female beavers did, however, increase time spent in the lodge during spring, which most likely relates to giving birth and weaning kits (Mayer et al. 2017a). Based on the increased lodge occupancy, a consequential reduction in foraging could be expected, but we did not observe this. The simultaneous reduction in travelling during spring could allow for more time spent in the lodge together with other activities not modelled in the current study (Sharpe and Rosell 2003), while foraging remained unaffected. Both males and females travelled more with increasing distance to the main lodge, and females even more than males at the furthest distances. This does not necessarily mean that females travel further from the lodge, but when observed far away, they are most likely travelling. The furthest distances away from the lodge likely represent the border with another territory, which is regularly patrolled and scent marked by the dominant pair (Rosell et al. 1998; Hohwieler et al. 2018). The purpose of travelling is often difficult to unravel and may relate to both foraging and patrolling (Graf et al. 2016). In roe deer (*Capreolus capreolus*), which have very low levels of body size dimorphism, males increase activity levels during periods when increased territorial defence is needed, suggesting that differing circadian activity rhythms between the sexes may be more pronounced in periods with different investment in reproduction or territorial protection (Pagon et al. 2013). Young beavers commonly disperse from their natal territory in spring in search of a new territory (Sun et al. 2000), and dominant male beavers may therefore increase patrolling and scent marking efforts during this time (Rosell et al. 1998).

Foraging behaviour and food use

The beavers were mostly observed foraging solitary, but when accompanied by another beaver, this was either their offspring or partner, which confirms previous studies (Brady and Svendsen 1981; McClanahan et al. 2020). Solitary foraging

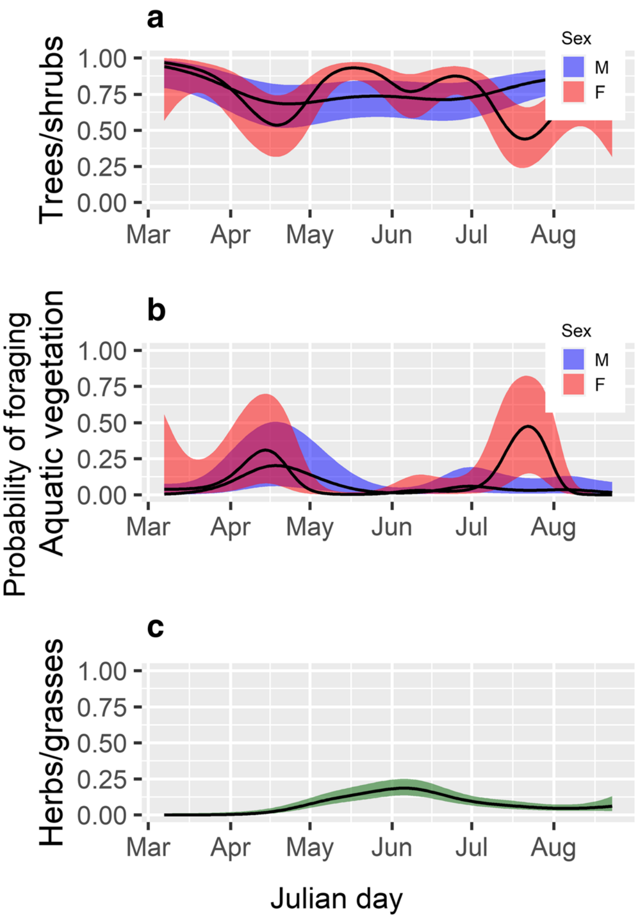

Fig. 5 Predicted effects of the probability of beaver use of trees/shrubs (**a**), aquatic vegetation (**b**) and herbs/grasses (**c**) across the study season (5 March–23 September). The lines represent the estimated smoother based on a GAMM model, while the polygons represent the 95% confidence interval around the estimates. The red lines represent females and the blue males. There was no difference between males and females for use of herbs/grasses, and both are represented with a green line. The predictions are based on beaver activity observations from spring to late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway

behaviour of a group-living species may occur due to increased predation risk involved with group foraging (Creel and Creel 2002). Elk (*Cervus canadensis*), for example, foraged in groups half the size when wolves (*C. lupus*) were present within the same drainage, compared to days when wolves were absent (Creel et al. 2005).

We confirmed that trees/shrubs were the most commonly used food item, followed by aquatic vegetation and herbs/grasses. Woody material from trees/shrubs is an important part of the beaver diet throughout the year, but has a high crude fibre content that represents a lower quality diet (Bełżecki et al. 2018). Deciduous trees/shrubs were the most common tree type used, but we also observed occasional foraging on conifers during spring (Jenkins 1979; Haarberg and Rosell 2006). Much of the energy in woody material is contained within the cell walls and hard to access, which may explain why beavers supplement with more nutritional foods during summer (Nolet et al. 1995). Another monomorphic species relying mostly on trees as food sources, the Finlayson's squirrel (*Callosciurus finlaysonii*), also displayed a seasonal shift from buds and tree bark towards more nutritional flowers, seeds and fruits during summer (Bertolino et al. 2004). We found a similar shift towards aquatic vegetation in spring. Several North American studies concluded that aquatic vegetation is a vital part of the beaver diet during summer (Svendsen 1980; Belovsky 1984; Milligan and Humphries 2010; Bergman et al. 2018). Fewer studies have reported Eurasian beavers foraging on aquatic vegetation, but it has been documented from early spring to autumn (Histøl 1989; Law et al. 2014a, 2014b). Beavers are energy maximizers and select food sources that return the most energy over time, but they also require a diverse diet to fulfil their nutritional needs (Belovsky 1984; Doucet and Fryxell 1993; Nolet et al. 1995). Seasonal variations in both availability and nutritional content of food items may have a large impact on choosy opportunistic foragers such as beavers and result in differing diet between males and females due to differing energy budgets.

Sex-specific seasonal food use

The beavers' use of food items varied according to the season, and males and females differed in seasonal use of trees/shrubs and aquatic vegetation, but not herbs/grasses. Females were less likely to use trees/shrubs between April and May, which is directly prior to the birthing period (Parker and Rosell 2001; Mayer et al. 2017b), but also after the reproductive period in July–August. In both these periods, the reduction of trees/shrubs was accompanied with a shift towards increased use of aquatic vegetation. Dietary differences between the sexes also occur in other monomorphic species such as thick-billed murres (*Uria lomvia*) and northern gannet (*Morus bassanus*) where females dove deeper than males, presumably to select different prey types (Lewis et al. 2002; Elliott et al. 2010). Differences in foraging locations may also relate to predation risk where one sex forages in high-risk locations, while the partner prioritizes safety over energy maximization and thereby increases overall reproductive success (Elliott et al. 2010). Beavers are most vulnerable to predation when foraging on land (Gable et al. 2018), and females shifting to increased use of aquatics during spring may represent a more risk-aversive foraging strategy (Fryxell and Doucet 1993). Aquatic vegetation also requires less handling time than other food resources (Fryxell and Doucet 1993; Severud et al. 2013), which may be beneficial for females while caring for kits in the lodge.

Different seasonal food use may also relate to nutrient availability and nutritional requirements of reproducing females. A seasonal shift from woody vegetation towards more aquatic vegetation and herbs/grasses is common when beavers diversify their diet in the summer to obtain additional nutrients (Brenner 1964; Nolet et al. 1995; Bełżecki et al. 2018), and is common also in other species foraging on trees (Bertolino et al. 2004). Beaver foraging on conifers mostly occurs during spring, which may suggest selection for certain temporally available nutrients (Jenkins 1979). Sami communities in Fennoscandia used to utilize Scots pine as a traditional food source, especially during spring and summer – most likely because of raised starch levels in the trees during that time (Rautio et al. 2013). Black bears also cause damage to managed conifer stands to gain access to sapwood during spring (Ziegltrum 2004). Beavers shifting towards aquatic vegetation in spring may be influenced by higher available levels of nitrogen, phosphorus and sodium during that time (Nolet et al. 1995; Cebrian and Lartigue 2004; Shurin et al. 2006). Wild animals are commonly sodium-deficient due to low availability, and an increased need for sodium uptake is common in spring, especially for reproducing females during gestation and lactation (Blair-West et al. 1968; Weeks Jr and Kirkpatrick 1976). Moose (*Alces alces*) also forage on aquatic plants during spring and early summer to fulfil sodium requirements (Fraser et al. 1982, 1984). Nutritional needs may explain the two peaks of female use of aquatic vegetation prior to and after the lactation period.

Conclusion

Observing beaver behaviour across seasons and nights over multiple years gave us a unique insight into their temporal activity and foraging behaviour. Females likely adapted their seasonal activity budgets to spend more time in the lodge during reproduction, but without reducing foraging activity, while compensating in summer and early autumn with increased travelling and reduction in time spent in lodge. Differences between males and females were especially apparent in the use of different food items, which may relate to varying strategies to deal with predation risk and nutritional and energetic requirements of reproducing females. Temporal modelling of activity budgets and foraging allowed us to identify subtle variations in activity budgets and foraging on different food items between the sexes. These differences suggest that seasonal adaptions may be vital for both survival and reproduction of monogamous and monomorphic species.

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Declarations

Ethics approval All animal capture and tagging methods were approved by the Directorate of Nature management (00/45-ARTS/VI/GSy, 2001/7552, 05/9639) and the Norwegian Experimental Animal Board (id 742), as well as special permission to capture beavers within the Nature Reserve of Årnesbukta (2000/1808, 2001/1661, 2006/2642). The use of animals adheres to the guidelines set forth by the Animal Behaviour Society/Association for the Study of Animal Behaviour (ASAB/ABS 2020) and guidelines and regulations of the University of South-Eastern Norway.

Conflict of interest The authors declare no conflict of interest.

References

Anderson DR (2007) Model based inference in the life sciences: a primer on evidence. Springer, New York

Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. J Wildlife Manage 74:1175–1178. https://doi.org/10.2193/2009-367

Arnold W, Ruf T, Loe LE, Irvine RJ, Ropstad E, Veiberg V, Albon SD (2018) Circadian rhythmicity persists through the polar night and midnight sun in Svalbard reindeer. Sci Rep 8:1–12. https://doi.org/10.1038/s41598-018-32778-4

ASAB/ABS (2020) Guidelines for the treatment of animals in behavioural research and teaching. Anim Behav 159:1–11. https://doi.org/10.1016/j.anbehav.2019.11.002

Barton K (2011) Model selection with MuMIn and GAMM. https://r-forge.r-project.org/scm/viewvc.php/*checkout*/pkg/inst/doc/gamm.pdf?revision=99&root=mumin&pathrev=103. Accessed at: 9 March 2021

Belovsky GE (1984) Summer diet optimization by beaver. Am Midl Nat 111:209–222. https://doi.org/10.2307/2425316

Bełżecki G, Miltko R, Kowalik B, Kędzierska A, Demiaszkiewicz AW, Lachowicz J, Giżejewski Z, Obidziński A, Giżejewski Z, McEwan NR (2018) Seasonal variations of the digestive tract of the Eurasian beaver *Castor fiber*. Mammal Res 63:21–31. https://doi.org/10.1007/s13364-017-0337-x

Bergman BG, Bump JK, Romanski MC (2018) Revisiting the role of aquatic plants in beaver habitat selection. Am Midl Nat 179:222–246. https://doi.org/10.1674/0003-0031-179.2.222

Bertolino S, Mazzoglio PJ, Vaiana M, Currado I (2004) Activity budget and foraging behavior of introduced *Callosciurus finlaysonii* (Rodentia, Sciuridae) in Italy. J Mammal 85:254–259. https://doi.org/10.1644/BPR-009

Bischof R, Loe LE, Meisingset EL, Zimmermann B, Moorter BV, Mysterud A (2012) A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? Am Nat 180:407–424. https://doi.org/10.1086/667590

Blair-West J, Coghlan JP, Denton DA, Nelson JF, Orchard E, Scoggins BA, Wright KM, Junquira CL (1968) Physiological, morphological and behavioural adaptation to a sodium deficient environment by wild native Australian and introduced species of animals. Nature 217:922–928. https://doi.org/10.1038/217922a0

Brady CA, Svendsen GE (1981) Social-behaviour in a family of beaver, *Castor canadensis*. Biol Behav 6:99–114

Brenner FJ (1964) Reproduction of the beaver in Crawford County, Pennsylvania. J Wildlife Manage 28:743–747. https://doi.org/10.2307/3798790

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal 80:385–399. https://doi.org/10.2307/1383287

Bryant JP, Provenza FD, Pastor J, Reichardt PB, Clausen TP, du Toit JT (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annu Rev Ecol Evol S 22:431–446. https://doi.org/10.1146/annurev.es.22.110191.002243

Burke CM, Montevecchi WA, Regular PM (2015) Seasonal variation in parental care drives sex-specific foraging by a monomorphic seabird. PLoS ONE. 10:e0141190. https://doi.org/10.1371/journal.pone.0141190

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Campbell RD (2010) Demography and life history of the Eurasian beaver *Castor fiber*. PhD thesis, Merton College, Oxford, UK

Campbell RD, Rosell F, Nolet BA, Dijkstra VAA (2005) Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? Behav Ecol Sociobiol 58:597–607. https://doi.org/10.1007/s00265-005-0942-6

Campbell RD, Newman C, Macdonald DW, Rosell F (2013) Proximate weather patterns and spring green-up phenology effect Eurasian beaver (*Castor fiber*) body mass and reproductive success: the implications of climate change and topography. Glob Change Biol 19:1311–1324. https://doi.org/10.1111/gcb.12114

Cebrian J, Lartigue J (2004) Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecol Monogr 74:237–259. https://doi.org/10.1890/03-4019

Clutton-Brock TH, Iason GR, Albon SD, Guinness FE (1982) Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. J Zool 198:227–236. https://doi.org/10.1111/j.1469-7998.1982.tb02072.x

R Core Team (2019) R: A language and environment for statistical computing. Computing, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org

Creel S, Creel NM (2002) The African wild dog: behavior, ecology, and conservation. Princeton University Press, Princeton, New Jersey

Creel S, Winnie J Jr, Maxwell B, Hamlin K, Creel M (2005) Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397. https://doi.org/10.1890/05-0032

Doolan SP, Macdonald DW (1996) Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. J Zool 239:697–716. https://doi.org/10.1111/j.1469-7998.1996.tb05472.x

Doucet CM, Fryxell JM (1993) The effect of nutritional quality on forage preference by beavers. Oikos 67:201–208. https://doi.org/10.2307/3545464

Drickamer LC, Vessey SH, Jakob EM (2002) Animal behavior, 5th edn. McGraw-Hill, New York

Eccard JA, Meyer J, Sundell J (2004) Space use, circadian activity pattern, and matting system of the nocturnal tree rat *Thallomys nigricauda*. J Mammal. 85:440–445. https://doi.org/10.1644/BEM-039

eKlima (2020) Gridded values for counties, with trend. Norwegian Meteorological Institute, https://seklima.met.no/observations/

Elliott KH, Gaston AJ, Crump D (2010) Sex-specific behavior by a monomorphic seabird represents risk partitioning. Behav Ecol 21:1024–1032. https://doi.org/10.1093/beheco/arq076

Fraser D, Thompson B, Arthur D (1982) Aquatic feeding by moose: seasonal variation in relation to plant chemical composition and use of mineral licks. Can J Zool 60:3121–3126. https://doi.org/10.1139/z82-396

Fraser D, Chavez ER, Palohelmo JE (1984) Aquatic feeding by moose: selection of plant species and feeding areas in relation to plant chemical composition and characteristics of lakes. Can J Zool 62:80–87. https://doi.org/10.1139/z84-014

Fryxell JM, Doucet CM (1993) Diet choice and the functional response of beavers. Ecology 74:1297–1306. https://doi.org/10.2307/1940060

Gable TD, Stanger T, Windels SK, Bump JK (2018) Do wolves ambush beavers? Video evidence for higher-order hunting strategies. Ecosphere 9:e02159. https://doi.org/10.1002/ecs2.2159

Gallant D, Bérubé CH, Tremblay E, Vasseur L (2004) An extensive study of the foraging ecology of beavers (*Castor canadensis*) in relation to habitat quality. Can J Zool 82:922–933. https://doi.org/10.1139/z04-067

Gallant D, Léger L, Tremblay É, Berteaux D, Lecomte N, Vasseur L (2016) Linking time budgets to habitat quality suggests that beavers (*Castor canadensis*) are energy maximizers. Can J Zool 94:671–676. https://doi.org/10.1139/cjz-2016-0016

Ganzhorn JU, Pietsch T, Fietz J, Gross S, Schmid J, Steiner N (2004) Selection of food and ranging behaviour in a sexually monomorphic folivorous lemur: *Lepilemur ruficaudatus*. J Zool 263:393–399. https://doi.org/10.1017/S0952836904005394

Gerwing TG, Johnson CJ, Alström-Rapaport C (2013) Factors influencing forage selection by the North American beaver (*Castor canadensis*). Mamm Biol 78:79–86. https://doi.org/10.1016/j.mambio.2012.07.157

Goryainova ZI, Katsman EA, Zavyalov NA, Khlyap LA, Petrosyan VG (2014) Evaluation of tree and shrub resources of the Eurasian beaver (*Castor fiber* L.) and changes in beaver foraging strategy after resources depletion. Russ J Biol Invasions 5:242–254. https://doi.org/10.1134/S207511171404002X

Graf PM, Mayer M, Zedrosser A, Hackländer K, Rosell F (2016) Territory size and age explain movement patterns in the Eurasian beaver. Mamm Biol 81:587–594. https://doi.org/10.1016/j.mambio.2016.07.046

Haarberg O, Rosell F (2006) Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. J Zool 270:201–208. https://doi.org/10.1111/j.1469-7998.2006.00142.x

Halley D, Rosell F (2002) The beaver's reconquest of Eurasia: status, population development and management of a conservation success. Mamm Rev 32:153–178. https://doi.org/10.1046/j.1365-2907.2002.00106.x

Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CE, Robinson BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6:e4794. https://doi.org/10.7717/peerj.4794

Hedd A, Montevecchi WA, Phillips RA, Fifield DA (2014) Seasonal sexual segregation by monomorphic sooty shearwaters *Puffinus griseus* reflects different reproductive roles during the pre-laying period. PLoS ONE 9:e85572. https://doi.org/10.1371/journal.pone.0085572

Hertel AG, Steyaert SM, Zedrosser A, Mysterud A, Lodberg-Holm HK, Gelink HW, Kindberg J, Swenson JE (2016) Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. Behav Ecol Sociobiol *70*:831–842. https://doi.org/10.1007/s00265-016-2106-2

Histøl T (1989) Sommerdiett hos bever *Castor fiber* L. i et utvalg av skogsvann i Vennesla kommune. Vest Agder Fauna 42:96–103

Hjønnevåg ME (2020) Selection of aquatic vegetation in river habitats by Eurasian beaver (*Castor fiber*) in South-Eastern Norway. University of South-Eastern Norway, Norway, MSc thesis

Hohwieler K, Rosell F, Mayer M (2018) Scent-marking behavior by subordinate Eurasian beavers. Ethology 124:591–599. https://doi.org/10.1111/eth.12762

Hood GA (2020) Not all ponds are created equal: long-term beaver (*Castor canadensis*) lodge occupancy in a heterogeneous landscape. Can J Zool 98:210–218. https://doi.org/10.1139/cjz-2019-0066

Humphries MM, Thomas DW, Hall CL, Speakman JR, Kramer DL (2002) The energetics of autumn mast hoarding in eastern chipmunks. Oecologia 133:30–37. https://doi.org/10.1007/s00442-002-1014-5

Hut RA, Kronfeld-Schor N, van der Vinne V, De la Iglesia H (2012) In search of a temporal niche: environmental factors. Progr Brain Res 199:281–304. https://doi.org/10.1016/B978-0-444-59427-3.00017-4

Jenkins SH (1979) Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112–116. https://doi.org/10.1007/bf00346408

Kile NB, Nakken PJ, Rosell F, Espeland S (1996) Red fox, *Vulpes vulpes*, kills a European beaver, *Castor fiber*, kit. Can Field-Nat 110:338–339

Krojerová-Prokešová J, Barančeková M, Hamšíková L, Vorel A (2010) Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources. J Zool 281:183–193. https://doi.org/10.1111/j.1469-7998.2010.00695.x

Law A, Bunnefeld N, Willby NJ (2014a) Beavers and lilies: selective herbivory and adaptive foraging behaviour. Freshw Biol 59:224–232. https://doi.org/10.1111/fwb.12259

Law A, Jones KC, Willby NJ (2014b) Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation. Aquat Bot 116:27–34. https://doi.org/10.1016/j.aquabot.2014.01.004

Lee TH (2002) Feeding and hoarding behaviour of the Eurasian red squirrel *Sciurus vulgaris* during autumn in Hokkaido, Japan. Acta Theriol 47:459–470. https://doi.org/10.1007/bf03192470

Lewis S, Benvenuti S, Dall-Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. Proc R Soc Lond B 269:1687–1693. https://doi.org/10.1098/rspb.2002.2083

Logan M, Sanson GD (2003) The effects of lactation on the feeding behaviour and activity patterns of free-ranging female koalas (*Phascolarctos cinereus* Goldfuss). Aust J Zool 51:415–428. https://doi.org/10.1071/ZO03017

Mayer M, Robstad C, Serra EP, Hohwieler K, Fuchs B, Evans AL, Arnemo JM, Zedrosser A, Rosell F (2017a) Exposure of the Eurasian beaver (*Castor fiber*) towards hunters during the spring hunt. Department of Natural Sciences and Environmental Health. University College of Southeast Norway. Bø i Telemark, Norway

Mayer M, Künzel F, Zedrosser A, Rosell F (2017b) The 7-year itch: non-adaptive mate change in the Eurasian beaver. Behav Ecol Sociobiol 71:32. https://doi.org/10.1007/s00265-016-2259-z

Mayer M, Frank S, Zedrosser A, Rosell F (2019) Causes and consequences of inverse density-dependent territorial behavior and aggression in a monogamous mammal. J Anim Ecol 89:577–588. https://doi.org/10.1111/1365-2656.13100

McClanahan K, Rosell F, Mayer M (2020) Minding your own business: low pair cohesion in a territorial, monogamous mammal. Anim Behav 166:119–128. https://doi.org/10.1016/j.anbehav.2020.05.008

McLellan BN, Hovey FW (1995) The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Can J Zool 73: 704–712. https://doi.org/10.1139/z95-082

Milligan HE, Humphries MM (2010) The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic-terrestrial ecosystem linkages in a subarctic environment. Oikos 119:1877–1886. https://doi.org/10.1111/j.1600-0706.2010.18160.x

Mott CL, Bloomquist CK, Nielsen CK (2011) Seasonal, diel, and ontogenetic patterns of within-den behavior in beavers (*Castor canadensis*). Mamm Biol 76:436–444. https://doi.org/10.1016/j.mambio.2010.09.002

Neuhaus P, Ruckstuhl K (2002) The link between sexual dimorphism, activity budgets, and group cohesion: the case of the plains zebra (*Equus burchelli*). Can J Zool 80:1437–1441. https://doi.org/10.1139/z02-126

Nielsen JM, Clare EL, Hayden B, Brett MT, Kratina P (2018) Diet tracing in ecology: method comparison and selection. Methods Ecol Evol 9: 278–291. https://doi.org/10.1111/2041-210X.12869

Nolet BA, Rosell F (1994) Territoriality and time budgets in beavers during sequential settlement. Can J Zool 72:1227–1237. https://doi.org/10.1139/z94-164

Nolet BA, Hoekstra A, Ottenheim MM (1994) Selective foraging on woody species by the beaver *Castor fiber*, and its impact on a riparian willow forest. Biol Conserv 70:117–128. https://doi.org/10.1016/0006-3207(94)90279-8

Nolet BA, van der Veer PJ, Evers E, Ottenheim MM (1995) A linear programming model of diet choice of free-living beavers. Neth J Zool 45:315–337. https://doi.org/10.1163/156854295X00339

Novak M (1999) Beaver. In: Novak M, Baker JA, Obbard ME, Mallock B (eds) Wild furbearer management and conservation in North America. Queens Printer for Ontario, Toronto, Canada

Owen-Smith N, Fryxell J, Merrill E (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. Phil Trans R Soc B 365:2267–2278. https://doi.org/10.1098/rstb.2010.0095

Pagon N, Grignolio S, Pipia A, Bongi P, Bertolucci C, Apollonio M (2013) Seasonal variation of activity patterns in roe deer in a temperate forested area. Chronobiol Int 30:772–785. https://doi.org/10.3109/07420528.2013.765887

Parker H, Rosell F (2001) Parturition dates for Eurasian beaver *Castor fiber*: when should spring hunting cease? Wildlife Biol 7:237–241. https://doi.org/10.2981/wlb.2001.015

Pedersen HC, Follestad A, Gjershaug JO, Nilsen EB (2016) Statusoversikt for jaktbart småvilt. NINA Rapport 1178, Trondheim

Pelletier F, Festa-Bianchet M (2004) Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*. Behav Ecol Sociobiol 56:546–551. https://doi.org/10.1007/s00265-004-0820-7

Pérez-Barbería FJ, Gordon IJ, Pagel M (2002) The origins of sexual dimorphism in body size in ungulates. Evolution 56:1276–1285. https://doi.org/10.1111/j.0014-3820.2002.tb01438.x

Pita R, Mira A, Beja P (2011) Circadian activity rhythms in relation to season, sex and interspecific interactions in two Mediterranean voles. Anim Behav 81:1023–1030. https://doi.org/10.1016/j.anbehav.2011.02.007

Potvin CL, Bovet J (1975) Annual cycle of patterns of activity rhythms in beaver colonies (*Castor canadensis*). J Comp Physiol 98:243–256. https://doi.org/10.1007/bf00656972

Ranheim B, Rosell F, Haga HA, Arnemo JM (2004) Field anaesthetic and surgical techniques for implantation of intraperitoneal radio transmitters in Eurasian beavers *Castor fiber*. Wildlife Biol 10:11–15. https://doi.org/10.2981/wlb.2004.004

Rautio AM, Norstedt G, Östlund L (2013) Nutritional content of scots pine inner bark in northern Fennoscandia. Econ Bot 67:363–377. https://doi.org/10.1007/s12231-013-9254-3

Richter L, Balkenhol N, Raab C, Reinecke H, Meißner M, Herzog S, Isselstein J, Signer J (2020) So close and yet so different: the importance of considering temporal dynamics to understand habitat selection. Basic Appl Ecol 43:99–109. https://doi.org/10.1016/j.baae.2020.02.002

Roberts TH, Arner DH (1984) Food habits of beaver in east-central Mississippi. J Wildlife Manag 48:1414–1419. https://doi.org/10.2307/3801808

Rödel HG, Valencak TG, Handrek A, Monclús R (2015) Paying the energetic costs of reproduction: reliance on postpartum foraging and stored reserves. Behav Ecol 27:748–756. https://doi.org/10.1093/beheco/arv217

Rosell F, Hovde B (2001) Methods of aquatic and terrestrial netting to capture Eurasian beavers. Wildlife Soc B 29:269–274 http://www.jstor.org/stable/3784008

Rosell F, Sun LX (1999) Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *Castor fiber*. Wildlife Biol 5:119–123. https://doi.org/10.2981/wlb.1999.015

Rosell F, Bergan F, Parker H (1998) Scent-marking in the Eurasian beaver (*Castor fiber*) as a means of territory defense. J Chem Ecol 24: 207–219. https://doi.org/10.1023/A:1022524223435

Rosell F, Zedrosser A, Parker H (2010) Correlates of body measurements and age in Eurasian beaver from Norway. Eur J Wildlife Res 56:43–48. https://doi.org/10.1007/s10344-009-0289-9

Ruckstuhl KE (2007) Sexual segregation in vertebrates: proximate and ultimate causes. Integr Comp Biol 47:245–257. https://doi.org/10.1093/icb/icm030

Ruckstuhl KE, Neuhaus P (2009) Activity budgets and sociality in a monomorphic ungulate: the African oryx (*Oryx gazella*). Can J Zool 87:165–174. https://doi.org/10.1139/Z08-148

Ruckstuhl KE, Clutton-Brock T, Neuhaus P (2005) Sexual segregation and the ecology of the two sexes. Cambridge University Press, Cambridge, UK

Severud WJ, Windels SK, Belant JL, Bruggink JG (2013) The role of forage availability on diet choice and body condition in American beavers (*Castor canadensis*). Mamm Biol *78*:87–93. https://doi.org/10.1016/j.mambio.2012.12.001

Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. Funct Ecol 17:66–74. https://doi.org/10.1046/j.1365-2435.2003.00705.x

Sharpe F, Rosell F (2003) Time budgets and sex differences in the Eurasian beaver. Anim Behav 66:1059–1067. https://doi.org/10.1006/anbe.2003.2274

Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. Proc R Soc Lond B 273:1–9. https://doi.org/10.1098/rspb.2005.3377

Speakman JR (2008) The physiological costs of reproduction in small mammals. Phil Trans R Soc B 363:375–398. https://doi.org/10.1098/rstb.2007.2145

Sun L (2003) Monogamy correlates, socioecological factors, and mating systems in beavers. In: Reichard UH, Boesch C (eds) Monogamy: mating strategies and partnerships in birds, humans and other mammals Cambridge University Press, Cambridge, UK

Sun L, Müller-Schwarze D, Schulte BA (2000) Dispersal pattern and effective population size of the beaver. Can J Zool 78:393–398. https://doi.org/10.1139/z99-226

Svendsen GE (1980) Seasonal change in feeding patterns of beaver in Southeastern Ohio. J Wildlife Manage 44:285–290. https://doi.org/10.2307/3808390

Swinnen KRR, Hughes NK, Leirs H (2015) Beaver (*Castor fiber*) activity patterns in a predator-free landscape. what is keeping them in the dark? Mamm Biol 80:477–483. https://doi.org/10.1016/j.mambio.2015.07.006

Vasey N (2005) Activity budgets and activity rhythms in red ruffed lemurs (*Varecia rubra*) on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. Am J Primatol 66:23–44. https://doi.org/10.1002/ajp.20126

Weeks HP Jr, Kirkpatrick CM (1976) Adaptations of white-tailed deer to naturally occurring sodium deficiencies. J Wildlife Manage 40:610–625. https://doi.org/10.2307/3800555

Welch CA, Keay J, Kendall KC, Robbins CT (1997) Constraints on frugivory by bears. Ecology. 78:1105–1119. https://doi.org/10.1890/0012-9658(1997)078[1105:COFBB]2.0.CO;2

Wilsson L (1971) Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). PhD thesis, Stockholm University, Stockholm, Sweden

Wood S, Scheipl F, Wood MS (2017) Package 'gamm4'. Am Stat 45:339

Ydenberg RC, Krebs JR (1987) The tradeoff between territorial defense and foraging in the great tit (*Parus major*). Am Zool 27:337–346. https://doi.org/10.1093/icb/27.2.337

Ziegltrum GJ (2004) Efficacy of black bear supplemental feeding to reduce conifer damage in western Washington. J Wildlife Manage 68: 470–474. https://doi.org/10.2193/0022-541X(2004)068[0470:EOBBSF]2.0.CO;2

Zoller H, Drygala F (2013) Activity patterns of the invasive raccoon dog (*Nyctereutes procyonoides*) in North East Germany. *Folia* Zool 62: 290–296. https://doi.org/10.25225/fozo.v62.i4.a6.2013

Zub K, Szafrańska P, Konarzewski M, Redman P, Speakman JR (2009) Trade-offs between activity and thermoregulation in a small carnivore, the least weasel *Mustela nivalis*. Proc R Soc Lond B 276: 1921–1927. https://doi.org/10.1098/rspb.2008.1936

Żurowski W (1992) Building activity of beavers. Acta Theriol 37:403–411

Żurowski W, Kisza J, Kruk A, Roskosz A (1974) Lactation and chemical composition of milk of the European beaver (*Castor fiber* L.). J Mammal 55:847–850. https://doi.org/10.2307/1379417

Zuur AF (2012) A beginner's guide to generalized additive models with R. Highland Statistics Limited Newburgh, New York

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science and Business Media, New York

Zuur AF, Saveliev AA, Ieno EN (2014) A beginner's guide to generalised additive mixed models with R. Highland Statistics, New York

Size is not everything: Differing activity and foraging patterns between the sexes in a monomorphic mammal

Behavioral Ecology and Sociobiology

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Table S1 Recorded behaviours of Eurasian beavers observed during spring-late summer in the years 2000, 2001, 2006 and 2007 in South-Eastern Norway. Behaviour category shows the main categories in which these behaviours were classified. The number of observations in each category is displayed as N

Behaviour category	**Behaviour**	**N**
Alerted	Alerted, sitting or laying while being attentive of the surroundings. Sniffing in the air.	54
Defensive	Tail slap, stick display, conflict with other beaver, scent mark	86
Dive	Diving, but not into the lodge or for foraging.	29
Foraging	Walking with food, eating, felling trees/shrubs, diving for aquatics	1687
Lodge	On land by lodge, inside lodge, inside burrow, dived into lodge	1873

Still	Sitting still, still in the water	162
Social/grooming	Play wrestling, unknown social behaviour, self-grooming, nose to nose interaction, mutual grooming	92
Travelling	Walking, swimming	1579

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Table S2 Model structure and selection of candidate models for predicting probability of the beavers' main activities: foraging, travelling and being in lodge from spring-late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway. Observations of beaver activity is collected from 41 beavers (N=5430). Each model was fitted with a GAMM with year and beaver ID as random variable. Each candidate model is described in terms of which explanatory variables are included, degrees of freedom (df), Akaike Information Criterion corrected for a small sample size (AIC_c), delta AIC (ΔAIC_c) and model weight (AICcw)

Forage probability	n=1682	**df**	**AIC_c**	**ΔAIC_c**	**AICcw**
Age + s(Julian_day) + Distance_lodge + s(Active_hou)		9	6011.60	0.00	0.62
Age + s(Julian_day) + Distance_lodge*Sex + s(Active_hou)		11	6013.10	1.51	0.29
Age + s(Julian_day) + Distance_lodge + s(Active_hou, by=Sex) + Sex		14	6018.30	6.68	0.02

Age + s(Julian_day, by=Sex) + Sex + Distance_lodge + s(Active_hou, by=Sex)	5	6021.20	9.65	0.00
Age+ Distance_lodge	4	6072.50	60.96	0.00
Distance_lodge	6	6073.70	62.09	0.00
Age + Distance_lodge + Sex	5	6074.30	62.75	0.00
s(Active_hou)	7	6086.20	74.61	0.00
s(Julian_day)+ s(Active_hou)	8	6090.00	78.40	0.00
s(Active_hou, by=Sex) + Sex	10	6094.30	82.74	0.00
s(Julian_day)+ s(Active_hou, by=Sex) + Sex	12	6098.10	86.55	0.00
s(Julian_day, by=Sex)+s(Active_hou, by=Sex) + Sex	4	6121.20	88.85	0.00
Distance_lodge + Sex	3	6121.20	109.62	0.00
1	0	6189.50	177.95	0.00
Age	4	6190.90	179.28	0.00
Sex	4	6191.00	179.40	0.00
s(Julian_day)	5	6193.50	181.88	0.00
s(Julian_day, by=Sex) + Sex	8	6197.30	185.70	0.00
Travelling probability n=1561	**df**	**AICc**	**ΔAIC$_c$**	**AICcw**
Age + s(Julian_day, by=Sex) + Distance_lodge*Sex + s(Active_hou)	12	5696.7	0	0.932
Age + s(Julian_day)+ Distance_lodge*Sex + s(Active_hou)	10	5701.9	5.23	0.068
Age + s(Julian_day)+ Distance_lodge + s(Active_hou)	14	5720.3	23.58	0
Age + s(Julian_day, by=Sex) + Sex + Distance_lodge + s(Active_hou, by=Sex)	16	5723.8	27.13	0
Age + s(Julian_day) + Distance_lodge + s(Active_hou, by=Sex) + Sex	12	5727.9	31.19	0
s(Julian_day) + s(Active_hou)	14	5770	73.28	0
s(Julian_day, by=Sex)+ Sex + s(Active_hou, by=Sex)	6	5777.8	81.08	0
s(Julian_day)+ s(Active_hou, by=Sex) + Sex	5	5779.1	82.4	0
s(Julian_day, by=Sex) + Sex	8	5801	104.28	0
s(Julian_day)	6	5809.5	112.75	0
Age+Distance_lodge + Sex	7	5833.8	137.07	0
Age+ Distance_lodge	11	5835.7	138.99	0
Distance_lodge	9	5839.1	142.41	0
s(Active_hou)	7	5851.7	154.96	0
s(Active_hou, by=Sex) + Sex	5	5858.2	161.5	0
Distance_lodge + Sex	5	5865.6	168.85	0
Age	7	5894.6	197.88	0
Sex	4	5897	200.29	0
1	3	5899.9	203.2	0
Lodge probability n=1870	**df**	**AICc**	**ΔAIC$_c$**	**AICcw**
Age + s(Julian_day, by=Sex)+ Sex + s(Active_hou)	11	5408.8	0	0.999
Age + s(Julian_day, by=Sex) + Sex+ s(Active_hou, by=Sex)	13	5424.3	15.47	0
s(Julian_day, by=Sex)+ Sex + s(Active_hou, by=Sex)	12	5425.1	16.25	0
Age + s(Julian_day)+s(Active_hou)	8	5443.7	34.88	0
s(Julian_day)+ s(Active_hou)	7	5446.7	37.93	0
Age+ s(Julian_day) + s(Active_hou, by=Sex) + Sex	11	5459.3	50.49	0

s(Julian_day)+ s(Active_hou, by=Sex) + Sex	10	5461.8	53	0
s(Active_hou)	5	5510.8	102.01	0
s(Active_hou, by=Sex) + Sex	8	5525	116.22	0
s(Julian_day, by=Sex) + Sex	8	5663.7	254.92	0
s(Julian_day)	5	5707.5	298.71	0
Age	4	5778	369.16	0
1	3	5780.5	371.69	0

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Behavioral Ecology and Sociobiology

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Table S3 Model structure and selection diagnostics of candidate models for predicting probability of beaver use of trees/shrubs, aquatic vegetation and herbs/grasses from spring-late summer during the years 2000, 2001, 2006 and 2007 in South-Eastern Norway. Observations of beaver activity is collected from 37 beavers (N=3312). Each model was fitted with a GAMM with year and beaver ID as random variables on the intercept Each candidate model is described in terms of which explanatory variables are included, degrees of freedom (df), Akaike Information Criterion corrected for a small sample size (AIC$_c$), delta AIC (ΔAIC$_c$) and model weight (AICcw)

Wood probability	**df**	#	**AICc**	**ΔAIC$_c$**	**AICcw**
s(Julian day, by=Sex) + Sex + Age	9	1	3636.5	0	0.587
s(Julian day, by=Sex) + Sex	8	3	3637.2	0.7	0.413
s(Julian day) + Age	6	2	3693.6	57.07	0.00
s(Julian day)	5	5	3694.3	57.8	0.00
Age	4	4	3733.4	96.96	0.00
1	3	0	3733.8	97.32	0.00

Aquatic probability	**df**	#	**AICc**	**ΔAIC$_c$**	**AICcw**
s(Julian day, by=Sex) + Sex	8	3	2386.9	0.00	0.72
s(Julian day, by=Sex) + Sex + Age	9	1	2388.7	1.85	0.28
s(Julian day)	5	5	2491.3	104.39	0.00
s(Julian day) + Age	6	2	2493.1	106.27	0.00
1	3	0	2659.4	272.57	0.00
Age	4	4	2661.4	274.57	0.00
Herb & grass probability	**df**	#	**AICc**	**ΔAIC$_c$**	**AICcw**
s(Julian day) + Age	6	2	2192.2	0.00	0.36
s(Julian day)	5	5	2192.8	0.55	0.27
s(Julian day, by=Sex) + Sex + Age	9	1	2193.2	0.98	0.22
s(Julian day, by=Sex) + Sex	8	3	2194.1	1.86	0.14
1	3	0	2276.6	84.41	0.00
Age	4	4	2276.9	84.64	0.00

Article 2

Lodberg-Holm, H. K., Garvik, E. S., Fountain, M. S. Reinhardt, S., & Rosell, F. Crop circles revealed? Spatio-temporal patterns of beaver selection for agriculture and foraging on cereals. Second revision submitted to: Agriculture, Ecosystems & Environment.

Crop circles revealed? Spatio-temporal patterns of beaver foraging on cereal fields

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ABSTRACT

The surface of the Earth is increasingly dominated by human-modified ecosystems. As natural habitats dwindle, some wildlife species adapt to a landscape increasingly dominated by agriculture. Crops offer a predictable and nutritious food source and may become an integral part of the diet of some species. Eurasian beavers (*Castor fiber*) are closely associated with forests and wetlands, but as they recolonize their previous range following centuries of persecution, they settle into a highly anthropogenic landscape. We aimed to investigate spatio-temporal patterns of beaver foraging on cereals and use of crop fields among individual beavers. Within the study area of the Norwegian beaver project in southeastern Norway, we surveyed signs of beaver foraging in cereal fields during summer and early autumn in 2019 and 2020 and tracked beaver movement using GPS loggers. Beavers foraged mostly on the kernels of wheat (*Triticum aestivum*), followed by oats (*Avena sativa*), barley (*Hordeum sativum*), and lastly rye (*Secale cereale*). The probability of foraging decreased with increasing width of the canopy-covered buffer zone, and with increasing elevational gain from water. Foraging increased when cereal plants ripened in the early autumn, and beavers removed larger areas when foraging further away from water. There were considerable differences between territories, and while we could not identify the drivers of these differences, we found increasing use of crop fields among beavers of good body condition. Cereals might provide a significant food source for this generalist and opportunistic species during late summer. As wildlife populations expand into agricultural land, crops may become an increasingly important part of their diet, which requires research attention to avoid conflicts and improve our understanding of wildlife foraging ecology within anthropogenic landscapes.

Keywords: Crop depredation, Eurasian beaver, *Castor fiber*, agriculture, cereals.

1. Introduction

Crop depredation has the potential to create extensive conflicts with human communities (Conover et al., 2018; de la Torre et al., 2021), but crops also provides an important food subsidy for a wide range of wildlife species (Fox et al., 2005; Oro et al., 2013). Crops may offer a more predictable food source as they occur in large quantities during the same time every year (Chiyo et al., 2005; de la Torre et al., 2021). Where agriculture have persisted over centuries, certain wildlife species becomes a permanent feature in the agricultural landscape, which they depend on both as a supplementary food source and habitat (Jacob and Hempel, 2003; Heroldová et al., 2021). The extent of crop depredation tend to increase close to forests and protected areas (Linkie et al., 2007; Lemessa et al., 2013) and often displays clear temporal patterns in relation to avoidance of humans (Bjørneraas et al., 2011; Regmi et al., 2013; Troup et al., 2020), crop availability and attractive phenological stages (Chiyo et al., 2005; Lande et al., 2014).

In Europe, vast areas have been converted to agriculture, especially for cereal production, such as wheat (*Triticum aestivum*), oats (*Avena sativa*), rye (*Secale cereale*), and barley (*Hordeum sativum*). These cereal fields provide habitats and supplementary food for a wide range of wildlife species (Vickery et al., 2002; Hofman-Kamińska and Kowalczyk, 2012). Generalist species such as European badgers (*Meles meles*) have in certain areas shifted foraging patterns to depend on cereals (Roper et al., 1995), which has completely altered the nutritional content of their diet (Remonti et al. 2011). Different species prefer different phenological stages and vegetative parts of the crops. While some species forage on the whole cereal plant (Putman and Moore, 1998; Hata et al., 2021), others prefer only the mature grain (Heroldová et al., 2008). Cereal plants and grains are particularly rich in carbohydrates whilst also being a good source of protein for wildlife (Heroldová et al., 2008; Remonti et al., 2011). Several species of geese (*Anser spp.*) breeding at northern latitudes have completely altered their habitat use and foraging patterns to depend on nutritious cereal crops, causing them to abandon natural feeding areas and facilitated an increase in reproduction and population size (Fox et al., 2005; Bjerke et al., 2014; Chudzińska et al., 2015). While crop depredation in some species is driven by a lack of natural foods (Hofman-Kamińska and Kowalczyk, 2012), for others it reflects a highly opportunistic behavior and is concentrated around times of high availability (Chiyo et al., 2005; Paolini et al., 2018).

The extent of crop depredation often differs in relation to physiological and demographic characteristics such as sex, where males tend to engage in more high-risk crop depredation (Ditmer et al., 2015a; Hata et al., 2021), while females are often more risk aversive (Vogel et al., 2020; de la Torre et al., 2021). Foraging for crops may also be influenced by age (Ditmer et al., 2015b; Hata et al., 2021), family structure and reproduction (Ditmer, 2014; Tiller et al., 2021), as well as crop availability within the animal's home range or migration routes (Naughton-Treves et al., 1998; Fox et al., 2005; Lemessa et al., 2013). As agricultural landscapes continue to expand, crops such as cereals become an increasingly important food source for many wildlife species (Oro et al., 2013). Research into crop depredation usually takes a anthropocentric perspective where the main focus is how to reduce conflicts between major crop depredating species and local farmers (Simonsen et al., 2016; Conover et al., 2018; de la Torre et al., 2021). However, even species not considered major pests may utilize crops with potential ecological implications (Oro et al., 2013), which merits research attention on how this impacts their foraging ecology.

Eurasian beavers (*Castor fiber*) commonly reside in landscapes dominated by agriculture; however, their interactions with crops are poorly understood. Following large-scale extermination up until the 20th century, Eurasian beavers, together with their close relative, the North American beaver (*C. canadensis*), are recovering throughout both continents (Gibson and Olden, 2014; Halley et al., 2021). Partly due to increased recognition of their role as ecosystem engineers by constructing dams and wetlands and thus increasing biodiversity, beavers are reintroduced throughout large parts of their historical range (Wright et al., 2002; Halley et al., 2021). They are opportunistic foragers, and as typical generalists, they forage on a wide variety of woody materials and plants to obtain different nutrients (Nolet et al., 1994; Vorel et al., 2015). As central-place foragers, beavers become more selective with increasing distance from their lodge or the water (McGinley and Whitham, 1985; Haarberg and Rosell, 2006), and rarely forage far from the water's edge (Donkor and Fryxell, 1999). During spring and summer, beavers shift their diet from relying mostly on trees towards a variety of herbaceous plants, grasses, and aquatic plants (Krojerová-Prokešová et al., 2010; Law et al., 2014). Despite being similar in body size, the diet of male and female beavers may differ (Bełżecki et al., 2018), and females that reproduce the following spring tend to gain more weight during autumn (Parker et al., 2017). Older beavers also tend to spend more time on land and more time foraging than younger beavers (Graf et al., 2016; Lodberg-Holm et al., 2021).

The historical range of beavers once consisted of forests and wetlands, which in many places have been converted into agriculture (Dewas et al., 2012; Wohl, 2021), offering beavers new and novel food sources. Research into the interactions between beavers and agriculture has focused mostly on damming and draining of water bodies causing flooding of agricultural fields (Dieter and McCabe, 1989; Nolet and Rosell, 1998). Beavers foraging on cereal crops have been briefly mentioned in a few publications but have rarely been the focus of research. One notable exception is the study by Mikulka et al. (2020) from the Czech Republic that documented foraging on wheat, and barley fields, as well as rape seed (*Brassica napus*), maize (*Zea mays*), and sugar beet (*Beta vulgaris*) close to water and the beaver lodge or burrow (Mikulka et al., 2020). Plant material from cereals have also been found in the stomach content and scats of Eurasian beavers (Krojerová-Prokešová et al., 2010; Bełżecki et al., 2018). In Finland, introduced North American beavers coexist with native Eurasian beavers, but Eurasian beavers tend to settle closer to agricultural areas compared to their North American relative (Alakoski et al., 2019). These settlement patterns may reflect availability of agricultural landscapes, or that these areas provide high quality habitat leading to higher densities (Alakoski, 2021). Overall, there has been limited research on where and when beavers forage on agricultural crops, and the drivers for why they are exploiting this novel food source.

The goal of this study was to investigate the extent and spatio-temporal patterns of beaver foraging on a novel food source for beavers, cereals (wheat, barley, oat, and rye). We wanted to determine the extent of foraging within different beaver territories and use of crop fields among individual beavers, as well as potential drivers of these differences. We hypothesized that beavers would focus their foraging where less vegetation separates the river and cereal field, and at lower elevation and slopes, that they would select for wheat and barley, and increase foraging in early autumn when the cereals matured. We also hypothesized that foraging on cereals would increase in territories with a higher coverage of agriculture and lower coverage of other important habitat types for beavers. Finally, we hypothesized that beaver use of crop fields would differ according to age, sex, reproductive status and body condition, as well as over years.

2. Methods

2.1 Study area

This study was conducted in three rivers (Sauar, Gvarv and Straumen) that empty into lake Norsjø in Midt-Telemark and Nome municipalities in Telemark, southeastern Norway. The rivers are between 30-150 m wide and are only partly ice-covered during winter (Herr and Rosell, 2004). The rivers meander through a landscape dominated by agriculture and boreal forests, with several villages and human settlements along the riverbanks. Agricultural production in the area is dominated by cereals, which constituted 60% of the land used for agriculture in 2019-2020 (Landbruksdirektoratet, 2021b). Among these, wheat and oat are the most commonly grown (39 and 38% of total planted cereal fields respectively), followed by barley (19%) and rye (5%) (Landbruksdirektoratet, 2021a). Farmers commonly rotate between cereal crops across years to reduce pesticide use and increase financial returns (Kvakkestad and Prestvik, 2016). Agricultural fields often have a buffer zone between the river and the field, while a few fields extend all the way down to the river. The mean daily temperature of the region is 6.5 °C and mean precipitation is 2.3 mm (eKlima, 2020). Beavers have occupied the area since the 1920s and are assumed to be at carrying capacity (Pinto et al., 2009; Mayer et al., 2020). The study area is part of a long-term research project on beavers within the Norwegian Beaver Project (NBP) that has monitored the resident beaver population since 1997. The density of beavers is on average 1.23 ± 0.32 SD beavers per km of shoreline with territory sizes of an average of 3.28 ± 1.45 SD km (Mayer et al., 2020). Wolves (*Canis lupus*) that commonly predate beavers (Gable et al., 2018) are not present within the study area, but there is a stable population of lynx (*Lynx lynx*) (Rovdata, 2021).

2.2 Field registrations

We surveyed cereal fields during late summer and early autumn 2019 and 2020, and registered signs of beaver foraging in 17 beaver territories along the main rivers within the study area. A previous beaver habitat selection study from the region observed that 95% of the GPS locations were located within 77 m from water (Steyaert et al., 2015). Still, we decided to survey cereal fields within 100 m from the riverbanks if cereals attract beavers at even further distances. To establish which areas to survey, we downloaded a land cover map of the rivers and the surrounding areas (FKB-AR5 4.6) (Kartverket, 2016). We initiated our survey while the cereal plants were still green and the grain immature in late July and continued until all fields were harvested in late September. We did not survey beaver foraging on cereal plants during spring or early summer and previous studies report that beaver foraging tends to focus on mature crops (Mikulka et al., 2020). During the first survey in each year, we visited all agricultural fields used for crop production to register those that contained cereals (wheat, barley, rye, or oat). In each cereal field, we surveyed signs of foraging along the field edges. We did not survey the interior of the fields to avoid damaging the crops. Beaver foraging is easily identified as beavers leave trails from the river to the field with cereal plants strewn in the path. Whenever we found such a trail leading to a cereal field, we also found signs of foraging on the edge of the field, and we never found trails leading further into the field. We also flew a drone over the interior of some fields to confirm that there were no foraging signs further into the field (Video A.1). We are therefore convinced that foraging by beavers was restricted to the edges and not the interior of the field. We registered the size of every foraged patch together with equally spaced control plots every 50 m along the edges of the fields, which represented unused locations not foraged by beavers. We could thereby contrast characteristics of foraged patches and unused locations using a resource selection design to identify landscape features that facilitated beaver foraging (Manly et al., 2007; Lele et al., 2013). Within the control plots, we surveyed the immediate surrounding area and if beaver foraging was observed within 2 m of the plot, we considered it a foraged patch instead. Each cereal field was surveyed 4-5 times during the study period until all cereal crops were harvested. The repeated surveys were conducted to explore how beaver foraging developed during the season, and to record when the cereal plants and kernels matured in the different fields. There were, on average, 11 days between each repeating survey. As some foraged patches appeared late in the field season, not all foraged patches were surveyed an equal number of times. We also did not revisit all control plots during each survey round, but each foraged and control plot were visited between 1-5 times during each field season. Different control plots were surveyed in each year. In 2019, we also documented the percent of cereal plants left within the foraging patch, along the trail, or in the water to describe beaver foraging behavior. The condition of the discarded plant material was classified as either intact (having every part of the cereal plant still attached, but removed from the ground), having only the stem (the whole stem and root without the kernel), or still in the ground without the kernel.

We distinguished patches foraged by beavers from areas where the cereals had naturally been flattened by rain, wind, or flooding, based on field signs of beaver activity. Beaver foraging was determined as cases where the cereal plants had been cut or pulled up, with a distinct trail leading down to the river, and with stems of cereal plants scattered along the trail and in the water. Foraging by other mammals such as roe deer (*Capreolus capreolus*) (Putman, 1986), or badgers (Roper et al., 1995) could be distinguished as these species forage on cereals plants on site, while beavers transport plant material down to the river. In 12 of the beaver-foraged patches within three beaver territories, we also installed wildlife cameras to observe how beavers cut and transported cereals, and to confirm that beavers were the culprit behind the growing crop circles that appeared in the field. We registered foraged patches and control plots using the ArcGIS application; Collector (ESRI 2013) installed on smart phones. We used a tape measurer to assist with the estimation of the size of the foraged patches. At both foraged and control plots, we registered the maturity of the cereal plants as green (at the earliest stages of immaturity, when the cereal plant is bright green), immature (the cereal plant is golden with soft kernels), and mature (golden cereal plant with hard kernels). Whenever we found a foraged patch, we registered vegetation cover along the beaver trail leading from the water to the foraged area. In the control plots that did not have such a trail, we surveyed along the most direct route between the field and the closest water. We visually estimated vegetation density as the proportional coverage of grass/field layer, bush, and trees. These three vegetation categories were distinguished from each other based on height. The grass/field layer defined as grass included vegetation reaching up to 40 cm, bush as from 40 cm to 150 cm, and trees as vegetation higher than 150 cm. Additionally, we registered crossing roads, including hiking trails and small paths, between the cereal field and the closest waterway.

The recorded foraged patches and the control plots were extracted from ArcGIS Online at the end of each field season. We created a plot ID for each foraged patch and control plot within each year, and those separated by less than 2 m were recorded as the same plot. We also generated an ID for each field surveyed in each year. Based on the most current GPS tagging data as part of a long-term research project within the NBP (Graf et al., 2016), and field observations of territorial border markings, we mapped the extent of each beaver territory. Within each river stretch included in a territory, we added surrounding areas within 100 m of the river, but not the water itself, to include the terrestrial habitats available to beavers. For each of the foraged plots, we extracted the size of the area foraged since our last survey. Elevation at each foraged and control plot was extracted from a digital elevation model with pixel size of 10 m x 10 m (Kartverket, 2019). We then estimated the height difference between each plot and the elevation at water level of the closest waterway. Slope was estimated based on the same elevation map using the “terrain” function in the R package “raster” (Hijmans, 2020). We used the proportional coverage of each vegetation type (grass, bush, and trees) within the buffer zone and multiplied this with the distance to the closest waterway as an index of the size of the vegetated buffer zone. We finally summarized the size of all the foraged patches within each territory across the two sampling years. We matched this with data on territory size and vegetative composition within each territory. Within a 100 m buffer zone of the river, we estimated the territory size in square meters, but excluded water from this estimate. Within the territories, we calculated the square meters of different habitat types. Human settlements and infrastructure were defined as developed, all agricultural areas used for crops as agriculture, and with an additional category including only cereal fields. Forests and wetlands were also included as habitat types. We also estimated the square meters of forest dominated by coniferous, deciduous and mixed forest within each beaver territory (Kartverket, 2016). We estimated the density of beavers in each territory by dividing the number of beavers residing in the territory with the estimated territory size. Demographic information associated with each beaver territory such as family size, age of the reproductive pair, and whether the pair reproduced that year or the following year was based on long-term monitoring of the beaver families in the area as part of the NBP (Mayer et al., 2020).

GPS tagging and data processing

To investigate individual use of crop fields among beavers and across years we utilized a long-term bio-logging dataset from the NBP. Beavers were live-captured and tagged with GPS loggers in 2010-2021. Beavers were captured from small motorboats at nighttime using nets and transferred to cloth sacks for handling without the use of anesthesia (Rosell and Hovde, 2001). The GPS loggers together with VHF transmitters were glued onto the lower back of the beaver using epoxy glue. The GPS was set to log a location every 15 min between 19:00-08:00 every night until the logger fell off or the beaver was recaptured after 2-3 weeks.

For more details on the attachment of loggers and equipment used see Robstad et al. (2021) and (Justicia et al., 2018; Mortensen et al., 2021). Each tagged beaver was weighed, and tail and body measurements were recorded to calculate the tail fat index, which indicates beaver body condition (Parker et al., 2017). Captured beavers were aged based on body weight at first capture, where those weighing ≥17 kg and ≤19.5 kg were defined as minimum age of two years old, while those >19.5 kg as minimum three years old (Campbell et al., 2005; Mayer et al., 2017). We added an additional year to the minimum age each subsequent year following the initial capture. The sex of the beaver was determined based on the color and viscosity of their anal gland secretion (Rosell and Sun, 1999). Reproduction was determined each year based on long-term monitoring of the resident beaver population. We screened the beaver GPS data and removed positions that were fixed using less than 4 satellites or with a HDOP value less than 5, in order to ensure spatial accuracy (Justicia et al., 2018). We only used GPS fixes during the months July-September when cereals are available within the study area. We calculated the proportion of GPS fixes within crop fields for each tagging event in comparison with other terrestrial habitat types. A tagging event was defined as a beaver tagged in a particular year. We only included fields used for crop production according to the landcover map (Kartverket, 2016), while we excluded all pastures. As farmers commonly rotate their crops, we could not determine whether other crops besides cereals were grown in these fields in certain years. However, as cereals are the most common crop in the study area, we assumed that most fields contained cereals during most study years. We linked the proportional of overlap of beaver GPS fixes within crop fields with information on the year of tagging, sex of the beaver, age, weight in kilograms, tail fat index, and whether the tagged beaver was a female that had reproduced either in the current or subsequent year.

2.3 Statistical procedures

We followed the protocol for data exploration by Zuur et al. (2010). All explanatory variables were checked for potential collinearity using both a Pearson correlation test with a cut-off value of 0.7, and variance inflation factors (VIF) (Zuur et al., 2010; Harrison et al., 2018). Collinear variables were never included in the same candidate model. We used generalized linear mixed effects models (GLMM) and the glmmTMB package (Brooks et al., 2017) for the analysis. We built a set of candidate models containing different combinations of the explanatory variables hypothesized as important to determine beaver foraging on cereals. Each candidate model set also included a null model containing only the intercept and random effects. We selected the most supported model through AICc model selection (Anderson and Burnham, 2004), using the model.sel function from the MuMIn package (Barton, 2020), and selected the top models within a ΔAICc <2. If there were several top models, we selected the most parsimonious (simplest) among these to avoid the inclusion of so-called pretending variables with limited statistical importance (Arnold, 2010). Variables included in the final model in which confidence intervals overlapped with zero were considered uninformative (Arnold, 2010). We used square meters of cereals removed by beavers as the response, but as this was rounded to the closest m^2, we modelled it as count data. The control plots created a high percentage of zeroes (79%) in the dataset, and we therefore divided the statistical models in two parts to avoid issues with overdispersion (Zuur and Ieno, 2016a). First we modelled the probability of beaver foraging to occur, and then we focused in on only the foraged areas and investigated which variables regulated the extent of foraging.

For the first part of the analysis, we used the entire dataset and included whether the beaver had foraged or not since the last visit as the response variable with a Bernoulli distribution (0 = not foraged since last survey, 1 = foraging had occurred since the last survey). Julian day, the maturity level of the cereals, the width of the vegetated buffer zone and distance to the river had collinearity issues and were therefore not included in the same analysis. There were few observations of roads or paths crossing between the river and the cereal field, and we therefore excluded this variable. We constructed candidate models with different combinations of the explanatory variables including Julian day, cereal species, width of the buffer zone covered by trees, bush or grass, slope, elevation difference from the water, and distance to closest river. In all models, we included year of sampling (2019 or 2020) as a fixed effect, and field ID and plot ID as nested random intercepts. In part two, we selected all observations where foraging had occurred since our last visit, thereby excluding all zero observations. We used square meters of cereals removed since last survey as the response variable and a gamma distribution to account for all zeros being excluded from the dataset (Zuur and Ieno, 2016a; Zuur et al., 2017). We used the same candidate models to model both what influenced the probability that foraging occurred and extent of foraging.

Following selection of the most parsimonious model, we simulated residuals from the model using the package DHARMa (Hartig, 2019), plotted these residuals against expected and fitted values to observe deviations from the expected distribution. Additionally, we plotted the model residuals against each explanatory variable included and not included in the most parsimonious model, while fitting a smoother to look for any non-linear patterns in the residuals (Zuur and Ieno, 2016b). If non-linear patterns were observed, either during data exploration or in the residuals of the full model, we refitted the model using a polynomial to allow for non-linear effects. To assist with model convergence, we scaled all numerical variables by subtracting the mean and dividing by the standard deviation of that variable (Zuur et al., 2009). We also plotted the residuals of the most parsimonious candidate model on a map to observe any spatial correlation in the residuals not explained by the spatial variables in the model (Zuur et al., 2017). We explored potential spatial correlation for each study area separately, and also used a semi-variogram to look for spatial correlation patterns in the model residuals (Zuur et al., 2017).

Finally, we modelled the total area of cereals foraged within each beaver territory during the two survey years, and the proportion of beaver GPS fixes within crop fields in each beaver-year. We first investigated whether the extent of cereal foraging within each territory was related to the habitat structure or territory size. We therefore summarized the total area of cereals foraged in each territory across the two field survey years and used this as the response in a new set of GLM models with a negative binomial distribution. Territory size in square meters, square meters of habitat type within the territories, as well as square meters of coniferous, deciduous, and mixed forest were included as potential explanatory variables. Finally, we used the proportion of GPS fixes within crop fields during each tagging event as the response and implemented linear models using a Gaussian distribution. Sex, age, weight, tail fat index, and whether the tagged beaver was a female that reproduced either in the current or following year were included as explanatory variables together with the year of tagging. Both the dataset for the extent of foraging within each territory and proportion GPS fixes within crop fields had relatively small sample sizes and we therefore constructed univariate candidate models containing only one explanatory variable in each model. The dataset containing proportion of GPS fixes overlapping with crop fields had missing values for certain variables. We therefore compared each univariate model with a null model and not with each other due to variable number of observations. All model comparisons were made using AICc model selection as described above. The geographical and statistical analyses were conducted in R version 4.0.3 (R Core Team, 2020).

3. Results

We surveyed a total of 619 plots within the two survey years and the three study rivers that included 17 beaver territories. We registered 172 patches foraged by beavers at least once during the season, and 447 control plots that were never foraged. Oat was the most common cereal species grown in 53 fields, followed by wheat in 25 fields, barley in 13 fields, and rye in three fields (Table 1). A total of 26 fields were not foraged by beavers. In 2019, we found few signs of beaver foraging during the first survey, while the cereal was still green. However, in 2020 a few large patches were foraged prior to the first survey, while the cereals were still immature. Most foraged patches expanded between each visit as the beavers continued to forage at the same location, and the largest foraged patch we identified measured 165 m^2 in a wheat field at the end of the summer. Beavers foraged on a larger proportion of mature oat, rye and wheat compared to immature or green cereals, but foraged slightly more on immature barley than mature barley (Fig. 1). Barley was the first species harvested by the farmer, and we never found barley fields unharvested after 30. August. The other cereal species were mostly harvested in mid-September.

The beavers began foraging at the edge of the field and then continued inward, constructing a circular area with one or several distinct trails leading down to the water (Video A.1). In total, we registered 3136 m^2 foraged by beavers during the two sampling years. Wheat was the most popular cereal and constituted 71.9% of the foraged cereals, followed by oat of 18.8%, barley of 7.7%, and rye of 1.6% (Fig. 1). At each foraged plot, the cereal plants were either cut close to the ground or pulled up with the roots. Footage from camera traps showed that beavers gathered bundles of cereal plants in their mouth and transported these down to the riverbank (Video A.2). Cereal plants left along the trail mostly had intact kernels, while cereal plants left floating in the water had the kernels removed. From the camera traps, we recorded beavers consuming the kernels in shallow water close to the riverbank. In one video, mallard ducks (*Anas platyrhynchos*) approached the beaver and foraged on the kernels simultaneously (Video A.3).

In the first part of the analysis, where we modelled the probability that a location was foraged by beavers, only one model came out as important (Table B.1). The model included elevational difference, Julian day, cereal species, maturity of the cereals, width of the vegetated buffer zone covered by trees and year of sampling (Table B.2). The probability of foraging was reduced with higher elevational difference from the river level, and very low at elevational differences greater than 5 m (Fig. 2A). The probability was reduced with increasing width of the forested buffer zone, and with a width of more than 20 m, it flattened to almost zero probability (Fig. 2B). The probability of foraging increased throughout the season with the highest probability at the very end of the sampling season (Fig. 2C). It also varied between species of cereals, with rye having the highest predicted probability of foraging. However, due to the low sample size of rye with only 14 plots in total and three foraged plots, this result had high level of uncertainty (Fig. 3A). Wheat had the second highest probability of foraging, followed by oat and barley (Fig. 3A). Locations with immature or mature grain had a higher probability of foraging compared to immature grain that was still green (Fig. 3B). The probability of foraging was higher in 2019 than in 2020 (Table B.2). The model explained much of the variability in the data with an r-squared conditional of 0.92, and an r-squared marginal of 0.45.

In the second part of the analysis, where we modeled the size of the foraged patches in cereal fields, three candidate models were among the most supported models (Table B.3). We selected the most parsimonious model that contained distance to the closest water, crop species, and year of sampling (Table B.4). The size of the foraged area increased with further distance from the closest waterway, but a few outliers further than 30 m away created high model uncertainty for the furthest distances (Fig. 4A). The model also confirmed that beavers removed the largest patches of cereals in wheat fields, followed by barley, oat, and finally rye (Fig. 4B). Larger areas were removed by beavers overall in 2019 compared to 2020 (Table. B.4). The top model had an r-squared conditional of 0.64 and a r-squared marginal of 0.16.

We also investigated the total area of cereals foraged in each beaver territory during the two sampling years combined, and in relation to habitat composition and territory size. Foraging on cereals was not observed within three beaver territories, while the total area of cereals removed for the remaining beaver territories varied between 4–1294 m^2. Two candidate models were among the top models to explain variations in the total area foraged in relation to habitat composition within each territory (Table B.5). This included the null model and the model containing the cover of agriculture within the territory. As the null model was among the top models this was the most parsimonious, showing that the size of the area used for cereals was not statistically important. However, it indicated a positive relationship in which beavers in territories with a larger coverage of cereals fields also foraged more on cereals.

We obtained GPS data from 27 beavers within 19 territories during 34 tagging events (eight beavers were tagged twice in different years) during the months July-September 2010-2021. This included 15 females and 12 males ranging in age from 1 to 12 years of age. The proportion of GPS fixes within crop fields ranged from 0.0-0.6 for different tagging events. Only three beavers had no GPS fixes within crop fields. When modelling the proportion of overlap with crop fields in relation to sex, age and whether the beaver was a female that reproduced the current or following year, the null model was most supported. The model containing weight of the beaver and year had the lowest AIC values, but the null models were also within < 2 ΔAICc (Table B.6). These models indicated that the proportion of GPS fixes on crop fields increased with weight of the beaver and over years, but these effects were not statistically important. The model containing tail fat index as a measure of body condition was more supported than the null model (Table B.6) and showed that the proportion of GPS fixes in crop fields increased in beavers with a better body condition (Table B.7 & Fig. 5)

4. Discussion

We found support for our first hypothesis of spatial patterns of beaver foraging on cereals. The probability of foraging dropped quickly with increasing width of the tree-covered buffer zone separating the cereal field from the water. Beaver foraging on cereals occurred mostly on fields with lower elevational gain. However, contrary to our expectations the beavers removed larger areas of cereals when foraging further away from water. The probability of foraging was overall highest for rye and wheat, which partly confirmed our hypothesis in terms of expected selection for wheat, but not for barley. The high probability of foraging on rye was influenced by low availability within the study area. Mature wheat was the most foraged cereal, followed by mature oat, immature barley, and mature rye. The probability of foraging was high for both immature and mature grain, but not when the immature grain was green. The probability of foraging increased until late September when all cereal fields were harvested by the farmers. We could not confirm that any of the variables related to habitat and demography were important to determine the size of the foraged areas in each territory. There was a tendency towards territories where extensive foraging was observed to also encompass more cereal fields, and that use of crop fields increased in beavers with higher body weight and over years. However, none of these relationships were statistically important. Beaver body condition increased use of crop fields and the extensive foraging on cereals identified in the field also indicates that cereals play a significant part in beaver foraging ecology.

4.1 Spatial and temporal patterns

The beavers displayed spatial foraging patterns and the probability of foraging increased in areas closer than 20 m away from water, and with lower elevational difference from the water level. This may reflect both where cereals are grown, as well as general habitat selection patterns of beavers that tend to avoid steep climbs and focus foraging activities within short distance to water (Pinto et al., 2009; Steyaert et al., 2015). Water represents safety and movement corridors for beavers, and we confirmed a lower probability of cereal foraging with increasing size of the tree covered buffer zone separating the field from the water. Previous studies found that beaver foraging on agricultural fields only occurred within an average distance of 7.5–14 m away from water, but with a maximum range of 20–26 m (Campbell et al., 2012; Mikulka et al., 2020). We found signs of foraging up to 50 m from the river, but most observations were made within 30 m. In addition to the distance to water, the vegetative composition of the buffer zone may also play an important role in determining foraging patterns.

For beavers in the current study, distance to water covered by trees was more important than distance alone in terms of probability of foraging. This may suggest that vegetated buffer zones either provide beavers with alternative food sources or hinders transportation of cereals down to the river. Despite our finding that larger vegetated buffer zones decreased the probability of beaver cereal foraging, we also found that when beavers foraged further away from water, they removed larger patches of cereals. This contrasts with previous studies of beaver foraging behavior on crops (Mikulka et al., 2020). It is, however, similar to patterns of beaver foraging in forests, where beavers felled larger trees further away from the river (Haarberg and Rosell, 2006; Raffel et al., 2009). This behavior may also reflect a behavior associated with central place foraging by increasing load sizes at further distances (Orians and Pearson, 1979).

Cereal foraging increased as cereals matured from the end of August to the middle of September, but beavers foraged both on the immature yellow cereal and the mature cereals. Agricultural crops are seasonally predictable (Oro et al., 2013), which means they are usually available in large quantities during the same time every year. Crop depredation often intensifies when crops are available or during certain attractive phenological stages (Putman, 1986; Roper et al., 1995; Chiyo et al., 2005). For beavers this seemed to be when cereals were mature, but they would also forage on the immature grains once the cereal plant changed color to yellow. In addition to the observed spatial and temporal patterns, beavers also displayed a clear preference for certain species.

4.2 Extent and benefits of cereal forage

We found that beavers foraged mostly on wheat, which reaffirms previous studies (Mikulka et al., 2020). They also foraged on oat, barley, and rye, but rye was so rare within the study area that it was difficult to conclude on the preference for this species. Cereals may provide additional nutrients for beavers who forage on a wide variety of plant material to meet nutritional demands (Nolet et al., 1994; Nolet et al., 1995). Wheat is also preferred by other rodents, probably due to higher digestibility compared to barley, with higher starch and sugar content, but lower potassium (Heroldová et al., 2008). Certain rodent species such as voles may reside permanently within agriculture and cause extensive crop damages (Heroldová et al., 2021), the impact of beaver foraging on cereal crops seemed less extensive. Still, cereals might provide an important food source in early autumn when the beavers start preparing for the leaner winter season. In Sweden, brown bears (*U. arctos)* forage extensively on oats that provided them with valuable nutrients during hyperphagia (Elfström et al., 2014; Steyaert et al., 2016). However, foraging on oats close to human settlements also exposed these bears to human hunters, and thereby functioning as an ecological trap for the species (Steyaert et al., 2016). Beaver hunting in Norway starts in October after the cereals have already been harvested, and we found no evidence that local farmers have initiated any deterring strategies directed towards beavers.

Beavers removed a total of 3,136 m^2 of cereals across the two years, and within 17 surveyed beaver territories, which is a smaller area per beaver territory than the 3,995 m^2 found in the Czech Republic across two years and only five beaver territories. The extent of foraging varied among territories, and while three territories displayed no signs of cereal foraging, one territory was alone responsible for 1,294 m^2 of foraged cereals. When beavers transport cereal plants down to the water for consumption; they may also increase availability for other species. One of our camera traps showed mallards foraging on the kernels together with a beaver, and this species is known to forage on several types of cereals (Sugden, 1979). Future research should investigate to what extent other species make use of the cereals deposited into rivers, streams, and lakes by beavers. Our study area supports a high density of beavers, but we still found relatively low levels of damage, and few complaints have been made to local authorities regarding beaver foraging on cereals (Roheim 2021, personal communication). There were by contrast more complains related to damming of productive forests and crops, as well as construction of burrows underneath agricultural fields (Roheim 2021, personal communication). Farmers in Scotland, where beavers have recently been introduced, also did not view beaver foraging as problematic despite occasional damages to crops (Campbell et al., 2012). In the US, beavers were listed among the 21 species causing most damage to agriculture, but it was not specified whether these damages were related to foraging or damming (Conover et al., 2018). Conflicts with beavers within agriculture may be reduced through lethal removal (Taylor and Singleton, 2014), but if the area is attractive to beavers new individuals may quickly recolonize it (Campbell et al., 2005). The use of predator smell can discourage beavers from using foraging trails and food items (Rosell and Czech, 2000; Severud et al., 2011), but covering a sufficiently large area using scent would most likely be challenging. As our results show probability of foraging on crops decreased with the width of the tree covered buffer zone, establishment of a large vegetated buffer zone between the river and cereal field may be the most effective way to reduce damages to crops (Dewas et al., 2012; Mikulka et al., 2020).

We only explored beaver foraging from the stage of immature cereals and until harvest, which means that we cannot rule out that beavers also forage on cereal seedlings shortly after sowing or leftover grains after harvest. Beavers in the Czech Republic were found to forage on the vegetative part of cereals during spring, but at very low levels compared to mature crops (Mikulka et al., 2020). We also found very few foraged cereal patches containing immature cereals during our first survey in both years, except for a few foraged patches of immature cereals during the first survey in 2020. Wildlife may utilize different parts of the cereal plant at different phenological stages. Pink-footed geese start foraging on cereal seeds directly after sowing (Simonsen et al., 2016). Roe deer and voles forage mostly on the vegetative part of the plant during early phenological stages (Putman, 1986; Heroldová et al., 2021). Other rodents prefer the nutritious grain heads after ripening (Heroldová et al., 2008; Elfström et al., 2014). Typical generalist species such as European badgers (Roper et al., 1995) and Svalbard pink-footed geese (*Anser brachyrhynchus*) (Simonsen et al., 2016) may utilize cereal crops throughout these different phenological stages. Pygmy field mice (*Apodemus microps*), however, waited for the grain to mature before foraging (Heroldová et al. 2007), which is similar to what we found in beavers. While some of these species rely on agricultural areas to complete important life stages such as reproduction, beaver use of agricultural crops seems more opportunistically.

4.3 Territorial and individual differences

We found large differences in the extent of foraging across beaver territories but failed to identify any clear relationship with variables that could explain these differences. In beaver territories with a high coverage of cereal fields, there was tendency that beavers foraged more extensively on cereals, but this relationship was not statistically important. In many species crop depredation is induced by low availability of natural food sources (Hofman-Kamińska and Kowalczyk, 2012; Barrio et al., 2013; Lemessa et al., 2013). We did not survey the availability of different plant materials within the beaver territories but used the square meter coverage of other habitat types as a proxy. Availability of these vegetation types did not influence the extent of cereal foraging, which seems to indicate that natural food availability is not a major driver of cereal foraging. Beavers do typically diversify their diet especially during summer to obtain sufficient nutrients and maximize energy intake (Belovsky, 1984; Doucet and Fryxell, 1993; Nolet et al., 1995), and foraging on cereals may also reflect their opportunistic and generalist diet.

We could not link the observed foraging in each territory to individual beavers, but instead we used GPS data showing beaver overlap with crop fields during the cereal season as an indication of individual variation in cereal foraging. Individual beavers differed in their overlap with crop fields with some displaying hardly any overlap, while others overlapped with crop fields for 60% of their terrestrial GPS fixes. We found no indication that either sex used these fields more, nor any impact of age, or reproductive status of females. In species such as Svalbard pink-footed geese and Greenland white-fronted geese (*A. albifrons flavirostris)* foraging on cereal fields during migration stop-overs have facilitated large increases in reproduction and population size leading to large scale conflicts with farmers (Fox et al., 2005; Simonsen et al., 2016). There were no indications of similar effects on beavers as the resident population size has remained stable and with low levels of reproduction. While size-dimorphic species such as black bears (*Ursus americanus*) and moose (*Alces alces*) display sex-specific use of agricultural fields related to more risk-aversive behavior in females (Bjørneraas et al., 2011; Ditmer et al., 2015b), we did not find that sex nor female reproductive status in the current or following year impacted use of crop fields. However, we found that beavers in good body condition had a higher proportional overlap with crop fields. As we recorded body weight prior to attaching the tag, we cannot conclude that these beavers improved their body condition through foraging on cereals fields, but it certainly indicates that individuals that spend time in these fields gain some benefits. In other species such as sika deer (*Cervus nippon*) (Hata et al., 2021), African elephants

(*Loxodonta africana*) (Chiyo et al., 2011) and black bears (Ditmer et al., 2015b) individuals that foraged in cereal fields also had a larger body size. However, in black bears this improvement in body condition did not necessarily impact reproductive output (Ditmer et al., 2015b), which is similar to our findings.

5. Conclusion

Species such as beavers rarely cause extensive damages when foraging on agricultural crops, and therefore tend to receive less research attention (Mikulka et al., 2020). Still, we have shown that beavers foraged extensively on cereals with clear spatial and temporal patterns and a preference for certain species and maturity levels. The extent of cereal foraging within each territory varied, but we could not conclude on what drives these patterns. However, beavers that used crop fields more also displayed a better body condition. Beaver foraging on cereals is probably a reflection of beavers flexible and opportunistic diet within a human dominated landscape. As agriculture already covers a large proportion of the Earth's surface and continues to expand, humans and wildlife increasingly overlap and utilize the same food sources (Ellis and Ramankutty, 2008), potentially leading to conflicts (Regmi et al., 2013; Tiller et al., 2021). Beavers are re-colonizing large parts of their historic range throughout Europe and North America in a highly anthropogenic landscape, which means foraging on crops may increase and become an important food subsidy for beavers. There is a potential for future increases in conflicts levels within these landscapes that should be mitigated by increasing the size of the vegetated buffer zones between crops fields and water, and installing drainage mechanisms in locations where beaver damming may damage crops (Campbell-Palmer et al., 2016). Survival of wildlife within human-dominated landscapes depends on our ability to coexist (Ellis and Ramankutty, 2008), and research into interactions between wildlife and agriculture may aid towards managing wildlife and their impacts in these landscapes.

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References

Alakoski, R., 2021. Factors affecting the distribution of the Eurasian beaver and the North American beaver in Finland. Department of biology. University of Turku, Turku, Finland.

Alakoski, R., Kauhala, K., Selonen, V., 2019. Differences in habitat use between the native Eurasian beaver and the invasive North American beaver in Finland. Biol. Invasions 21, 1601–1613.

Anderson, D., Burnham, K., 2004. Model selection and multi-model inference. Springer-Verlag, New York.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's information criterion. J. Wildl. Manage. 74, 1175-1178.

Barrio, I.C., Bueno, C.G., Villafuerte, R., Tortosa, F.S., 2013. Rabbits, weeds and crops: Can agricultural intensification promote wildlife conflicts in semiarid agro-ecosystems? J. Arid Environ. 90, 1-4.

Barton, K., 2020. MuMIn: Multi-model Inference. R package version 1.43.17.

Belovsky, G.E., 1984. Summer diet optimization by beaver. Am. Midl. Nat. 111, 209-222.

Bełżecki, G., Miltko, R., Kowalik, B., Demiaszkiewicz, A.W., Lachowicz, J., Giżejewski, Z., Obidziński, A., McEwan, N.R., 2018. Seasonal variations of the digestive tract of the Eurasian beaver Castor fiber. Mammal Res. 63, 21-31.

Bjerke, J.W., Bergjord, A.K., Tombre, I.M., Madsen, J., 2014. Reduced dairy grassland yields in central Norway after a single springtime grazing event by pink-footed geese. Grass Forage Sci 69, 129-139.

Bjørneraas, K., Solberg, E.J., Herfindal, I., Moorter, B.V., Rolandsen, C.M., Tremblay, J.-P., Skarpe, C., Sæther, B.-E., Eriksen, R., Astrup, R., 2011. Moose Alces alces habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biol 17, 44-54.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378-400.

Campbell-Palmer, R., Gow, D., Campbell, R., Dickson, H., Girling, S., Gurnell, J., Halley, D., Jones, S., Lisle, S., Parker, H., Schwab, G., Rosell, F., 2016. The Eurasian Beaver Handbook: Ecology and Management of *Castor fiber*. Pelagic Publishing, UK, Exeter.

Campbell, R.D., Harrington, A., Ross, A., Harrington, L., 2012. Distribution, population assessment and activities of beavers in Tayside. Scottish Natural Heritage Commissioned Report No. 540.

Campbell, R.D., Rosell, F., Nolet, B.A., Dijkstra, V.A.A., 2005. Territory and group sizes in Eurasian beavers (Castor fiber): echoes of settlement and reproduction? Behav. Ecol. Sociobiol. 58, 597-607.

Chiyo, P.I., Cochrane, E.P., Naughton, L., Basuta, G.I., 2005. Temporal patterns of crop raiding by elephants: a response to changes in forage quality or crop availability? Afr. J. Ecol. 43, 48-55.

Chiyo, P.I., Lee, P.C., Moss, C.J., Archie, E.A., Hollister-Smith, J.A., Alberts, S.C., 2011. No risk, no gain: effects of crop raiding and genetic diversity on body size in male elephants. Behav. Ecol. 22, 552-558.

Chudzińska, M.E., van Beest, F.M., Madsen, J., Nabe-Nielsen, J., 2015. Using habitat selection theories to predict the spatiotemporal distribution of migratory birds during stopover – a case study of pink-footed geese Anser brachyrhynchus. Oikos 124, 851-860.

Conover, M.R., Butikofer, E., Decker, D.J., 2018. Wildlife damage to crops: Perceptions of agricultural and wildlife leaders in 1957, 1987, and 2017. Wildl. Soc. Bull. 42, 551-558.

de la Torre, J.A., Wong, E.P., Lechner, A.M., Zulaikha, N., Zawawi, A., Abdul-Patah, P., Saaban, S., Goossens, B., Campos-Arceiz, A., 2021. There will be conflict – agricultural landscapes are prime, rather than marginal, habitats for Asian elephants. Anim. Conserv.

Dewas, M., Herr, J., Schley, L., Angst, C., Manet, B., Landry, P., Catusse, M., 2012. Recovery and status of native and introduced beavers *Castor fiber* and *Castor canadensis* in France and neighbouring countries. Mamm Rev 42, 144-165.

Dieter, C.D., McCabe, T.R., 1989. Factors influencing beaver lodge-site selection on a prairie river. Am. Midl. Nat. 122, 408-411.

Ditmer, M.A., 2014. American black bears: strategies for living in a fragmented, agricultural landscape. University of Minnesota, Saint Paul.

Ditmer, M.A., Burk, T.E., Garshelis, D.L., 2015a. Do innate food preferences and learning affect crop raiding by American black bears? Ursus 26, 40-52.

Ditmer, M.A., Garshelis, D.L., Noyce, K.V., Haveles, A.W., Fieberg, J.R., 2015b. Are American black bears in an agricultural landscape being sustained by crops? J. Mammal. 97, 54-67.

Donkor, N.T., Fryxell, J.M., 1999. Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. For. Ecol. Manag. 118, 83-92.

Doucet, C.M., Fryxell, J.M., 1993. The effect of nutritional quality on forage preference by beavers. Oikos 67, 201-208.

eKlima, 2020. Gridded values for counties, with trend. Norwegian Meteorological Institute.

Elfström, M., Davey, M.L., Zedrosser, A., Müller, M., De Barba, M., Støen, O.-G., Miquel, C., Taberlet, P., Hackländer, K., Swenson, J.E., 2014. Do Scandinavian brown bears approach settlements to obtain high-quality food? Biol. Conserv. 178, 128-135.

Ellis, E.C., Ramankutty, N., 2008. Putting people in the map: anthropogenic biomes of the world. Front Eco Environ 6, 439-447.

Fox, A.D., Madsen, J., Boyd, H., Kuijken, E., Norriss, D.W., Tombre, I.M., Stroud, D.A., 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. Glob. Change Biol. 11, 881-893.

Gable, T.D., Windels, S.K., Romanski, M.C., Rosell, F., 2018. The forgotten prey of an iconic predator: a review of interactions between grey wolves *Canis lupus* and beavers *Castor* spp. Mammal Review 48, 123-138.

Gibson, P.P., Olden, J.D., 2014. Ecology, management, and conservation implications of North American beaver (Castor canadensis) in dryland streams. Aquat Conserv 24, 391-409.

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

Haarberg, O., Rosell, F., 2006. Selective foraging on woody plant species by the Eurasian beaver (Castor fiber) in Telemark, Norway. J. Zool. 270, 201-208.

Halley, D.J., Saveljev, A.P., Rosell, F., 2021. Population and distribution of beavers Castor fiber and Castor canadensis in Eurasia. Mam Rev 51, 1-24.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6, e4794.

Hartig, F., 2019. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.

Hata, A., Nakashita, R., Anezaki, T., Minami, M., Fukue, Y., Higuchi, N., Uno, H., Nakajima, Y., Saeki, M., Kozakai, C., 2021. Agricultural crop consumption induces precocious maturity in deer by improving physical and reproductive performance. Ecosphere 12, e03464.

Heroldová, M., Šipoš, J., Suchomel, J., Zejda, J., 2021. Influence of crop type on common vole abundance in Central European agroecosystems. Agric Ecosys Environ 315, 107443.

Heroldová, M., Tkadlec, E., Bryja, J., Zejda, J., 2008. Wheat or barley?: Feeding preferences affect distribution of three rodent species in agricultural landscape. Appl. Anim. Behav. Sci. 110, 354-362.

Herr, J., Rosell, F., 2004. Use of space and movement patterns in monogamous adult Eurasian beavers (Castor fiber). J. Zool. 262, 257-264.

Hijmans, R.J., 2020. raster: Geographic Data Analysis and Modeling. R package version 3.3-7.

Hofman-Kamińska, E., Kowalczyk, R., 2012. Farm crops depredation by European bison (Bison bonasus) in the vicinity of forest habitats in northeastern Poland. Environ Manage 50, 530-541.

Jacob, J., Hempel, N., 2003. Effects of farming practices on spatial behaviour of common voles. J. Ethol. 21, 45-50.

Justicia, L.S., Rosell, F., Mayer, M., 2018. Performance of GPS units for deployment on semiaquatic animals. PLoS One 13, e0207938.

Kartverket, 2016. FKB-AR5.

Kartverket, 2019. DTM 10.

Krojerová-Prokešová, J., Barančeková, M., Hamšíková, L., Vorel, A., 2010. Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources. J. Zool. 281, 183-193.

Kvakkestad, V., Prestvik, A., 2016. Integrert plantevern hos norske kornbønder. Resultater fra en spørreundersøkelse om holdninger til og bruk av integrert plantevern. NIBIO, Ås, Norway.

Landbruksdirektoratet, 2021a. PT-900 Antallstatistikk - per 1.10.

Landbruksdirektoratet, 2021b. PT-912 Antall dekar og søkere med de ulike vekstgruppene.

Lande, U.S., Loe, L.E., Skjærli, O.J., Meisingset, E.L., Mysterud, A., 2014. The effect of agricultural land use practice on habitat selection of red deer. European Journal of Wildlife Research 60, 69-76.

Law, A., Bunnefeld, N., Willby, N.J., 2014. Beavers and lilies: selective herbivory and adaptive foraging behaviour. Freshw. Biol. 59, 224-232.

Lele, S.R., Merrill, E.H., Keim, J., Boyce, M.S., 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. J Anim Ecol 82, 1183-1191.

Lemessa, D., Hylander, K., Hambäck, P., 2013. Composition of crops and land-use types in relation to crop raiding pattern at different distances from forests. Agric Ecosys Environ 167, 71-78.

Linkie, M., Dinata, Y., Nofrianto, A., Leader-Williams, N., 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. Anim. Conserv. 10, 127-135.

Lodberg-Holm, H.K., Steyaert, S.M.J.G., Reinhardt, S., Rosell, F., 2021. Size is not everything: differing activity and foraging patterns between the sexes in a monomorphic mammal. Behav. Ecol. Sociobiol. 75, 76.

Manly, B., McDonald, L., Thomas, D., McDonald, T.L., Erickson, W.P., 2007. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media.

Mayer, M., Frank, S.C., Zedrosser, A., Rosell, F., 2020. Causes and consequences of inverse density-dependent territorial behaviour and aggression in a monogamous mammal. J Anim Ecol 89, 577-588.

Mayer, M., Künzel, F., Zedrosser, A., Rosell, F., 2017. The 7-year itch: non-adaptive mate change in the Eurasian beaver. Behav. Ecol. Sociobiol. 71, 32.

McGinley, M.A., Whitham, T.G., 1985. Central place foraging by beavers (Castor canadensis): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (Populus fremontii). Oecologia 66, 558-562.

Mikulka, O., Homolka, M., Drimaj, J., Kamler, J., 2020. European beaver (Castor fiber) in open agricultural landscapes: crop grazing and the potential for economic damage. Eur. J. Wildl. Res. 66, 101.

Mortensen, R.M., Reinhardt, S., Hjønnevåg, M.E., Wilson, R.P., Rosell, F., 2021. Aquatic habitat use in a semi-aquatic mammal: the Eurasian beaver. Animal Biotelemetry 9, 35.

Naughton-Treves, L., Treves, A., Chapman, C., Wrangham, R., 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. J Appl Ecol 35, 596-606.

Nolet, B.A., Hoekstra, A., Ottenheim, M.M., 1994. Selective foraging on woody species by the beaver Castor fiber, and its impact on a riparian willow forest. Biol. Conserv. 70, 117-128.

Nolet, B.A., Rosell, F., 1998. Comeback of the beaver Castor fiber: An overview of old and new conservation problems. Biol. Conserv. 83, 165-173.

Nolet, B.A., Van Der Veer, P.J., Evers, E.G.J., Ottenheim, M.M., 1995. A linear programming model of diet choice of free-living beavers. Neth. J. Zoo 45, 315-337.

Orians, G.H., Pearson, N.E., 1979. On the theory of central place foraging. In: Horn, J., Stairs, G.R., Mitchell, R.D. (Eds.), Analysis of ecological systems. Ohio State Press, Columbus, pp. 155-177.

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

Paolini, K.E., Strickland, B.K., Tegt, J.L., VerCauteren, K.C., Street, G.M., 2018. Seasonal variation in preference dictates space use in an invasive generalist. PLOS ONE 13, e0199078.

Parker, H., Zedrosser, A., Rosell, F., 2017. Age-specific reproduction in relation to body size and condition in female Eurasian beavers. J. Zool. 302, 236-243.

Pinto, B., Santos, M.J., Rosell, F., 2009. Habitat selection of the Eurasian beaver (Castor fiber) near its carrying capacity: an example from Norway. Can. J. Zool. 87, 317-325.

Putman, R.J., 1986. Foraging by roe deer in agricultural areas and impact on arable crops. J Appl Ecol 23, 91-99.

Putman, R.J., Moore, N.P., 1998. Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. Mamm Rev 28, 141-164.

R Core Team, 2020. R: A language and environment for statistical computing. . R Foundation for Statistical Computing, Vienna, Austria.

Raffel, T.R., Smith, N., Cortright, C., Gatz, A.J., 2009. Central place foraging by beavers (Castor canadensis) in a complex lake habitat. Am. Midl. Nat. 162, 62-73.

Regmi, G.R., Nekaris, K.A.-I., Kandel, K., Nijman, V., 2013. Crop-raiding macaques: predictions, patterns and perceptions from Langtang National Park, Nepal. Endanger Species Res 20, 217-226.

Remonti, L., Balestrieri, A., Prigioni, C., 2011. Percentage of protein, lipids, and carbohydrates in the diet of badger (Meles meles) populations across Europe. Ecol. Res. 26, 487-495.

Robstad, C.A., Lodberg-Holm, H.K., Mayer, M., Rosell, F., 2021. The impact of bio-logging on body weight change of the Eurasian beaver. Plos one 16, e0261453.

Roper, T.J., Findlay, S.R., Lüps, P., Shepherdson, D.J., 1995. Damage by badgers Meles meles to wheat Triticum vulgare and barley Hordeum sativum crops. J Appl Ecol 32, 720-726.

Rosell, F., Czech, A., 2000. Responses of foraging Eurasian beavers Castor fiber to predator odours. Wildlife Biol 6, 13-21.

Rosell, F., Hovde, B., 2001. Methods of aquatic and terrestrial netting to capture Eurasian beavers. Wildl. Soc. Bull. 29, 269-274.

Rosell, F., Sun, L.X., 1999. Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *Castor fiber*. Wildlife Biol 5, 119-123.

Rovdata, 2021. Bestandsstatus - Gaupe.

Severud, W.J., Belant, J.L., Bruggink, J.G., Windels, S.K., 2011. Predator cues reduce American beaver use of foraging trails. Hum-Wild Interact 5, 296-305.

Simonsen, C.E., Madsen, J., Tombre, I.M., Nabe-Nielsen, J., 2016. Is it worthwhile scaring geese to alleviate damage to crops? – An experimental study. J Appl Ecol 53, 916-924.

Steyaert, S.M.J.G., Zedrosser, A., Elfström, M., Ordiz, A., Leclerc, M., Frank, S.C., Kindberg, J., Støen, O.-G., Brunberg, S., Swenson, J.E., 2016. Ecological implications from spatial patterns in human-caused brown bear mortality. Wildlife Biol 22, 144-152.

Steyaert, S.M.J.G., Zedrosser, A., Rosell, F., 2015. Socio-ecological features other than sex affect habitat selection in the socially obligate monogamous Eurasian beaver. Oecologia 179, 1023-1032.

Sugden, L.G., 1979. Grain Consumption by Mallards. Wildl. Soc. Bull. 7, 35-39.

Taylor, J.D., Singleton, R.D., 2014. The evolution of flow devices used to reduce flooding by beavers: A review. Wildl. Soc. Bull. 38, 127-133.

Tiller, L.N., Humle, T., Amin, R., Deere, N.J., Lago, B.O., Leader-Williams, N., Sinoni, F.K., Sitati, N., Walpole, M., Smith, R.J., 2021. Changing seasonal, temporal and spatial crop-raiding trends over 15 years in a human-elephant conflict hotspot. Biol. Conserv. 254, 108941.

Troup, G., Doran, B., Au, J., King, L.E., Douglas-Hamilton, I., Heinsohn, R., 2020. Movement tortuosity and speed reveal the trade-offs of crop raiding for African elephants. Anim. Behav. 168, 97-108.

Vickery, J., Carter, N., Fuller, R.J., 2002. The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. Agric Ecosyst Environ 89, 41-52.

Vogel, S.M., Lambert, B., Songhurst, A.C., McCulloch, G.P., Stronza, A.L., Coulson, T., 2020. Exploring movement decisions: Can Bayesian movement-state models explain crop consumption behaviour in elephants (Loxodonta africana)? J Anim Ecol 89, 1055-1068.

Vorel, A., Válková, L., Hamšíková, L., Maloň, J., Korbelová, J., 2015. Beaver foraging behaviour: Seasonal foraging specialization by a choosy generalist herbivore. Behav. Ecol. Sociobiol. 69, 1221-1235.

Wohl, E., 2021. Legacy effects of loss of beavers in the continental United States. Environ. Res. Lett. 16, 025010.

Wright, J.P., Jones, C.G., Flecker, A.S., 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132, 96-101.

Zuur, A.F., Ieno, E.N., 2016a. Beginner's guide to zero-inflated models with R. Highland Statistics Limited Newburgh, United Kingdom.

Zuur, A.F., Ieno, E.N., 2016b. A protocol for conducting and presenting results of regression-type analyses. Methods Ecol. Evol. 7, 636-645.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3-14.

Zuur, A.F., Ieno, E.N., Saveliev, A.A., 2017. Spatial, temporal and spatial–temporal ecological data analysis with R-INLA. Highland Statistics Ltd, Newburgh, United Kingdom.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology. Springer Science and Business Media, New York.

Tables

Table 1: Overview of data collected investigating foraging on cereals by Eurasian beavers (*Castor fiber*) 2019 and 2020 in southeastern Norway. The table contains an overview of the species of cereal surveyed, the number of fields identified for each crop, number of foraged patches, and the mean and max size in m^2 of each foraged patches. Also included is the total area of cereal removed across the two survey years and date of the last observation before the crop was harvested.

Cereal species	**No. of fields**	**No. of foraged patches**	**Mean size of foraged patch**	**Max size of foraged patch**	**Total foraged area**	**Last observation before harvest**
Barley	13	35	2.9	12	54 m^2	30-Aug
Oat	53	27	10.8	70	469 m^2	17-Sep
Rye	3	3	5	12	19 m^2	10-Sep
Wheat	25	79	20.8	165	2596 m^2	15-Sep

Figures legends

Fig. 1. Proportion of barley (*Hordeum sativum*), oat (*Avena sativa*), rye (*Secale cereale*) and wheat (*Triticum aestivum*) foraged by Eurasian beavers (*Castor fiber*) in southeastern Norway 2019 and 2020. The proportion foraged of each maturity level is also shown.

Fig. 2. Probability of foraging on cereals within Eurasian beaver (*Castor fiber*) territories in southeastern Norway, 2019 and 2020. Foraging probability has been predicted in relation to elevational gain from water level in meters (A) and width of the buffer area between the field and the river covered by trees (B) and days since January 1 (Julian day) converted to date for visualization purposes. All predictions are based on a generalized linear mixed effect model (GLMM) with a Bernoulli distribution contrasting foraged and control plots within cereal fields less than 100 m from water. Model estimates have been converted from the logit scales to probabilities, and the colored area represents the 95% confidence intervals.

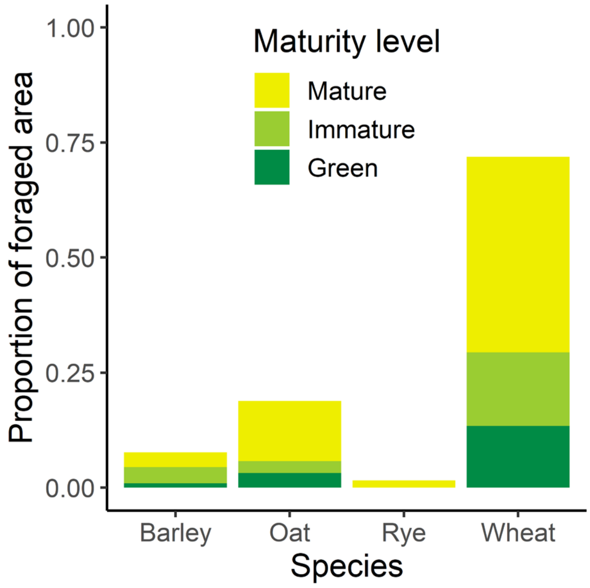
Fig. 3. Probability of foraging on cereals within Eurasian beaver (*Castor fiber*) territories in southeastern Norway, 2019 and 2020. Predictions of foraging probability have been predicted for each species of cereal (A) and maturity level (B). All predictions are based on a generalized linear mixed effect model with a Bernoulli distribution contrasting foraged and control plots within cereal fields. Model estimates have been converted from the logit scales to probabilities, and the horizontal bars represents the 95% confidence intervals.

Fig. 4. Predicted size of cereal patches (m^2) foraged by beavers (*Castor fiber*) in cereal fields in southeastern Norway, 2019 and 2020, in relation to distance from closest waterway (A) and species of cereal (B). Predictions are based on a generalized linear mixed effect model with a gamma distribution modelling square meters of cereal removed between subsequent surveys.

Model estimates have been converted back to the scale of the original data, and colored area in A and the vertical bars in B represents the 95% confidence intervals. The blue points represent each foraged patch recorded in the field.

Fig. 5. Predicted effect of tail fat index as a measure of body condition on the proportion of GPS fixes within crop fields for each tagging event (beaver-year) of Eurasian beavers (*Castor fiber*) in southeastern Norway, 2010-2021. All predictions are based on a linear regression model with a Gaussian distribution and the colored area represents the 95% confidence intervals.

Figure 1



Maturity level
Mature
Immature
Green
Proportion of foraged area
1.00
0.75
0.50
0.25
0.00
Barley
Oat
Rye
Wheat
Species

Figure 2

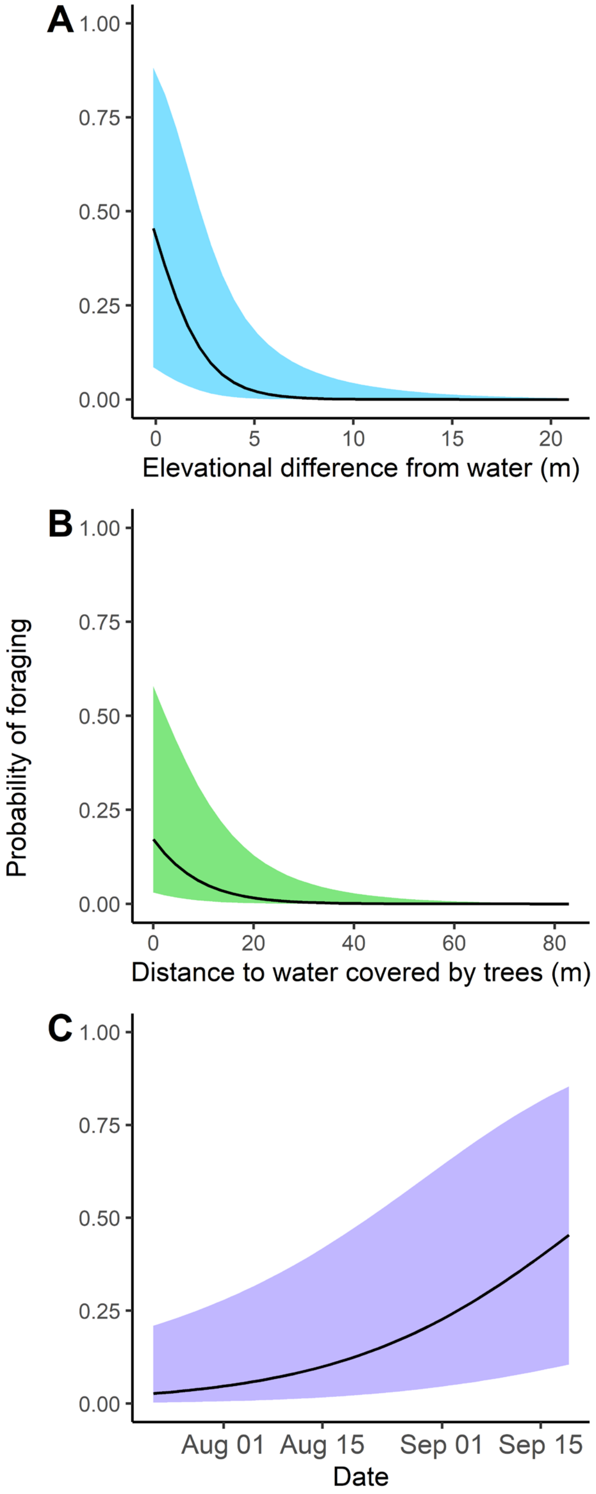

A
B
C
Probability of foraging
1.00
0.75
0.50
0.25
0.00
0
5
10
15
20
Elevational difference from water (m)
0
20
40
60
80
Distance to water covered by trees (m)
Aug 01
Aug 15
Sep 01
Sep 15
Date

Figure 3

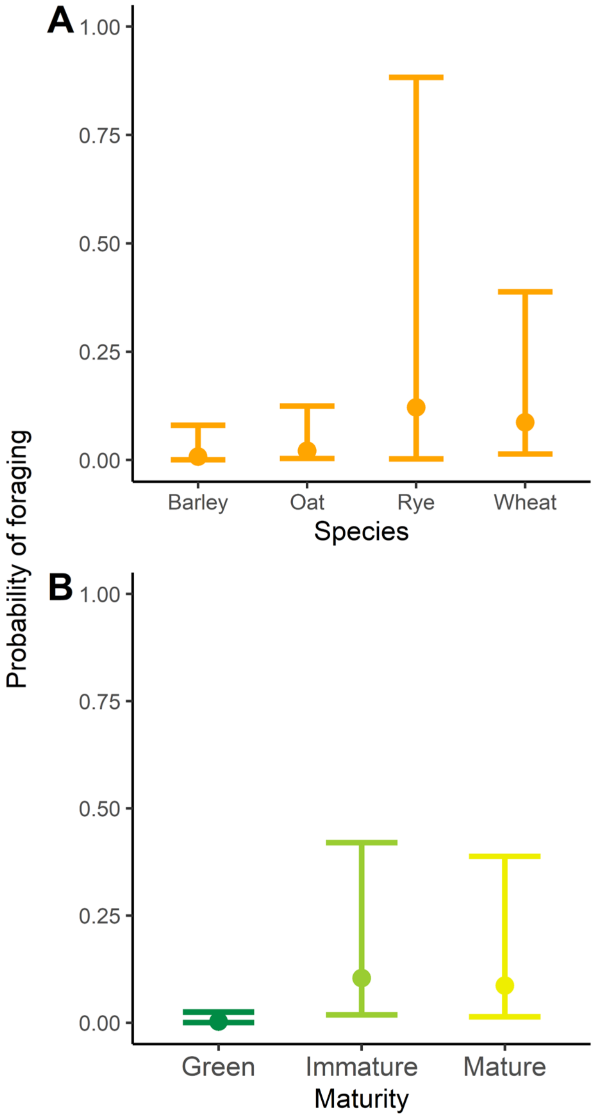

A
B
Probability of foraging
1.00
0.75
0.50
0.25
0.00
Barley
Oat
Rye
Wheat
Species
1.00
0.75
0.50
0.25
0.00
Green
Immature
Mature
Maturity

Figure 4

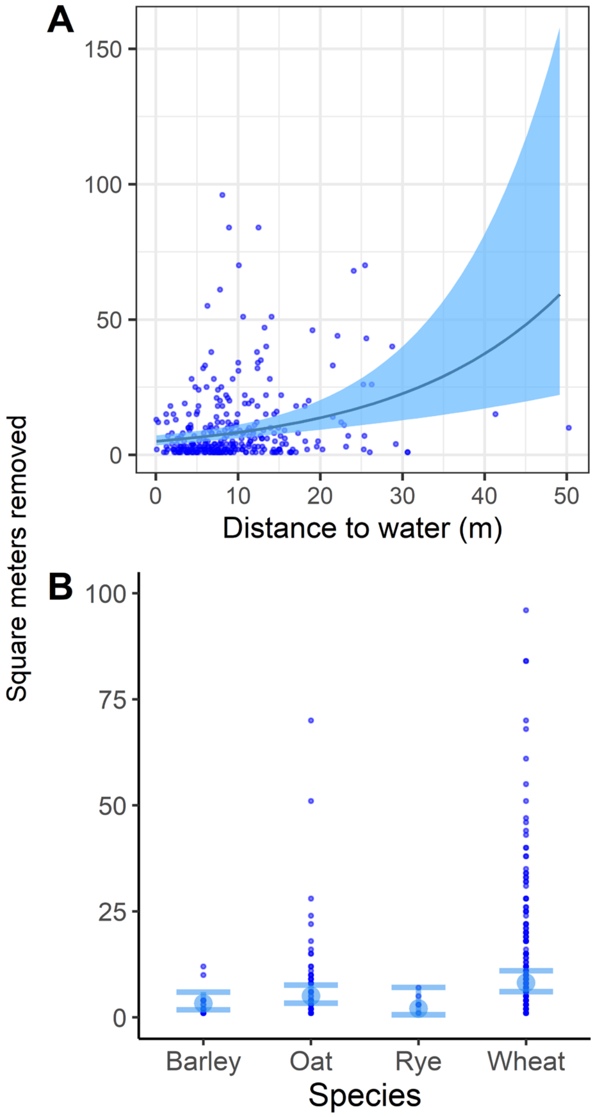
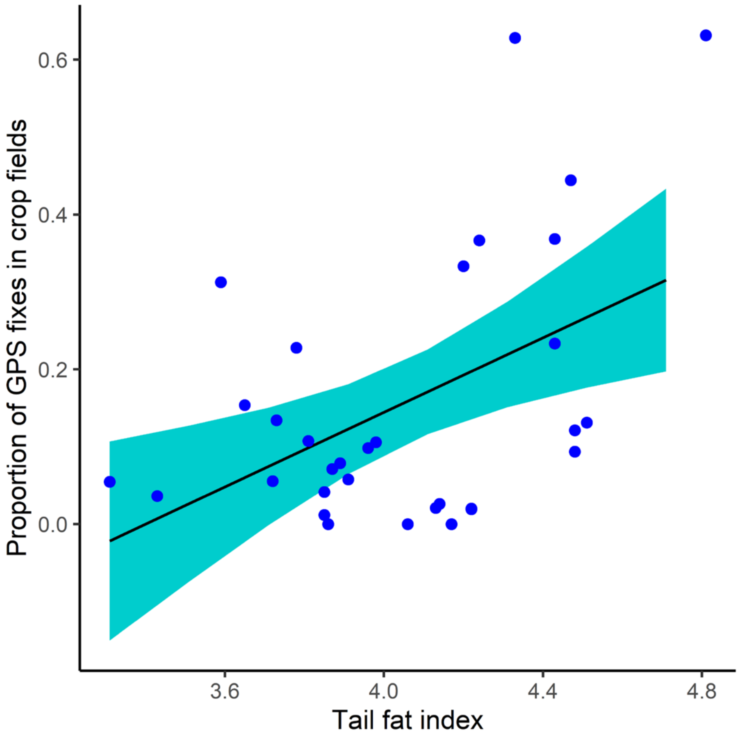

A
150
100
50
0
0
10
20
30
40
50
Distance to water (m)
Square meters removed
B
100
75
50
25
0
Barley
Oat
Rye
Wheat
Species

Figure 5


0.6
0.4
0.2
0.0
Proportion of GPS fixes in crop fields
3.6
4.0
4.4
4.8
Tail fat index

Appendix

Video A.1. Patches in cereal fields foraged by Eurasian beavers (*Castor fiber*) in southeastern Norway, 2020. Only the patches located close to the edge of the field and with trails leading down to the river are made by beavers. Drone footage: James Stensby Fountain, editing: Hanna Kavli Lodberg-Holm.

Video A.2. A Eurasian beaver (*Castor fiber*) transporting cereal plants down to the river and foraging on cereal kernels in the shallow water in southeastern Norway, 2019. The metal frame that is visible on the video is part of another research project where the PIT tag in the neck of the beaver was logged when the beaver moved through the frame. This data was not used for the current research project. Camera trap footage: Peter Farsund.

Video A.3. A Eurasian beaver (*Castor fiber*) foraging on cereals in the shallow water in southeastern Norway, 2019. Three mallard ducks (*Anas platyrhynchos*) swim past and start foraging on one of the kernels that the beaver has transported into the water. Camera trap footage: Elise Solheim Garvik/Marte Stensby Fountain.

Videos are available in the USN Research Data Archive:
https://figshare.com/s/b356c374a3af8ca005d5

Table B1: Model selection table for the candidate models exploring probability of foraging in cereal fields of Eurasian beavers (*Castor fiber*) in southeastern Norway, 2019 and 2020 (n=1457). Each model explores whether beaver foraging was observed or not coded using a Bernoulli distribution and generalized linear mixed effects models (GLMM). The intercept, degrees of freedom (df), log likelihood (logLik), Akaike information criterion adjusted for a small sample size (AICc), AICc delta (ΔAICc) and model weight (w) are provided for each candidate model. The table also indicates which of the following explanatory variables are included in each candidate model. The top models within ΔAICc < 2 units are marked in bold.

Intercept	**Water distance**	**Elevational gain**	**Julian day**	**Cereal maturity**	**Slope**	**Cereal species**	**Year**	**Bush index**	**Grass index**	**Tree index**	**df**	**logLik**	**AICc**	**ΔAICc**	**w**
-8.32		**-2.06**	**0.82**	**+**		**+**	**+**			**-1.42**	**12.00**	**-440.58**	**905.38**	**0.00**	**0.65**
-8.09		-1.96	0.80	+		+	+	-0.25	-0.22	-1.43	14.00	-439.69	907.68	2.30	0.21
-8.10		-1.96	0.80	+	0.01	+	+	-0.24	-0.22	-1.42	15.00	-439.69	909.71	4.34	0.07
-7.66	-1.40	-2.02	0.87	+		+	+				12.00	-443.49	911.20	5.83	0.04
-7.65	-1.41	-2.02	0.87	+	-0.03	+	+				13.00	-443.48	913.21	7.83	0.01
-7.85			0.82	+		+	+	-0.46		-1.61	12.00	-444.71	913.64	8.26	0.01
-8.06			0.83	+		+	+			-1.67	11.00	-445.84	913.85	8.47	0.01
-7.29	-1.74		0.90	+		+	+				11.00	-448.76	919.71	14.33	0.00
-8.75	-1.36	-2.08		+		+	+				11.00	-449.83	921.83	16.46	0.00
-9.18				+		+	+			-1.72	10.00	-451.28	922.71	17.33	0.00
-8.43	-1.70			+		+	+				10.00	-455.48	931.12	25.74	0.00

-7.06			0.94	+			+				7.00	-464.01	942.11	36.73	0.00
-4.13		-1.52	1.47			+	+			-1.04	10.00	-472.32	964.80	59.42	0.00
-3.66	-1.52		1.52			+	+				9.00	-477.82	973.76	68.39	0.00
-2.29		-0.85			-0.04		+	-0.34	-0.27	-0.87	9.00	-561.33	1140.78	235.40	0.00
-2.29							+	-0.40	-0.25	-0.99	7.00	-564.90	1143.88	238.50	0.00
-3.23	-0.73	-1.03				+	+				9.00	-563.47	1145.07	239.69	0.00
-3.08	-0.94					+	+				8.00	-569.34	1154.78	249.40	0.00
-2.36		-1.18			0.04		+				6.00	-577.26	1166.59	261.21	0.00
-3.03											3.00	-597.35	1200.71	295.34	0.00

Table B2: Model summary of the most supported candidate model exploring probability of foraging on cereals among Eurasian beavers (*Castor fiber*) in southeastern Norway, 2019 and 2020 (n=1457). The model estimates are based on a generalized linear mixed effects model (GLMM) with a Bernoulli distribution and plot and field ID included as nested random terms. For each variable included in the model, we report the model estimates (β), standard error (SE), z value, and lower (2.5%) and upper (97.5%) confidence intervals. For the random terms (PlotID and FieldID) the variance, standard deviation (SD) and the lower (2.5%) and upper (97.5%) confidence intervals are provided. Also provided are the conditional and marginal r-squared for the model.

Fixed terms	**β**	**SE**	**z value**	**2.50%**	**97.50%**	**R2 (cond.)**	**R2 (marg.)**
Intercept (Barley, 2019)	-8.32	1.43	-5.81	-11.12	-5.51	0.92	0.45
SpeciesOat	0.97	0.84	1.15	-0.68	2.62		
SpeciesRye	2.82	2.12	1.33	-1.33	6.97		
SpeciesWheat	2.45	0.88	2.77	0.71	4.18		
Julian day	0.82	0.26	3.17	0.31	1.33		
MaturityImmature	3.72	0.60	6.24	2.55	4.88		
MaturityMature	3.51	0.71	4.94	2.12	4.91		
Elevation	-2.06	0.73	-2.82	-3.50	-0.63		
Tree index	-1.42	0.38	-3.77	-2.16	-0.68		
Year2020	-2.61	0.60	-4.39	-3.78	-1.45		
Random terms	**Variance**	**SD**		**2.50%**	**97.50%**		
PlotID:FieldID	4.97	2.23		1.65	3.02		
FieldID	15.58	3.95		2.60	6.00		

Table B3: Model selection table for the candidate models exploring the size of the area foraged by Eurasian beavers (*Castor fiber*) in cereal fields of southeastern Norway, 2019 and 2020 (n=300). Each model is fitted as a generalized linear mixed effect model (GLMM) with a gamma distribution. The intercept, degrees of freedom (df), log likelihood (logLik), Akaike information criterion adjusted for a small sample size (AICc), AICc delta (ΔAICc) and model weight (w) are provided for each candidate model. The table also indicates which of the explanatory variables are included in each candidate model. Whether a variable is fitted as a polynomial and the degree of polynomial is indicated with (poly) followed by the degrees. The top models within ΔAICc < 2 units are marked in bold.

Intercept	**Water distance**	**Julian day**	**Maturity**	**Poly (Elevation, 2)**	**Slope**	**Species**	**Year**	**Bush index**	**Grass index**	**Tree index**	**df**	**logLik**	**AICc**	**ΔAICc**	**w**
1.25	**0.40**			+		+	+				**11**	**-928.62**	**1880.15**	**0.00**	**0.33**
1.18	**0.33**					+	+				**9**	**-930.95**	**1880.53**	**0.38**	**0.27**
1.20	**0.32**	**0.07**				+	+				**10**	**-930.33**	**1881.41**	**1.26**	**0.18**
1.13	0.39		+	+		+	+				13	-927.79	1882.85	2.70	0.09
1.05	0.32		+			+	+				11	-930.19	1883.30	3.15	0.07
1.12	0.39	0.00	+	+		+	+				14	-927.79	1885.06	4.91	0.03
1.09	0.32	0.02	+			+	+				12	-930.17	1885.42	5.27	0.02
1.11	0.39	0.00	+	+	-0.02	+	+				15	-927.77	1887.23	7.08	0.01
1.01			+			+	+			-0.04	11	-937.97	1898.86	18.71	0.00
0.99		0.11		+		+	+			-0.02	12	-937.61	1900.31	20.16	0.00
1.11		0.06	+			+	+			-0.03	12	-937.78	1900.65	20.50	0.00
1.97		0.11	+				+				8	-942.96	1902.41	22.26	0.00
1.10		0.06	+			+	+	0.03		-0.04	13	-937.69	1902.65	22.50	0.00
1.01		0.07	+	+		+	+			-0.02	14	-937.29	1904.06	23.91	0.00
1.73											4	-948.81	1905.76	25.61	0.00
1.96				+	-0.06		+				8	-944.91	1906.32	26.17	0.00
1.96							+	0.02	-0.06	-0.04	8	-944.98	1906.45	26.30	0.00
0.99		0.06	+	+		+	+	0.04	-0.05	-0.03	16	-937.11	1908.14	27.99	0.00
0.87		0.05	+	+	-0.10	+	+	0.04	-0.05	-0.03	17	-936.11	1908.40	28.25	0.00
1.96				+	-0.07		+	0.03	-0.06	-0.04	11	-944.51	1911.94	31.79	0.00

Table B4: Model summary of the most supported candidate model exploring size of patches foraged on cereal fields by Eurasian beavers (*Castor fiber)* in southeastern Norway, 2019 and 2020 (n=300). For each variable included in the model estimates (β), standard error (SE), z value, and lower (2.5%) and upper (97.5%) confidence intervals are provided. For the random terms (PlotID and FieldID) the variance, standard deviation (SE) and the lower (2.5%) and upper (97.5%) confidence intervals are provided. Also provided are the conditional and marginal r-squared for the model.

Fixed terms	**β**	**SE**	**z value**	**2.50%**	**97.50%**	**R2 (cond.)**	**R2 (marg.)**
Intercept (Barley, 2019)	1.18	0.31	3.87	0.59	1.78	0.64	0.16
SpeciesOat	0.43	0.36	1.21	-0.27	1.14		
SpeciesRye	-0.45	0.70	-0.65	-1.82	0.92		
SpeciesWheat	0.92	0.33	2.79	0.27	1.56		
Water distance	0.33	0.08	4.22	0.18	0.49		
Year2020	-0.39	0.20	-1.97	-0.78	0.00		
Random terms	**Variance**	**SD**		**2.50%**	**97.50%**		
New_plotID:FieldID	0.71	0.84		0.72	1.00		
FieldID	0.00	0.07		0.00	36.37		

Table B5: Model selection table for the candidate models exploring the total area of cereals foraged within each territory of Eurasian beavers (*Castor fiber*) in southeastern Norway in 2019 and 2020 combined (n=17). Each model is fitted as a generalized linear model (GLM) with a negative binomial distribution. The intercept, degrees of freedom (df), log likelihood (logLik), Akaike information criterion adjusted for a small sample size (AICc), AICc delta (ΔAICc) and model weight (w) are provided for each candidate model. The top models within ΔAICc < 2 units are marked in bold.

Intercept	**Developed**	**Agriculture**	**Open**	**Cereals**	**Conifer**	**Deciduous**	**Mixed forest**	**Forest**	**Wetland**	**Territory size**	**df**	**logLik**	**AICc**	**ΔAICc**	**w**
3.33				**0.00**							**3.00**	**-94.93**	**197.72**	**0.00**	**0.37**
5.22											**2.00**	**-97.09**	**199.04**	**1.33**	**0.19**
6.05										0.00	3.00	-96.77	201.38	3.66	0.06
5.05									0.00		3.00	-96.86	201.56	3.85	0.05
5.00							0.00				3.00	-96.93	201.70	3.98	0.05
5.64		0.00									3.00	-96.94	201.72	4.00	0.05
5.31	0.00										3.00	-97.02	201.89	4.18	0.05
5.39					0.00						3.00	-97.04	201.92	4.20	0.05
5.37								0.00			3.00	-97.06	201.96	4.25	0.04
5.11			0.00								3.00	-97.07	202.00	4.28	0.04
5.24						0.00					3.00	-97.09	202.03	4.31	0.04

Table B6: Model selection table for the candidate models investigating proportion of GPS fixes overlapping with crop fields for each beaver-year of Eurasian beavers (*Castor fiber*) in southeastern Norway 2010-2021 in relation to physiological variables. Some physiological variables had missing values and we therefore compared each model with a null model fitted to the same dataset. The number of observations per dataset is given as N. Each model is fitted as linear model with a Gaussian distribution. The intercepts, degrees of freedom (df), log likelihood (logLik), Akaike information criterion adjusted for a small sample size (AICc), AICc delta (ΔAICc) and model weight (w) are provided for each candidate model. The top models within ΔAICc < 2 units are marked in bold.

Variable	**N**	**Intercept**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Null model	34	0.153	2	12.63	-20.90	0.00	0.75
Age		0.181	3	12.74	-18.70	2.19	0.25
Null model	34	**0.15**	**2**	**12.63**	**-20.90**	**0.76**	**0.41**
Year		**-22.66**	**3**	**14.22**	**-21.60**	**0.00**	**0.59**
Null model	34	0.153	2	12.63	-20.90	0.00	0.76
Sex		0.161	3	12.68	-18.60	2.30	0.24
Null model	34	**0.1529**	**2**	**12.627**	**-20.9**	**0**	**0.759**
Female reproduction		0.1582	3	12.685	-18.6	2.3	0.241
Null model	24	**0.1144**	**2**	**20.305**	**-36**	**0**	**0.786**
Female reproduction +1yr		0.1155	3	20.315	-33.4	2.61	0.214
Null model	33	**0.1464**	**2**	**12.605**	**-20.8**	**0.95**	**0.384**
Weight		**-0.3201**	**3**	**14.292**	**-21.8**	**0**	**0.616**
Null model	32	0.1559	2	11.039	-17.7	5.85	0.051
Tail fat index		**-0.8187**	**3**	**15.185**	**-23.5**	**0**	**0.949**

Table B7: Model summary of the most supported candidate models exploring proportions of GPS fixes overlapping with crop fields within each tagging event (beaver-year) of Eurasian beavers (*Castor fiber*) in southeastern Norway, 2010-2021. Tail fat index as a measure of body condition was the only statistically important variable and here are the model estimates (β), standard error (SE), t value, and lower (2.5%) and upper (97.5%) confidence intervals. Also provided are the conditional and marginal r-squared for the model.

Fixed terms	**β**	**SE**	**z value**	**2.50 %**	**97.50 %**	**R2 (cond.)**	**R2 (marg.)**
(Intercept)	-0.82	0.33	-2.49	-1.49	-0.15	0.23	0.20
TailFatIndex	**0.24**	**0.08**	**2.98**	**0.08**	**0.41**		

Article 3

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Individual variation and spatio-temporal trends in terrestrial habitat selection of Eurasian beavers

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Open research statement

Data and/or code are provided as private-for-peer review via the following link:

https://figshare.com/s/ed505be9d5c208faeb60

Abstract

Habitat selection is key to understand animal ecology and encompasses all resources and threats that affect animal occupancy. Animals often display individual selection patterns, while varying food availability and human disturbances affects temporal patterns. Habitat selection patterns may differ among individuals sometimes driven by age and sex, but fewer sex-specific differences are expected in monogamous species. We investigated individual, seasonal, and circadian habitat selection of monogamous and monomorphic Eurasian beavers (*Castor fiber*) by attaching GPS loggers on 74 beavers in 104 tagging events, 2009-2021. We modelled beaver habitat selection within terrestrial environments and wetlands using resource selection functions and a Bayesian framework. We investigated individual variability in relation to beaver density, age, reproductive effort, and body condition. Lastly, we explored seasonal and circadian habitat selection of the socio-reproductive groups. On a population level, beavers selected against increasing distance to water and elevational gain, as well as against crops, developed- and open areas. We found considerable individual variation and age was the best predictor to explain these. There were distinct temporal trends for certain habitat types, and the socio-reproductive groups differed in seasonal selection for crops and developed areas. The reproductively active pair displayed mostly similar circadian trends, which differed from the non-reproductive for certain habitat types. Temporal patterns may reflect the temporally dynamic environment with varying food availability and risk, but also different strategies of the socio-reproductive groups. Exploring individual variability as well as temporal trends revealed nuances of habitat selection within this monogamous and group-living species.

Keywords: *Habitat selection, Eurasian beaver, Castor fiber, spatio-temporal, individual variation, INLA-SPDE*

Introduction

Habitat selection includes all physical, chemical, and biological resources as well as environmental conditions that affect occupancy, survival, and reproduction of animals, which is key to understand animal ecology and evolution (Northrup et al. 2021; McGarigal et al. 2016). Habitat selection occurs on different levels where the first-order refers to the geographical range of the species, second-order refers to placement of the home range, third-order to habitat patches within the home range, and fourth-order selection to resources within habitat patches (McGarigal et al. 2016; Johnson 1980). Habitat selection is highly dynamic and varies in relation to physical needs, environmental conditions (William et al. 2018), perceived risk from humans (DeCesare et al. 2012), presence of predators (Joly et al. 2017), interactions with conspecifics (Richter et al. 2020; McLoughlin et al. 2002), and availability of food resources (Dupke et al. 2017; McLoughlin et al. 2002). Habitat selection consists of choices made by individuals, but for practical reasons is often modelled at the population level. However, individual differences are also interesting to explore, especially when linked to demographic variables that may drive individual variability (Mayor et al. 2009; Northrup et al. 2021).

A wide range of demographic and physiological mechanisms may affect habitat selection such as sex, age, reproduction, population density, and intraspecific competition (Northrup et al. 2021). Males and females can display highly different selection patterns, and ignoring these differences may exaggerate or underestimate selection for certain habitats (Dupke et al. 2017). While females often select for habitats with lower risk of encountering humans, predators and conspecifics (McLoughlin et al. 2002; Joly et al. 2017), males sometimes select more for risky habitats that entail a higher risk of encountering humans but also obtaining abundant food sources (Merkle et al. 2013; Chiyo et al. 2011; Ditmer et al.

2015). Such differences have often been studied in polygamous or size-dimorphic species where differences are driven by disparities in physical requirements, vulnerability to predation, competition, or mating systems (Oliveira et al. 2018; Creel et al. 2005). However, behavioral differences in monogamous species have received less research attention as they usually display less sexual dimorphism both in terms of morphology and behavior (Kleiman 1977).

Certain behavioral differences are still found in monogamous species, but often restricted to certain time periods such as the reproductive period. Studies of monogamous sea birds have shown that female sooty shearwaters (*Puffinus griseus*) travelled further to forage prior to egg laying (Hedd et al. 2014), and female thick-billed murres (*Uria lomvia*) and northern gannets (*Morus bassanus*) dove deeper than males during the breeding season (Elliott, Gaston, and Crump 2010; Lewis et al. 2002). These are monomorphic species with similar body size and a high degree of co-parenting, indicating that sex-specific behavioral differences are not always driven by body size. Monogamy is found in fewer than 9% of mammal species and co-parenting between males and females have been identified in 56% of these (Lukas and Clutton-Brock 2013). Fewer studies appear to have explored sex-specific behavioral differences in these species. In the monogamous rodent, crested porcupine (*Hystrix cristata*) no differences were found between males and females neither in terms of territory size nor habitat selection (Mori et al. 2014; Lovari, Sforzi, and Mori 2013). However, these studies only considered annual habitat selection or within pre-defined seasons, which may miss more subtle different temporal nuances between the sexes in monogamous mammals.

Resources and threats within habitats are rarely static but change across time, which animals respond to by adapting temporal habitat selection. Temporal trends have received less attention in habitat selection studies, but several studies have indicated highly different seasonal and diurnal patterns (McGarigal et al. 2016; Dupke et al. 2017; Mayor et al. 2009) as well as interannual variation (Uboni et al. 2015). Seasonal food availability and quality often induce shifts in habitat selection, such as brown bears (*Ursus arctos*) selecting for berry areas to gain weight prior to hyperphagia (Hertel et al. 2016; Welch et al. 1997), red deer (*Cervus elaphus*) using pastures more in spring and fall (Godvik et al. 2009) or jumping the green wave by tracking phenological green-up to summer foraging sites (Bischof et al. 2012). At fine temporal scales, circadian rhythm, rumination cycles, weather, olfactory cues, and especially human disturbances, tend to have a large impact on animal habitat selection (Richter et al. 2020; Christiansen et al. 2017). Red deer and roe deer (*Capreolus capreolus*) for example selected for open areas with higher food quality during night, while selecting for higher vegetation cover during daytime, when exposed to human disturbance (Dupke et al. 2017; Richter et al. 2020).

Animal reactions to anthropogenic disturbances and food availability is often species-specific but can also vary according to sex and reproductive status (Oliveira et al. 2018; McLoughlin et al. 2002; Joly et al. 2017). Female red deer selected stronger for fertilized meadows than males (Lande et al. 2014), and were also more willing to risk crossing roads to access such areas (Meisingset et al. 2013). However, female moose accompanied by calves selected stronger for forests and avoided open areas in contrast to males and non-reproducing females that did not strongly avoid these areas (Bjørneraas et al. 2012). Increased energy use of females especially during lactation might increase foraging needs and create differences in habitat selection patterns (Ruckstuhl 2007; Clutton-Brock et al. 1982). This might induce temporal differences even between the sexes of monogamous species such as racoon dogs (*Nyctereutes procyonoides*), where both activity patterns and space use differed between males and females during reproduction (Drygala et al. 2008; Zoller and Drygala 2013). Group-living species are often assumed to have similar habitat selection patterns, and individuals of the same family are often merged during analyses (Uboni et al. 2015).

However, differences in habitat selection and foraging behavior may even occur among individuals within the same family unit (Sheppard et al. 2018; Robertson et al. 2014). Different habitat selection choices may ultimately affect fitness both through reproduction and survival (Ofstad et al. 2020; McLoughlin et al. 2007), but such consequences are rarely studied as it requires long-term monitoring of populations (Gaillard et al. 2010; Clutton-Brock and Sheldon 2010).

We used a monogamous, monomorphic, and group-living species, the Eurasian beaver (*Castor fiber*) and a long-term dataset from the Norwegian Beaver Project (NBP) to investigate individual differences and temporal patterns of habitat selection. The Eurasian beaver and its close relative, the North American beaver (*C. canadensis*) function as ecosystem engineers with large impacts on the structure of ecosystems (Rosell et al. 2005; Hood and Larson 2015). As central place foragers they concentrate foraging activities around their lodge or water, where they might deplete food resources (Fryxell 1992), while becoming more selective with increasing distance (Haarberg and Rosell 2006; Gallant et al. 2004). Beavers are nocturnal and mostly reside within lodges or burrows during daytime (Mott, Bloomquist, and Nielsen 2011; Sharpe and Rosell 2003). They reside in family groups where the reproductively active pair maintains an exclusive territory shared with offspring from the current and previous years (Nolet and Rosell 1994; Mayer, Zedrosser, and Rosell 2017c). Females give birth sometime in May-June and are subsequently more restricted to the lodge during lactation (Wilsson 1971; Żurowski et al. 1974), but the reproductive pair later display a high level of co-parenting (Sun 2003; Wilsson 1971). Beavers change their diet from mainly foraging on trees in winter, towards more herbaceous and aquatic vegetation in summer (Milligan and Humphries 2010; Nolet, Hoekstra, and Ottenheim 1994), and may display sex-specific patterns in activity and food use (Lodberg-Holm et al. 2021; Sharpe and Rosell 2003; Herr and Rosell 2004). Several studies have explored beaver habitat selection in relation to placement of territories or lodges (Scrafford et al. 2018; Curtis and Jensen 2004; Hood 2020), selection of habitats and food sources within territories (Francis et al. 2017; Wang, McClintic, and Taylor 2019; Pinto, Santos, and Rosell 2009; Steyaert, Zedrosser, and Rosell 2015), and within aquatic environments (Bergman, Bump, and Romanski 2018; Mortensen et al. 2021). However, individual variation and temporal trends related to socio-reproductive status have not previously been investigated to the best of our knowledge.

Our goal was to study individual and temporal third-order habitat selection of Eurasian beavers within terrestrial environments, including potential drivers of individual differences, and temporal trends specific to different socio-reproductive groups. We hypothesized that beavers would display individual differences impacted by reproductive effort, age, body condition and beaver density. Secondly, we hypothesized that we would find temporal trends related to seasonal food availability and daily human activity patterns. Finally, we hypothesized that temporal habitat selection would differ amongst social-reproductive groups that have different energetic needs and social responsibilities.

Methods

Study area

The study area encompasses three main rivers (Sauar, Gvarv and Straumen) that all empty into lake Norsjø. The rivers run through Midt-Telemark and Nome municipalities located in southeastern Norway. The rivers are between 30-150 m wide, and the sections included as part of the study area extend approximately 32 km, while they meander through a rolling landscape dominated by boreal forests, crops, pastures, and small villages. The rivers provide a stable water supply and are too wide for beavers to construct dams (Herr and Rosell 2004). Parts of the rivers are surrounded by fields used for pastures and crop production, mostly for cereals such as wheat (*Triticum aestivum*), oat (*Avena sativa*), barley (*Hordeum sativum*), and rye (*Secale cereale*). Human activity in the area increases during summers an influx of summer tourists and increased boat traffic (Flemsæter, Stokowski, and Frisvoll 2020). Forested areas along the rivers are dominated by grey alder (*Alnus incana*), birch (*Betula* spp.), Norway spruce (*Picea abies*), rowan (*Sorbus aucuparia*), bird cherry (*Prunus padus*), alder-buckthorn (*Rhamnus frangula*), common ash (*Fraxinus excelsior*), and red elderberry (*Sambucus racemosa*) (Haarberg and Rosell 2006). The mean daily temperature in the region is 6.5°C with a mean precipitation of 2.3mm (eKlima 2020). All large carnivores except lynx (*Lynx lynx*) have been extirpated from the area (Rosell and Sanda 2006).

Study population and live-captures

After centuries of prosecution, beavers have been reintroduced throughout Europe and North America to restore the species as well as their ecological functions (Halley, Saveljev, and Rosell 2021). Beavers have persisted within the study area since the 1920s, and are probably close to carrying capacity (Rosell and Hovde 2001). Hunting pressure has been low and approximately 5% of the known population were harvested between 2009 and 2014 (Graf, Mayer, et al. 2016) with highest outtakes during April and May (Parker et al. 2002). Reproducing females are disproportionally shot by human hunters during this spring hunt (Parker et al. 2002), which cause has not yet been identified (Mayer et al. 2017). Local beavers usually disperse at around two years of age, but may delay dispersal for five more years to increase body mass and gain a competitive advantage (Mayer, Zedrosser, and Rosell 2017a).

Beavers were live-captured using nets from small motorboats during nighttime (Rosell and Hovde 2001). Post-capture, we transferred the beaver to a cloth sack to allow handling without the use of anesthesia. Every beaver was tagged using metal or plastic ear tags (Sharpe and Rosell 2003), in addition to a passive integrated responder tag (PIT) inserted into the neck to identify individual beavers (Briggs, Robstad, and Rosell 2021). Each beaver was weighed and body length and various tail measurements were recorded to calculate tail fat index as a measure of body condition (Parker, Zedrosser, and Rosell 2017; Rosell, Zedrosser, and Parker 2010). We aged the beavers based on their body weight at first capture where those weighing ≥17 kg and ≤19.5 kg were defined as minimum age of two years old, while those >19.5 kg as minimum three years old (Campbell et al. 2005; Mayer, Zedrosser, and Rosell 2017b). An additional year was added to the minimum age following the initial capture. We determined sex of the beaver based on the color of the anal gland secretion (Rosell and Sun 1999). Socio-reproductive status was determined based on observations of reproduction in the current or previous years, and whether there were other adult beavers present within the same territory (Campbell et al. 2013). Beavers that had not yet reproduced and were still living in their parents' territory, were classified as non-reproductive beavers, while the rest were categorized as reproductively active males or females. Reproduction and family size were determined from long-term monitoring as well as genetic testing to determine parentage (Nimje et al. 2021; Mayer, Zedrosser, and Rosell 2017c). To estimate reproductive effort, we calculated the average number of kits produced by each beaver in each year in which that beaver has been monitored. We used family size as a measure of beaver density within each territory.

The NBP has developed a novel method to tag beavers with data loggers glued onto the lower back of the beaver (Graf, Hochreiter, et al. 2016), which has previously provided information on territorial behavior (Graf, Mayer, et al. 2016; Mayer et al. 2020), spatial movement patterns (Cabré et al. 2020; McClanahan, Rosell, and Mayer 2020), as well as habitat selection (Steyaert, Zedrosser, and Rosell 2015; Mortensen et al. 2021). Beavers residing within the study area were instrumented with data loggers to monitor their spatial movements during the ice-free season between March and November. In most years, the reproductive pair was prioritized due to concerns that non-reproductive beavers may disperse, causing problems to recover the tags (Mayer, Zedrosser, and Rosell 2017c). We fitted beavers with a GPS logger, either G1G 134A (24 g; Sirtrack, Havelock North, New Zealand, TGB-317/315GX (Telenax, Playa del Carmen, Mexico), or model Gipsy 5 (TechnoSmart, Via Antonio Signorini 20 – 00134 – Rome, Italy) (Justicia, Rosell, and Mayer 2018). We also attached a VHF transmitter (Reptile glue-on, series R1910; Advanced Telemetry Systems, Isanti, MN, USA), with a weight of 10 g. In most tagging events, we also equipped beavers with a Daily Diary (52 x 29 x 22 mm, 62 g with waterproof casing) developed by SLAM lab at Swansea University, UK, or a tri-axial accelerometer logger (TAA) (15 × 90 mm, 62 g; JUV Elektronik, Schleswig-Hollstein, GER), but these were not used in the current study.

The loggers were attached to a piece of polyester using epoxy glue and plastic straps and covered with a durable small-meshed net to increase the surface area. The combined weight of the data loggers and materials used for attachment never exceeded 2% of the beaver's body weight (Robstad et al. 2021). The tag was glued approximately 15 cm above the base of the tail using fast-drying two-component epoxy glue. The GPS units were set to log positions every 15 minutes between 19:00 and 07:00/08:00, which covered the beavers' active period outside the lodge (Sharpe and Rosell 2003). Some of the GPS devices have been previously tested and had locational error of 15.7 ± 21.9 m during field testing and a fix rate of 86.2 ± 10.3% while deployed on beavers (Justicia, Rosell, and Mayer 2018). After one to six weeks, data loggers were recovered either by re-capturing the beaver and carefully cutting the tag away from the outer fur. If the tag fell off by itself, it was retrieved from the water, on land, or inside the lodge. All handling of beavers was conducted in the field, and they were released within 40 min at the same location as the capture. The capture and handling methods were approved by Norwegian Experimental Animal Board (FOTS id 742, id 2170, 2579, 4384, 6282, 8687, 15947, 19557) and the Norwegian Directorate for Nature Management (2008/14367 ART-VI-ID, archive code 444.5, 446.15/3, 14415).

Data preparation

To improve spatial accuracy of GPS locations, we removed those with horizontal dilution of precision (HDOP) value >5 and three or fewer satellites (Justicia, Rosell, and Mayer 2018). We also excluded GPS locations from capture nights when beavers may change their behavior (Graf, Hochreiter, et al. 2016). For each tagging event (beaver-year), we constructed a 95% minimum convex polygon (MCP) home range, and excluded locations outside that may represent exploratory trips into neighboring territories (Mayer, Zedrosser, and Rosell 2017b). We buffered these territory estimates with 100 m to include areas that beavers swim past but rarely visited, as potentially available habitats. Beavers rarely move further than 60-77 m away from the safety of water (Donkor and Fryxell 1999; Steyaert, Zedrosser, and Rosell 2015), but may venture further when attracted by especially attractive food sources (Northcott 1971). We excluded areas further than 100 m away from water to avoid inclusion of unrealistically large inland areas where the rivers meander. We excluded GPS locations in the water and focused our sampling on available habitats within terrestrial habitats and wetlands. In each home range, we created random points at a rate of 5:1 compared to GPS locations to represent habitat availability (Mayer et al. 2019).

For each GPS or random location, we extracted the habitat type from a national map of natural resources in Norway (FKB-AR5) (Kartverket 2016). We merged the habitat types, human settlements, roads and railways as developed areas, all agricultural fields used for crop production as crops, while pastures and open habitats were defined as open areas. Wetlands and forest were included as separate categories, and we extracted the dominant forest type within each forest patch (coniferous, deciduous, or mixed forest). For our first analysis, we used habitat types as continuous variables by extracting the percentage cover in a circular buffer around each location. We chose a buffer radius of 15 m, which is similar to the locational error of GPS units used in the study (Justicia, Rosell, and Mayer 2018). For our second analysis, we extracted habitat types as a categorical variable. We also estimated the Euclidian distance from each location to the closest water and developed area. Elevation was extracted from a digital elevation model (10 x 10 m) (Kartverket 2019), and slope was calculated using the "terrain" function in the R package raster (Hijmans 2020). We estimated the elevational gain from every location to the closest water and used this for all subsequent analyses. Dates were transformed into Julian day, which we defined as the number of nights since January 1 each year. Seasons were defined as spring (March-May) summer (June-August) and fall (September-November). Hour of the night was transformed into active hour, where hour 1 represented the first hour of logging at 19:00 and the last active hour as 08:00.

Statistical analysis

For all analyses, we followed the recommended steps by Zuur, Ieno, and Elphick (2010) for data exploration. We checked the potential collinearity of explanatory variables using a Pearson correlation test with a cutoff value of 0.7, as well as variance inflation factors (VIF) with a cutoff value of 10 (Harrison et al., 2018; Zuur et al., 2010). We avoided collinear variables within the same model. To check model assumptions, we plotted the residuals for each model against fitted values and against each numerical variable included or not included in the model to check for non-linear patterns (Zuur and Ieno 2016). All statistical and spatial analyses were conducted in R version 4.1.2.

Population-level model

To explore population-level habitat selection patterns, we fitted resource selection functions (RSF) with generalized linear mixed effects models (GLMM) and a Bayesian framework using integrated nested Laplace approximations (INLA) (Rue, Martino, and Chopin 2009). Whether the location represented a GPS or random location was included as the response using a Bernoulli distribution (1 = GPS location, 0 = random location). We applied weighted logistic regression with large weight on random locations to ensure robustness of the estimates (Northrup et al. 2021; Fieberg et al. 2021). A weight of 1 was used on the GPS locations and a weight of 1000 on the random locations (Muff, Signer, and Fieberg 2020). The percentage of each habitat type, elevation, slope, distance to closest water and developed areas were included as potential explanatory variables. Percentage forest cover displayed collinearity issues, and we therefore created a new forest variable, containing only percentage dominated by either deciduous or mixed forest while excluding coniferous forest, as the beaver diet relies mostly on deciduous trees (Haarberg and Rosell 2006; Nolet, Hoekstra, and Ottenheim 1994). Year of tagging and beaver ID were included as random slopes, while year was included as a random intercept. We included both random intercepts and slopes to account for among individual variation in selection estimates (Muff, Signer, and Fieberg 2020), and to enable us to investigate the causes of individual variation in the next part of the analysis. We gave the random intercepts a large fixed prior to avoid variation in the intercepts simply due to different distribution of habitats (Muff, Signer, and Fieberg 2020). We used penalized complexity (PC) priors for the hyperparameters of the random slopes instead of the default gamma priors as these may overfit the model (Muff, Signer, and Fieberg 2020; Zuur 2017). All numerical variables were scaled by subtracting the mean and dividing by the standard deviation to assist model convergence (Zuur 2017).

The full model including all fixed and random effects was compared with a null model containing only the random intercept (Forstmeier and Schielzeth 2011; Harrison et al. 2018), using deviance information criterion (DIC) (Xi et al. 2021; Zuur 2017). We also provide the Watanabe-Akaike information criterion (WAIC), which has similarities to leave-one-out cross validation methods (Vehtari, Gelman, and Gabry 2015). However, WAIC may encounter problems when applied to time series and spatial data, we therefore chose to focus on DIC for model comparisons (Gelman, Hwang, and Vehtari 2014). If the full model was more supported than the null model, we dropped one variable at the time that was considered uninformative (95% credible intervals overlapped with zero), starting with the variable with the largest standard error. When only statistically important terms were retained, we used this as a final model.

Individual modelling

We extracted individual estimates of habitat selection for each beaver-year from the full model in the previous analysis (Forstmeier and Schielzeth 2011) and used these selection estimates for the next step of the analysis (Northrup et al. 2021). First, we visualized individual variation by plotting the selection estimates for each habitat variable in each beaver-year. We then modeled the estimates of selection for each habitat variable using age, body condition, reproductive effort, and beaver density as explanatory variables (Northrup et al. 2021). Tail measurements were not recorded in every tagging event and tagging events with missing values were therefore excluded from the analysis. For each habitat type, we created a full model including all explanatory variables and beaver family ID as a random intercept. We used linear mixed effects models and a Gaussian distribution to model variation in the individual selection estimates for each habitat type in INLA. We used the reciprocal of variance for each individual estimate as a weighting factor to place more weight on estimates with lower model uncertainty. We used the same model selection procedure as described above.

Temporal models

To explore temporal trends in beaver habitat selection, we used the same dataset and the RSF framework, but this time applying generalized additive mixed models (GAMM) to investigate seasonal (Julian day) and circadian (active hour) trends. Temporal trends in habitat selection studies are often investigated by dividing days or hours into categories, which risk oversimplifying temporal trends (Richter et al. 2020). We instead included day of the year and hour as continuous variables. Habitat types were included as categories to fit interactions between these and Julian day or active hour. Forests were retained as one habitat type including all forest types for this analysis. We included the other continuous variables (elevation, slope, distance to water and developed areas) if these were retained in the final model from the previous population-level models. To reduce model complexity, we constructed separate model sets investigating seasonal and circadian trends but used a similar model structure in both model sets. We used unpenalized cubic regression splines that use only fixed model terms and thereby reduced the number of hyperparameters to estimate (Zuur and Ieno 2018). The smoothCon function from the mgcv package (Wood and Wood 2015) was used to construct smoothers for both Julian day and active hour, while limiting the number of knots to 5, to avoid oversmoothing. We modelled temporal habitat selection for each social-reproductive group, which we defined as reproductively active males and females, and non-reproductive beavers. We did not separate between non-reproductive males and non-reproductive females as we did not expect differences between them prior to reproduction, and due to a smaller sample size of these beavers. We lacked data on non-reproductive beavers during summer, and we therefore merged this group with the reproductive males for the seasonal models but retained them as a separate group for the circadian models.

We included beaver ID as a random intercept to account for repeated sampling of the same individual, while we accounted for possible spatial autocorrelation and missing spatial variables by fitting various spatial-temporal models using stochastic partial differential equations (INLA-SPDE) (Beguin et al. 2012; Lezama-Ochoa et al. 2020). These models are useful to deal with some of the statistical challenges of spatio-temporal data and are increasingly applied to model species distributions and habitat selection (Lezama-Ochoa et al. 2020; Sadykova et al. 2017; Xi et al. 2021; Beguin et al. 2012). We first created a mesh covering the study area with non-overlapping triangles using Delaunay triangularization (Appendix S2: Fig. S1). Matérn correlation estimated whether locations closer in space were more similar than those spaced further apart and the distance in which this correlation fades (Zuur 2017). For mathematical details on how this is estimated see Illian, Sørbye, and Rue (2012) and Lindgren, Rue, and Lindström (2011). A prior for the range in which this spatial dependency likely diminishes must be provided based on the biology of the species (Illian, Sørbye, and Rue 2012). We used average length of beaver territories within the study area, which is 3550 ± 1591 m (Graf, Mayer, et al. 2016), and set 3.5 km as a prior for the range. We first fit a basic GAMM model without spatial autocorrelation and then extended this model to SPDE models using different spatio-temporal autocorrelation structures (Zuur 2017). First, we fit a SPDE model for all the sampling years combined. Then, we added a temporal element and constructed a replicate spatial autocorrelation model, which estimates the same strength of spatial autocorrelation in each year but allows for different spatial patterns every year (Zuur and Ieno 2018). Lastly, we fit a spatio-temporal model with residual autoregressive correlation (AR1), which means that spatial correlation patterns were allowed to change gradually across time where years close together are predicted to be more similar than those further apart (Zuur 2017). AR1 requires regularly spaced data, but as we lacked data from 2017, we had to create regularly spaced time-knots (every second year) to fit this model (Zuur 2017). We compared the four model structures and a null model using DIC for each social-reproductive group with Julian day as the smoother, and retained the most supported model structure also for the circadian models.

Results

We obtained GPS locations from 74 beavers in 104 different tagging events within 19 families. Thirteen beavers were tagged twice, five were tagged three times and two beavers were tagged four times in different years. Only two beavers were tagged during the first year in 2009, while no beavers were tagged in 2017. The dataset included 33 females (nine non-reproductive and 25 reproductively active) and 41 male beavers (10 non-reproductive and 32 reproductively active) with an average age of 6.3±3.5 SD. Two of the non-reproductive beavers found their own territories and became reproductively active in later years. The tagging periods lasted 2-22 days with an average of 10.3±4.3 SD days. In total, the dataset consisted of 82,628 locations with 13,776 used and 68,652 available locations. Most beaver GPS locations were in forests (74.8%), followed by wetlands (8.9%), open areas (8.6%), crops (6.6%) and developed areas (1.1%).

Population-level

In the first population-level analysis, the final model contained elevation, distance to water and the percentage crops, developed- and open areas (Appendix S1: Table S1). The beavers selected against increased elevation, increasing distance to water, crops, developed- and open areas (Appendix S1: Table S2 and Appendix S2: Fig. S2). We found considerable individual variation in most habitat variables when visualizing the individual selection estimates from the full model (Fig. 1). Distance to water displayed the least individual variation, with all beavers except one selecting against increasing distance to water and only six beavers (5.8%) displaying no clear selection patterns (Fig. 1). Most beavers selected against increased elevational gain (31.7%) with many displaying no clear selection patterns (66.3%), and only two beavers selecting for increased elevational gain (Fig. 1). Most selection estimates in relation to developed areas had credible intervals overlapping with zero indicating no clear selection patterns (60.3%), but the remaining (30.8%) selected against and only two beavers selected for developed areas (Fig. 1). Half of the beavers selected against crops (50%) and open areas (45.2%) with few beavers selecting for a higher cover of these two habitat types (7.7% and 6.7% respectively) (Fig. 1). Slope and wetland were not retained in the population-level model and most individual estimates overlapped with zero indicating no clear selection patterns (81.7% and 86.5% respectively). The few beavers that displayed any selection patterns for these variables selected against slope and wetlands (10.6%) while eight beavers selected for steeper slopes and three for wetlands. Distance to developed areas and forests were not retained in the population-level model, and we found considerable individual variation with beavers selecting both for (24.0% and 26.9% respectively) or against (32.7% and 18.3% respectively) (Fig. 1).

Individual variation

We extracted selection estimates for all 104 tagging events, but after excluding those with missing values, 90 selection estimates was retained to explore drivers of individual variability. The full models were always more supported than the null model, except when modelling variability in selection for developed areas, where the null model was most supported (Appendix S1: Table S3). Age of the beaver was retained in the models investigating individual variability in selection for elevation, slope, crops, percentage forest and open areas (Appendix S1: Table S4). With increasing age, beavers strengthened their selection against elevation while weakening their selection against a higher percentage of crops and open areas (Fig. 2). While younger beavers generally selected against forests, older beavers selected for forests. Average reproduction was retained in the models for elevational gain, slope, open areas, and distance to developed areas (Appendix S1: Table S4). While the impact of average reproduction was negligible for selection for slopes and distance to developed areas, beavers with higher average reproduction weakened their selection against elevational gain but displayed slightly stronger selection against open areas (Appendix S1: Table S5 and Fig. 3). Family size as a measure of beaver density was retained in all models except for elevational gain and forest (Appendix S1: Table S4). However, family size explained little of the variation in most selection estimates. Selection against distance to water and crops, however, weakened slightly in beavers from larger families (Appendix S1: Table S5 and Fig. 4). Finally, tail fat index was retained in the models looking into individual variation in selection for distance to developed areas and water, slope, crops, forest, and open areas (Appendix S1: Table S4). Selection against crops and steeper slopes strengthened in beavers in a good body condition, while selection against distance to water weakened (Appendix S1: Table S5 and Fig. 5).

Temporal trends

Finally, we modelled the seasonal and circadian trends for each socio-reproductive group. The spatio-temporal model with time knots was most supported for all socio-reproductive groups except reproductively active males (Appendix S1: Table S6). For reproductively active males, the spatial-temporal replicate model was most supported and used to model the circadian trends of this group. However, for the seasonal models, we combined reproductively active males and non-reproductive and used the spatio-temporal time knot model that was most supported for this combined group. The posterior marginal distributions of the coefficients of the predictors are presented in the appendix (Appendix S1: Table S7 and Table S8), together with visualizations of the spatial random fields indicating spatial clusters of beaver locations unexplained by the model (Appendix S2: Fig. S3-S6). The seasonal smoothers interacting with habitat types displayed the clearest seasonal trends in relation to selection for crops that moved from strong selection against crops in spring, to selection for crops in July that continued until fall. However, reproductively active females selected slightly stronger for crops compared to the remaining beavers (Fig. 6). There were no seasonal trends in selection for forests. Reproductively active females displayed no seasonal trends in selection for developed areas, but the remaining beavers selected against developed areas during July-

September (Fig. 6). Reproductively active males and non-reproductive beavers selected for open areas and wetlands in early spring and shifted to selection against these in late summer. Females selected against wetlands in early summer, but they displayed no clear selection for or against any other habitat variables, with the exception of crops, during the remainder of the season (Fig. 6).

Lastly, we modelled patterns of circadian habitat selection, this time including non-reproductive beavers as a separate group (Appendix S1: Table S9-S11). The three groups displayed the largest differences in circadian selection of crops with reproductively active males selecting for crops during evening and avoiding them in the morning (Fig. 7). Reproductively active females had the opposite pattern with selection against crops in the evening and selection for crops during morning. The non-reproductive beavers displayed no clear circadian selection patterns for or against crops (Fig. 7). There were limited diurnal trends in selection for forests, but reproductively active males and non-reproductive beavers both selected weakly for forest during the last hour of the morning. Non-reproductive beavers selected for developed areas in the morning, while the reproductively active pair displayed no clear circadian selection patterns for developed areas. Non-reproductive beavers also selected against open areas in the evening, while switching to selection for these areas after 3 am (Fig. 7). The reproductively active pair selected for open areas in the middle of the night but avoided these areas in the evening and morning (Fig. 7). They also displayed similar patterns in selection for wetlands in the evening and morning, while the non-reproductive selected against wetlands during this time. The non-reproductive instead selected for wetlands for a few hours after 3 am (Fig. 7).

Discussion

We have shown that Eurasian beaver habitat selection is highly dynamic and varies among individuals and across time, sometimes with socio-reproductive groups displaying different seasonal and circadian patterns. On a population-level, we found that distance to water and elevational gain as well as crops, developed- and open areas, were avoided by beavers. As we hypothesized, beavers displayed much individual variation in selection for certain habitat variables. Some of the individual variability could be explained by age, reproduction, density, and body condition. Age had the strongest impact. Older beavers displayed weaker selection against crops while selecting for forests and open areas, and more strongly against elevation. We also identified temporal trends in habitat selection, which might reflect seasonal food availability and human disturbances, giving support to our second hypothesis. Male reproductive beavers and non-reproductive beavers displayed the clearest seasonal trends by selecting for open areas and wetlands in spring while all beavers switched to crops in late summer and autumn. The reproductive males and non-reproductive beavers avoided developed areas in summer, but reproductively active females displayed no temporal selection patterns other than an avoidance of wetlands in early summer and selection for crops in late summer and fall. The reproductively active pair selected for crops at different times of the night but displayed similar circadian selection patterns for other habitat types, which sometimes differed from non-reproductive beavers. This illustrated that temporal habitat selection may differ between socio-reproductive groups as hypothesized.

Individual variation

We found considerable individual variation in selection for certain habitat variables. Beavers varied most in selection of forests and distance to developed areas, which probably affected the lack of population-level trends for these habitat variables. Similar individual variability was found in Canadian elk in relation to selection for forest and roads, which made it difficult to predict population-level trends (Newediuk, Prokopenko, and Vander Wal 2022).

Accounting for such variability may change the conclusions of habitat selection models and predict completely opposite selection patterns (Gillies et al. 2006). Individual selection patterns in habitat selection can also have direct implications for reproductive success and mortality such as Norwegian female moose experiencing higher mortality when selecting for grasslands during the hunting season (Ofstad et al. 2020). Individual differences may therefore cause selective pressure on certain animal behaviors with unknown long-term evolutionary impacts on populations (Lodberg-Holm et al. 2019; Madden and Whiteside 2014).

We also investigated potential drivers of individual variability, but no explanatory variables could account for complete shifts in the direction of selection. However, the strength of selection changed among beavers with certain traits. The largest differences were related to beaver age, where older beavers selected less strongly against open areas and crops, while selecting stronger for forests. Beavers tend to increase foraging and time spent on land during senescence (Lodberg-Holm et al. 2021; Graf, Mayer, et al. 2016), and these patterns may reflect older beavers foraging more in these habitat types. Habitat selection and foraging often differs among age groups such as subadult male deer foraging less while being more vigilant than adults (Pecorella et al. 2018) and young bearded seals (*Erignathus barbatus*) staying closer to the sea ice edge than adults (Cameron et al. 2018). Such differences are often driven by avoidance of conspecifics and competitive exclusion from dominant males. However, a trait of monogamous mammals such as beavers, is that juveniles are retained within the family group for longer and the subject of higher parental investment (Kleiman 1977; Mayer, Zedrosser, and Rosell 2017c). Non-reproductive beavers also help out raising their siblings and gain more experience and improved body condition prior to dispersal (McTaggart and Nelson 2003; Mayer, Zedrosser, and Rosell 2017a). Social exclusion of younger beavers from certain habitats seems unlikely due to low levels of aggression observed between family members (Mott, Bloomquist, and Nielsen 2011). Younger beavers selected less strongly against elevation, which could reflect increased exploratory movements in younger individuals searching for their own territory (Mayer, Zedrosser, and Rosell 2017b) or the need to gain more weight prior to dispersal (Mayer, Zedrosser, and Rosell 2017a), causing them to seek out higher quality food resources at higher elevations. Young cave salamanders also increased risks by staying closer to the cave entrance than adults to obtain better foraging opportunities and weight gain (Ficetola, Pennati, and Manenti 2013). Within beaver territories, high-quality food and preferred tree species are often depleted closer to water where beavers forage more intensely (Fryxell 1992; Nolet, Hoekstra, and Ottenheim 1994), which may motivate young beavers to climb higher to obtain high-quality forage.

Exploring individual habitat selection also enabled us to investigate trends in relation to reproductive effort, body condition and density. Average reproduction did not explain much variability in most habitat variables. However, we found that beavers with higher average reproduction selected less strongly against increasing elevation, while individuals in good body condition and from larger families weakened their selection against increasing distance from water. Beavers with a better body condition, however, selected stronger against crops, while at high densities, beavers displayed no clear selection for or against crops. Studies of other crop depredating species such as American black bears (*U. americanus*) (Ditmer et al. 2015), sika deer (*C. nippon*) (Hata et al. 2021) and African elephants (*Loxodonta africana*) (Chiyo et al. 2011) have indicated that crop foraging increased body size. As we only studied selection and not crop use, it is difficult to connect body condition with the extent of foraging. Crops are also available during a very short period in our study area, and effects on body condition should probably be investigated specifically during that time.

Temporally variable food sources

While beavers selected against crops, developed- and open areas, there were temporal differences indicating seasonal shifts. Reproductively active males and non-reproductive beavers selected for wetlands and open areas during spring, while all beavers selected for crops from July until late fall. Seasonal shifts in habitat selection often reflect changes in food availability such as male roe deer selecting for higher vegetation biomass during summer (Dupke et al. 2017). Open areas, such as pastures may provide highly digestible and nutritious fodder for herbivores such as red deer and moose (Godvik et al. 2009; Lande et al. 2014; Ofstad et al. 2020). Beavers are a typical generalist relying on a wide range of vegetation types and their diet usually differs considerably across seasons as beavers shift foraging towards herbs, grasses, and aquatic vegetation to obtain a variety of nutrients (Svendsen 1980; Nolet et al. 1995; Milligan and Humphries 2010). Especially aquatic vegetation contains high sodium content as well as other nutrients that attracts both beavers and species such as moose during spring and early summer (Fraser, Chavez, and Palohelmo 1984; Fraser, Thompson, and Arthur 1982; Law, Bunnefeld, and Willby 2014). Increased selection for open areas and wetlands may reflect a general dietary change towards non-woody foraging items as these appear in spring (Svendsen 1980; Roberts and Arner 1984), but still at low availabilities that encourage selection (Godvik et al. 2009). These seasonal switches to obtain nutritious foods are common in many species such as red deer migrating to gain access to early plant phenological stages (Bischof et al. 2012) and brown bears foraging on highly digestible berries with high sugar content during hyperphagia (Welch et al. 1997; Hertel et al. 2016). Another highly temporal food source that beavers have access to are crops, in which beavers displayed the strongest seasonal switch.

Beaver foraging on crops has received limited research attention but been mentioned in a few publications (Campbell et al. 2012; Bełżecki et al. 2018; Krojerová-Prokešová et al.

2010; Ulicsni et al. 2020) and most often observed close to water and the beaver lodge (Mikulka et al. 2020). Cereals are the dominant crop type in our study area and may provide wildlife with high nutrient content (Heroldová et al. 2008) and cause a wide range of species to shift habitat selection away from natural habitats and food sources (Fox et al. 2005; Roper et al. 1995). Crop-depredation often occurs during certain phenologically attractive stages (Putman 1986; Roper et al. 1995; Chiyo et al. 2005), and beavers also switch to selection for crops in late summer when cereals matured in our study area (Lodberg-Holm et al., unpublished).

Forests represent more natural foraging areas for beavers (Barela et al. 2020; John and Kostkan 2009; Pinto, Santos, and Rosell 2009), but we found no clear population-level nor temporal selection for forests. Forests were the most common habitat type within the study area, and contained the majority of GPS-fixes, indicating frequent use. Resource selection functions do not, however, measure quantity use, but the probability that when a habitat type or resource is encountered, it will be selected by the animal (Lele et al. 2013). Selection is estimated from the ratio of available and used locations in each habitat type (Fieberg et al. 2021), which means that beavers may display a functional response by not selecting strongly for forests due to the high availability (Newediuk, Prokopenko, and Vander Wal 2022; Godvik et al. 2009). Beavers also prefer certain forest characteristics such as intermediate densities of trees and shrubs (Curtis and Jensen 2004; Gerwing, Johnson, and Alström-Rapaport 2013; Francis et al. 2017), avoiding coniferous and mixed forests (Wang, McClintic, and Taylor 2019), and strong selection for willows (*Salix* spp.) (Fustec et al. 2001; John, Baker, and Kostkan 2010). Roe deer and moose also displayed preferences for forest characteristics such as high availability of herbs and forests of high productivity that may provide them with nutritious fodder (Bjørneraas et al. 2012; Mysterud et al. 1999). More detailed vegetation mapping may have revealed clearer selection patterns of beavers. The spatial random fields from the INLA-SPDE models also indicated clusters of beaver use unexplained by the model, which could be specific vegetation patches or lodge and burrow locations. In addition to seasonal trends driven by food availability, other temporal trends may relate more to potential risks perceived by beavers.

Human disturbances and perceived predation risk

Beavers selected against increasing distance to water and elevational gain. This is unsurprising and reflect typical behavior of a central place forager (Steyaert, Zedrosser, and Rosell 2015; Haarberg and Rosell 2006). Beavers risk being predated (Gable et al. 2016) or shot by human hunters when on land (Parker et al. 2001), and water therefore represents safety. Despite most large carnivores that predate beavers not being present within the study area, beavers still responded to the smell of predators (Rosell and Czech 2000; Rosell and Sanda 2006), suggesting that anti-predator instincts are intact. Staying close to water when moving on land is also common in other semi-aquatic species such as wood turtles (*Clemmys insculpta*) (Compton, Rhymer, and McCollough 2002), and southern water voles (*Arvicola sapidus*) that find refuge from predators, food sources and a medium for movement in open water (Mate et al. 2013). Avoidance of open- and developed areas may represent avoidance of humans and less food availability in most seasons. For both ungulates and brown bears, grazing in open areas entails a high risk of being killed by human hunters (Godvik et al. 2009; Ofstad et al. 2020; Steyaert et al. 2016). Beavers might perceive similar risks despite being hunted mostly in spring (Parker and Rosell 2012). Several studies have shown that wildlife avoids developed and other human-manipulated areas such as elk avoiding roads (Prokopenko, Boyce, and Avgar 2017), wolves avoiding human developed areas (O'Neil, Beyer, and Bump 2019), and crested porcupines avoiding agriculture year around (Mori et al. 2014). While beavers avoided direct overlap with developed areas, they did not respond to distance to developed areas. A study from North America similarly found that beaver presence in ponds was not impacted by distance to roads (Hood 2020). Compared to species such as woodland caribou (*Rangifer tarandus caribou*) and semi-domesticated reindeer (*R. t. tarandus*), that avoids these areas at distances up to several kilometers (DeCesare et al. 2012; Pape and Löffler 2015), beavers did not react as strongly to developed areas on the population-level. Beavers have in fact been found to select for roads in previous studies, especially if they find attractive roadside vegetation (Curtis and Jensen 2004; Steyaert, Zedrosser, and Rosell 2015).

Temporal trends in habitat selection may reveal differences among socio-reproductive groups even for monogamous and monomorphic species such as beavers. Reproductively active males and non-reproductive beavers avoided developed areas during summer, but reproductively active females displayed no such patterns. The study area has an influx of summer tourists (Flemsæter, Stokowski, and Frisvoll 2020), and we expected an increased avoidance of human-dominated areas during this time. Deer and roe deer in Germany acted similarly by shifting seasonal habitat selection towards more vegetation cover in response to increased human activity during summer (Richter et al. 2020; Dupke et al. 2017). Female mammals are often more risk aversive than males (Vogel et al. 2020; de la Torre et al. 2021; Joly et al. 2017), especially those accompanied by dependent young (Bjørneraas et al. 2011; Ditmer et al. 2015). Beavers, however, usually move around their territory solitarily (McClanahan, Rosell, and Mayer 2020) and are rarely accompanied by kits (Lodberg-Holm et al. 2021), implying that female beavers may not be as risk aversive as females belonging to other species. This may reflect a characteristic of monogamous animals where females share the responsibility of offspring with males (Kleiman 1977; Sun 2003). In monomorphic sea birds, females accepted more risk to obtain better quality food when the male cared for the offspring (Elliott, Gaston, and Crump 2010; Lewis et al. 2002). A similar pattern was found in monogamous racoon dogs where males remained by the den taking care of pups, while the female selected for habitats and foraged further away (Drygala et al. 2008; Zoller and Drygala 2013). We found that females selected stronger for crops during fall, which could be a compensation for increased energy use during reproduction, but they did not select stronger for any other seasonally available habitat types. Their avoidance of wetlands in June may simply be a results of more time spent in the lodge lactating during that time (Mayer et al. 2017).

We also found differences in circadian habitat selection specific to socio-reproductive groups. Surprisingly, we found no circadian trends in relation to developed areas for the reproductively active pair, but clearer patterns in selection for wetlands and open areas. The reproductively active pair selected stronger for wetlands during morning and evening, while selecting for open areas during the middle of the night. Wetlands could act as refuges from humans by being less accessible, while also being important habitats for beavers (Francis et al. 2017; Wang, McClintic, and Taylor 2019). Open areas on the other hand are more exposed, and are often avoided by wildlife during daytime (Godvik et al. 2009; Dupke et al. 2017). However, non-reproductive beavers displayed opposite patterns by selecting for both developed- and open areas during morning, while selecting for wetlands during hours of darkness. The reproductively active pair differed in circadian selection for crops with males selecting for them in the evening and females during morning. Individuals with overlapping home ranges may display niche specialization and focus on different food sources to reduce competition (Robertson et al. 2014; Sheppard et al. 2018; O'Brien et al. 2020). However, animals may also reduce competition by adjusting circadian foraging patterns such as platypuses (*Ornithorhynchus anatinus*) foraging at different times of the day to avoid conspecifics, but still share their burrows (Bethge et al. 2009). Differing circadian trends in beavers may represent a similar strategy to reduce competition, reflect more accumulated experience by the reproductive pair, or simply to increase the efficiency of territorial defense (McClanahan, Rosell, and Mayer 2020).

Conclusions

Habitat selection is complex and tend to vary among individuals and across time and space, calling for investigations of the interplay between these dimensions rather than simplifying them in search of “one model fits all” (Pape and Löffler 2015). We found extensive individual differences in habitat selection of Eurasian beavers, some of which were affected by demographic and physiological variables. Differences may relate to personality traits in wildlife (Hertel et al. 2019; Aliperti et al. 2021), individual niche specializations (Bolnick et al. 2003; Dall et al. 2012) or strategies to reduce competition within social groups (O'Brien et al. 2020; Robertson et al. 2014). When individual variation outweighs population-level trends, it also implies different impacts of environmental change and management actions, which calls for increased research attention (Milligan, Berkeley, and McNew 2020; O'Brien et al. 2020). Despite beavers being monogamous and assumed to display low levels of behavioral sexual dimorphism, socio-reproductive groups differed in seasonal and circadian trends, which might easily be overlooked without considering temporal trends. Much of the individual differences remains unexplained and new research questions emerge. As an ecosystem engineer, beavers contribute to shape landscapes, and their habitat selection patterns are therefore not only important to understand the ecology of the species but may have wider landscape-scale implications.

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Literature cited

Aliperti, J.R., B.E. Davis, N.A. Fangue, A.E. Todgham, and D.H. Van Vuren. 2021. "Bridging animal personality with space use and resource use in a free-ranging population of an asocial ground squirrel." *Animal Behaviour* 180:291-306.

Barela, I., L.M. Burger, J. Taylor, K.O. Evans, R. Ogawa, L. McClintic, and G. Wang. 2020. "Relationships between survival and habitat suitability of semi-aquatic mammals." *Ecology and Evolution* 10 (11):4867– 4875.

Beguin, J., S. Martino, H. Rue, and S.G. Cumming. 2012. "Hierarchical analysis of spatially autocorrelated ecological data using integrated nested Laplace approximation." *Methods in Ecology and Evolution* 3 (5):921-929.

Bełżecki, G., R. Miltko, B. Kowalik, A.W. Demiaszkiewicz, J. Lachowicz, Z. Giżejewski, A. Obidziński, and N.R. McEwan. 2018. "Seasonal variations of the digestive tract of the Eurasian beaver Castor fiber." *Mammal Research* 63 (1):21-31.

Bergman, B.G., J.K. Bump, and M.C. Romanski. 2018. "Revisiting the role of aquatic plants in beaver habitat selection." *The American Midland Naturalist* 179 (2):222-246.

Bethge, P., S. Munks, H. Otley, and S. Nicol. 2009. "Activity patterns and sharing of time and space of platypuses, Ornithorhynchus anatinus, in a subalpine Tasmanian lake." *Journal of Mammalogy* 90 (6):1350-1356.

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 (4):407-424.

Bjørneraas, K., I. Herfindal, E.J. Solberg, B.-E. Sæther, B. van Moorter, and C.M. Rolandsen. 2012. "Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore." *Oecologia* 168 (1):231-243.

Bjørneraas, K., E.J. Solberg, I. Herfindal, B.V. Moorter, C.M. Rolandsen, J.-P. Tremblay, C. Skarpe, B.-E. Sæther, R. Eriksen, and R. Astrup. 2011. "Moose Alces alces habitat use at multiple temporal scales in a human-altered landscape." *Wildlife Biology* 17 (1):44-54.

Bolnick, Daniel I., R. Svanbäck, James A. Fordyce, Louie H. Yang, Jeremy M. Davis, C.D. Hulsey, and Matthew L. Forister. 2003. "The ecology of individuals: incidence and implications of individual specialization." *The American Naturalist* 161 (1):1-28.

Briggs, A.J.A., C.A. Robstad, and F. Rosell. 2021. "Using radio-frequency identification technology to monitor Eurasian beavers." *Wildlife Society Bulletin* 45 (1):154-161.

Cabré, L.B., M. Mayer, S. Steyaert, and F. Rosell. 2020. "Beaver (Castor fiber) activity and spatial movement in response to light and weather conditions." *Mammalian Biology* 100:261–271.

Cameron, M.F., K.J. Frost, J.M. Ver Hoef, G.A. Breed, A.V. Whiting, J. Goodwin, and P.L. Boveng. 2018. "Habitat selection and seasonal movements of young bearded seals (Erignathus barbatus) in the Bering Sea." *PLoS ONE* 13 (2):e0192743.

Campbell, R.D., A. Harrington, A. Ross, and L. Harrington. 2012. Distribution, population assessment and activities of beavers in Tayside. Scottish Natural Heritage Commissioned Report No. 540.

Campbell, R.D., C. Newman, D.W. Macdonald, and F. Rosell. 2013. "Proximate weather patterns and spring green-up phenology effect Eurasian beaver (Castor fiber) body mass and reproductive success: the implications of climate change and topography." *Global Change Biology* 19 (4):1311-1324.

Campbell, R.D., F. Rosell, B.A. Nolet, and V.A.A. Dijkstra. 2005. "Territory and group sizes in Eurasian beavers (Castor fiber): echoes of settlement and reproduction?" *Behavioral Ecology and Sociobiology* 58 (6):597-607.

Chiyo, P.I., E.P. Cochrane, L. Naughton, and G.I. Basuta. 2005. "Temporal patterns of crop raiding by elephants: a response to changes in forage quality or crop availability?" *African Journal of Ecology* 43 (1):48-55.

Chiyo, P.I., P.C. Lee, C.J. Moss, E.A. Archie, J.A. Hollister-Smith, and S.C. Alberts. 2011. "No risk, no gain: effects of crop raiding and genetic diversity on body size in male elephants." *Behavioral Ecology* 22 (3):552-558.

Christiansen, F., N. Esteban, J.A. Mortimer, A.M. Dujon, and G.C. Hays. 2017. "Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking." *Marine biology* 164 (1):10.

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 (10):562-573.

Clutton-Brock, T.H., G.R. Iason, S.D. Albon, and F.E. Guinness. 1982. "Effects of lactation on feeding behaviour and habitat use in wild Red deer hinds." *Journal of Zoology* 198 (2):227-236.

Compton, B.W., J.M. Rhymer, and M. McCollough. 2002. "Habitat selection by wood turtles (Clemmys insculpta): an application of paired logistic regression." *Ecology* 83 (3):833-843.

Creel, S., J. Winnie Jr, B. Maxwell, K. Hamlin, and M. Creel. 2005. "Elk alter habitat selection as an antipredator response to wolves." *Ecology* 86 (12):3387-3397.

Curtis, P.D., and P.G. Jensen. 2004. "Habitat features affecting beaver occupancy along roadsides in New York state." *Journal of Wildlife Management* 68 (2):278-287.

Dall, S.R., A.M. Bell, D.I. Bolnick, and F.L. Ratnieks. 2012. "An evolutionary ecology of individual differences." *Ecology letters* 15 (10):1189-1198.

de la Torre, J.A., E.P. Wong, A.M. Lechner, N. Zulaikha, A. Zawawi, P. Abdul-Patah, S. Saaban, B. Goossens, and A. Campos-Arceiz. 2021. "There will be conflict – agricultural landscapes are prime, rather than marginal, habitats for Asian elephants." *Animal Conservation* 24 (5):720-732.

DeCesare, N.J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G.J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K.G. Smith, L.E. Morgantini, M. Wheatley, and M. Musiani. 2012. "Transcending scale dependence in identifying habitat with resource selection functions." *Ecological Applications* 22 (4):1068-1083.

Ditmer, M.A., D.L. Garshelis, K.V. Noyce, A.W. Haveles, and J.R. Fieberg. 2015. "Are American black bears in an agricultural landscape being sustained by crops?" *Journal of Mammalogy* 97 (1):54-67.

Donkor, N.T., and J.M. Fryxell. 1999. "Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario." *Forest Ecology and Management* 118 (1-3):83-92.

Drygala, F., H. Zoller, N. Stier, H. Mix, and M. Roth. 2008. "Ranging and parental care of the raccoon dog Nyctereutes procyonoides during pup rearing." *Acta Theriologica* 53 (2):111-119.

Dupke, C., C. Bonenfant, B. Reineking, R. Hable, T. Zeppenfeld, M. Ewald, and M. Heurich. 2017. "Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources." *Ecography* 40 (8):1014-1027.

eKlima. 2020. "Gridded values for counties, with trend." Norwegian Meteorological Institute, accessed 2 March 2020.

Elliott, K.H., A.J. Gaston, and D. Crump. 2010. "Sex-specific behavior by a monomorphic seabird represents risk partitioning." *Behavioral Ecology* 21 (5):1024-1032.

Ficetola, G.F., R. Pennati, and R. Manenti. 2013. "Spatial segregation among age classes in cave salamanders: habitat selection or social interactions?" *Population Ecology* 55 (1):217-226.

Fieberg, J., J. Signer, B. Smith, and T. Avgar. 2021. "A 'How to' guide for interpreting parameters in habitat-selection analyses." *Journal of Animal Ecology* 90 (5):1027-1043.

Flemsæter, F., P. Stokowski, and S. Frisvoll. 2020. "The rhythms of canal tourism: Synchronizing the host-visitor interface." *Journal of Rural Studies* 78:199-210.

Forstmeier, W., and H. Schielzeth. 2011. "Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse." *Behavioral Ecology and Sociobiology* 65 (1):47-55.

Fox, A.D., J. Madsen, H. Boyd, E. Kuijken, D.W. Norriss, I.M. Tombre, and D.A. Stroud. 2005. "Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations." *Global Change Biology* 11 (6):881-893.

Francis, R.A., J.D. Taylor, E. Dibble, B. Strickland, V.M. Petro, C. Easterwood, and G. Wang. 2017. "Restricted cross-scale habitat selection by American beavers." *Current Zoology* 63 (6):703-710.

Fraser, D., E.R. Chavez, and J.E. Palohelmo. 1984. "Aquatic feeding by moose: selection of plant species and feeding areas in relation to plant chemical composition and characteristics of lakes." *Canadian Journal of Zoology* 62 (1):80-87.

Fraser, D., B.K. Thompson, and D. Arthur. 1982. "Aquatic feeding by moose: seasonal variation in relation to plant chemical composition and use of mineral licks." *Canadian Journal of Zoology* 60 (12):3121-3126.

Fryxell, J.M. 1992. "Space use by beavers in relation to resource abundance." *Oikos* 64:474-478.

Fustec, J., T. Lode, D. Le Jacques, and J.P. Cormier. 2001. "Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire." *Freshwater Biology* 46 (10):1361-1371.

Gable, T.D., S.K. Windels, J.G. Bruggink, and A.T. Homkes. 2016. "Where and how wolves (*Canis lupus*) kill beavers (*Castor canadensis*)." *PloS One* 11 (12):e0165537.

Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. "Habitat–performance relationships: finding the right metric at a given spatial scale." *Philosophical Transactions of the Royal Society B: Biological Sciences* 365 (1550):2255-2265.

Gallant, D., C.H. Bérubé, E. Tremblay, and L. Vasseur. 2004. "An extensive study of the foraging ecology of beavers (Castor canadensis) in relation to habitat quality." *Canadian Journal of Zoology* 82 (6):922-933.

Gelman, A., J. Hwang, and A. Vehtari. 2014. "Understanding predictive information criteria for Bayesian models." *Statistics and Computing* 24 (6):997-1016.

Gerwing, T.G., C.J. Johnson, and C. Alström-Rapaport. 2013. "Factors influencing forage selection by the North American beaver (Castor canadensis)." *Mammalian Biology* 78 (2):79-86.

Gillies, C.S., M. Hebblewhite, S.E. Nielsen, M.A. Krawchuk, C.L. Aldridge, J.L. Frair, D.J. Saher, C.E. Stevens, and C.L. Jerde. 2006. "Application of random effects to the study of resource selection by animals." *Journal of Animal Ecology* 75 (4):887-898.

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 (3):699-710.

Graf, P.M., J. Hochreiter, K. Hackländer, R.P. Wilson, and F. Rosell. 2016. "Short-term effects of tagging on activity and movement patterns of Eurasian beavers (Castor fiber)." *European Journal of Wildlife Research* 62 (6):725-736.

Graf, P.M., M. Mayer, A. Zedrosser, K. Hackländer, and F. Rosell. 2016. "Territory size and age explain movement patterns in the Eurasian beaver." *Mammalian Biology* 81 (6):587-594.

Halley, D.J., A.P. Saveljev, and F. Rosell. 2021. "Population and distribution of beavers Castor fiber and Castor canadensis in Eurasia." *Mammal Review* 51 (1):1-24.

Harrison, X.A., L. Donaldson, M.E. Correa-Cano, J. Evans, D.N. Fisher, C.E.D. Goodwin, B.S. Robinson, D.J. Hodgson, and R. Inger. 2018. "A brief introduction to mixed effects modelling and multi-model inference in ecology." *PeerJ* 6:e4794.

Hata, A., R. Nakashita, T. Anezaki, M. Minami, Y. Fukue, N. Higuchi, H. Uno, Y. Nakajima, M. Saeki, and C. Kozakai. 2021. "Agricultural crop consumption induces precocious maturity in deer by improving physical and reproductive performance." *Ecosphere* 12 (4):e03464.

Hedd, A., W.A. Montevecchi, R.A. Phillips, and D.A. Fifield. 2014. "Seasonal sexual segregation by monomorphic sooty shearwaters Puffinus griseus reflects different reproductive roles during the pre-laying period." *PLoS One* 9 (1):e85572.

Heroldová, M., E. Tkadlec, J. Bryja, and J. Zejda. 2008. "Wheat or barley?: Feeding preferences affect distribution of three rodent species in agricultural landscape." *Applied Animal Behaviour Science* 110 (3):354-362.

Herr, J., and F. Rosell. 2004. "Use of space and movement patterns in monogamous adult Eurasian beavers (Castor fiber)." *Journal of Zoology* 262 (3):257-264.

Hertel, A.G., M. Leclerc, D. Warren, F. Pelletier, A. Zedrosser, and T. Mueller. 2019. "Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife." *Animal Behaviour* 147:91-104.

Hertel, A.G., S.M.J.G. Steyaert, A. Zedrosser, A. Mysterud, H.K. Lodberg-Holm, H.W. Gelink, J. Kindberg, and J.E. Swenson. 2016. "Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape." *Behavioral Ecology and Sociobiology* 70 (6):831-842.

raster: geographic data analysis and modeling. R package version 3.3-7.

Hood, G.A. 2020. "Not all ponds are created equal: long-term beaver (Castor canadensis) lodge occupancy in a heterogeneous landscape." *Canadian Journal of Zoology* 98 (3):210-218.

Hood, G.A., and D.G. Larson. 2015. "Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands." *Freshwater Biology* 60 (1):198-208.

Haarberg, O., and F. Rosell. 2006. "Selective foraging on woody plant species by the Eurasian beaver (Castor fiber) in Telemark, Norway." *Journal of Zoology* 270 (2):201-208.

Illian, J.B., S.H. Sørbye, and H. Rue. 2012. "A toolbox for fitting complex spatial point process models using integrated nested laplace approximation (INLA) " *The Annals of Applied Statistics* 6 (4):1499-1530.

John, F., S. Baker, and V. Kostkan. 2010. "Habitat selection of an expanding beaver (Castor fiber) population in central and upper Morava River basin." *European Journal of Wildlife Research* 56 (4):663-671.

John, F., and V. Kostkan. 2009. "Compositional analysis and GPS/GIS for study of habitat selection by the European beaver, *Castor fiber* in the middle reaches of the Morava River." *Folia Zoologica* 58 (1):76-86.

Johnson, D.H. 1980. "The comparison of usage and availability measurements for evaluating resource preference." *Ecology* 61 (1):65-71.

Joly, K., M.S. Sorum, T. Craig, and E.L. Julianus. 2017. "The effects of sex, terrain, wildfire, winter severity, and maternal status on habitat selection by moose in north-central Alaska." *Alces: A Journal Devoted to the Biology and Management of Moose* 52:101-115.

Justicia, L.S., F. Rosell, and M. Mayer. 2018. "Performance of GPS units for deployment on semiaquatic animals." *PLoS ONE* 13 (12):e0207938.

Kartverket. 2016. FKB-AR5.

Kartverket. 2019. DTM 10.

Kleiman, D.G. 1977. "Monogamy in mammals." *The Quarterly Review of Biology* 52 (1):39-69.

Krojerová-Prokešová, J., M. Barančeková, L. Hamšíková, and A. Vorel. 2010. "Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources." *Journal of Zoology* 281 (3):183-193.

Lande, U.S., L.E. Loe, O.J. Skjærli, E.L. Meisingset, and A. Mysterud. 2014. "The effect of agricultural land use practice on habitat selection of red deer." *European Journal of Wildlife Research* 60 (1):69-76.

Law, A., N. Bunnefeld, and N.J. Willby. 2014. "Beavers and lilies: selective herbivory and adaptive foraging behaviour." *Freshwater Biology* 59 (2):224-232.

Lele, S.R., E.H. Merrill, J. Keim, and M.S. Boyce. 2013. "Selection, use, choice and occupancy: clarifying concepts in resource selection studies." *Journal of Animal Ecology* 82 (6):1183-1191.

Lewis, S., S. Benvenuti, L. Dall–Antonia, R. Griffiths, L. Money, T.N. Sherratt, S. Wanless, and K.C. Hamer. 2002. "Sex-specific foraging behaviour in a monomorphic seabird." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269 (1501):1687-1693.

Lezama-Ochoa, N., M.G. Pennino, M.A. Hall, J. Lopez, and H. Murua. 2020. "Using a Bayesian modelling approach (INLA-SPDE) to predict the occurrence of the spinetail devil ray (Mobular mobular)." *Scientific Reports* 10 (1):18822.

Lindgren, F., H. Rue, and J. Lindström. 2011. "An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach." *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73 (4):423-498.

Lodberg-Holm, H.K., H.W. Gelink, A.G. Hertel, J.E. Swenson, M. Domevscik, and S.M.J.G. Steyaert. 2019. "A human-induced landscape of fear influences foraging behavior of brown bears." *Basic and Applied Ecology* 35:18-27.

Lodberg-Holm, H.K., S.M.J.G. Steyaert, S. Reinhardt, and F. Rosell. 2021. "Size is not everything: differing activity and foraging patterns between the sexes in a monomorphic mammal." *Behavioral Ecology and Sociobiology* 75 (4):76.

Lovari, S., A. Sforzi, and E. Mori. 2013. "Habitat richness affects home range size in a monogamous large rodent." *Behavioural Processes* 99:42-46.

Lukas, D., and T.H. Clutton-Brock. 2013. "The Evolution of Social Monogamy in Mammals." *Science* 341 (6145):526-530.

Madden, J.R., and M.A. Whiteside. 2014. "Selection on behavioural traits during 'unselective' harvesting means that shy pheasants better survive a hunting season." *Animal Behaviour* 87:129-135.

Mate, I., J. Barrull, M. Salicrú, J. Ruiz-Olmo, and J. Gosàlbez. 2013. "Habitat selection by Southern water vole (Arvicola sapidus) in riparian environments of Mediterranean mountain areas: a conservation tool for the species." *Acta Theriologica* 58 (1):25-37.

Mayer, M., S.C. Frank, A. Zedrosser, and F. Rosell. 2020. "Causes and consequences of inverse density-dependent territorial behaviour and aggression in a monogamous mammal." *Journal of Animal Ecology* 89 (2):577-588.

Mayer, M., C. Robstad, E.P. Serra, K. Hohwieler, B. Fuchs, A.L. Evans, J.M. Arnemo, A. Zedrosser, and F. Rosell. 2017. Exposure of the Eurasian beaver (*Castor fiber*) towards hunters during the spring hunt. Department of Natural Sciences and Environmental Health, University College of Southeast Norway. Bø i Telemark, Norway

Mayer, M., W. Ullmann, R. Heinrich, C. Fischer, N. Blaum, and P. Sunde. 2019. "Seasonal effects of habitat structure and weather on the habitat selection and home range size of a mammal in agricultural landscapes." *Landscape Ecology* 34 (10):2279-2294.

Mayer, M., A. Zedrosser, and F. Rosell. 2017a. "Couch potatoes do better: Delayed dispersal and territory size affect the duration of territory occupancy in a monogamous mammal." *Ecology and Evolution* 7 (12):4347-4356.

Mayer, M., A. Zedrosser, and F. Rosell. 2017b. "Extra-territorial movements differ between territory holders and subordinates in a large, monogamous rodent." *Scientific Reports* 7 (1):15261.

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

Mayor, S.J., D.C. Schneider, J.A. Schaefer, and S.P. Mahoney. 2009. "Habitat selection at multiple scales." *Écoscience* 16 (2):238-247.

McClanahan, K., F. Rosell, and M. Mayer. 2020. "Minding your own business: low pair cohesion in a territorial, monogamous mammal." *Animal Behaviour* 166:119-128.

McGarigal, K., H.Y. Wan, K.A. Zeller, B.C. Timm, and S.A. Cushman. 2016. "Multi-scale habitat selection modeling: a review and outlook." *Landscape Ecology* 31 (6):1161-1175.

McLoughlin, P.D., R.L. Case, R.J. Gau, D.H. Cluff, R. Mulders, and F. Messier. 2002. "Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic." *Oecologia* 132 (1):102-108.

McLoughlin, P.D., J.-M. Gaillard, M.S. Boyce, C. Bonenfant, F. Messier, P. Duncan, D. Delorme, B.V. Moorter, S. Saïd, and F. Klein. 2007. "Lifetime reproductive success and composition of the home range in a large herbivore." *Ecology* 88 (12):3192-3201.

McTaggart, S.T., and T.A. Nelson. 2003. "Composition and demographics of beaver (Castor canadensis) colonies in central Illinois." *The American Midland Naturalist* 150 (1):139-150, 12.

Meisingset, E.L., L.E. Loe, Ø. Brekkum, B. Van Moorter, and A. Mysterud. 2013. "Red deer habitat selection and movements in relation to roads." *The Journal of Wildlife Management* 77 (1):181-191.

Merkle, J.A., H.S. Robinson, P.R. Krausman, and P. Alaback. 2013. "Food availability and foraging near human developments by black bears." *Journal of Mammalogy* 94 (2):378-385.

Mikulka, O., M. Homolka, J. Drimaj, and J. Kamler. 2020. "European beaver (Castor fiber) in open agricultural landscapes: crop grazing and the potential for economic damage." *European Journal of Wildlife Research* 66 (6):101.

Milligan, H.E., and M.M. Humphries. 2010. "The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic-terrestrial ecosystem linkages in a subarctic environment." *Oikos* 119 (12):1877-1886.

Milligan, M.C., L.I. Berkeley, and L.B. McNew. 2020. "Habitat selection of female sharp-tailed grouse in grasslands managed for livestock production." *PLoS ONE* 15 (6):e0233756.

Mori, E., S. Lovari, A. Sforzi, G. Romeo, C. Pisani, A. Massolo, and L. Fattorini. 2014. "Patterns of spatial overlap in a monogamous large rodent, the crested porcupine." *Behavioural Processes* 107:112-118.

Mortensen, R.M., S. Reinhardt, M.E. Hjønnevåg, R.P. Wilson, and F. Rosell. 2021. "Aquatic habitat use in a semi-aquatic mammal: the Eurasian beaver." *Animal Biotelemetry* 9 (1):35.

Mott, C.L., C.K. Bloomquist, and C.K. Nielsen. 2011. "Seasonal, diel, and ontogenetic patterns of within-den behavior in beavers (Castor canadensis)." *Mammalian Biology* 76 (4):436-444.

Muff, S., J. Signer, and J. Fieberg. 2020. "Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation." *Journal of Animal Ecology* 89 (1):80-92.

Mysterud, A., P.K. Larsen, R.A. Ims, and E. Østbye. 1999. "Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability?" *Canadian Journal of Zoology* 77 (5):776-783.

Newediuk, L., C.M. Prokopenko, and E. Vander Wal. 2022. "Individual differences in habitat selection mediate landscape level predictions of a functional response." *Oecologia* 198 (1):99-110.

Nimje, P.S., M. Mayer, A. Zedrosser, M. Sæbø, and F. Rosell. 2021. "Territory acquisition and mate choice in a monogamous mammal, the Eurasian beaver." *Animal Behaviour* 178:165-173.

Nolet, B.A., A. Hoekstra, and M.M. Ottenheim. 1994. "Selective foraging on woody species by the beaver Castor fiber, and its impact on a riparian willow forest." *Biological Conservation* 70 (2):117-128.

Nolet, B.A., and F. Rosell. 1994. "Territoriality and time budgets in beavers during sequential settlement." *Canadian Journal of Zoology* 72 (7):1227-1237.

Nolet, B.A., P.J. Van Der Veer, E.G.J. Evers, and M.M. Ottenheim. 1995. "A linear programming model of diet choice of free-living beavers." *Netherlands Journal of Zoology* 45 (3):315-337.

Northcott, T.H. 1971. "Feeding Habits of Beaver in Newfoundland." *Oikos* 22 (3):407-410.

Northrup, J.M., E. Vander Wal, M. Bonar, J. Fieberg, M.P. Laforge, M. Leclerc, C.M. Prokopenko, and B.D. Gerber. 2021. "Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution." *Ecological Applications* 32 (1):e02470.

O'Brien, O., S.J. Allen, M. Krützen, and R.C. Connor. 2020. "Alliance-specific habitat selection by male Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia." *Animal Behaviour* 164:39-49.

O'Neil, S.T., D.E. Beyer, and J.K. Bump. 2019. "Territorial landscapes: incorporating density-dependence into wolf habitat selection studies." *Royal Society Open Science* 6 (11):190282.

Ofstad, E.G., S.S. Markussen, B.-E. Sæther, E.J. Solberg, M. Heim, H. Haanes, K.H. Røed, and I. Herfindal. 2020. "Opposing fitness consequences of habitat use in a harvested moose population." *Journal of Animal Ecology* 89 (7):1701-1710.

Oliveira, T., F. Urra, J.M. López-Martín, E. Ballesteros-Duperón, J.M. Barea-Azcón, M. Moléon, J.M. Gil-Sánchez, P.C. Alves, F. Díaz-Ruíz, P. Ferreras, and P. Monterroso. 2018. "Females know better: Sex-biased habitat selection by the European wildcat." *Ecology and Evolution* 8 (18):9464-9477.

Pape, R., and J. Löffler. 2015. "Ecological dynamics in habitat selection of reindeer: an interplay of spatial scale, time, and individual animal's choice." *Polar Biology* 38 (11):1891-1903.

Parker, H., and F. Rosell. 2012. Beaver management in Norway-A review of recent literature and current problems. Norway: Telemark University College.

Parker, H., F. Rosell, T. Hermansen, G. Sørløkk, and M. Stærk. 2002. "Sex and age composition of spring-hunted Eurasian beaver in Norway." *The Journal of Wildlife Management* 66 (4):1164-1170.

Parker, H., F. Rosell, T.A. Hermansen, G. Sørløkk, and M. Stærk. 2001. "Can beaver *Castor fiber* be selectively harvested by sex and age during spring hunting?" The European Beaver in a new millennium. Proceedings of 2nd European Beaver Symposium, 27-30 Sept. 2000, Bialowieza, Poland.

Parker, H., A. Zedrosser, and F. Rosell. 2017. "Age-specific reproduction in relation to body size and condition in female Eurasian beavers." *Journal of Zoology* 302 (4):236-243.

Pecorella, I., N. Fattorini, E. Macchi, and F. Ferretti. 2018. "Sex/age differences in foraging, vigilance and alertness in a social herbivore." *acta ethologica* 22:1-8.

Pinto, B., M.J. Santos, and F. Rosell. 2009. "Habitat selection of the Eurasian beaver (Castor fiber) near its carrying capacity: an example from Norway." *Canadian Journal of Zoology* 87 (4):317-325.

Prokopenko, C.M., M.S. Boyce, and T. Avgar. 2017. "Characterizing wildlife behavioural responses to roads using integrated step selection analysis." *Journal of Applied Ecology* 54 (2):470-479.

Putman, R.J. 1986. "Foraging by roe deer in agricultural areas and impact on arable crops." *Journal of Applied Ecology* 23 (1):91-99.

Richter, L., N. Balkenhol, C. Raab, H. Reinecke, M. Meißner, S. Herzog, J. Isselstein, and J. Signer. 2020. "So close and yet so different: The importance of considering temporal dynamics to understand habitat selection." *Basic and Applied Ecology* 43:99-109.

Roberts, T.H., and D.H. Arner. 1984. "Food habits of beaver in East-Central Mississippi." *The Journal of Wildlife Management* 48 (4):1414-1419.

Robertson, A., R.A. McDonald, R.J. Delahay, S.D. Kelly, and S. Bearhop. 2014. "Individual foraging specialisation in a social mammal: the European badger (Meles meles)." *Oecologia* 176 (2):409-421.

Robstad, C.A., H.K. Lodberg-Holm, M. Mayer, and F. Rosell. 2021. "The impact of bio-logging on body weight change of the Eurasian beaver." *PLoS ONE* 16 (12):e0261453.

Roper, T.J., S.R. Findlay, P. Lüps, and D.J. Shepherdson. 1995. "Damage by badgers Meles meles to wheat Triticum vulgare and barley Hordeum sativum crops." *Journal of Applied Ecology* 32 (4):720-726.

Rosell, F., O. Bozsér, P. Collen, and H. Parker. 2005. "Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems." *Mammal Review* 35 (3-4):248-276.

Rosell, F., and A. Czech. 2000. "Responses of foraging Eurasian beavers Castor fiber to predator odours." *Wildlife Biol* 6:13-21.

Rosell, F., and B. Hovde. 2001. "Methods of aquatic and terrestrial netting to capture Eurasian beavers." *Wildlife Society Bulletin* 29 (1):269-274.

Rosell, F., and J. Sanda. 2006. "Potential risks of olfactory signaling: the effect of predators on scent marking by beavers." *Behavioral Ecology* 17 (6):897-904.

Rosell, F., and L.X. Sun. 1999. "Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *Castor fiber*." *Wildlife Biology* 5 (2):119-123.

Rosell, F., A. Zedrosser, and H. Parker. 2010. "Correlates of body measurements and age in Eurasian beaver from Norway." *European Journal of Wildlife Research* 56 (1):43-48.

Ruckstuhl, K.E. 2007. "Sexual segregation in vertebrates: proximate and ultimate causes." *Integrative and Comparative Biology* 47 (2):245-257.

Rue, H., S. Martino, and N. Chopin. 2009. "Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations." *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 71 (2):319-392.

Sadykova, D., B.E. Scott, M. De Dominicis, S.L. Wakelin, A. Sadykov, and J. Wolf. 2017. "Bayesian joint models with INLA exploring marine mobile predator–prey and competitor species habitat overlap." *Ecology and Evolution* 7 (14):5212-5226.

Scrafford, M.A., D.B. Tyers, D.T. Patten, and B.F. Sowell. 2018. "Beaver habitat selection for 24 Yr since reintroduction north of Yellowstone National Park." *Rangeland Ecology & Management.*

Sharpe, F., and F. Rosell. 2003. "Time budgets and sex differences in the Eurasian beaver." *Animal Behaviour* 66 (6):1059-1067.

Sheppard, C.E., R. Inger, R.A. McDonald, S. Barker, A.L. Jackson, F.J. Thompson, E.I.K. Vitikainen, M.A. Cant, and H.H. Marshall. 2018. "Intragroup competition predicts individual foraging specialisation in a group-living mammal." *Ecology Letters* 21 (5):665-673.

Steyaert, S.M.J.G., A. Zedrosser, M. Elfström, A. Ordiz, M. Leclerc, S.C. Frank, J. Kindberg, O.-G. Støen, S. Brunberg, and J.E. Swenson. 2016. "Ecological implications from spatial patterns in human-caused brown bear mortality." *Wildlife Biology* 22 (4):144-152, 9.

Steyaert, S.M.J.G., A. Zedrosser, and F. Rosell. 2015. "Socio-ecological features other than sex affect habitat selection in the socially obligate monogamous Eurasian beaver." *Oecologia* 179 (4):1023-1032.

Sun, L. 2003. "Monogamy correlates, socioecological factors, and mating systems in beavers." *Monogamy: mating strategies and partnerships in birds, humans and other mammals (UH Reichard and C. Boesch, eds.). Cambridge University Press, Cambridge, United Kingdom*:138-146.

Svendsen, G.E. 1980. "Seasonal change in feeding patterns of beaver in southeastern Ohio." *The Journal of Wildlife Management* 44 (1):285-290.

Uboni, A., D.W. Smith, J.S. Mao, D.R. Stahler, and J.A. Vucetich. 2015. "Long- and short-term temporal variability in habitat selection of a top predator." *Ecosphere* 6 (4):art51.

Ulicsni, V., D. Babai, E. Juhász, Z. Molnár, and M. Biró. 2020. "Local knowledge about a newly reintroduced, rapidly spreading species (Eurasian beaver) and perception of its impact on ecosystem services." *PLoS ONE* 15 (5):e0233506.

Vehtari, A., A. Gelman, and J. Gabry. 2015. "Efficient implementation of leave-one-out cross-validation and WAIC for evaluating fitted Bayesian models." *arXiv preprint arXiv:1507.04544*.

Vogel, S.M., B. Lambert, A.C. Songhurst, G.P. McCulloch, A.L. Stronza, and T. Coulson. 2020. "Exploring movement decisions: Can Bayesian movement-state models explain crop consumption behaviour in elephants (Loxodonta africana)?" *Journal of Animal Ecology* 89 (4):1055-1068.

Wang, G., L.F. McClintic, and J.D. Taylor. 2019. "Habitat selection by American beaver at multiple spatial scales." *Animal Biotelemetry* 7 (1):10.

Welch, C.A., J. Keay, K.C. Kendall, and C.T. Robbins. 1997. "Constraints on frugivory by bears." *Ecology* 78 (4):1105-1119.

William, G., G. Jean-Michel, S. Sonia, B. Christophe, M. Atle, M. Nicolas, P. Maryline, and C. Clément. 2018. "Same habitat types but different use: evidence of context-dependent habitat selection in roe deer across populations." *Scientific Reports* 8 (1):5102.

Wilsson, L. 1971. "Observations and experiments on the ethology of the European beaver (*Castor fiber* L.)." *Viltrevy* 8 (3):160-203.

Wood, S., and M.S. Wood. 2015. "Package ‘mgcv’." *R package version* 1:29.

Xi, C., Z. Wu, T. Qian, L. Liu, and J. Wang. 2021. "A Bayesian model for estimating the effects of human disturbance on wildlife habitats based on nighttime light data and INLA-SPDE." *Applied Spatial Analysis and Policy.*

Zoller, H., and F. Drygala. 2013. "Activity patterns of the invasive raccoon dog (Nyctereutes procyonoides) in North East Germany." *Folia Zoologica* 62 (4):290-296, 7.

Żurowski, W., J. Kisza, A. Kruk, and A. Roskosz. 1974. "Lactation and chemical composition of milk of the European beaver (*Castor fiber* L.)." *Journal of Mammalogy* 55 (4):847-850.

Zuur, A. 2017. *Beginner’s guide to spatial, temporal and spatial-temporal ecological data analysis with R-Inla: Using Glm and Glmm Volume I.* Vol. 973745327, *Highland Statistics Ltd., Sl OCLC.*

Zuur, A.F., and E.N. Ieno. 2016. "A protocol for conducting and presenting results of regression-type analyses." *Methods in Ecology and Evolution* 7 (6):636-645.

Zuur, A.F., and E.N. Ieno. 2018. *Beginner's guide to spatial, temporal and spatial-temporal ecological data analysis with R-INLA.: GAM and Zero-inflated models*: Highland Statistics Limited.

Zuur, A.F., E.N. Ieno, and C.S. Elphick. 2010. "A protocol for data exploration to avoid common statistical problems." *Methods in Ecology and Evolution* 1 (1):3-14.

Figure legends

Fig. 1: Individual selection estimates for Eurasian beaver (*Castor fiber*) selection of percentage habitat types, elevation, slope and distance to water and developed areas in southeastern Norway, 2009-2021. Each point represents a specific beaver-year while the vertical lines represent the 95% credible intervals of each estimate. The dashed red line represents zero and individual estimates with credible intervals that overlap with this line means that the beaver does not display selection either for or against the habitat variable in question. Estimates above this line indicates selection for the habitat variable in questions and estimates bellow the lines indicates selection against.

Fig. 2: Individual habitat selection estimates of Eurasian beavers (*Castor fiber*) (N=90) in southeastern Norway, 2009-2021. Predicted effect of age is obtained from a linear mixed effect model using integrated nested Laplace approximation (R-INLA) while accounting for beaver family ID as a random effect. Estimates above the stabled line indicates selection for the habitat variable in question and estimates bellow the lines indicates selection against.

Fig. 3: Variation in individual habitat selection of Eurasian beavers (*Castor fiber*) (N=90) in southeastern Norway, 2009-2021. Predicted effect of average yearly reproduction is obtained from a linear mixed effect model using integrated nested Laplace approximation (R-INLA) while accounting for beaver family ID as a random effect. Estimates above the stabled line indicate selection for the habitat variable in question and estimates bellow the lines indicates selection against.

Fig. 4: Variation in individual habitat selection of Eurasian beavers (*Castor fiber*) (N=90) in southeastern Norway, 2009-2021. Predicted effect of family size as a measure of density is obtained from a linear mixed effect model using integrated nested Laplace approximation (R-INLA) while accounting for beaver family ID as a random effect. Estimates above the stabled line indicate selection for the habitat variable in question and estimates bellow the lines indicate selection against.

Fig 5: Variation in individual habitat selection of Eurasian beavers (*Castor fiber*) (N=90) in southeastern Norway, 2009-2021. Predicted effect of tail fat index as a measure of body condition is obtained from a linear mixed effect model using integrated nested Laplace approximation (R-INLA) while accounting for beaver family ID as a random effect. Estimates above the stabled line indicate selection for the habitat variable in question and estimates bellow the lines indicate selection against.

Fig. 6: Habitat selection estimate smoothers for Julian day interacting with habitat types for Eurasian beavers (*Castor fiber*) (N=104) in southeastern Norway, 2009-2021. Months have been added to aid visual interpretation. A generalized additive mixed model using integrated nested Laplace approximation and stochastic partial differential equations (INLA-SPDE) was fitted for each socio-reproductive group. This includes reproductively active females (Reprod. females), and combined group of reproductively active males and non-reproductive beavers (Other beavers). The stapled black line represents zero, which means no selection for or against the habitat variable in question. Estimates above the stabled line indicates selection for the habitat variable in question and estimates bellow the lines indicates selection against.

Fig. 7: Habitat selection estimate smoothers for active hour interacting with habitat types for Eurasian beavers (*Castor fiber*) (N=104) in southeastern Norway, 2009-2021. Active hour has been converted into a 24-hour format to aid interpretation. A generalized additive mixed model using integrated nested Laplace approximation and stochastic partial differential equations (INLA-SPDE) was fitted for each socio-reproductive group. This includes reproductively active females (Reprod. females), reproductively active males (Reprod. Males) and non-reproductive beavers (Other beavers). The stapled black line represents zero, which means no selection for or against the habitat variable in question. Estimates above the stabled line indicates selection for the habitat variable in question and estimates bellow the lines indicates selection against. The lighter background represents the range of sundown to sunrise to times across the study period, while the dark represents the minimum hours of darkness.

Figure 1

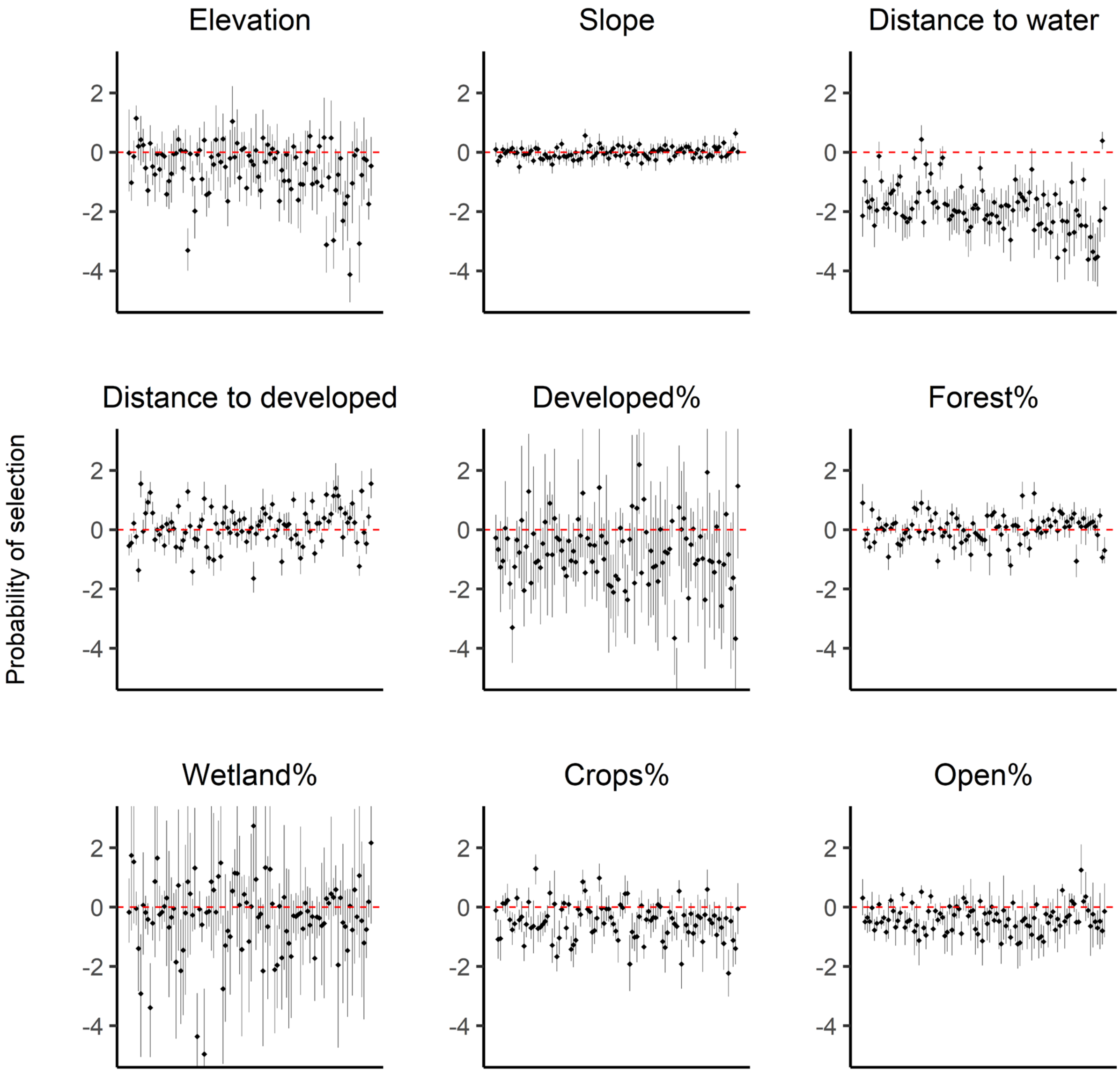
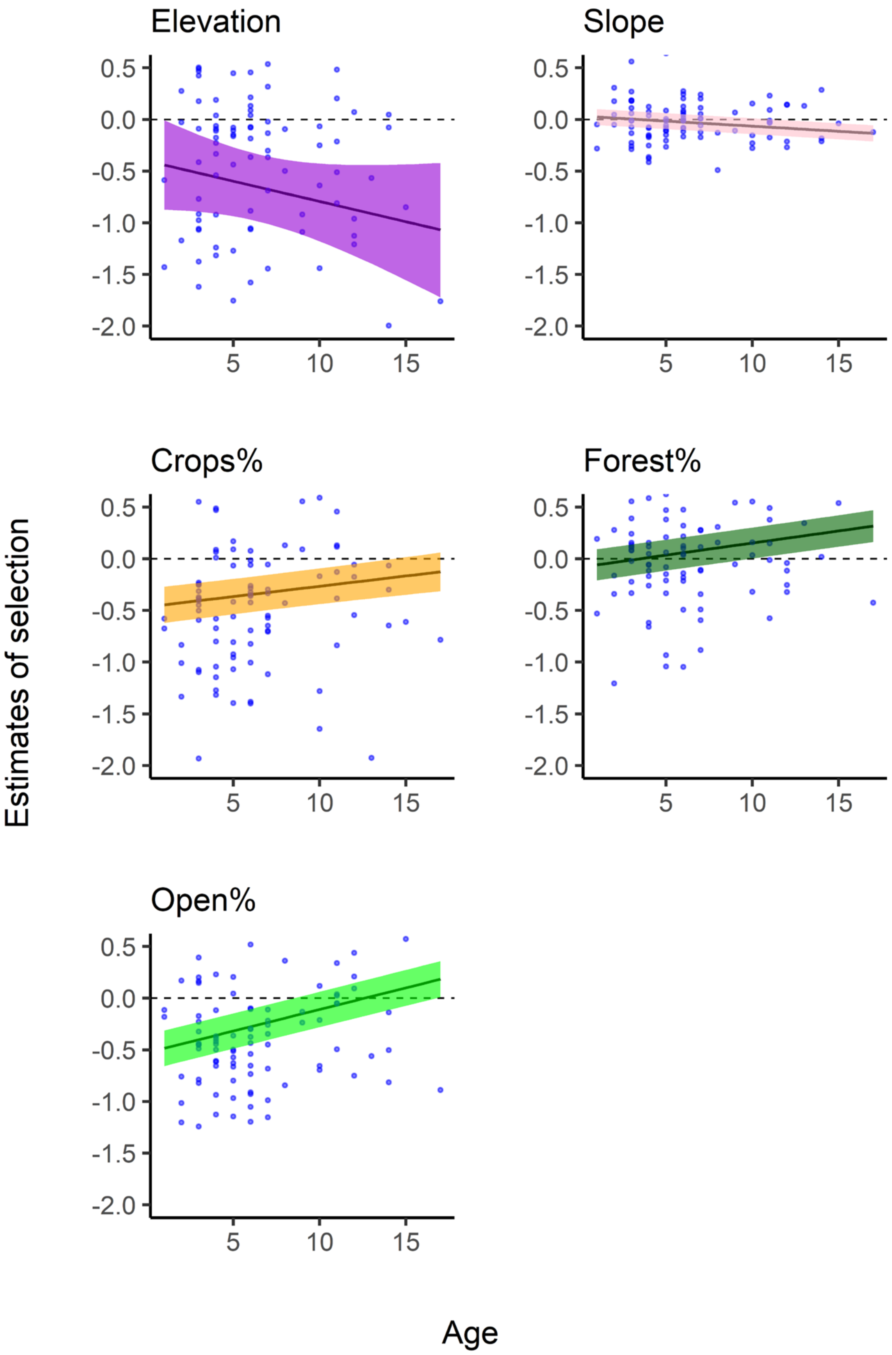

Elevation
Slope
Distance to water
Distance to developed
Developed%
Forest%
Wetland%
Crops%
Open%
Probability of selection
2
0
-2
-4

Figure 2


Elevation
Slope
Crops%
Forest%
Open%
Estimates of selection
Age
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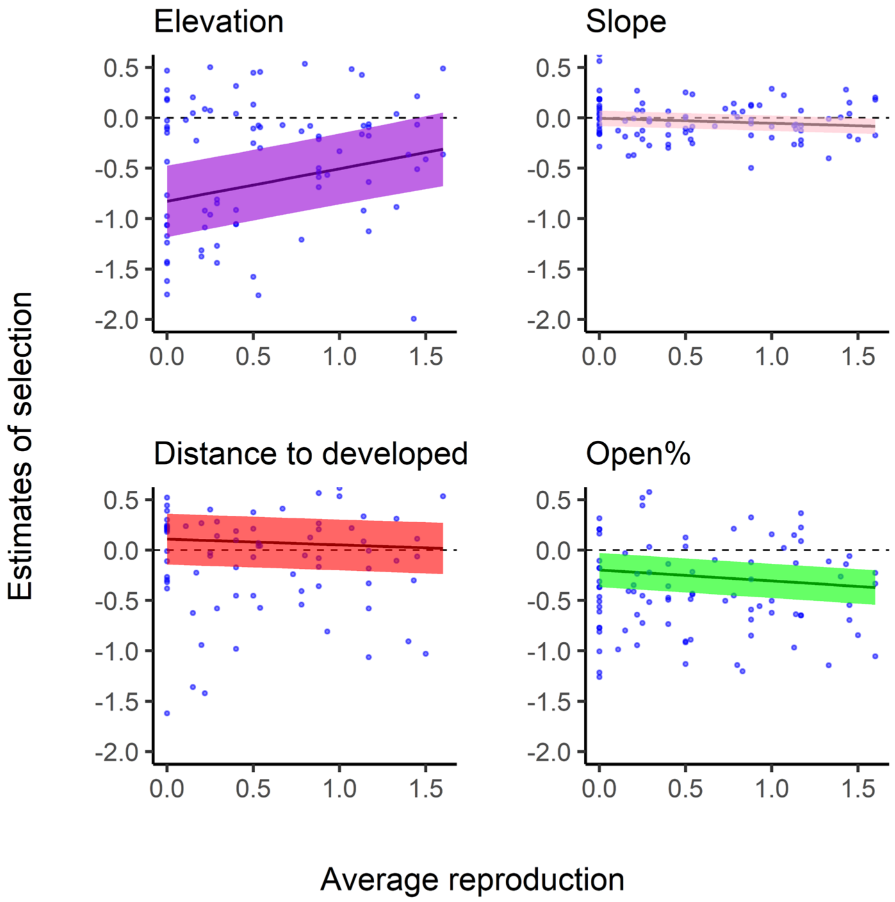
0.0
-0.5
-1.0
-1.5
-2.0
5
10
15

Figure 3


Elevation
Slope
Distance to developed
Open%
Estimates of selection
Average reproduction
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-0.5
-1.0
-1.5
-2.0
0.0
0.5
1.0
1.5

Figure 4

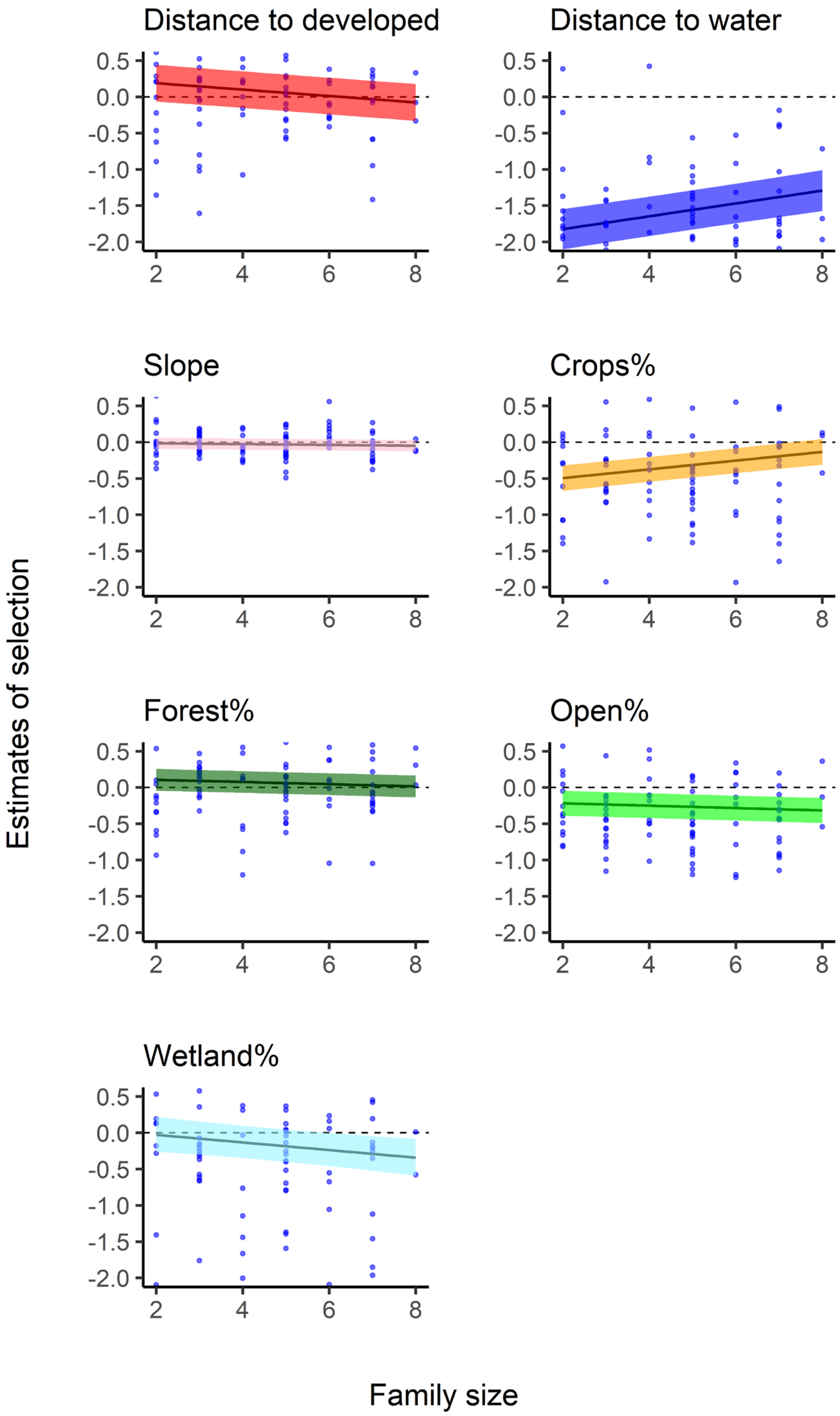

Distance to developed
Distance to water
Slope
Crops%
Forest%
Open%
Wetland%
0.5
0.0
-0.5
-1.0
-1.5
-2.0
2
4
6
8
Estimates of selection
Family size

Figure 5

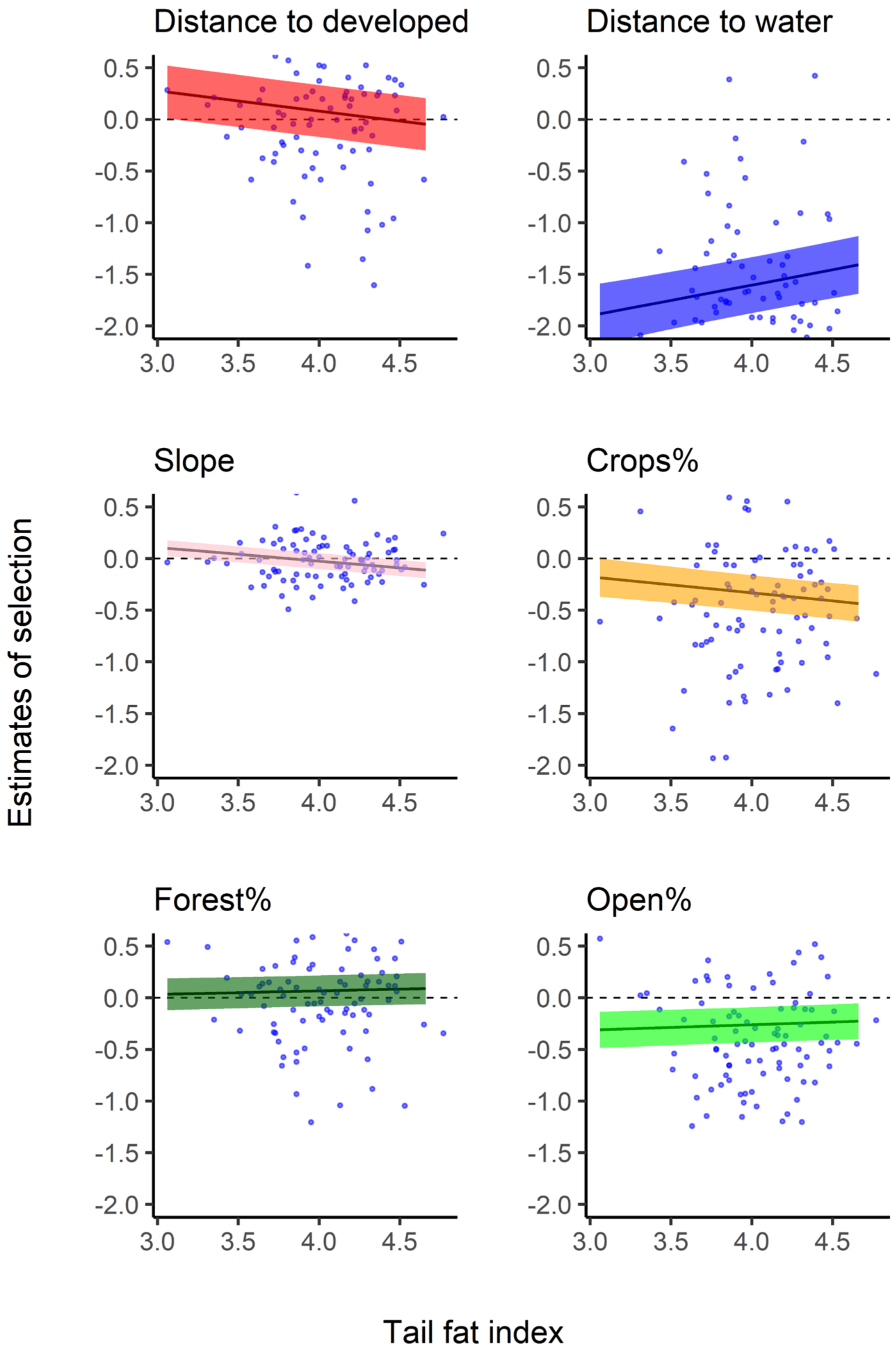
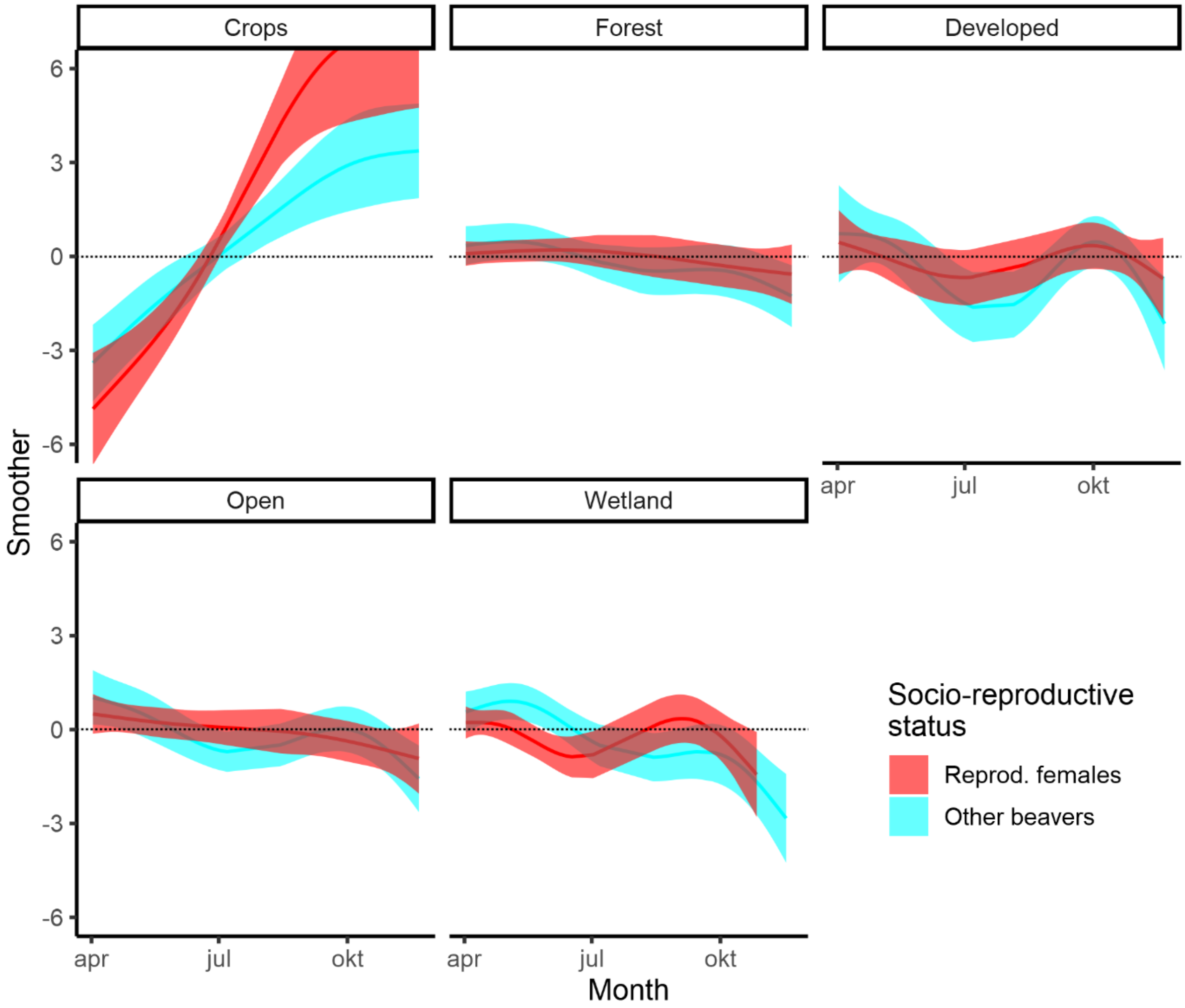

Distance to developed
Distance to water
Slope
Crops%
Forest%
Open%
0.5
0.0
-0.5
-1.0
-1.5
-2.0
3.0
3.5
4.0
4.5
Estimates of selection
Tail fat index

Figure 6


Crops
Forest
Developed
Open
Wetland
6
3
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-3
-6
Smoother
apr
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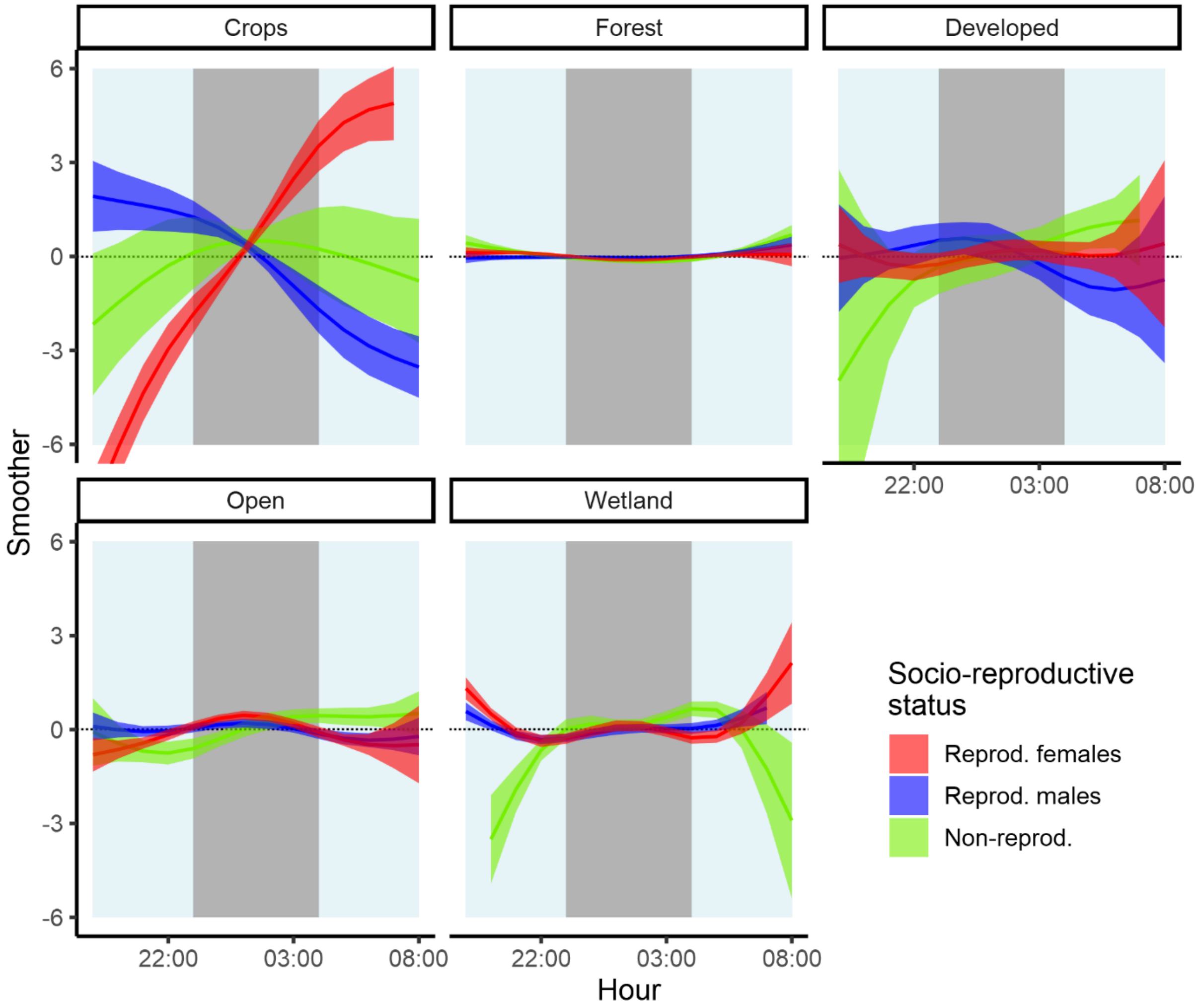
okt
Month
Socio-reproductive status
Reprod. females
Other beavers

Figure 7


Crops
Forest
Developed
Open
Wetland
Smoother
6
3
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-3
-6
22:00
03:00
08:00
Hour
Socio-reproductive status
Reprod. females
Reprod. males
Non-reprod.

Supplementary tables

Table S1: Model selection for the population-level models for habitat selection of Eurasian beavers (*Castor fiber*) (N=104) in southeastern Norway, 2009-2021, with one unimportant variable with credible intervals overlapping with zero is dropped in each round. Each model was fit as a generalized mixed effects models with integrated nested Laplace approximation (R-INLA) including beaver ID and year as random effects. The plus signs represents whether the variable was retained in the model. In the final model, all variables retained were considered statistically important. Elevation implies elevational gain from the closest river, Dist. water to water is the distance to the closest waterway and distance to developed is the distance to the closest human developed area (settlement, road or railway). Crops%, developed%, wetland% and open% stands for the percentage of these habitat types surrounding each beaver or random location. Forest% stands for the percentage of deciduous and mixed forests but excluding coniferous forest.

	Explanatory variables								
Model	Elevation	Slope	Distance to water	Distance to developed	Developed%	Crops%	Forest%	Wetland%	Open%
1	+	+	+	+	+	+	+	+	+
2	+	+	+	+	+	+	+		+
3	+	+	+		+	+	+		+
4	+	+	+		+	+			+
5	+		+		+	+			+

Table S2: Posterior marginal distributions for the coefficients of the predictors for population-level Eurasian beaver (*Castor fiber*) habitat selection in southeastern Norway, 2009-2021 (N=104). The posterior distributions were estimated using generalized mixed effects models with integrated nested Laplace approximation (R-INLA) while accounting for beaver ID and year as random effects. Elevation means elevational gain from the closest river, distance to water is the distance to the closest waterway, while crops%, developed%, and open% stands for the percentage of these habitat types surrounding each beaver or random location. All explanatory variables were centered prior to model fitting.

Parameter	**Mean**	**Sd**	**2.5th percentile**	**97.5th percentile**
Intercept	42.30	181.38	-313.80	398.11
Elevation	-0.56	0.11	-0.77	-0.36
Distance to water	-1.81	0.09	-2.00	-1.63
Developed%	-1.02	0.20	-1.42	-0.63
Crops%	-0.50	0.06	-0.63	-0.37
Open%	-0.41	0.06	-0.53	-0.29

Table S3: Comparisons between the full model and a null model for each model set investigating how individual habitat selection varies in relation to potential demographic and physiological characteristics of Eurasian beavers (*Castor fiber*) in southeastern-Norway (N=104). Each model was fit as a linear mixed effects models with integrated nested Laplace approximation (R-INLA) with beaver family ID as a random intercept. Deviance information criterion (DIC) and Watanabe-Akaike information criterion (WAIC) are given for each model. The most supported model based on the lowest DIC values is shown in bold.

Model	**DIC**	**WAIC**
Crop		
Full model	**1848.90**	2623.77
Null model	2076.00	2653.29
Developed		
Full model	665.86	721.35
Null model	**663.53**	702.68
Distance to developed		
Full model	**1731.90**	3461.57
Null model	2168.33	3438.10
Distance to water		
Full model	**1859.16**	2470.11
Null model	2022.45	2499.37
Elevation		
Full model	**1413.77**	1757.32
Null model	1475.70	1763.78
Forest		
Full model	**1558.07**	4966.27
Null model	1984.53	4884.68
Open		
Full model	**779.56**	2538.03
Null model	1089.16	2828.34
Slope		
Full model	**-12098.33**	-5068.85
Null model	-10357.32	-4789.34
Wetland		
Full model	**707.00**	707.00
Null model	715.77	776.33

Table S4: Model selection for exploring individual variation in habitat selection of Eurasian beavers (*Castor fiber*) (N=90) in southeastern Norway, 2009-2021 in relation to beaver-specific demographic and physiological variables. These include age of the beaver, tail fat index as a measure of body condition, average yearly reproduction, and family size as a measure of density. Each model was fit as a generalized mixed effects models with integrated nested Laplace approximation (R-INLA) with beaver family ID as a random intercept. One unimportant parameter with 95% credible intervals overlapping with zero is dropped in each round and the plus sign indicates which variables are retained in each round. In the final model, all parameters retained were considered statistically important.

Habitat variable	**Variables**			
Crop%	Age	Tail fat index	Average reproduction	Family size
1	+	+	+	+
2	+	+		+
Distance to developed				
1	+	+	+	+
2		+	+	+
Distance to water				
1	+	+	+	+
2	+	+		+
3		+		+
Elevation				
1	+	+	+	+
2	+		+	+
3	+		+	
Forest%	+	+	+	+
1	+	+		+
2				
Open%				
1	+	+	+	+
2	+		+	+
3	+		+	
Slope				
1	+	+	+	+
Wetland%				
1	+	+	+	+
2	+		+	+

3	+	+
4		+

Table S5: Posterior marginal distributions of the predictor coefficients for individual habitat selection estimates of Eurasian beavers (*Castor fiber*) (N=90) in southeastern Norway, 2009-2021. Selection estimates for each habitat variable were used as the response variables modelled with linear mixed models using integrated nested Laplace approximation (R-INLA). For each estimate, the standard deviation (sd) and the 95% credible intervals are displayed for each fixed variable retained in the final model.

Parameter	**Mean**	**sd**	**2.5th percentile**	**97.5th percentile**
Crop%				
Intercept	-0.12	0.18	-0.48	0.24
Age	0.02	0.00	0.01	0.03
Tail fat index	-0.16	0.04	-0.23	-0.08
Family size	0.06	0.01	0.04	0.08
Distance to developed				
Intercept	1.14	0.16	0.82	1.46
Tail fat index	-0.20	0.03	-0.26	-0.15
Average reproduction	-0.06	0.02	-0.09	-0.02
Family size	-0.04	0.01	-0.05	-0.03
Distance to water				
Intercept	-3.14	0.28	-3.69	-2.60
Tail fat index	0.28	0.06	0.16	0.39
Average reproduction	0.09	0.01	0.07	0.12
Elevation				
Intercept	-0.72	0.18	-1.07	-0.37
Age	-0.01	0.01	-0.03	0.00
Average reproduction	0.33	0.05	0.22	0.43
Forest%				
Intercept	-0.16	0.11	-0.37	0.05
Age	0.02	0.00	0.02	0.03
Tail fat index	0.04	0.02	0.00	0.07
Family size	-0.02	0.00	-0.03	-0.01
Open%				
Intercept	-0.61	0.12	-0.85	-0.37
Age	0.04	0.00	0.04	0.05
Tail fat index	0.05	0.02	0.01	0.10
Average reproduction	-0.11	0.02	-0.14	-0.08
Family size	-0.02	0.00	-0.02	-0.01
Slope				
Intercept	0.59	0.05	0.50	0.68

Age	-0.01	0.00	-0.01	-0.01
Tail fat index	-0.13	0.01	-0.14	-0.12
Average reproduction	-0.05	0.00	-0.06	-0.04
Family size	0.00	0.00	-0.01	0.00
Wetland%				
Intercept	0.06	0.14	-0.21	0.35
Family size	-0.05	0.02	-0.08	-0.01

Table S6: Model selection of generalized additive mixed models with integrated nested Laplace approximation using stochastic partial differential equations (INLA-SPDE) modelling habitat selection of Eurasian beavers (*Castor fiber*) (N=104) in southeastern Norway, 2009-2021. Five models were fitted for each social-reproductive group (reproductive males, reproductive females, and non-reproductive individuals) and deviance information criterion (DIC) and Watanabe-Akaike information criterion (WAIC) are given for each model. The most supported model is shown in bold.

Model	**DIC**	**WAIC**
Male/Non reproductive combined		
Bernoulli GAMM	146789.70	146828.80
Bernoulli GAMM + spatial correlation	134530.60	135051.20
Bernoulli GAMM + space-time correlation	129869.90	208255.20
Bernoulli GAMM + space-time correlation with knots	**129827.10**	186043.20
Null model	158967.90	158969.60
Reproductive females		
Bernoulli GAMM	94821.22	94881.87
Bernoulli GAMM + spatial correlation	88488.97	89190.84
Bernoulli GAMM + space-time correlation	86142.97	106038.20
Bernoulli GAMM + space-time correlation with knots	**86057.41**	89907.94
Null model	103452.40	103452.70
Non-reproductive		
Bernoulli GAMM	76491.23	76509.36
Bernoulli GAMM + spatial correlation	45399.04	77326.04
Bernoulli GAMM + space-time correlation	44756.03	512021.79
Bernoulli GAMM + space-time correlation with knots	**44731.50**	377709.84
Null model	54972.75	54973.11
Reproductive males		
Bernoulli GAMM	95760.25	95790.62
Bernoulli GAMM + spatial correlation	87102.04	88505.61
Bernoulli GAMM + space-time correlation	**83788.58**	2373523.04
Bernoulli GAMM + space-time correlation with knots	84427.00	391357.41
Null model	158968.30	158970.10

Table S7: Posterior marginal distributions for the coefficients of the predictors of seasonal habitat selection for reproductively active male and non-reproductive Eurasian beavers (*Castor fiber*) (N=65) in south-eastern Norway, 2009-2021. Smoothers have been fitted for Julian day interacting with habitat type using generalized additive mixed models with integrated nested Laplace approximation using stochastic partial differential equations (INLA-SPDE). Each habitat variable was included as a categorical variable interacting with smoothers for Julian day, beaver ID was included as a random term and spatio-temporal correlation accounted for using residual autoregressive correlation (AR1).

Parameter	**Mean**	**SD**	**2.5th percentile**	**0. 97.5th percentile**
Intercept (Crop)	-0.37	30.64	-60.52	59.74
HabitatForest	0.83	0.08	0.68	1.00
HabitatDeveloped	-0.97	0.22	-1.41	-0.56
HabitatOpen	0.22	0.12	0.00	0.45
HabitatWetland	0.80	0.17	0.47	1.13
Elevation	-0.23	0.05	-0.34	-0.13
WaterDistance	-2.01	0.05	-2.11	-1.91
Jul1.crop	1.22	0.70	-0.15	2.60
Jul2.crop	0.82	2.01	-3.13	4.77
Jul3.crop	-0.95	2.01	-4.88	3.00
Jul4.crop	0.90	0.62	-0.31	2.11
Jul1.for	0.61	0.57	-0.51	1.72
Jul2.for	-2.96	1.60	-6.10	0.18
Jul3.for	1.74	1.48	-1.17	4.66
Jul4.for	0.29	0.49	-0.68	1.25
Jul1.dev	1.82	1.39	-0.94	4.50
Jul2.dev	7.94	4.37	-0.74	16.42
Jul3.dev	-9.91	4.55	-18.64	-0.77
Jul4.dev	1.65	1.35	-1.09	4.23
Jul1.ope	0.54	0.77	-0.97	2.04
Jul2.ope	-3.50	2.02	-7.46	0.47
Jul3.ope	-5.18	2.30	-9.68	-0.67
Jul4.ope	-0.02	0.64	-1.29	1.25
Jul1.wet	-0.08	0.75	-1.56	1.39
Jul2.wet	-3.36	2.20	-7.66	0.98
Jul3.wet	-3.46	2.57	-8.48	1.61
Jul4.wet	-0.62	0.68	-1.98	0.70

Table S8: Posterior marginal distributions for the coefficients of the predictors of seasonal habitat selection for reproductively active female Eurasian beavers (*Castor fiber*) (N=39) in southeastern Norway, 2009-2021. Smoothers have been fitted for Julian day interacting with habitat type using generalized additive mixed models with integrated nested Laplace approximation using stochastic partial differential equations (INLA-SPDE). Each habitat variable was included as a categorical variable interacting with smoothers for Julian day, beaver ID was included as a random term and spatio-temporal correlation accounted for using residual autoregressive correlation (AR1).

Parameter	**Mean**	**SD**	**2.5th percentile**	**0. 97.5th percentile**
Intercept (Crop)	-0.39	30.76	-60.79	59.96
HabitatForest	0.52	0.08	0.37	0.68
HabitatDeveloped	-0.53	0.19	-0.90	-0.17
HabitatOpen	0.14	0.11	-0.08	0.36
HabitatWetland	0.24	0.14	-0.04	0.52
Elevation	-0.16	0.05	-0.26	-0.06
WaterDistance	-1.88	0.05	-1.97	-1.78
Jul1.Crop	-3.47	0.82	-5.09	-1.86
Jul2.Crop	1.50	2.22	-2.82	5.90
Jul3.Crop	4.47	2.52	-0.41	9.49
Jul4.Crop	-3.57	0.86	-5.28	-1.91
Jul1.Forest	0.24	0.63	-1.01	1.48
Jul2.Forest	0.03	1.19	-2.31	2.37
Jul3.Forest	0.37	1.20	-1.99	2.72
Jul4.Forest	-0.11	0.46	-1.02	0.80
Jul1.Developed	-1.74	1.09	-3.92	0.36
Jul2.Developed	2.54	2.90	-3.07	8.31
Jul3.Developed	2.04	2.91	-3.58	7.83
Jul4.Developed	-1.83	1.07	-3.96	0.23
Jul1.Open	-0.33	0.85	-1.98	1.33
Jul2.Open	0.03	1.61	-3.12	3.21
Jul3.Open	0.30	1.80	-3.20	3.86
Jul4.Open	-0.69	0.67	-2.01	0.62
Jul1.Wetland	2.28	0.76	0.79	3.78
Jul2.Wetland	4.84	2.49	-0.04	9.71
Jul3.Wetland	5.33	2.49	0.46	10.23
Jul4.Wetland	-1.84	0.68	-3.18	-0.50

Table S9: Posterior marginal distributions for the coefficients of the predictors of circadian habitat selection for reproductively active female Eurasian beavers (*Castor fiber*) (N=39) in southeastern Norway, 2009-2021. Smoothers have been fitted for hour of the night interacting with habitat type using generalized additive mixed models with integrated nested Laplace approximation using stochastic partial differential equations (INLA-SPDE). Each habitat variable was included as a categorical variable interacting with smoothers for Julian day, beaver ID was included as a random term and spatio-temporal correlation accounted for using residual autoregressive correlation (AR1).

	β	**sd**	**0.025**	**0.975**
Intercept (Crop)	-0.36	30.67	-60.57	59.79
HabitatForest	0.49	0.07	0.35	0.63
HabitatDeveloped	-0.41	0.15	-0.71	-0.11
HabitatOpen	0.16	0.10	-0.03	0.36
HabitatWetland	0.00	0.13	-0.26	0.25
Elevation	-0.13	0.05	-0.23	-0.03
WaterDistance	-1.90	0.05	-2.00	-1.80
Hour1.Crop	-0.42	0.38	-1.19	0.32
Hour2.Crop	3.24	0.91	1.49	5.06
Hour3.Crop	5.95	1.49	3.09	8.95
Hour4.Crop	0.12	0.37	-0.60	0.85
Hour1.Forest	-0.05	0.11	-0.26	0.17
Hour2.Forest	0.37	0.26	-0.15	0.88
Hour3.Forest	0.36	0.45	-0.52	1.25
Hour4.Forest	-0.01	0.12	-0.24	0.21
Hour1.Developed	0.65	0.74	-0.80	2.12
Hour2.Developed	-1.59	1.73	-4.89	1.91
Hour3.Developed	-2.52	3.12	-8.41	3.86
Hour4.Developed	-0.23	0.79	-1.87	1.23
Hour1.Open	-0.30	0.33	-0.95	0.34
Hour2.Open	-0.93	0.75	-2.38	0.56
Hour3.Open	-0.61	1.38	-3.26	2.17
Hour4.Open	0.30	0.36	-0.42	0.99
Hour1.Wetland	0.48	0.36	-0.22	1.20
Hour2.Wetland	-4.34	0.82	-5.95	-2.71
Hour3.Wetland	-7.37	1.40	-10.07	-4.58
Hour4.Wetland	0.41	0.41	-0.42	1.21

Table S10: Posterior marginal distributions for the coefficients of the predictors of circadian habitat selection for non-reproductive Eurasian beavers (*Castor fiber*) (N=21) in southeastern Norway, 2009-2021. Smoothers have been fitted for hour of the night interacting with habitat type using generalized additive mixed models with integrated nested Laplace approximation using stochastic partial differential equations (INLA-SPDE). Each habitat variable was included as a categorical variable interacting with smoothers for Julian day, beaver ID was included as a random term and spatio-temporal correlation accounted for using residual autoregressive correlation (AR1).

	β	**sd**	**0.025**	**0.975**
Intercept (Crop)	-0.30	31.00	-61.17	60.51
HabitatForest	1.74	0.14	1.47	2.01
HabitatDeveloped	1.22	0.30	0.57	1.76
HabitatOpen	1.48	0.18	1.12	1.83
HabitatWetland	3.43	0.21	3.02	3.84
Elevation	-1.53	0.09	-1.71	-1.36
WaterDistance	-0.70	0.05	-0.80	-0.60
Hour1.Crop	-0.67	0.69	-2.02	0.67
Hour2.Crop	0.63	1.50	-2.21	3.69
Hour3.Crop	2.47	2.57	-2.33	7.77
Hour4.Crop	0.28	0.66	-1.06	1.52
Hour1.Forest	-0.12	0.14	-0.39	0.16
Hour2.Forest	-0.42	0.31	-1.03	0.19
Hour3.Forest	-1.17	0.50	-2.14	-0.19
Hour4.Forest	0.19	0.13	-0.06	0.44
Hour1.Developed	-1.22	1.82	-5.25	1.88
Hour2.Developed	2.18	3.42	-3.91	9.53
Hour3.Developed	4.38	6.29	-6.48	18.18
Hour4.Developed	2.11	2.09	-1.38	6.78
Hour1.Open	1.06	0.51	0.03	2.06
Hour2.Open	-1.40	1.09	-3.51	0.78
Hour3.Open	-2.12	1.75	-5.48	1.40
Hour4.Open	-0.47	0.43	-1.29	0.39
Hour1.Wetland	-0.50	0.55	-1.58	0.57
Hour2.Wetland	4.80	1.30	2.36	7.47
Hour3.Wetland	10.55	2.75	5.42	16.23
Hour4.Wetland	-0.08	0.63	-1.37	1.12

Table S11: Posterior marginal distributions for the coefficients of the predictors of circadian habitat selection for reproductively active male Eurasian beavers (*Castor fiber*) (N=44) in southeastern Norway, 2009-2021. Smoothers have been fitted for hour of the night interacting with habitat type using generalized additive mixed models with integrated nested Laplace approximation using stochastic partial differential equations (INLA-SPDE). Each habitat variable was included as a categorical variable interacting with smoothers for Julian day, beaver ID was included as a random term and spatio-temporal correlation accounted for using a replicate spatial autocorrelation model.

Parameter	**Mean**	**SD**	**2.5th percentile**	**0. 97.5th percentile**
Intercept (Crop)	-0.43	31.18	-61.64	60.73
HabitatForest	0.79	0.07	0.65	0.94
HabitatDeveloped	-0.52	0.22	-0.97	-0.10
HabitatOpen	0.16	0.11	-0.05	0.36
HabitatWetland	0.67	0.13	0.41	0.92
Elevation	-0.24	0.06	-0.35	-0.13
WaterDistance	-2.03	0.05	-2.13	-1.93
Hour1.Crop	-1.00	0.36	-1.70	-0.30
Hour2.Crop	-0.68	0.78	-2.18	0.89
Hour3.Crop	-0.33	1.29	-2.80	2.28
Hour4.Crop	0.96	0.34	0.28	1.61
Hour1.Forest	-0.14	0.10	-0.35	0.07
Hour2.Forest	-0.08	0.23	-0.53	0.38
Hour3.Forest	-0.29	0.37	-1.02	0.45
Hour4.Forest	0.20	0.10	0.01	0.40
Hour1.Developed	-0.94	1.08	-3.07	1.16
Hour2.Developed	-1.33	2.44	-6.01	3.57
Hour3.Developed	-1.47	3.94	-8.82	6.66
Hour4.Developed	0.51	0.97	-1.55	2.27
Hour1.Open	0.07	0.27	-0.46	0.60
Hour2.Open	-0.98	0.61	-2.16	0.22
Hour3.Open	-1.21	0.97	-3.09	0.72
Hour4.Open	-0.03	0.24	-0.50	0.43
Hour1.Wetland	0.70	0.25	0.21	1.20
Hour2.Wetland	-1.81	0.60	-2.99	-0.62
Hour3.Wetland	-2.80	0.82	-4.40	-1.17
Hour4.Wetland	-0.21	0.24	-0.68	0.25

Supplementary figures

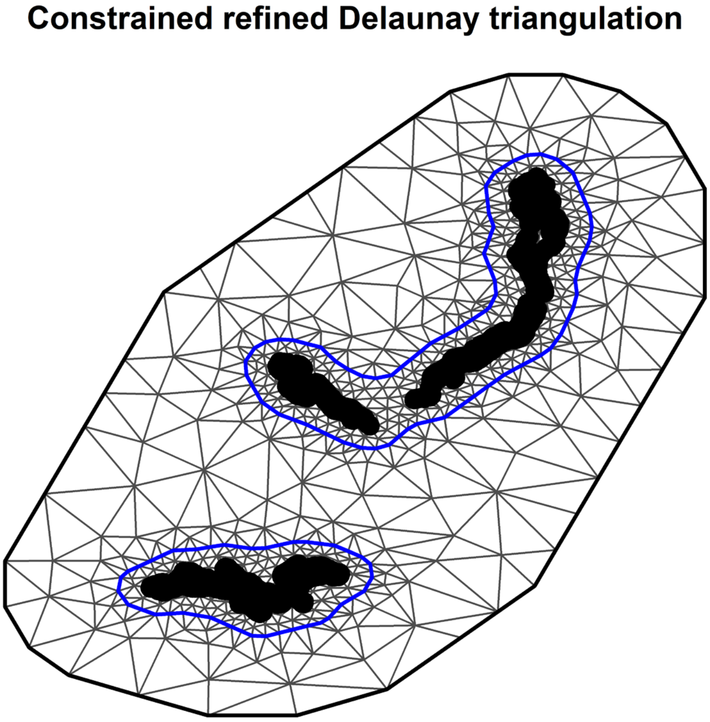

Figure S1: Example of one of the spatial meshes created using Delaunay triangularization overlaying the three study rivers, which was used to estimate the stochastic partial differential equations (INLA-SPDE) for the spatial temporal models. This particular mesh is made for reproductively active female Eurasian beavers (*Castor fiber*) (N=39) within southeastern Norway (2009-2021). The black areas represent GPS and available locations of the female reproductively active beavers.

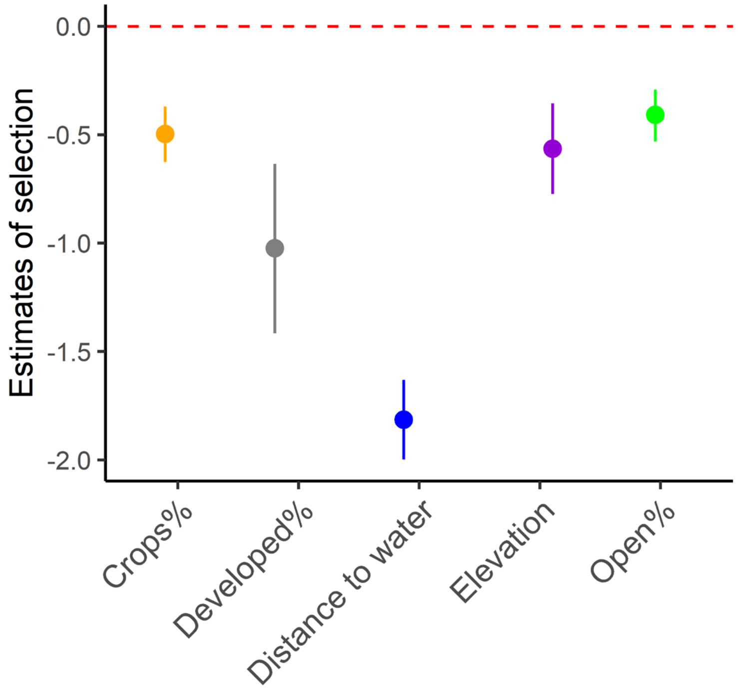

Fig. S2: Population-level selection estimates of Eurasian beaver (*Castor fiber*) (N=104) habitat selection in southeastern Norway 2009-2021. These are obtained from a generalized linear mixed effects model using a binomial distribution with integrated nested Laplace approximation (R-INLA) while accounting for beaver ID and year as random effects. The 95% credible intervals are displayed for around each fixed variable as vertical lines. The dashed red line represents zero and individual estimates with credible intervals overlapping this line implies no selection for or against the variable in question. Estimates above the line indicates selection for the variable in question and estimates bellow the lines indicates selection against.

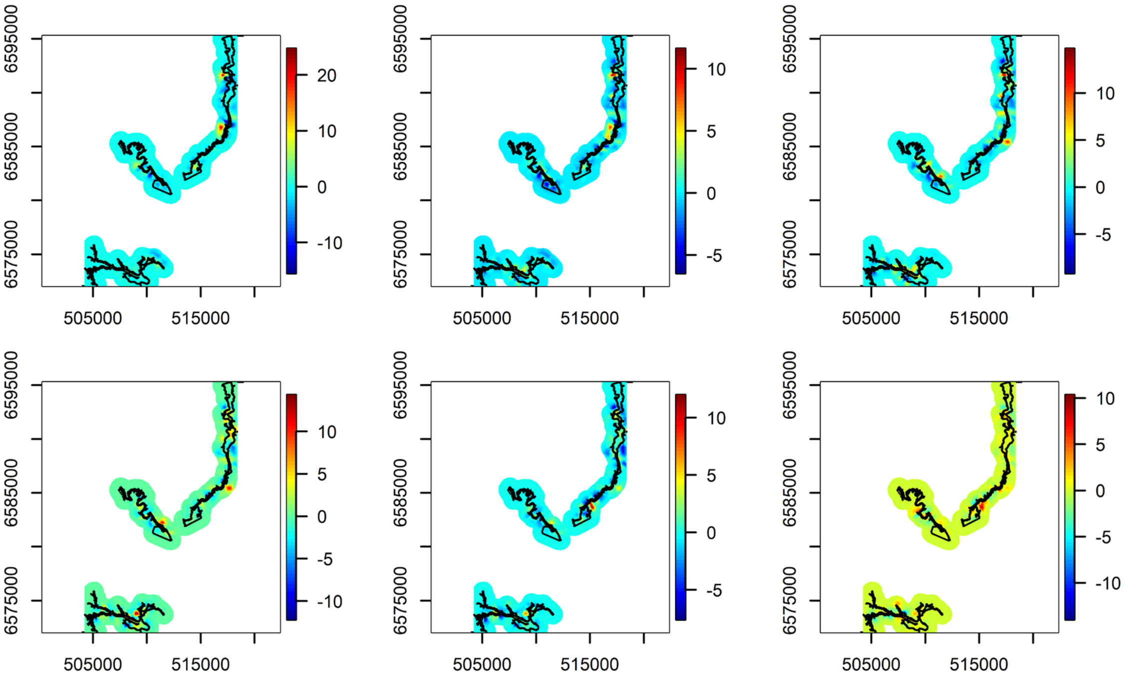

Figure S3: Spatial-random field for each time knot for reproductive female Eurasian beavers (*Castor fiber*) in southeastern-Norway (2009-2021) (N=39). The spatial field displays the predicted probability of beaver presence across the landscape not explained by a generalized additive mixed effect model using integrated nested Laplace approximation and stochastic partial differential equations (INLA-SPDE). Higher values represent a higher probability for beaver presence, while lower represents low probability of beaver presence.

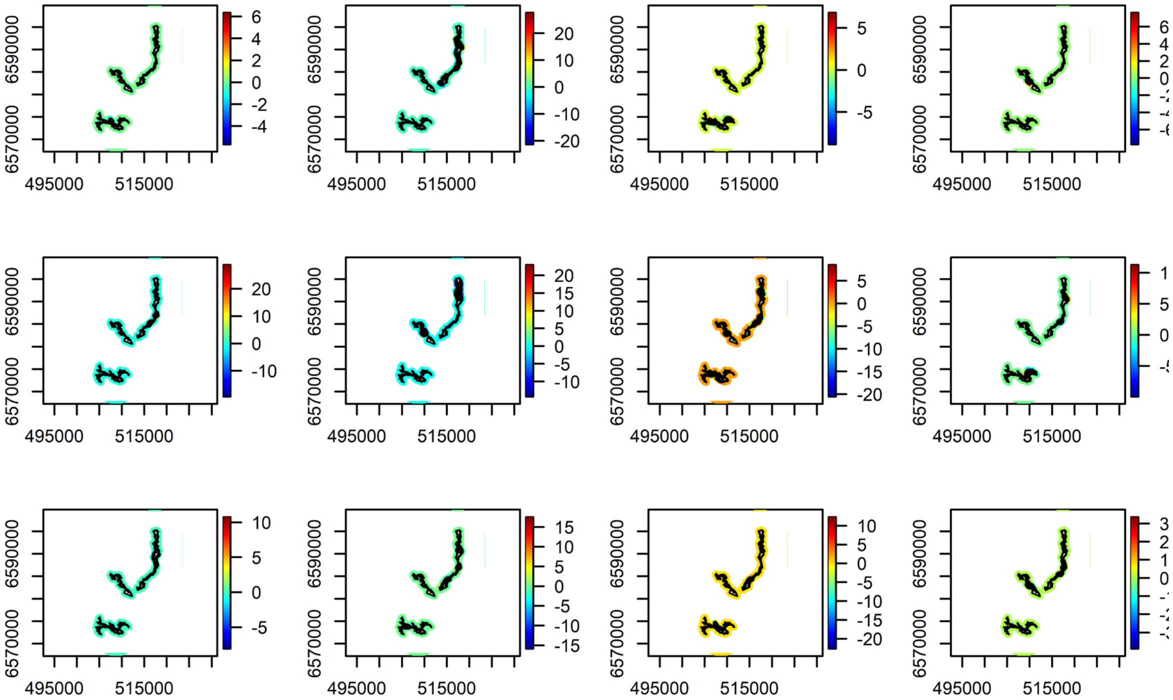

Figure S4: Spatial-random field for each year for reproductive male Eurasian beavers (*Castor fiber*) (N=44) in southeastern Norway, 2009-2021 The spatial field displays the predicted probability of beaver presence across the landscape not explained by a generalized additive mixed effect model using integrated nested Laplace approximation and stochastic partial differential equations (INLA-SPDE). Higher values represent a higher probability for beaver presence, while lower represents low probability of beaver presence.

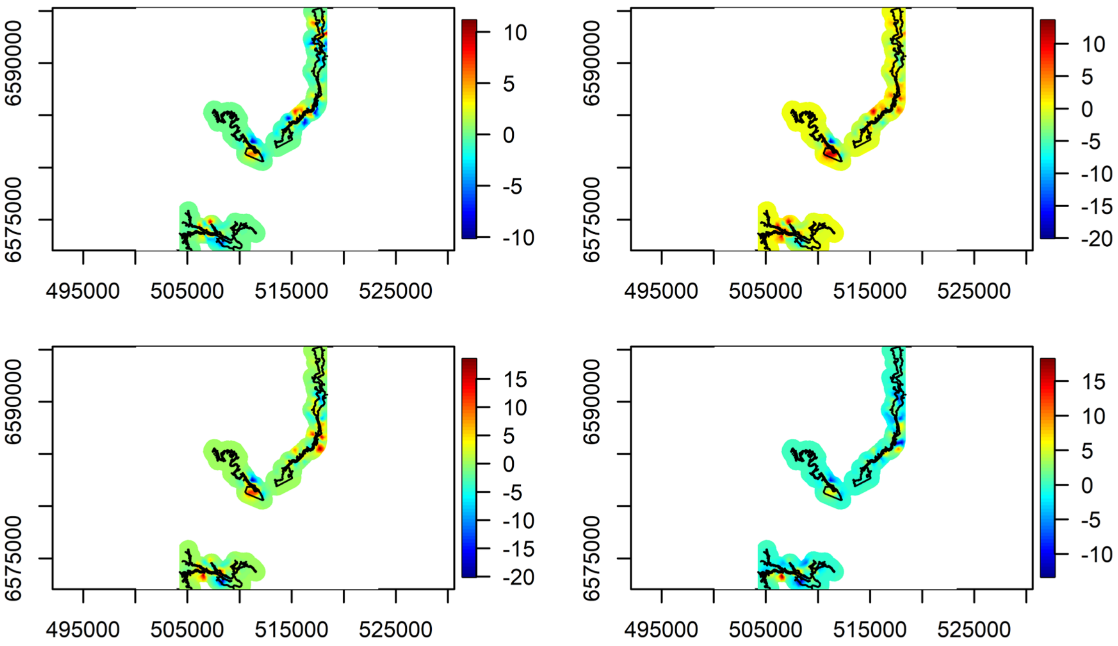

Figure S5: Spatial-random field for each time knot for non-reproductive Eurasian beavers (*Castor fiber*) (N=21) in southeastern-Norway, 2009-2021 The spatial field displays the predicted probability of beaver presence across the landscape not explained by a generalized additive mixed effect model using integrated nested Laplace approximation and stochastic partial differential equations (INLA-SPDE). Higher values represent a higher probability for beaver presence, while lower represents low probability of beaver presence.

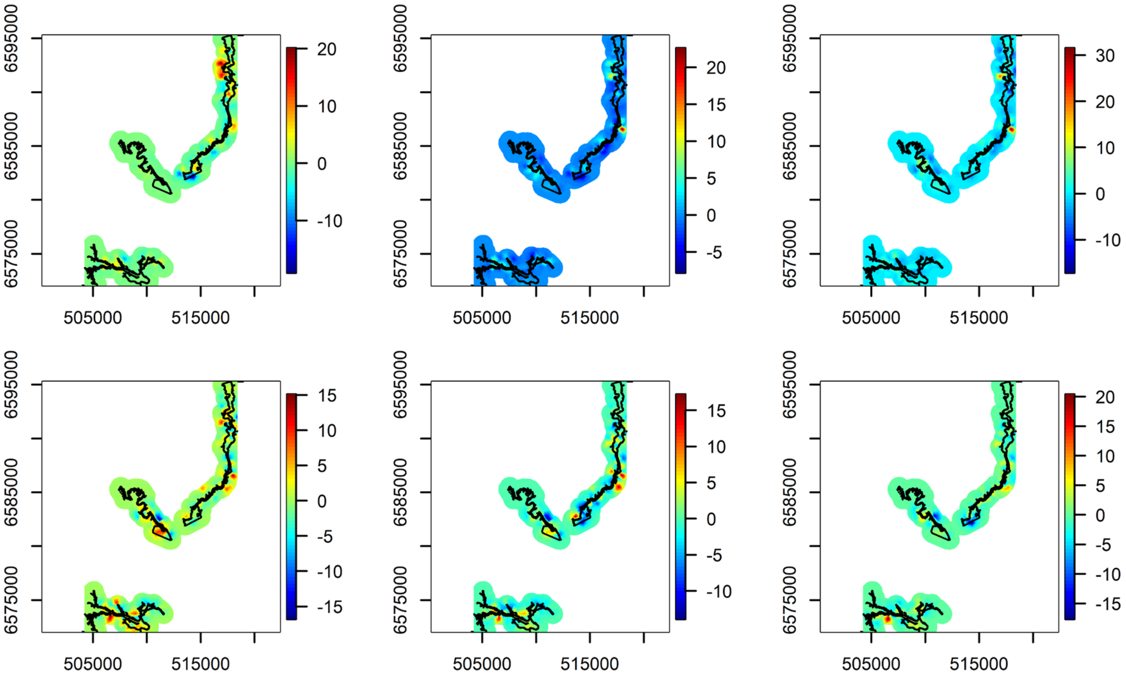

Figure S6: Spatial-random field for each time knot for non-reproductive and male reproductive Eurasian beavers (*Castor fiber*) (N=65) in southeastern Norway, 2009-2021. The spatial field displays the predicted probability of beaver presence across the landscape not explained by a generalized additive mixed effect model using integrated nested Laplace approximation and stochastic partial differential equations (INLA-SPDE). Higher values represent a higher probability for beaver presence, while lower represents low probability of beaver presence.

Article 4

Robstad, C. A., Lodberg-Holm, H. K., Mayer, M., & Rosell, F. (2021). The impact of bio-logging on body weight change of the Eurasian beaver. PLOS ONE, 16(12), e0261453.

PLOS ONE

RESEARCH ARTICLE

The impact of bio-logging on body weight change of the Eurasian beaver

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Abstract

Bio-logging is a common method to collect ecological data on wild animals, but might also induce stress, reduce body condition, and alter behavior. Eurasian beavers (*Castor fiber*) are a semi-aquatic and nocturnal species that are challenging to observe in the wild. Bio-loggers are hence useful tools to study their behaviour and movements, but this raises concerns of potential negative impacts of tagging. To investigate the potential negative impacts of glue-on tags, we compared body weight change for tagged and untagged Eurasian beavers. We hypothesized that tagged beavers would gain less body weight compared to untagged beavers, and that weight change might be affected by tagging length, tag weight, water temperature and the season of tagging. Daily percentage body weight change in relation to initial body weight during the first capture was compared during 57 tagging periods (18±7 days) and 32 controls periods (64±47 days). Body weight change varied between the two groups, with untagged beavers on average gaining daily weight whilst tagged beavers on average lost weight daily, indicating a negative effect of tagging. The average reduction in percentage body weight change per day for tagged beavers was small (0.1 ± 0.3%), and with large individual variation. Neither tag weight, number of tagging days, nor season were important in explaining body weight change of tagged animals. In other words, we found that tagging reduced daily body weight during the tagging period but were unable to determine the mechanism(s) responsible for this decline. Detrimental effects of tagging have important implications for animal welfare and can introduce bias in data that are collected. This calls for careful consideration in the use of tags. We conclude that studies investigating the effects of tagging should consider individual variation in the effects of tagging and, where possible, compare tagged animals with a control group.

Introduction

Bio-logging studies, i.e. using animal-borne devices to gather information on animal behavior, movement, physiology, and environmental conditions, are key to increasing our

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understanding of animal behavior and ecology [1, 2]. However, negative impacts of attaching instruments to animals can be substantial, yet are not always considered [3]. Generally speaking, the impact of tag weight is a primary concern, and contemporary guidelines endorse continued miniaturization of tags [4]. The total weight of a tag should not exceed 0.7–10% of body weight depending on the species and recommendations from different authors [5–9]. Moreover, negative effects from bio-logging can be caused by capture stress [8, 10] and vary depending on the attachment method [11]. For example, increased drag from external tags affects energy expenditure, locomotion, and swimming speed [12], especially for aquatic and semi-aquatic species [13–16]. Tagging may negatively impact both body condition and life history traits such as reproduction, parental care, and survival [17, 18]. Such detrimental impacts raise concerns around animal welfare and ethics. In addition, if the body condition, energy expenditure or activity patterns of animals are affected, this can produce biased data that does not reflect the true behaviour of the species [19, 20]. The effects of tag attachment vary among species, individuals [16], and geographic regions [21], and require species-specific adaptations [22]. Impacts from tagging and capture may also vary according to the sex and age of an animal [14, 23]. Assessments should therefore be made to the extent of the tag impact through species-specific studies using different tag types [18]. Importantly, the effects of tagging on animal behaviour and body condition are often not fully understood due to the difficulty in comparing tagged animals with a control group of untagged individuals [24]. This should be investigated and assessed whenever possible [25]. External attachment mechanisms for bio-logging devices such as harnesses, backpacks, collars, and glue-on tags have been used for scientific studies of numerous taxa from invertebrates to mammals [26–29]. The glue-on method is commonly used on animals that are unsuitable to tag with a collar, and involves gluing the tag directly onto the fur or skin of the animal with fast-curing adhesives [30, 31]. However, several studies have found that such tags may impact animals negatively. For example, glue-on tags affected swimming speed due to increased drag in Hawaiian monk seals (*Monachus schauinslandi*) [32], increased trip duration in Antarctic fur seals (*Arctocephalus gazella*) [33], changed foraging behavior in harbour seals (*Phoca vitulina*) [34], and caused skin abrasions on Weddell seals (*Leptonychotes weddellii*) and southern elephant seals (*Mirounga leonina*) [35]. Gluing tags onto the fur is a common method for tagging semi-aquatic mammals. For animals that are insulated by blubber, such as pinnipeds, glue-on tags are expected to have limited impact on body temperature, despite potential heat leakage at the site of tag attachment (e.g. in grey seals) [36]. However, semi-aquatic species that rely on a water-resistant fur for insulation [37] may be more vulnerable to heat loss from glue-on tags that impair the insulating properties of their pelage [38, 39].

The Eurasian beaver (*Castor fiber*) together with the closely related North American beaver (*C. canadensis*) are semi-aquatic and nocturnal, which makes it challenging to observe their behavior and habitat use [40, 41]. Therefore, bio-logging is a powerful tool to study their secret lives [42–44]. As ecosystem engineers that have large impacts on their surrounding ecosystems [45, 46], they are often the focus of ecological studies in which bio-loggers are a valuable tool. However, beavers have fusiform body shapes and thick necks with small heads that render the common tagging method of collaring impossible [41, 47, 48]. Other methods to collect data on beavers include surgically implanted transmitters [47, 49, 50], and securing devices using a hole made in the beaver's tail [51–55]. However, implants can cause extended recovery and surgical complications [56], while tail mounting may cause tail injuries and reduce body weight gain during winter [55]. Due to these challenges, glue-on tags have been utilized as an alternative method for beaver bio-logging by the Norwegian Beaver Project (NBP) [42, 44, 57].

A study investigating short-term changes in post-tagging behaviour of beavers following tagging with glue-on tags, found only minor alterations in behaviour through reduced activity levels of individuals, and four beavers remained in their lodge until the next day following attachment of glue-on tags [58]. Another long-term study within the same population found that the number of captures and handling events negatively affected beaver reproduction during the first years of monitoring, but this effect subsided during the later years of the study, possibly due to habituation of older beavers captured several times throughout their life [59]. The same study found no long-term effects related to whether a beaver had carried a tag in its lifetime on body condition, survival or reproduction [59].

Changes to body condition or body weight in beavers as a result of glue-on tags have not yet been studied during the tagging period. Beavers usually gain body weight from spring to fall and decrease body weight in winter when food availability is scarce [60, 61]. Young beavers tend to gain more body weight than adults, with the weight of beavers peaking at around 10 years of age, and adult females tend to have larger body masses than males in spring and summer [59]. The aim of this study was to investigate potential negative impacts of tagging on the body weight change of beavers by comparing tagged and untagged (control) individuals. We also aimed to identify variables related to tagging that could influence weight change, while controlling for potential effects of year, age, and sex. We hypothesized that glue-on tags would reduce the rate of body weight gain in beavers and predicted that tagged beavers would gain less body weight during the tagging period compared to untagged beavers. Secondly, we hypothesized that negative impacts of tagging on beaver body weight would be exaggerated during the colder months in spring and fall, and at colder water temperatures when beavers spend more energy on thermoregulation, and have lower food access compared to the warmer summer months [45]. Lastly, we hypothesized that the negative effect of tagging on body weight change might be exaggerated by the increased tag weight and duration of the tagging period.

Materials and methods

Study area and beaver population

We studied beavers in the NBP study site. This site consists of three connected rivers–Gvarv (59˚ 386' N, 09˚ 179' E), Straumen (59˚ 29' N, 09˚ 153' E), and Sauar (59˚ 444' N, 09˚ 307' E)–which all discharge into lake Norsjø in Vestfold and Telemark County, Norway. The mean annual air temperature is 4.6 Celsius and annual precipitation is 790 mm [59, 62]. Human settlements, semi-agricultural landscapes, and forested woodlands are scattered throughout the study area [62]. Eurasian beavers have inhabited the area since the 1920s [63]. Hunting pressure in the area is low [64], and the population is considered to be at carrying capacity [42, 62, 64]. Beaver territories border each other, so there are few unoccupied stretches of the river. In total, 25–30 beaver families inhabit the study area and they have been continuously monitored since 1997 [42, 65, 66].

Capture and handling, and details of study individuals

We studied 57 beavers that had been captured as part of ongoing research. Specifically, every year between March and November, beavers were captured as part of a long-term capture-mark-recapture study and for tagging purposes [65, 67]. The NBP has studied beavers for over 20 years with 1,560 live captures. We attempted to reduce capture-related stress by not capturing the same beaver several times a year, which resulted in a lower sample size of untagged beavers (control group) compared to tagged beavers. Beavers were caught at night with nets from a boat or onshore [68], and transferred into a cloth bag for handling. All beavers included in this study were handled while awake with no use of anesthesia. Captured animals were microchipped and ear-tagged for identification [69]. Each beaver was sexed, based on the color and viscosity of the anal-gland secretion [70], weighed (tagged beavers were weighed with the tag during attachment, and without the tag after removal) and measured for body size, tail length, and tail thickness [65, 71]. Beavers were subsequently released back to the place of capture after 20–40 minutes. Age was assigned based on body weight if not captured for the first time as a kit or yearling. Individuals captured for the first time weighing between >17 and <19.5 kg were assigned a minimum age of two years and a minimum age of three years when over >19.5 kg [72]. We classified the beavers into age groups based on prior knowledge of rate of body weight change for different ages. Beavers aged between 2–3 years were defined as 'young' (i.e. individuals that are still growing), those between 4–10 were classified as 'adult' (fully grown with a lower body weight gain compared to young beavers). Beavers aged 11–17 were classified as 'old' (showing signs of senescence, such as loss of body weight). The average age when beavers in our study population tend to die or disappear is 9–10 years independent of their sex [67], but beavers in the wild can live up to 20–24 years of age [73–75]. We have had several beavers older than 10 years in our study area, with a maximum age of 17 included in the dataset [65, 76].

Tagging procedure

Since 2009, glue-on tags have been the main attachment method under the NBP. From 2009 to 2020, beavers were equipped with tags sized approximately 12 × 12 x 1.2 cm with tag weight varying according to logger weight and the materials used (total logger weight: 159 ± 36 g, range: 124–267 g). Every tag unit consisted of a VHF transmitter (18 × 35 mm, 10 g; Reptile glue-on series R1910; Advanced Telemetry Systems, Isanti, MN, USA) in combination with a global positioning system (GPS) device–model G1G 134A; Sirtrack, Havelock North, NZ (50 × 70 mm, 24 g), or model Gipsy 5 GPS; TechnoSmart, Rome, Italy, (48×21 mm, 27.8 g). Most beavers were also equipped with triaxial accelerometers (15 × 90 mm, 62 g; JUV Elektronik, Schleswig-Hollstein, GER) or a Daily Diary (52 x 29 x 22 mm, 62 g with waterproof casing) developed by the SLAM lab at Swansea University, UK. During a few tagging sessions, a time-depth recorder (67 x 17 mm, 30 g; model MK9 Archival Tag, Wildlife Computers Inc, Redmond, WA, USA) was used instead of a GPS or accelerometer. The loggers were attached to a piece of coarse polyester, secured with cable ties and glue (both to the polyester and to each other), to assure all parts remained in one unit until retrieval of the tag.

The tag was glued onto the lower back of the beaver, 15 cm above the base of the tail irrespective of beaver body size, using a two-component epoxy resin (System Three Resins, Auburn WA, USA) [58] (Fig 1). Note that tags were covered with a 4.5 mm mesh net (Mørenot Fishery AS, Møre and Romsdal) on both sides to prevent the glue from reaching the skin of the beaver which may cause heat or chemical burns (Fig 1). After attaching the tag to the beaver, we waited for the glue to harden, and rinsed the beaver and tag with cold water if we registered a rise in temperature that may harm the beaver. Temperatures above 50˚C cause damage to the skin of animals [77], but laboratory analysis using similar glues as we applied, showed that three types of epoxy glue never reached temperatures above 34˚C [35]. We monitored the temperature of the glue with our hands while wearing latex gloves. The whole capture, handling and attachment process took between 20–40 minutes. Tagged beavers were usually recaptured after 2–3 weeks, and the tag was cut out of the fur using a scalpel, which took approximately 10–40 minutes. We defined the tagging period from the time the tag was attached on the beaver until the beaver was recaptured and the tag removed. If the tag fell off by itself, the beaver was not recaptured, and the body weight difference from the beginning to the end of the tagging period could not be estimated. These tagging events were therefore not included in the analysis. The weight of each tag was estimated by adding together the weights

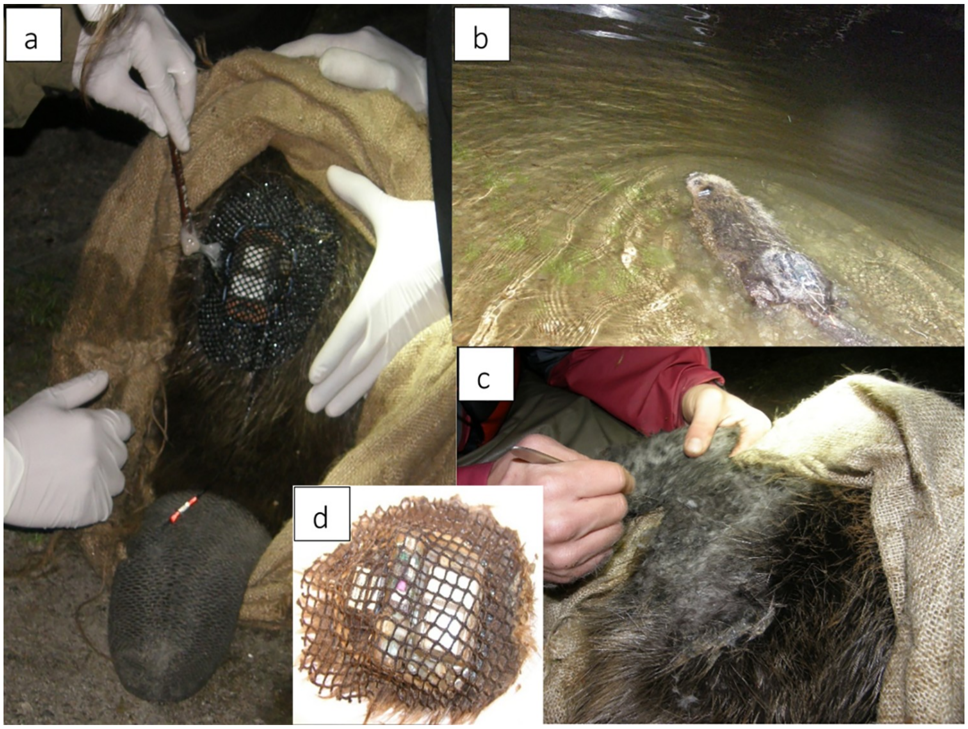

Fig 1. Process of tagging a Eurasian beaver (*Castor fiber*) using glue-on tags within the study area in southeastern Norway. Attachment of the tag using two-component epoxy glue (a), release of the beaver with the tag attached (b), removal of tag by cutting it out of the outer fur using a scalpel (c), and the tag following removal (d). Photos: Patricia Graf.

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of the individual loggers and an average weight of the materials used for attachment. We weighed 21 tags post-removal (and after having removed the data loggers) to estimate the average weight of the glue and materials used for attachment; this was 90 ± 27 g, and we therefore added this as a constant to each tag weight.

Ethical statement

Ethical committees within the Norwegian Food Safety Authority (most recent authorization FOTS ID 15947) and the Norwegian Directorate for Nature Management (most recent authorization 2014/14415 ART-VI-ID) approved this study, including all handling and tagging procedures. To our knowledge, none of the beavers in this study were injured due to capture and handling. Unfortunately, one beaver was found deceased in the entrance of the lodge during the tagging period but cause of death and whether it was related to tagging could not be determined based on a necropsy by the Norwegian Veterinary Institute. The study complied with the ASAB/ABS Guidelines for the treatment of animals in behavioral research and teaching [78]. The study was also carried out in compliance with the ARRIVE guidelines [79].

Data preparation

We used percentage body weight change between initial and the subsequent capture of tagged and untagged beavers as an indicator of change in body condition. Tagged beavers were included if their body weight was measured both when the tag was attached (capture) and removed (recapture). Untagged beavers were only included in the control group if captured twice between March–November in a given year, in order to calculate their daily body weight change between the two captures. We first estimated total body weight change (%) between the two captures, and then divided this by the number of days between capture and recapture to obtain daily body weight change (%) in relation to the initial body weight (at first capture). The percentage weight of the tag in relation to the initial beaver body weight was also calculated, which we hereby refer to as relative tag weight (%).

Glue-on tags were only used on beavers after 2009, so we only included observations of tagged beavers during or following that year (2009–2020), while observations of untagged beavers were included from 2006–2020. Prior to 2006, the beavers were weighed with less accuracy, and these observations were therefore not included. Four of the female territory owners included in the study were pregnant in the period between captures. We conducted our analysis both with and without these individuals included, and because they did not impact the model selection or model estimates, they were retained in the dataset. Similarly, four tagged beavers were older than the maximum age of the untagged beavers (13 years old), which increased the average age of the tagged beavers. We also tried to exclude these older tagged beavers from the analysis, but this did not influence model selection or model estimates, and they were therefore retained in the dataset. Most of the study beavers have been monitored over many years, and some were included several times in the dataset, either as tagged or untagged (S1 File).

We defined season according to the months in which the majority of the days between captures fell within. Observations with the majority of days during March-May were defined as spring, June-August as summer, and September-November as fall. We obtained average water temperature measurements in Celsius from the Norwegian Water Resources and Energy Directorate (NVE) for each river system during the periods beavers carried the tags. Water temperatures were not monitored within the study area itself, and we therefore had to rely on data from the same watershed to indicate water temperature. For Sauar, we used water temperature data from Kirkvoll located on the Tinnåa river that runs into Heddal lake, which represents the start of Sauar river. For Straumen, we obtained water temperatures from Kilen in the Kilåi river than runs into Flåvatn, which represents the start of the Straumen river. For Gvarv, we used water temperature information from the Hørte river, which merges with the Gvarv river just above the study area.

Statistical analysis

We divided the analysis into two parts. First, we modelled the daily body weight change (%) as a function of tagging status (tagged or untagged), including age group, season and sex as possible confounding variables. Second, for tagged beavers, we modelled total body weight change (%) in relation to initial weight as a function of tagging season, relative tag weight (%), average water temperature during the tagging period, sex, age group, and the duration of tagging. We excluded the six tagged beavers for which we could not obtain water temperature data in this analysis. For both analyses, we used linear mixed models (LMM) with a Gaussian distribution and the R package lme4 [80]. Beaver ID and year were included as crossed random effects on the intercept in both analyses to account for pseudoreplication of repeated sampling of the same individual and yearly variations. In part one of the analysis we included interactions between the tagging status of the beaver (tagged or untagged) and its sex, age group and the season of tagging. The recommended steps from Zuur, Ieno and Elphick [81] were followed for data exploration. All numerical variables were tested for collinearity and were found not to be correlated (Pearson r coefficient <0.6) and with a cut-off of variance inflation factor (VIF) < 3 [82]. We visually assessed collinearity between numerical and categorical variables using boxplots. The beavers' social status was collinear with age and was therefore excluded from the analysis. Season of tagging and water temperature were also collinear, so we included them both in different models.

We constructed a set of candidate models with separate combinations of the explanatory variables for both parts of the analysis. Model selection was based on Akaike's Information Criterion (AICc) values for small sample sizes [83, 84], and carried out with the R package MuMln using the "model.sel" function [85]. To avoid selecting complex models that add little additional information compared to a similar nested model, we selected the most parsimonious model among the candidate models separated with less than <2 ΔAICc from the top model [86, 87]. For each explanatory variable included in the most parsimonious model, we calculated the 95% confidence interval, and if it overlapped with zero, the variable was considered uninformative. We plotted the Pearson residuals of the most parsimonious model against fitted values to inspect for non-normality and heterogeneity [88]. We also plotted the model residuals against each variable included and not included in the most parsimonious model, and fitted a smoother to check for potential non-linear patterns in the residuals. Lastly, we simulated residuals from the model using the package DHARMa and plotted the residuals against expected and fitted values to observe deviations from the expected distribution [89]. All data analyses were performed with R version 4.0.3 (R Development Core Team 2020).

Results

We analyzed beaver body weight change across 89 periods (tagging periods or between captures of untagged beavers) of 57 individual beavers (S1 File). We included 57 tagging periods (20 females, 22 males), and 32 control periods (14 females, 13 males). Of these,11 beavers were tagged more than once, while 13 were included with more than one control period, and 13 beavers were included as both tagged and controls at different times (S1 File). The mean age of the two groups differed by 1.8 years, and the mean number of days between captures was 18 ± 7 days for tagged beavers and 64 ± 47 days for untagged (Table 1). Water temperature varied among tagging periods between 1.29 to 15.87 Celsius. The relative tag weight (%) constituted 0.8 ± 0.2% (range, 0.5–1.4%) of the initial body weight of the beavers. Between captures, untagged beavers gained an average of 23 g per day, while body weight of the tagged beavers declined by 13.7 g daily (Table 1). Percentage daily body weight change was on average 0.1% for untagged and -0.1% for tagged beavers, but with considerable individual variation (Fig 2). The largest decline in body weight among the tagged beavers was for an individual that lost 2,333 g (11.5% reduction) over a 14-day tagging period; this constituted 0.8% daily weight loss. Amongst the tagged beavers, 57% of the tagging periods caused a decline in body weight, but 42% of the tagged beavers gained body weight. Two (7%) of the untagged beavers declined in body weight between captures, while 93% gained body weight. Visual observations during tag removal indicated that the amount of fur remaining post-tagging varied. The extent was not documented consistently, but we believe it had a negligible impact on measured body weight.

Table 1. Overview of the two Eurasian beaver (*Castor fiber)* groups (tagged and untagged) in relation to number of days between captures, and total and daily body weight change between the captures in southeastern Norway 2006–2020. Each variable is presented as the mean with standard deviation and the total range within the parenthesis.

	Tagged	Untagged
Days between captures	18 ± 6.6 days (8–43)	64 ± 46.8 (5–139)
Age	6.7 ± 3.5 years (2–17)	4.9 ± 3.0 years (2–13)
Average total body weight change	-220.7 ± 953.5 g (-2,333–2,077.8)	1,156.9 ± 953.5 g (-500–3,500)
Average daily body weight change	-13.7 ± 59.4 g (-166.64–115.43)	23 ± 3.0 g (-66.67–149.63)
Average daily body weight change %	-0.1 ± 0.3% (-0.82–0.57)	0.1 ± 0.2% (-0.27–0.75)

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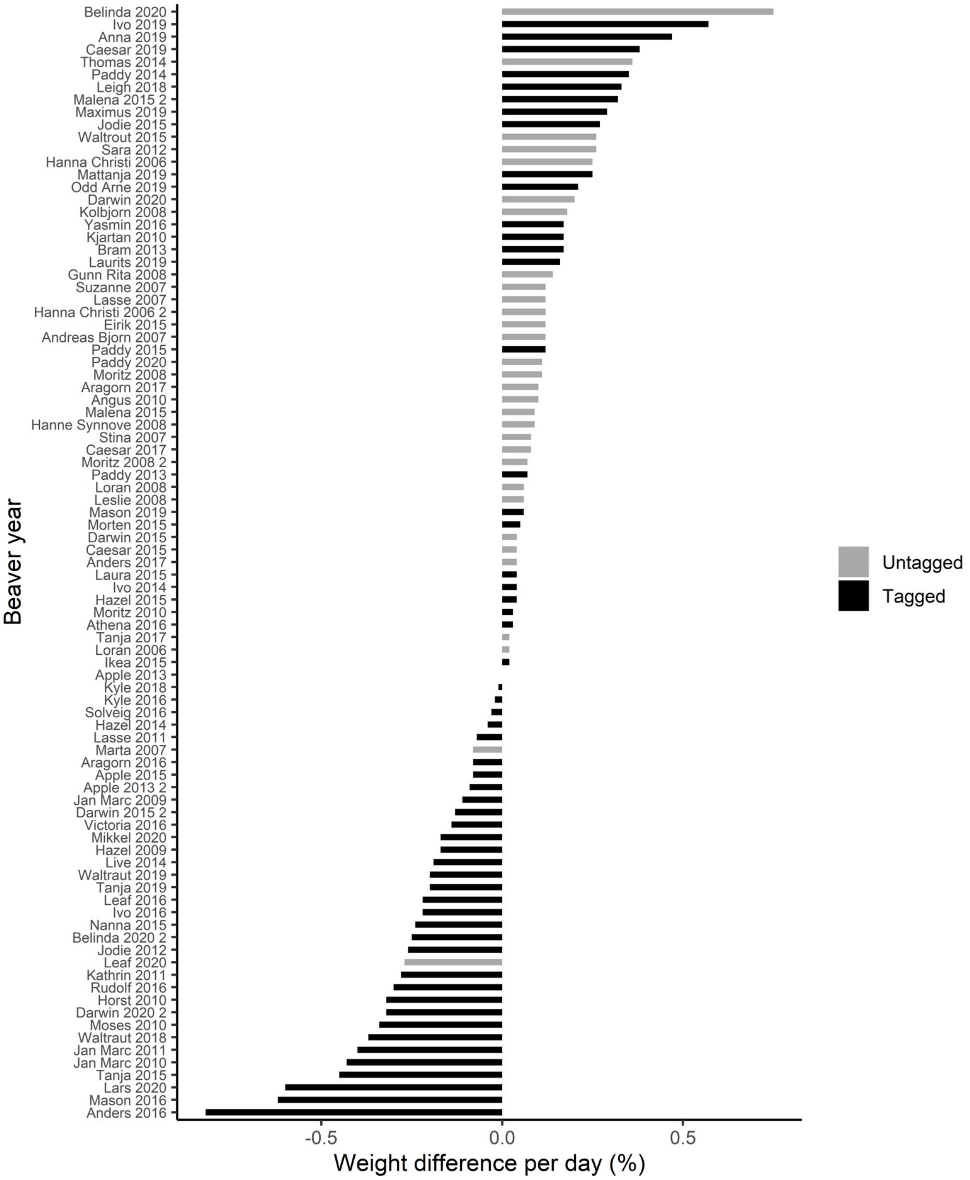

Fig 2. Daily percentage body weight change between captures for Eurasian beavers (*Castor fiber*) in southeastern Norway 2006–2020. Tagged beavers are shown in black while untagged are shown in dark grey.

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For some beavers, underfur appeared intact, while others had open patches with no underfur remaining.

Daily weight change (%) in tagged versus untagged beavers

The most supported model retained tag presence and age group as fixed effects (Table 2). Predicted daily body weight change of tagged beavers was -0.04 g (CI: -0.18–0.09), while predicted daily body weight change of untagged beavers was 0.20 g (CI: 0.07–0.32; Fig 3 & Table 3). Age group was uninformative (95% confidence intervals overlapped zero) in explaining daily body weight change for tagged and untagged beavers (Table 3). The interactions between tag presence and either sex or season were unsupported. The diagnostic plots indicated acceptable model fit using a Gaussian distribution (S1 File).

Table 2. The model selection results investigating the percentage daily body weight change between two subsequent captures of Eurasian beavers (*Castor fiber*) in southeastern Norway (2006–2020). Each model represents a linear mixed effect model with year and beaver ID included as random effects. Potential fixed effects included in each candidate model are age group of the beaver, season of tagging, sex of the beaver, and whether the beaver was tagged or not. The plus signs indicate which variables were included in each candidate model. Degrees of freedom (df), log likelihood (logLik) and model AIC weight (w) are provided for each candidate model. Results for the best supported model are shown in bold.

Intercept	AgeG	Season	Sex	Tag	AgeG*Tag	Season *Tag	Sex *Tag	df	logLik	AICc	ΔAICc	w
-0.04	+			+				**7**	**4.36**	**6.66**	**0.00**	**0.90**
0.00								4	-2.27	13.01	6.35	0.04
0.08	+							6	-0.47	13.96	7.30	0.02
-0.09	+	+	+	+		+		12	6.55	15.01	8.34	0.01
0.09	+		+					7	-0.39	16.16	9.49	0.01
0.03	+	+						8	0.48	16.83	10.17	0.01
-0.08	+	+	+	+		+	+	13	6.57	17.72	11.06	0.00
-0.08	+	+	+	+		+	+	13	6.57	17.72	11.06	0.00
-0.11	+	+	+	+	+	+		14	6.76	20.15	13.49	0.00
-0.11	+	+	+	+	+	+	+	15	6.76	23.05	16.39	0.00

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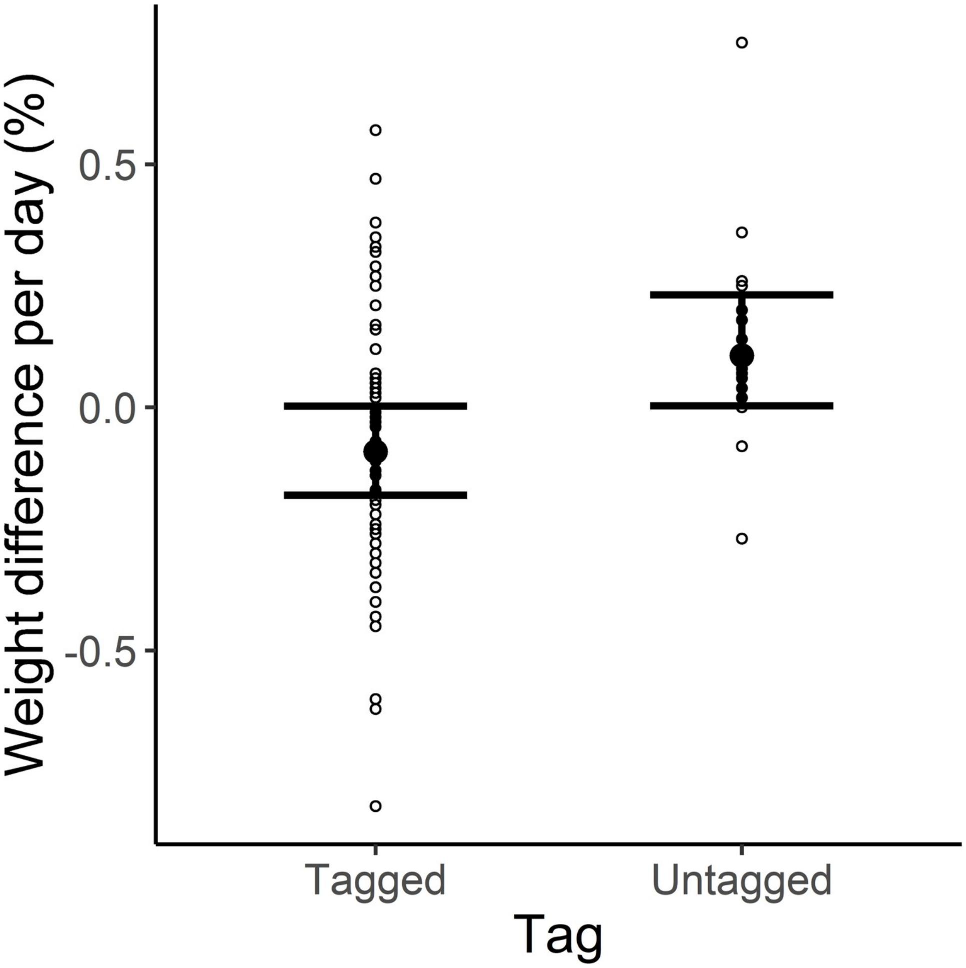

Fig 3. Estimated daily weight change (%) between captures for tagged and untagged Eurasian beavers (*Castor fiber*) in southeastern Norway (2006–2020). The prediction is based on a linear mixed effects model using percent daily body weight change as the response variable. The horizontal lines represent the 95% confidence intervals around each mean.

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Table 3. Effect size (β), adjusted standard error (SE), lower (LCI), and upper (UCI) 95% confidence interval of explanatory variables in the most parsimonious model analyzing percentage daily body weight change between two subsequent captures of Eurasian beavers (*Castor fiber*) in southeastern Norway (2006–2020). The intercept includes the 'young' age group of beavers. The informative parameters are shown in bold, and the marginal (R^2m) and conditional (R^2c) R squared is given for the model overall.

	β	SE	LCI	UCI	R^2m	R^2c
Intercept (Tagged)	−0.04	0.07	−0.18	0.09	0.16	0.40
TagUntagged	**0.20**	**0.06**	**0.07**	**0.32**		
AgeGroup (Adult)	−0.05	0.06	−0.16	0.07		
AgeGroup (Old)	0.00	0.09	−0.18	0.18		

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Total weight change (%) in tagged beavers between tag attachment and removal

The null model was the most supported model; none of the explanatory variables (relative weight of tag (%), average water temperature during the tagging period, sex, age group, season, and length of the tagging period) were retained in the model selection to explain total body weight change (%) (Table 4).

Discussion

We investigated the effects of glue-on tags on body weight change of Eurasian beavers. We found support for our first hypothesis that tagging reduced beaver body weight gain during the tagging period (and actually led to body weight loss) compared to untagged beavers that generally gained body weight. Our hypothesis that tagged beavers should gain less body weight during the colder months of the year or with colder water temperature was unsupported. Moreover, we found no evidence that relative tag weight or the number of tagging days affected beaver body weight. The tagged beavers did, however, display individual variation

Table 4. The model selection result, investigating percentage body weight change during tagging of Eurasian beavers (*Castor fiber*) in South-Eastern Norway (2009–2020). Each model represents a linear mixed effects model with beaver ID included as a random effect. Potential fixed effects included in each candidate model are tag weight as a percent of initial beaver body mass (tag weight %), age group of the beaver, number of days tagged, season of tagging, sex, and average water temperature during the tagging period. The plus signs indicate the categorical variables included, and values are given for numerical variables that were included in each candidate model. The intercept includes the 'young' age group of beavers. Candidate models were ranked based on AICc, and the range of ΔAICc <2 are shown in bold. Degrees of freedom (df), log likelihood (logLik) and AIC weight (w) is provided for each candidate model.

Intercept	Age group	Relative tag weight %	Tagging days	Season	Sex	Average water temperature	df	logLik	AICc	delta	w
−1.44							**4.00**	**−144.08**	**297.03**	**0.00**	**0.78**
−1.59	+						6.00	−143.96	301.83	4.80	0.07
−3.22	+		0.09				7.00	−143.37	303.35	6.32	0.03
−0.37	+					−0.14	7.00	−143.47	303.53	6.50	0.03
−0.14	+	−2.12					7.00	−143.75	304.10	7.07	0.02
−1.40	+				+		7.00	−143.89	304.39	7.36	0.02
−2.05	+		0.10			−0.14	8.00	−142.79	305.01	7.98	0.01
−1.54	+			+			8.00	−143.22	305.88	8.85	0.01
−1.90	+	−1.75	0.09				8.00	−143.23	305.88	8.85	0.01
−3.36	+		0.10	+			9.00	−142.66	307.70	10.67	0.00
−1.93	+		0.10		+	−0.14	9.00	−142.73	307.86	10.83	0.00
−1.79	+	−1.65	0.09		+		9.00	−143.15	308.70	11.66	0.00
−1.81	+	−2.10	0.09	+			10.00	−142.44	310.39	13.36	0.00
0.07	+	−2.46	0.09		+	−0.16	10.00	−142.46	310.42	13.39	0.00
−1.79	+	−2.00	0.09	+	+		11.00	−142.41	313.59	16.56	0.00

https://doi.org/10.1371/journal.pone.0261453.t004 with some tagged beavers gaining body weight, while most lost body weight during tagging. The average daily weight loss in tagged beavers of 13 g (0.1%) appears small, but importantly indicates that tagged beavers were (on average) unable to gain weight compared to untagged beavers that gained 23 g (0.1%) daily. This difference between the two groups, as well as some tagged beavers displaying considerable declines in body weight, indicates that tagging can have a negative impact on beavers.

Control groups

We included a control group of untagged beavers in our study, who mostly increased daily body weight between captures in line with previous studies [61]. Comparing tagged animals with a control group may help quantify the impact of tagging and avoid conclusions based on statistical artifacts that may arise without one [90]. While the weight loss of tagged beavers in our study was small on average, this was in direct contrast to untagged beavers who saw a small increase in body weight. Many bio-logging studies lack a control group due to the challenges with monitoring wild animals that are not tagged, which may influence the conclusions of these studies. Other semi-aquatic mammals such as the Eurasian otter (*Lutra lutra*) [91] and platypus (*Ornithorhynchus anatinus*) [92] tagged with glue-on tags displayed no apparent adverse effects. However, the authors did not compare the tagged animals with an untagged control group, which may impact the results.

Defining a true control group to include in wildlife studies can bring additional challenges. In the current study, there was a large difference in the number of days between the captures in the control group (mean = 64 days) and the tagged individuals (mean = 18 days). This could potentially lead to biases, requiring a careful interpretation of the results. In wild populations, it can be challenging to capture a sufficient number of individuals (both for logistic and economic reasons) to have a control group that is directly comparable to the tagged animals. Here, we accounted for confounding variables such as age group, sex, season, year and individual variation. Despite controlling for these, we failed to identify any variables related to the tagging process aside from the presence of a tag that drove the observed negative effects, suggesting further investigation is needed.

Relative tag weight and drag

The decline in body weight of tagged beavers was not exaggerated by the relative weight of the tag. If added weight was the main cause for the lower body weight gain, we would expect beavers that carried heavier tags, or carried the tag over a longer period to display the strongest decline in body weight. The tags made up between 0.5–1.3% of the initial body weight of the tagged beaver, which is well below both the 3% and 5% limits suggested by several studies [7]. A meta-analysis reviewing 214 studies of birds tagged using various tag types and attachment methods, found that negative effects of tagging were only apparent when tags weighed more than 1% of the bird's body weight [17]. As most of our tags were below this 1% threshold, we would not expect to observe a strong effect due to relative tag weight.

The shape of the tag and its location on the body of an animal may be more important than tag weight, as these factors directly impact tag-induced drag; something that is essential for animals moving in fluid media [12, 93]. For example, drag created by an external tag might increase energy expenditure, thereby increasing foraging time [94, 95]. A simulation study on grey seals (*Halichoerus grypus*) showed that shape of a tag is much more important than its size, e.g. a larger but more streamlined tag can reduce drag by 22% in swimming seals compared to a smaller but conventionally shaped tag [93]. We did not record the size or shape of the tag attached to beavers, and can therefore not directly analyze the drag impact. However, the relatively slow swimming speed of Eurasian beavers compared to other aquatic or semi-aquatic species may make them less susceptible to negative impacts from tag-induced drag. Indeed, drag is influenced by the speed and acceleration of the tagged animal, with slower moving animals not relying on high acceleration to capture prey being less impacted [9]. Great cormorants (*Phalacrocorax carbo*) were only negatively affected by drag from a tag at swimming speeds >1.4 m/s [4]. Beavers rarely swim faster than 0.8 m/s when swimming at the surface [96], and 0.6 m/s when diving [97]. The tags used on beavers here are usually above the surface of the water when beavers are swimming, and the beavers spend only 3% of their active time diving [57]. Thus, we speculate that the tag-induced drag impact of the glue-on tags used here may have been relatively small. However, we cannot make certain conclusions regarding drag in tagged beavers, and future studies should attempt to address this.

Tagging season and tag removal

The season of tagging did not impact body weight change of the beavers, and neither did water temperature in the river. A study of the impacts of tags on North American beavers in Minnesota, USA, that used different tagging methods (tail tags and implants) found no difference in body weight between tagged and untagged individuals during summer, but tagged animals lost more body weight in winter [55]. We did not tag beavers during the winter months, which might partly explain why we did not observe a seasonal effect. Beavers may be more susceptible to negative tagging effects during winter due to the colder winter temperatures and lower access to green plants during this time. In ice free areas beavers may even increase their active time and time spent foraging during winter, and tagging during this time may represent an additional stressor [96]. Semi-aquatic species are in an especially energetic precarious position due to changing temperature conditions in water and on land [37]. A major concern with attaching a tag to the fur of a semi-aquatic animal is how it impacts the thermal insulation properties of the fur [36]. Beaver fur consists of a protective overlayer of coarse guard hairs and an underlayer of fur-wool [98], functioning as a thermal barrier in both air and water [99]. Beavers groom regularly to maintain the waterproof properties of the fur [100, 101] and a glued patch will impair their ability to groom that patch, which might cause heat loss. Additionally epoxy used to attach the tag has a higher thermal conductivity than fur, and therefore may act as a source of increased energy expenditure [36]. Grey seals tagged with glue-on tags displayed no apparent heat loss when wet, but heat loss was clear when animals were dry [36]. We would recommend that future studies apply thermal imaging to measure differences in surface temperature of tagged beavers both when they are wet and dry.

Following tag removal, we observed cases in which the underfur was left intact, but also occasions where patches with no underfur were left on the beaver. Fur loss may be exaggerated by excessive amounts of glue and attachment too close to the skin. The damaged patch left after tagging beavers with glue on tags usually takes 3 to 4 months to be restored [58]. Thus, the open patch may be a source of heat loss until the fur is regrown, further reducing body weight because resources are invested into thermoregulation. Future studies should explore whether the negative effects on body weight continues after tag removal. Skin irritation or major wounds following tagging has not previously been documented with glue-on tags on beavers, with the exception of one beaver included in our study with a small wound underneath the logger. Tagging of nutria (*Myocastor coypus*) using glue-on tags on the tail caused sloughing of the skin [102], which we did not observe in our beavers. There is always a trade-off between minimizing the amount of glue in order to reduce damage to the beaver fur, and so minimize the compromise to thermal insulation and using sufficient amounts to ensure that the tag remains attached to the beaver for the required duration.

Tagging length, handling and individual variation

The length of the tagging periods varied between 8 to 43 days. While we attempted to recapture beavers after 2–3 weeks for tag removal, some were retrieved earlier due to different battery capacities of the loggers. Some beavers also evaded capture and carried the tag for longer time periods. Despite the considerable variation, we did not find that tagging length affected body weight change. A comprehensive long-term study in the same population of Eurasian beavers found that beaver body mass and litter size (in old individuals only) decreased with increasing number of captures [59]. However, this effect was less clear during the later years of the project, indicating possible habituation towards capture and handling [59]. A previous tagging study from the same area also found that tagged beavers tend to spend more time in the lodge during the night they were tagged compared to later in the tagging period [58]. Upon capture, tagged beavers are typically handled for longer time periods than non-tagged beavers, due to the extra time required to attach and remove the tag. However, as we cannot monitor the spatial movements of untagged beavers, we cannot conclude on whether this behavior is driven by the capture itself or related to carrying the tag. Future tagging studies should attempt to reduce handling time during tagging as much as possible to mitigate any potential negative impacts.

We found considerable individual variation among the tagged beavers, and while the majority lost body weight during tagging, some tagged beavers also gained body weight. In comparison only two of the untagged beavers lost body weight between captures. This indicates that it is unusual for beavers to lose body weight between spring and autumn (March and November). Thus, body weight loss in 57% of the tagged beavers is a cause for concern. Habituation to both capture and tagging could go some way to explain why some tagged beavers gained body weight, and this would be interesting to explore in future studies with additional data on body weight gain of the same individuals during several tagging periods.

Conclusion

Our study emphasizes the importance of using a control group to investigate tagging effects on wildlife. We found a negative effect on beaver body weight change during the tagging period, but with considerable individual variation amongst tagged individuals. These findings might have implications regarding animal welfare and the validity of data collected [103, 104]. The large variation among tagged beavers illustrates how effects of tagging should not only be studied by comparing averages among tagged and untagged individuals, but also by analyzing individual impacts. The negative effect of tagging did not vary as a function of the confounding variables (sex, age, relative tag weight, tagging duration, season, water temperature) we examined. This means we found no support for our hypothesis that relative tag weight would negatively impact tagged beavers, but the drivers of the observed body weight loss should be investigated further. The observed changes in body weight might be caused by stress associated with capture [105, 106] as tagging usually requires longer handling time, and such impacts on body condition do not necessarily mean that the beavers change their activity patterns or spatial movements [58], or prolonged effects after tag removal, but this should be investigated further. Especially the duration of weight loss in tagged beavers remains uncertain, and this should be explored in relation to environmental conditions and food availability that may exaggerate negative effects during tagging. Glue-on tags are used as a relatively short-term tagging method on beavers, and the cumulative body weight loss observed was not extensive in comparison to their total body weight. Nevertheless, any decrease in body weight gain during tagging may be important in terms of individual animal welfare especially considering that untagged animals by comparison tended to increase their body weight. Assessing potential negative impacts of tagging on both a population and individual level should therefore be a priority for all research projects applying tags on wild animals.

Supporting information

S1 File. This file contains all the supporting tables and figures.
(DOCX)

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References

1. Börger L, Bijleveld AI, Fayet AL, Machovsky-Capuska GE, Patrick SC, Street GM, et al. Biologging special feature. J Anim Ecol. 2020; 89:6–15. https://doi.org/10.1111/1365-2656.13163 PMID: 32091640
2. Kays R, Crofoot MC, Jetz W, Wikelski M. Terrestrial animal tracking as an eye on life and planet. Science. 2015; 348(6240):aaa2478. https://doi.org/10.1126/science.aaa2478 PMID: 26068858
3. McIntyre T, editor Animal telemetry: tagging effects 2015: American Association for the Advancement of Science.
4. Vandenabeele S, Shepard E, Grémillet D, Butler P, Martin G, Wilson R. Are bio-telemetric devices a drag? Effects of external tags on the diving behaviour of great cormorants. Mar Ecol Prog Ser. 2015; 519:239–49. https://doi.org/10.3354/meps11058

5. Brooks C, Bonyongo C, Harris S. Effects of global positioning system collar weight on zebra behavior and location error. J Wildl Manage. 2008; 72(2):527–34. https://doi.org/10.2193/2007-061
6. Casper RM. Guidelines for the instrumentation of wild birds and mammals. Anim Behav. 2009; 78 (6):1477–83. https://doi.org/10.1016/j.anbehav.2009.09.023
7. Portugal SJ, White CR. Miniaturization of biologgers is not alleviating the 5% rule. Methods Ecol Evol. 2018; 9(7):1662–6. https://doi.org/10.1111/2041-210X.13013
8. Sikes RS, Gannon WL. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of mammalogy. 2011; 92(1):235–53. https://doi.org/10.1644/10-MAMM-F-355.1
9. Wilson RP, Rose KA, Gunner R, Holton MD, Marks NJ, Bennett NC, et al. Animal lifestyle changes acceptable mass limits for attached tags. bioRxiv. 2021:2021.04.27.441641. https://doi.org/10.1098/rspb.2021.2005 PMID: 34702077
10. Baylis AMM, Page B, Staniland I, Arnould JPY, McKenzie J. Taking the sting out of darting: risks, restraint drugs and procedures for the chemical restraint of Southern Hemisphere otariids. Mar Mamm Sci. 2015; 31(1):322–44. https://doi.org/10.1111/mms.12148
11. Vandenabeele SP. Avian rucksacks for science: in search for minimum-impact tagging procedures for birds: Swansea University (United Kingdom); 2013.
12. Rosen DAS, Gerlinsky CG, Trites AW. Telemetry tags increase the costs of swimming in northern fur seals, *Callorhinus ursinus*. Mar Mamm Sci. 2018; 34(2):385–402. https://doi.org/10.1111/mms.12460
13. Tudorache C, Burgerhout E, Brittijn S, van den Thillart G. The effect of drag and attachment site of external tags on swimming eels: experimental quantification and evaluation tool. PLoS One. 2014; 9 (11):e112280. https://doi.org/10.1371/journal.pone.0112280 PMID: 25409179
14. Bouyoucos IA, Suski CD, Mandelman JW, Brooks EJ. Effect of weight and frontal area of external telemetry packages on the kinematics, activity levels and swimming performance of small-bodied sharks. J Fish Biol. 2017; 90(5):2097–110. https://doi.org/10.1111/jfb.13290 PMID: 28239865
15. van der Hoop JM, Fahlman A, Hurst T, Rocho-Levine J, Shorter KA, Petrov V, et al. Bottlenose dolphins modify behavior to reduce metabolic effect of tag attachment. J Exp Biol. 2014; 217(23):4229–36. https://doi.org/10.1242/jeb.108225 PMID: 25324344
16. Lear KO, Gleiss AC, Whitney NM. Metabolic rates and the energetic cost of external tag attachment in juvenile blacktip sharks *Carcharhinus limbatus*. J Fish Biol. 2018; 93(2):391–5. https://doi.org/10.1111/jfb.13663 PMID: 30241112
17. Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, et al. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. Methods Ecol Evol. 2018; 9(4):946–55. https://doi.org/10.1111/2041-210X.12934
18. Barron DG, Brawn JD, Weatherhead PJ. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods Ecol Evol. 2010; 1(2):180–7. https://doi.org/10.1111/j.2041-210X.2010.00013.x
19. Murray DL, Fuller MR. A critical review of the effects of marking on the biology of vertebrates. In: Boitani L, K. FT, editors. Research techniques in animal ecology: controversies and consequences. New York: Columbia University Press; 2000. p. 15–64.
20. Saraux C, Le Bohec C, Durant JM, Viblanc VA, Gauthier-Clerc M, Beaune D, et al. Reliability of flipper-banded penguins as indicators of climate change. Nature. 2011; 469(7329):203–6. https://doi.org/10.1038/nature09630 PMID: 21228875
21. White GC, Garrott RA. Analysis of wildlife radio-tracking data: Elsevier; 2012.
22. Williams HJ, Taylor LA, Benhamou S, Bijleveld AI, Clay TA, de Grissac S, et al. Optimizing the use of biologgers for movement ecology research. J Anim Ecol. 2020; 89(1):186–206. https://doi.org/10.1111/1365-2656.13094 PMID: 31424571
23. Jung TS, Konkolics SM, Kukka PM, Majchrzak YN, Menzies AK, Oakley MP, et al. Short-term effect of helicopter-based capture on movements of a social ungulate. J Wildl Manage. 2019; 83(4):830–7. https://doi.org/10.1002/jwmg.21640
24. Baker JD, Johanos TC. Effects of research handling on the endangered Hawaiian monk seal. Mar Mamm Sci. 2002; 18(2):500–12. https://doi.org/10.1111/j.1748-7692.2002.tb01051.x
25. Bank MS, Franklin WL, Sarno RJ. Assessing the effect of radiocollars on juvenile guanaco survival. Oecologia. 2000; 124(2):232–4. https://doi.org/10.1007/s004420050011 PMID: 28308183
26. Hetem RS, Strauss WM, Fick LG, Maloney SK, Meyer LC, Shobrak M, et al. Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis? Zoology. 2012; 115(6):411–6. https://doi.org/10.1016/j.zool.2012.04.005 PMID: 23036437

27. Stewart J, Hazen E, Foley D, Bograd S, Gilly W. Marine predator migration during range expansion: Humboldt squid *Dosidicus gigas* in the northern California Current System. Mar Ecol Prog Ser. 2012; 471:135–50. https://doi.org/10.3354/meps10022

28. McFarland R, Hetem RS, Fuller A, Mitchell D, Henzi SP, Barrett L. Assessing the reliability of biologger techniques to measure activity in a free-ranging primate. Anim Behav. 2013; 4(85):861–6. https://doi.org/10.1016/j.anbehav.2013.02.005

29. Watts C, Empson R, Thornburrow D, Rohan M. Movements, behaviour and survival of adult Cook Strait giant weta (*Deinacrida rugosa; Anostostomatidae: Orthoptera*) immediately after translocation as revealed by radiotracking. J Insect Conserv. 2012; 16(5):763–76. https://doi.org/10.1007/s10841-012-9461-8

30. Brien M, Webb G, Manolis C, Lindner G, Ottway D. A method for attaching tracking devices to crocodilians. Herpetol Rev. 2010; 41(3):305.

31. Fedak MA, Anderson SS, Curry MG. Attachment of a radio tag to the fur of seals. J Zool. 1983; 200 (2):298–300. https://doi.org/10.1111/j.1469-7998.1983.tb05794.x

32. Littnan CL, Baker JD, Parrish FA, Marshall GJ. Effects of video camera attachment on the foraging behavior of immature Hawaiian monk seals. Mar Mamm Sci. 2004; 20(2):345–52.

33. Boyd IL, Lunn NJ, Barton T. Time budgets and foraging characteristics of lactating antarctic fur seals. J Anim Ecol. 1991; 60(2):577–92. https://doi.org/10.2307/5299

34. Bowen W, Tully D, Boness DJ, Bulheier B, Marshall G. Prey-dependent foraging tactics and prey profitability in a marine mammal. Mar Ecol Prog Ser. 2002; 244:235–45. https://doi.org/10.3354/meps244235

35. Field IC, Harcourt RG, Boehme L, De Bruyn PN, Charrassin J-B, McMahon CR, et al. Refining instrument attachment on phocid seals. Mar Mamm Sci. 2011. https://doi.org/10.1111/j.1748-7692.2011.00519.x

36. McCafferty DJ, Currie J, Sparling CE. The effect of instrument attachment on the surface temperature of juvenile grey seals (*Halichoerus grypus*) as measured by infrared thermography. Deep Sea Res. 2007; 54(3):424–36. https://doi.org/10.1016/j.dsr2.2006.11.019

37. Fish FE. Biomechanics and energetics in aquatic and semiaquatic mammals: platypus to whale. Physiol Biochem Zool. 2000; 73(6):683–98. https://doi.org/10.1086/318108 PMID: 11121343.

38. Hartung R. Energy metabolism in oil-covered ducks. J Wildl Manage. 1967:798–804. https://doi.org/10.2307/3797987

39. Jenssen BM. Review article: Effects of oil pollution, chemically treated oil, and cleaning on thermal balance of birds. Environ Pollut. 1994; 86(2):207–15. https://doi.org/10.1016/0269-7491(94)90192-9 PMID: 15091638

40. Barnes WJ, Dibble E. The effects of beaver in riverbank forest succession. Can J Bot. 1988; 66(1):40–4. https://doi.org/10.1139/b88-005

41. Wheatley M. Beaver, *Castor canadensis*, home range size and patterns of use in the taiga of southeastern Manitoba: I. Seasonal variation. Can Field-Nat. 1997; 111(2):204–10.

42. Steyaert SMJG, Zedrosser A, Rosell F. Socio-ecological features other than sex affect habitat selection in the socially obligate monogamous Eurasian beaver. Oecologia. 2015; 179(4):1023–32. https://doi.org/10.1007/s00442-015-3388-1 PMID: 26260166

43. Francis RA, Taylor JD, Dibble E, Strickland B, Petro VM, Easterwood C, et al. Restricted cross-scale habitat selection by American beavers. Curr Zool. 2017; 63(6):703–10. https://doi.org/10.1093/cz/zox059 PMID: 29492032

44. Mayer M, Frank SC, Zedrosser A, Rosell F. Causes and consequences of inverse density-dependent territorial behaviour and aggression in a monogamous mammal. J Anim Ecol. 2020; 89(2):577–88. https://doi.org/10.1111/1365-2656.13100 PMID: 31469174

45. Rosell F, Bozsér O, Collen P, Parker H. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mamm Rev. 2005; 35(3–4):248–76. https://doi.org/10.1111/j.1365-2907.2005.00067.x

46. Wright JP, Jones CG, Flecker AS. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia. 2002; 132(1):96–101. https://doi.org/10.1007/s00442-002-0929-1 PMID: 28547281

47. Davis JR, Von Recum AF, Smith DD, Guynn DC. Implantable telemetry in beaver. Wildl Soc Bull. 1984; 12(3):322–4.

48. Guynn DC Jr, Davis JR, Von Recum AF. Pathological potential of intraperitoneal transmitter implants in beavers. J Wildl Manage. 1987; 51(3):605–6. https://doi.org/10.2307/3801277

49. McKinstry MC, Anderson SH. Survival, fates, and success of transplanted beavers, *Castor canadensis*, in Wyoming. Can Field-Nat. 2002; 116(1):60–8.

50. Ranheim B, Rosell F, Haga HA, Arnemo JM. Field anaesthetic and surgical techniques for implantation of intraperitoneal radio transmitters in Eurasian beavers Castor fiber. Wildlife Biol. 2004; 10(1):11–5. https://doi.org/10.2981/wlb.2004.004

51. Rothmeyer SW, McKinstry MC, Anderson SH. Tail attachment of modified ear-tag radio transmitters on beavers. Wildl Soc Bull. 2002; 30(2):425–9.

52. Baker BW, Hill E. Beaver (*Castor canadensis*). Beaver (*Castor canadensis*). 2nd ed. Baltimore, MD: Johns Hopkins University Press; 2003.

53. Arjo WM, Joos RE, Kochanny CO, Harper JL, Nolte DL, Bergman DL. Assessment of transmitter models to monitor beaver *Castor canadensis* and *C. fiber* populations. Wildlife Biol. 2008; 14(3):309–17. https://doi.org/10.2981/0909-6396(2008)14[309:AOTMTM]2.0.CO;2

54. Bloomquist CK, Nielsen CK, Shew JJ. Spatial organization of unexploited beavers (*Castor canadensis*) in southern Illinois. Am Midl Nat. 2012; 167(1):188–97. https://doi.org/10.1674/0003-0031-167.1.188

55. Smith JB, Windels SK, Wolf T, Klaver RW, Belant JL. Do transmitters affect survival and body condition of American beavers *Castor canadensis*? Wildlife Biol. 2016; 22(3):117–23. https://doi.org/10.2981/wlb.00160

56. Wheatley M. A new surgical technique for implanting radio transmitters in beavers, *Castor canadensis*. Can Field-Nat. 1997; 111(4):601–6.

57. Graf PM, Wilson RP, Sanchez LC, Hackländer K, Rosell F. Diving behavior in a free-living, semi-aquatic herbivore, the Eurasian beaver *Castor fiber*. Ecol Evol. 2018; 8(2):997–1008. https://doi.org/10.1002/ece3.3726 PMID: 29375773

58. Graf PM, Hochreiter J, Hackländer K, Wilson RP, Rosell F. Short-term effects of tagging on activity and movement patterns of Eurasian beavers (*Castor fiber*). Eur J Wildl Res. 2016; 62(6):725–36. https://doi.org/10.1007/s10344-016-1051-8

59. Mortensen RM, Rosell F. Long-term capture and handling effects on body condition, reproduction and survival in a semi-aquatic mammal. Sci Rep. 2020; 10(1):17886. https://doi.org/10.1038/s41598-020-74933-w PMID: 33087816

60. Smith DW, Jenkins SH. Seasonal change in body mass and size of tail of northern beavers. J Mammal. 1997; 78(3):869–76. https://doi.org/10.2307/1382945

61. Campbell RD. Demography and life history of the Eurasian beaver *Castor fiber*. Oxford, UK: Oxford University; 2010.

62. Pinto B, Santos MJ, Rosell F. Habitat selection of the Eurasian beaver (*Castor fiber*) near its carrying capacity: an example from Norway. Can J Zool. 2009; 87(4):317–25. https://doi.org/10.1139/Z09-015

63. Olstad O. Beverens (*Castor fiber*) utbredelse i Norge. Statens viltundersøkelser Nytt Mag Naturvidensk. 1937; 77:217–73.

64. Parker H, Rosell F, Hermansen T, Sørløkk G, Stærk M. Sex and age composition of spring-hunted Eurasian beaver in Norway. J Wildl Manag. 2002; 66(4):1164–70. https://doi.org/10.2307/3802949

65. Campbell RD, Newman C, Macdonald DW, Rosell F. Proximate weather patterns and spring green-up phenology effect Eurasian beaver (*Castor fiber*) body mass and reproductive success: the implications of climate change and topography. Glob Chang Biol. 2013; 19(4):1311–24. https://doi.org/10.1111/gcb.12114 PMID: 23504905

66. Campbell RD, Rosell F, Nolet BA, Dijkstra VAA. Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? Behav Ecol Sociobiol. 2005; 58(6):597–607. https://doi.org/10.1007/s00265-005-0942-6

67. Mayer M, Künzel F, Zedrosser A, Rosell F. The 7-year itch: non-adaptive mate change in the Eurasian beaver. Behav Ecol Sociobiol. 2017; 71(2):32. https://doi.org/10.1007/s00265-016-2259-z

68. Rosell F, Hovde B. Methods of aquatic and terrestrial netting to capture Eurasian beavers. Wildl Soc Bull. 2001; 29:269–74.

69. Sharpe F, Rosell F. Time budgets and sex differences in the Eurasian beaver. Anim Behav. 2003; 66(6):1059–67. https://doi.org/10.1006/anbe.2003.2274

70. Rosell F, Sun LX. Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *Castor fiber*. Wildlife Biol. 1999; 5(2):119–23. https://doi.org/10.2981/wlb.1999.015 WOS:000080973800006.

71. Mayer M, Zedrosser A, Rosell F. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. Animal Behaviour. 2017; 123:375–82. https://doi.org/10.1016/j.anbehav.2016.11.020

72. Rosell F, Zedrosser A, Parker H. Correlates of body measurements and age in Eurasian beaver from Norway. Eur J Wildl Res. 2010; 56(1):43–8. https://doi.org/10.1007/s10344-009-0289-9

73. Brown MK. Two old beavers from Adirondacks. N Y game fish. 1979; 26:92.

74. Gorbunova V, Bozzella MJ, Seluanov A. Rodents for comparative aging studies: from mice to beavers. Age. 2008; 30(2–3):111–9. https://doi.org/10.1007/s11357-008-9053-4 PMID: 19424861

75. Larson JS. Age structure and sexual maturity within a western Maryland beaver (*Castor canadensis*) population. J Mammal. 1967; 48(3):408–13. https://doi.org/10.2307/1377773

76. Nimje P, Tinnesand HV, Buesching CD, Sæbø M, Senn H, Zedrosser A, et al. Almost faithful: SNP markers reveal low levels of extra-pair paternity in the Eurasian beaver. Under review Ecology and Evolution. 2019. https://doi.org/10.7287/peerj.preprints.27866v1

77. Leach E, Peters R, Rossiter R. Experimental thermal burns, especially the moderate temperature burn. Q J Exp Physiol. 1943; 32(1):67–86. https://doi.org/10.1113/expphysiol.1943.sp000875

78. ASAB/ABS. Guidelines for the treatment of animals in behavioural research and teaching. Anim Behav. 2020; 159:I–XI. https://doi.org/10.1016/j.anbehav.2019.11.002

79. Percie du Sert N, Ahluwalia A, Alam S, Avey MT, Baker M, Browne WJ, et al. Reporting animal research: Explanation and elaboration for the ARRIVE guidelines 2.0. PLOS Biol. 2020; 18(7): e3000411. https://doi.org/10.1371/journal.pbio.3000411 PMID: 32663221

80. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using *lme4*. J Stat Soft. 2015; 67(1):48. Epub 2015-10-07. https://doi.org/10.18637/jss.v067.i01

81. Zuur AF, Ieno EN, Elphick CS. A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol. 2010; 1(1):3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

82. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology. New York: Springer Science and Business Media; 2009.

83. Burnham KP, Anderson DR, Huyvaert KP. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol. 2011; 65(1):23–35.

84. Anderson D, Burnham K. Model selection and multi-model inference. Second ed. New York: Springer-Verlag; 2004. 10 p.

85. Barton K. MuMIn: Multi-model Inference. R package version 1.43.17. 1.43.17 ed2020.

86. Arnold TW. Uninformative parameters and model selection using Akaike's information criterion. J Wildl Manage. 2010; 74(6):1175–8. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

87. Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CED, et al. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ. 2018; 6:e4794. https://doi.org/10.7717/peerj.4794 PMID: 29844961

88. Zuur AF, Ieno EN. A protocol for conducting and presenting results of regression-type analyses. Methods Ecol Evol. 2016; 7(6):636–45. https://doi.org/10.1111/2041-210X.12577

89. Hartig F. DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. 0.3.3.0 ed2020.

90. Authier M, Péron C, Mante A, Vidal P, Grémillet D. Designing observational biologging studies to assess the causal effect of instrumentation. Methods Ecol Evol. 2013; 4(9):802–10. https://doi.org/10.1111/2041-210X.12075

91. Néill LÓ, Wilson P, de Jongh A, de Jong T, Rochford J. Field techniques for handling, anaesthetising and fitting radio-transmitters to Eurasian otters (*Lutra lutra*). Eur J Wildl Res. 2008; 54(4):681. https://doi.org/10.1007/s10344-008-0196-5

92. Bethge P, Munks S, Otley H, Nicol S. Activity patterns and sharing of time and space of platypuses, *Ornithorhynchus anatinus*, in a subalpine tasmanian Lake. J Mammal. 2009; 90(6):1350–6. https://doi.org/10.1644/08-mamm-a-355r.1

93. Kay WP, Naumann DS, Bowen HJ, Withers SJ, Evans BJ, Wilson RP, et al. Minimizing the impact of biologging devices: Using computational fluid dynamics for optimizing tag design and positioning. Methods Ecol Evol. 2019; 10(8):1222–33. https://doi.org/10.1111/2041-210X.13216

94. Wilson RP, Grant WS, Duffy DC. Recording devices on free-ranging marine animals: does measurement affect foraging performance? Ecology. 1986; 67(4):1091–3. https://doi.org/10.2307/1939832

95. Culik B, Wilson RP. Swimming energetics and performance of instrumented adélie penguins (*Pygoscelis adeliae*). J Exp Biol. 1991; 158(1):355–68. https://doi.org/10.1242/jeb.158.1.355

96. Nolet BA, Rosell F. Territoriality and time budgets in beavers during sequential settlement. Can J Zool. 1994; 72(7):1227–37. https://doi.org/10.1139/z94-164

97. Allers D, Culik Boris M. Energy requirements of beavers (*Castor canadensis*) swimming underwater. Physiol Zool. 1997; 70(4):456–63. https://doi.org/10.1086/515852 PMID: 9237306.

98. Novak M. Wild furbearer management and conservation in North America: Ontario Ministry of Natural Resources; 1987.

99. Irving L. Aquatic mammals. Comparative physiology of thermoregulation: Elsevier; 1973. p. 47–96.

100. Wilsson L. Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). Viltrevy. 1971; 8(3):160–203.

101. Walro JM, Svendsen GE. Castor sacs and anal glands of the North American beaver (*Castor canadensis*): their histology, development, and relationship to scent communication. J Chem Ecol. 1982; 8 (5):809–19. https://doi.org/10.1007/BF00994781 PMID: 24415179

102. Merino S, Carter J, Thibodeaux G. Testing tail-mounted transmitters with *Myocastor coypus* (nutria). Southeast Nat. 2007; 6(1):159–64. https://doi.org/10.1656/1528-7092(2007)6[159:TTTWMC]2.0.CO;2

103. Cleasby IR, Morrissey BJ, Bolton M, Owen E, Wilson L, Wischnewski S, et al. What is our power to detect device effects in animal tracking studies? Methods Ecol Evol. 2021; 12(7):1174–85. https://doi.org/10.1111/2041-210X.13598

104. Soulsbury CD, Gray HE, Smith LM, Braithwaite V, Cotter SC, Elwood RW, et al. The welfare and ethics of research involving wild animals: A primer. Methods Ecol Evol. 2020; 11(10):1164–81. https://doi.org/10.1111/2041-210X.13435

105. Kock MD, Clark RK, Franti CE, Jessup DA, Wehausen JD. Effects of capture on biological parameters in free-ranging bighorn sheep (*Ovis canadensis*): evaluation of normal, stressed and mortality outcomes and documentation of postcapture survival. J Wildl Dis. 1987; 23(4):652–62. https://doi.org/10.7589/0090-3558-23.4.652 PMID: 3682092.

106. Meyer LCR, Fick L, Matthee A, Mitchell D, Fuller A. Hypothermia in captured impala (*Aepyceros melampus*): a fright not flight response. J Wildl Dis. 2008; 44(2):404–16. https://doi.org/10.7589/0090-3558-44.2.404 PMID: 18436672.

Supporting information

Table S1: Overview of tagging periods and control periods of Eurasian beavers (*Castor fiber*) in southeastern Norway (2009-2020). Name of the beaver, age, days between subsequent captures, initial weight at first capture, season and whether it was tagged or not is provided for every period. Also included is how many tagging periods and control periods included for each beaver.

Name	**Age**	**Tagged**	**Number of tagging periods**	**Number of control periods**	**Days between captures**	**Initial weight (kg)**	**Season**
Anders	5	No	1	1	108	19.80	Summer
Anders	4	Yes	1	1	14	20.23	Spring
Andreas Bjorn	3	No	0	1	93	18.60	Summer
Angus	2	No	0	1	68	16.00	Summer
Anna	7	Yes	1	0	15	23.12	Spring
Apple	3	No	2	1	28	21.50	Autumn
Apple	3	Yes	2	1	19	21.38	Autumn
Apple	5	Yes	2	1	20	20.83	Spring
Aragorn	3	No	1	1	132	18.80	Summer
Aragorn	2	Yes	1	1	31	22.38	Autumn
Asle	4	No	0	1	116	18.00	Spring
Athena	6	Yes	1	0	12	21.93	Spring
Belinda	3	No	1	1	6	20.02	Autumn
Belinda	3	Yes	1	1	12	20.92	Autumn
Bram	14	Yes	1	0	19	19.38	Summer
Caesar	3	No	1	2	139	23.50	Summer
Caesar	5	No	1	2	108	20.70	Summer
Caesar	7	Yes	1	2	14	17.52	Spring
Carl	5	No	0	1	125	17.00	Summer
Chris	5	No	0	2	83	20.00	Summer
Chris	5	No	0	2	84	19.00	Spring
Darwin	5	No	2	2	126	20.00	Summer
Darwin	10	No	2	2	65	18.90	Summer
Darwin	5	Yes	2	2	15	19.38	Spring
Darwin	10	Yes	2	2	22	20.32	Summer

Eirik	3	No	0	1	13	19.50	Spring
Franky	6	No	0	1	58	23.00	Summer
Frode	5	No	0	2	103	21.50	Spring
Frode	5	No	0	2	31	22.50	Summer
Froydis	4	No	0	1	111	19.50	Spring
Gronn	5	No	0	1	110	20.50	Summer
Gunn Rita	4	No	0	1	16	22.00	Summer
Hanna Christi	3	No	0	2	23	20.50	Autumn
Hanna Christi	3	No	0	2	133	17.60	Summer
Hanne	3	No	0	1	62	22.00	Summer
Hanne Synnove	4	No	0	1	71	22.00	Summer
Harald	5	No	0	1	69	21.50	Summer
Havar	3	No	0	1	46	19.00	Spring
Hazel	5	Yes	4	0	43	24.27	Autumn
Hazel	9	Yes	4	0	9	20.83	Spring
Hazel	10	Yes	4	0	39	22.33	Autumn
Hazel	11	Yes	4	0	21	21.83	Spring
Helgenen	4	No	0	1	86	20.00	Summer
Horst	6	Yes	1	0	18	22.83	Autumn
Ikea	13	Yes	1	0	17	22.73	Autumn
Ivo	4	Yes	3	0	14	20.88	Spring
Ivo	6	Yes	3	0	14	18.98	Spring
Ivo	9	Yes	3	0	18	20.42	Summer
Jan Marc	5	Yes	3	0	20	22.37	Spring
Jan Marc	6	Yes	3	0	20	22.83	Autumn
Jan Marc	6	Yes	3	0	15	21.93	Summer
Jobu	4	No	0	1	103	18.00	Summer
Jodie	14	Yes	2	0	13	24.83	Spring
Jodie	17	Yes	2	0	22	19.83	Spring
Jon	5	No	0	2	154	20.50	Summer
Jon	3	No	0	2	145	21.00	Summer
Jorn	5	No	0	2	132	20.00	Summer
Jorn	8	No	0	2	59	19.00	Spring
Kathrin	7	Yes	1	0	12	25.34	Autumn
Kjartan	8	Yes	1	0	29	23.38	Autumn
Kolbjorn	3	No	0	1	15	18.50	Summer
Kyle	4	Yes	2	0	15	22.88	Autumn
Kyle	6	Yes	2	0	14	22.43	Summer
Lars	5	Yes	1	0	12	23.72	Autumn
Lasse	3	No	1	1	27	19.00	Spring

Lasse	7	Yes	1	1	25	22.88	Spring
Laura	2	Yes	1	0	14	20.88	Spring
Laurits	13	Yes	1	0	22	18.82	Spring
Leaf	6	No	1	1	6	24.70	Autumn
Leaf	3	Yes	1	1	15	20.88	Autumn
Leigh	12	Yes	1	0	18	22.63	Spring
Leslie	2	No	0	1	9	18.00	Summer
Live	5	Yes	1	0	8	23.35	Autumn
Loran	7	No	0	2	107	24.50	Summer
Loran	9	No	0	2	124	24.00	Summer
Malena	7	No	1	1	48	24.00	Spring
Malena	7	Yes	1	1	14	24.88	Spring
Marta	7	No	0	1	26	25.50	Spring
Mason	3	Yes	2	0	12	14.58	Spring
Mason	6	Yes	2	0	27	17.67	Spring
Mattanja	3	Yes	1	0	12	17.82	Spring
Maximus	2	Yes	1	0	13	16.92	Spring
Mikkel	7	Yes	1	0	17	25.22	Summer
Moritz	3	No	1	2	15	23.40	Summer
Moritz	3	No	1	2	133	21.40	Summer
Moritz	5	Yes	1	2	17	24.88	Summer
Morten	6	Yes	1	0	20	18.83	Spring
Moses	7	Yes	1	0	14	23.83	Summer
Nanna	5	Yes	1	0	20	22.88	Spring
Odd Arne	5	Yes	1	0	14	24.52	Summer
Oddi	5	No	0	1	44	18.00	Spring
Orjan	3	No	0	3	154	23.00	Summer
Orjan	5	No	0	3	86	24.00	Summer
Orjan	8	No	0	3	68	24.00	Spring
Paddy	12	No	3	1	57	25.30	Summer
Paddy	5	Yes	3	1	10	24.83	Spring
Paddy	6	Yes	3	1	13	25.83	Autumn
Paddy	7	Yes	3	1	23	25.33	Spring
Randi	5	No	0	1	29	20.50	Summer
Rudolf	6	Yes	1	0	14	20.88	Spring
Sara	4	No	0	1	36	22.50	Spring
Solveig	3	Yes	1	0	29	21.18	Autumn
Sonja	5	No	0	1	127	23.50	Summer
Stina	4	No	0	2	81	19.50	Spring
Stina	10	No	0	2	38	21.00	Spring
Suzanne	4	No	0	1	88	17.60	Summer
Takehode	4	No	0	2	91	20.00	Spring
Takehode	4	No	0	2	70	23.50	Summer

Tanja	13	No	2	1	117	19.50	Summer
Tanja	11	Yes	2	1	19	21.88	Summer
Tanja	15	Yes	2	1	22	18.42	Summer
Terje	7	No	0	1	119	20.00	Summer
Thatcher	8	No	0	1	93	23.00	Summer
Thomas	3	No	0	1	5	22.00	Spring
Trude	4	No	0	1	133	22.00	Summer
Unni	2	No	0	2	39	20.00	Summer
Unni	5	No	0	2	42	24.00	Spring
Victoria	4	Yes	1	0	15	22.08	Spring
Waltraut	6	Yes	2	1	13	24.58	Autumn
Waltraut	7	Yes	2	1	16	23.02	Summer
Waltraut	3	No	2	1	70	19.00	Autumn
Yasmin	4	Yes	1	0	14	22.68	Spring

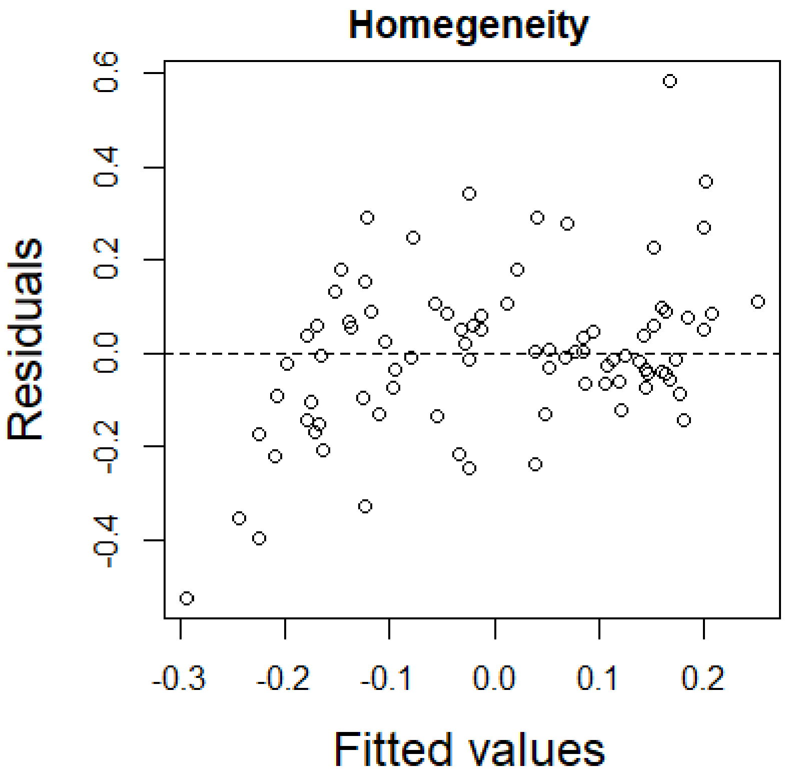

Fig. S1: Residuals versus fitted values from the most parsimonious model analyzing percentage daily body weight change between two subsequent captures of Eurasian beavers (*Castor fiber*) in southeastern Norway (2006-2020).

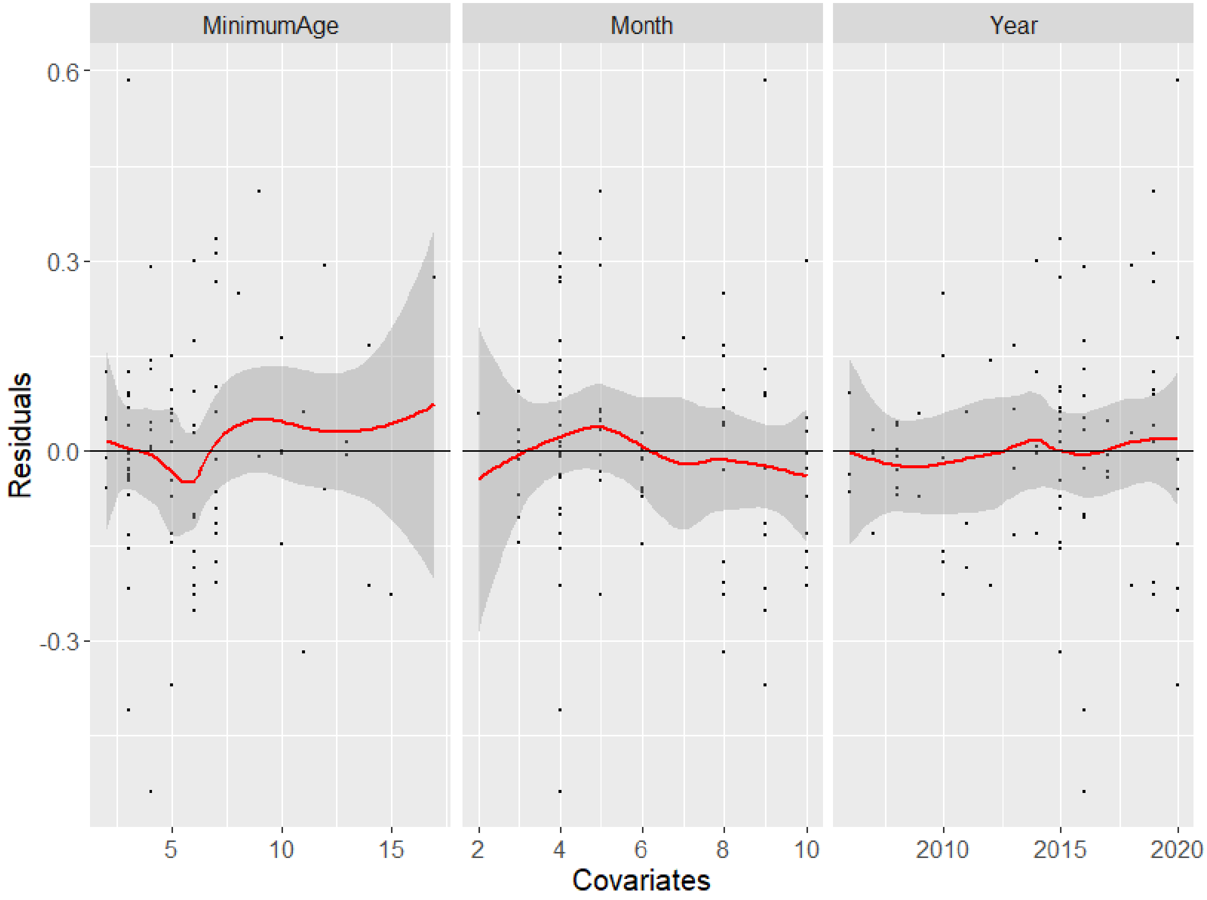

Fig. S2: Model residuals plotted against each numerical variable included and not included in the most parsimonious model analyzing percentage daily body weight change between two subsequent captures of Eurasian beavers (*Castor fiber*) in southeastern Norway (2006-2020). A smoother have been fitted to visualize any non-linear patterns in the residuals.

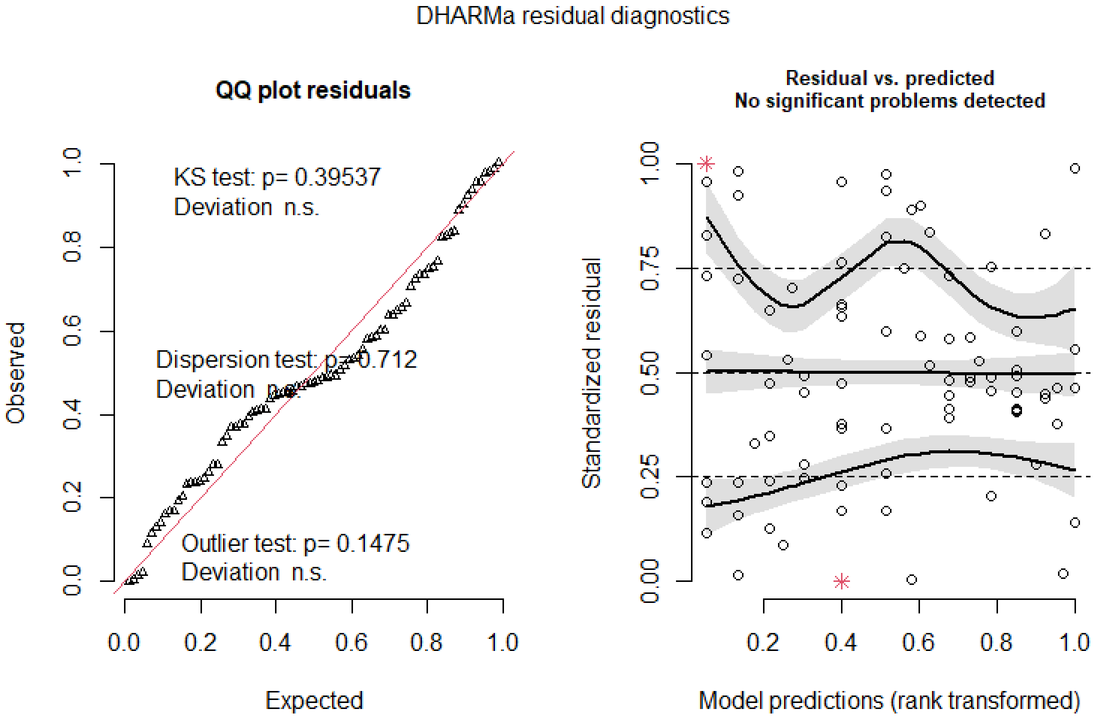

Fig. S3: Simulated residuals from model simulations using the DHARMa package from the most parsimonious model analyzing percentage daily body weight change between two subsequent captures of Eurasian beavers (*Castor fiber*) in southeastern Norway (2006-2020). The left panels show deviations from the expected distribution, while the right panel displays residuals against fitted values. The KS test results tests for whether the correct distribution is utilized.

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