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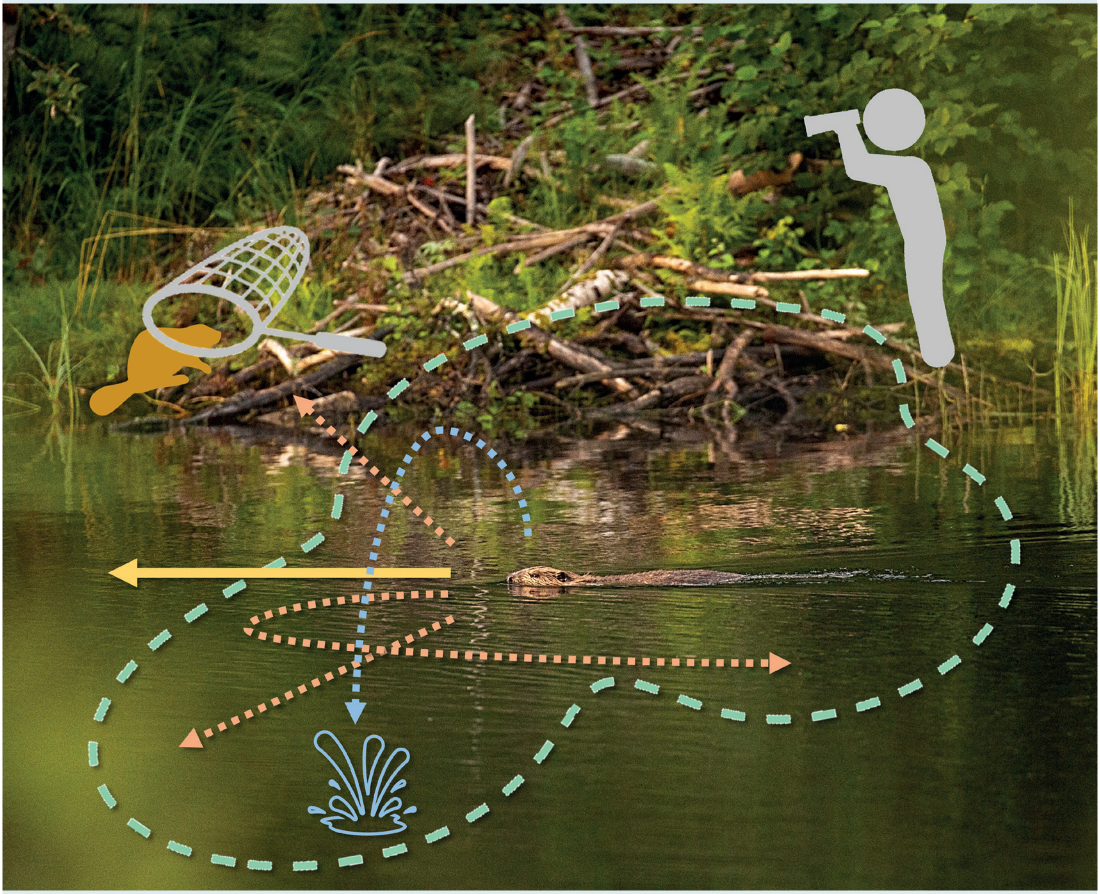
Rasmus Mohr Mortensen

Territorial movement behaviour in the Eurasian beaver



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Territorial movement behaviour in the Eurasian beaver

A PhD dissertation in
Ecology

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Abstract

It can be challenging to observe and quantify natural behaviour in wild free-ranging animals. Species that are reclusive or exploit multiple environments, such as semi-aquatic mammals, may be particularly difficult to study. Fortunately, deployment of animal-borne telemetry devices has rapidly improved our understanding of movement, behaviour, and physiology in free-ranging individuals with increasing spatiotemporal resolution and accuracy. However, deployment of tracking devices often requires multiple capture and handling events of individuals, and ecologists may additionally use long-term individual-based studies to get a better understanding of patterns and mechanisms. This, together with the tracking device itself, may have considerable behavioural effects on the individual and potentially have considerable consequences for individual fitness and the dynamics of the population.

In this thesis, we aimed to investigate natural spatiotemporal dynamics in the territorial movement behaviour in free-ranging individuals of a territorial, semi-aquatic mammal, the Eurasian beaver (*Castor fiber*). We combined a long-term individual-based monitoring project (the Norwegian Beaver Project) with sophisticated animal-borne dataloggers to study the natural movement behaviour of various individuals throughout the night and across seasons in habitats that are often difficult to observe (e.g., the aquatic environment). Furthermore, we evaluated short- and long-term effects from repeated capture and handling of individuals which can have considerably effects on the reliability of our ecological research.

In the first part, we showed how the combination of fine-scaled dead-reckoned movement tracks together with behavioural segmentation of the tracks can reveal how individuals allocate time to various activities, with focus on aquatic behaviours. We show how individuals perform dives of short duration and allocate little time to diving activities, indicating the energetic constraints. Furthermore, we show how timing and location of diving activities are highly shaped according to the activity peaks of predators, as well as by activities connected to the territory borders.

In the second part, we investigated how individuals moved and exploited the territory. Beavers strongly selected, both aquatic and terrestrial, habitats located closer to the riverbank, indicating the energetic costs. Habitat use and movement patterns revealed how beavers perceive the aquatic environment as safe and suggest that movement and selection of habitats are highly shaped according to individuals' perception of risk, social interactions, and energetic requirements.

In the third part, we investigated short- and long-term effects of repeated capture and handling according to movement behaviour and fitness-related metrics. We show that adult individuals can adjust their movements according to perceived risk and disturbances within the territory, both in the short- and in the long-term, whereas younger individuals may be less capable of adjusting, possibly because of varying energetic requirements related to their fitness potential. Consequently, capture and handling may cause territorial animals to exploit the territory, temporally and spatially, in a less predictable manner to reduce potential risk from predators and researchers in the field. Lastly, we show how repeated capture and handling can affect important life stages in individuals. Body mass in dominant individuals were negatively affected by number of capture events, however, other individuals may not be able to adapt to the increased stress because of other ecological drivers. Number of captures furthermore negatively affected reproduction in the early years of monitoring, but the effect decreased with time, indicating possible habituation. We found no effects on survival.

Overall, we show the potential of using multiple biologging data to improve our knowledge and understanding of animal movement and behavioural dynamics in wild free-ranging individuals that may be challenging to study. Furthermore, we illustrate the validity of long-term individual-based studies and show the importance of investigating several condition-related categories, at multiple times, when evaluating the consequences of capturing and handling individual animals.

Keywords: Animal welfare, biologging, capture stress, movement ecology, research ethics, territoriality.

List of papers

Paper I

Mortensen, R.M., Reinhardt, S., Hjønnevåg, M.E., Wilson, R.P., and Rosell, F. (2021). Aquatic habitat use in a semi-aquatic mammal: the Eurasian beaver. Animal Biotelemetry, 9(1), 1-19. doi: 10.1186/s40317-021-00259-7

Paper II

Mortensen, R.M., Wilson, R.P., and Rosell, F. (*Manuscript*). A territorial semi-aquatic mammal reduces predictable movements within the territory as a response to short- and long-term capture effects. *Prepared for submission to Movement Ecology*.

Paper III

Mortensen, R.M. and Rosell, F. (2020). Long-term capture and handling effects on body condition, reproduction, and survival in a semi-aquatic mammal. Scientific Reports, 10(1), 1-16. doi: 10.1038/s41598-020-74933-w

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1 Background

1.1 Animals navigating in various ecological landscapes

How wild free-ranging animals move and distribute themselves in the landscape is highly influenced by a variety of ecological factors that act across multiple spatial and temporal scales (Nathan *et al.*, 2008). Moving step-by-step from one location to another, animals constantly undergo decision-making processes as they have to trade-off investments of time and energy into various activities and behaviours to maximize their lifetime reproductive success (Mangel and Clark, 1986). Their decisions to invest time and energy into specific activities or behaviours can have severe consequences for their ultimate fitness (Brown *et al.*, 2013), which emphasises the importance of understanding these behavioural dynamics (Nathan *et al.*, 2008; Kays *et al.*, 2015; Shaw, 2020). However, understanding the choices of an animal's specific behaviour is complex, as an individual's behaviour at a given time will be shaped by its internal physiological condition, the ecological conditions in the surrounding environment, and its capacity to perceive and process information of these and other ecological factors (Nathan *et al.*, 2008; Sih *et al.*, 2010; Lewis *et al.*, 2021; Little *et al.*, 2022). Improved knowledge on the causes, patterns, mechanisms, and consequences of animal movement is needed to determine the behavioural dynamics of individuals as well as the structure of animal populations and ecosystems (Nathan *et al.*, 2008; Shaw, 2020; Little *et al.*, 2022).

Fundamentally, an animal may have an internal need to move to a different location which can be driven by such factors as the animal's need to gain energy, reproduce, avoid predation, or engage in social activities (Nathan *et al.*, 2008; Gallagher *et al.*, 2017; Tucker *et al.*, 2018). This may vary among individuals and across multiple spatial and temporal scales according to both internal and external ecological factors (Little *et al.*, 2022). Whether the individual animal can act on this internal state may first depend on its biomechanical capacity of actually moving, i.e., whether it is capable of running, swimming, and/or flying, which consequently may restrict the space use of the animal to certain environments (Dickinson *et al.*, 2000). Second, the individual must obtain and process information that enables it to navigate in space and time, selecting where and when to move based on its perception of internal and external spatiotemporal cues and/or its memory of past, learned, or genetically coded experiences (Nathan *et al.*, 2008; Little *et al.*, 2022). The individual's ability to sense and react to this information about the spatiotemporal structure and dynamics of its environment, including other individuals in the same environment, will determine whether it for example can move according to specific food items, mates, predators, and conspecifics (Nathan *et al.*, 2008; Gallagher *et al.*, 2017; Tucker *et al.*, 2018; Ariano-Sánchez *et al.*, 2022; Little *et al.*, 2022).

Animal movement involves significant energy expenditure (Dickinson *et al.*, 2000). The energy landscape that the animal moves within is shaped by various physical features, such as varying terrain profiles and substrates, which influence the energy required for movement (Shepard *et al.*, 2013). Consequently, the costs of moving through the landscape are highly variable and animals may avoid steep slopes, deep dives, or strong currents to reduce cost of transport (Dickinson *et al.*, 2000; Wilson *et al.*, 2012; Shepard *et al.*, 2013; Gallagher *et al.*, 2017). Animals will attempt to minimise travelling costs between two points and hence are expected to display a movement trajectory where the sum of cost of all speeds and turns across the landscape is minimised (Wilson *et al.*, 2012; Gallagher *et al.*, 2017). However, moving in the landscape, animals will have to trade-off the costs of movement in their physical landscape with a multitude of ecological landscapes, such as the availability of resources and foraging possibilities (i.e., resource landscape), the risk of being predated (i.e., predator landscape), and interactions with competitors and group members (i.e., social landscape) (Gallagher *et al.*, 2017; Abrahms *et al.*, 2021; Williams and Safi, 2021; Finnerty *et al.*, 2022). All together they constitute a landscape intrinsically linked by various risks and rewards. How the animal ultimately decides to move depends on its perception and expectation of these ecological landscapes that furthermore may be more or less predictable in time and space (Riotte-Lambert and Matthiopoulos, 2020; Abrahms *et al.*, 2021; Williams and Safi, 2021).

Foraging is one of the most discussed drivers of animal movement. Animals moving according to food resources that are distributed in the landscape with spatially varying abundance, timing, ephemerality, and predictability illustrate how individuals make foraging decisions to maximize their energy intake (MacArthur and Pianka, 1966; Gallagher *et al.*, 2017; Abrahms *et al.*, 2021; Mortensen *et al.*, 2022). Similarly, the concept of landscape of fear explains how predator avoidance also influences animal movement and may restrict how animals exploit resources (Laundré *et al.*, 2010; Bleicher, 2017; Gallagher *et al.*, 2017). The fear of being killed by a predator is known to significantly alter the physiology, behaviour, and life history in prey species, and anti-predatory responses facilitate the individual prey's recognition, avoidance, and defence against potential predators (Lima and Dill, 1990). However, as individuals rarely know the exact whereabouts of a predator in the landscape, they may need to maintain some level of background fear (Smith and Parker, 1976; Brown *et al.*, 1999). Predators do not only have a direct lethal effect on the prey species, but indirectly influence movement patterns, habitat selection, and activity patterns of their prey towards less risky behaviours (Creel *et al.*, 2005; Fortin *et al.*, 2005; Creel and Christianson, 2008; Thaker *et al.*, 2011). Animals may change their movement behaviour in response to experienced predation risk, e.g., by increasing vigilance when foraging, assembling in groups to reduce individual predation risk, or avoid risky habitat types (Lima and Dill, 1990; Brown *et al.*, 1999; Gallagher *et al.*, 2017; Mortensen *et al.*, 2022).

Besides managing a continuous predation risk, individuals may invest time and energy in social interactions (Snijders *et al.*, 2017). The social structure and social organisation of individuals in a landscape may be an important driver of movement, influencing for example how individuals may collaborate and/or compete with each other when exploiting various resources or search and find mating partners (Morales *et al.*, 2010; Wey *et al.*, 2015; Armansin *et al.*, 2020; Hansen *et al.*, 2021; Little *et al.*, 2022). One way to ensure access to resources, including food items, breeding partners, and safe spaces, is to defend them against conspecifics and other species, i.e., showing territorial behaviour (Kaufmann, 1983; Dunham *et al.*, 1995; Maher and Lott, 1995).

A territory can be defined as an area in time and space that is defended by an individual or several mutually tolerant individuals to exclude competitors and to ensure exclusive resource use to the territory holder(s) (Maher and Lott, 1995). Once an individual has established its territory, it must defend the valuable resources against potential intruders by patrolling the territory and its borders (Maher and Lott, 1995; Amsler, 2010). Defending a territory is associated with costs related to time, energy expenditure, and the risk of injury when engaging in potential conflicts with intruders (Amsler, 2010). To minimize these costs, territorial individuals may advertise their territory occupancy as well as evaluate intruders via various types of visual, acoustic, and olfactory signalling (Gosling and Mckay, 1990; Rosell *et al.*, 1998; Gardner and Graves, 2005; Thomsen *et al.*, 2007). These signals allow the territory holders to assess the potential threat of an intruder, as well as the amount of time and energy that needs to be invested in the territorial defence (Ydenberg and Krebs, 1987; Adams, 2001; Graf *et al.*, 2016b). This may vary according to various characteristics of both the territory holder and the intruding individual, such as sex, age, and reproductive status (Brick, 1998; Cross *et al.*, 2014; Mayer *et al.*, 2017c). For example, many territorial animals respond less aggressively towards neighbouring individuals than to complete strangers, because neighbours typically respect the territory borders, whereas unfamiliar individuals are probably more likely to challenge for territorial dominance (Ydenberg and Krebs, 1987; Temeles, 1994; Sillero-Zubiri and Macdonald, 1998). However, territory borders need to be maintained and patrolled often, and in species with high competition between neighbours, territory holders may respond more aggressively towards neighbours than strangers (Muller and Manser, 2007). Patrolling the territory has shown to be an important driver of spatial movements (Amsler, 2010; Graf *et al.*, 2016b). Studies show that animals might trade-off patrolling and scent marking with other ecological important activities, such as foraging (Amsler, 2010; Graf *et al.*, 2016b; Vogt *et al.*, 2016). In general, the costs of territoriality appear to increase with territory size, but costs and benefits of various territory sizes may be more complex (Kacelnik *et al.*, 1981; Righton *et al.*, 1998; Adams, 2001; Lopez-Sepulcre and Kokko, 2005).

1.2 Tracking the natural movement behaviour in wild animals

Previously, to gain insight into the natural behaviour of wild animals, ecologists had to go out in the field and do actual observations of their study species, as direct observations or tracks of the animal were the only ways to measure its movements, behaviours, and associated time budgets (Brown *et al.*, 2013; Evans *et al.*, 2013; Wilmers *et al.*, 2015). However, the presence of an observer may cause changes in the expressed behaviours of the observed individuals, especially when animals are naturally reclusive or perceive humans as a threat (Ordiz *et al.*, 2012; Bleicher and Rosenzweig, 2018; Tucker *et al.*, 2018). Even animals that may not appear to directly react to human presence or to a given method of capture and handling, may still alter their behaviour in subtle ways (Elliott, 2016). With technological advances, deployment of animal-borne telemetry devices has rapidly improved our understanding of animal movement, behaviour, and physiology with increasing spatiotemporal resolution and accuracy (Evans *et al.*, 2013; Wilmers *et al.*, 2015; Williams *et al.*, 2021; Nathan *et al.*, 2022). Additionally, this improved ecological information has enabled us to evaluate how our research methods potentially affect the behaviour of our study animals (Kays *et al.*, 2015; Wilson *et al.*, 2018a; Kay *et al.*, 2019), and, maybe just as important, the reliability of our research data (Jewell, 2013).

The need to locate, observe, and record the natural behaviour in free-ranging animals with minimal interactions from human observers has advanced the technological development within the field of biotelemetry remarkably (Kays *et al.*, 2015; Wilmers *et al.*, 2015; Nathan *et al.*, 2022). Locating animals in time and space using tracking devices has evolved from manual tracking of animal-borne radio transmitters and acoustic signals to automated GPS loggers that uses satellite-based positioning systems (Ropert-Coudert *et al.*, 2012; Brown *et al.*, 2013; Evans *et al.*, 2013; Wilmers *et al.*, 2015; Sherub *et al.*, 2017). Some sensor types have even enabled remote monitoring of animals' internal physiological state (Ropert-Coudert *et al.*, 2012; Wilson *et al.*, 2015; Williams *et al.*, 2021). The development of smaller and lighter bio-logging devices with increasing memory storage capacity has revolutionised the bio-logging business, reducing many of the limitations from the past, such as bias from human presence in the landscape and the abilities of the observer in habitats of various accessibility (Hebblewhite and Haydon, 2010; Wilson *et al.*, 2015; Elliott, 2016; Hughey *et al.*, 2018). The benefits of the technological development are obvious and include the ability to collect accurate fine-scale spatiotemporal location data on an increasing size range of animals, diversity of taxa, over several spatial scales, and environments (Hebblewhite and Haydon, 2010; Wilson *et al.*, 2015; Elliott, 2016; Nathan *et al.*, 2022). However, the costs of using the newest equipment also pose some limitations, and it has been argued that the use of costly tracking devices may result in smaller sample sizes and weaker study designs, potentially weakening the ecological conclusions we can draw from the tracking data (Hebblewhite and Haydon, 2010). Because of the many possibilities of obtaining data with these tracking devices, we may even end up with more data than we as researchers are capable of analysing (Pimm *et al.*, 2015; Williams *et al.*, 2020).

A record of precise animal locations tells us where the animal was, and potentially how long it stayed there, but it tells little about what the animal was actually doing while it was tracked (Cagnacci *et al.*, 2010; Hebblewhite and Haydon, 2010). Until the development of animal-borne accelerometers, the behavioural context had to be inferred or otherwise recorded using direct observation methods (Brown *et al.*, 2013). An accelerometer is a flexible piezoelectric sensor which measures the changes in velocity (i.e., acceleration) as the animal moves (Dow *et al.*, 2009; Brown *et al.*, 2013). Three sensors that are aligned orthogonally to one another, enable measurements in three dimensions, which makes it possible to quantify fine-scaled body movements and body postures of the animal unlimited by observer bias, visibility of the animal, or the spatial scale (Shepard *et al.*, 2008a; Soltis *et al.*, 2012; Brown *et al.*, 2013; Hughey *et al.*, 2018).

To understand how the large sets of remotely collected acceleration waveforms (i.e., several hertz), including processed associated statistical derivatives, translate to actual behaviours in the animals, researchers analysing accelerometers must be able to assign these waveforms to their corresponding well-defined behaviour. Generally, this involves synchronised ground-truthed observations of various behaviours in relation to the measurements recorded via the accelerometer (Brown *et al.*, 2013). This process has to be accurate for each behaviour in its quantification of variation and must be consistent across several subjects of the same species to ensure valid behavioural classification, and hereby associated time-budgets and energy expenditure outside of the ground-truthed data (Graf *et al.*, 2015; Chimienti *et al.*, 2022). Several studies have demonstrated that tri-axial accelerometers can elucidate the behaviour of free-ranging animals with only minor disturbance and allow identification of complex behavioural traits, even with highly varying appearance (e.g. Wilson *et al.*, 2008; McClune *et al.*, 2014; Graf *et al.*, 2015; Wang *et al.*, 2015; Chimienti *et al.*, 2016; Hammond *et al.*, 2016; Wilson *et al.*, 2016; Studd *et al.*, 2019; Chimienti *et al.*, 2021). Often, sophisticated statistical machine learning methods are used to classify the behavioural activities based on the waveform patterns of the acceleration, which can be divided into two general categories of unsupervised and supervised learning. Supervised learning approaches come handy when the objective is to do classification and there is a set of pre-defined behavioural activities, whereas unsupervised learning approaches can be used to learn new aspects of animal behaviour by describing observed patterns in the data (Nathan *et al.*, 2012; Leos-Barajas *et al.*, 2017; Wang, 2019). One of the benefits of the first is that interpretation can be relatively straightforward as behavioural categories are well defined, whereas the categories obtained from the latter may not necessarily match specific animal behaviours (Leos-Barajas *et al.*, 2017).

However, not all behaviours are well described by accelerometers as interpretation of movement-based acceleration can be confounded by external forces not generated by the animal themselves, such as the motion of waves or wind on the animal (Halsey *et al.*, 2011), or when velocity of the animal is constant and there is little or no animal-induced acceleration, as seen in marine or aerial species during gliding (Bidder *et al.*, 2012a; Williams *et al.*, 2015). Many of these challenges can be resolved by coupling acceleration data with other tri-axial sensors, e.g., magnetometers that measure angular rotation (Williams *et al.*, 2017). The use of accelerometers and magnetometers in tandem can enhance the acquisition of metrics useful for quantifying animal behaviour in various habitats, as well as enabling dead-reckoning animal movement trajectories (Wilson *et al.*, 2007; Wilson *et al.*, 2008; Bidder *et al.*, 2012b; Bidder *et al.*, 2015).

Dead-reckoning is originally a nautical technique that has been implemented for animal movement analysis (Bidder *et al.*, 2015; Gunner *et al.*, 2021a). It has been adopted to reconstruct three-dimensional movement paths in space over time as an alternative to VHF and GPS telemetry by sequentially integrating calculated travel vectors (Bidder *et al.*, 2015; Gunner *et al.*, 2021a). Dead-reckoning calculates the vector of travel by advancing a predetermined position based on vector calculations on the magnetic heading of the animal, the change in vertical axis, and velocity over an elapsed time interval (Bidder *et al.*, 2015), often using dynamic body acceleration (DBA) as a proxy for speed (Bidder *et al.*, 2012b; Qasem *et al.*, 2012). DBA metrics appear to be powerful proxies for movement-based energy expenditure (Halsey *et al.*, 2011; Qasem *et al.*, 2012; Wilson *et al.*, 2020), and have been tested and calibrated on various taxa during different modes of activity, such as walking, flying, and swimming (Halsey *et al.*, 2008; Gleiss *et al.*, 2011; Halsey *et al.*, 2011; Fahlman *et al.*, 2013; Wilson *et al.*, 2022).

However, dead-reckoning animal movement tracks using DBA as the speed metric can be difficult, as perturbations in for example substrate type and inclination can alter the relationship between dynamic acceleration and speed, resulting in cumulative errors over time of the travel vector sequence (Shepard *et al.*, 2008b; Bidder *et al.*, 2015; Dewhirst *et al.*, 2016). To correct for this, frequent ground-truthing obtained from actual observations or a secondary telemetry source, such as GPS or VHF, is needed (Bidder *et al.*, 2015; Wensveen *et al.*, 2015; Dewhirst *et al.*, 2016; Gunner *et al.*, 2021b). Altogether, dead-reckoning has the potential to provide a complete continuous record of animal locations and movement, which can improve our understanding of animal movement ecology and reveal the fine-scaled use of various habitats that may be under-sampled by other tracking methods (Bidder *et al.*, 2015; Gunner *et al.*, 2021a). Coupled with behavioural segmentation of the movement track, we may be able to get a better understanding of the, sometimes unwatchable, behaviours in free-ranging wild animals

(Brown *et al.*, 2013; Williams *et al.*, 2016; Williams *et al.*, 2020). Ultimately, we may be able to answer *what* the animals do and how much time they spend on various activities, *where* and *when* do they move, and *why* do they move and behave as they do (Nathan *et al.*, 2008).

1.3 Effects of capture and handling

Deployment of tracking devices on wild animals often requires multiple capture and handling events of individual animals, and ecologists may additionally use long-term individual-based studies to get a better understanding of ecological patterns and mechanisms, which too may require repeated capture and handling of individuals (Clutton-Brock and Sheldon, 2010). However, capturing, handling, and even just observing wild animals may pose some challenges regarding what ecological conclusions can be made (Ordiz *et al.*, 2012; Bleicher and Rosenzweig, 2018; Tucker *et al.*, 2018).

Besides the risk of physical injuries, capturing and handling an animal is expected to induce immediate physiological and behavioural changes in the individual for it to cope with the experienced disturbance (Arnemo *et al.*, 2006; Harcourt *et al.*, 2010). Often focus is on the direct harm immediately following a capture event, and researchers may consider methods of capture and handling successful when the individual survives through the capturing process without any noticeable harms to the animal (Holt *et al.*, 2009). However, animals may hide symptoms that make them appear vulnerable (Jordan, 2005). Consequently, mortality rates or physical injuries at or near time of capture are insufficient to successfully assess various capture and handling procedures. Often researchers only evaluate the effects of capture and handling using a limited number of parameters associated to, e.g., physiology or reproduction, and seldom several categories at the same time (Kukalová *et al.*, 2013). However, we may not be able to detect a change in some parameters (Igual *et al.*, 2005), or parameters may not be affected despite the level of experienced stress (Wingfield and Sapolsky, 2003) as animals may habituate to cope with the experienced stress (Grissom and Bhatnagar, 2009; Blumstein, 2016). Several physical, physiological, and behavioural effects should therefore be evaluated at multiple times, and in multiple ways, in a long-term scale (Wilson and McMahon, 2006; Jewell, 2013).

Numerous studies have shown how individuals that have been captured and handled respond with changes in their movement, behaviour, and physiology (Kukalová *et al.*, 2013). Some species may decrease movement rates and activity levels for a period of time before returning to pre-capture levels (Cattet *et al.*, 2008; Morellet *et al.*, 2009; Bergvall *et al.*, 2021), whereas others may temporarily increase their activity levels following capture and handling (Shuert *et al.*, 2021). Other species may flee from the area, avoiding the site of capture, or may increase the use of habitats that offer shelter (Morellet *et al.*, 2009; Kukalová *et al.*, 2013). Other human activities, such as hunting, have been found to result in similar behavioural changes (Ordiz *et al.*, 2012; Moen *et al.*, 2019; Ordiz *et al.*, 2019; Græsli *et al.*, 2020; Meisingset *et al.*, 2022). However, studies may often only evaluate the potential capture stress that appears in the immediate days, weeks, or in the following breeding season after a capture and handling event (Kukalová *et al.*, 2013). Even long-term studies that aim to investigate capture and handling effects over several seasons may fail to evaluate any long-term effects of their procedures, as they only evaluate effects within each year or season (Laurenson and Caro, 1994; Deguchi *et al.*, 2014; Grisham *et al.*, 2015). Additionally, responses to capture and handling events may vary dynamically between individuals according to ecological factors and previous experiences, as the potential fitness consequences may differ between various ecological groups and life stages (Morellet *et al.*, 2009; Kukalová *et al.*, 2013; Brivio *et al.*, 2015).

1.4 Ecology of beavers

In this thesis, we use the Eurasian beaver (*Castor fiber*) as a model organism. Beavers (including the North American beaver (*C. canadensis*)) are socially monogamous, territorial rodents that inhabit various freshwater bodies (Steyaert *et al.*, 2015). In their territory, they build and use one or several lodges that can be both the well-known constructions of sticks, mud, and vegetation along the riverbank, but also can be made up of more discreet burrows dug into the brink of the riverbank (Wilsson, 1971; Rosell and Campbell-Palmer, 2022). Beavers live in family groups consisting of a dominant breeding pair, kits of the year, and older non-breeding offspring (i.e., subordinates) (Campbell *et al.*, 2005; Mayer *et al.*, 2017b). At northern latitudes, up to five kits are born around May (Campbell *et al.*, 2005; Parker *et al.*, 2017). Kits are weaned within the lodge in their first months, but usually emerge from the lodge in July when they start feeding on their own (Campbell *et al.*, 2005). Before being weaned, family members provide the kits with twigs and leaves of deciduous trees, on which beavers predominantly feed (Zurowski *et al.*, 1974; Campbell *et al.*, 2005). However, they also forage on aquatic vegetation (Nolet and Rosell, 1994; Haarberg and Rosell, 2006; Parker *et al.*, 2007b; Milligan and Humphries, 2010; Bergman and Bump, 2018) and may as well forage on more anthropogenic food resources, such as cereal fields (Lodberg-Holm *et al.*, 2022). They are central-place foragers and foraging appear to mostly occurs within 50 m from the riverbank (Fryxell and Doucet, 1991; Basey and Jenkins, 1995; Haarberg and Rosell, 2006; Steyaert *et al.*, 2015).

Beavers allocate a lot of time and energy to territorial defence, and they advertise territory occupancy mainly through scent-marking near territory borders (Rosell and Nolet, 1997; Rosell *et al.*, 1998). But territory dominance may also be communicated more actively in agonistic encounters with extra-familial individuals through tail-slapping, fighting, or even stick display (Thomsen *et al.*, 2007). Beavers have two main scent-producing organs. They use scent marking with castoreum as a territorial marker (Rosell *et al.*, 1998; Rosell, 2003), whereas scent marking with the anal gland secretion is used to code for individual information (Rosell and Bergan, 1998), such as species (Rosell and Sun, 1999), sex (Rosell and Sundsdal, 2001; Cross *et al.*, 2014), dominance (Tinnesand *et al.*, 2013), individuality, and kinship (Sun and Muller-Schwarze, 1998). Scent-marking tends to peak in the spring when subordinate individuals, usually around 2-3 years old, disperse to establish or take over a territory of their own (Rosell *et al.*, 1998; Mayer *et al.*, 2017c). But subordinate individuals have also been observed to delay their dispersal until seven years of age to await physical and behavioural maturation before acquisition of a territory (Mayer *et al.*, 2017b). Territorial scent-marking is mainly performed by dominant individuals in the family group (Hohwieler *et al.*, 2018), and more frequently by male individuals (Rosell and Thomsen, 2006) and individuals of larger territory ranges (Graf *et al.*, 2016b), but family members of all age-classes, sexes, and social ranks have been found to participate in the defence of the territory (Rosell *et al.*, 2000).

Being semi-aquatic mammals, beavers exploit both terrestrial and aquatic habitats. Although their semi-aquatic lifestyle make them somewhat less adapted for the aquatic environment, beavers are highly connected to water which they specifically use for movement and safety (Basey and Jenkins, 1995; Gable *et al.*, 2016; Graf *et al.*, 2016b; Bartra Cabré *et al.*, 2020). Therefore, whether they are foraging, collecting building resources, or scent-marking, they tend to stay close to the riverbank (Fryxell and Doucet, 1993; Rosell and Nolet, 1997; Steyaert *et al.*, 2015; Graf *et al.*, 2016b). Furthermore, beavers can be seen constructing rather complex dam systems if water levels are deemed too low in a territory (Hartman and Törnlöv, 2006; Hood and Larson, 2015). This natural management of the ecosystem facilitates an ecological heterogeneity that creates habitats for a number of organisms (Rosell *et al.*, 2005; Jones *et al.*, 2009; Hood and Larson, 2014; Law *et al.*, 2014; Hood and Larson, 2015; Orazi *et al.*, 2022).

Although beavers are socially monogamous (Herr and Rosell, 2004), activities do appear to vary between individuals. Overall, time-budgets of males and females appear to be similar, but male individuals generally seem to allocate more time to travelling than females (Sharpe and Rosell, 2003). Activities also appear to vary according to age as older individuals have been found to spend more time on land and near territorial borders, which suggest increased experience and boldness (Graf *et al.*, 2016b). However, older beavers spending less time in water, moving shorter distances, and generally reducing their activities may also indicate senescence (Bartra Cabré *et al.*, 2020). Patrolling activities seem to be prioritised among individuals occupying larger territories as they appear to trade-off the costs of patrolling larger territories against the benefits of foraging closer towards the riverbank (Graf *et al.*, 2016b). Both territory size and social rank have been found to affect extraterritorial movement trips among individuals (Mayer *et al.*, 2017c). Furthermore, subordinate individuals have been observed to forage more on aquatic vegetation, which may be linked to increased risk-avoidance (Svendsen, 1980). General movement activities have also been found to vary temporally, peaking in the middle of the night (Graf *et al.*, 2016a) and changing through the seasons according to light and weather conditions (Bartra Cabré *et al.*, 2020).

As a relatively long-lived rodent, living in social family groups that execute highly territorial behaviour consisting of visual, auditory, and chemical communication, beavers can be a useful model species when studying various ecological questions (Rosell and Campbell-Palmer, 2022). Understanding the behavioural ecology of beavers is also interesting in the context of management. This is particularly relevant as beavers are being reintroduced within their previous ranges in both Europe and North America to restore their ecological function within the landscape (Halley *et al.*, 2021), but also increasingly inhabit areas within highly anthropogenic landscapes (Dewas *et al.*, 2012), which potentially may cause an increasing number of conflicts between human and wildlife.

2 Objectives

As indicated in the previous chapter, the behavioural ecology of beavers has been extensively studied over the years, utilizing various methods ranging from direct observations of behavioural activities to deployment of animal-borne dataloggers that may reduce the effects of observers and increase the possibilities of studying these elusive animals in unobservable habitats (Hebblewhite and Haydon, 2010; Brown *et al.*, 2013). However, even with the technological development of sophisticated dataloggers, ecological research on animals is often dependent on capturing and handling individuals, sometimes multiple times, in order to attach dataloggers on individuals or obtain metrics of individuals over time in relation to ecological questions (Clutton-Brock and Sheldon, 2010). This, together with the tracking device itself, may have considerable effects on the behaviour and physiology of the individuals (Arnemo *et al.*, 2006; Harcourt *et al.*, 2010; Kay *et al.*, 2019) and potentially have considerable consequences for individuals' fitness and the dynamics of the population (Pelletier *et al.*, 2004; Cattet *et al.*, 2008; Brivio *et al.*, 2015). However, researchers often only account for these effects in the short term (Jewell, 2013; Bergvall *et al.*, 2021).

The aim of this thesis was to investigate spatiotemporal patterns of territorial movements and behavioural activities in individuals of a free-ranging territorial, semi-aquatic mammal, using the Eurasian beaver as a model species. By combining a long-term individual-based monitoring project (i.e., the Norwegian Beaver Project – hereafter the NBP) with sophisticated animal-borne dataloggers, we aimed to study the natural movement behaviour of various individuals throughout the night and across seasons in habitats that are difficult to observe (i.e., the aquatic environment), but also evaluate short- and long-term effects from repeated capture and handling of individuals which may affect the conclusions of our ecological research. Our overall aim was to answer: 1) *what* are beavers doing in the wild? 2) how do beavers use their territory? (i.e., *when* and *where*), and 3) how are beavers affected by long-term individual-based research?

2.1 What are beavers doing in the wild? **(Paper I)**

Technological developments within biotelemetry have dramatically improved our ability to describe movement and behaviours in free-ranging animals. Specifically, animal-borne accelerometers provide information on body posture, movement, and movement-based energy expenditure (Wilson *et al.*, 2008; Qasem *et al.*, 2012), and several studies have demonstrated the potential of using acceleration to elucidate behaviour in wild animals that are hard to study without bias (Brown *et al.*, 2013). In beavers, seven behaviours were previously classified with high precision and accuracy using tri-axial acceleration (Graf *et al.*, 2015). Behaviours can be combined with fine-scale animal movement determined by dead-reckoning (Bidder *et al.*, 2015; Williams *et al.*, 2017; Gunner *et al.*, 2021a) to provide information on what animals do in the spaces they reside (Wilson *et al.*, 2008).

In paper I, we focused on the aquatic behaviour in beavers. Despite beavers being semi-aquatic, most studies focus on their use of terrestrial habitat components. By using fine-scaled dead-reckoned animal tracks to determine spatial and temporal locations of aquatic dives, we examined the spatiotemporal patterns of aquatic (diving) behaviour in Eurasian beavers. Hereby, we attempted to investigate *what* beavers are doing (i.e., classifying behavioural activities), and with focus on aquatic behaviour, *when* and *where* are they diving. As time invested in various behavioural activities may vary among individuals and in time and space, we investigated how diving behaviour varied throughout the night between individuals of various ages, sizes, sex, social ranks, and range sizes.

2.2 How do beavers use their territory? **(Paper I and II)**

How animals move in the landscape is affected by a suite of factors, including the cost of movement, likelihood of predation, resource distribution, reproduction, and social interactions (Gallagher *et al.*, 2017; Abrahms *et al.*, 2021; Williams and Safi, 2021; Finnerty *et al.*, 2022). To identify important spatiotemporal characteristics within the territory, we investigated how habitat selection and movement patterns varied among tracked individuals.

In paper I, we specifically investigated the aquatic habitats selected by individuals for diving activities by combining sophisticated animal-attached data loggers (GPS and Daily Diary units), that allow determination of animal behaviour with locations, with a comprehensive assessment of aquatic habitat characteristics. Assuming that diving events represented the aquatic habitat use in beavers, we hypothesized that habitat use varied temporally and spatially between individuals and by the habitat composition within their individual territories.

In paper II, we deployed GPS loggers on individual beavers to investigate how fine-scaled habitat selection and movement patterns varied spatially, temporally, and among individuals. We furthermore examined movement activity on a night-scale by investigating how nightly range size, distance moved, night duration, and emergence time from the lodge varied temporally through the tracking, over the year, and between individuals. By investigating the patterns of individual movement and habitat use, we aimed to get a better understanding of the ecological dynamics that shape the behavioural choices of the beaver.

2.3 How are beavers affected by long-term individual-based research? (Paper II and III)

Researchers often focus on the direct harm following a capture event, and methods are considered successful when the animal survives through the capture process without any noticeable injuries (Holt *et al.*, 2009). However, animals often hide symptoms that make them appear vulnerable (Jordan, 2005) and even animals that do not appear to react to human presence or to a given method of capture and handling may still change their behaviour in subtle ways (Elliott, 2016).

Using a long-term individual-based monitoring project (i.e., the NBP), we aimed to evaluate short- and long-term effects of repeatedly capturing and handling individuals, expecting that individual beavers and monitored populations would be negatively affected by the long-term research (Fig. 1). In paper II, we investigated how habitat selection and movement patterns were affected in the short-term as an effect of nights since capture, as well as in the long-term as a function of capture intensity and years of study, while accounting for ecological differences between individuals. In paper III, we investigated how body condition, reproduction, and survival were affected by long-term repeated capture and handling of individuals by investigating the effects of number of captures, years of study, and deployment of telemetry devices while accounting for ecological variation between individuals.

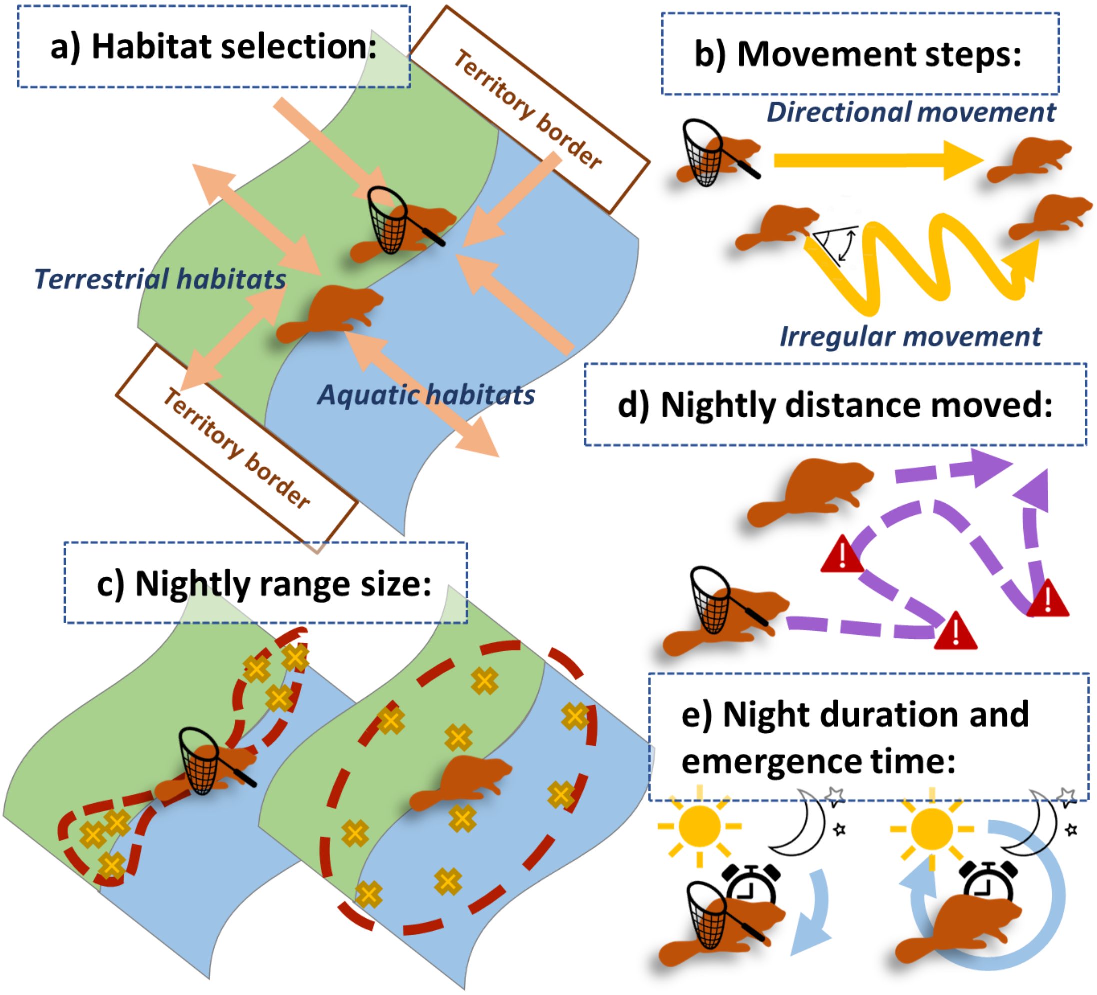

Figure 1. Schematic overview illustrating how movement behaviour in individual beavers may be affected by long-term repeated capture and handling (From paper II).

3 Methods

3.1 Study populations and study area

For all studies included in this thesis, we used individuals from three Eurasian beaver populations inhabiting rivers in Vestfold and Telemark County in south-eastern Norway (Fig. 2). The three study rivers are located at the lower reaches of the rivers Straumen, Gvarv, and Sauar that all empty into the larger Lake Norsjø. The rivers are generally slow flowing with stable water levels because of natural lakes and man-made impoundments along parts of their length (Pinto *et al.*, 2009), although seasonal flooding events do occur. All three rivers meander through a varying landscape of farmlands, fields, and small villages interspersed with riparian mixed forests (Haarberg and Rosell, 2006; Pinto *et al.*, 2009).

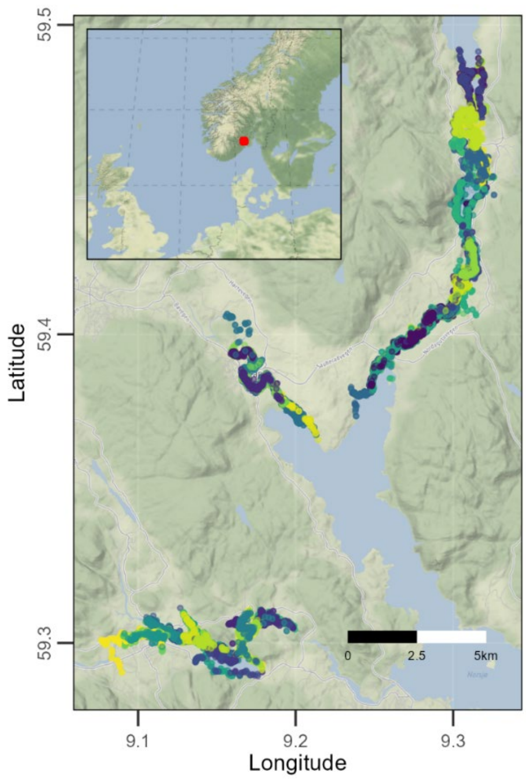

Figure 2. Overview of the three study rivers that constitute the Norwegian Beaver Project. Coloured points represent GPS fixes obtained from tracking 78 adult individual Eurasian beavers with GPS loggers from 2009 to 2021 (total of 116 tracks). The red point in the inset map indicates the position of the study area in south-eastern Norway (From paper II).

The study rivers are part of a larger monitoring and research project, the NBP, where individuals in the area have been monitored through an extensive live-capture program since 1997. This long-term individual-based monitoring project aims to annually capture all newcomers (kits of the year and dispersers from territories outside the study sites), enabling identification of individual beavers at later encounters and estimations of family group sizes. The populations in the area are believed to be at carrying capacity as the three main rivers contain about 30 distinguishable territories that vary in size from 1 to 8 km bank length with family groups of on average 4 individuals per territory (Campbell *et al.*, 2005; Graf *et al.*, 2016b; Mayer *et al.*, 2020b). Territory borders were identified based on scent mound concentrations and sight observations of patrolling known beavers in the field, as well as GPS data of dominant individuals.

Predation pressure from natural predators along the rivers is minimal as wolves (*Canis lupus*) and bears (*Ursus arctos*) are functionally extinct in the area, and lynx (*Lynx lynx*) only occur at low densities (Herfindal *et al.*, 2005; Rosell and Sanda, 2006). However, hunting occurs in the area from October to May, and human disturbances may in general affect behaviours of individuals (Parker and Rosell, 2001; Parker *et al.*, 2002; Parker *et al.*, 2007a; Swinnen *et al.*, 2015).

3.2 Capture protocol

Every study in this thesis made use of live-captured individuals captured between March and November each year. Individual beavers were usually detected at darker hours (i.e., dawn, dusk, and night) from a motorboat using searchlights and nudged to a potential capture site, enabling effective and safe captures for both the beaver and the fieldworker. An effective live-capturing method has been developed by the NBP and used throughout the period of monitoring in all rivers where individuals are captured using large diving-nets in shallow water or with land-nets (Rosell and Hovde, 2001). Following capture, individuals were transferred to land and immobilized in cloth sacks, enabling easy handling without anaesthesia. Individual beavers were identified via microchips (PIT tags) and unique combinations of plastic and metal ear-tags (Sharpe and Rosell, 2003; Mayer *et al.*, 2022). In the cloth sacks, individuals were weighed to the nearest 100 g and body and tail dimensions were measured to estimate body condition (i.e., tail fat index: Parker *et al.*, 2017). Especially the dimensions of the tail may be relevant as the tail functions as a fat storage in beavers (Aleksiuk, 1970).

First time captured, individuals were sexed based on the colour and viscosity of their anal gland secretion (Rosell and Sun, 1999). Individuals that were captured first time as kits (0 years) or yearlings (1 year) were assigned an exact age, i.e., number of experienced winters, based on their body size (Rosell *et al.*, 2010). Larger individuals were assigned a minimum age based on body mass at first capture (Rosell *et al.*, 2010); minimum 2 years when body mass was between 17 to 19.5 kg inclusive, and minimum 3 years when body mass was above 19.5 kg. When evaluating social rank, the adult territorial residents of each sex were in most cases assigned territorial dominance in a family group, which was additionally verified by eventual dispersal of the alternative same-sex candidate, the greatest body weight among same-sex group members, or lactation signs in females (i.e., large nipples of >0.5 cm). Individuals dispersing into a territory were believed to have achieved the dominant breeding position in a family group when the previous dominant same-sex individual had disappeared, or conditions outlined above was applicable. Unless proven otherwise, dominant individuals were assumed to maintain their social rank in a family group until they died or disappeared from the territory (Mayer *et al.*, 2017a). All captured beavers were released near the capture site and/or within their territory after approximately 20-40 minutes of handling time (Rosell and Hovde, 2001).

3.3 Deployment of dataloggers

During the duration of the NBP, we have captured and deployed various dataloggers on adult individuals. For this thesis, individuals were equipped with GPS loggers and daily diary units (including accelerometer, magnetometer, thermometer, Wildbyte technologies (Wilson *et al.*, 2008)) to infer movement and behaviours, as well as VHF transmitters used for locating lost dataloggers and/or individuals for recapture and observations. All dataloggers were combined with netting into one unit and glued onto the fur on the lower back of the beavers using a two-component epoxy resin, approximately 15 cm above the tail following the spine. This was done to ensure as identical a placement as possible on different individuals (Graf *et al.*, 2015; Chimienti *et al.*, 2022). After two to three weeks, dataloggers were removed from the tracked individuals if they had not fallen off by themselves. To extend battery life, GPS loggers were typically programmed to take a fix position every 15 minutes, at least between 7 pm and 7 am local time to reduce numbers of unsuccessful GPS fix attempts from within beaver lodges. Daily diary units were usually programmed to continuously measure acceleration, magnetic heading, and temperature with up to 40 Hz.

To improve precision, GPS positions were filtered to only include positions with more than three satellites and horizontal dilution of precision (HDOP) values below ten or positions with three satellites and HDOP values below five (Lewis *et al.*, 2007; Schlippe Justicia *et al.*, 2018). Additionally, we removed all GPS positions that resulted in unlikely movement steps between consecutive positions, which we defined as movement rates faster than 3 meters per second. In total, 5.8% of the obtained GPS positions were removed from the data set (not including unsuccessful fix attempts).

3.4 Ethical note

All capture and handling procedures were approved by the Norwegian Experimental Animal Board (Most recent authorization: FOTS ID19557) and by the Norwegian Directorate for Nature Management (Most recent authorization: 2014/14415). Our study met the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching (Buchanan *et al.*, 2012). All methods were performed in accordance with the relevant guidelines and regulations (Kilkenny *et al.*, 2010). No individuals were injured during capture and handling, and they were all successfully released. To minimize potential risks, the NBP prioritized capturing and handling only individuals that were necessary for the monitoring and experiments with clear objectives.

3.5 Identification of movement and behavioural activities

In paper I, we used data on acceleration and magnetic heading obtained from the daily diary units of nine individuals to infer both fine-scale movement and behavioural activities. Using dead-reckoning we accurately predicted and reconstructed individuals' fine-scale three-dimensional movement paths in space and time by sequentially integrating calculated travel vectors (Bidder *et al.*, 2015; Gunner *et al.*, 2021a). To ground-truth the dead-reckoned paths, we used GPS positions that were filtered according to number of satellites, horizontal dilution of precision values, and unlikely movement steps to reduce location error (Lewis *et al.*, 2007; Schlippe Justicia *et al.*, 2018).

To identify diving locations for paper I, we divided the dead-reckoned movement tracks into ten second bursts and used various derivatives (i.e., mean and standard deviation) of the acceleration to assign behavioural activities to each burst based on the acceleration-based behavioural classification model by Graf *et al.* (2015). This random forest classification model has shown to clearly differentiate the acceleration pattern between seven behaviours: swimming, diving, sleeping, feeding, standing, walking, and grooming (Graf *et al.*, 2015). To furthermore filter out potentially falsely classified diving events, we focused on diving sections where the previous 10 second bursts were additionally predicted to be swimming. This enabled us to identify the number of nightly diving events for each individual as well as spatiotemporal locations of these.

In paper II, movement was evaluated through the tracks of the filtered GPS positions to maximize sample size, using movement tracks from 75 adult individuals (33 F, 42 M, total of 112 GPS tracks). For the analysis, we only kept fixes that represented 15-min (± 1 min) movement steps (i.e., straight lines connecting consecutive GPS positions), hereby obtaining equal sampling rates. Movement patterns were described step by step through step length (i.e., 15-min movement rate) and turn angle that may indicate whether an individual is travelling through or exploiting an area, respectively. Movement patterns were also evaluated on a coarser nightly scale by analysing the effects on nightly range sizes (i.e., 95% autocorrelated kernel density estimates - AKDE), minimum total distance moved (i.e., Euclidean distance between steps from the earliest GPS positions to the last GPS position of the tracking night), night duration (i.e., time difference between the earliest and last GPS position of each tracking night), and emergence time from lodge at individual tracking nights (i.e., earliest GPS position of the tracking night). For the night-scale analyses, we removed the capture night and last night of tracking as these will constitute somewhat incomplete tracking nights.

In both paper I and II, using the GPS positions, we calculated 95% AKDE (Fleming *et al.*, 2015) to estimate the territory range sizes, which in our beaver populations correspond to home range sizes (Rosell and Campbell-Palmer, 2022), as well as the nightly ranges of each beaver. In paper III, range distribution was indicated through territory size, using km bank length within the territory as a proxy.

3.6 Habitat assessment

In paper I, we visited and assessed the aquatic habitat of all diving locations as well as random aquatic locations available within the territories of each tracked beaver. All diving locations and potential diving locations were visited between June and October 2019. We only sampled sites with a water depth of less than 10 m since vegetation growth here is more abundant due to light conditions (Middelboe and Markager, 1997), whilst also attempting to account for previously known diving depths in beavers (Graf *et al.*, 2018). At each diving location, vegetation was sampled using a 1 x 1 m quadrat with an aluminium frame. The sampling quadrat was placed as close to the diving location as wind and currents would allow. A GoPro camera (GoPro Hero5) was attached to the top of the sampling construction, keeping the sampling quadrat within the view of the camera. At each site, the quadrat was left at the bottom. After sediment had settled, pictures and films of the underwater vegetation were recorded. When possible, aquatic plants and physical characteristics were recorded *in situ* using an aqua scope. Plant material was collected with a rake when identification of species required closer inspection. We quantified species abundance as coverage in percentage, rounding to the nearest 5 percent (Kent, 2012). Habitat at each site was categorised according to physical characteristics (i.e., water depth and sediment type), spatial characteristics (i.e., distance to riverbank, main beaver lodge, and territory border), and characteristics of the aquatic vegetation (i.e., cover and species richness).

In paper II, habitat at each movement step, as well as at each random potential movement step, was evaluated according to their spatial location, i.e., distance from water, distance from riverbank, and distance from territory borders. Here, we did not include distance from lodge as positions from the lodge cannot be successfully obtained via GPS, which can result in masking behaviours connected to the lodge. However, these behaviours may be expressed through the reversed distance from territory borders.

3.7 Evaluation of capture effects

In paper II, the effects of capture and handling was evaluated in the scale of consecutive movement steps (15-min steps) as well as on a night scale using the GPS tracking data described above (i.e., 112 tracks from 75 adult individuals) which was obtained between 2009 and 2021. We assessed how repeated capture and handling potentially affect short- and long-term spatial activities in beavers by comparing how, respectively, habitat selection, fine-scaled movement patterns, nightly range size, night duration, and emergence time varied by capture and handling intensity (i.e., number of captures per living year), years of study (i.e., years since 1997), and nights since capture. Nights since capture was used to indicate the short-term capture and handling effects to the individual, whereas capture intensity and years of study were used as proxies to indicate long-term effects on movement behaviour in the individual and its population, respectively. In a study system as ours where most individuals are captured first time as kits and several individuals are monitored, and hence captured, several times throughout their life, we chose to not use number of captures alone as it was highly correlated with age of the beavers ($r > 0.7$). However, age additionally represents the number of captures and years of study of the individual, implicitly. Effects of capture and handling were analysed while also accounting for spatiotemporal and ecological variation.

In paper III, we evaluated the effects of repeated capture and handling using the NBP's longitudinal individual-based monitoring data from 1998 to 2018 including 436 individuals which have been captured 1421 times. While accounting for temporal and ecological variation, we investigated the effects of capture and handling events (i.e., number of experienced events of capture and handling of the individual), years of study, and deployment of tracking devices (i.e., whether the individual had experienced a deployment in its lifetime) on measures related to body condition, reproduction, and survival. Body condition was indicated by using the ratio of the tail size (seasonally variable) to body length (seasonally stable) as an index of tail fat content (i.e., tail fat index), which has previously been used as a proxy for body condition (Parker *et al.*, 2007a; Parker *et al.*, 2017). Additionally, we evaluated the effects on body mass (i.e., body weight) and body size (i.e., body length). Reproduction was evaluated in dominant female individuals through the annual reproduction and annual reproductive success of breeding pairs, using the recorded number of kits in a given year as a proxy for reproductive success in each territory. Survival was analysed by using the capture observations in a capture-mark-recapture (CMR) framework as an estimation of apparent survival, which may reflect the actual survival of individuals, but which potentially may include emigration of individuals from the study area too (Lebreton *et al.*, 1992; Borchers *et al.*, 2014; Fouchet *et al.*, 2016). We furthermore used continuous occupancy of the same territory in dominant individuals as a proxy for survival by assuming that dominant individuals may perish when they lose territory dominance and do not overtake a new territory within the study area (Mayer *et al.*, 2017b).

3.8 Statistical analyses

Our first objective was to investigate *what* behavioural activities beavers are doing in the wild with focus on aquatic activities, and furthermore investigate *when* and *where* beavers are diving. In paper I, we used generalized linear mixed-effects models (GLMMs) with Poisson error distribution, log link, and beaver ID as a random effect to analyse how the number of identified diving events each night varied between individuals and component of their territories, including the effects of sex (i.e., female or male), social rank (i.e., dominant or subordinate), age (i.e., years), body size (i.e., body mass, body length, and tail fat index), range size (i.e., 95% AKDE), territory size (i.e., km bank length), and territory characteristics (i.e., mean water depth, mean vegetation cover, and mean species richness).

We investigated *when* and *where* diving activities occur within the territory, by evaluating how individuals' hourly diving probability (i.e., whether a diving event would occur within a given hour or not) varied through the night and between individuals by fitting GLMMs with Bernoulli distribution, logit link, with beaver ID and tracking night as random effects. We analysed how hourly diving probability varied according to spatiotemporal effects (i.e., Julian night, hour of the night, distance to riverbank, lodge, and territory border), individual differences (i.e., sex, social rank, age, body size, and range size), and between components of the territory (i.e., territory size, mean water depth, mean vegetation cover, and mean species richness).

Our second objective was to investigate how beavers use their territory. In paper I, we investigated what habitats were selected for diving activities by using a resource selection function (RSF) to compare third order habitat selection of diving locations with random available aquatic sites within the territory (Johnson, 1980; Manly *et al.*, 2002; Johnson *et al.*, 2006; Lele *et al.*, 2013; Northrup *et al.*, 2022). We fitted GLMMs with Bernoulli distribution, logit link, and beaver ID as a random effect to compare whether aquatic habitats of varying water depth, sediment type, distance to riverbank, lodge, and territory border, vegetation cover, and species richness were used more than what was generally available within each territory. Vegetation cover and species richness were evaluated both according to an overall total cover and total number of species, as well as by specific focal species that appeared to be of potential importance for the diving locations. These focal species were identified in a detrended correspondence analysis (DCA) using the R package 'vegan' (Oksanen *et al.*, 2013). From the ordination, comparing plant species with use, we could identify species that appeared to be of potential importance to the beavers when diving. For the subsequent RSF, we included variables for the number of focal species present at a site and vegetation cover of these focal species in addition to the total number of plant species and cover.

Additionally, we analysed individual differences in diving selection in univariate models weighted by the number of identified dives by fitting the above RSF to each individual (Gillies *et al.*, 2006; Muff *et al.*, 2020; Ariano-Sánchez *et al.*, 2022; Mortensen *et al.*, 2022). Hereby, we investigated how individual diving selection varied according to individual differences, such as age, sex, body size, social rank, and range size, as well as territorial differences, such as territory size, water depth, vegetation cover, and species richness (Mysterud and Ims, 1998; McLoughlin *et al.*, 2010).

To investigate the various purposes of diving events in the territory (i.e., *why* do they dive?), we fitted GLMMs with beaver ID as random effect to investigate how diving locations varied spatially within the territory according to temporal variations (i.e., Julian night and hour of the night), environmental characteristics (i.e., water depth, sediment type, vegetation cover, and species richness), and individual differences (i.e., age, sex, body size, social rank, territory size, and range size). A similar analysis was done using only dives located within 150 m of the main beaver lodge, assuming that these diving locations to a higher degree may represent resource needs related to behavioural activities connected to the lodge.

In paper II, we investigated the general habitat selection of beavers and additionally investigated how individuals move around within the territory (i.e., *where* do they go, *when* do they go there, and *who* go there?). Habitat selection and movement are highly conditional on each other (i.e., movement capacity decides what habitats are available for the individual in time and space, whereas local habitat conditions also affect how an animal may move in that given habitat) (Avgar *et al.*, 2013; Avgar *et al.*, 2015). Therefore, to evaluate habitat selection and movement while simultaneously accounting for differing selection and movement behaviours, habitat selection and movement were analysed by using a conditional logistic regression in an integrated step selection function (hereafter iSSF) to compare observed and random available movement steps (i.e., steps which the beaver could have done) (Forester *et al.*, 2009; Avgar *et al.*, 2016;

Fieberg *et al.*, 2021). By restricting the analysis to only include possible steps at any given time, we may be able to get a better understanding on how the animal perceives the environment and navigates in time and space (Nathan *et al.*, 2008; Little *et al.*, 2022). However, ecological drivers may act differently to various spatial and temporal scales (McLoughlin *et al.*, 2010), which emphasises the importance of evaluating movement behaviour at several scales.

The iSSF were performed by fitting a mixed conditional logistic Poisson model with stratum-specific fixed intercepts and incorporated individual-specific slopes for the covariates for habitat selection (i.e., distance from water, riverbank, and territory borders at the end of a step) and movement (i.e., step length and turn angle) to accommodate inter-individual heterogeneity in the iSSF (Duchesne *et al.*, 2010; Muff *et al.*, 2020; Ariano-Sánchez *et al.*, 2022). We generated ten random available movement steps for each observed movement step. This was done by randomly selecting step lengths and turn angles from a gamma distribution and a von Mises distribution, respectively (Thurfjell *et al.*, 2014; Duchesne *et al.*, 2015). We parameterised these distributions based on the observed movement patterns of the tracked individuals using the R package 'amt' (Signer *et al.*, 2019). We investigated the effects of spatial variations (i.e., habitat at beginning of a step), temporal variations (i.e., hours since sunset and Julian night), and ecological variations (i.e., age, sex, social rank, body mass, and range size) by including interactions of them with the variables for habitat selection and movement.

Habitat covariates were interpreted by calculating the relative selection strength (Avgar *et al.*, 2017). We calculated the relative probability of selecting a step at a given distance to a feature (i.e., riverbank, water, or territory border) compared with the probability of selecting a step within 0.01 m from the riverbank or territory border. We used the movement coefficients (i.e., step length, natural logarithm of step length, and cosine of turn angle) from the iSSF to adjust the initial population-level gamma and von Mises distributions of step length and turn angles, respectively, to evaluate the movement patterns irrespective of the habitat selection (Fieberg *et al.*, 2021). We calculated the mean step lengths (i.e., movement rates) by multiplying the adjusted shape and scale parameters from the gamma distribution (Scrafford *et al.*, 2018).

In paper II, we additionally evaluated territorial movement patterns on a coarser night-scale by investigating how nightly range sizes, minimum total distance moved, night duration, and emergence time from lodge varied temporally (i.e., Julian night) and between individuals (i.e., age, sex, social rank, and body mass). We analysed the nightly movement activities by fitting GLMMs with log-normal (for nightly range size, minimum total distance moved, and night duration) or Gaussian distributions (for emergence time from the lodge) with individual, territory, and tracking year as random effects to account for differences between these.

For our third objective, we wanted to investigate how beavers are affected by long-term repeated capture and handling events. In paper II, we analysed short- and long-term effects of capture and handling on habitat selection and movement by including interaction of capture-effects covariates (i.e., capture intensity, years of study, and nights since capture) with covariates for habitat selection and movement in the above-mentioned iSSF. Hereby, we attempted to account for ecological dynamics related to the spatiotemporal variation and individual differences described above. Similarly, we included interactions for capture and handling between the temporal and ecological variables in the GLMMs for night-scale movement patterns to investigate whether nightly movement activity patterns were influenced by how much individuals and their populations previously had been captured and monitored.

In paper III, we investigated how metrics related to body condition (i.e., tail fat index, body mass, and body length), reproduction (i.e., annual reproduction and annual reproductive success), and survival (i.e., annual survival and probability of keeping territory dominance) were affected by long-term repeated capture and handling of individuals by investigating the effects of number of captures, years of study, and deployment of telemetry devices while accounting for ecological variation between individuals. For the analyses of body condition indices, we fitted GLMMs, separately for young (i.e., kits and yearlings) and adult (i.e., >2 years) individuals, with Gaussian distribution and capture year, beaver ID, and study river as random effects. For young individuals, we analysed the capture effects (i.e., number of capture events, years of study) while also accounting for season (i.e., spring: March-May, summer: June-August, and autumn: September-November) and individual ecological differences (i.e., sex, age, territory size, and family group size). Similar GLMMs were built for adult individuals, additionally analysing the effect of having carried a telemetry device in its lifetime up to the given capture event, accounting for social rank at the capture event, and the individual's family origin (i.e., immigrant or resident).

Long-term effects of capture and handling on annual reproduction were evaluated in dominant female individuals by fitting GLMMs with a binomial distribution and logit link and capture year, beaver ID, and study river as random effects to analyse the effects of capture and handling, while accounting for individual and ecological variations (i.e., age, reproduction in the previous year, territory size, family origin, and family group size). GLMMs with a Poisson distribution and log link with a similar covariate structure were fitted to investigate the long-term effects of capture and handling on annual reproductive success (i.e., litter size).

We evaluated the long-term effects of capture and handling on survival by investigating annual survival in a CMR framework. We chose to fit our model for survival in a continuous time open capture-recapture model (CMRCT) using the R package 'CMRCT' (Fouchet *et al.*, 2016), which can be applied to studies where the duration of and the time lag between capture sessions are unconstrained. Classical CMR models require discrete-time assumptions (Lebreton *et al.*, 1992) that introduce constraints in the CMR protocols (Borchers *et al.*, 2014; Fouchet *et al.*, 2016). Using the CMRCT model, we analysed how annual survival varied with effects of capture and handling, capture season, and ecological variation among individuals (i.e., sex, age, territory size, and family group size). Furthermore, we used individuals' retainment of dominance status in a family group as a proxy for annual survival among adult individuals, which we evaluated by fitting GLMMs with binomial distribution and logit link and capture year, beaver ID, and study river as random effects. We investigated how probability of staying dominant in a family group in the following year varied among dominant individuals according to capture effects and ecological differences among individuals (i.e., sex, age, territory size, and family group size).

Model construction and selection

All analyses were conducted in R (R Core Team, 2022). In both paper I, II, and III, we build and constructed many of our models using the R package 'glmmTMB' (Magnusson *et al.*, 2017). In all analyses, explanatory variables were checked for collinearity using Pearson's r with a threshold of 0.6 and variance inflation factors (VIF) with values less than 3 (Zuur *et al.*, 2009). For all analyses, a list of ecologically relevant candidate models was created using relevant combinations of the fixed effects mentioned above. Linearity of variables were tested in univariate mixed-effect models with either linear or squared variables. In paper II, covariates were scaled by standard deviation and centred to improve interpretation of relative relevance among included covariates.

Model selection in all analyses, except for the CMRCT model, was based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002), and carried out using the R package 'MuMIn' (Barton, 2018). In paper I and II, the most parsimonious models were identified within ΔAICc < 2 (Burnham and Anderson, 2002; Arnold, 2010). In paper III, we performed model averaging over the most parsimonious models within ΔAICc < 4 (Burnham and Anderson, 2002; Arnold, 2010). Both methods attempt to deal with model selection uncertainty by optimising the trade-off between fit and model complexity (Harrison *et al.*, 2018). Consequently, uninformative variables would ideally be left out or given less importance in the final models. For the CMRCT model in paper III, the R package did not offer any model selection function. Therefore, we decided to fit all variables and interactions in a global model and removed uninformative variables, according to above, by backwards selection until the final model consisted only of variables that had a statistically clear effect (Arnold, 2010).

In all models, variables that included zero within their 95% confidence interval (CI) were considered statistically unclear effects (i.e., uninformative) (Arnold, 2010). In paper II, confidence intervals were additionally bootstrapped with 10,000 simulations (however, the iSSF was only bootstrapped using 2000 simulations, as it was computationally heavy to fit) by treating tracking nights as sampling units to obtain robust estimates (Fieberg *et al.*, 2020). In all papers, models were visually validated using the R package 'DHARMa' (Hartig, 2017) to plot standardised model residuals against the fitted values (Zuur *et al.*, 2009). When applicable, we furthermore checked for dispersion and zero-inflation using (Harrison *et al.*, 2018).

4 Results and discussion

4.1 What are beavers doing in the wild? (Paper I)

Aquatic behaviour in free-ranging individuals

In paper I, focusing on diving activities among the tracked individuals, we only identified an average of (mean ± SD) 9.5 ± 3.1 dives per night, whereas a previous study in beavers identified 40 dives per night (Graf *et al.*, 2018). We found no clear differences among any of the ecological groups included in the analysis. The differences in number of identified dives may relate to temporal resolution of the classification as well as the diversity of dives, and between individuals, which may not be accounted for in the model (Chimienti *et al.*, 2022). Especially our temporal resolution of 10 second acceleration bursts may not be fine enough to separate between consecutive diving events that may be lumped together in our analysis. Seasonal variations in expression of behavioural activities may also explain why we observed fewer dives. We only included observations from April to June, whereas Graf *et al.* (2018) additionally included observations from the autumn (September to October) where diving conditions may be more favourable, because of increased water temperature and life history patterns (Mayer *et al.*, 2017c; Graf *et al.*, 2018).

We found that the majority of the identified diving events were of relatively short duration, lasting between 10 and 110 seconds, with the majority (80%) lasting 10 seconds. Additionally, individuals only spend on average 1.6 ± 1.3 percent of their nightly time-budget on diving activities. That the tracked individuals allocated little time to diving activities matches previous findings in beavers (Allers and Culik, 1997; Graf *et al.*, 2018). Beavers do not rely on aquatic foraging alone, which may explain why they invest relatively little time in diving activities. Similar patterns of short duration diving have been found among semi-aquatic generalist carnivores (Allers and Culik, 1997; Vogel *et al.*, 1998; Harrington *et al.*, 2012; Bagniewska *et al.*, 2015). These observed diving patterns for semi-aquatic animals may relate to the fact that they in general tend to be less specialised for the aquatic environment, whereby other means of foraging may be energetically easier to exploit (Fish, 2000; Fish *et al.*, 2002).

The low number and short duration of diving events may indicate that beavers preferably dive to bring large quantities of vegetation to the surface rather than consuming small amounts of vegetation while underwater. Hereby, they save energy and minimize heat loss by not diving repeatedly to exploit resources at depth (Wilson *et al.*, 1992; Ciancio *et al.*, 2016). The energetic cost of diving has earlier been indicated by high DBA values when beavers descent, indicating the work done against buoyancy (Graf *et al.*, 2018), which has also been found for many birds because of their air-filled plumage (Wilson *et al.*, 1992). Whereas birds have been shown to use this buoyancy for passive ascents, minimizing the energetic costs (Wilson *et al.*, 2010), beavers also expressed high DBA values during their return to the surface, which is suggested to represent the transportation of vegetation to the surface for consumption (Graf *et al.*, 2018). Consequently, this is most advantageous when the individual can bring large amounts of food to the surface in one dive, without the need for multiple, energetically costly dives in repetitive feeding bouts, such as those performed in some carnivorous species (De Leeuw, 1999; Bagniewska *et al.*, 2013).

To investigate *when* and *where* diving activities occur, we analysed individuals' hourly diving probability. Hourly diving probability varied through the night, decreasing in the final hours of the night (i.e., early morning) and with increasing distance from the territory borders (Fig. 3). We did not find any other clear spatiotemporal effects on hourly diving probability and observed no clear differences between individuals or as a function of habitat components. In contrast, other studies of beavers have observed increased amounts of diving activities in the final hour of the night (Graf *et al.*, 2018). However, they did note considerable variation in this pattern. Another study found a peak in general movement-based activities (expressed through ODBA) in the middle of the beavers' principal activity period (Graf *et al.*, 2016a). As diving generally is expressed through a relatively high DBA compared to other behavioural activities, diving patterns in beavers may implicitly be represented by this general pattern of activity throughout the night (Graf *et al.*, 2015; Wilson *et al.*, 2020). Aquatic activities peaking in the middle of the active period have been observed in other semi-aquatic mammals too, such as American mink (*Neogale vison*), that appear to perform temporal niche shifts to avoid interspecific aggression from their competitors (Hays *et al.*, 2007; Harrington *et al.*, 2009).

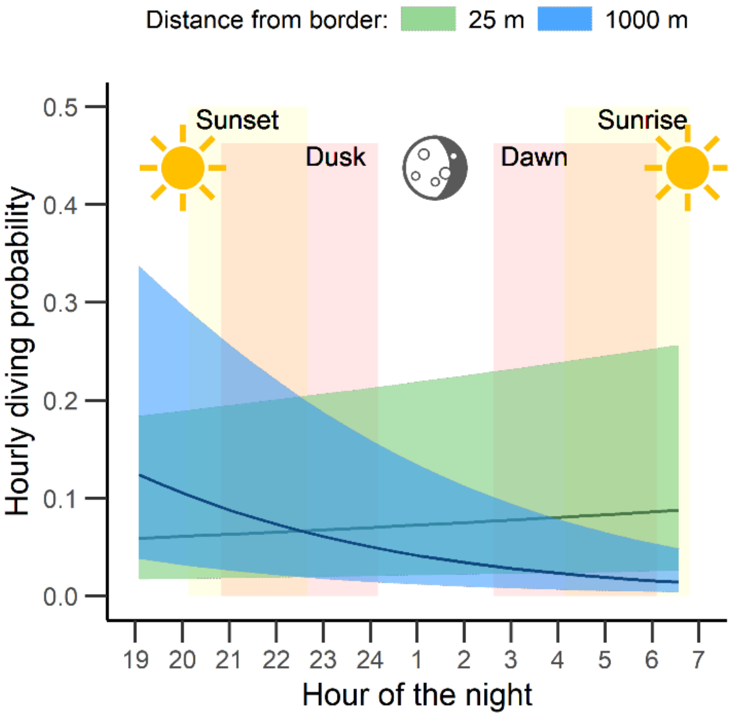

Figure 3. The predicted relationship ± 95% confidence interval between hourly diving probability, time of night, and distance from territory border among nine individuals in a Eurasian beaver population in south-eastern Norway. Yellow boxes represent time of sunset and sunrise through the tracking period. Red boxes represent time of dusk and dawn through the tracking period (From paper I).

This temporal variation in diving activities may be shaped according to the activity peaks of beaver-predating animals. When beavers bring aquatic resources onto the riverbank to be handled, their risk of predation increases (Gable *et al.*, 2016; Gable *et al.*, 2021). They are at a particular risk when on land because of their poor eyesight (i.e., they lack *tapetum lucidum*) (Rodriguez-Ramos Fernandez and Dubielzig, 2013). They therefore highly depend on olfaction cues to detect potential nearby threats (Campbell-Palmer and Rosell, 2010). Consequently, they may not detect nearby predators, such as wolves and Eurasian lynx that have advanced night vision (Maffei *et al.*, 1990; Ollivier *et al.*, 2004). In wolves, predation events have been observed to peak at dawn, dusk, and during moonlit nights (Theuerkauf *et al.*, 2003) and wolves have also been observed to ambush beavers when they leave the water (Gable *et al.*, 2021), which could explain why beavers would reduce movement-based activities at dusk and dawn. Natural predators are mostly absent in our study area, but behavioural activities are known to be influenced by historical threats (Rosell and Sanda, 2006; Swinnen *et al.*, 2015). In addition, human activities, which are naturally reduced at night, may also influence the observed activity levels of beavers (Swinnen *et al.*, 2015; Gallant *et al.*, 2016).

Through diving beavers get access to important aquatic resources, including food and building materials. The observed decreased hourly diving probability with increasing distance from the territory borders may indicate a possible depletion of aquatic resources near beaver lodges that often are located in central parts of the territory (Birt *et al.*, 1987; Elliott *et al.*, 2009). This could be expected to be related to the size of territory (Campbell *et al.*, 2005), but we found no clear effects, possibly because of our limited sample size. The increased diving probability near the borders of the territory may furthermore relate to activities of territorial defence. Diving near the borders may help reduce the risk of aggressive territorial encounters by letting territorial intruders swim away unseen (Lima, 1993; Nolet and Rosell, 1994; Mayer *et al.*, 2020b).

4.2 How do beavers use their territory? (Paper I and II)

Movement and habitat use in aquatic habitats

Beavers expressed a high selection for aquatic habitats, including diving habitats, located closer to the riverbank (Fig. 5a and 4a). Additionally, in paper I, we found that diving habitats with clay sediments, which may be an important building material for lodges and dams (Gurnell, 1998), were selected more than aquatic habitats with mud, sand, or rock sediment (Fig. 4b). Diving events within 150 m of the beaver lodge furthermore occurred more frequently on habitats with clay and muddy sediments, indicating the specific importance of fine sediment for various building constructions (Woo and Waddington, 1990; Gurnell, 1998). Furthermore, we found that diving selection probability increased when several of either quillwort (*Isoetes* spp.), shoreweed (*Littorella uniflora*), and stonewort (*Nitella* spp.) were present in an aquatic habitat (Fig. 4c), indicating that they may represent important food resources for the beaver in the spring and early summer (Simonsen, 1973).

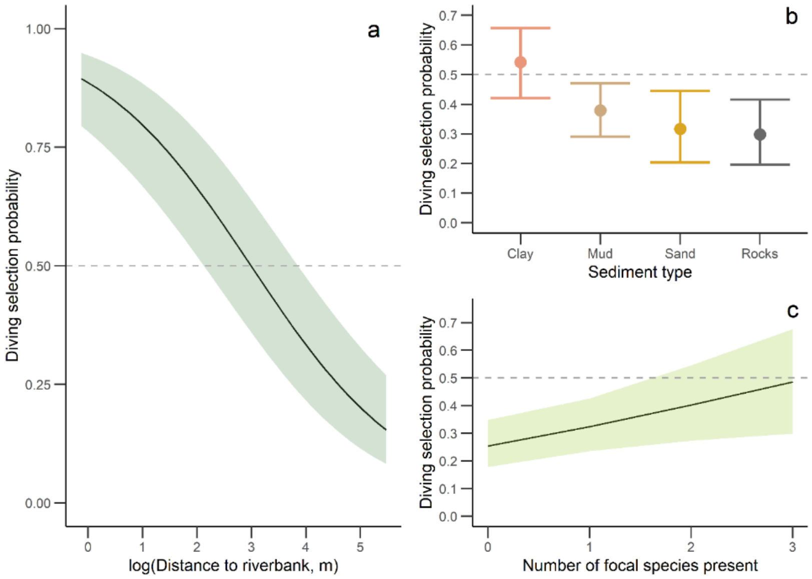

Figure 4. The predicted relationship ± 95 % confidence interval between diving selection probability and (a) distance to riverbank, (b) sediment type, and (c) number of focal vegetation species present among nine individuals in a Eurasian beaver population in southeastern Norway (From paper I).

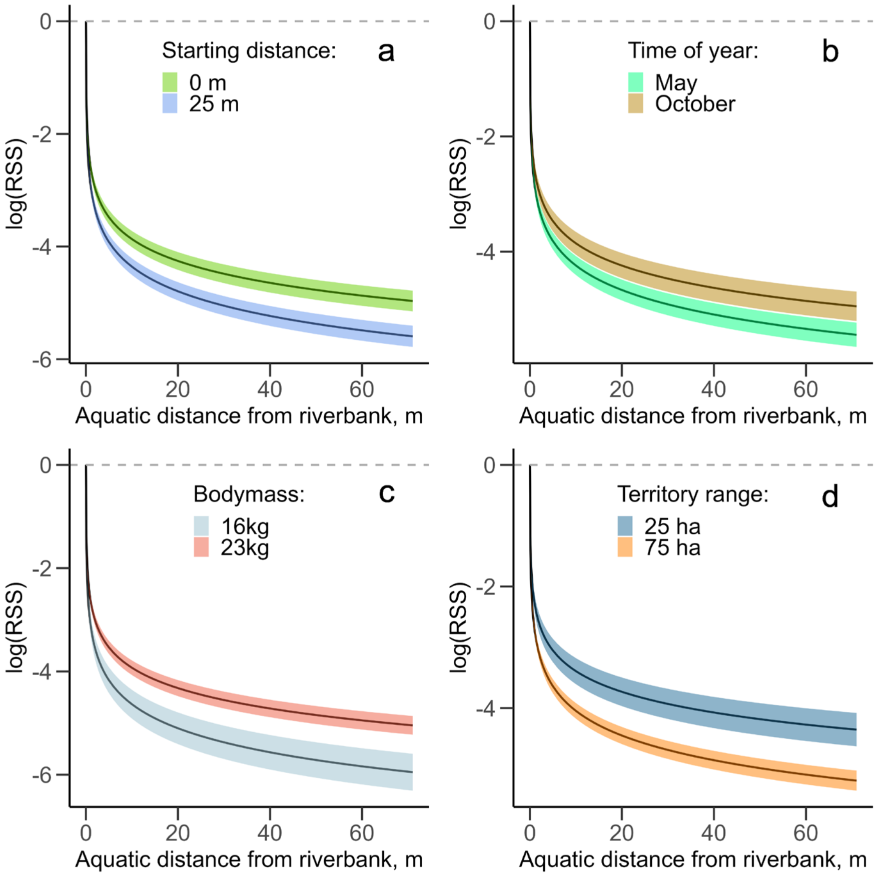

Figure 5. The predicted relationship with 95% confidence intervals of the integrated step selection function showing the relative selection strength (RSS) for (a) spatial variation (i.e., starting habitat in beginning of a step), (b) temporal variation (i.e., Julian night), and (c-d) ecological variation (body size and territory range) among 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. All values show the relative probability of selecting a step compared with the probability of selecting a step just next to the riverbank (From paper II).

Selection for habitats located closer to the riverbank increased with increasing distance to the riverbank (Fig. 5a). The selection for both aquatic habitats and diving habitats closer to the riverbank probably reflect the energetic constraints of bringing resources (i.e., food and building materials) to the riverbank as well as the beavers' preference for travelling along the riverbank (Lardet, 1988; Hays *et al.*, 2007; Graf *et al.*, 2016b; Graf *et al.*, 2018). The aquatic distance to the riverbank may further reflect how aquatic foraging options decrease with distance as macrophyte growth is highly dependent on water depth and light penetration (Middelboe and Markager, 1997). Short and shallow dives closer to the riverbank may also be energetically cheaper for a semi-aquatic animal like the beaver that has high buoyancy (Fish *et al.*, 2002).

In both paper I and II, we found that individuals that exploited larger range areas expressed a higher selection for aquatic habitats closer to the riverbank (Fig. 5d and 6a). These individuals may have a greater need to stay closer to the riverbank because they invest more time and energy in territory patrolling (Graf *et al.*, 2016b). Individuals using larger range areas or inhabiting larger territories may also experience a reduced risk of resource depletion, whereas individuals restricted to smaller territory ranges may be forced to be less selective and therefore exploit foraging areas further away from the riverbank (Campbell *et al.*, 2005; Goryainova *et al.*, 2014). Additionally, larger territory ranges may include more areas of shallow water, which, depending on the time individuals will spend on diving, can be energetically easier to exploit for a semi-aquatic animal as the beaver (Fish *et al.*, 2002).

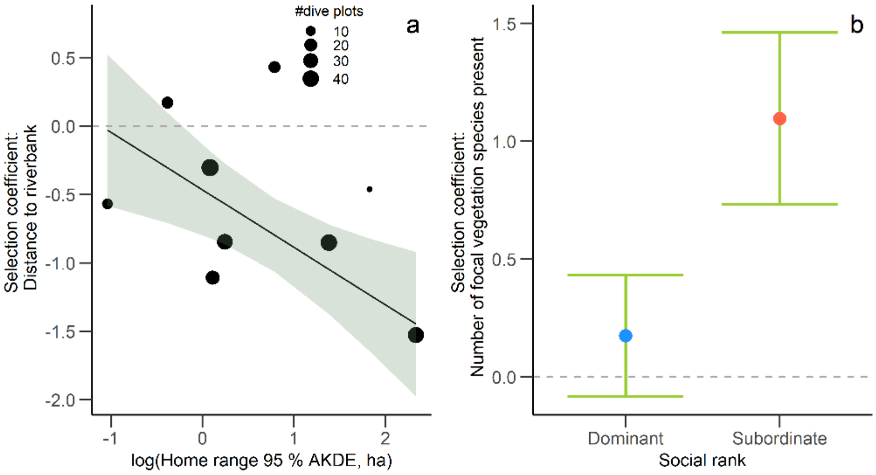

Figure 6. The predicted relationship ± 95 % confidence interval between (a) selection coefficients for distance to riverbank and home range size (AKDE, autocorrelated kernel density estimate) and (b) selection coefficients for number of focal vegetation species present and social rank among nine individuals in a Eurasian beaver population in southeastern Norway (From paper I).

In paper I, when we investigated the characteristics of the spatially varying dives within the territory, we found that water depth at diving locations generally increased with increasing distance from the riverbank (Fig. 7a), which again may represent these high energetic costs of diving away from the riverbank. But diving locations further from the riverbank were also characterised by having higher amounts of quillwort, shoreweed, and stonewort present (Fig. 7b), indicating the interplay of depth and distance energetics in a semi-aquatic animal, which have to be balanced with the calorific value of high quality food resources and their location (Wilson *et al.*, 1992; Fish *et al.*, 2002; Ciancio *et al.*, 2016). Additionally, dives located further from the beaver lodge also had higher amounts of vegetation cover (Fig. 7c) which may similarly indicate the energetic trade-offs a central place foraging individual experiences (Benkwitt, 2016; Gallagher *et al.*, 2017).

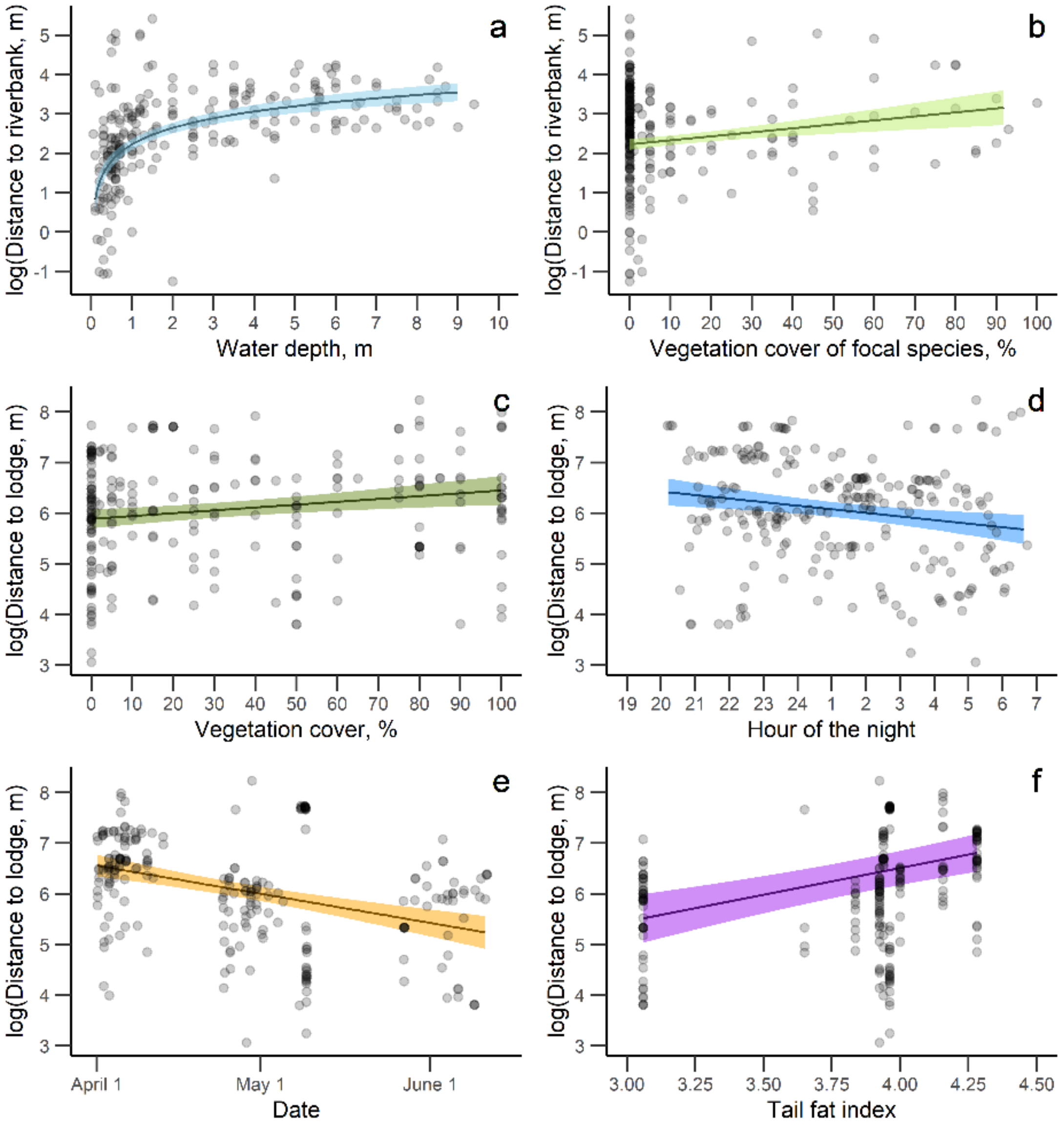

Figure 7. The predicted relationship ± 95 % confidence interval between distance to riverbank and beaver lodge and (a) water depth, (b) vegetation cover of focal species, (c) vegetation cover, (d) hour of the night, (e) Julian day, and (f) tail fat index among dives of nine individuals in a Eurasian beaver population in southeastern Norway. Points represent actual distances (From paper I).

Although beavers mainly forage on woody vegetation, aquatic vegetation seems to be seasonally important (Rosell and Campbell-Palmer, 2022). Incorporating aquatic vegetation into a varied diet could be a strategy to minimize risk of nutrient deficiency (Nolet *et al.*, 1994), which seasonally may be beneficial to some individuals, such as lactating females that may experience increased energetic requirements (Logan and Sanson, 2003; Zoller and Drygala, 2013). Other studies in semi-aquatic mammals show how male and female individuals in two species of shrew (*Neomys fodiens* and *Sorex coronatus*) use separate foraging habitats during the breeding season to ensure adequate food supply (Cantoni, 1993). In our beaver population, males and females have previously shown seasonally differing aquatic foraging patterns with females peaking in the spring and late summer, whereas males foraged on aquatic vegetation in the spring (Lodberg-Holm *et al.*, 2021). However, we did not find any selection differences between male and female individuals regarding selection of aquatic habitats in either paper I or paper II. But when we investigated the temporal variation in aquatic habitat use, we found that selection for aquatic habitats closer to the riverbank decreased through the season (Fig. 5b), following the growth of aquatic vegetation. In paper I, we also saw that diving distance to the lodge decreased from early spring to summer (Fig. 7e). Both may relate to increased parenting responsibilities that require adults to stay closer to the lodge when the kits are born in mid-May (Parker and Rosell, 2001).

A higher use of aquatic vegetation may be a risk-avoiding strategy, minimizing predation risk on land (Fryxell and Doucet, 1993; Gable *et al.*, 2021), and could be preferred by parenting individuals to ensure the growth and survival of their offspring (Dale *et al.*, 1996). Furthermore, we found that subordinate individuals appeared to have a stronger selection for the focal aquatic plant species than dominant individuals (Fig. 6b). This may be linked to them having higher energetic requirements resulting from activities related to their attempts to dominate a territory of their own, e.g., when performing extra territorial movements (Mayer *et al.*, 2017c). Adult beavers have previously been found to forage less on aquatic vegetation than subadult individuals (i.e., 2-year-old) (Svendsen, 1980). This may relate to younger individuals being less risk-willing as they potentially face higher fitness costs in terms of future reproductive success (Mayer *et al.*, 2017b), therefore adjusting their foraging strategy accordingly (Gallagher *et al.*, 2017; Mayer *et al.*, 2020a). Similarly, we found that dives located closer to the lodge were done more frequently by individuals with lower tail fat index (Fig. 7f), which may indicate territorial constraints as individuals with higher body condition may be better suited to cope with the increased cost of patrolling and protecting territory borders (Amsler, 2010; Graf *et al.*, 2016b).

In paper II, we found that smaller individuals had a stronger selection for aquatic habitats closer to the riverbank (Fig. 5c). This may at first seem contradictory to the other results, but it may again represent the high energetic costs of utilizing the aquatic environment, making it more beneficial to exploit shallow aquatic habitats. On the other hand, the aquatic environment is as an important means of transportation within and between territories, for example when patrolling or investigating territory borders, and may even help reduce aggressive territorial encounters between individuals (Lima, 1993; Nolet and Rosell, 1994; Mayer *et al.*, 2020b). This may explain why larger individuals, who often may be dominant with territorial responsibilities or a subordinate in search for a territory, may utilize a wider range of the aquatic environment compared to smaller and possibly younger individuals (Mayer *et al.*, 2017c).

When evaluating the movement patterns of individuals in the aquatic environment, we did not find any changes in movement rate according to the distance to the riverbank, despite that being further out in the river may represent higher energetic costs. This may indicate how beavers perceive the aquatic environment as generally safe (Graf *et al.*, 2016b; Bartra Cabré *et al.*, 2020). We found that directionality of the movement track decreased with increasing aquatic distance to the riverbank (Fig. 8d), which may represent how individuals bring back aquatic resource to the riverbank for handling and/or consumption (Hays *et al.*, 2007; Graf *et al.*, 2018). Nevertheless, the increased directionality may also be an artefact from our sampling interval of 15-min steps. Individuals crossing the rivers are expected to travel somewhat perpendicular to the riverbank to minimize energetic costs of travelling (Wilson *et al.*, 2013; Gallagher *et al.*, 2017). However, as individuals may come from a trajectory along the riverbank, the actual turn in the trajectory when crossing the river may not be visible in our data. Consequently, this may explain why we observe higher turn angles further out in the river.

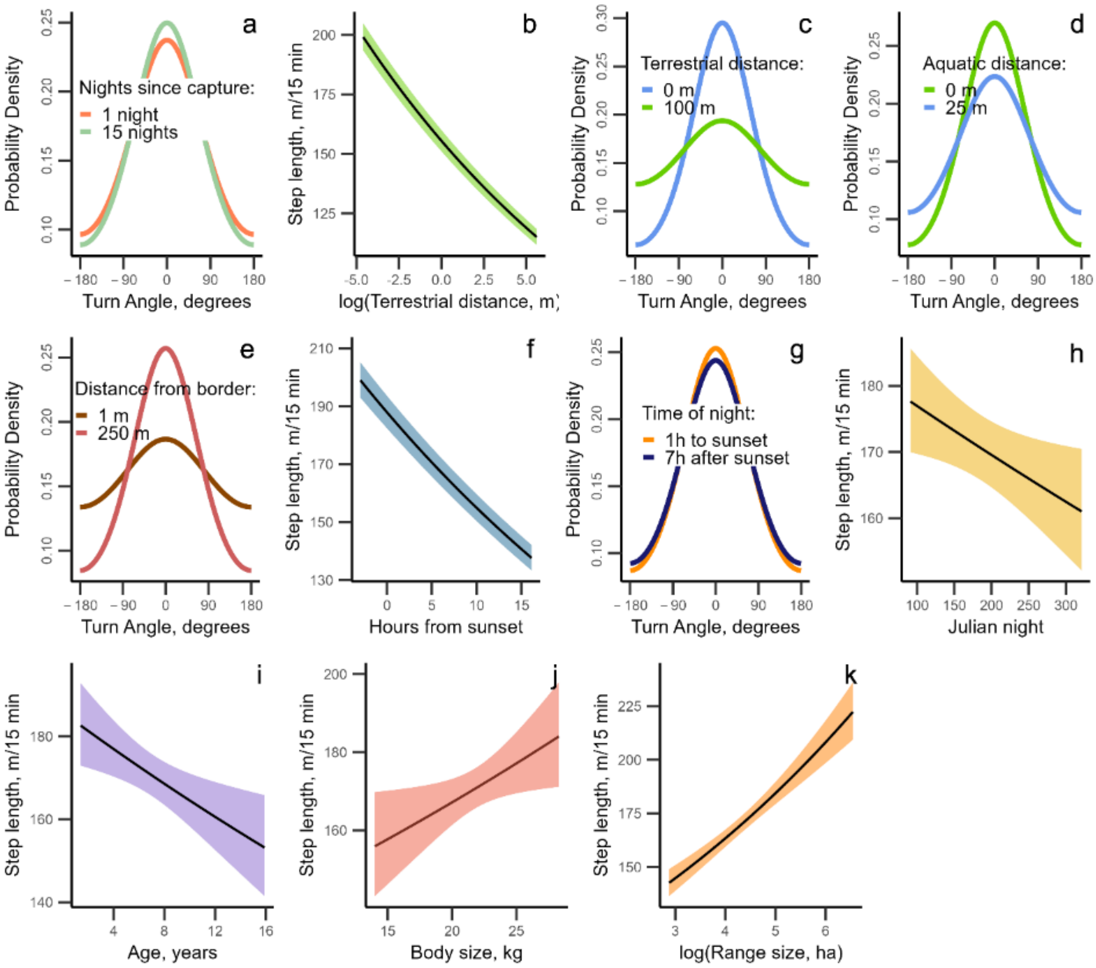

Figure 8. The predicted relationship between step length, turn angles, and (a) capture effects (nights since capture), (b-e) spatial variation (starting habitat at beginning of a step), (f-h) temporal variation (hours from sunset and Julian night), and (i-k) ecological variation (age, body size, and nightly range size) according to the integrated step selection function among 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Shaded areas in step length subplots represent 95% confidence intervals. Higher density around 0 in turn angle subplots indicate more directional movement (From paper II).

Movement and habitat use in terrestrial habitats

In paper II, we investigated how beavers moved between and selected for terrestrial habitats with varying distance to the riverbank. Not surprisingly, as beavers are at a particular risk when exploiting terrestrial habitats (Basey and Jenkins, 1995; Gable *et al.*, 2016; Gable *et al.*, 2021), we found a strong selection for terrestrial habitats located closer to the riverbank (Fig. 9). Although one would expect beavers to select terrestrial habitats in the middle of the night when it is darkest, as have been showed in other studies (Graf *et al.*, 2016a; Bartra Cabré *et al.*, 2020; Mori *et al.*, 2022), we did not find any variation throughout the night. However, we did see that individuals expressed more directional movement with longer steps temporally closer to sunset (Fig. 8f), suggesting higher risk alertness when moving within the territory (McClintic *et al.*, 2014). In contrast, we found that terrestrial movement became shorter and less directional the further individuals moved inland (Fig. 8c) and selection for habitats near the riverbank similarly reduced (Fig. 9a), although these habitats remained preferred. This may relate to optimal foraging theory, explaining how individuals maximize reward while minimizing transit time and energy expenditure (Houston and McNamara, 1985; Wetterer, 1989).

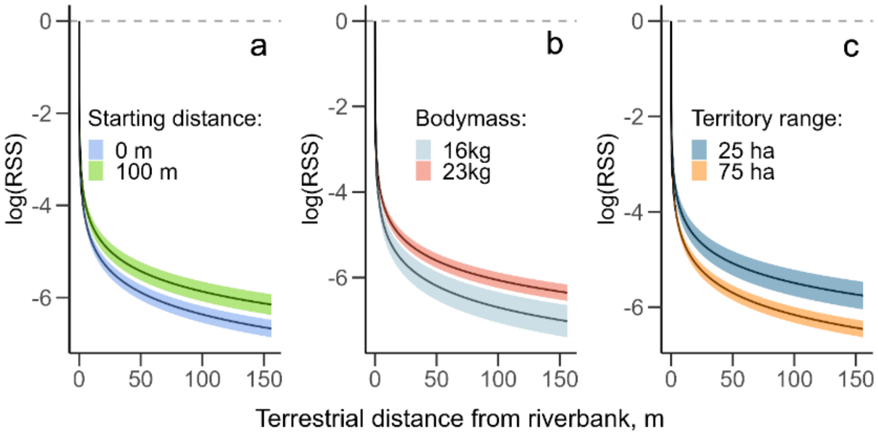

Figure 9. The predicted relationship with 95% confidence intervals of the integrated step selection function showing the relative selection strength (RSS) for terrestrial habitats as a function of (a) spatial variation (i.e., starting habitat in beginning of a step) and (b-c) ecological variation (body size and territory range) among 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. All values show the relative probability of selecting a step compared with the probability of selecting a step just next to the riverbank (Adapted from paper II).

Travelling in terrestrial habitats can be risky for a beaver, and our results suggest that individuals may want to maximize habitat exploitation of these terrestrial resources instead of frequently travelling back and forth from the riverbank (Basey and Jenkins, 1995). The decreased movement rate, we observed on land (Fig. 8b), may also indicate the increased energetic costs when bringing food items back to the riverbank for handling (Fryxell and Doucet, 1991; Wilson *et al.*, 2013).

When we investigated which individuals used the terrestrial habitats, we found that larger individuals and individuals with smaller range sizes selected terrestrial habitats more than others (Fig. 9b-c). Again, this may indicate the high costs of terrestrial habitats. As in the aquatic environment, individuals that exploit larger range areas may have a greater need to stay closer to the riverbank due to them allocating more time and energy to territory patrolling, whereas individuals exploiting smaller ranges may be able to forage further inland away from the riverbank (Graf *et al.*, 2016b). However, individuals restricted to smaller range areas may also be forced to exploit terrestrial foraging areas further away from the riverbank because of limited food resources in or near the aquatic environment (Campbell *et al.*, 2005; Goryainova *et al.*, 2014).

Larger individuals may be older or have higher energetic requirements due to, e.g., reproduction (Logan and Sanson, 2003; Sharpe and Rosell, 2003; Zoller and Drygala, 2013), making them more risk-willing to cover their energy expenditure. But larger individuals may also just be in a better condition to cope with the increased predation risk, as well as the cost of patrolling and protecting territory borders (Amsler, 2010; Graf *et al.*, 2016b). This was further indicated by the fact that larger individuals appeared to move faster (Fig. 8j), but also moved longer distances in the night (Fig. 10i), even though they emerged later from the lodge (Fig. 10p), suggesting general increased nightly activity. However, emerging later from the lodge may be a way to reduce potential risks, which they may need to compensate for in the rest of the night (Rosell and Sanda, 2006; Swinnen *et al.*, 2015; Bartra Cabré *et al.*, 2020).

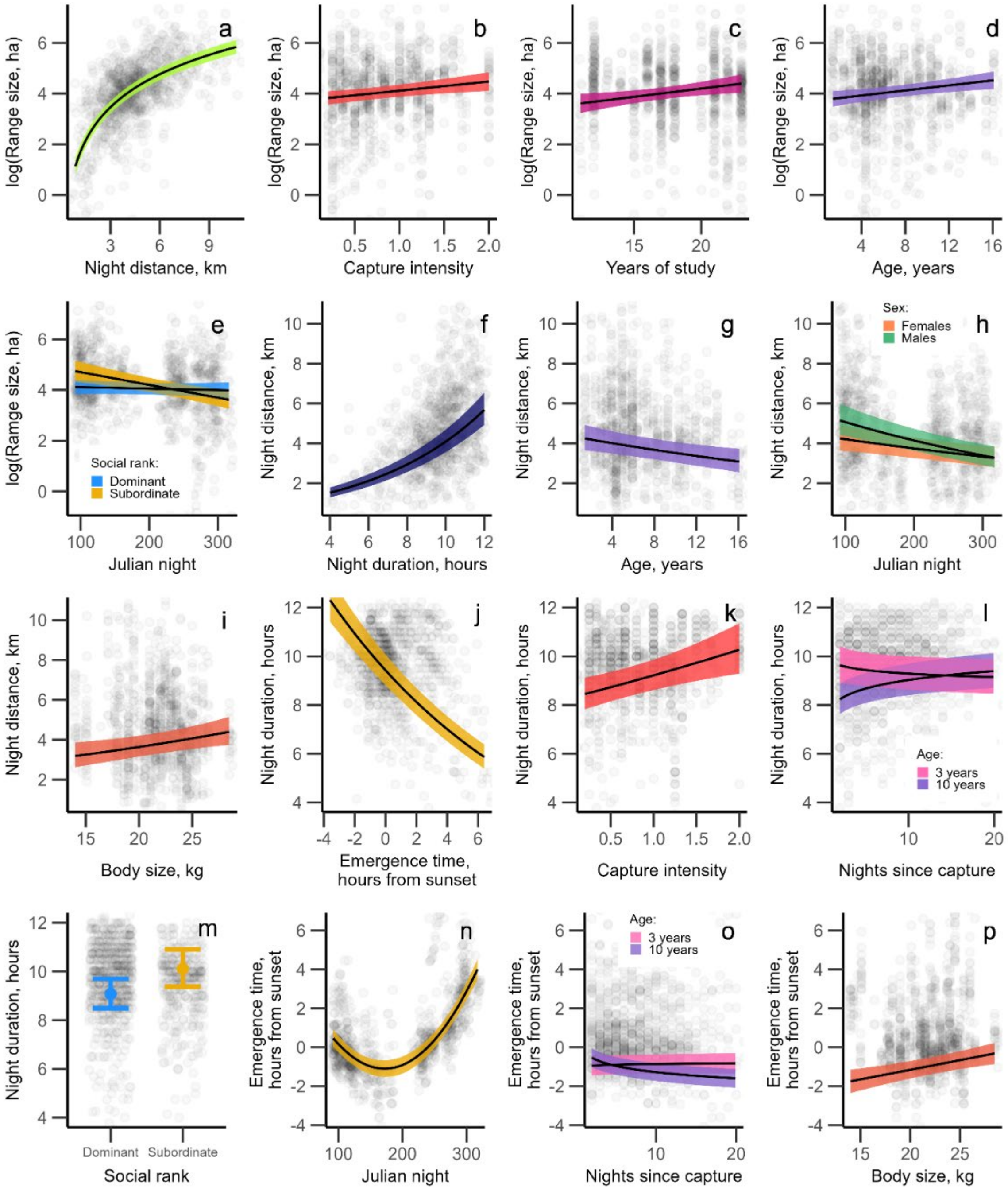

Figure 10. The predicted relationship with 95% confidence intervals between (a-e) nightly range size, (f-i) total distance moved in the night, (j-m) night duration, (n-p) emergence time from the lodge, and variables for capture and handling (capture intensity, years of study, and nights since capture), temporal variation (Julian night), and ecological variation (age, sex, social rank, and body size) in 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Grey points represent raw data (From paper II).

Movement and habitat use near territorial borders

When investigating beavers' movement behaviour in habitats according to distance from territory borders, we found a high selection for territorial habitats which additionally increased with distance to the borders (Fig. 11a). This emphasizes their strong territorial behaviour as they spend huge amount of resources advertising territory occupancy, mainly through scent-marking near territory borders (Rosell and Nolet, 1997; Rosell *et al.*, 1998). Selection for habitats closer to the territory borders was stronger in the beginning of the night (Fig. 11b), suggesting that patrolling behaviour may be an activity that is prioritized when individuals emerge from the lodge. This corresponds well with the findings from paper I where we found increased early activity peaks near the borders, as well as increased diving away from the lodge (i.e., closer to the borders) earlier in the night and in the season (Fig. 7d-e). In other territorial mammals we see similar increased visits to territory borders with increasing time since last visit (Schlägel *et al.*, 2017).

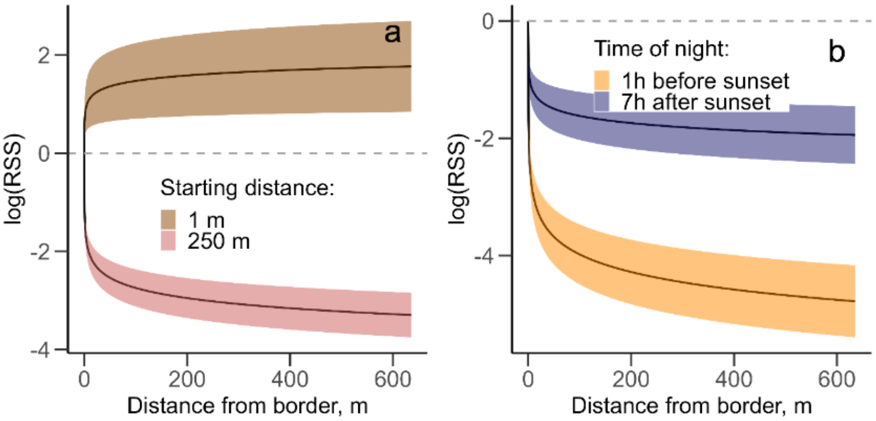

Figure 11. The predicted relationship with 95% confidence intervals of the integrated step selection function showing the relative selection strength (RSS) for terrestrial habitats as a function of (a) spatial variation (i.e., starting habitat in beginning of a step) and (b-c) ecological variation (body size and territory range) among 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. All values show the relative probability of selecting a step compared with the probability of selecting a step just next to the riverbank (From paper II).

When we evaluated the movement patterns according to the territory borders, we observed increased directional movement with increasing distance to the borders (Fig. 8e), which may indicate how individuals in our relatively linear study areas tend to travel along the riverbank to and from the borders of the territory (Graf *et al.*, 2016b). However, this may also imply that individuals spend relatively short time at the borders as we found that individuals' movements at the borders were more irregular and selected for habitats further away from the border (Fig. 11a). It is energetically costly to defend a territory (Amsler, 2010; Graf *et al.*, 2016b) and reducing the time spent at the borders may help reduce aggressive territorial encounters with neighbours and intruders (Lima, 1993; Nolet and Rosell, 1994; Amsler, 2010; Mayer *et al.*, 2020b).

Studies of beavers determined that scent-marking at territory borders is mainly performed by dominant individuals and more frequently by males (Rosell and Thomsen, 2006; Hohwieler *et al.*, 2018) that also spend more time on patrolling in the spring when subordinates individuals disperse to establish or take over a territory of their own (Rosell *et al.*, 1998; Sharpe and Rosell, 2003; Mayer *et al.*, 2017c). This corresponds well with our findings, as we found increased movement rates in the spring (Fig. 8h), which may be related to the increased patrolling or exploration of new territories in dominant and subordinate individuals, respectively (Amsler, 2010; Graf *et al.*, 2016b; Mayer *et al.*, 2017c). Similar increases in territorial defence during and after reproduction have been found in other mammals, such as coyotes (*Canis latrans*) that increase territorial defence during and immediately following the breeding period to keep exclusive access to breeding partners and food resources (Gese, 2001). Time allocated for patrolling may also vary according to the familiarity of the individuals in the neighbouring territories, as is seen in North American red squirrels (*Tamiasciurus hudsonicus*) (Siracusa *et al.*, 2019).

When we evaluated movement patterns at the night-scale, we found that male individuals moved faster in the spring compared to females (Fig. 10h). Females, on the other hand, may have to allocate more time and resources in the spring to reproduction (Logan and Sanson, 2003; Sharpe and Rosell, 2003; Zoller and Drygala, 2013). Additionally, we observed seasonal difference between social ranks as dominant individuals did not vary their nightly range size throughout the year, whereas subordinate individuals increased their range sizes considerably in the spring (Fig. 10e).

This most likely represents the increased energetic costs of defending a territory that continuously needs to be patrolled (Amsler, 2010; Campbell *et al.*, 2017; Parker *et al.*, 2017; Hohwieler *et al.*, 2018). This becomes especially important in the spring when the subordinate individuals searching for available territories increase their exploration of nearby territories to gain information on population density and available mates before dispersing (Mayer *et al.*, 2017c).

4.3 How are beavers affected by long-term individual-based research? (Paper II and III)

Short-term capture effects on movement and habitat selection

In the short-term, contrary to our expectations, we found that individuals expressed less directional movement in the nights just following a capture event (Fig. 8a). Initially, we expected individuals to express higher directionality in their movements (i.e., longer steps, smaller turn angles) following a capture event to minimize time spend in a habitat that may appear risky, as is seen in some deer species that flee following a capture event (Morellet *et al.*, 2009). However, we found no clear changes in movement rate in the individuals as a function of nights since capture. Consequently, this may relate to the highly territorial identity of beavers that can be rather predictable in their use of habitats within the territory (Gable *et al.*, 2021). Our results indicate that in the short term, when individuals may perceive an increased risk because of a capture event, highly territorial mammals such as beavers may cope with the increased stress by reducing directionality of their movements. By becoming more irregular in their movements within the territory, individuals may appear less predictable, which may protect them from potential threats (Gable *et al.*, 2021), including predators and researchers in the field, while still being capable to fulfil their requirements for energy, social interactions, and territorial defence (Amsler, 2010; Graf *et al.*, 2016b; Gallagher *et al.*, 2017).

According to our predictions, we also found, that older individuals in the short term delayed their emergence time and shortened their activity period in the first nights following capture and handling (Fig. 10l and fig. 10o). Other studies have similarly reported anecdotally how captured individuals may spend more time within their lodges in the immediate time following a capture event (Sharpe and Rosell, 2003; Ranheim *et al.*, 2004). Studies in other mammals have reported similar short temporary changes in movement and activity among individuals, lasting from hours to a few weeks (Cattet *et al.*, 2008; Morellet *et al.*, 2009; Kukalová *et al.*, 2013; Bergvall *et al.*, 2021; Shuert *et al.*, 2021). Other types of human disturbances have also been found to drive some mammals to become more nocturnal in their activities (Ordiz *et al.*, 2012; Gaynor *et al.*, 2018).

In contrast to our results, an earlier study from the NBP showed only very minimal reduced activity in the first week post-capture, and no effects on night length or movement rate (Graf *et al.*, 2016a). However, the observed differences between them and our study may relate to sample size and study design, as we also find that the effect of reduced night duration appear to decrease with time (Fig. 10l). The fact that older individuals changed their emergence and activity behaviour more than younger individuals may indicate that they are more capable of adjusting their behaviour to the experienced capture stress. Younger individuals may on the other hand not be able to reduce risky activities more than they are already doing in order to fulfil their energetic requirements, and may even express alertness already (Svendsen, 1980; Gallagher *et al.*, 2017). Adult individuals in other mammals have similarly been reported to react stronger to human disturbances than younger individuals (Loehr *et al.*, 2005).

Overall, our results indicate that individuals that invest time and energy in defending a territory may additionally be strongly influenced by other ecological dynamics related to, e.g., social interactions and competition (Amsler, 2010; Shaw and Couzin, 2013; Gallagher *et al.*, 2017; Palmer *et al.*, 2022). These dynamics may require them to maintain their movement patterns irrespective of the experienced capture stress in the short-term (Gill *et al.*, 2001). In roe deer (*Capreolus capreolus*), females have been shown to respond less than males to experienced capture stress, because female individuals have higher need for social interactions to form maternal clans (Morellet *et al.*, 2009). In beavers, the presence of other, and possibly stronger, ecological drivers may additionally explain why we found no short-term capture effects on habitat selection, nightly range size, or distance moved in the night (Gill *et al.*, 2001).

Long-term capture effects on movement and habitat selection

When we evaluated the long-term effects on movement behaviour, we found no clear effects of repeated capture and handling on movement rate or habitat selection. However, in a study system like ours, older individuals will naturally have experienced more capture events than younger. Accordingly, we did find that older individuals had decreased movement rate compared to younger individuals (Fig. 8i). This was also the case when we investigated the effects on night-scale (Fig. 10g). However, this was contrary to our predictions, as beavers have been shown to increase their movement in risky (i.e., unknown) habitats (McClintic *et al.*, 2014; Mayer *et al.*, 2017c) and mammals generally increase their movement as a response to human disturbances (Doherty *et al.*, 2021), but studies across terrestrial mammals in areas with high human impact have also shown substantial decreases in movement (Tucker *et al.*, 2018).

In our study, we also found that older individuals expressed larger nightly range sizes compared to younger individuals (Fig. 10d), even after correcting for total distance moved in the night (Fig. 10a). This may relate to younger individuals being less risk-willing and therefore less willing to stay in the same potentially risky area. Individuals moving around in the landscape without really exploiting any areas could theoretically decrease the estimated range size even when the younger individuals in total would move longer distances in the night. However, for a territorial mammal, a decreased movement rate (i.e., shorter steps) may also be a way to move around the territory while being more alert, though another study in North American beavers found that individuals moved faster further away from the lodge (i.e., risky habitat) to reduce predation risk (McClintic *et al.*, 2014).

Even after we corrected for age in the analysis, we found long-term capture effects on range size areas, as both individuals that had experienced higher capture intensity (i.e., captures per living year) and individuals from populations that had been studied for longer periods expressed larger nightly ranges (Fig. 10b-c). Over the years of being monitored, individuals may increase their range area as the territories may experience some depletion of resources (Birt *et al.*, 1987; Elliott *et al.*, 2009; Goryainova *et al.*, 2014). However, increased nightly range sizes in these individuals and populations may additionally be a consequence of long-term capture stress (Gill *et al.*, 2001). Having experienced increased disturbances in their lifetime, these individuals may perceive larger areas of their territory as risky. Therefore, they may use proportionally more of their territory range each night to appear less predictable for predators and researchers in the field (Ofstad *et al.*, 2016; Gable *et al.*, 2021). However, changes in range sizes as a function of human disturbances can vary considerably among mammals (Doherty *et al.*, 2021). The increased nightly range size, we observed, may also explain why we do not find any proportional changes in habitat selection among the individuals as we would expect the amount of available habitat to follow range size (Graf *et al.*, 2016b), although functional responses in habitat use may change habitat preferences (Mysterud and Ims, 1998).

We expected that individuals would decrease the duration of the night they were active with increasing capture intensity, but instead we found that individuals that had experienced higher capture intensity were active for a longer part of the night (Fig. 10k). This additionally supports the idea that beaver individuals may spatially and temporally extend their activities in the night to reduce risks (Ofstad *et al.*, 2016; Bartra Cabré *et al.*, 2020), and that individuals are capable of adjusting their movement behaviour according to the perceived risks and disturbances within the territory range, as is seen in other mammals too (Ordiz *et al.*, 2012; Palmer *et al.*, 2017; O’Donnell and delBarco-Trillo, 2020; Mortensen *et al.*, 2022). By adjusting their behaviour, individuals may to some degree be able to counteract the increased stress they experience from long-term repeated capture and handling. Territorial individuals that are somewhat restricted to a specific range area because of other ecological factors may even respond by habituating to being handled and other human activities in the area (Amsler, 2010; Shaw and Couzin, 2013; Gallagher *et al.*, 2017; Palmer *et al.*, 2022). Similar responses of habituation to human activities and disturbances have been found in several other mammals, as well as bird species (Baudains and Lloyd, 2007; Ditmer *et al.*, 2019; Ordiz *et al.*, 2019; O’Donnell and delBarco-Trillo, 2020; Barocas *et al.*, 2022).

Long-term capture effects on body condition, reproduction, and survival

When evaluating capture effects on body condition indices among the individuals, we found no clear effects of number of capture and handling events, years of monitoring, or from carrying a telemetry device on the variability in tail fat index or body length. However, we did find a clear decrease in body mass with increasing capture and handling events among dominant individuals (Fig. 12). Other studies in beavers have observed increased weight loss and decreased tail area in the following winter following deployment of tracking devices (Smith *et al.*, 2016), and in our population, tagged individuals have been observed to lose body weight in the short term, although the responsible mechanism behind is unknown (Robstad *et al.*, 2021). Our results from paper III furthermore indicate that this weight loss does not appear to affect individuals in the long-term. Body size can be an important feature of social status which is highly influenced by agonistic interactions between individuals (Bernstein, 1981). In beavers only the dominant individuals in a territory breeds, and in other social rodents body size have also shown to correlate well with reproduction (Huang *et al.*, 2011). Consequently, as dominant individuals may have increased energy expenditure due to territorial defence and reproduction (Campbell *et al.*, 2017; Parker *et al.*, 2017; Hohwieler *et al.*, 2018), they may be more susceptible to experienced capture stress (Pelletier *et al.*, 2004; Taillon and Côté, 2006).

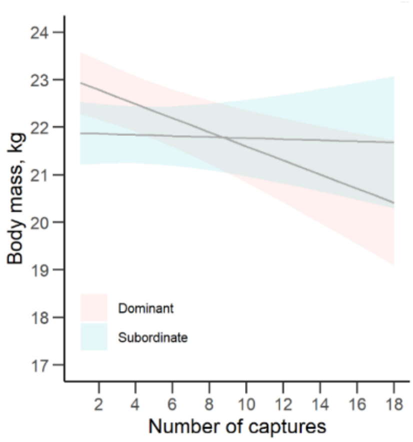

Figure 12. The predicted relationship with 95% confidence intervals body mass as a function of number of capture and handling events and social rank among adult individuals in a Eurasian beaver population in southeastern Norway between 1998 and 2018 (From paper III).

Focusing on reproduction among dominant female individuals, we found clear effects of number of capture and handling events and years of monitoring on both probability of reproducing and annual number of kits produced (Fig. 13a-b). Annual litter size furthermore decreased among older females that had experiences more capture and handling events (Fig. 13c). Interestingly, we found varying capture effects on the reproductive success over the more than twenty years of monitoring. Repeated capture and handling events had strong negative effects on annual reproduction in the early years of the monitoring program, which decreased considerably in the latter years and may indicate habituation to the experienced capture and handling stress (Grissom and Bhatnagar, 2009; Blumstein, 2016). Habituation responses to handling and human activities have been found for behaviours related to breeding in shorebirds (Baudains and Lloyd, 2007), as well as spatial behaviour and alertness in both birds and mammals (Van Oers and Carere, 2007; Ellenberg *et al.*, 2012; Vincze *et al.*, 2016; Seress *et al.*, 2017; Ditmer *et al.*, 2019; Ordiz *et al.*, 2019). Some behaviour may even be shaped by parental habituation (Schell *et al.*, 2018).

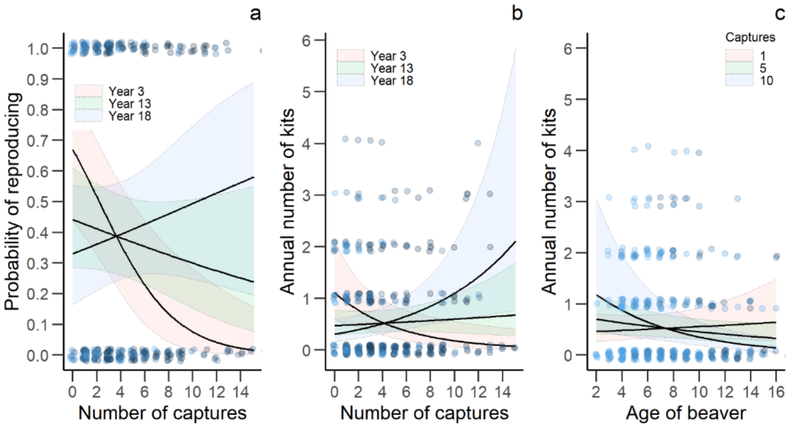

Figure 13. The predicted relationship with 95% confidence intervals of (a) probability of reproducing as a function of number of capture and handling and years of monitoring, and (b-c) annual litter size as a function of number of capture and handling, years of monitoring, and age among dominant female individuals in a Eurasian beaver population in southeastern Norway between 1998 and 2018 (From paper III).

We found no clear short- or long-term capture effects on survival probability in our population. Similar results have been found in beavers comparing the effects of radio-transmitters over a study period of eight years (Smith *et al.*, 2016). In our study, we found that survival increased with age among dominant individuals, whereas it decreased with age among subordinate individuals (Fig. 14). With increasing age, subordinate individuals may be more challenged to find a territory of their own (Mayer *et al.*, 2017a). In other rodents (North American red squirrels) this have shown to result in lower survival or accepting a territory of lesser quality (Larsen and Boutin, 1994). Dominant individuals may on the other hand be more socially anchored in a territory and family group, potentially making them more resilient to changes (Larsen and Boutin, 1994). However, the final fate of many individuals may be hidden and more details on the actual time of death of individuals may reveal the true effects of long-term repeated capture and handling which otherwise may go undetected (Laurenson and Caro, 1994; Cattet *et al.*, 2008).

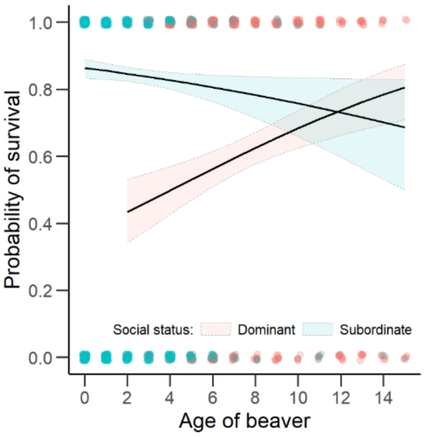

Figure 14. The predicted relationship with 95% confidence intervals of probability of surviving as a function of age and social rank among adult individuals in a Eurasian beaver population in southeastern Norway between 1998 and 2018 (From paper III).

5 Concluding remarks and future perspectives

In this thesis, we show the potential of using valuable biologging data to improve our knowledge and understanding of animal movement and the spatiotemporal behavioural dynamics in wild free-ranging individuals. Species that are naturally reclusive or utilize various environments, such as semi-aquatic mammals, may be difficult to study, and traditional methods to record animal locations, e.g., GPS loggers, may for example under sample use of the aquatic environment.

Focusing on diving activities, we show how the potential of combining fine-scaled dead-reckoned movement tracks together with acceleration-based behavioural classification. With high spatiotemporal resolution, we can identify *when*, *where*, and *how much* time each free-ranging individual invested into various behavioural activities, while reducing the limitations of the past (Brown *et al.*, 2013; Kays *et al.*, 2015). We provide new knowledge on the aquatic behavioural activities in a semi-aquatic mammal, showing how energetic constraints may shape the extend of diving events and the time allocated for diving activities, but also show the importance of aquatic behaviours for collecting resources and relieving social encounters. Future studies, investigating the consequences of investing more time in aquatic behaviours relative to terrestrial activities may further indicate their ecological importance for individual fitness.

Using a supervised learning approach with pre-defined behavioural categories, as we did, may pose some challenges. Some behaviours may be masked by others, including behaviours that may not be pre-defined, as they may show similar patterns of acceleration (Graf *et al.*, 2015). Therefore, clearly describing and defining the behavioural types an animal may express while being tracked, hereby including samples representing the variations of each, become crucial when building an acceleration-based classification model (Graf *et al.*, 2015; Chimienti *et al.*, 2022). This may include sampling ground-truthed behaviours from several individuals, deployments, over time, and in multiple environments. However, obtaining ground-truthed observations of all relevant behaviours will naturally be challenging, especially in shy and reclusive species.

Temporal resolution of the segmentation may also be important as behavioural activities of shorter duration may be masked when summarising acceleration into burst as we did (Bom *et al.*, 2014). A more detailed inspection of the fine-scale acceleration and derived body postures (i.e., what bodily movements constitute a given behaviour (Wilson *et al.*, 2018b)) may improve the classification and provide more information on the actual behavioural activity (Chimienti *et al.*, 2016; Gunner *et al.*, 2020). Placing the behavioural activities into a larger context (i.e., what the animal did before and after an activity), as we did in the short-term, could furthermore improve the behavioural classification and would furthermore help understand the ecological aspects of similar behaviours in various contexts (Leos-Barajas *et al.*, 2017). To further investigate the drivers of animal behaviour, classification may not be the goal *per se*. Instead, unsupervised machine learning approaches, such as hidden Markov models, could be used to learn new aspects of animal behaviour by describing patterns in the tracking data, identifying behavioural modes state-switching dynamics, and how these are driven by various environmental and ecological factors (Patterson *et al.*, 2009; Nathan *et al.*, 2012; Leos-Barajas *et al.*, 2017; Wang, 2019). Evaluating patterns in the acceleration instead of pre-defined behavioural activities may also be a way to investigate the behavioural dynamics that take place within the unobservable beaver lodges, where it is difficult to obtain good ground-truthed samples.

Evaluating movement tracks, we showed how territorial semi-aquatic mammals move and select aquatic, terrestrial, and border habitats within their territorial range. Habitat use and movement patterns varied spatially, temporally, and ecologically among individuals, indicating how the movement behaviour is highly shaped according to energetic requirements (i.e., physical landscape), access and exploitation of resources (i.e., resource landscape), perception of risk and disturbances (i.e., predator landscape), and social interactions within and between family groups (i.e., social landscape). This knowledge on the movement behavioural dynamics in a territorial semi-aquatic mammal may be further improved with the use of more fine-scaled tracking data, hereby validating and explaining in more detail how free-ranging individuals perceive the landscape and choose where to go (Nathan *et al.*, 2008; Shaw, 2020; Little *et al.*, 2022). For example, the use of continuous dead-reckoned movement tracks of several individuals in various ecological contexts may give us an accurate description of exactly where the individual went and how long it stayed in various parts of the landscape according to various environmental and ecological factors. These more or less continuous movement tracks of individuals may furthermore be compared experimentally in time and space to, e.g., physical features of the landscape, the presence of scats from predators, and scent marks or other social cues from intruding individuals to further investigate the details and variations of individual beavers' perception of their energy landscape, landscape of fear, and social landscape, respectively (Gallagher *et al.*, 2017; Hohwieler *et al.*, 2018).

Although technological developments in the tracking technology have revolutionised our ability to obtain detailed movement trajectories with high spatial and temporal resolution, the use of these also poses some challenges (Evans *et al.*, 2013; Wilmers *et al.*, 2015; Williams *et al.*, 2021; Nathan *et al.*, 2022). The environmental and ecological data we use to characterise the various ecological landscapes that our study animals move within, seldom match the fine-scaled resolution of tracking data. Often, we end up comparing the dynamic tracking data to static maps of the landscape that do not represent the ecological dynamics that changes over time (Abrams, 2006; Neumann *et al.*, 2015; Williams *et al.*, 2020). The possibilities of remote sensing keep improving, but applying additional sensors to animal-borne tracking devices may enable real time sampling of the habitat, climate, and other individuals as it goes (Wilson *et al.*, 2008; Williams and Safi, 2021), and has for example been used to study movement-related thermoregulation in an ectotherm (Ariano-Sánchez *et al.*, 2022). Altogether, these fine-scaled data on the environment may reveal the ecological landscapes that shape the movement of an animal (Gallagher *et al.*, 2017; Abrahms *et al.*, 2021; Williams and Safi, 2021; Finnerty *et al.*, 2022). Utilizing several environmental data streams may also be used with our beaver tracking data to explain the dynamic differences in the movement patterns, for example, distinguishing between various foraging types and trips to the territory borders, which may have different purposes, e.g., active signalling with stick display or more passive signalling using scent marking (Thomsen *et al*., 2007; Hohwieler *et al.*, 2018).

However, as a consequence of the many possibilities of obtaining ecological data from tracking devices, we may end up with more data than we are capable of managing and analysing (Pimm *et al.*, 2015; Williams *et al.*, 2020; Nathan *et al.*, 2022). High resolution tracking data may further be limited by the fact that several statistical methods, such as conventional range estimating techniques, require independent data points, which is an assumption violated by the high serial autocorrelation of most tracking data nowadays (Fleming *et al.*, 2015; Patterson *et al.*, 2017). We used and accounted for some of the autocorrelation when investigating the movement patterns of individuals by for example fitting continuous-time movement models to more accurately estimate the range utilization of the individuals (Fleming *et al.*, 2015) or restricting the selection function to only include possible steps performed by the individuals (Thurfjell *et al.*, 2014; Avgar *et al.*, 2016). However, much information may be hidden in the autocorrelation structure, which could be used in specifically developed statistical analyses in the future to identify spatiotemporal behavioural dynamics among individuals.

Capturing and handling wild animals raise some important issues on research ethics and animal welfare (Powell and Proulx, 2003; Jordan, 2005). Furthermore, it can be quite costly to deploy innovative tracking devices on wild animals, which consequently may result in smaller sample sizes and weaker study designs (Hebblewhite and Haydon, 2010). To not limit the ecological conclusions that can be drawn from the tracking data, tracking protocols need to be well thought through according to what ecological individuals are needed to answer a given research question (Lindenmayer and Likens, 2009; Williams *et al.*, 2020). Tracking many individuals with high spatiotemporal resolution for a longer period of time, preferably simultaneously, may reveal several interesting dynamics about individual animals' movement behaviour (Nathan *et al.*, 2022). Especially in a territorial animal like the beaver, where we show how the movement behaviour is strongly shaped by the social landscape, obtaining simultaneous fine-scaled information on as many individuals within the family group and neighbouring family groups as possible, may be needed to investigate with more detail how individual beavers perceive and act on the social landscape (Williams and Safi, 2021). An obvious challenge is to deploy tracking devices that will stay on the beaver for a long period of time. The gluing method of the NBP will last some weeks before it naturally falls off the beaver, hence, new attachment methods should be tested to maximize the amount of data from each tracked individual.

Lifelong habitat use and movement patterns varying between individuals will ultimately affect individual fitness (Nathan *et al.*, 2008; Kays *et al.*, 2015; Shaw, 2020). We showed how beavers that repeatedly experienced disturbances did not flee from the area, as is seen in other herbivorous mammals (Morellet *et al.*, 2009). Individuals adjusted their movement behaviour, both in the short and in the long term, according to the perceived disturbance risk, while continuously navigating and exploiting their territory according to their ecological landscapes, but in a less predictable manner. While obtaining lifetime tracks from wild individuals may prove to be practically challenging, relating individuals' space use to fitness-related measures, such as body condition, reproduction, and survival, may reveal the important ecological and evolutionary consequences of various movement decisions and events (Kays *et al.*, 2015).

We related capture protocols of the NBP to fitness-related measures. Besides the disturbance and risk of injuries during and immediately after being captures and handled, individuals may experience physiological and behavioural changes that may have consequences in the long-term, which may considerably challenge the ecological reliability of our data (Jewell, 2013). We showed how repeated capture and handling of individuals over twenty years of monitoring can have clear consequences on important life stages in a semi-aquatic mammal. According to the adjustments we found in the movement behaviour of individuals to counteract the experienced disturbances, we showed how individuals over time appeared to habituate to the capture and handling stress (Grissom and Bhatnagar, 2009; Blumstein, 2016). Overall, our results illustrate the validity of long-term individual-based studies and show the importance of investigating several condition-related categories when evaluating the consequences of capturing and handling individual animals (Wilson and McMahon, 2006; Cattet *et al.*, 2008; Jewell, 2013). To fully understand the fitness effects of various capture procedures, several capture and handling effects related to categories, such as body condition, reproduction, and survival, need to be evaluated repeatedly at multiple points in time. To further validate the fitness consequences, future studies should relate the lifelong differences and experiences of individuals, including ecological dynamics and anthropogenic disturbances, to measures such as lifetime reproduction success and age of mortality. In relatively long-lived mammals like beavers, it may take time to gather a large enough data set with several generations to be able to investigate the true ecological effects of repeated capture and handling of individuals.

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Paper I

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Animal Biotelemetry

RESEARCH **Open Access**

Aquatic habitat use in a semi-aquatic mammal: the Eurasian beaver

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Abstract

Background: Semi-aquatic mammals exploit resources both on land and in water and may require both to meet their habitat requirements including food- and building resources, refuges, and for social interactions with conspecifics. Within this, the specific availability of both terrestrial and aquatic resources is expected to impact individual fitness. Beavers are highly dependent on water for movement and protection from predators. They are central place foragers and mostly forage on woody vegetation near water although aquatic vegetation may also be an important food resource. However, little is known about their use of aquatic habitats. We aimed to address this knowledge gap by dead-reckoning fine-scale movement tracks and classifying fine-scale diving events, which we then related to the spatial distribution of aquatic vegetation and habitat components within the territory.

Results: Overall, there was a statistically clear decrease in probability that diving would occur at dawn and with increasing distance from territory borders. In addition, the distance from the lodge at which animals dived decreased through the night and during the spring/early summer. There was strong selection for diving habitats located closer to the riverbank, with stronger selection for these areas being observed in individuals with larger home ranges. We saw a higher selection for diving above clay sediment, and within 150 m from the lodge, presumably because mud and clay sediment tended to be located closer to the lodge than sand and rock sediment. Furthermore, we found a clear selection for diving in the presence of quillwort (*Isoetes* spp.), shoreweed (*Littorella uniflora*), and stonewort (*Nitella* spp.). Selection for these focal species was stronger among subordinate individuals. Individuals with lower body condition dived closer to the beaver lodge, and dives located further from the lodge were associated with high densities of aquatic vegetation.

Conclusion: We provide new knowledge on the aquatic habitat use in a semi-aquatic mammal and show how energetic constraints may shape how beavers spatially use the aquatic environment, whereby short and shallow dives appear most beneficial. We show how aquatic habitats may have great importance for both foraging, building materials and safety, and discuss to how they may affect the fitness of individuals.

Keywords: Aquatic foraging, Behavioural ecology, *Castor fibre*, Dead-reckoning, Habitat selection, Movement ecology, Resource selection functions

Background

Animal movements are affected by a suite of factors, including the cost of movement [1–6], likelihood of predation [7–11], resource distribution [12–14], reproduction [15, 16], and social interactions [12, 17–19]. This, in part, explains why there is so much interest in animal movement ecology, but elucidating causality to explain

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animal movement is challenging as behavioural ecologists have to juggle with multiple interacting factors [20, 21].

A major movement delimitator results from competition, when animals may exclude potential competitors from an area by being territorial [22, 23]. As a result, some individuals end up defending habitats that do not have favourable combinations of essential resources, and thus have to trade-off resources within their ultimate habitat acquisition [24–26]. Consequently, some species benefit by being generalists rather than specialists, because the consequences of losing a resource are less severe since animals can exploit a greater variety of resources [27–30]. For example, semi-aquatic mammals have adapted to exploit resources on land and in water, and individuals of this group may express considerable plasticity to meet their habitat requirements according to the available food resources, shelter, and social interactions [31–33].

Habitat selection happens at various spatial scales [34] and is described as the use of resources (habitat) in a manner that is disproportionate to their availability [35]. Critically, resource-use may not necessarily be directly proportional to resource availability, but it may also be modulated by other ecological factors such as competition and predation [25, 36–38]. Although it has always been a challenge to quantify which habitats animals have available to them, and how much they use them, today, this information is important to inform space-value discussions so that confounding ecological variables affecting habitat value for the animal can be put into context [39–41].

In this study, we examine aquatic habitat use in Eurasian beavers (*Castor fibre*) to identify important characteristics of aquatic habitats within beaver territories and investigate potential differences in aquatic habitat use among individuals. To achieve our aim, we combine sophisticated animal-attached tags (GPS loggers and Daily Diary units), that allow determination of animal behaviour with locations, with a comprehensive assessment of aquatic habitat characteristics.

Technological developments have hugely enhanced what animal biotelemetry can do for us, elucidating, for example, fine-scale spatiotemporal location data on an increasing range of animals across various environments [40–43]. In particular, tri-axial accelerometers are increasingly being used to study wild animals [44, 45], because they allow determination of an individual's behaviour [46]. They have been used to classify behaviour and activity level patterns in beavers, distinguishing seven behaviours with high precision, including swimming and diving [47, 48]. These behaviours can be combined with fine-scale animal movement determined by dead-reckoning [49–51] to provide information on what animals do in the spaces they inhabit [52]. Altogether, fine-scale information on behaviour and movement, obtained from the use of acceleration and dead-reckoning, respectively, are being used increasingly to study wild animals that are hard to observe directly and/or without bias [44, 49, 52–56].

Beavers are socially monogamous, monomorphic, nocturnal mammals that inhabit various freshwater bodies [38, 57]. They live in family groups consisting of the dominant breeding pair, kits of the year, and older non-breeding offspring [33, 58, 59]. Beavers reach sexual maturity during their second winter [59], and give birth to one to five kits in mid-May at northern latitudes [57]. The kits emerge from the lodge in July when they start feeding on their own [33]. At around 2–3.5 years old, beavers tend to disperse from their natal territory to establish their own territory [15, 60].

Beavers are central place foragers, mostly foraging near water and their lodges [61–63]. Their diet consists mainly of woody vegetation but varies seasonally, and comprised primarily bark from deciduous trees during winter to more nutritiously rich deciduous leaves, aquatic vegetation, and herbaceous plants in spring and summer [64–72]. In some areas, aquatic plants may seasonally account for up to 90% of the diet [65, 66, 73]. Aquatic vegetation may offer some nutritional benefits over terrestrial vegetation, including better digestibility, higher crude protein, and higher sodium and iron content [64, 66, 74, 75]. Low concentrations of secondary compounds might also make aquatic vegetation more palatable [66], but this may vary with species [76]. Seasonally, rhizomes of aquatic plants can provide great nutritional value in winter and spring when plants store nutrients in the rhizomes in preparation for spring growth [77, 78]. Diet variation may depend on nutrient content and digestibility of available forage as individual beavers attempt to maximize energy intake over time [66, 76, 79–81]. Beaver foraging behaviour varies according to environmental factors that affect the distribution of food items [82], but ecological factors such as food plant density, human disturbance, presence of conspecifics, and predator activity may also affect their foraging choices and foraging locations [67, 83, 84]. No clear dietary differences have been found between sexes, ages, or social ranks in beavers [65, 69, 85], but several studies indicate that foraging behaviour may differ seasonally as territorial movements vary among individuals [86–88]. Furthermore, individuals may be affected by various ecological conditions during their lifetime, such as loss and acquisition of territories [15, 89], that can affect their behavioural time-budgets and consequently their body condition, reproduction, and survival [57, 90].

Water acts as a refuge for beavers [91] and is specifically used to minimize predation risk when foraging on land [92]. Even though beavers depend on the aquatic environment for movement and safety [83, 86, 87, 93] and may even manipulate the environment to optimize aquatic conditions [82, 94], aquatic behaviour and habitat use have not been well studied in these animals. Although beavers use aquatic habitats for foraging [64–66, 71], protection from predators [92, 95], and collecting resources for lodge- and dam-building [96, 97], aquatic habitats may be particularly important when terrestrial vegetation is difficult to access, or is of low nutritional quality [38, 64, 66, 75, 98]. However, their spatial exploitation of the aquatic components of their territory is poorly understood. Research has found, however, that habitat use may differ between age groups and according to risk levels [87]. Diving behaviour has been studied using accelerometers, which has highlighted a preference for short (< 30 s) and shallow (up to 4 m, but most < 1 m) dives, which indicate some form of aquatic resource selection, although the link between diving and space use is vague [99]. Being only semi-aquatic [cf. 100], beavers may experience a higher cost exploiting aquatic resources [101, 102] than a fully aquatic equivalent may do. This may explain why studies have found them to be diving for less than 3% of their nightly activity budget [99]. However, energy requirements have been reported to compare well with more fully aquatic mammals and birds [101].

Using fine-scaled dead-reckoned animal tracks to determine spatial and temporal locations of aquatic dives, we aim to examine important characteristics of aquatic habitat use by Eurasian beavers and investigate potential individual differences. Assuming that dives indicate aquatic habitat use in beavers, we hypothesize that habitat use vary temporally and spatially between individuals of various ages, sexes, social ranks, and by the composition of biotic and abiotic factors within their individual territories.

Methods

Study site

Our study site was located at the lower reaches of the river Sauar in Vestfold and Telemark County, southeastern Norway (Fig. 1). The river drains the lake Heddalsvatnet in the north and forms part of the catchment of the lake Norsjø in the south, stretching over approximately 13 km with a width of 45–250 m. The river sections are generally slow-flowing with stable water levels because of natural lakes and man-made impoundments along part of its length [103], although flooding events frequently occur. The river flows through small villages, farmlands and fields interspersed with riparian woodland that comprised mostly Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birch (*Betula* spp.), grey alder (*Alnus incana*), aspen (*Populus tremula*) and mountain ash (*Sorbus aucuparia*) [62, 103].

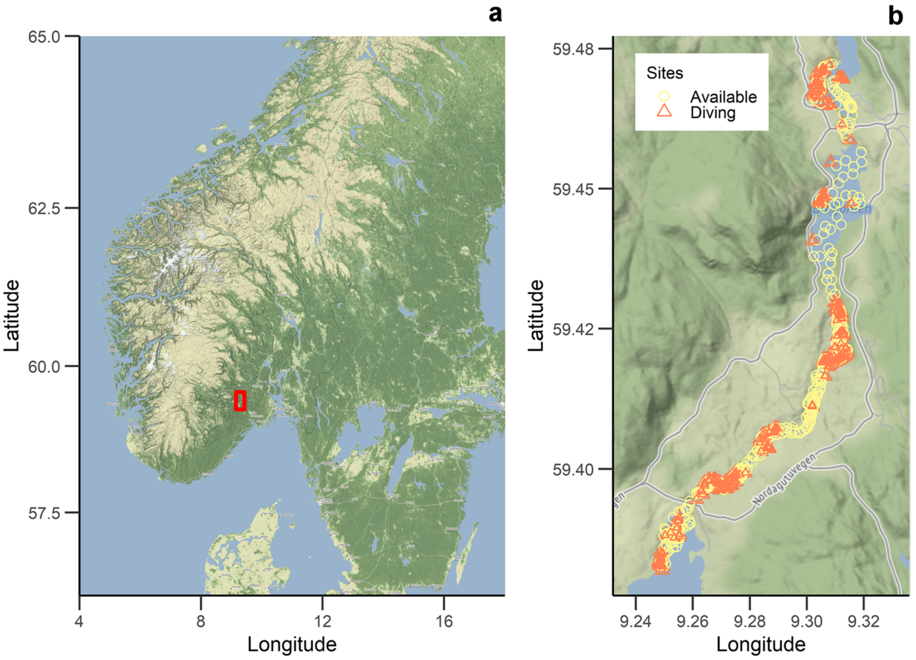

Fig. 1 **a** The location of the study site (red square) in Telemark and Vestfold County, Norway. **b** Overview of study river with random available sites (yellow circles) and identified beaver diving locations (red triangles) within beaver territories

Beavers have inhabited the area since the 1920s when they recolonized the rivers [104]. The population is at carrying capacity, as territories of various sizes directly border each other [33]. Territory borders are identified based on scent mound concentrations, sight observations of known patrolling beavers backed up by GPS data. The main river contains ten distinguishable territories inhabited by approximately 32 individuals [33, 57]. Predation pressure is low as wolves (*Canis lupus*) and bears (*Ursus arctos*) are functionally extinct in the area, and lynx (*Lynx lynx*) only occur at low densities [84, 105].

The study river is part of a larger monitoring project where beavers in the area have been monitored through an extensive capture programme, the Norwegian Beaver Project (NBP), since 1997 [57]. The long-term monitoring project aims to capture all newcomers (kits and dispersers from outside the study site) annually, enabling identification of individuals at later encounters and family group sizes.

Capture and tracking protocol

Individuals were detected from a motorboat using searchlights and captured at night with large diving-nets in shallow water or with land-nets [106]. Captured individuals were immobilized in cloth sacks, enabling easy handling without anaesthesia, and identified via microchips (PIT tag) and unique combinations of plastic and metal ear-tags. Beavers were weighed to the nearest 100 g. Body length was measured following the curvature of the spine from nose tip to the base of the tail. Tail length was measured from the base to the tip of the tail, and tail width was measured from edge to edge of the dorsal surface at the midpoint between tail base and tip. Measurements of body length and tail proportions in cm were used to calculate tail fat index ((tail length × tail width)/body length), representing the body condition of beavers [57, 59].

Individuals were sexed based on the colour and viscosity of their anal gland secretion [107] and assigned a minimum age based on body mass at first capture [57, 108]; minimum 2 years (subadult) when body mass was between 17 to 19.5 kg inclusive, and minimum 3 years (adult) when body mass was above 19.5 kg. Territorial dominance was in most cases attributed to adult territorial residents of each sex. Territorial dominance was verified by eventual dispersal of the alternative candidate, greatest body weight among same-sex group members or lactation in females (large nipples, i.e. >0.5 cm). Individuals dispersing into a territory were posited to have achieved the dominant breeding position when the previous dominant same-sex individual had disappeared, or evidence outlined above was applicable. Unless proven otherwise, dominant individuals were assumed to maintain their social rank until they died or disappeared from the territory [109].

We captured and equipped nine beavers (five males, four females, Table 1) with GPS loggers (Gipsy-5, Techno Smart) and daily diary units (including accelerometer, magnetometer, thermometer, Wildbyte technologies [52]) in the spring and early summer of 2018 (one beaver) and 2019 (eight beavers). The data loggers were glued onto the fur on the lower back of the beavers, approximately 15 cm above the tail following the spine, and were removed again after 2 to 3 weeks if they had not fallen off by themselves [47]. To extend battery life, GPS loggers were programmed to take a fix position every 15 min between 7 p.m. and 7 a.m. to reduce numbers of unsuccessful GPS fix attempts from within the beaver lodges. Daily diary units logged continuously at 40 Hz. From the GPS positions, we identified territory borders to estimate territory size, expressed in bank length (km) and calculated 95% autocorrelated kernel density estimates (AKDE) to estimate the overall space use (home range) of each beaver [110]. Captured beavers were released near the capture site within their territory after approximately 40 min of handling time [106].

Identification of dives

Accelerometers in tandem with magnetometers can be used in dead-reckoning to accurately predict and reconstruct animals' fine-scale three-dimensional movement paths in space and time by sequentially integrating calculated travel vectors [49, 51]. However, the estimated movement track accumulates error and therefore drifts over time, so it needs to be corrected through ground-truthing, e.g. correcting the track according to GPS fixes [49].

We calibrated the daily diary data in the software DDMT (Daily Diary Multiple Trace, Wildbyte Technologies). Using the acceleration and magnetism data, we dead-reckoned the movement track of each beaver in the software Framework4 [111]. The dead-reckoned movement tracks were hereafter corrected using the GPS positions as ground-truthing [49]. GPS positions were filtered to remove positions with horizontal dilution of precision (HDOP) values above five and with less than four available satellites to reduce the effects of imprecise GPS positions [112, 113].

To identify diving locations, we divided the dead-reckoned movement tracks into ten second bursts and used the acceleration to assign behavioural activities to each burst based on the acceleration-based behavioural classification model by Graf et al. [47]. The classification model can clearly differentiate the acceleration between seven behaviours: swimming, diving, sleeping, feeding, standing, walking, and grooming. To furthermore filter out

Table 1 Overview of tracked individuals with daily diaries and GPS loggers in a population of Eurasian beavers in southeastern Norway

Beaver	Tracking period	Nights	Dives	Territory size, km	Home range, ha	Sex	Age, years	Social rank	Mass, kg	Body length, cm	Tail fat index
Anna	April 2–April 15 2019	13	92	4.9	1.3	F	7	Dominant	23.3	85.5	4.3
Ceasar	April 2–April 9 2019	7	143	4.9	1.1	M	9	Dominant	17.7	81.0	3.9
Dylan	May 9–May 11 2018	2	110	6.6	10.3	M	6	Dominant	21.2	82.0	4.0
Laurits	April 26–May 7 2019	12	37	2.2	0.4	M	13	Dominant	19.0	77.5	3.8
Mason	April 2–April 10 2019	7	49	3.4	2.2	M	6	Subordiante	17.9	72.0	4.2
Mattanja	April 25–May 4 2019	9	89	2.2	4.0	M	3	Subordinate	18.0	72.0	3.9
Maximus	April 25–April 29 2019	4	9	6.6	6.2	M	2	Subordinate	17.1	79.0	3.6
Tanja	May 28–June 13 2019	17	269	4.4	1.1	F	16	Dominant	18.6	75.0	3.1
Tatjana	April 2–April 6 2019	4	47	3.4	0.7	F	3	Subordinate	16.4	70.0	4.0

potentially falsely classified dives, we focused on diving sections where the previous 10-s bursts were additionally predicted to be swimming.

Assessment of aquatic habitats

We visited and assessed the aquatic habitat of all diving locations as well as random aquatic locations available within the territories of each beaver between June and October 2019 (Fig. 1b). We only sampled sites with a water depth of less than 10 m since vegetation growth here is more abundant due to light conditions [114], whilst also accounting for known diving depths in beavers [99].

For vegetation sampling at each location, sites were sampled using a 1 × 1 m quadrat with an aluminium frame. The quadrat was placed as close to the location as wind and currents allowed. The frame construction had a pyramidal shape, enabling a GoPro camera (GoPro Hero5) to be attached to the top, 0.8 m above the surface, which would keep the quadrat within the camera view. The quadrat was left at the bottom of the site after sediment settled, and pictures and films were recorded. When water depth allowed it, aquatic plants and physical characteristics were recorded in situ using an aqua scope. Aquatic plants were collected with a rake when identification required closer inspection. Plant species identification followed the database of Artsdatabanken [115]. Species abundance was quantified as coverage in percentage, rounding to the nearest 5% [116]. Plants with less than 5% cover were registered as 1% per species.

We categorized each site according to physical characteristics [water depth and sediment type (clay, mud, sand, and rock)], spatial characteristics (distance to riverbank, beaver lodge, and territory border), and characteristics of the aquatic vegetation. We characterized the aquatic vegetation by cover and species richness (number of species) to evaluate importance of quantity and diversity, respectively.

Statistical analysis

We used generalized linear mixed-effects models (GLMMs) with Poisson distribution, log link, and beaver ID as a random effect to investigate how the number of identified dives per night varied between individuals and components of the territories. We analysed the effects of sex (male, female), social rank (dominant, subordinate), age (years), body size (body mass, body length, and tail fat index), and home range size (95% AKDE), and the effects of territory size (bank length in km), mean water depth (m) and mean vegetation cover and species richness.

Using GLMMs with Bernoulli distribution, logit link, with beaver ID and tracking night as random effects, we also investigated how hourly diving probability (1 = a diving event was identified within a given hour, 0 = no diving events were identified within a given hour) varied through the night and between individuals. We analysed the effects of spatiotemporal variables (date, hour of the night, distance to riverbank, lodge, and territory border), individual differences (sex, social rank, age, body sizes, and home range size), and between components of the territories (territory size, mean water depth, mean vegetation cover, and mean species richness).

We used a detrended correspondence analysis (DCA) from the R package 'vegan' v. 2.5–7 [117] to assess the general distribution pattern of the aquatic vegetation in the study river in relation to physical (water depth and sediment type), spatial (distance to riverbank, beaver lodge, and territory border) and vegetation characteristics (vegetation cover and species richness) of the sites. A matrix including aggregated abundance per species was used for the DCA. However, species that only occurred in five sites or less were removed from the matrix. The correlation between the aquatic species compositions and physical, spatial, and vegetation characteristics of the sites were assessed by passively fitting them to the ordination (permutations = 999). From the ordination, comparing species with use, we could furthermore identify species that appeared to be of potential importance to the beavers when diving. For the subsequent resource selection functions, we included variables for the number of focal species present at a site and vegetation cover of these focal species.

We investigated the aquatic habitat selection within territories using GLMMs with Bernoulli distribution, logit link, and beaver ID as a random effect (1 = diving site, 0 = random available site within the territory) [34, 35]. We analysed whether aquatic habitats located at varying water depths, sediment types, distances to riverbank, beaver lodge, and territory border, or with varying vegetation cover (overall and focal species), and species richness (overall and focal species) were used more than was generally available in the territories [35, 118]. Additionally, we analysed the variations in diving selection among individuals in univariate models weighted by number of identified dives by fitting the resource selection function to each individual [119]. This enabled us to analyse how the individual diving selection coefficients varied between beavers of different age, sex, body size, and social rank that furthermore inhabit territories of different size and with varying amount of available water depth, vegetation cover (overall and focal species), and species richness (overall and focal species) [13, 25, 119]. As dives may have different purposes according to their spatial location, we furthermore investigated how log transformed distance to the lodge and riverbank varied temporally (date and hour of the night), by environmental characteristics (depth, sediment, vegetation cover, species richness), and among individuals of different age, sex, body size, social rank, territory size, and home range by using GLMMs with gaussian distribution and beaver ID as a random effect. To examine characteristics associated to the proximate area of the beaver lodge, we furthermore analysed how dives within 150 m of the beaver lodge varied according to the above variables using univariate GLMMs with Gaussian distribution and beaver ID as a random effect.

In all analyses, a list of candidate models was created using ecologically relevant combinations of fixed effects to account for variability in endogenous (such as sex, age, and social rank) and exogenous factors (such as territory size, vegetation composition) that may be important in describing the ecology of beavers (Fig. 2). Because of the sample size, individual effects (sex, age, social rank, territory size, and home range size) should be interpreted with care as they only imply possible ecological effects that should be investigated with more individuals in future studies. We included spatiotemporal interactions (between hour and distance to riverbank, lodge, and territory border, respectively) in the analysis for diving probability, but excluded interactions in all other analyses because of the limited sample size. Individual selection coefficients were similarly analysed in univariate models because of the limited sample size. The fixed effects used in all analyses were not correlated (Pearson *r* coefficients less than 0.5) and variance inflation factor values were less than 3 [120].

Model selection was based on Akaike's information criterion corrected for small sample size [121], and carried out using the R packages 'glmmTMB' v. 1.0.2.1 [122] and 'MuMIn' v. 1.43.17 [123]. The most parsimonious models within $\Delta AICc < 2$ were chosen as the best models to describe the variation [121, 124]. In each model, variables that included zero within their 95% confidence interval (CI) were considered uninformative and reported as unclear effects [124]. The best models were visually validated using the R package 'DHARMa' v. 0.4.1 [125] to plot standardized model residuals against the fitted values [120] and, when relevant, furthermore checked for zero-inflation. Top candidate models for all analyses can be found in the supplemental material (Additional file 1). All analyses were conducted in R 4.0.3 [126].

Results

Nine beavers were tracked with data loggers (Wildbyte technologies, Daily Diaries [52]) and GPS loggers (Techno Smart) affixed to the lower back for a total of 77 nights. Identified diving events lasted between 10 and 110 s, with the majority (80%) lasting 10 s or less. We identified on average (mean ± SD) 9.5 ± 3.1 dives per night for each beaver. We found no clear differences in the number of dives per night between males and females (10.9 ± 3.3 and 8.8 ± 3.0, respectively), among dominants and subordinates (12.9 ± 3.6 and 6.4 ± 2.5, respectively) or as a function of age, body size and tail fat index (Additional file 1). Furthermore, territory size, home range size, mean water depth in territory, and mean vegetation cover and species richness in territory did not have a clear effect on the number of identified dives per night (Additional file 1).

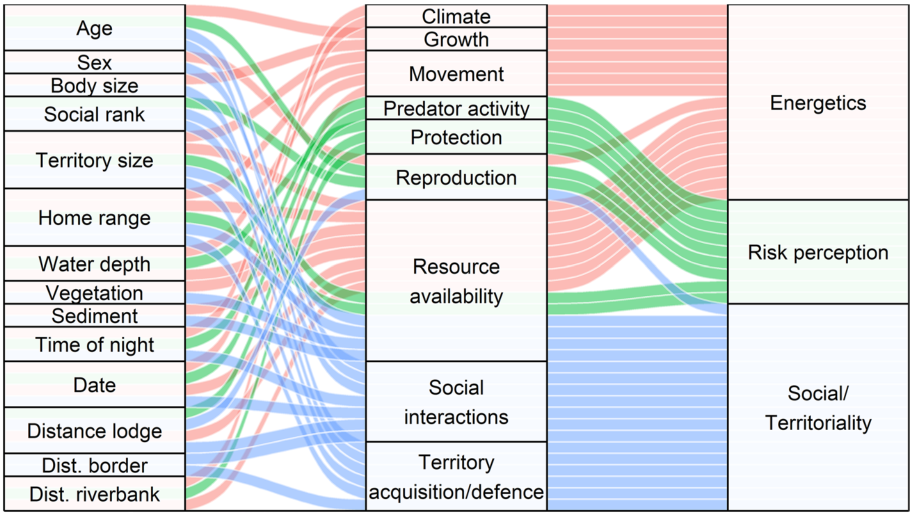

Fig. 2 Alluvial diagram showing how covariates included in the analyses (left) may relate to various ecological mechanisms (middle) which ecologically may have physical, behavioural, and social consequences (right) for the fitness of beavers

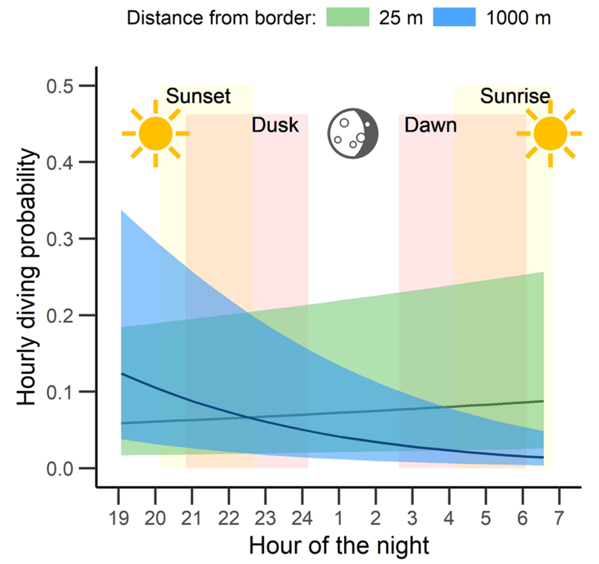

Fig. 3 The predicted relationship ± 95% confidence interval between hourly diving probability, time of night, and distance from territory border among nine individuals in a Eurasian beaver population in southeastern Norway. Yellow boxes represent time of sunset and sunrise through the tracking period. Red boxes represent time of dusk and dawn through the tracking period

Table 2 Effect size (*β*), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of nightly diving probability among nine individuals in a Eurasian beaver population in southeastern Norway

Variable	Estimate *β*	SE	LCI	UCI
Intercept	**− 2.970**	**0.652**	**− 4.247**	**− 1.692**
Hour	**− 0.114**	**0.002**	**− 0.119**	**− 0.110**
Log (distance to territory border)	**− 0.184**	**0.007**	**− 0.197**	**− 0.171**
Hour × log (distance to territory border)	**− 0.064**	**0.002**	**− 0.069**	**− 0.059**
Marginal R^2: 0.01	**Conditional R^2**: 0.84			

Effects were modelled using a GLMM with Bernoulli distribution. Beaver ID and tracking night were included as random effects. Informative parameters are given in bold

Diving probability

Hourly diving probability varied through the night, decreasing over the final hours of the night (Fig. 3) and with increasing distance from the territory borders (Table 2, Fig. 3). We found no differences in hourly diving probability between sexes, social ranks, age, or relative to body size and tail fat index. Furthermore, we found no clear effect of date, distance to riverbank, distance from the lodge, territory size, home range size, mean water depth in territory and mean vegetation diversity within the territory on nightly diving probability (Table 2, Additional file 1).

Table 3 Detrended correspondence analysis results for aquatic vegetation sites in a population of Eurasian beaver in southeastern Norway

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.62	0.60	0.43	0.42
Axis lengths	6.15	4.94	4.30	3.51
Proportion explained %	9.63	9.39	6.78	6.52
Cumulative prop. explained %	9.63	19.02	25.80	32.32

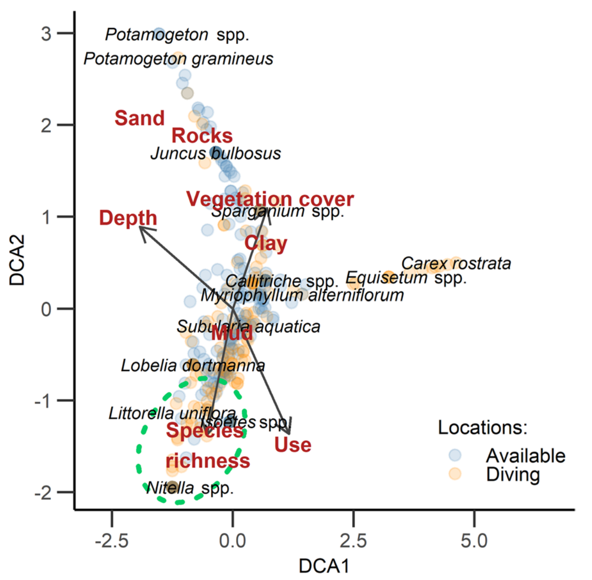

Fig. 4 Detrended correspondence analysis (DCA) of aquatic vegetation sites (points) within territories of nine individuals in a Eurasian beaver population in southeastern Norway. Arrows represent passively fitted environmental gradients and red labels represent environmental centroids. The green ellipse encircles species that may represent important resources at diving locations of the beavers

Characterization of aquatic vegetation

The DCA ordination described up to 32.3% of the variation in the aquatic vegetation composition within the beaver territories with DCA1 and DCA2 describing 9.6 and 9.4% of the variation, respectively (Table 3). The aquatic vegetation within the territories showed great variation and differed clearly with increasing water depth, vegetation cover, species richness, and sediment type (Fig. 4). Diving sites and random available sites within the beaver territories clearly differed in species composition. Diving sites were especially associated with varying amounts of quillwort (*Isoetes* spp.), shoreweed (*Littorella uniflora*), and stonewort (*Nitella* spp.) (Fig. 4). Furthermore, sites were predominantly more used for diving with decreasing water depths, increasing species richness, and decreasing vegetation cover. A list of all aquatic species can be found in Additional file 1.

Table 4 Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of diving location selection among nine individuals in a Eurasian beaver population in southeastern Norway

Variable	Estimate β	SE	LCI	UCI
Intercept	**− 0.934**	**0.216**	**− 1.358**	**− 0.510**
Log (distance to riverbank)	**− 0.686**	**0.086**	**− 0.855**	**− 0.517**
$\text{Sediment}_{\text{Clay}}$	**0.857**	**0.265**	**0.337**	**1.376**
$\text{Sediment}_{\text{Sand}}$	− 0.349	0.308	− 0.952	0.254
$\text{Sediment}_{\text{Rocks}}$	− 0.461	0.286	− 1.022	0.100
Number of focal species present	**0.340**	**0.141**	**0.065**	**0.616**

Marginal R^2: 0.19 **Conditional R^2**: 0.26

Effects were modelled using a GLMM with Bernoulli distribution. Beaver ID was included as random effect. Informative parameters are given in bold

Reference level for sediment = Mud

Resource selection of aquatic habitats within the territory

We found a clear diving selection for aquatic locations closer to the riverbank but found no clear diving selection as a function of distance from lodge, distance from territory border, or water depth (Table 4, Fig. 5a, Additional file 1). Diving selection probability varied as a function of sediment type. Locations having either mud, sand, or rock sediment were less selected than locations with clay sediment (Table 4, Fig. 5b). Furthermore, diving selection probability increased when several of either quillwort, shoreweed, and stonewort were present, but we found no effect of vegetation cover, overall species richness, or vegetation cover of the focal species on the diving selection probability (Table 4, Fig. 5c, Additional file 1).

Individual diving selection coefficients varied among individuals and territories. Individuals exploiting larger home ranges (i.e. 95% AKDE) had a weaker selection for

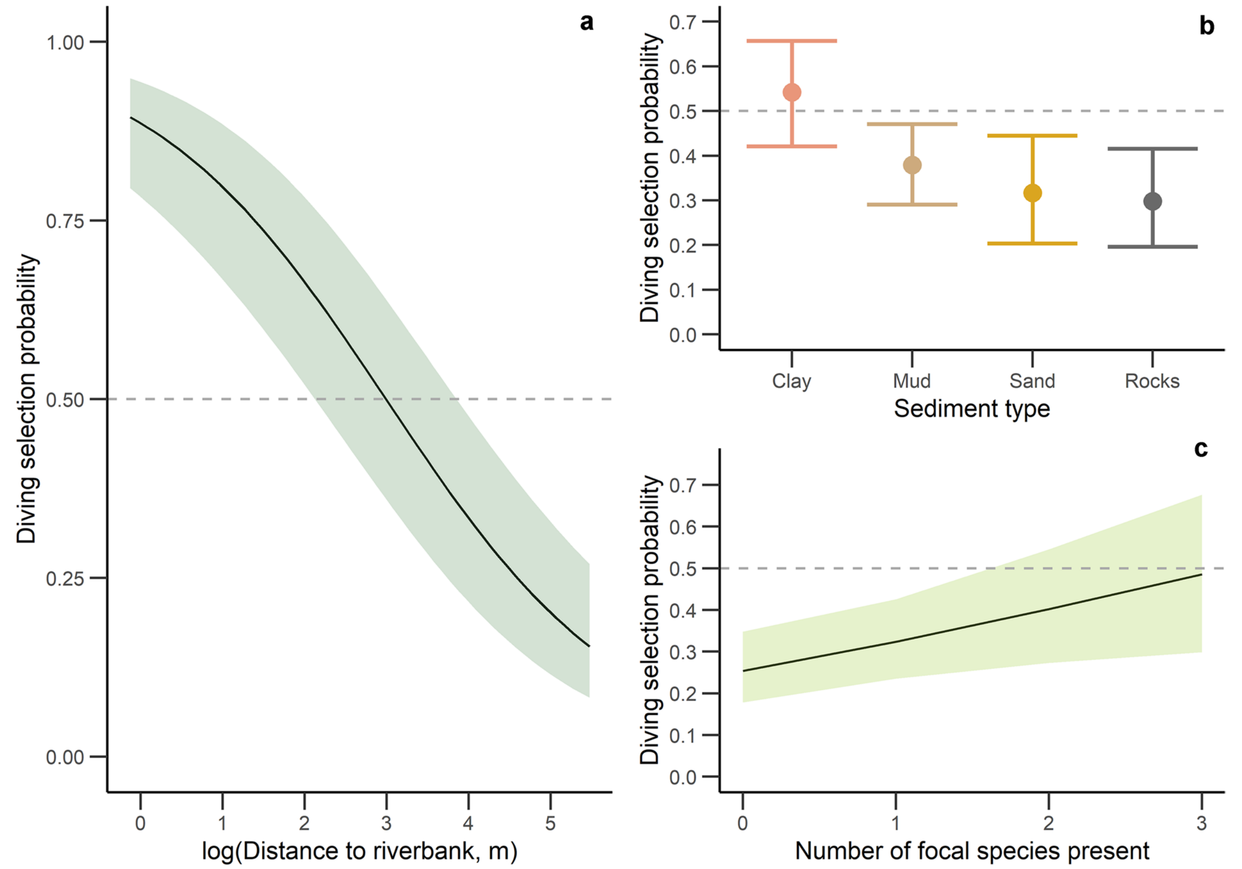

Fig. 5 The predicted relationship ± 95% confidence interval between diving selection probability and **a** distance to riverbank, **b** sediment type and **c** number of focal vegetation species present among nine individuals in a Eurasian beaver population in southeastern Norway

diving locations closer to the riverbank than individuals with smaller home ranges (Table 5, Fig. 6a). We found no clear context dependent effects on selection coefficients for the various sediment types (Additional file 1). Social rank had an effect on diving selection for number of focal species present which were stronger among subordinate individuals than dominant individuals (Table 5, Fig. 6b). We found no conditional effects of other variables on the selection coefficients (Additional file 1).

Table 5 Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of individual selection coefficient for distance to riverbank and number of focal species present among nine individuals in a Eurasian beaver population in southeastern Norway

Variable	Estimate β	SE	LCI	UCI
Selection for distance to riverbank				
Intercept	**−0.465**	**0.169**	**−0.864**	**−0.067**
Log (home range)	**−0.420**	**0.142**	**−0.757**	**−0.084**
R^2: 0.56 $R^2_{adjusted}$: 0.49				
Selection for number of focal species present				
Intercept	0.175	0.131	−0.135	0.485
Social rank$_{subordinate}$	**0.922**	**0.228**	**0.384**	**1.460**
R^2: 0.70 $R^2_{adjusted}$: 0.66				

Effects were modelled using a GLM with gaussian distribution. Analyses were weighed by number of diving sites for each individual. Informative parameters are given in bold

Reference level for social rank = Dominant

We found that diving locations further from the riverbank had a deeper water depth and higher vegetation cover of focal species compared to diving locations closer to the riverbank (Table 6, Fig. 7a, b). Diving locations located further from the beaver lodge had a higher vegetation cover than diving locations closer to the beaver lodge (Table 6, Fig. 7c). Diving distance to the beaver lodge also increased with increasing tail fat index and decreased during the night and during the spring/early summer (Table 6, Fig. 7d–f). Focusing on dives within 150 m of the beaver lodge, we found a difference among sediment types with dives located on clay and mud sediment being closer to the lodge than dives located on sand and rock (Table 6, Fig. 8).

Discussion

We provide new knowledge on aquatic habitat use in a semi-aquatic mammal, the Eurasian beaver, by examining finely resolved information on beaver movement and diving in relation to fine-scaled qualitative assessments of aquatic habitat characteristics within beaver territories. We observed clear spatiotemporal variations in hourly diving probability but found no differences among individuals or territories. Beavers selected for both spatial,

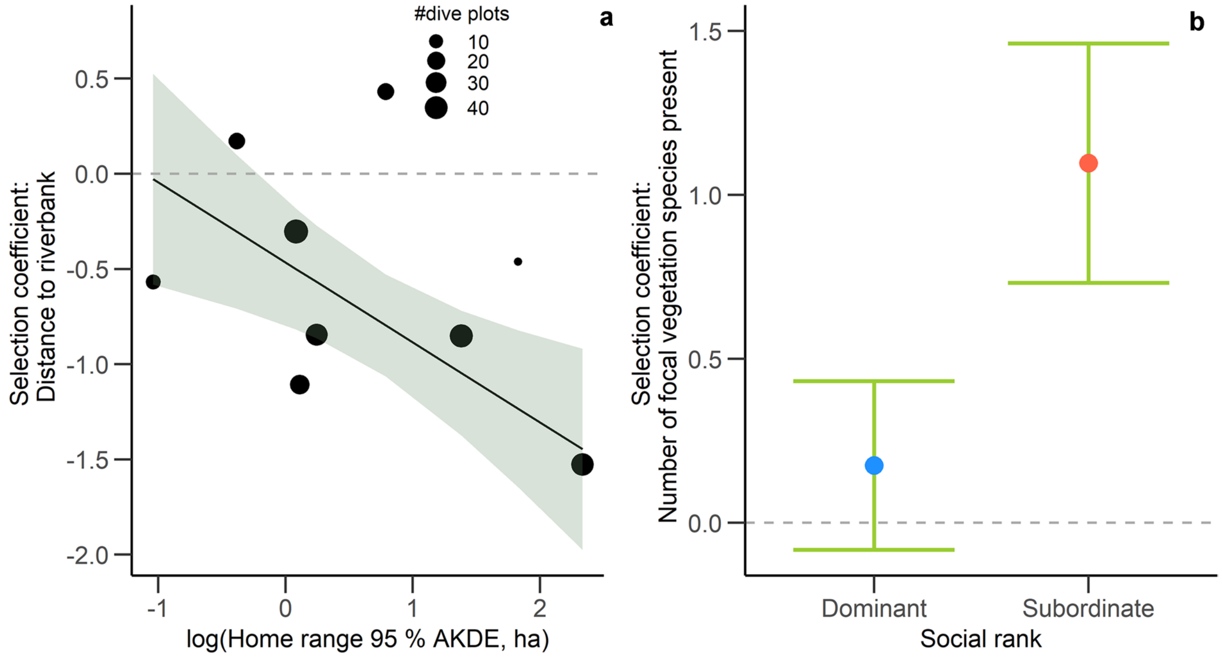

Fig. 6 The predicted relationship ± 95% confidence interval between **a** selection coefficients for distance to riverbank and home range size (AKDE, autocorrelated kernel density estimate) and **b** selection coefficients for number of focal vegetation species present and social rank among nine individuals in a Eurasian beaver population in southeastern Norway

Table 6 Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analyses of distance to riverbank and distance to beaver lodge among dives of nine individuals in a Eurasian beaver population in southeastern Norway

Variable	Estimate β	SE	LCI	UCI
Distance to riverbank				
Intercept	**2.226**	**0.071**	**2.087**	**2.365**
Log (water depth)	**0.603**	**0.053**	**0.499**	**0.708**
Vegetation cover of focal species	**0.010**	**0.003**	**0.005**	**0.015**
Marginal R^2: 0.35 **Conditional R^2**: 0.35				
Distance to beaver lodge				
Intercept	**5.801**	**0.410**	**−0.375**	**11.976**
Vegetation cover	**0.006**	**0.002**	**0.002**	**0.009**
Hour	**−0.071**	**0.023**	**−0.116**	**−0.025**
Julian day	**−0.019**	**0.003**	**−0.025**	**−0.012**
Tail fat index	**1.059**	**0.023**	**0.635**	**1.483**
Marginal R^2: 0.18 **Conditional R^2**: 0.19				
Distance to beaver lodge (dives within 150 m)				
Intercept	**4.227**	**0.091**	**4.049**	**4.404**
$\text{Sediment}_{\text{Clay}}$	−0.098	0.152	−0.395	0.199
$\text{Sediment}_{\text{Sand}}$	**0.670**	**0.240**	**0.201**	**1.140**
$\text{Sediment}_{\text{Rocks}}$	**0.309**	**0.147**	**0.021**	**0.597**
Marginal R^2: 0.25 **Conditional R^2**: 0.25				

Effects were modelled using a GLMMs with gaussian distribution. Beaver ID was included as random effect. Informative parameters are given in bold

Reference level for sediment = Mud

physical and vegetation characteristics in their diving locations, highlighting the degree of choice they exercise for foraging behaviour although selection strength varied between individuals. Furthermore, spatial variations among dives indicate the energetic variability in aquatic habitat use. Often studies in freshwater-inhabiting semi-aquatic mammals focus on the use of terrestrial habitat components, but we show how components of aquatic habitats similarly may be an important resource which can potentially have considerable fitness consequences for a semi-aquatic mammal like the beaver.

Diving patterns

The majority of our identified diving events were short, which matches previous findings for beavers [99, 101] and other semi-aquatic mammals [127–129]. Beavers have previously been reported to spend less than 3% of their nightly activity budget on diving activities which corresponds well with their role as generalist herbivores that do not rely solely on aquatic foraging [99]. Similar diving patterns have been found among semi-aquatic generalist carnivores and may relate to semi-aquatic animals being less specialized for the aquatic environment [101, 129–131]. Beavers may preferably dive to bring large quantities of vegetation to the surface rather than consuming small amounts of vegetation underwater, saving energy by not diving repeatedly to exploit resources at depth, thereby also minimizing heat loss [132, 133]. In fact, an extensive study on diving in beavers by Graf et al. [99] found that animals had high dynamic body acceleration (DBA) (a good proxy for movement-based energy expenditure [134]) for the descent, indicating work done against appreciable buoyancy, as has been noted for many birds with their air-filled plumage [133]. Curiously though, in stark contrast to birds, which use this buoyancy for passive ascents [135], beavers also had high DBA values during their return to the surface, which was suggested to be due to animals having to transport vegetation from the bottom to the surface for consumption [99]. Similar behaviour is commonly observed in water birds such as Eurasian coots (*Fulica atra*) when foraging on aquatic vegetation [136, 137], but also in semi-aquatic carnivores such as American mink (*Neovison vison*) that occasionally consume aquatic food items at the surface or on the riverbank [128, 138]. Critically, this behaviour is most advantageous when large amounts of food can be brought to the surface during one dive, which can then be consumed at leisure without the need for multiple, energetically onerous dives in repetitive feeding bouts such as those performed by carnivorous species [138, 139].

We found a decreased hourly diving probability in the early morning which is contrary to the findings of Graf et al. [99], although they had appreciable variation. Other studies have found a peak in general activity (measured via overall body dynamic acceleration) in the middle of the beavers' principal activity period, suggesting increased activity in the middle of the night [48]. Diving generally has a high overall body dynamic acceleration compared to other behavioural activities and therefore a higher movement-based energy cost [47, 134]. Diving patterns in beavers may be implicitly represented by this general activity pattern, peaking in the middle of the principal activity period, as aquatic habitat use may be costly for a semi-aquatic mammal [101, 140]. Similar diving patterns peaking in the middle of the activity period have been found in other semi-aquatic mammals, such as American mink, that perform temporal niche shifts to avoid interspecific aggression from competitors [128, 141].

Diving patterns may be structured according to the activity peaks of potential terrestrial predators [142]. When beavers bring aquatic resources onto the riverbank to be handled, their risk of predation increases [93, 95]. Beavers are at a particular risk when on land because of their poor eyesight under low light conditions (i.e. they lack *tapetum lucidum*) [143] and dependence on

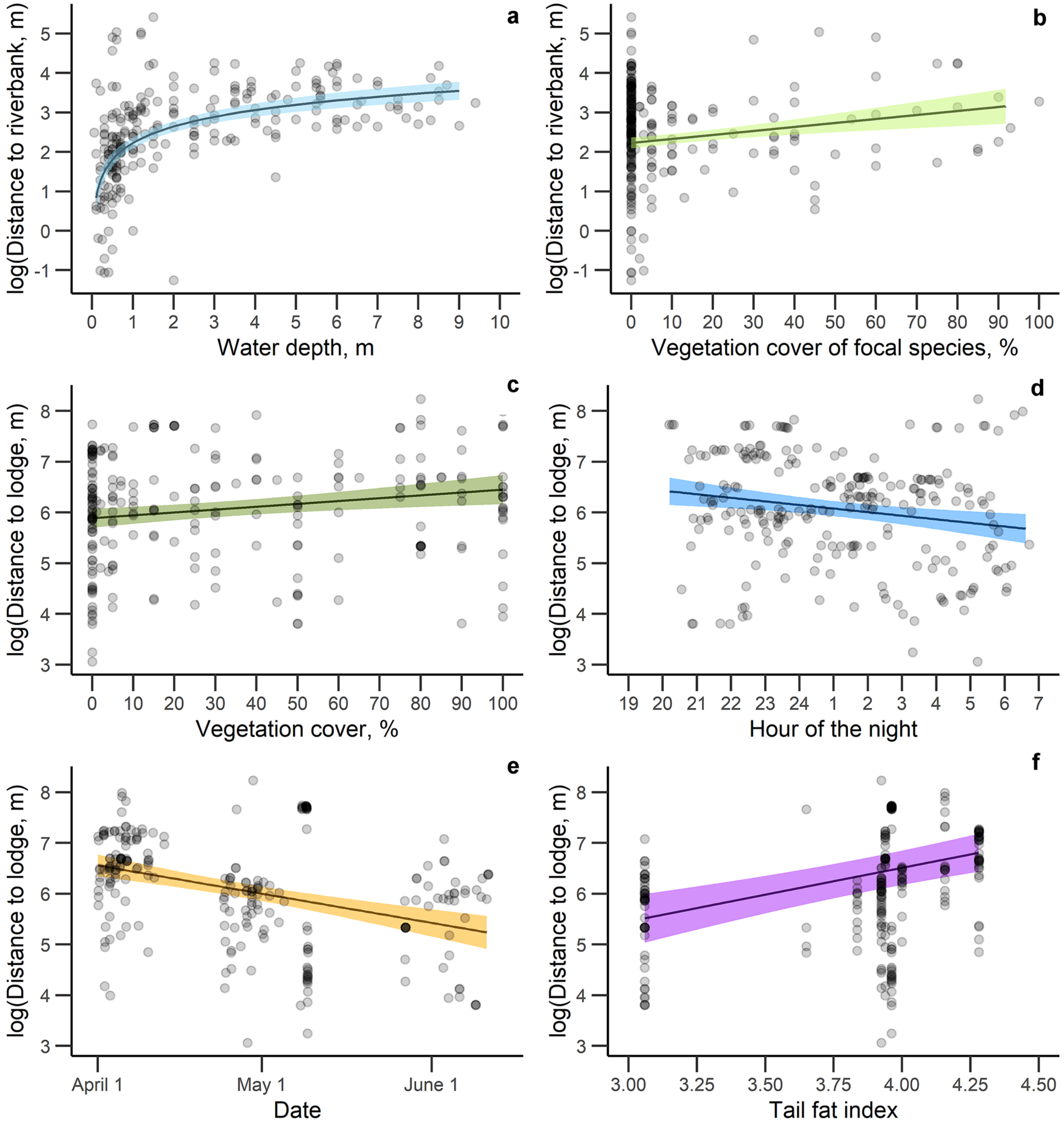

Fig. 7 The predicted relationship ± 95% confidence interval between distance to riverbank and beaver lodge and **a** water depth, **b** vegetation cover of focal species, **c** vegetation cover, **d** hour of the night, **e** Julian day, and **f** tail fat index among dives of nine individuals in a Eurasian beaver population in southeastern Norway. Points represent actual distances

olfaction to detect potential risks [144]. Consequently, they may not detect potential predators, such as wolves (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) that have advanced night vision [145, 146], before being detected themselves. However, wolves have been observed to predate more at dawn, dusk, and during moonlit nights [142], which could increase the benefits of being most active (including diving) in the middle of the night when it is darkest. In North America, beavers make up a large proportion of wolf diet, especially during summer when wolves have been observed to ambush beavers at frequently used locations [95]. Natural predators are absent in our study area, but behavioural activities are known to be influenced by historical threats [84, 147]. In addition,

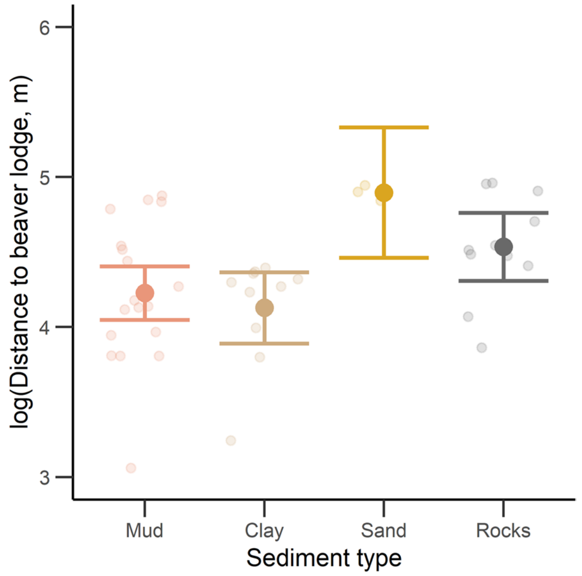

Fig. 8 The predicted relationship ± 95% confidence interval between distance to beaver lodge and sediment type among dives within 150 m of the beaver lodge of nine individuals in a Eurasian beaver population in southeastern Norway. Points represent actual distances

human activities both on land and on water, which are naturally reduced at night, may also influence the activity levels of beavers [147]. Consequently, diving for food resources at dusk and dawn may be perceived to be too risky for beavers.

Diving is presumably not just shaped by risks, but also allows the animals to have access to important aquatic resources [4, 81]. Hourly diving probability decreased with increasing distance from the territory borders which may indicate a possible depletion of aquatic resources near beaver lodges that are often located in central parts of the territory [cf. 148,149]. Although this may be expected to be related to territory size [33], we did not find this, possibly because our sample size was too small. Diving near the borders may also relate to territorial defence activities, which may help reduce aggressive territorial encounters when territorial intruders swim away unseen [89, 150, 151]. However, we were unable to quantify territorial behaviour.

Diving selection

We found a high selection for diving closer to the riverbank. Similar short and shallow dives have been found in other studies of semi-aquatic mammals which probably reflect the energetic constraints of bringing food resources to the riverbank for consumption and a preference for travelling along the riverbank [86, 99, 127, 128]. Association with a riverbank can, in some senses, be treated as a central place [152], which makes clear the energetic costs of leaving the central place to acquire food. In that sense, the decreasing tendency to dive with increasing distance from the riverbank ties in with optimal foraging theory, which has animals maximizing reward and minimizing transit time and energy [153, 154]. Distance to the riverbank may also reflect decreasing aquatic foraging options in terms of decreased macrophyte growth which is highly dependent on water depth and light penetration [114]. But short shallow dives may also be preferred as they are energetically cheaper for semi-aquatic animals like beavers that have high buoyancy [140]. In general, diving locations in semi-aquatic carnivores have been shown to follow distributions of aquatic food resources [127, 155]. We noted that selection for diving locations near the riverbank was statistically stronger among individuals that exploited a larger home range: individuals that exploit a larger home range may have a greater need to stay closer to the riverbank due to higher territory patrolling efforts whereas individuals exploiting smaller home ranges may be able to forage further away from the riverbank [86]. Individuals using larger areas or inhabiting larger territories may also have reduced resource depletion so that, conversely, beavers restricted to smaller areas may be forced to exploit foraging areas further away from the riverbank [33, 156]. Larger home ranges may also have a greater area of shallow water, which, depending on the time spent diving, can be energetically easier to exploit for a semi-aquatic animal [140]. Conversely, individuals with smaller home ranges may have to exploit all habitats to fulfil their energetic requirements [33]. We saw that water depth at the diving locations generally increased with increasing distance from the riverbank, which presumably represent higher energetic costs of diving away from the riverbank, but dives at longer distances from the riverbank also had higher amounts of quillwort, shoreweed, and stonewort present, possibly due to the Ashmole's halo effect [148, 149] operating on animals preferentially associated with the shoreline. This indicates the interplay of depth and distance energetics in a semi-aquatic animal, which have to be balanced with the calorific value of the food plants and their location [132, 133, 140].

Beavers had a higher selection for diving at locations with clay sediment, which may be an important building material for lodges and dams [96], although dams are not present in our study site, and beavers may additionally make use of burrows dug into the riverbank whereby the clay sediment aids in enhancing the structural integrity of those burrows [157, 158]. Lodges and dams are mostly repaired in the autumn [159, 160], but may be repaired after flooding events too [161]. Mud is also widely used for beaver constructions [97], although mud substrates, despite being highly abundant in the study area, seemed not to be selected. Beavers continuously need to apply fresh mud and other fine debris to seal their constructions as it is continuously washed away [96, 97]. We found that dives on mud and clay sediment within 150 m of the beaver lodge were generally located closer to the beaver lodges than dives located on sand and rock sediment which, we believe, indicates the importance of fine sediment for building constructions. However, we cannot rule out that mud and clay sediment may contain advantageous foraging options, although our ordination did not show strong correlation between mud and clay sediment with aquatic species richness or vegetation cover.

We found a higher selection for diving locations with presence of species of quillwort, shoreweed, and stonewort, which may represent important food resources for the beaver. Other studies have similarly found a high preference for quillwort in the early summer [73], and algae like stonewort may be selected for its protein content and other nutrients [65]. Although beavers mainly forage on woody vegetation, aquatic vegetation seems to be seasonally important, with studies additionally reporting beavers foraging on, among others, water lilies (*Nymphaea* spp.), pondweed (*Potamogeton* spp.), water horsetail (*Equisetum* spp.), waterweed (*Elodea* spp.), and water lobelia (*Lobelia dortmanna*) [64–66, 68, 69, 71, 98]. Incorporating aquatic vegetation into a varied diet could be a strategy to minimize risk of nutrient deficiency [162], which may be seasonally beneficial to some individuals (e.g. females during lactation when energetic requirements increase) [163, 164]. However, we did not find any selection differences between males and females which may be because of our limited number of individuals. Other studies on semi-aquatic mammals show how males and females in two species of shrew (*Neomys fodiens* and *Sorex coronatus*) use separate foraging habitats during the breeding season [165]. Males and females in our population have been shown to differ seasonally in aquatic foraging with peaks in the spring and late summer for females, whereas males only foraged on aquatic vegetation in the spring [166]. We found that selection for the focal plant species were statistically stronger among subordinate individuals, which may be linked to their higher energetic requirements resulting from their activities related to attempts to become dominant in a territory [57] (e.g. performing more extra territorial movements [15]). A higher use of aquatic vegetation may also be a risk-avoiding strategy, minimizing predation risk on land [92, 95]. In other studies, adult beavers have been found to forage less on aquatic vegetation than subadult individuals (i.e. 2-year-old) [65] which may be less risk-willing as they potentially face higher fitness costs in terms of future reproductive success [167] and therefore adjust their foraging strategy accordingly [4, 168]. Similarly, we found that beavers with lower tail fat index tended to dive closer to their lodge, which may be a consequence of territorial constraints as individuals with higher body condition may be better able to cope with the increased cost of patrolling and protecting territory borders [18, 86]. Diving locations located further from the beaver lodge also had higher amounts of vegetation cover which indicate the energetic trade-offs between costs and benefits that a central place foraging individual experiences [4, 169]. Diving distance to the lodge decreased through the night which may indicate a functional change in the purpose of the dive. As dives further from the lodge occurred at locations with more aquatic vegetation, these dives may be intended for foraging whereas dives later in the night may be used for building activities. We also saw that diving distance to the lodge decreased from early spring to summer, which may relate to increased parenting activities that require the beaver to stay closer to the lodge when the kits are born in mid-May [58]. Diving for food resources may be perceived as less risk-taking than going on land [87] and could be preferred by parenting individuals to ensure the growth and survival of their offspring [170].

Methodological limitations

Using dead-reckoning together with an acceleration-based behavioural classification model to identify the temporal and spatial distribution of clear diving events, we identified considerably fewer diving events than a previous study in beavers that identified typically 40 dives per night [99]. This may be related to seasonal variations as we only tracked beavers from April to June, whereas Graf et al. [99] also included observations from the autumn (September to October) where diving conditions may be more favourable, because of increased water temperature and life history patterns [15, 57, 99]. But dives may also be masked by our method. Despite a high classification accuracy of diving events from the model by Graf et al. [47], some events may not be identified because some behavioural activities, including behaviours not described by the model, can have similar patterns and mask each other [47]. Therefore, it is important to clearly define each behavioural activity in an acceleration-based classification model, but also to include enough variations of each activity from several individuals to improve the precision of the model. Different diving styles may be misclassified as other behavioural categories if the behavioural classification model is not trained on several variations of each behavioural category but only includes typical acceleration patterns for each behavioural category. For example, the ecological difference between a 'dive' and an 'almost dive' may be minimal when a beaver can access aquatic resources by just sticking its head underwater, but they may fall within two different behavioural categories because of variable acceleration patterns. The acceleration can also be affected by external environmental forces such as wave actions [134], which can be corrected by incorporating magnetism in the classification [50]. We also only gathered acceleration in 10 s bursts for the classification model, which may mask some of the diving events of shorter duration. A more detailed inspection of the fine-scale acceleration and body postures may improve the classification and provide more information on the actual behavioural activity [171, 172]. Placing the behavioural activities into a larger context (i.e. what the animal did before and after an activity) would furthermore help understand the ecological significance of each activity. In addition, the ability of dead-reckoning procedures is spatially limited by the precision of the GPS positions that are used to ground-truth the dead-reckoned movement tracks [49, 51], which means that we will have introduced some spatial error in the locations of the diving events [112, 113]. However, this potential error will be consistent along the tracking period making it less likely to bias our results. The high classification accuracy of the model together with the filtering of less likely diving locations (e.g. on land or not in combination with swimming) improve our confidence in our ability to classify relevant diving locations in our beaver population.

Conclusion

By coupling fine-scaled information on individual beavers' movement and diving with comprehensive qualitative assessments of aquatic habitat characteristics within beaver territories, we provided new knowledge on the aquatic habitat use by a freshwater semi-aquatic mammal. We showed how energetic constraints may shape beavers' spatial use of the aquatic environment, and how aquatic habitats may have great importance for both foraging, building materials and safety, even in absence of natural predators. However, future studies should investigate the importance of aquatic habitat use relative to terrestrial habitat use. Several groups of individuals experiencing various ecological conditions may benefit greatly from the use of aquatic resources, consequently affecting their body condition, reproduction, and survival [57, 90], which should be investigated further in future studies including more individuals and populations.

Supplementary Information

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Additional file 1: S1. The model selection results for the best candidate models investigating the number of dives per night among nine beavers in a Eurasian beaver population in south-eastern Norway. **S2.** The model selection results for the best candidate models investigating the diving probability among nine beavers in a Eurasian beaver population in south-eastern Norway. **S3.** List of aquatic species abundance in Saua river in south-eastern Norway. **S4.** The model selection results for the best candidate models investigating the diving habitat selection among nine beavers in a Eurasian beaver population in south-eastern Norway. **S5.** The model selection results for the best candidate models investigating the individual context-dependent diving selection for distance to riverbank among nine beavers in a Eurasian beaver population in south-eastern Norway. **S6.** The model selection results for the best candidate models investigating the individual context-dependent diving selection for clay sediment among nine beavers in a Eurasian beaver population in south-eastern Norway. **S7.** The model selection results for the best candidate models investigating the individual context-dependent diving selection for mud sediment among nine beavers in a Eurasian beaver population in south-eastern Norway. **S8.** The model selection results for the best candidate models investigating the individual context-dependent diving selection for sand sediment among nine beavers in a Eurasian beaver population in south-eastern Norway. **S9.** The model selection results for the best candidate models investigating the individual context-dependent diving selection for rock sediment among nine beavers in a Eurasian beaver population in south-eastern Norway. **S10.** The model selection results for the best candidate models investigating the individual context-dependent diving selection for species richness of focal species among nine beavers in a Eurasian beaver population in south-eastern Norway. **S11.** The model selection results for the best candidate models investigating the diving distance to riverbank among nine beavers in a Eurasian beaver population in south-eastern Norway. **S12.** The model selection results for the best candidate models investigating the diving distance to beaver lodge among nine beavers in a Eurasian beaver population in south-eastern Norway. **S13.** The model selection results for the best candidate models investigating the diving distance to beaver lodge among dives within 150 m of the lodge of nine beavers in a Eurasian beaver population in south-eastern Norway.

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Authors' contributions

FR founded the NBP and RMM obtained additional supporting funding for this subproject. RMM, SR, MEH, and FR developed the study design. MEH led the field work of the study with support from RMM, SR and FR. RMM performed the statistical analyses with support from SR and MEH. RMM wrote the manuscript with support from SR, RPW and FR. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

All capture and handling procedures were approved by the Norwegian Experimental Animal Board (FOTS ID15947) and by the Norwegian Directorate for Nature Management (2014/14415). Our study met the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching [173]. No individuals were injured during capture and handling, and they were all successfully released. All methods were performed in accordance with the relevant guidelines and regulations [174]. No short-term effects have been observed on the movement after tagging [48]. Body mass of dominant individuals have been observed to decrease with number of capture and handling events, but no statistically clear effects have been observed on survival or other body condition indices [57]. Number of capture and handling events was also observed to affect reproduction, but the population seemed habituated to repeated capture and handling in the long-term [57]. To minimize potential risks, the NBP prioritized capture and handling individuals that were necessary for the monitoring and experiments with clear objectives.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Publisher's Note

Aquatic habitat use in a semi-aquatic mammal, the Eurasian beaver

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S1: The model selection results for the best candidate models investigating the number of dives per night among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	deltaAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
0	**3**	**-245.99**	**498.31**	**0.00**	**0.10**	**0.00**	**0.92**
9	4	-245.10	498.76	0.46	0.08	0.16	0.92
10	4	-245.19	498.94	0.64	0.07	0.12	0.92
2	4	-245.42	499.40	1.10	0.06	0.07	0.92
5+9	5	-244.30	499.45	1.14	0.06	0.28	0.92
4	4	-245.46	499.47	1.17	0.06	0.07	0.91
5+10	5	-244.35	499.55	1.24	0.05	0.26	0.92
12	4	-245.72	499.99	1.68	0.04	0.04	0.91
5	4	-245.72	500.00	1.70	0.04	0.03	0.91
1	4	-245.80	500.16	1.86	0.04	0.03	0.92
2+5	5	-244.71	500.26	1.95	0.04	0.10	0.91
6	4	-245.86	500.28	1.98	0.04	0.02	0.92
3	4	-245.93	500.41	2.11	0.03	0.01	0.92
7	4	-245.96	500.47	2.17	0.03	0.00	0.92
8	4	-245.97	500.49	2.18	0.03	0.00	0.92
2+5+9	6	-243.67	500.54	2.23	0.03	0.30	0.92
2+9	5	-244.86	500.57	2.27	0.03	0.18	0.92
2+5+10	6	-243.78	500.76	2.45	0.03	0.27	0.91
10+11	5	-244.96	500.77	2.47	0.03	0.18	0.92
2+10	5	-244.97	500.79	2.48	0.03	0.15	0.92

0 = null, 1 = Sex, 2 = Social rank, 3 = Age, 4 = Territory size, 5 = Home range size, 6 = Body mass, 7 = Body length, 8 = Tail fat index, 9 = Vegetation cover, 10 = Species richness, 11 = Water depth

S2: The model selection results for the best candidate models investigating the diving probability among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	deltaAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
1+6+12+13	7	-97600.51	195215.01	0.00	0.16	0.07	0.84
1+6+11+12+13	8	-97599.67	195215.33	0.32	0.13	0.07	0.84
1+4+12+13	7	-97601.03	195216.07	1.06	0.09	0.05	0.84
1+4+11+12+13	8	-97600.19	195216.39	1.37	0.08	0.05	0.84
1+12+13	**6**	**-97602.43**	**195216.87**	**1.85**	**0.06**	**0.01**	**0.84**
1+11+12+13	7	-97601.59	195217.18	2.17	0.05	0.01	0.84
1+5+12+13	7	-97601.64	195217.29	2.27	0.05	0.04	0.84
1+5+11+12+13	8	-97600.80	195217.60	2.59	0.04	0.04	0.84
1+10+12+13	7	-97602.12	195218.24	3.22	0.03	0.02	0.84
1+7+12+13	7	-97602.13	195218.27	3.26	0.03	0.02	0.84
1+3+12+13	7	-97602.14	195218.28	3.27	0.03	0.02	0.84
1+2+12+13	7	-97602.21	195218.42	3.41	0.03	0.02	0.84
1+8+12+13	7	-97602.23	195218.47	3.45	0.03	0.02	0.84
1+9+12+13	7	-97602.26	195218.51	3.50	0.03	0.02	0.84
1+10+11+12+13	8	-97601.28	195218.56	3.54	0.03	0.02	0.84
1+7+11+12+13	8	-97601.29	195218.59	3.57	0.03	0.02	0.84
1+3+11+12+13	8	-97601.30	195218.60	3.59	0.03	0.02	0.84
1+2+11+12+13	8	-97601.37	195218.74	3.73	0.02	0.02	0.84
1+8+11+12+13	8	-97601.39	195218.78	3.77	0.02	0.02	0.84
1+9+11+12+13	8	-97601.41	195218.83	3.82	0.02	0.02	0.84

1 = Hour 2 = Julian day, 3 = Sex, 4 = Age, 5 = Territory size, 6 = Home range size, 7 = Social rank, 8 = Tail fat index, 9 = Vegetation cover, 10 = Species richness, 11 = Distance to riverbank, 12 = Distance to border, 13 = Hour x Distance to border

S3: List of aquatic species abundance in Saua river in south-eastern Norway.

SCIENTIFIC NAME	COMMON NAME	MEAN ABUNDANCE (%)	SD
Alisma plantago-aquatica	Water plantain	>0.01	0.04
Callitriche hamulata	Intermediate water starwort	4.76	12.48
Callitriche spp.	Starworts	0.37	4.28
Carex rostrata	Bottle sedge	0.91	8.24
Elodea canadensis	Canadian pondweed	0.46	5.59
Equisetum fluviatile	Water horsetail	1.77	10.70
Equisetum hyemale	Rough horsetail	>0.01	0.08
Isoetes echinospora	Spring quillwort	1.80	7.74
Isoetes lacustris	Quillwort	0.59	6.19
Juncus bulbosus	Bulbous rush	6.21	18.59
Lemna minor	Common duckweed	>0.01	0.12
Littorella uniflora	Shoreweed	2.98	13.09
Lobelia dortmanna	Water lobelia	2.64	7.35
Lysimachia thyrsiflora	Tufted loosestrife	0.02	0.32
Menyanthes trifoliata	Bogbean	>0.01	0.08

Myriophyllum alterniflorum	Alternate water-milfoil	2.03	8.56
Nitella spp.	Stoneworts	4.45	13.72
Nuphar spp.	Water lilies	0.01	0.21
Nuphar lutea	Yellow water lily	0.16	2.66
Potamogeton alpinus	Red pondweed	0.20	4.18
Potamogeton berchtoldii	Small pondweed	0.52	4.84
Potamogeton gramineus	Various-leaved pondweed	1.21	8.47
Potamogeton natans	Broad-leaved pondweed	0.03	0.51
Potamogeton perfoliatus	Perfoliate pondweed	0.05	1.25
Potamogeton spp.	Pondweeds	0.24	2.61
Ranunculus reptans	Creeping spearwort	0.03	0.46
Sparganium angustifolium	Floating bur-reed	0.22	3.22
Sparganium spp.	Bur-reeds	1.24	4.71
Subularia aquatica	Water awlwort	8.95	20.10
Utricularia spp.	Bladderworts	0.12	1.30

S4: The model selection results for the best candidate models investigating the diving habitat selection among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	**df**	**log likelihood**	**AICc**	**deltaAICc**	**weight**	**$R^2_{marginal}$**	**$R^2_{conditional}$**
1+5+8	**7**	**-394.01**	**802.17**	**0.00**	**0.23**	**0.19**	**0.26**
1+3+5+8	8	-393.42	803.03	0.86	0.15	0.19	0.26
1+2+5+8	8	-393.94	804.08	1.91	0.09	0.19	0.26
1+4+5+8	8	-394.01	804.21	2.04	0.08	0.19	0.26
1+2+3+5+8	9	-393.33	804.92	2.75	0.06	0.19	0.26
1+3+4+5+8	9	-393.42	805.08	2.91	0.05	0.19	0.26
1+5+6	7	-395.67	805.48	3.31	0.04	0.19	0.25
1+3+5+6	8	-394.91	806.01	3.84	0.03	0.19	0.25
1+5	6	-396.95	806.02	3.85	0.03	0.19	0.24
1+2+4+5+8	9	-393.94	806.13	3.96	0.03	0.19	0.26
1+5+9	7	-396.07	806.28	4.11	0.03	0.19	0.25
1+3+5	7	-396.33	806.82	4.65	0.02	0.19	0.25
1+2+3+4+5+8	10	-393.33	806.97	4.80	0.02	0.20	0.26
1+4+5	7	-396.53	807.21	5.04	0.02	0.19	0.24
1+3+5+9	8	-395.51	807.21	5.04	0.02	0.19	0.25
1+2+5+6	8	-395.66	807.52	5.35	0.02	0.19	0.25
1+4+5+9	8	-395.85	807.89	5.72	0.01	0.19	0.25
1+5+7	7	-396.93	808.02	5.85	0.01	0.19	0.24
1+2+5	7	-396.94	808.03	5.86	0.01	0.19	0.24
1+2+3+5+6	9	-394.90	808.05	5.88	0.01	0.19	0.25

1 = Distance to riverbank, 2 = Distance to territory border, 3 = Distance to lodge, 4 = Water depth, 5 = Sediment, 6 = Vegetation cover, 7 = Species richness, 8 =Number of focal species present, 9 = Vegetation cover$_{\text{focal species}}$

S5: The model selection results for the best candidate models investigating the individual context-dependent diving selection for distance to riverbank among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	**df**	**log likelihood**	**AICc**	**deltaAICc**	**weight**	**R^2**	**$R^2_{adjusted}$**
Home range size	**3**	**-4.54**	**19.88**	**0.00**	**0.39**	**0.56**	**0.49**
Distance to riverbank	3	-5.63	22.05	2.18	0.13	0.43	0.35
Null	2	-8.18	22.37	2.49	0.11	0.00	0.00
Body mass	3	-6.47	23.73	3.86	0.06	0.32	0.22
Body length	3	-6.52	23.85	3.97	0.05	0.31	0.21
Distance to lodge	3	-6.83	24.46	4.58	0.04	0.26	0.15
Sex	3	-7.32	25.44	5.57	0.02	0.17	0.06
Vegetation cover	3	-7.44	25.68	5.80	0.02	0.15	0.03
Territory size	3	-7.50	25.80	5.93	0.02	0.14	0.02
Age	3	-7.62	26.05	6.17	0.02	0.12	-0.01
Tail fat index	3	-7.67	26.15	6.27	0.02	0.11	-0.02
Vegetation cover$_{\text{focal species}}$	3	-7.68	26.17	6.29	0.02	0.11	-0.02
Water depth	3	-7.70	26.20	6.32	0.02	0.10	-0.03
Social rank	3	-7.72	26.24	6.36	0.02	0.10	-0.03
Species richness	3	-7.77	26.33	6.45	0.02	0.09	-0.04
Number of focal species present	3	-7.92	26.64	6.77	0.01	0.06	-0.08
Distance to territory border	3	-8.10	27.00	7.12	0.01	0.02	-0.12
Julian day	3	-8.15	27.10	7.22	0.01	0.01	-0.13

S6: The model selection results for the best candidate models investigating the individual context-dependent diving selection for clay sediment among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	**df**	**log likelihood**	**AICc**	**deltaAICc**	**weight**	**R^2**	**$R^2_{adjusted}$**
Null	**2**	**-11.47**	**32.93**	**0.00**	**0.99**	**0.00**	**0.00**
Distance to riverbank	3	-7.42	44.84	11.91	0.00	0.80	0.74
Species richness	3	-7.64	45.28	12.35	0.00	0.78	0.71
Vegetation cover	3	-7.66	45.31	12.38	0.00	0.78	0.71
Body length	3	-8.30	46.61	13.68	0.00	0.72	0.62
Social rank	3	-9.00	48.01	15.08	0.00	0.63	0.50
Number of focal species present	3	-9.15	48.31	15.38	0.00	0.60	0.47
Distance to lodge	3	-9.23	48.47	15.54	0.00	0.59	0.45
Territory size	3	-9.26	48.51	15.58	0.00	0.59	0.45
Vegetation cover$_{\text{focal species}}$	3	-9.54	49.08	16.14	0.00	0.54	0.38
Water depth	3	-10.39	50.78	17.85	0.00	0.35	0.13
Age	3	-10.88	51.75	18.82	0.00	0.21	-0.05
Amount of sand	3	-10.88	51.75	18.82	0.00	0.21	-0.05
Amount of mud	3	-11.30	52.60	19.67	0.00	0.06	-0.25
Julian day	3	-11.31	52.61	19.68	0.00	0.06	-0.25
Body mass	3	-11.36	52.73	19.80	0.00	0.04	-0.28
Tail fat index	3	-11.42	52.85	19.92	0.00	0.02	-0.31
Amount of clay	3	-11.46	52.91	19.98	0.00	0.00	-0.33
Home range size	3	-11.46	52.92	19.99	0.00	0.00	-0.33

S7: The model selection results for the best candidate models investigating the individual context-dependent diving selection for mud sediment among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	**df**	**log likelihood**	**AICc**	**deltaAICc**	**weight**	**R^2**	**$R^2_{adjusted}$**
Distance to lodge	3	-11.26	33.32	0.00	0.20	0.50	0.43
Body length	3	-11.45	33.69	0.38	0.17	0.48	0.41
Territory size	3	-11.86	34.51	1.20	0.11	0.43	0.35
Null	**2**	**-14.39**	**34.78**	**1.47**	**0.10**	**0.00**	**0.00**
Social rank	3	-12.11	35.01	1.70	0.09	0.40	0.31
Number of focal species present	3	-12.20	35.20	1.88	0.08	0.39	0.30
Distance to riverbank	3	-12.76	36.31	2.99	0.05	0.30	0.21
Vegetation cover$_{focal\ species}$	3	-12.78	36.37	3.05	0.04	0.30	0.20
Species richness	3	-12.86	36.52	3.20	0.04	0.29	0.19
Vegetation cover	3	-13.89	38.58	5.27	0.01	0.11	-0.02
Julian day	3	-13.89	38.58	5.27	0.01	0.11	-0.02
Body mass	3	-14.18	39.16	5.84	0.01	0.05	-0.09
Age	3	-14.21	39.22	5.90	0.01	0.04	-0.10
Home range size	3	-14.22	39.24	5.92	0.01	0.04	-0.10
Water depth	3	-14.22	39.25	5.93	0.01	0.04	-0.10
Tail fat index	3	-14.24	39.28	5.96	0.01	0.03	-0.10
Distance to territory border	3	-14.32	39.45	6.13	0.01	0.02	-0.13
Amount of mud	3	-14.37	39.54	6.22	0.01	0.01	-0.14
Sex	3	-14.37	39.54	6.23	0.01	0.00	-0.14

S8: The model selection results for the best candidate models investigating the individual context-dependent diving selection for sand sediment among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	**df**	**log likelihood**	**AICc**	**deltaAICc**	**weight**	**R^2**	**$R^2_{adjusted}$**
Null	**2**	**-10.28**	**28.57**	**0.00**	**0.51**	**0.00**	**0.00**
Social rank	3	-7.27	32.55	3.98	0.07	0.63	0.54
Distance to riverbank	3	-7.37	32.73	4.17	0.06	0.62	0.53
Vegetation cover	3	-7.59	33.19	4.62	0.05	0.59	0.49
Distance to lodge	3	-7.71	33.42	4.85	0.05	0.58	0.47
Territory size	3	-7.72	33.45	4.88	0.04	0.57	0.47
Species richness	3	-7.91	33.82	5.25	0.04	0.55	0.43
Body length	3	-8.20	34.39	5.82	0.03	0.50	0.38
Number of focal species present	3	-8.62	35.25	6.68	0.02	0.43	0.28
Vegetation cover$_{focal\ species}$	3	-8.83	35.66	7.09	0.01	0.38	0.23
Age	3	-8.86	35.72	7.16	0.01	0.38	0.22
Water depth	3	-9.26	36.52	7.96	0.01	0.29	0.11
Amount of sand	3	-9.81	37.63	9.06	0.01	0.14	-0.07
Julian day	3	-9.98	37.96	9.39	0.00	0.10	-0.13
Amount of mud	3	-10.01	38.02	9.45	0.00	0.09	-0.14
Body mass	3	-10.13	38.26	9.69	0.00	0.05	-0.19
Tail fat index	3	-10.22	38.45	9.88	0.00	0.02	-0.23
Amount of rocks	3	-10.24	38.47	9.90	0.00	0.02	-0.23
Amount of clay	3	-10.25	38.51	9.94	0.00	0.01	-0.24

S9: The model selection results for the best candidate models investigating the individual context-dependent diving selection for rock sediment among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	deltaAICc	weight	R^2	$R^2_{adjusted}$
Body length	3	-5.58	25.17	0.00	0.24	0.64	0.56
Null	**2**	**-9.11**	**25.23**	**0.06**	**0.24**	**0.00**	**0.00**
Distance to lodge	3	-5.68	25.36	0.20	0.22	0.62	0.55
Distance to riverbank	3	-6.95	27.90	2.73	0.06	0.46	0.35
Territory size	3	-7.13	28.25	3.08	0.05	0.43	0.32
Social rank	3	-7.38	28.77	3.60	0.04	0.39	0.27
Amount of clay	3	-8.25	30.50	5.33	0.02	0.22	0.06
Tail fat index	3	-8.40	30.80	5.63	0.01	0.18	0.02
Julian day	3	-8.46	30.91	5.74	0.01	0.17	0.01
Body mass	3	-8.56	31.12	5.96	0.01	0.15	-0.03
Amount of mud	3	-8.63	31.26	6.10	0.01	0.13	-0.05
Sex	3	-8.83	31.65	6.49	0.01	0.08	-0.11
Number of focal species present	3	-8.83	31.67	6.50	0.01	0.08	-0.11
Amount of rocks	3	-8.86	31.73	6.56	0.01	0.07	-0.12
Amount of sand	3	-8.96	31.92	6.75	0.01	0.04	-0.15
Vegetation $cover_{focal\ species}$	3	-9.02	32.05	6.88	0.01	0.03	-0.17
Species richness	3	-9.02	32.05	6.88	0.01	0.03	-0.17
Water depth	3	-9.09	32.17	7.01	0.01	0.01	-0.19
Distance to territory border	3	-9.10	32.19	7.03	0.01	0.00	-0.19
Home range size	3	-9.10	32.20	7.03	0.01	0.00	-0.19

S10: The model selection results for the best candidate models investigating the individual context-dependent diving selection for species richness of focal species among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	deltaAICc	weight	R^2	$R^2_{adjusted}$
Social rank	**3**	**-2.39**	**15.58**	**0.00**	**0.78**	**0.70**	**0.66**
Age	3	-5.39	21.58	5.99	0.04	0.42	0.33
Null	2	-7.82	21.65	6.06	0.04	0.00	0.00
Territory size	3	-6.25	23.29	7.71	0.02	0.30	0.19
Species richness	3	-6.32	23.44	7.86	0.02	0.28	0.18
Water depth	3	-6.33	23.45	7.87	0.02	0.28	0.18
Body length	3	-6.36	23.52	7.94	0.01	0.28	0.17
Vegetation cover	3	-6.42	23.65	8.07	0.01	0.27	0.16
Distance to lodge	3	-6.87	24.54	8.96	0.01	0.19	0.08
Vegetation $cover_{focal\ species}$	3	-6.97	24.75	9.17	0.01	0.17	0.05
Home range size	3	-7.00	24.80	9.22	0.01	0.17	0.05
Number of focal species present	3	-7.06	24.91	9.33	0.01	0.16	0.04
Tail fat index	3	-7.33	25.45	9.87	0.01	0.10	-0.02
Sex	3	-7.55	25.89	10.31	0.00	0.06	-0.07
Julian day	3	-7.58	25.97	10.38	0.00	0.05	-0.08

Body mass	3	-7.66	26.13	10.55	0.00	0.03	-0.10
Distance to territory border	3	-7.73	26.25	10.67	0.00	0.02	-0.12
Distance to riverbank	3	-7.76	26.32	10.74	0.00	0.01	-0.13

S11: The model selection results for the best candidate models investigating the diving distance to riverbank among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	deltaAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
1+3+12	6	-320.12	652.60	0.00	0.16	0.36	0.36
1+3	**5**	**-321.40**	**653.06**	**0.45**	**0.12**	**0.35**	**0.35**
1+3+4	6	-320.80	653.96	1.35	0.08	0.36	0.36
1+3+9	6	-320.99	654.35	1.74	0.07	0.36	0.36
1+3+14	6	-321.04	654.43	1.83	0.06	0.36	0.36
1+3+5	6	-321.26	654.89	2.29	0.05	0.35	0.35
1+3+13	6	-321.31	654.99	2.38	0.05	0.35	0.35
1+3+6	6	-321.32	655.00	2.40	0.05	0.35	0.35
1+3+8	6	-321.36	655.08	2.47	0.05	0.35	0.35
1+3+10	6	-321.36	655.09	2.49	0.05	0.35	0.35
1+3+7	6	-321.39	655.13	2.53	0.04	0.35	0.35
1+2+14	6	-321.40	655.16	2.56	0.04	0.35	0.35
1+3+11	6	-321.40	655.16	2.56	0.04	0.35	0.35
1+2+12	6	-321.52	655.40	2.80	0.04	0.35	0.35
1+2+13	6	-321.98	656.32	3.71	0.02	0.35	0.35
1+2+10	6	-322.09	656.55	3.95	0.02	0.35	0.35
1+2	5	-323.19	656.64	4.03	0.02	0.34	0.34
1+2+5	6	-322.35	657.07	4.47	0.02	0.35	0.35
1+2+4	6	-322.72	657.80	5.19	0.01	0.35	0.35
1+2+8	6	-323.04	658.44	5.83	0.01	0.34	0.34

1 = Water depth, 2 = Vegetation cover, 3 = Vegetation cover$_{\text{focal species}}$, 4 = Sex, 5 = Age, 6 = Territory size, 7 = Home range size, 8 = Social rank, 9 = Body mass, 10 = Tail fat index, 11 = Body length, 12 = Hour, 13 = Julian day, 14 = Time in current territory

S12: The model selection results for the best candidate models investigating the diving distance to beaver lodge among nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	deltaAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
3+9+10	**6**	**-327.27**	**666.90**	**0.00**	**0.37**	**0.18**	**0.19**
3+8+9	**6**	**-327.54**	**667.44**	**0.54**	**0.28**	**0.18**	**0.20**
6+9+10	6	-329.15	670.66	3.76	0.06	0.17	0.17
2+8+9	8	-327.23	671.09	4.18	0.05	0.18	0.20
1+9+10	6	-329.47	671.30	4.39	0.04	0.17	0.18
2+9+10	8	-327.45	671.52	4.62	0.04	0.18	0.19
3+6+10	6	-329.81	671.98	5.08	0.03	0.17	0.17
7+9+10	6	-330.03	672.42	5.52	0.02	0.17	0.17
4+9+10	6	-330.31	672.99	6.08	0.02	0.16	0.17
3+7+10	6	-330.45	673.26	6.35	0.02	0.17	0.17

9+10	5	-331.81	673.88	6.98	0.01	0.15	0.16
3+10	5	-331.82	673.91	7.00	0.01	0.15	0.16
1+8+9	6	-330.81	673.98	7.08	0.01	0.16	0.19
4+8+9	6	-331.16	674.68	7.78	0.01	0.16	0.18
2+6+10	8	-329.10	674.83	7.93	0.01	0.17	0.17
3+5+10	6	-331.28	674.92	8.01	0.01	0.16	0.16
3+8	5	-332.36	674.98	8.08	0.01	0.15	0.17
5+9+10	6	-331.32	675.00	8.10	0.01	0.16	0.16
2+3+8	8	-329.24	675.11	8.21	0.01	0.17	0.19
8+9	5	-332.49	675.23	8.33	0.01	0.15	0.18

1 = Water depth, 2 = Sediment, 3 = Vegetation cover, 4 = Species richness, 5 = Sex, 6 = Territory size, 7 = Social rank, 8 = Tail fat index, 9 = Hour, 10 = Julian day

S13: The model selection results for the best candidate models investigating the diving distance to beaver lodge among dives within 150 m of the lodge of nine beavers in a Eurasian beaver population in south-eastern Norway. Models were ranked based on AICc.

Variables	**df**	**log likelihood**	**AICc**	**deltaAICc**	**weight**	**$R^2_{marginal}$**	**$R^2_{conditional}$**
Sediment	**6**	**-19.42**	**53.25**	**0.00**	**0.40**	**0.25**	**0.25**
Hour	4	-23.75	56.59	3.34	0.08	0.08	0.08
Julian day	4	-23.90	56.88	3.64	0.06	0.07	0.07
Water depth	4	-23.96	57.01	3.76	0.06	0.07	0.07
Body length	4	-23.99	57.06	3.81	0.06	0.06	0.06
Null	3	-25.37	57.36	4.12	0.05	0.00	0.00
Time in current territory	4	-24.15	57.39	4.14	0.05	0.06	0.06
Tail fat index	4	-24.63	58.34	5.09	0.03	0.04	0.04
Age	4	-24.83	58.73	5.49	0.03	0.03	0.03
Territory size	4	-24.89	58.85	5.61	0.02	0.02	0.02
Sex	4	-24.90	58.88	5.63	0.02	0.02	0.02
Vegetation cover	4	-24.95	58.98	5.73	0.02	0.02	0.02
Body mass	4	-25.20	59.48	6.24	0.02	0.01	0.01
Home range size	4	-25.29	59.67	6.42	0.02	0.00	0.00
Vegetation coverfocal species	4	-25.31	59.71	6.46	0.02	0.00	0.00
Number of focal species present	4	-25.33	59.75	6.50	0.02	0.00	0.00
Social rank	4	-25.36	59.80	6.56	0.02	0.00	0.00
Species richness	4	-25.36	59.80	6.56	0.02	0.00	0.00

Paper II

Mortensen, R.M., Wilson, R.P., and Rosell, F. (*Manuscript*). A territorial semi-aquatic mammal reduces predictable movements within the territory as a response to short- and long-term capture effects. *Prepared for submission to Movement Ecology*.

A territorial semi-aquatic mammal reduces predictable movements as a response to short- and long-term capture effects

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Abstract

Background: Ecologists often use long-term individual-based studies, involving repeated capture and handling of individuals, to understand and explain patterns in behavioural ecology. Often focus is on the direct harm following a capture event. However, captures may cause long-term effects, potentially changing individuals' behaviour to an extent that may make our conclusions ecologically unreliable. Some animals exhibit temporary flight responses to avoid capture sites, but territorial animals may not have the same options, because of other stronger ecological factors, such as competition and social interactions. We aimed to investigate how the movement behaviour in a territorial semi-aquatic mammal is affected by repeated capture and handling events, using the Eurasian beaver (*Castor fiber*) as a model species.

Methods: We analysed movement trajectories of 75 adult individuals (33 F, 42 M, total of 112 GPS tracks) from a long-term (approx. 25 years) individual-based monitoring program, the Norwegian Beaver Project. We examined movement patterns at two temporal scales (15-min steps and night-scale). To investigate effects of repeated capture and handling, we evaluated how habitat selection, movement steps, and nightly movement activities (range sizes, distances moved, night duration, and emergence times from the lodge) were affected in the short- (nights since capture) and in the long-term (experienced capture intensity and years of study), while correcting for temporal and ecological variation between individuals.

Results: Movement patterns generally varied spatially, temporally, and among individuals. We found no short- or long-term capture effects on individuals' habitat selection. In the short-term, individuals decreased directionality of steps just after a capture event. We found no long-term effects on movement steps, but older individuals that may have experienced more captures moved slower than younger individuals. We found no short-term effects on nightly range size but capture intensity and years of study increased range size, which furthermore increased with age. We found no clear short- or long-term effects on nightly distances moved, but older individuals moved shorter distances in total. Older individuals furthermore emerged later from the lodge and reduced night duration following a capture event, and individuals with high capture intensity were active for a longer time of the night.

Conclusions: Our results indicate that particularly adult individuals of territorial, semi-aquatic mammals can adjust their movements according to perceived risk and disturbances within territory ranges, both in the short- and in the long-term, whereas younger individuals may be less capable of adjusting because of energetic requirements related to their fitness potential. In territorial animals, these behavioural adjustments may cause individuals to exploit their territory, temporally and spatially, in a less predictable manner, reducing the potential risk from predators and researchers in the field.

Keywords: Animal welfare, Capture stress, Integrated step selection function, Long-term individual-based study, Movement ecology, Research ethics, Semi-aquatic, Trapping effects, Territoriality

Introduction

How animals use the landscape is fundamentally shaped by their internal need to move to a new location, their physical movement capacity, and their capacity to navigate themselves in space and time in the landscape, which all together are dynamically influenced by external factors such as distribution of resources, predators, and social interactions [1-3]. To understand and elucidate these causes, mechanisms, and spatiotemporal patterns of animal movement, ecologists often have to make use of long-term individual-based studies [4]. This may require repeated capture and handling of individuals and populations, which can have considerable fitness consequences [5-7].

Capturing and handling an animal is expected to induce immediate physiological and behavioural adjustments in the individual to cope with the experienced disturbance, which may result in an intense stress response that can have physical, physiological, and behavioural consequences [8, 9]. Researchers often focus on the direct harm following a capture event, and methods are considered successful when the animal survives through the capture process without any noticeable injuries [10]. However, animals often hide symptoms that make them appear vulnerable [11], making mortality rates and physical injuries at or near time of capture insufficient to successfully assess capture and handling procedures without also evaluating other physical, physiological, and behavioural effects at multiple times, and in multiple ways, on a long-term scale [7, 12, 13].

To gain insight into the behaviour of wild animals, direct observations were previously the only way to measure animal movements, behaviours, and their associated time budgets [14-16]. However, due to observer effects, human presence may cause a change in the expressed behaviours, especially when animals are naturally reclusive or perceive humans as a threat [3, 17]. Even animals that do not appear to react to human presence or to a given method of capture and handling may still change their behaviour in subtle ways [7, 18]. With technological advances, deployment of animal-borne telemetry devices has rapidly improved our understanding of animal movement, behaviour, and physiology [15, 19, 20], and has additionally enabled us to evaluate how our research methods potentially affect the behaviour of our study animals.

Several studies have found short-term modifications in movement and behaviour among captured individuals [21]. Studies in bears (*Ursus* arctos and *U. americanus*) and roe deer (*Capreolus capreolus*) found temporary decreases in movement rates and activity levels among captured individuals which lasted up to a month before returning to normal levels [6, 22, 23], whereas narwhals (*Monodon monoceros*) have been found to temporary increase their activity levels and swimming behaviour up to 24 hours immediately following long handling time [24]. In species such as edible dormice (*Glis glis*), grey-sided voles (*Clethrionomys rufocanus*), and roe deer, captured individuals have been found to exhibit temporary flight responses, avoid the capture site, switch nest box, or increase use of habitats that offer shelter in the immediate time following capture and handling [21, 22]. Other anthropogenic activities, such as hunting, have been found to result in similar behavioural changes in wild animals [25-29]. However, studies often only evaluate capture stress that appears in the immediate days, weeks, or the following breeding season after handling [21]. Even long-term studies that investigate effects of capture and handling over several years sometimes fail to evaluate long-term effects of their procedures as only effects within each year or season are evaluated [30-32]. Overall responses to capture and handling may additionally vary dynamically between individuals according to ecological factors such as sex, age, body condition, social status, seasonality, and previous experience, as the potential fitness consequences of repeated capture and handling can differ between these groups [5, 7, 21, 22], but often these ecological individual differences are not accounted for when analysing potential capture effects.

In this study, we examine fine-scale spatial behaviour at two temporal scales in a territorial, semi-aquatic mammal and investigate how repeated capture and handling events may have short- and long-term effects on individuals' movement behaviour. To achieve our aim, we use thirteen years of GPS data from three populations of Eurasian beavers (*Castor fiber*) which have been extensively monitored through a long-term individual-based capture program (the Norwegian Beaver Project – hereafter NBP) since 1997 [7].

Beavers are socially monogamous, highly territorial , semi-aquatic rodents [33-36] that, because of their characteristic behavioural ecology and effects on their surroundings [37], have been used as a model species in numerous research projects to answer various ecological questions (see also *methods*). Several of these projects required repeated capture, handling, and deployment of telemetry devices on individuals, which potentially can affect animal welfare and the quality of the research [7, 12]. Studies in beavers have reported short-term effects on body weight after tagging [38, 39], but weight loss seem to be compensated in the longer run [7, 40]. In a study looking at the long-term effects of capture and handling, body mass of dominant individuals were observed to decrease with number of experienced capture and handling events, but no statistically clear effects were found for survival or other body condition indices [7]. Additionally, they found that number of experienced capture and handling events affected reproduction, but the populations showed signs of habituation in the long-term [7]. A study on North American beavers (*C. canadensis*) showed how translocated individuals on a fine-scale (5-min steps) moved similarly to resident individuals (i.e. non-translocated), but on a coarse-scale (up to 6 months post-release) moved farther from release sites and faster than resident individuals [41]. However, movement rates decreased with time, indicating settlement in new territories. Studies have anecdotally reported how captured beavers spend more time within their lodges in the first few days post-release [42, 43] and move faster with increasing distance from safer locations, such as their lodge or territory [44, 45]. Short-term effects of capture, handling, and tagging on movement patterns have previously been investigated in 29 beavers in our populations, but they found no effects within the first week after release [46]. We include the same individuals in our capture-effect study on movement behaviour, but we take a completely different analytical perspective on the topic by additionally investigating various long-term effects, as well as including several more individuals from a longer range of years.

Using fine-scaled information on individual movement tracks in three populations that have experienced almost 25 years of repeated capture and handling of individuals, we aim to investigate how repeated capture and handling events in both the short- and the long-term may affect movement patterns at two temporal scales (15-min steps and night-scale) in a territorial semi-aquatic mammal, using the Eurasian beaver as a model species. Assuming that repeated capture and handling induce a stress response in monitored individuals, we hypothesize that repeated capture and handling affect spatiotemporal movements of individuals (Fig. 1), both in the short-term of the actual tracking period (i.e. nights since capture), but also in the long-term of individuals' future movement patterns (i.e. capture intensity and years of study), which consequently may affect their lifetime fitness [7]. In the short term, we expect movement patterns temporally closer to the capture event to be most affected. In the long term, over the years of monitoring, we expect movement patterns of individuals that have experienced more capture events or individuals of populations that have experienced less capture and handling (i.e. earlier years of monitoring) to be negatively affected by capture stress. We furthermore expect spatial movement variations according to e.g. distance to the riverbank (i.e. known habitats). Overall, we expect individuals to be less risk-willing in their territorial movement behaviour 1) immediately following capture and handling and 2) when they, or 3) their population, have experienced more capture and handling events. We predict that these individuals will select even stronger for terrestrial and aquatic habitats closer to the riverbank and away from the territory borders to avoid risky habitats (Fig. 1a), and express more directional movement (i.e. longer step length, smaller turn angles) to minimize time spend in a habitat (Fig. 1b). On a night scale, we expect them to spend less time in the same area and therefore have narrower (i.e. smaller) nightly ranges (Fig. 1c), move longer distances in the night (when accounting for night duration) (Fig. 1d), but also emerge later from the lodge and be active for a shorter time duration during the night (Fig. 1e).

Methods

Study animal

For our study, we make use of Eurasian beavers from a long-term individual-based study in Norway, the NBP. Beavers are socially monogamous, territorial rodents that inhabit various freshwater bodies [33, 35]. They live in family groups consisting of a dominant breeding pair, kits of the year, and older non-breeding offspring (i.e. subordinates) [36]. At northern latitude, up to five kits are born around May [7, 36, 47], which emerge from the lodge in July when they start feeding on their own [36]. Beavers advertise territory occupancy mainly through scent-marking near territory borders [48, 49]. Scent-marking peaks in spring when subordinate individuals, usually 2-3 years old, disperse to establish or take over a territory [45, 48]. Studies have found that scent-marking is mainly performed by dominant individuals [50], and more frequently by males [51], but family members of all age classes, sexes, and social ranks participate in the territorial defence [52].

Beavers are highly connected to water which is specifically used for movement and safety [34, 35, 53-55]. Foraging, collection of building resources, territorial scent-marking, and social interactions in both terrestrial and aquatic habitats all happen in close proximity of the riverbank [34, 35, 49, 56]. However, territorial activities vary between individuals. Although time-budgets of males and females appear similar, males seem to allocate more time to travelling [42]. Older beavers have been found to spend more time on land and near territorial borders, suggesting increased experience and boldness [34]; however, older beavers spending less time in water, moving shorter distances, and generally reducing their activities may also indicate senescence [53]. Beavers seem to trade-off the costs of patrolling larger territories against the benefits of foraging closer towards the riverbank [34, 35], and both territory size and social rank have been found to affect extraterritorial movement trips [45]. Furthermore, subordinates have a higher use of aquatic vegetation, which may be linked to increased risk-avoidance [35, 57]. Movement activities have also been found to vary temporally peaking in the middle of the night [35, 46] and changing through the years according to light and weather conditions [53].

Study site

Our three study sites are located at the lower reaches of the rivers Straumen, Gvarv, and Sauar in Vestfold and Telemark County, south-eastern Norway (Fig. 2). The rivers are generally slow flowing with stable water levels because of natural lakes and man-made impoundments along part of their length [58], although flooding events do occur. All rivers meander through a landscape of farmlands, fields, and small villages interspersed with riparian mixed forests [58, 59].

The study rivers are part of a larger monitoring and research project where individuals in the area have been monitored through an extensive capture program, the Norwegian Beaver Project (NBP), since 1997 [7]. The long-term monitoring project aims to annually capture all newcomers (kits and dispersers from territories outside the study site), enabling identification of individuals at later encounters and family group sizes. The populations are at carrying capacity, as main rivers contain about 30 distinguishable territories from 1 to 8 km bank length that directly border each other with family groups of on average 4 individuals per territory [7, 34, 36, 60]. Predation pressure is low as wolves (*Canis lupus*) and bears (*Ursus arctos*) are functionally extinct in the area, and lynx (*Lynx lynx*) only occur at low densities [61, 62].

Capture protocol

Individuals were detected from a motorboat using searchlights and captured at night with large diving-nets in shallow water or with land-nets [63]. Captured individuals were immobilized in cloth sacks, enabling easy handling without anaesthesia, and identified via microchips (PIT tags) and unique combinations of plastic and metal ear-tags [42, 64]. In the cloth sacks, individuals were weighed and measured to estimate body condition [See also: 7]. First time captured, individuals were sexed based on the colour and viscosity of their anal gland secretion [65] and assigned a minimum age based on body mass at first capture [7, 66]; minimum 2 years when body mass was between 17 to 19.5 kg inclusive, and minimum 3 years when body mass was above 19.5 kg. The adult territorial residents of each sex were in most cases assigned territorial dominance, which was additionally verified by eventual dispersal of the alternative candidate, the greatest body weight among same-sex group members, or lactation signs in females (large nipples, i.e. > 0.5 cm). Individuals dispersing into a territory were posited to have achieved the dominant breeding position when the previous dominant same-sex individual had disappeared, or conditions outlined above was applicable. Unless proven otherwise, dominant individuals were assumed to maintain their social rank until they died or disappeared from the territory [7, 67]. Captured beavers were released near the capture site within their territory after approximately 20-40 minutes of handling time [63].

GPS Tracking

For this study, we captured and equipped 78 adult individuals (42 males, 36 females) from 26 territories with various GPS loggers from 2009 to 2021 (total tracks = 116). Some individuals were additionally equipped with other data loggers such as daily diary units (including accelerometer, magnetometer, thermometer, Wildbyte technologies [68]). The data loggers were glued onto the fur on the lower back of the beavers using a two-component epoxy resin, approximately 15 cm above the tail following the spine, and were removed again after two to three weeks if they had not fallen off by themselves [69]. To extend battery life, GPS loggers were typically programmed to take a fix position every 15 minutes, at least between 7 pm and 7 am to reduce numbers of unsuccessful GPS fix attempts from within beaver lodges.

To improve precision, GPS positions were filtered to only include positions with more than three satellites and horizontal dilution of precision (HDOP) values below ten or positions with three satellites and HDOP values below five [70, 71]. Additionally, we removed all GPS positions that resulted in unlikely movement steps between consecutive positions, which we defined as movements faster than 3 meters per second. In total, 5.8% of the obtained GPS positions were removed from the data set (not including unsuccessful fix attempts). Using the GPS positions, we calculated 95% autocorrelated kernel density estimates [AKDE, 72] to estimate the territory range sizes, which in our populations correspond to home range sizes [73], as well as the nightly ranges of each beaver.

Evaluating responses to repeated capture and handling

Consecutive movement steps were used to evaluate how repeated capture and handling events potentially may affect short- and long-term spatial activity in beavers by comparing how habitat selection, movement steps, nightly range size, night duration, and emergence time varied by capture and handling intensity, years of study, and nights since capture. We used nights since capture to indicate the short-term capture and handling effects to the individual, whereas capture intensity of the individual (captures per living year) and years of study (years since 1997) were used to indicate long-term effects on movement behaviour of the individual and its population, respectively. We did not use number of captures alone as it is highly correlated with age of the beavers ($r > 0.7$) in a study system like ours where most individuals are captured first time as kits and several individuals are monitored throughout their life (i.e. several capture events).

The age variable will therefore additionally represent number of captures and years of study of the individual, implicitly.

Habitat selection and movement steps

To evaluate how capture and handling events affect habitat selection and movement steps of beavers, we filtered our GPS tracks (*n* = 112; individuals who were not weighed before tracking were removed from the analysis) to only include 15-min (± 1 min) movement steps (i.e. straight lines connecting consecutive GPS positions), resulting in 3,591 individual bursts of 112 tracks. Since step length and turn angle require two and three consecutive fixes to be calculated, respectively, we ended up with 20,367 steps. As habitat selection and movement are interconnected [74], we used an integrated step selection function (iSSA) to compare observed and random available steps (i.e. steps which the animal could have taken), hereby evaluating habitat selection and movement while simultaneous accounting for differing selection and movement behaviours [74, 75]. We generated ten random available steps for each observed step by randomly selecting step lengths and turn angles from a gamma distribution and a von Mises distribution, respectively [76, 77], which we parameterised based on the observed movement patterns of the individuals using the R package 'amt' [78].

As beavers are territorial and highly connected to both terrestrial and aquatic habitats near the riverbank [34, 35], we evaluated habitat selection (i.e. habitats at the end of observed steps compared to habitats at the end of random available steps) as a function of distance from water (i.e. terrestrial habitats), distance from riverbank (i.e. aquatic habitats), and distance from territory borders. Distance from lodge was not included as positions from the lodge cannot be successfully obtained via GPS, which may mask behaviours connected to the lodge. However, these behaviours can to some degree be expressed through reversed distance from territory borders. Distances were log-transformed as we expected animals to respond stronger to features when they were closer to them. Movement steps were described through step length and turn angle. We used step length and the natural logarithm of step length to modify the initial population-level gamma scale and shape parameters, respectively, and cosine of turn angles to modify the initial turn angle distribution [74]. We furthermore included an interaction between step length (shape parameter) and turn angle as they naturally may be correlated [74]. We investigated effects of capture and handling (capture intensity, years of study, and nights since capture), spatial variation (habitat at beginning of a step), temporal variation (hours since sunset, Julian night (i.e. night following Julian day), and ecological variation (age, sex, social rank (i.e. dominant or subordinate), body mass, and territory size) by including interactions of them with the variables for habitat selection (i.e. terrestrial and aquatic distance from riverbank and distance from territory border) and movement (ln(step length) and cos(turn angle)).

To interpret the habitat covariates, we calculated the relative selection strength [79]. For terrestrial and aquatic distances from riverbank and distance from territory border, we calculated the relative probability of selecting a step at a given distance compared with the probability of selecting a step within 0.01 m from the riverbank or territory border. To understand movement patterns irrespective of habitat selection, we used the movement coefficients from the iSSA to adjust the initially observed gamma and von Mises distributions of step length and turn angles, respectively [74]. Mean step lengths (i.e. movement rates) were calculated by multiplying the adjusted shape and scale parameters from the gamma distribution [80].

Nightly movement activities

As the effects of capture and handling events on movement behaviour may be more visible on a coarser scale, we investigated how nightly range sizes, minimum total distance moved, night duration, and emergence time from lodge at individual tracking nights (*n* = 1,270) varied by repeated capture and handling. Nightly range sizes were estimated using GPS positions of each night to calculate 95% AKDE [72]. We calculated minimum total distance moved in the night as Euclidean distance moved between steps by each individual from the earliest GPS positions to the last GPS position of the tracking night. Night duration was estimated using the time difference between the earliest and last GPS position of each tracking night. Emergence time from the lodge was assumed to correspond to the time of the earliest GPS position of the tracking night.

Statistical analysis

We analysed habitat selection and movement steps of the beavers by using conditional logistic regressions in an iSSA [75, 81]. Following Muff*, et al.* [82], we fitted a mixed conditional logistic Poisson model with stratum-specific fixed intercepts. We incorporated individual-specific slopes for covariates for habitat selection (i.e. distance to water, riverbank, and territory borders) and movement (i.e. step length and turn angle) to accommodate inter-individual heterogeneity in the iSSA [82-84]. We created a list of candidate models by first defining a base model that consisted of covariates for habitat selection and movement. Hereafter, we combined the base model with combinations of interactions for spatiotemporal effects (habitat at beginning of step, hours from sunset, and Julian night), capture and handling (capture intensity, years of study, and nights since capture) and ecological variation (age, sex, social rank, body mass, and territory size), assuming that each effect always affected all covariates for habitat selection and movement, respectively. Since the iSSA was computationally heavy to fit and to reduce complexity, we chose to just include two-way interactions.

Measures of nightly movement activity (i.e. nightly range size, distance moved, emergence time from lodge, and night duration) were analysed using generalized linear mixed-effects models (GLMMs) with log-normal (for nightly range size, distance moved, and night duration) or Gaussian distributions (for emergence time from lodge), and individual, territory, and tracking year as random effects to account for differences between these. Capture night and last night with GPS positions were removed in these analyses due to them being somewhat incomplete tracking nights. For the four analyses, a list of candidate models was created using relevant combinations of variables for capture and handling (capture intensity, years of study, and nights since capture), temporal variation (Julian night), ecological variation (age, sex, social rank, and body mass), and relevant variables of other nightly movement activities (i.e. nightly range size may to some degree depend on distance moved in the night, distance moved may depend on night duration and time of emergence from lodge, whereas night duration to some degree may depend on emergence time from the lodge). We included interactions between all variables and variables for capture and handling to investigate whether nightly movement activity patterns were influenced by how much individuals and populations previously had been captured and monitored, as well as interactions for seasonality between sex and social ranks [7].

Model selection in all analyses was based on Akaike's Information Criterion corrected for small sample size (AICc) [85], and carried out using the R package 'MuMIn' v. 1.43.17 [86] to choose the most parsimonious models within ΔAICc < 2 [85, 87]. In each model, variables that included zero within their 95% confidence interval (CI) were considered statistically unclear effects [87]. Confidence intervals were bootstrapped with 10,000 simulations (however, the iSSA was only bootstrapped using 2000 simulations, because it was computationally heavy to fit) by treating tracking nights as sampling units to obtain robust estimates [88]. Tracking nights were also used as sampling unit in the bootstrapped iSSA to preserve correlation between movement steps in a track [74]. Models were visually validated using the R package 'DHARMa' v. 0.4.1 [89] to plot standardised model residuals against the fitted values [90]. Top candidate models for all analyses can be found in the supplemental material (Additional file 1).

In all analyses explanatory variables were scaled by standard deviation, centred, and checked for collinearity using Pearson's *r* (threshold: $r < 0.6$) and variance inflation factors (VIF < 3) [90]. All analyses were conducted in R 4.2.1 [91].

Results

Habitat selection

We found no clear effects of repeated capture and handling on habitat selection among individuals. In the short-term, beavers did not vary their selection for terrestrial and aquatic habitats close to the riverbank or habitats close to the territory borders as a function of nights since capture (Table 1, S1). Neither did individuals that had experienced more captures in their life or were part of populations that had been studied for a longer period differ in selection for terrestrial and aquatic habitats closer to the riverbank or habitats closer to the territory borders (Table 1).

Both on land and in water, beavers generally selected for habitats located closer to the riverbank and habitats closer to the territory border (Table 1). Selection strength for habitats located closer to riverbank varied by the individuals' starting distance relative to the riverbank (Table 1). We saw that selection for terrestrial habitats closer to the riverbank decreased with increasing terrestrial distance from the riverbank (Fig. 3a), whereas selection for aquatic habitats closer to the riverbank increased with increasing starting distance from the riverbank (Fig. 3b). Individuals also increased their selection for habitats closer to the territory borders with increasing starting distance from the territory borders (Table 1, Fig. 3c). We found a clear change in habitat selection through the night as selection for habitats closer to the territory borders were stronger earlier in the night (Fig. 3d), but no nightly patterns were found for terrestrial and aquatic proximity to the riverbank (Table 1). Seasonally, selection for aquatic habitats closer to the riverbank decreased with Julian night (Fig. 3e), but we found no clear seasonal change in selection for terrestrial proximity to the riverbank or among habitats closer to the territory borders throughout the year (Table 1).

We found no clear differences in habitat selection as a function of age, sex, or social rank (Table S1). Selection for both terrestrial and aquatic habitats closer to the riverbank was stronger for smaller individuals compared to larger individuals (Fig. 3f-g), but we found no clear effects on selection for habitats closer to territory borders as a function of body size (Table 1). Individuals with larger territory ranges expressed stronger selection for terrestrial and aquatic habitats closer to the riverbank (Fig. 3h-i), but no clear selection patterns were found for habitats closer to the territory borders (Table 1).

Movement steps

Analysing selection-independent movement patterns, we found no short-term effects of repeated capture and handling in step length as a function of nights since capture (Table 2), but individuals expressed decreased directionality (i.e. turn angle) in the first tracking nights (Table 2, Fig. 4a). We found no clear pattern changes in either step length or turn angle as a function of capture intensity (Table 2) or years of monitoring (Table S1).

Longer steps generally occurred with more directional movement (i.e. low turn angle, Table 2). On land, movement varied with habitat as steps situated further from the riverbank resulted in shorter steps and higher turn angles (Table 2, Fig. 4b-c). Step lengths did not change as a function of aquatic distance to the riverbank (Table 2), but turn angles became less directional with increasing aquatic distance from the riverbank (Fig. 4d). We found no clear changes in step length patterns as a function of distance from territory borders (Table 2), but turn angles became more directional with increasing distance from territory borders (Fig. 4e). Movement patterns also varied through the night as beavers moved with longer and more directional steps earlier in the night and with shorter and more irregular steps (i.e. higher turn angles) in the end of the night (Table 2, Fig. 4f-g). Step lengths decreased with increasing Julian night as individuals moved with longer steps in the spring than in the autumn where steps were shorter (Fig. 4h), but we found no clear seasonal changes in turn angle patterns (Table 2).

Step length decreased with increasing age as older beavers moved with shorter steps than younger beavers (Fig. 4i), but we saw no clear changes in directionality as a function of age (Table 2). Step length increased with age and territory range size as larger individuals and individuals with larger territory ranges expressed longer step lengths (Fig. 4j-k), but we found no clear directional pattern changes as a function of body size or territory range size (Table2). Furthermore, we found no clear changes in movement patterns as a function of sex or social rank (Table S1).

Nightly movement activities

Naturally, nightly range sizes increased as beavers moved further distances in the night (Table 3, Fig. 5a). Capture history appeared to affect individuals' nightly range size as individuals that had experienced more captures in their lifetime had larger nightly range sizes compared to individuals that had experienced fewer captures in their lifetime (Table 3, Fig. 5b). A similar trend was found over the years of study as individuals from populations that had been studied for a longer time had larger nightly range sizes (Table 3, Fig. 5c). Nightly range sizes also increased with increasing age (Table 3, Fig. 5d). In the short term, we found no differences in nightly range size as a function of nights since capture (Table S2). Seasonally, we found that subordinate individuals had larger nightly range sizes in the spring which decreased over the year, whereas the nightly range sizes of dominant individuals stayed the same over the seasons (Table 3, Fig. 5e). We found no differences between sexes or individuals of different body sizes (Table S2).

Individuals that were active for a longer time during the night also moved longer distances (Table 4, Fig. 5f). We found no clear effects of capture history (i.e. capture intensity and years of study) or nights since capture (Table S3), but older individuals moved less in the night compared to younger individuals (Table 3, Fig. 5g). We found that individuals generally moved less in the night as a function of Julian night as nightly distance moved decreased from spring to autumn, but especially males moved further distances in the spring compared to females (Table 4, Fig. 5h). Furthermore, we found that larger individuals moved longer distances in the night than smaller individuals (Table 4, Fig. 5i). We found no clear differences in nightly distance moved between individuals of different social rank (Table S3).

Night duration decreased with emergence time from the lodge (i.e. hours from sunset) (Table 5, Fig. 5j). Individuals that had experienced more captures were generally active for a longer period of the night (Table 5, Fig. 5k), but we found no effect of years of study (Table S4). Younger individuals generally did not change the length of their nights as a function of nights since capture, but older individuals increased their night duration with nights since capture (Table 5, Fig. 5l). Dominant individuals were furthermore active for a shorter period of the night compared to subordinate individuals (Table 4, Fig. 5m). We found no clear differences on night duration as a function of sex or body size (Table S4).

Emergence time from the lodge varied seasonally over the year with length of the night as individuals emerged before sunset in the summer and after sunset in the spring and autumn (Table 6, Fig. 5n). Individuals generally emerged later from their lodge in the nights just following a capture event and especially older individuals emerged later from the lodge in the first nights following a capture event compared to younger individuals (Table 6, Fig. 5o). Furthermore, we found that larger individuals emerged later from the lodge compared with smaller individuals (Table 6, Fig. 5p).

Discussion

By GPS tracking individuals from three Eurasian beaver populations that have been intensively studied for almost 25 years [7, 64], we provide important knowledge on short- and long-term capture effects in a semi-aquatic mammal by evaluating how individuals' movement behaviour at two temporal scales are affected by repeated capture and handling events. We show how beavers' movement patterns vary spatially, temporally, and among individuals, and show how repeated capture and handling events may cause individuals to change their movement patterns both in the short- and in the long-term.

Short-term effects of repeated capture and handling

In the short-term individuals were less directional in their movement in the nights just following a capture event, contrary to our predictions. We expected individuals to express higher directionality (i.e. longer steps, smaller turn angles) to minimize time spend in a potentially risky habitat as is seen in some deer species that flee following a capture event [22]. However, we found no changes in step length as a function of nights since capture. Altogether this may relate to beavers being highly territorial and rather predictable in their use of habitats within the territory [92]. Our results may indicate that in the short term, when perceiving increased risk because of capture events, highly territorial mammals such as beavers may cope with the increased stress by reducing directionality of their movement steps. Being more irregular in their movement within the territory may make them less predictable and protect them from potential threats [92], such as predators and researchers in the field, while still being capable to fulfil their requirements for energy, social interactions, and territorial defence [2, 34, 93].

In the short term, according to our predictions, we also found, that older individuals appeared to delay their emergence time and shorten their active period in the first nights following a capture event. Similar patterns describing how captured beavers are spending more time within their lodges immediately following release have been reported anecdotally by other studies [42, 43]. Relatively short temporary changes in movement and activity behaviour lasting from hours to a few weeks have also been reported in other mammals [6, 21-24], and mammals have shown to become more nocturnal with increasing human disturbance [94]. In contrast to our results, an earlier study from our populations showed only very minimal reduced activity in the first week post-capture and no effects on night length or displacement rate [46]. However, these differences may be related to sample size and study design as our findings on reduced night duration also appeared to decrease with time. The fact that older individuals changed their emergence and activity behaviour more than younger individuals may relate to them being more risk-willing in general [35, 53] and, therefore, adjust their behaviour to the increased capture stress, whereas younger individuals may not be able to reduce risky activities more than they are already doing in order to fulfil their energetic requirements and may express alertness already [2, 35, 57]. Also in other mammals, adults have been reported to react stronger to disturbances than younger individuals [95]. The movement behaviour of territorial species that defend a territory may be strongly influenced by other ecological dynamics related to e.g. social interactions and competition [2, 93, 96, 97], which may require them to maintain their movement patterns irrespective of the experienced capture stress in the short-term [98]. In roe deer that, although being seasonally territorial, exhibit temporary flight responses and avoid capture sites, females have been shown to respond less than males, because of their higher need for social interactions to form maternal clans [22]. The presence of other stronger ecological drivers in beavers may also explain why we found no short-term capture effects on habitat selection, nightly range size, or distance moved in the night [98].

Long-term effects of repeated capture and handling

In the long-term, we found no effects of repeated capture and handling on habitat selection or movement steps, but older individuals, which, in a study system as ours, naturally have experienced more capture events, appeared to move slower (i.e. shorter steps) than younger individuals. This was also the case on the night-scale. This was contrary to our expectations as beavers in risky (i.e. unknown) habitats have been shown to increase movement [44, 45] and mammals generally show an increase in movement to human disturbances [99], but studies across terrestrial mammals in areas with higher human impact have also shown substantial decreases in movement [3]. However, we also found that older individuals expressed larger nightly range sizes compared to younger individuals, even after correcting for total distance moved in the night. This may relate to younger individuals being less risk-willing and, therefore, less willing to stay in the same potentially risky area. With our method of range estimation [AKDE, 72], moving around and not really exploiting any areas could decrease home range size even when they in total move longer distances in the night. However, for a territorial mammal, shorter steps may also be a way to move around the territory with higher alertness, though another study in North American beavers found that movement steps were faster further away from the lodge (i.e. risky habitat) to reduce predation risk [44].

Even after correcting for age, we found long-term capture effects on range size as both individuals that had experienced higher capture intensity (i.e. captures per living year) and populations that had been studied for more years expressed higher nightly ranges. Over the years of monitoring, individuals may increase ranges as territories may experience some depletion of resources [35, 100-102]. However, although contrary to our predictions, increased nightly range sizes of these individuals and populations may also be a consequence of long-term capture stress [98]. Because they have experienced increased disturbance in their lifetime, these individuals may perceive larger parts of their territory as risky and may therefore use proportionally more of their territory each night to appear less predictable for predators and field-researchers [92, 103], whereas other individuals may express a more systematic use of specific parts of their territory. However, changes in range sizes according to human disturbances vary greatly among mammals [99]. Increasing their nightly range size may also explain why we do not observe any proportional changes in habitat selection as available habitat probably would follow range size [34, 35].

Contrary to our predictions that individuals would decrease night duration with increased capture intensity, we found that individuals that experienced higher capture intensity appeared to be active for a longer period of the night. This additionally supports that beavers may extend their nightly activities both spatially and temporally to reduce risk [35, 53, 103], and are capable of adjusting their movement behaviour according to perceived risks and disturbances within their territory, as is seen in other mammals [104-106]. Consequently, this may explain why no capture effects have been found on reproduction and survival in our beaver populations in the long term, although reproduction seemed to be affected in the early years of the NBP [7]. These behavioural adjustments may to some degree counteract the increased stress individuals experience from the repeated capture and handling in the long-term, and territorial animals that are somewhat restricted to a certain area because of other ecological factors may even respond with habituation to handling and human activities [2, 93, 96, 97]. Similar habituation responses to human activities and disturbances have been observed in other mammals and birds [27, 105, 107-109]. However, caution should still be taken when capturing and handling animals. Body mass of dominant individuals in our study populations has previously been shown to be negatively affected by number of captures [7]. Body size is an important feature of social status, which is highly influenced by agonistic interactions between individuals [110]. In beavers only the dominant pair of a territory breeds, and in other social rodents body size has similarly been shown to correlate with reproduction [111]. Consequently, as dominant individuals have higher energy expenditure due to increased territorial defence and reproduction [47, 50, 112], they may be more susceptible to capture stress [7, 113, 114]. However, other individuals may not be able to respond to the increased stress [98]. This emphasizes the importance of having clear adaptive objectives and framing tractable questions to help resolve what and how much that needs to be monitored in a given research project and to ensure reliable ecological research data [12, 115].

Ecological variations among individuals

In beavers, foraging, collection of building resources, territorial scent-marking, and social interactions in both terrestrial and aquatic habitats all happen in close proximity of the riverbank [34, 35, 49, 56]. Naturally, we also found strong selection for habitats located closer to the riverbank.

Selection for terrestrial habitats may, to a large degree, be shaped by predation risk [54, 55, 92], as beavers are at a particular risk when on land because of their poor eyesight under low light conditions [116], and dependence on olfaction to detect potential risks [117]. Consequently, potential predators, such as wolves and Eurasian lynx that have advanced night vision [118, 119], may detect the beaver before it detects them. In North America, beavers make up a large proportion of wolf diet during summer [92]. However, wolves have been observed to predate more at dawn, dusk, and during moonlit nights [120], which could increase the benefits of selecting more terrestrial habitats in the middle of the night when it is darkest. Other studies have similarly showed how beavers' movement activities vary temporally, peaking in the middle of the night [35, 46, 121] and changing through the year according to light and weather conditions [53], even though natural predators are absent in our study area. However, behavioural activities are known to be influenced by historical threats [61, 122], and human activities, both on land and on water, and are naturally reduced at night, which may also influence the activity levels of beavers [122]. Similar changes in activity according to human disturbances have also been found in other mammals [94]. Although we did not find any changes in habitat selection through the night, we did observe that individuals expressed more directional movement with longer steps temporally closer to sunset, suggesting higher risk alertness when moving within the territory [44]. In contrast, we did observe, that movement became shorter and less directional the further individuals moved inland and selection for the riverbank similarly reduced. This may relate to optimal foraging theory, which has animals maximizing reward and minimizing transit time and energy [123, 124].

Terrestrial travels can be risky for a beaver, and our results suggest that individuals may want to maximize habitat exploitation when utilizing terrestrial resources instead of frequently travelling back and forth from the riverbank [54]. Shorter steps on land may also indicate the increased energetic costs of terrestrial movement and especially when bringing food items back to the riverbank [125, 126]. Terrestrial trips were furthermore selected more by larger individuals and individuals with smaller home ranges, which may represent the high cost of utilizing terrestrial habitats. Individuals that exploit a larger home range may have a greater need to stay closer to the riverbank due to higher territory patrolling efforts whereas individuals exploiting smaller home ranges may be able to forage further inland away from the riverbank [34, 35]. Individuals using larger areas or inhabiting larger territories may also have reduced resource depletion or greater areas that are energetically easier to exploit, whereas beavers restricted to smaller areas may be forced to exploit foraging areas further away from the riverbank [36, 100]. Larger individuals may be older or have higher energetic requirements due to e.g. reproduction [7, 42, 127, 128]. This may make them more risk-willing, and larger individuals may be better able to cope with the increased predation risk, as well as the cost of patrolling and protecting territory borders [34, 93]. This was further indicated by the fact that larger individuals generally moved faster (i.e. longer steps) and longer distances in the night even though they also emerged later from the lodge, suggesting increased nightly activity. However, their later emergence from the lodge may be a way to reduce potential risks, which they may need to compensate for in the rest of the night [53, 61, 122].

Individuals' selection for aquatic habitats closer to the riverbank probably reflect the energetic constraints of bringing food resources to the riverbank for consumption as well as their preference for travelling along the riverbank [34, 35, 129-131]. Aquatic distance to the riverbank may also reflect decreasing aquatic foraging options in terms of decreased macrophyte growth, which is highly dependent on water depth and light penetration [132], and short and shallow dives closer to the riverbank may be preferred as they are energetically cheaper for semi-aquatic animals like beavers that have high buoyancy [133]. Similar diving patterns have been shown for other semi-aquatic mammals [130, 131, 134].

As with selection for terrestrial habitats, we found that individuals that exploited a larger home range also expressed a higher selection for aquatic habitats closer to the riverbank. Again, this may be connected to higher patrolling efforts and resource depletion within the territory [34, 36, 100], as larger home ranges may have a greater area of shallow water, which, depending on the time spent diving, can be energetically easier to exploit for a semi-aquatic animal [133]. Other studies in beavers have shown similar patterns in diving behaviour and furthermore showed that dives at longer distances from the riverbank also had higher amounts of potentially important food resources [35], making these energetically costly dives beneficial [133, 135, 136]. Similar to selection for terrestrial habitats, we found that smaller individuals had a stronger selection for aquatic habitats closer to the riverbank, although other studies in beavers have found that especially subordinate individuals may utilize aquatic resources more than dominant individuals [35, 57]. However, water depth may also increase with distance to the riverbank, which presumably represents higher energetic costs [35, 133]. Despite representing higher energetic costs, we did not find any changes in movement rate according to the distance to the riverbank, which may represent how beavers perceive the aquatic environment as generally safe [34, 35, 53]. Directionality of steps decreased with increasing aquatic distance to the riverbank, indicating how beavers bring aquatic resources back to the riverbank for handling and consumption [129, 130]. The increased directionality with increasing aquatic distance to the riverbank may also be an artefact from our sampling interval (i.e. 15 min), as beavers crossing the rivers supposedly travels somewhat perpendicular to the riverbank, depending on water flow, to minimize energetic costs of travelling [2, 126]. However, as individuals may come from a trajectory along the riverbank, the actual turn when crossing the river may not be visible from our sampling, leading to high turn angles far out in the river.

Although we found that selection for aquatic habitats closer to the riverbank weakened through the season following the growth of aquatic vegetation [35, 137]; utilization of the aquatic environment is presumably not just shaped by risks when foraging, but also allows the animals to have access to other important aquatic resources [2, 138]. The aquatic environment generally constitutes as an important means of safe transportation within the territory, for example when patrolling territory borders, and may even help reduce aggressive territorial encounters [35, 60, 139, 140]. This may explain why larger individuals, who often may be dominant with territorial responsibilities or an subordinate in search for a territory [7], may utilize a wider range of the aquatic environment compared to smaller and possibly younger individuals [7, 45].

Individuals' strong selection for habitats closer to the territory borders, which additionally increased with distance to the borders, emphasizes the strong territorial behaviour of beavers as they spend huge resources advertising territory occupancy, mainly through scent-marking near territory borders [48, 49]. We found that selection for habitats closer to the territory borders was stronger earlier in the night, suggesting that patrolling behaviour may be prioritized when individuals emerge from the lodge. Early activity peaks near the borders have also been found in other studies [35] and other territorial mammals similarly show increased visits to territory borders with increasing time since last visit [141]. Similarly, we observed more directional movements with increasing distance to the borders, which may indicate how beavers travels along the riverbank to and from the borders [34]. However, our results may also imply that beavers spend relatively short time at the borders as movements when at the borders were more irregular and selection for habitats further away from the border increased. Territorial defence activities are costly [34, 93] and reducing time spent at the borders may help reduce aggressive territorial encounters [35, 60, 93, 139, 140]. In beavers scent-marking at territory borders is mainly performed by dominant individuals and more frequently by males [50, 51] that also spend more time on patrolling in the spring when subordinates individuals disperse to establish or take over a territory [42, 45, 48]. Our findings match these patterns, as we generally found increased movement rates in the spring, which may be related to the increased patrolling or exploration of territories [34, 45, 93]. Similar increases in territorial defence during and after reproduction are found in other mammals [142]. Looking at night-scale especially males moved further distances in the night in spring compared to females that may allocate more time and resources in the spring to parenting activities [42, 127, 128]. We also found seasonal differences between social ranks as dominant individuals did not change their nightly range size throughout the year, but subordinate individuals increased their range sizes in the spring. This most likely represents the increased energetic costs of defending a territory [47, 50, 93, 112], which is especially important in the spring when subordinates increase exploration of neighbouring territories to gain information on population density and available mates before dispersing [45].

Conclusion

By evaluating various movement patterns among individuals of a highly territorial, semi aquatic mammal, the Eurasian beaver, that have been studied and exposed to repeated capture and handling events for almost 25 years, we provide important new knowledge on short- and long-term capture effects. We show how movement patterns vary spatially, temporally, and among individuals. Furthermore, we show how territorial semi-aquatic mammals as beavers are capable of adjusting their movement behaviour according to perceived risks and disturbances within their territories, both in the short- and in the long-term. Both in the immediate time following a capture as well as among individuals that may experience increased capture stress in the long-term, we observed how individuals changed directionality of their steps and increased, both temporally and spatially, their area of activity. Highly territorial animals such as beavers, which because of other ecological dynamics, are somewhat restricted to an area may benefit from these behavioural adjustments that make temporal and spatial movements patterns within the territory less predictable, thereby enabling exploitation of the territory while reducing risks from predators and field-researchers [92].

Our results emphasize the importance of evaluating effects of capture and handling at multiple scales and at multiple times during a research project, as repeated capture and handling events may affect individuals in the long term [7]. Furthermore, we illustrate the validity of long-term individual-based studies for assessing the quality and reliability of ecological research data used when analysing the behavioural ecology of wild animals, which altogether may reduce bias and promote animal welfare [12].

Declarations

Ethics approval and consent to participate

All capture and handling procedures were approved by the Norwegian Experimental Animal Board (Most recent authorization: FOTS ID19557) and by the Norwegian Directorate for Nature Management (Most recent authorization: 2014/14415). Our study met the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching [143]. All methods were performed in accordance with the relevant guidelines and regulations [144]. No individuals were injured during capture and handling, and they were all successfully released. No short-term effects have been observed on movement after tagging [46], but tagged individuals have been observed to lose body weight, but with large individual variation, although the responsible mechanism is unknown [38]. Body mass of dominant individuals have been observed to decrease with number of capture and handling events, but no statistically clear effects have been observed on survival or other body condition indices [7]. Number of capture and handling events were also observed to affect reproduction, but the population seemed habituated to repeated capture and handling in the long-term [7]. To minimize potential risks, the NBP prioritized capturing and handling only individuals that were necessary for the monitoring and experiments with clear objectives.

Consent for publication

Not applicable.

Availability of data and materials

The datasets used and analysed during the current study are available from *INSERT FIGSHARE LINK* (will be activated upon acceptance of publication).

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

FR founded and managed the NBP. RMM obtained additional supporting funding for this subproject. RMM and FR developed the study design with support from RPW. FR led the field work of the overall study with support from RMM and other participant of the Norwegian Beaver Project through the years. RMM performed the statistical analyses. RMM, RPW, and FR interpreted the results. RMM wrote the manuscript with support from RPW and FR. All authors read and approved the final manuscript.

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Figures

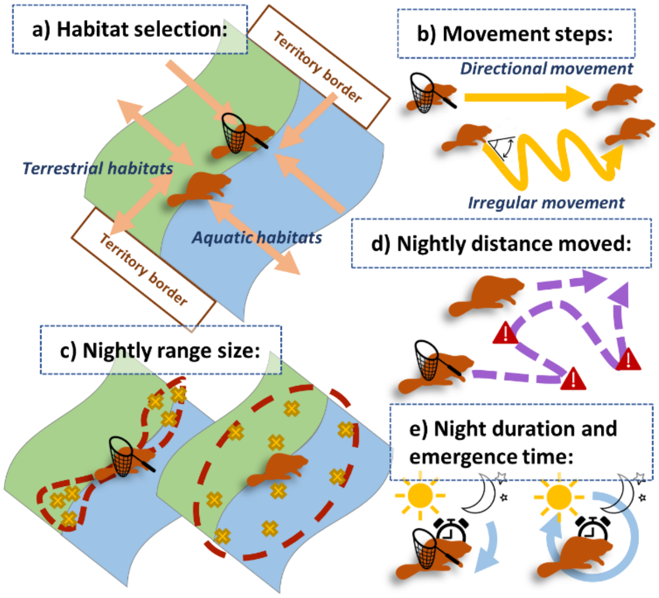

Figure 1. Visualisation of our predictions for how a semi-aquatic territorial mammal as the Eurasian beaver may respond to repeated capture and handling events both in the short and in the long term. We expected individuals to be less risk-willing immediately following capture and handling and when they, or their population, had experienced more capture and handling events, which we predicted would affect individuals': (a) habitat selection (arrows indicate selection direction for terrestrial, aquatic, and border habitats); (b) movement steps (top arrow indicates long straight steps, bottom arrow indicates short tortuous steps); (c) nightly range size (points indicate GPS fixes that are either concentrated in few areas or well distributed in the territory); (d) total distance moved in the night (indicated by arrows - warning signs indicate areas perceived risky by the beaver); and (e) night duration (length of blue arrows) and time of emergence from lodge (beginning of blue arrow from the top of circle). Expected capture effects of nights since capture, capture intensity, and years of study according to above are indicated by beavers with a capture net.

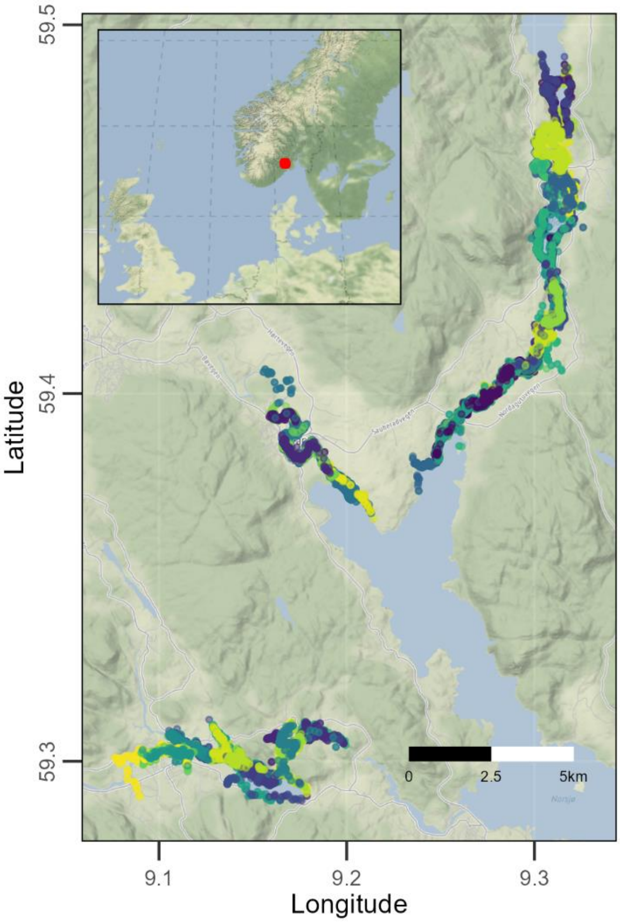

Figure 2. Overview of the three study rivers with movement steps obtained from tracking 78 adult individual Eurasian beavers (colours of point) with GPS loggers from 2009 to 2021 (total of 116 tracks). Red point on inset map indicates the position of our study area in south-eastern Norway.

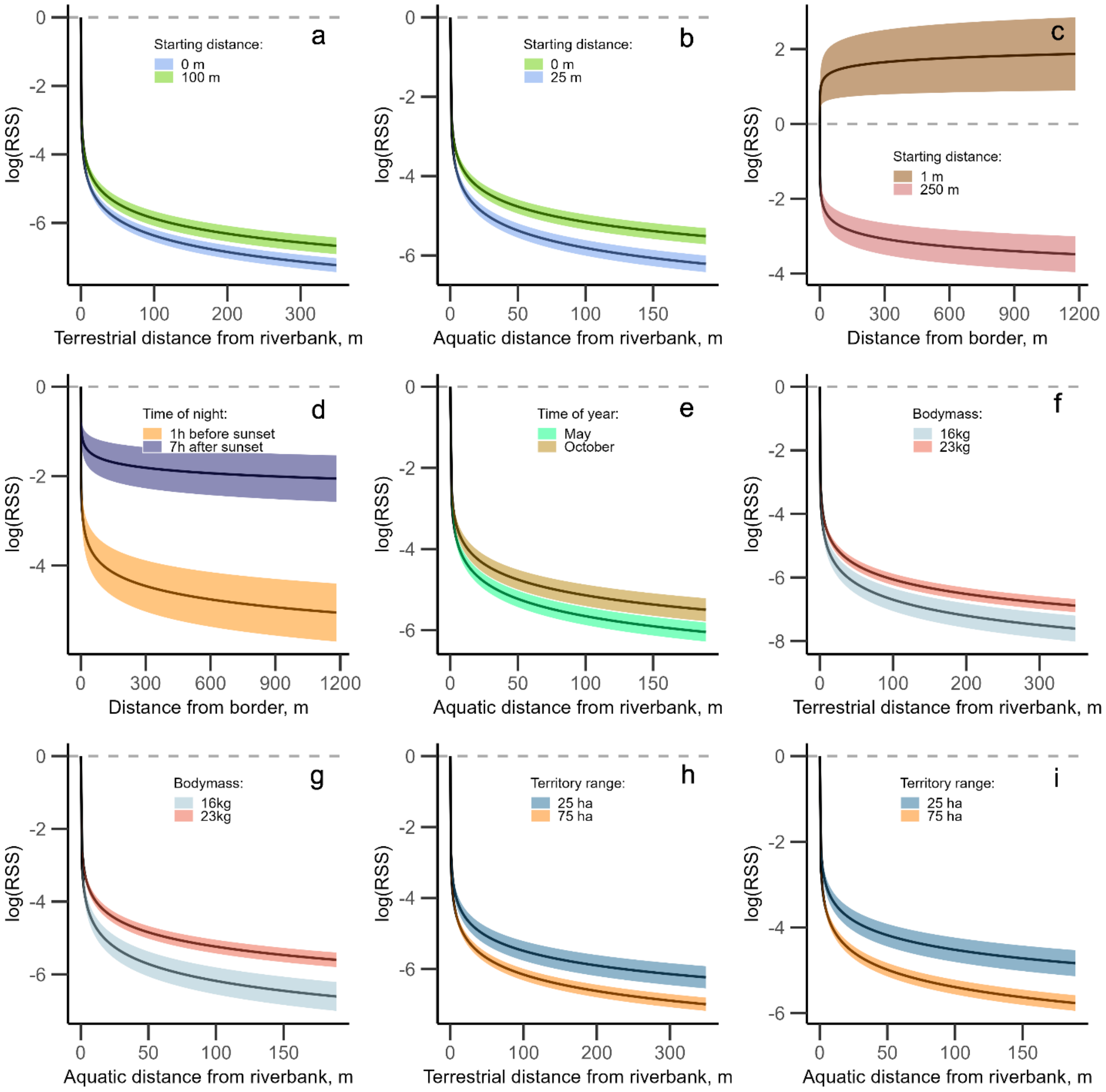

Figure 3. The predicted relationship with 95% confidence intervals of the integrated step selection function showing the relative selection strength (RSS) for (a-c) spatial variation (starting habitat in beginning of a step), (d-e) temporal variation (hours from sunset and Julian night), and (f-i) ecological variation (body size and territory range) among 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. All values show the relative probability of selecting a step compared with the probability of selecting a step just by the feature (riverbank or territory border).

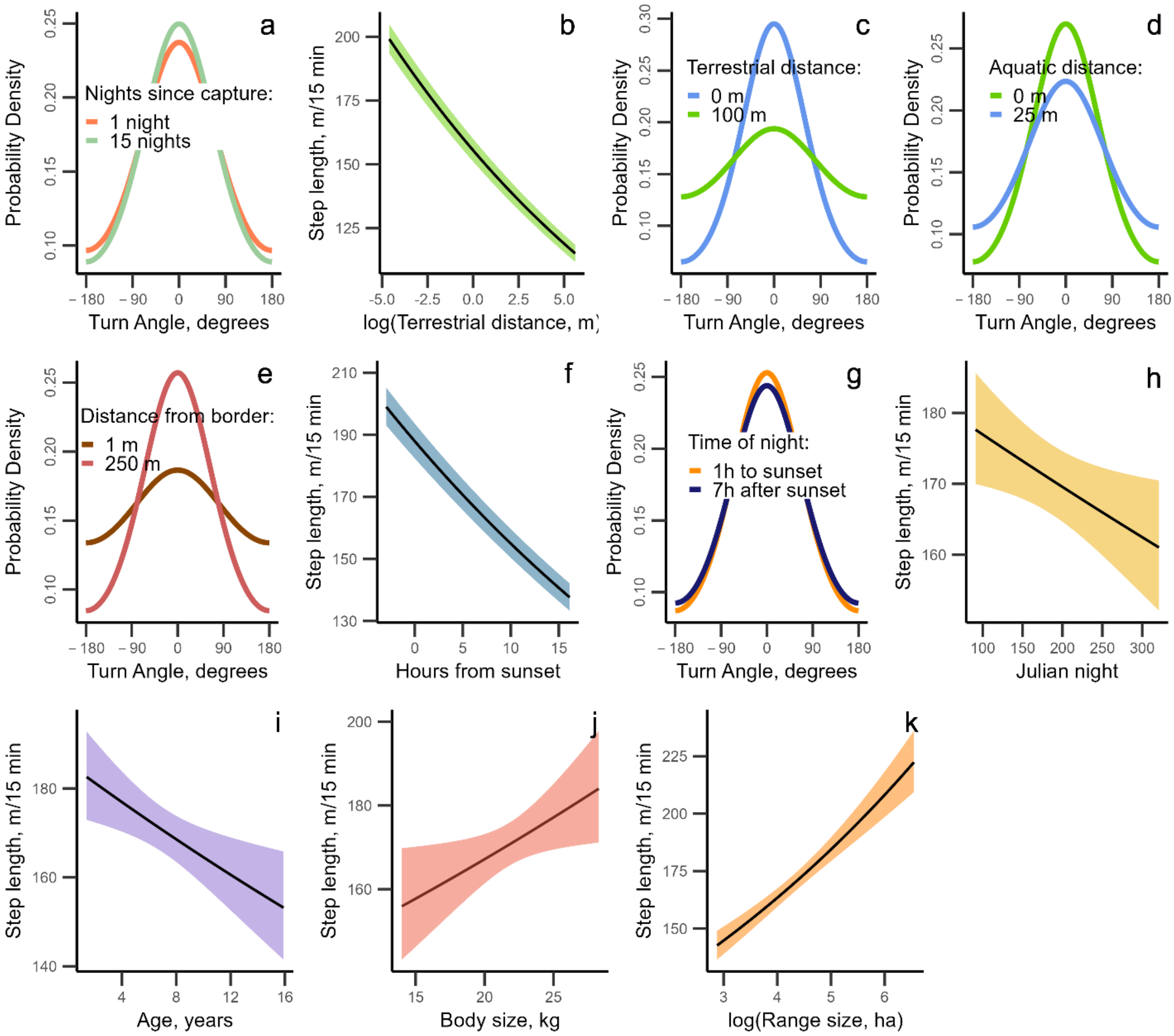

Figure 4. The predicted relationship between step length, turn angles, and (a) capture effects (nights since capture), (b-e) spatial variation (starting habitat at beginning of a step), (f-h) temporal variation (hours from sunset and Julian night), and (i-k) ecological variation (age, body size, and nightly range size) according to the integrated step selection function among 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Shaded areas in step length subplots represent 95% confidence intervals. Higher density around 0 in turn angle subplots indicate more directional movement.

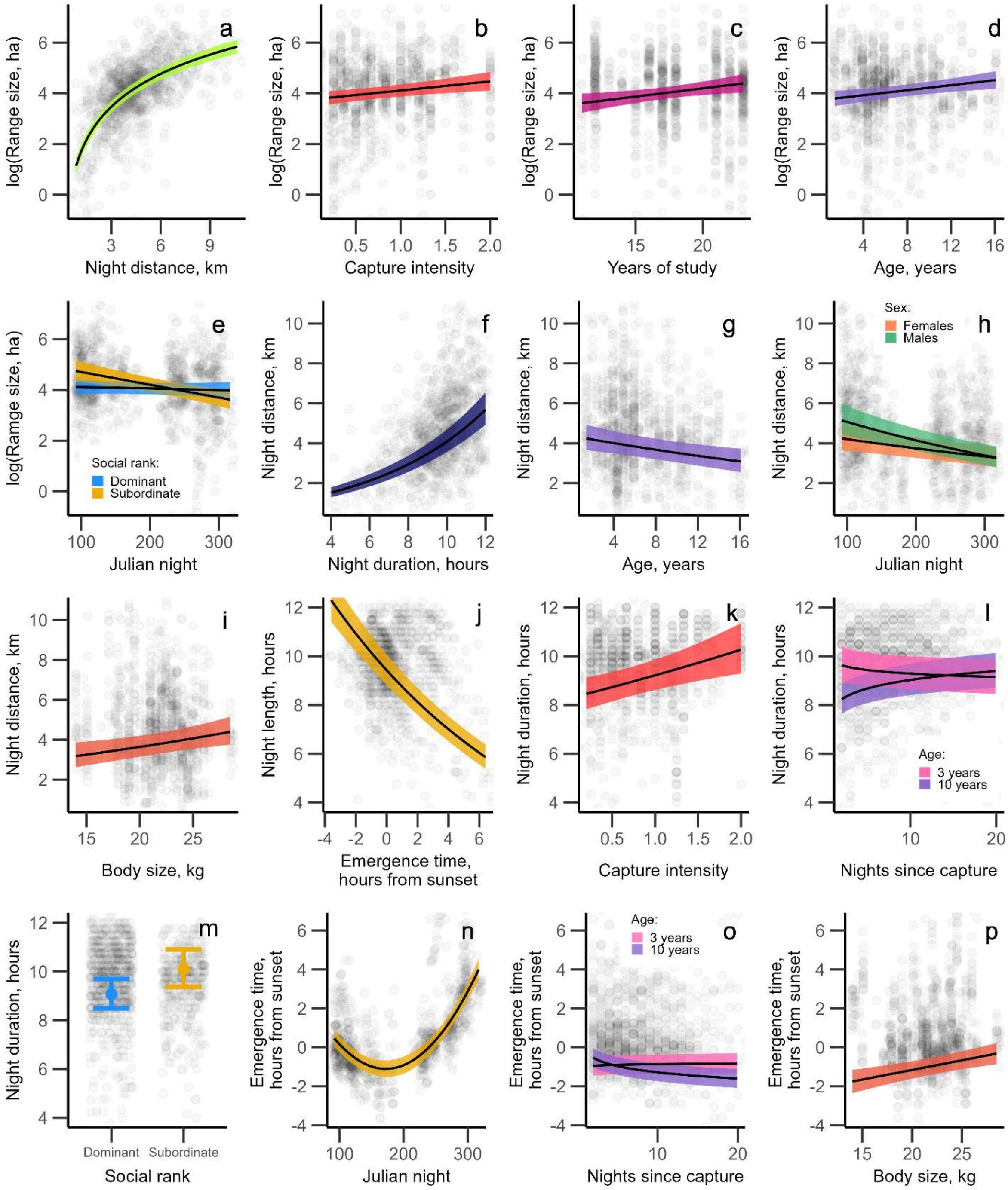

Figure 5. The predicted relationship with 95% confidence intervals between (a-e) nightly range size, (f-i) total distance moved in the night, (j-m) night duration, (n-p) emergence time from the lodge, and variables for capture and handling (capture intensity, years of study, and nights since capture), temporal variation (Julian night), and ecological variation (age, sex, social rank, and body size) in 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Grey points represent raw data.

Tables

Table 1. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables used in an iSSA to analyse habitat selection in 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Statistically clear effects are given in bold.

Variable	Estimate β	SE	LCI	UCI
log(Distance2Water$_{end}$)	**-2.761**	**0.048**	**-2.855**	**-2.666**
log(Distance2Riverbank$_{end}$)	**-2.232**	**0.045**	**-2.319**	**-2.144**
log(Distance2Border$_{end}$)	**-0.291**	**0.025**	**-0.340**	**-0.241**
log(Distance2Water$_{end}$) x log(Distance2Water$_{start}$)	**0.082**	**0.018**	**0.047**	**0.117**
log(Distance2Riverbank$_{end}$) x log(Distance2Riverbank$_{start}$)	**-0.116**	**0.017**	**-0.148**	**-0.083**
log(Distance2Border$_{end}$) x log(Distance2Border$_{start}$)	**-0.123**	**0.013**	**-0.148**	**-0.097**
log(Distance2Water)$_{end}$ x Time2Sunset	0.041	0.027	-0.012	0.094
log(Distance2Riverbank$_{end}$) x Time2Sunset	0.044	0.025	-0.006	0.094
log(Distance2Border$_{end}$) x Time2Sunset	**0.107**	**0.014**	**0.080**	**0.134**
log(Distance2Water$_{end}$) x Julian Night	0.064	0.051	-0.036	0.163
log(Distance2Riverbank$_{end}$) x Julian Night	**0.112**	**0.047**	**0.020**	**0.204**
log(Distance2Border$_{end}$) x Julian Night	-0.023	0.026	-0.074	0.027
log(Distance2Water$_{end}$) x log(Territory range size)	**-0.233**	**0.048**	**-0.326**	**-0.139**
log(Distance2Riverbank$_{end}$) x log(Territory range size)	**-0.279**	**0.044**	**-0.366**	**-0.192**
log(Distance2Border$_{end}$) x log(Territory range size)	-0.001	0.024	-0.048	0.046
log(Distance2Water$_{end}$) x Body size	**0.120**	**0.049**	**0.024**	**0.217**
log(Distance2Riverbank$_{end}$) x Body size	**0.164**	**0.045**	**0.075**	**0.253**
log(Distance2Border$_{end}$) x Body size	-0.041	0.025	-0.091	0.008

Table 2. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables used in an iSSA to analyse fine-scale movement in 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Statistically clear effects are given in bold.

Variable	Estimate β	SE	LCI	UCI
ln(Step length)	**0.357**	**0.024**	**0.311**	**0.404**
cos(Turn angle)	**-1.098**	**0.048**	**-1.193**	**-1.004**
Step length	0.000	0.000	-0.001	0.000
ln(Step length) x cos(Turn angle)	**0.236**	**0.010**	**0.218**	**0.255**
ln(Step length) x log(Distance2Water$_{start}$)	**-0.166**	**0.017**	**-0.200**	**-0.132**
cos(Turn angle) x log(Distance2Water$_{start}$)	**-0.480**	**0.030**	**-0.539**	**-0.420**
ln(Step length) x log(Distance2Riverbank$_{start}$)	0.023	0.018	-0.012	0.057
cos(Turn angle) x log(Distance2Riverbank$_{start}$)	**-0.220**	**0.030**	**-0.280**	**-0.161**
ln(Step length) x log(Distance2Border$_{start}$)	-0.012	0.009	-0.031	0.006
cos(Turn angle) x log(Distance2Border$_{start}$)	**0.283**	**0.013**	**0.257**	**0.309**
ln(Step length) x Time2Sunset	**-0.061**	**0.008**	**-0.078**	**-0.045**
cos(Turn angle) x Time2Sunset	**-0.039**	**0.014**	**-0.066**	**-0.012**
ln(Step length) x Julian Night	**-0.069**	**0.024**	**-0.115**	**-0.022**
cos(Turn angle) x Julian Night	-0.028	0.028	-0.084	0.027
ln(Step length) x Capture Intensity	-0.031	0.022	-0.074	0.013
cos(Turn angle) x Capture Intensity	0.044	0.027	-0.008	0.096
ln(Step length) x log(Nights since capture)	0.011	0.008	-0.004	0.027
cos(Turn angle) x log(Nights since capture)	**0.032**	**0.014**	**0.005**	**0.059**
ln(Step length) x Age	**-0.062**	**0.023**	**-0.108**	**-0.016**
cos(Turn angle) x Age	-0.013	0.028	-0.069	0.042
ln(Step length) x log(Territory range size)	**0.122**	**0.022**	**0.079**	**0.164**
cos(Turn angle) x log(Territory range size)	0.032	0.026	-0.019	0.084
ln(Step length) x Body size	**0.081**	**0.024**	**0.034**	**0.128**
cos(Turn angle) x Body size	0.011	0.029	-0.045	0.068

Table 3. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of nightly range size variations in 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Statistically clear effects are given in bold.

Variable	Estimate β	SE	LCI	UCI
Intercept	4.060	0.118	3.829	4.290
Capture intensity	**0.170**	**0.056**	**0.059**	**0.280**
Years of study	**0.244**	**0.094**	**0.061**	**0.428**
Julian night	-0.044	0.063	-0.169	0.080
Age	**0.179**	**0.054**	**0.072**	**0.285**
Socialrank$_{Subordinate}$	0.180	0.131	-0.076	0.435
log(Night distance)	**0.942**	**0.038**	**0.867**	**1.017**
Julian night x Socialrank$_{Subordinate}$	**-0.339**	**0.118**	**-0.569**	**-0.108**
Marginal R^2	0.45	**Conditional R^2**	0.57	

Table 4. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of nightly minimum distance moved in 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Statistically clear effects are given in bold.

Variable	Estimate β	SE	LCI	UCI
Intercept	1.328	0.071	1.190	1.467
Julian night	**-0.088**	**0.023**	**-0.134**	**-0.042**
Age	**-0.078**	**0.024**	**-0.126**	**-0.030**
Sex$_{Male}$	**0.108**	**0.052**	**0.006**	**0.209**
Body size	**0.067**	**0.024**	**0.021**	**0.113**
Night duration	**0.272**	**0.012**	**0.248**	**0.297**
Julian night x Sex$_{Male}$	**-0.065**	**0.033**	**-0.128**	**-0.001**
Marginal R^2	0.33	**Conditional R^2**	0.64	

Table 5. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of night duration in 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Statistically clear effects are given in bold.

Variable	**Estimate β**	**SE**	**LCI**	**UCI**
Intercept	2.205	0.034	2.139	2.272
Capture intensity	**0.051**	**0.015**	**0.022**	**0.080**
log(Nights since capture)	**0.012**	**0.005**	**0.001**	**0.022**
Age	**-0.031**	**0.014**	**-0.059**	**-0.004**
Socialrank$_{\text{Subordinate}}$	**0.108**	**0.027**	**0.056**	**0.160**
Emergence time	**-0.142**	**0.008**	**-0.158**	**-0.126**
log(Nights since capture) x Age	**0.024**	**0.005**	**0.014**	**0.035**
Marginal R^2	0.31	**Conditional R^2**	0.67	

Table 6. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of emergence time from the lodge in 75 adult individuals (112 tracks) of Eurasian beavers that were GPS tracked from 2009-2021 in three rivers in southeastern Norway. Statistically clear effects are given in bold.

Variable	**Estimate β**	**SE**	**LCI**	**UCI**
Intercept	-0.995	0.221	-1.429	-0.562
log(Nights since capture)	**-0.133**	**0.035**	**-0.200**	**-0.065**
Julian night	**0.771**	**0.064**	**0.645**	**0.897**
JulNights^2	**1.415**	**0.109**	**1.200**	**1.629**
Age	-0.110	0.089	-0.284	0.064
Body size	**0.298**	**0.078**	**0.145**	**0.451**
log(Nights since capture) x Age	**-0.157**	**0.033**	**-0.222**	**-0.092**
Marginal R^2	0.45	**Conditional R^2**	0.70	

Repeated capture and handling affect movement and activity patterns in a semi-aquatic mammal

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S1: The model selection results for the best candidate models investigating fine-scale habitat selection and movement across 75 individuals of Eurasian beavers that in the years 2009-2021 were tracked with GPS loggers in three rivers in southeastern Norway (total tracks: 112). Models were ranked based on AICc. Most parsimonious model within ΔAICc < 2 in bold.

Model variables	df	log likelihood	AICc	ΔAIC$_c$	weight
ln(Step length) + cos(turn angle) + Step length + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + ln(Step length):Age + cos(turn angle):Age + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	**47**	**-192260.84**	**384615.71**	**0.00**	**0.35**
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) +	53	-192255.44	384616.90	1.20	0.19

D2Riverbank$_{\text{end}}$:ln(Home range) + D2Border$_{\text{end}}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + ln(Step length):Age + cos(turn angle):Age + D2Water$_{\text{end}}$:Sex$_{\text{Male}}$ + D2Riverbank$_{\text{end}}$:Sex$_{\text{Male}}$ + D2Border$_{\text{end}}$:Sex$_{\text{Male}}$ + D2Water$_{\text{end}}$:Socialrank$_{\text{Subordinate}}$ + D2Riverbank$_{\text{end}}$:Socialrank$_{\text{Subordinate}}$ + D2Border$_{\text{end}}$:Socialrank$_{\text{Subordinate}}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{\text{end}}$:Bodymass + D2Riverbank$_{\text{end}}$:Bodymass + D2Border$_{\text{end}}$:Bodymass					
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{\text{end}}$ + D2Riverbank$_{\text{end}}$ + D2Border$_{\text{end}}$ + ln(Step length):D2Water$_{\text{start}}$ + cos(turn angle):D2Water$_{\text{start}}$ + ln(Step length):D2Riverbank$_{\text{start}}$ + cos(turn angle):D2Riverbank$_{\text{start}}$ + ln(Step length):D2Border$_{\text{start}}$ + cos(turn angle):D2Border$_{\text{start}}$ + D2Water$_{\text{end}}$:D2Water$_{\text{start}}$ + D2Riverbank$_{\text{end}}$:D2Riverbank$_{\text{start}}$ + D2Border$_{\text{end}}$:D2Border$_{\text{start}}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{\text{end}}$:Time2sunset + D2Riverbank$_{\text{end}}$:Time2sunset + D2Border$_{\text{end}}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{\text{end}}$:Julian night + D2Riverbank$_{\text{end}}$:Julian night + D2Border$_{\text{end}}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{\text{end}}$:ln(Home range) + D2Riverbank$_{\text{end}}$:ln(Home range) + D2Border$_{\text{end}}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + ln(Step length):Age + cos(turn angle):Age + D2Water$_{\text{end}}$:Sex$_{\text{Male}}$ + D2Riverbank$_{\text{end}}$:Sex$_{\text{Male}}$ + D2Border$_{\text{end}}$:Sex$_{\text{Male}}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{\text{end}}$:Bodymass + D2Riverbank$_{\text{end}}$:Bodymass + D2Border$_{\text{end}}$:Bodymass	50	-192259.09	384618.19	2.49	0.10
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{\text{end}}$ + D2Riverbank$_{\text{end}}$ + D2Border$_{\text{end}}$ + ln(Step length):D2Water$_{\text{start}}$ + cos(turn angle):D2Water$_{\text{start}}$ + ln(Step length):D2Riverbank$_{\text{start}}$ + cos(turn angle):D2Riverbank$_{\text{start}}$ + ln(Step length):D2Border$_{\text{start}}$ + cos(turn angle):D2Border$_{\text{start}}$ + D2Water$_{\text{end}}$:D2Water$_{\text{start}}$ + D2Riverbank$_{\text{end}}$:D2Riverbank$_{\text{start}}$ + D2Border$_{\text{end}}$:D2Border$_{\text{start}}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{\text{end}}$:Time2sunset + D2Riverbank$_{\text{end}}$:Time2sunset + D2Border$_{\text{end}}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{\text{end}}$:Julian night + D2Riverbank$_{\text{end}}$:Julian night + D2Border$_{\text{end}}$:Julian night + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{\text{end}}$:ln(Home range) + D2Riverbank$_{\text{end}}$:ln(Home range) + D2Border$_{\text{end}}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):Age + cos(turn angle):Age + D2Water$_{\text{end}}$:Sex$_{\text{Male}}$ + D2Riverbank$_{\text{end}}$:Sex$_{\text{Male}}$ + D2Border$_{\text{end}}$:Sex$_{\text{Male}}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{\text{end}}$:Bodymass + D2Riverbank$_{\text{end}}$:Bodymass + D2Border$_{\text{end}}$:Bodymass	50	-192259.09	384618.19	2.49	0.10

ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + ln(Step length):Nights + cos(turn angle):Nights + D2Water$_{end}$:Socialrank$_{Subordinate}$ + D2Riverbank$_{end}$:Socialrank$_{Subordinate}$ + D2Border$_{end}$:Socialrank$_{Subordinate}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	48	-192261.69	384619.40	3.70	0.06
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + D2Water$_{end}$:Socialrank$_{Subordinate}$ + D2Riverbank$_{end}$:Socialrank$_{Subordinate}$ + D2Border$_{end}$:Socialrank$_{Subordinate}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	48	-192262.01	384620.05	4.34	0.04
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset +	45	-192265.18	384620.37	4.67	0.03

D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass					
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Years + cos(turn angle):Years + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	45	-192265.18	384620.38	4.68	0.03
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Age + cos(turn angle):Age + D2Water$_{end}$:Sex$_{Male}$ + D2Riverbank$_{end}$:Sex$_{Male}$ + D2Border$_{end}$:Sex$_{Male}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	48	-192262.25	384620.52	4.82	0.03
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ +	51	-192259.87	384621.77	6.07	0.02

ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + D2Water$_{end}$:Nights + D2Riverbank$_{end}$:Nights + D2Border$_{end}$:Nights + D2Water$_{end}$:Socialrank$_{Subordinate}$ + D2Riverbank$_{end}$:Socialrank$_{Subordinate}$ + D2Border$_{end}$:Socialrank$_{Subordinate}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass					
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):Age + cos(turn angle):Age + D2Water$_{end}$:Sex$_{Male}$ + D2Riverbank$_{end}$:Sex$_{Male}$ + D2Border$_{end}$:Sex$_{Male}$ + D2Water$_{end}$:Socialrank$_{Subordinate}$ + D2Riverbank$_{end}$:Socialrank$_{Subordinate}$ + D2Border$_{end}$:Socialrank$_{Subordinate}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	53	-192258.70	384623.43	7.73	0.01
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ +	49	-192262.80	384623.62	7.91	0.01

D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + D2Water$_{end}$:Sex$_{Male}$ + D2Riverbank$_{end}$:Sex$_{Male}$ + D2Border$_{end}$:Sex$_{Male}$ + D2Water$_{end}$:Socialrank$_{Subordinate}$ + D2Riverbank$_{end}$:Socialrank$_{Subordinate}$ + D2Border$_{end}$:Socialrank$_{Subordinate}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass					
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Age + cos(turn angle):Age + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	43	-192268.89	384623.80	8.09	0.01
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Capture intensity + cos(turn angle):Capture intensity + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	43	-192269.02	384624.05	8.34	0.01

ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + ln(Step length):Years + cos(turn angle):Years + D2Water$_{end}$:Sex$_{Male}$ + D2Riverbank$_{end}$:Sex$_{Male}$ + D2Border$_{end}$:Sex$_{Male}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	48	-192264.33	384624.69	8.98	0.00
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + D2Water$_{end}$:Sex$_{Male}$ + D2Riverbank$_{end}$:Sex$_{Male}$ + D2Border$_{end}$:Sex$_{Male}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass	46	-192266.38	384624.77	9.07	0.00
ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$ + ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn	44	-192268.60	384625.23	9.52	0.00

angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + D2Water$_{end}$:Socialrank$_{Subordinate}$ + D2Riverbank$_{end}$:Socialrank$_{Subordinate}$ + D2Border$_{end}$:Socialrank$_{Subordinate}$ + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass					
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ln(Step length) + cos(turn angle) + ln(Step length) + ln(Step length):ta + D2Water$_{end}$ + D2Riverbank$_{end}$ + D2Border$_{end}$ + ln(Step length):D2Water$_{start}$ + cos(turn angle):D2Water$_{start}$	54	-192258.98	384625.99	10.29	0.00

+ ln(Step length):D2Riverbank$_{start}$ + cos(turn angle):D2Riverbank$_{start}$ + ln(Step length):D2Border$_{start}$ + cos(turn angle):D2Border$_{start}$ + D2Water$_{end}$:D2Water$_{start}$ + D2Riverbank$_{end}$:D2Riverbank$_{start}$ + D2Border$_{end}$:D2Border$_{start}$ + ln(Step length):Time2sunset + cos(turn angle):Time2sunset + D2Water$_{end}$:Time2sunset + D2Riverbank$_{end}$:Time2sunset + D2Border$_{end}$:Time2sunset + ln(Step length):Julian night + cos(turn angle):Julian night + D2Water$_{end}$:Julian night + D2Riverbank$_{end}$:Julian night + D2Border$_{end}$:Julian night + ln(Step length):Nights + cos(turn angle):Nights + ln(Step length):ln(Home range) + cos(turn angle):ln(Home range) + D2Water$_{end}$:ln(Home range) + D2Riverbank$_{end}$:ln(Home range) + D2Border$_{end}$:ln(Home range) + D2Water$_{end}$:Nights + D2Riverbank$_{end}$:Nights + D2Border$_{end}$:Nights + ln(Step length):Age + cos(turn angle):Age + D2Water$_{end}$:Sex$_{Male}$ + D2Riverbank$_{end}$:Sex$_{Male}$ + D2Border$_{end}$:Sex$_{Male}$ + D2Water$_{end}$:Socialrank$_{Subordinate}$ + D2Riverbank$_{end}$:Socialrank$_{Subordinate}$ + D2Border$_{end}$:Socialrank$_{Subordinate}$ + ln(Step length):Bodymass + cos(turn angle):Bodymass + D2Water$_{end}$:Bodymass + D2Riverbank$_{end}$:Bodymass + D2Border$_{end}$:Bodymass					

S2: The model selection results for the best candidate models investigating nightly home range size across 75 individuals of Eurasian beavers that in the years 2009-2021 were tracked with GPS loggers in three rivers in south-Eastern Norway. Models were ranked based on AICc. Most parsimonious model within ΔAICc < 2 in bold.

Model variables	**df**	**log likelihood**	**AICc**	**ΔAIC$_c$**	**weight**	**R$^2_{marginal}$**	**R$^2_{conditional}$**
1+2+4+5+7+9+18	**12**	**-1550.70**	**3125.70**	**0.00**	**0.12**	**0.45**	**0.57**
1+2+4+5+6+7+9+18	13	-1549.96	3126.26	0.57	0.09	0.45	0.56
1+2+4+5+6+7+9+17+18	14	-1549.13	3126.65	0.95	0.08	0.45	0.56
1+2+4+5+6+7+8+9+18	14	-1549.42	3127.23	1.54	0.06	0.45	0.56
1+2+4+5+7+8+9+18	13	-1550.48	3127.30	1.60	0.05	0.45	0.57
1+2+4+5+7+9+11+18	13	-1550.50	3127.34	1.64	0.05	0.45	0.57
1+2+4+5+6+7+8+9+17+18	15	-1548.49	3127.43	1.73	0.05	0.46	0.56
1+2+4+5+7+9+14+18	13	-1550.61	3127.57	1.87	0.05	0.45	0.56
1+2+4+5+7+9+10+18	13	-1550.63	3127.61	1.92	0.05	0.45	0.57
1+2+4+5+7+9+13+18	13	-1550.64	3127.63	1.94	0.05	0.45	0.57
1+2+3+4+5+7+9+18	13	-1550.70	3127.74	2.05	0.04	0.45	0.57
1+2+4+5+6+7+9+11+18	14	-1549.75	3127.90	2.21	0.04	0.45	0.56
1+2+3+4+5+7+9+15+18	14	-1549.84	3128.08	2.38	0.04	0.45	0.57
1+2+4+5+6+7+9+10+18	14	-1549.89	3128.17	2.47	0.04	0.45	0.56
1+2+4+5+6+7+9+11+17+18	15	-1548.86	3128.17	2.47	0.04	0.45	0.56
1+2+3+4+5+7+9+16+18	14	-1549.89	3128.17	2.48	0.03	0.45	0.56
1+2+4+5+6+7+9+14+18	14	-1549.91	3128.22	2.52	0.03	0.45	0.56
1+2+4+5+6+7+9+12+18	14	-1549.93	3128.25	2.55	0.03	0.45	0.56
1+2+4+5+6+7+9+13+18	14	-1549.95	3128.29	2.59	0.03	0.45	0.56
1+2+3+4+5+6+7+9+18	14	-1549.96	3128.31	2.61	0.03	0.45	0.56

1 = Capture intensity, 2 = Years of study, 3 = Nights since capture, 4 = Julian night, 5 = Age, 6 = Sex, 7 = Social rank, 8 = Body size, 9 = Night distance, 10 = Capture intensity x Years of study, 11 = Capture intensity x Age, 12 = Capture intensity x Sex, 13 = Capture intensity x Social rank, 14 = Years of study x Social rank, 15 = Nights since capture x Age, 16 = Nights since capture x Social rank, 17 = Julian night x Sex, 18 = Julian night x Social rank

S3: The model selection results for the best candidate models investigating nightly minimum distance moved across 75 individuals of Eurasian beavers that in the years 2009-2021 were tracked with GPS loggers in three rivers in south-Eastern Norway. Models were ranked based on AICc. Most parsimonious model within ΔAICc < 2 in bold.

Model variables	**df**	**log likelihood**	**AICc**	**ΔAIC_c**	**weight**	**$R^2_{marginal}$**	**$R^2_{conditional}$**
1+2+4+5+6+8+9+10+11	14	-378.38	785.16	0.00	0.09	0.37	0.65
4+5+6+7+8+9+11	12	-380.52	785.32	0.16	0.08	0.33	0.65
1+2+4+5+6+7+8+9+10+11	15	-377.59	785.63	0.47	0.07	0.37	0.66
2+4+5+6+7+8+9+11	13	-379.68	785.71	0.55	0.07	0.36	0.66
1+2+4+5+6+8+9+10	13	-379.80	785.93	0.77	0.06	0.36	0.65
2+4+5+6+8+9+11	12	-380.84	785.97	0.81	0.06	0.36	0.64
4+5+6+8+9+11	**11**	**-381.92**	**786.09**	**0.93**	**0.06**	**0.33**	**0.64**
4+5+6+7+8+9+11+12	13	-379.93	786.19	1.04	0.05	0.33	0.65
1+2+4+5+6+7+8+9+10+11+12	16	-376.98	786.46	1.30	0.05	0.36	0.66
1+2+4+5+6+7+9+10+11	14	-379.06	786.50	1.34	0.05	0.37	0.66
2+4+5+6+7+8+9+11+12	14	-379.09	786.57	1.41	0.04	0.36	0.66
1+2+3+4+5+6+8+9+10+11	15	-378.07	786.58	1.42	0.04	0.37	0.65
3+4+5+6+7+8+9+11	13	-380.19	786.72	1.56	0.04	0.33	0.65
1+2+3+4+5+6+7+8+9+10+11	16	-377.26	787.03	1.87	0.04	0.37	0.66
2+3+4+5+6+7+8+9+11	14	-379.36	787.10	1.94	0.03	0.36	0.66
1+2+3+4+5+6+8+9+10	14	-379.37	787.13	1.97	0.03	0.37	0.65
1+2+4+5+6+7+8+9+10	14	-379.39	787.17	2.01	0.03	0.36	0.66
1+2+4+5+6+7+9+10	13	-380.45	787.25	2.09	0.03	0.37	0.66
1+2+4+5+6+7+9+10+11+12	15	-378.44	787.32	2.16	0.03	0.37	0.66
1+4+5+6+7+8+9+11	13	-380.50	787.35	2.19	0.03	0.33	0.65

1 = Capture intensity, 2 = Years of study, 3 = Nights since capture, 4 = Julian night, 5 = Age, 6 = Sex, 7 = Social rank, 8 = Body size, 9 = Night distance, 10 = Capture intensity x Years of study, 11 = Capture intensity x Age, 12 = Capture intensity x Sex, 13 = Capture intensity x Social rank, 14 = Years of study x Social rank, 15 = Nights since capture x Age, 16 = Nights since capture x Social rank, 17 = Julian night x Sex, 18 = Julian night x Social rank

S4: The model selection results for the best candidate models investigating night length across 75 individuals of Eurasian beavers that in the years 2009-2021 were tracked with GPS loggers in three rivers in south-Eastern Norway. Models were ranked based on AICc. Most parsimonious model within ΔAICc < 2 in bold.

Model variables	**df**	**log likelihood**	**AICc**	**ΔAIC_c**	**weight**	**$R^2_{marginal}$**	**$R^2_{conditional}$**
1+2+3+4+6+7+8+11	13	333.12	-639.89	0.00	0.23	0.32	0.67
1+2+3+4+6+8+11	12	331.79	-639.29	0.60	0.17	0.32	0.67
1+3+4+6+7+8+11	12	331.27	-638.24	1.65	0.10	0.31	0.68
1+3+4+6+8+11	**11**	**330.16**	**-638.07**	**1.83**	**0.09**	**0.31**	**0.67**
1+2+3+4+5+6+7+8+11	14	333.18	-637.96	1.93	0.09	0.32	0.67
1+2+3+4+5+6+8+11	13	332.04	-637.73	2.16	0.08	0.32	0.67
1+3+4+5+6+8+11	12	330.43	-636.58	3.32	0.04	0.31	0.67
1+3+4+5+6+7+8+11	13	331.36	-636.38	3.52	0.04	0.31	0.68
1+2+3+6+7+8+10	12	329.97	-635.64	4.25	0.03	0.33	0.68
1+2+3+4+6+7+8+10	13	330.98	-635.63	4.26	0.03	0.33	0.67
1+2+3+4+6+8+10	12	329.82	-635.35	4.54	0.02	0.32	0.66
1+3+4+6+8+10	11	328.02	-633.79	6.10	0.01	0.31	0.67
1+2+3+4+5+6+8+10	13	330.06	-633.79	6.10	0.01	0.32	0.66
1+2+3+4+5+6+7+8+10	14	331.05	-633.71	6.18	0.01	0.33	0.67
1+3+4+6+7+8+10	12	328.98	-633.67	6.22	0.01	0.31	0.67
1+2+3+5+6+7+8+10	13	329.98	-633.61	6.28	0.01	0.33	0.68
1+2+3+6+8+10	11	327.72	-633.20	6.69	0.01	0.32	0.69
1+2+3+6+7+8+9	12	328.49	-632.68	7.21	0.01	0.31	0.70
1+2+3+4+7+8+11	12	328.42	-632.55	7.34	0.01	0.31	0.64
1+3+4+5+6+8+10	12	328.29	-632.29	7.60	0.01	0.32	0.67

1 = Capture intensity, 2 = Years of study, 3 = Nights since capture, 4 = Julian night, 5 = Age, 6 = Sex, 7 = Social rank, 8 = Body size, 9 = Night distance, 10 = Capture intensity x Years of study, 11 = Capture intensity x Age, 12 = Capture intensity x Sex, 13 = Capture intensity x Social rank, 14 = Years of study x Social rank, 15 = Nights since capture x Age, 16 = Nights since capture x Social rank, 17 = Julian night x Sex, 18 = Julian night x Social rank

S5: The model selection results for the best candidate models investigating nightly emergence time across 110 individuals of Eurasian beavers that in the years 2009-2021 were tracked with GPS loggers in three rivers in south-Eastern Norway. Models were ranked based on AICc. Most parsimonious model within ΔAICc < 2 in bold.

Model variables	**df**	**log likelihood**	**AICc**	**ΔAIC_c**	**weight**	**$R^2_{marginal}$**	**$R^2_{conditional}$**
3+4+5+6+7+9+11+12	13	-1683.1	3392.6	0.0	0.2	0.4	0.7
2+3+4+5+6+7+9+11+12	14	-1682.5	3393.3	0.7	0.1	0.4	0.7
3+4+5+6+9+11	**11**	**-1685.7**	**3393.6**	**1.0**	**0.1**	**0.5**	**0.7**
2+3+4+5+6+9+11	12	-1685.1	3394.4	1.8	0.1	0.5	0.7
3+4+5+6+7+8+9+11+12	14	-1683.1	3394.6	2.0	0.1	0.4	0.7
1+3+4+5+6+7+9+11+12	14	-1683.1	3394.6	2.0	0.1	0.4	0.7
3+4+5+6+8+9+11	12	-1685.4	3395.1	2.5	0.0	0.5	0.7
1+2+3+4+5+6+7+9+11+12	15	-1682.4	3395.3	2.7	0.0	0.4	0.7

2+3+4+5+6+7+8+9+11+12	15	-1682.4	3395.3	2.7	0.0	0.4	0.7
3+4+5+6+7+9+11	12	-1685.6	3395.5	2.9	0.0	0.5	0.7
1+3+4+5+6+9+11	12	-1685.7	3395.6	3.0	0.0	0.5	0.7
1+3+4+5+7+9+10+12	13	-1684.7	3395.8	3.2	0.0	0.4	0.7
2+3+4+5+6+8+9+11	13	-1684.9	3396.1	3.4	0.0	0.5	0.7
2+3+4+5+6+7+9+11	13	-1685.0	3396.4	3.8	0.0	0.5	0.7
3+4+5+6+7+8+9+11+12+13	15	-1683.0	3396.4	3.8	0.0	0.4	0.7
1+2+3+4+5+6+9+11	13	-1685.0	3396.4	3.8	0.0	0.5	0.7
1+2+3+4+5+7+9+10+12	14	-1684.1	3396.6	4.0	0.0	0.4	0.7
1+3+4+5+6+7+8+9+11+12	15	-1683.1	3396.6	4.0	0.0	0.4	0.7
3+4+5+6+8+9+11+13	13	-1685.3	3396.9	4.3	0.0	0.5	0.7
3+4+5+6+7+8+9+11	13	-1685.4	3397.0	4.4	0.0	0.5	0.7

1 = Capture intensity, 2 = Years of study, 3 = Nights since capture, 4 = Julian night, 5 = Age, 6 = Sex, 7 = Social rank, 8 = Body size, 9 = Night distance, 10 = Capture intensity x Years of study, 11 = Capture intensity x Age, 12 = Capture intensity x Sex, 13 = Capture intensity x Social rank, 14 = Years of study x Social rank, 15 = Nights since capture x Age, 16 = Nights since capture x Social rank, 17 = Julian night x Sex, 18 = Julian night x Social rank

Paper III

Mortensen, R.M. and Rosell, F. (2020). Long-term capture and handling effects on body condition, reproduction, and survival in a semi-aquatic mammal. Scientific Reports, 10(1), 1-16. doi: 10.1038/s41598-020-74933-w

scientific reports

OPEN

Long-term capture and handling effects on body condition, reproduction and survival in a semi-aquatic mammal

Rasmus M. Mortensen & Frank Rosell

In long-term individual-based field studies, several parameters need to be assessed repeatedly to fully understand the potential fitness effects on individuals. Often studies only evaluate capture stress that appears in the immediate weeks or breeding season and even long-term studies fail to evaluate the long-term effects of their capture procedures. We investigated effects of long-term repeated capture and handling of individuals in a large semi-aquatic rodent using more than 20 years of monitoring data from a beaver population in Norway. To investigate the effects, we corrected for ecological factors and analysed the importance of total capture and handling events, years of monitoring and deployment of telemetry devices on measures related to body condition, reproduction and survival of individual beavers. Body mass of dominant individuals decreased considerably with number of capture events (107 g per capture), but we found no statistically clear short or long-term effects of capture and handling on survival or other body condition indices. Annual litter size decreased with increasing number of captures among older individuals. Number of captures furthermore negatively affected reproduction in the beginning of the monitoring, but the effect decreased over the years, indicating habituation to repeated capture and handling. By assessing potential impacts on several fitness-related parameters at multiple times, we can secure the welfare of wild animal populations when planning and executing future conservation studies as well as ensure ecologically reliable research data.

Studying individuals of a population repeatedly over longer time periods yields substantial scientific insights on age-related changes in various vital rates such as growth[1], reproductive performance[2] and survival[3], but also enables possibilities to connect events and changes at one life-history stage to those of another[4].

Capture and handling events are expected to induce immediate physiological and behavioural adjustments for the individual to cope with the disturbance, which may result in an intense stress response that can have physical, physiological and behavioural consequences[5,6]. These potential changes in behavioural patterns can affect body condition as well as vital rates and may consequently negatively influence mating success and fitness[7–9].

To evaluate these potential capture and handling effects, researchers often focus on the immediate harm that could be caused, such as mortalities and physical injuries. Capture and handling methods are often considered efficient as long as the animal survives through the process without noticeable injuries[10]. However, animals often hide symptoms that make them appear vulnerable[11]. Mortality rates and physical injuries at time of capture are not sufficient to successfully assess capture and handling procedures, as the full impact cannot be determined without also evaluating physical, behavioural and physiological effects at multiple times on a long-term scale[12,13].

When evaluating the more indirect effects of capture and handling in a wide range of species, researchers have, among other things, analysed changes in various body condition indices[9,14–16], reproductive performance[8,17–22] and mortality[5,10,23–29]. Most studies only evaluate capture and handling effects using a limited number of parameters associated to, for example, physiology or reproduction, and seldom several categories[30]. However, we might not be able to detect changes in some parameters[22], or parameters might not be affected despite the level of stress[31] and animals may habituate to cope with stress[32]. Often effects are only evaluated on a time scale from a couple of weeks to a year after capture, which may relate to limitations of the measured parameters and constraints related to the framework of the project[33]. Even long-term studies that last several seasons are mostly evaluated within each season[30], although capture and handling may affect individuals at later life stages and across generations[18,34].

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To determine the full impact of repeated capture and handling, we need more evidence-based knowledge on physical, behavioural and physiological effects at both short and longer time-scales to understand how capture and handling procedures might affect body condition as well as vital rates that consequently may negatively influence reproductive performance and survival[8,9].

We use Eurasian beavers (*Castor fiber*) as a model species to study long-term effects of repeated capture and handling in a highly territorial, semi-aquatic mammal. Beavers (including *C. canadensis*) have been intensively studied describing, among other things, reproduction[35–37], territorial communication[38–41], resource and habitat use[42–45] and time-budgets[46–48]. However, effects of capturing and handling individuals, as well as deploying telemetry devices, which have taken place in several of these research projects, have not been investigated besides short-term effects of tagging[16,49]. One would expect these procedures to induce stress responses that may affect short term body condition measures (fat storage in the tail[37]) and behaviour of the beavers. However, these behavioural changes may also affect body condition in the long term and potentially affect the whole population, negatively influencing mating success and survival at several life-history stages and in coming generations[4].

In our study, we aim to investigate the effects of long-term capture, handling and tagging in a large semi-aquatic rodent, using monitoring data of a beaver population in south-eastern Norway which has experienced repeated capture and handling events since 1997. To investigate the long-term effects, we corrected for ecological factors and analysed the importance of capture and handling events, years of monitoring and deployment of telemetry devices on measures related to body condition, reproduction and survival of individual beavers, all of which ultimately affect fitness of individuals.

Results

We made on average (mean ± SD) 65.8 ± 8.1 annual captures (median = 63). Kits were captured up to four times (mean = 1.1 ± 1.1, median = 1). Captured yearlings experienced up to five captures (mean = 1.9 ± 1.4, median = 2) and subadults up to seven captures (mean = 3.0 ± 1.7, median = 3), including captures in previous life stages. Adult beavers were captured up to twenty-five times in their lifetime (mean = 5.1 ± 2.3, median = 4). Dominant adults experienced more captures than subordinates ($\text{mean}_{\text{dominant}} = 6.3 \pm 2.5$, $\text{median}_{\text{dominant}} = 5$, $\text{mean}_{\text{subordinate}} = 2.6 \pm 1.6$, $\text{median}_{\text{subordinate}} = 2$) and males and females were captured equally ($\text{mean}_{\text{males}} = 4.4 \pm 2.1$, $\text{median}_{\text{males}} = 3$, $\text{mean}_{\text{females}} = 4.1 \pm 2.0$, $\text{median}_{\text{females}} = 3$).

Body condition indices. We found no statistically clear effects of the number of capture and handling events, years of monitoring or from carrying telemetry devices on the variability of the tail fat index in our population. Tail fat index varied clearly with capture season and age among both young and adult individuals (Table 1). It increased clearly over time among individuals, resembling increase in body growth. Among adult individuals, tail fat index increased up to approximately eight years, after which it decreased (Fig. 1). Furthermore, we found statistically clear intra-annual variation in tail fat index among adults with tail fat clearly increasing between spring and autumn (Table 1, Fig. 1). No statistically clear differences were found among young males and females, but adult females had smaller tail fat index than males (Table 1).

We found a statistically clear negative effect of capture events on the body mass of dominant individuals, but found no statistically clear effects on other individuals, of years of monitoring, or from carrying telemetry devices (Table 2, Fig. 2). Body mass increased clearly within the year from spring to autumn and with increasing age up to approximately 10 years (Fig. 2). Young individuals from larger territories had smaller body weights than young individuals from smaller territories (Table 2, Fig. 2). As expected, dominant beavers had larger body mass than subordinates (Table 2, Fig. 2). We found no statistically clear differences between young males and females, but adult females were clearly bigger than males in spring and summer (Table 2, Fig. 2).

No statistically clear effects were found of either number of capture and handling events, years of monitoring or carrying telemetry devices on body length (Table 3). Body length increased clearly within the year from spring to autumn and with increasing age up to approximately 10 years (Fig. 3). Young individuals from larger territories were smaller than young individuals from smaller territories. We found no statistically clear differences in body size among sexes or social rank.

Reproduction. Between 1998 and 2018, we observed 65 dominant females, which produced 1–4 kits in reproducing years. They reproduced on average every 2.5 ± 0.6 years during the duration of their territory occupancy.

Number of capture and handling events and years of monitoring had statistically clear effects on both yearly reproduction and annual number of kits produced among females in our population (Table 4, Fig. 4). An increasing number of capture events seemed to have a negative effect in the early monitoring years on both yearly reproduction and annual number of offspring. However, this effect became less clear over the years of the monitoring program. Furthermore, we found a statistically clear negative effect of number of capture and handling events on annual number of offspring produced by older beavers (Table 4, Fig. 4). We found no statistically clear differences among the other investigated variables.

Survival. No statistically clear effects were found of number of capture and handling events, years of monitoring or carrying telemetry devices on annual survival (Table 5). Only social status, age and family group size had statistically clear effects on annual survival (Table 5). We found a clear increasing probability of annual survival with age for dominant individuals, whereas annual survival decreased with age for subordinates and with increasing family group size (Fig. 5).

We found no statistically clear effects of number of capture and handling events, years of monitoring or carrying telemetry devices on the probability of staying dominant in a territory the following year (Table 6). We found

Variables	Estimate	SE	LCI	UCI	$R^2_{marginal}$	$R^2_{conditional}$
Young (kits and yearlings)						
Intercept	**1.496**	**0.089**	**1.322**	**1.670**	0.56	0.73
Captures	0.001	0.014	− 0.026	0.028		
Years of monitoring	0.002	0.004	− 0.006	0.010		
Sex (male)	− 0.018	0.037	− 0.090	0.054		
Age	**1.051**	**0.050**	**0.952**	**1.150**		
Season (summer)	**0.486**	**0.061**	**0.366**	**0.606**		
Season (autumn)	**0.784**	**0.068**	**0.651**	**0.917**		
Log (territory size)	− 0.079	0.051	− 0.179	0.021		
Family group size	− 0.003	0.008	− 0.019	0.013		
Adults (2 + years)						
Intercept	**3.641**	**0.107**	**3.431**	**3.852**	0.12	0.48
Captures	− 0.005	0.006	− 0.017	0.007		
Years of monitoring	0.000	0.002	− 0.004	0.003		
Carried telemetry device (yes)	− 0.006	0.021	− 0.047	0.034		
Sex (male)	**0.131**	**0.038**	**0.055**	**0.206**		
Age	**0.100**	**0.022**	**0.058**	**0.142**		
Age^2	**− 0.006**	**0.001**	**− 0.008**	**− 0.004**		
Social status (subordinate)	− 0.145	0.079	− 0.299	0.009		
Origin (resident)	− 0.001	0.016	− 0.033	0.031		
Season (summer)	0.022	0.032	− 0.040	0.084		
Season (autumn)	**0.131**	**0.052**	**0.029**	**0.233**		
Log (territory size)	− 0.008	0.018	− 0.043	0.028		
Family group size	0.001	0.004	− 0.006	0.008		
Captures: social status (subordinate)	0.000	0.003	− 0.006	0.006		
Season (summer): sex (male)	− 0.011	0.035	− 0.080	0.059		
Season (autumn): sex (male)	− 0.061	0.074	− 0.206	0.083		
Social status (subordinate): age	0.018	0.011	− 0.005	0.040		

Table 1. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of tail fat index in a Eurasian beaver population in south-eastern Norway between 1998 and 2018 ($n_{young} = 333$, $n_{adults} = 828$). Beaver ID, capture year and river were included as random effects. We performed model averaging of best models (ΔAICc < 4) to estimate the effect size of each variable. Informative parameters are given in bold. Reference level of sex: female. Reference level of season: spring. Reference level of carried telemetry device: no. Reference level of social status: dominant. Reference level of origin: immigrant.

a decreasing probability of staying dominant with increasing age and an increasing probability with increasing family group size (Table 6, Fig. 6). No statistically clear differences were found for other investigated variables.

Discussion

By evaluating at multiple points in time on a long-term scale, how more than twenty years of repeated capture and handling of individuals in a beaver population affect body condition, reproductive performance and survival, we thoroughly investigate capture and handling effects on important vital rates that ultimately influence fitness of the animals[4]. We found statistically clear effects of repeated capture and handling on body mass of dominant individuals, but found no statistically clear effects of repeated capture and handling on any of the other body condition indices or annual survival probability. However, we observed statistically clear changes through the years in reproductive performance of dominant females, clarifying the importance of investigating several parameter categories when evaluating the consequences of capturing and handling individual animals[9,12,13]. To fully understand fitness effects of capture procedures, one should repeatedly evaluate capture and handling effects at several points in times. Often studies only evaluate capture stress that appears in the immediate days, weeks or the following breeding season after handling[30]. Even long-term studies that investigate capture and handling effects for several years sometimes fail to evaluate long-term effects of their procedures, since they only evaluate short-term effects within each year and season[50–52]. But as we show, capture effects might also have longer-term consequences for individuals, indicating the need for repeated evaluations of condition and fitness. However, this may prove unviable because of limited timeframes or other constraints within the framework of the project that may challenge such long-term continuity[33].

Body condition.

Body condition indices resemble snapshots of the physiological state of an animal, indicating e.g. past foraging success or ability to cope with environmental pressures[14,53], which may impact other life-

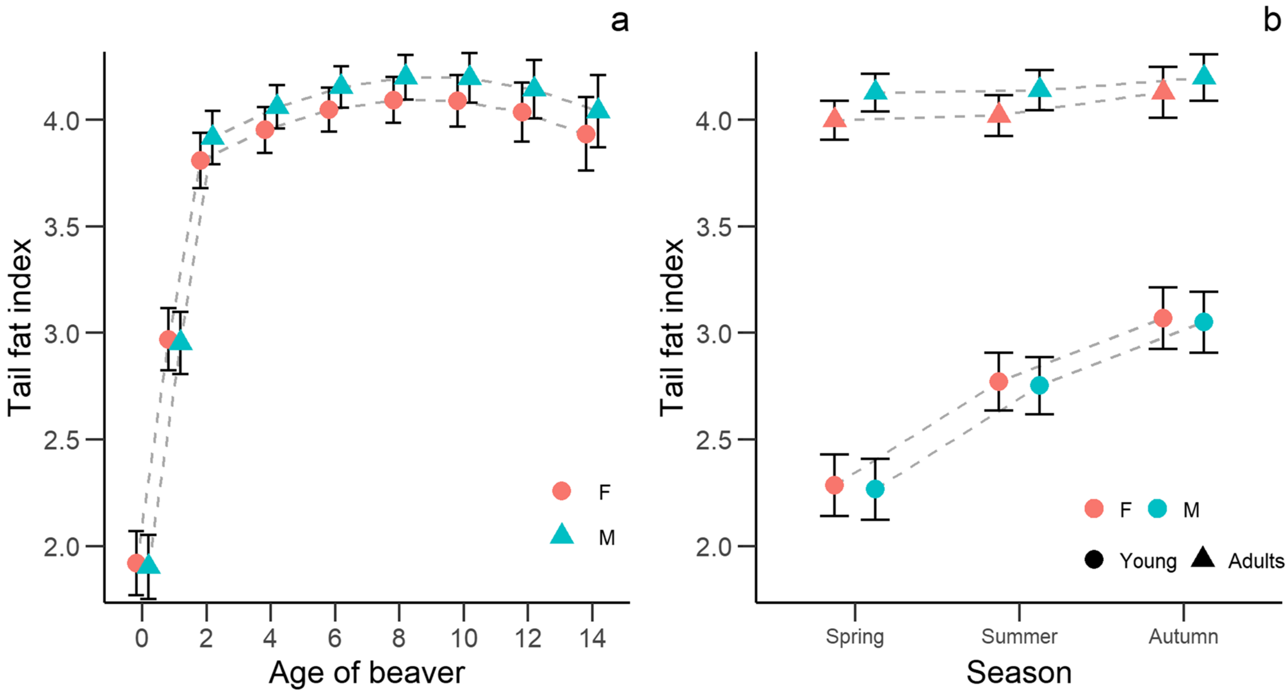

Figure 1. The predicted relationship ± 95% confidence interval between age, sex and tail fat index (**a**) and age, sex, season and tail fat index (**b**) in a Eurasian beaver population in south-eastern Norway between 1998 and 2018.

history stages, future reproductive success, and ultimately evolutionary fitness[54,55]. We therefore expected to find variations in size and mass in our population related to number of capture and handling events experienced by each individual, as well as a development over the years of the Norwegian Beaver Project (NBP) as an indication of experienced long-term stress. While several studies have observed negative effects of repeated captures on body condition, body mass and length, only few studies have looked at long-term effects[30]. In long-term studies, up to 21 years, bears that experienced more recaptures had a poorer age-specific body condition[9]. Similar negative effects have been found among rodents live-trapped over two years[15]. Neither tail fat index nor body length were affected short or long-term by repeated captures and handling in our population. However, we did find a clear decrease in body mass with increasing capture and handling events among dominant individuals. Other studies in beavers have observed greater weight loss and decrease in tail area over the following winter when being equipped with transmitters[16]. We might expect more short-term effects within days post-capture related to the individuals staying more in lodge and being less active as an immediate response to the capture event[49].

Tail fat index, body mass and body size increased considerably between life stages of beavers, reflecting their growth rate. Furthermore, they increased over the year, especially among young individuals, which increase relatively more in mass and size. But also adults showed seasonal variations similar with findings in other populations[56].

Females in the reproductive age generally had smaller tail size and higher body mass in spring and summer when reproduction occurs, indicating differentiation in allocation of time and energy among sexes. Comparing time-budgets of males and females, no differences were found[46], which is expected in monogamous animals[57]. Males allocated more time to travel which might indicate an increased patrolling effort or search for food items, whereas females might spend more time on parenting activities, which our results support.

Only body mass was greater among dominant individuals, indicating this as an important feature of social status[58], whereas tail size and body length might be more socially stable to maximize fitness of individuals[37]. Social rank is highly shaped by agonistic interactions between individuals[59], where body size can be an important factor[60]. However, the social hierarchy may also be influenced by affiliative interactions[61]. In beavers only the dominating pair breed. Also among high ranked individuals in other social rodents have body size correlated with greater reproductive success[62]. In our population, body mass decreased among dominant individuals with increasing number of capture and handling events. Dominants have a higher energy expenditure due to increased territorial defence and reproduction[36,37,41], which may suggest they might be more susceptible to capture stress[7,60].

Young individuals of larger territories were found to have lower body mass and smaller body length, which might be a result of parents spending more time on patrolling than parenting[47]. Generally, costs of defending a territory are positively correlated with territory size[63] and young individuals might suffer as a consequence. Larger territories may have fewer quality food resources and might be larger to provide adequate resource availability[64–66]. However, we found no effect of territory size among adults suggesting that territorial behaviour in our population, to a lesser degree, follows the availability of food resources[67].

Variables	Estimate	SE	LCI	UCI	$R^2_{marginal}$	$R^2_{conditional}$
Young (kits and yearlings)						
Intercept	**4.673**	**0.256**	**4.172**	**5.174**	0.87	0.93
Captures	0.078	0.109	− 0.135	0.291		
Years of monitoring	0.011	0.020	− 0.028	0.050		
Sex (male)	− 0.010	0.076	− 0.160	0.140		
Age	**7.997**	**0.201**	**7.603**	**8.391**		
Season (summer)	**3.765**	**0.204**	**3.364**	**4.166**		
Season (autumn)	**5.570**	**0.236**	**5.108**	**6.033**		
Log (territory size)	**− 0.453**	**0.143**	**− 0.734**	**− 0.172**		
Family group size	− 0.087	0.049	− 0.183	0.010		
Adults (2 + years)						
Intercept	**21.983**	**0.283**	**21.428**	**22.538**	0.48	0.78
Captures	**− 0.148**	**0.044**	**− 0.235**	**− 0.062**		
Years of monitoring	− 0.012	0.028	− 0.067	0.043		
Carried telemetry device (yes)	0.003	0.065	− 0.126	0.131		
Sex (male)	**− 1.084**	**0.253**	**− 1.581**	**− 0.587**		
Age	**0.684**	**0.047**	**0.591**	**0.777**		
Age^2	**− 0.088**	**0.007**	**− 0.102**	**− 0.075**		
Social status (subordinate)	**− 0.539**	**0.179**	**− 0.889**	**− 0.189**		
Origin (resident)	0.001	0.096	− 0.186	0.188		
Season (summer)	**0.939**	**0.205**	**0.537**	**1.341**		
Season (autumn)	**1.265**	**0.237**	**0.801**	**1.730**		
Log (territory size)	− 0.006	0.058	− 0.120	0.108		
Family group size	− 0.059	0.042	− 0.141	0.023		
Captures: years of monitoring	0.010	0.006	− 0.002	0.022		
Captures: social status (subordinate)	**0.137**	**0.042**	**0.055**	**0.219**		
Captures: age	− 0.016	0.009	− 0.033	0.001		
Season (summer): sex (male)	0.462	0.268	− 0.064	0.987		
Season (autumn): sex (male)	**0.703**	**0.317**	**0.082**	**1.324**		
Social status (subordinate): age	0.010	0.035	− 0.059	0.079		

Table 2. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of body mass in a Eurasian beaver population in south-eastern Norway between 1998 and 2018 ($n_{young} = 340$, $n_{adults} = 916$). Beaver ID, capture year and river were included as random effects. We performed model averaging of best models (ΔAICc < 4) to estimate the effect size of each variable. Informative parameters are given in bold. Reference level of sex: female. Reference level of season: spring. Reference level of carried telemetry device: no. Reference level of social status: dominant. Reference level of origin: immigrant.

Reproduction. Capture and handling may have further deleterious effects on individuals beyond the immediate event of capture, potentially affecting the following breeding season, but may also have long-term consequences for the reproductive success of handled individuals[20]. We did not find any statistically clear effects of repeated captures and handling on the annual probability of reproducing in our population, which is consistent with results from other long-term studies[6,68]. Studies in ungulates lasting up to 15 years found no evidence of lowered calving success among immobilized individuals[8,20]. However, we did find a decrease in annual litter size with increasing capture and handling events among older individuals. Other studies lasting up to 30 years in ungulates, birds, bears, as well as other species, have similarly showed negative effects on breeding success of repeated capture and handling[17,19,24,52,69,70]. Even though several studies investigated capture and handling effects over several years and seasons, most focus on effects in the current or subsequent breeding season, only assessing short-term effects in species that goes through several seasons. However, capture and handling might induce long-term effects, influencing reproduction in future life-history stages[4,71]. Not evaluating the long-term effects, we risk overlooking important fitness effects[9,52].

In our study, we found varying capture effects on the reproductive success over more than 20 years of monitoring. Repeated capture and handling had strong negative effects on annual reproduction in the early years of monitoring, which decreased considerably in recent years, indicating habituation to capture and handling stress[32,72]. To our knowledge, similar reproduction responses to repeated capture events have not been observed in other long-term studies, but habituation responses to handling and human activities have been found for behaviour related to breeding in shorebirds[73] and spatial behaviour and alertness in birds and mammals[74–79]. Some behaviour might even be shaped by parental habituation[34]. Additionally, habituation might be affected by the number of experimenters[80], requiring thoughtful planning of experimental setups to minimize observational effects.

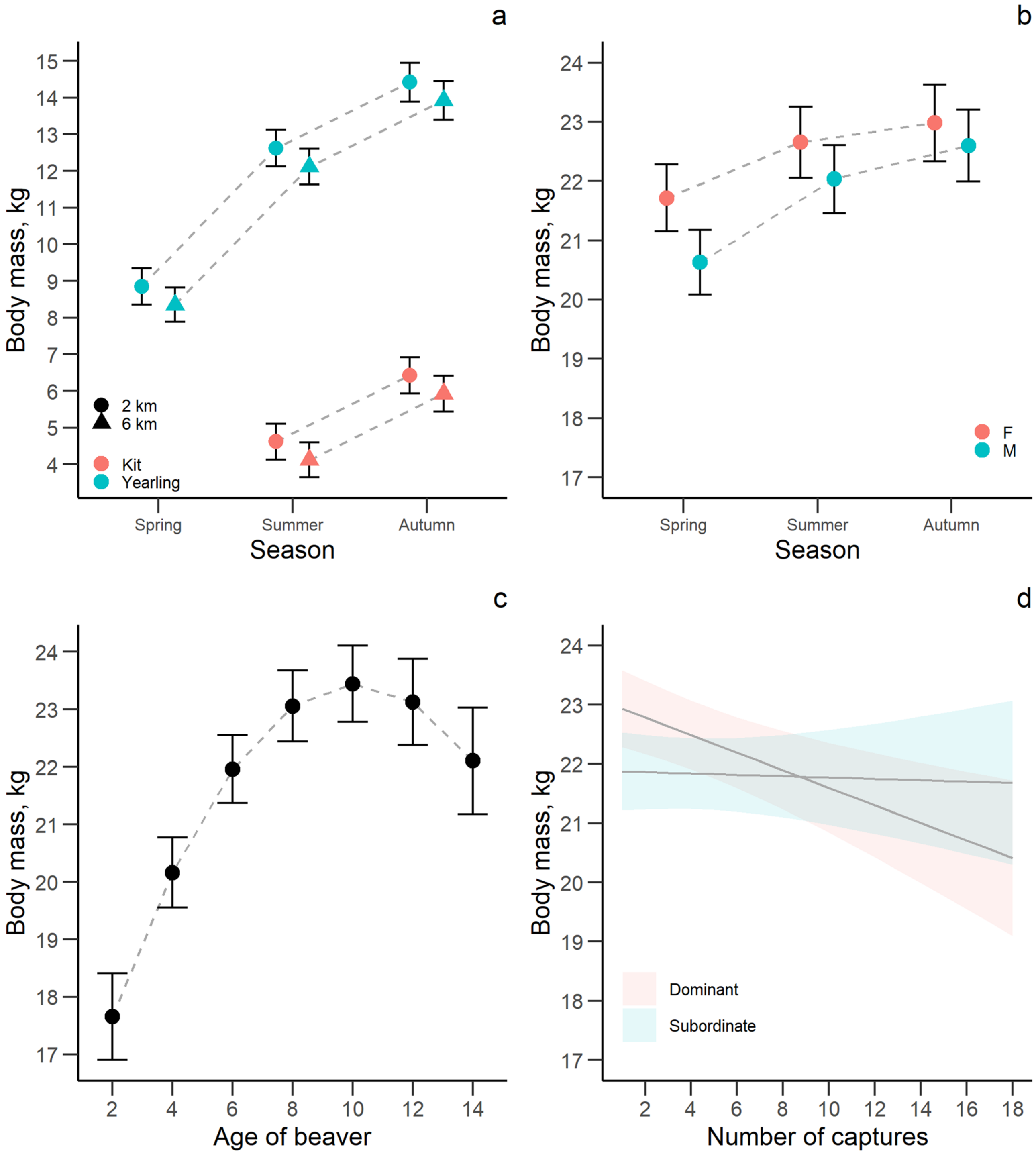

Figure 2. The predicted relationship ± 95% confidence interval between age, territory size and body mass in young beavers (**a**), between season, sex and body mass in adult beavers (**b**), between age, and body mass in adult beavers (**c**) and between number of captures, social status and body mass in adult beavers (**d**) in a Eurasian beaver population in south-eastern Norway between 1998 and 2018.

Survival. Mortality rates and physical injuries at time of capture are not sufficient to successfully assess capture and handling effects, as animals often hide symptoms to avoid further harm[10,11]. Several studies have found negative effects of capture and handling on survival in birds and mammals in the weeks after capture[5,21,23,26,27,29] while others observe no effects[19,22,28,51,81], but most studies do not address long-term effects. A seven year penguin study found decreased annual survival[25], but survival varied considerably between years, underlining the challenge of finding clear capture and handling effect on survival of individuals[10]. We found no statistically clear short or long-term capture effects on survival in our population. Similar results were found comparing the

Variables	Estimate	SE	LCI	UCI	$R^2_{marginal}$	$R^2_{conditional}$
Young (kits and yearlings)						
Intercept	**40.410**	**0.880**	**38.686**	**42.134**	0.78	0.84
Captures	0.018	0.199	− 0.372	0.408		
Years of monitoring	0.046	0.065	− 0.082	0.173		
Sex (male)	0.058	0.288	− 0.507	0.622		
Age	**19.164**	**0.612**	**17.965**	**20.364**		
Season (summer)	**6.274**	**0.715**	**4.874**	**7.675**		
Season (autumn)	**10.511**	**0.801**	**8.940**	**12.082**		
Log (territory size)	**− 1.528**	**0.475**	**− 2.459**	**− 0.598**		
Family group size	− 0.103	0.141	− 0.379	0.174		
Adults (2 + years)						
Intercept	**78.953**	**0.374**	**78.220**	**79.686**	0.35	0.56
Captures	− 0.018	0.051	− 0.117	0.081		
Years of monitoring	0.023	0.036	− 0.048	0.094		
Carried telemetry device (yes)	− 0.572	0.413	− 1.382	0.238		
Sex (male)	− 0.110	0.246	− 0.592	0.371		
Age	**0.826**	**0.095**	**0.641**	**1.012**		
Age^2	**− 0.108**	**0.011**	**− 0.131**	**− 0.086**		
Social status (subordinate)	0.072	0.319	− 0.553	0.698		
Origin (resident)	0.105	0.263	− 0.411	0.620		
Season (summer)	**1.379**	**0.257**	**0.876**	**1.883**		
Season (autumn)	**2.077**	**0.319**	**1.451**	**2.703**		
Log (territory size)	− 0.039	0.135	− 0.304	0.225		
Family group size	− 0.081	0.076	− 0.230	0.068		
Captures: social status (subordinate)	0.023	0.063	− 0.100	0.146		
Social status (subordinate): age	0.232	0.128	− 0.019	0.483		

Table 3. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of body size in a Eurasian beaver population in south-eastern Norway between 1998 and 2018 ($n_{young} = 333$, $n_{adults} = 829$). Beaver ID, capture year and river were included as random effects. We performed model averaging of best models ($\Delta AICc < 4$) to estimate the effect size of each variable. Informative parameters are given in bold. Reference level of sex: female. Reference level of season: spring. Reference level of carried telemetry device: no. Reference level of social status: dominant. Reference level of origin: immigrant.

effects of transmitters over eight years in beavers[16]. However, more details on actual time of death of individuals may reveal capture and handling-related effects that otherwise may go undetected[9,52].

Social status had a strong impact on annual survival in our population and handling procedures that affect the possibility to obtain or hold a social rank might have considerable consequences[7]. Subordinate individuals may be more challenged than territory holders to find a territory of their own, which may result in lower survival or accepting a territory of lesser quality as seen in other rodents[82]. Being potentially physiologically pressured (e.g. from growing) and operating in a highly tense social landscape[83], we would expect high capture intensity in combination to further affect survival[7], whereas dominant individuals might be more socially anchored in a territory and therefore more resilient[82]. We found a statistically clear decrease in survival of subordinates with increasing age and with increasing family group size which indicate they might be better off leaving their family group after some time. Subordinate beavers have been shown to make explorative trips to neighbouring and distant territories before they disperse from their natal family group[84] and might experience increased mortality risk when exploring potential territories[85–87].

Dominant individuals might need time to establish in a territory and build up their family group. Accordingly, we found a higher probability of staying dominant for individuals in larger family groups. A high number of individuals in a territory might indicate high territory quality[88] which the prolonged territory occupancy might reflect. Furthermore, the relationship between larger family groups and territory occupancy might reflect the benefits of social behaviour in beavers[89]. Other rodent studies found an increased survival and reproductive success among individuals that were translocated to new territories together with familiar conspecifics[90,91]. Not surprisingly, the probability of keeping dominance decreased with increasing age, indicating senescence[83,92].

Conclusion

Using a semi-aquatic mammal as a model species, we here present clear insights on how long-term monitoring studies including repeated capturing and handling of individuals affect the wellbeing of wild animal populations by evaluating changes in several fitness-related parameters. Our results, based on more than 20 years of a unique long-term individual-based field study, show how repeated capture and handling can have clear effects on

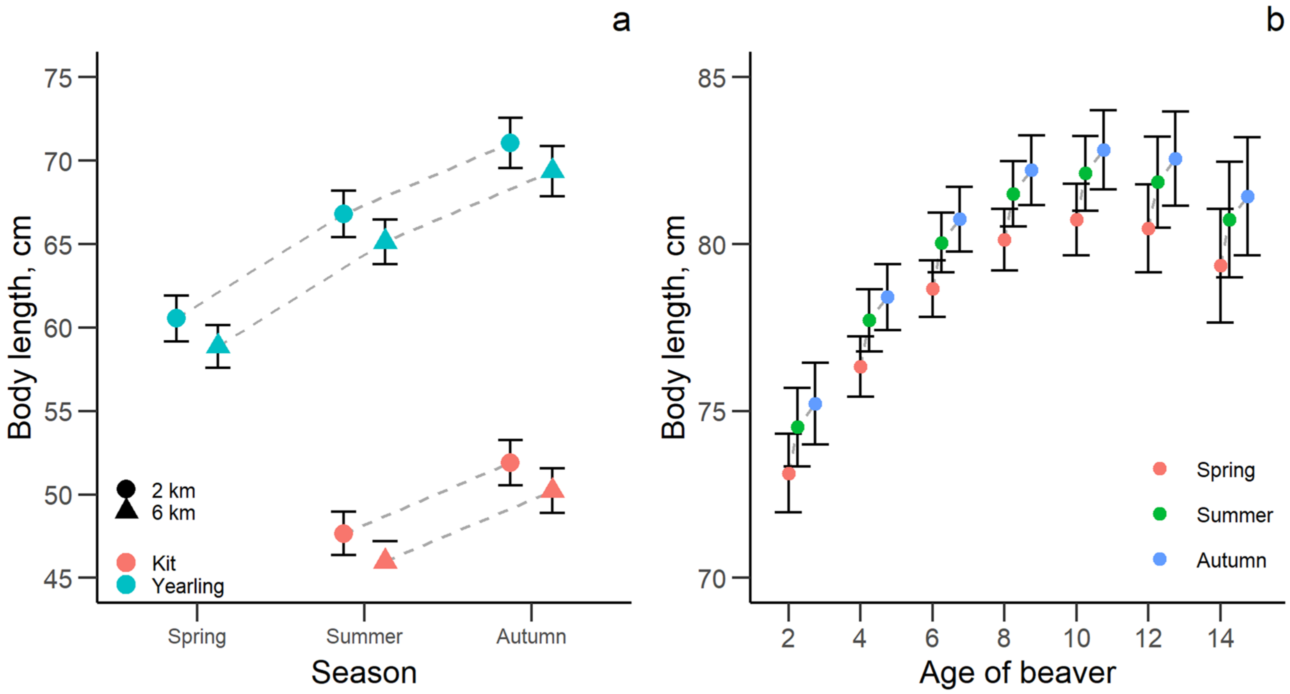

Figure 3. The predicted relationship ± 95% confidence interval between age, territory size and body length in young beavers (**a**) and between age, season and body length in adult beavers (**b**) in a Eurasian beaver population in south-eastern Norway between 1998 and 2018.

important life stages in a semi-aquatic mammal. We illustrate the validity of long-term individual-based studies which have great potential in the planning and execution of future wildlife and conservation studies to promote the welfare of wild populations and ensure reliable research data[12].

Long-term individual-based studies should always evaluate the potential bias created. Our results confirm the importance of having a clear adaptive objective when assessing effects of repeated capture and handling. Setting clear objectives and framing tractable questions will help resolve on what to monitor and assess, allowing the monitoring program to evolve and develop in response to new information and new questions[93].

Methods

Study animal.

Beavers are socially monogamous, semi-aquatic nocturnal mammals that inhabit various freshwater bodies[42]. They live in family groups consisting of the dominant breeding pair, kits of the year and older non-breeding offspring[94]. Beavers reach sexual maturity during their second winter[37] and give birth to one to five kits in mid-May, which emerge from the lodge during July when they start feeding on their own on twigs and leaves of deciduous trees like the adults[94]. Around 2–3 years old, beavers disperse to establish a territory of their own[84,95].

Beavers are highly territorial and announce territory occupation mainly by scent marking, primarily at territorial borders[39]. All adults take part in territorial defence, but males allocate more time to patrolling and scent marking[46].

Study site.

Our study site is located at the lower reaches of the rivers Straumen, Gvarv and Sauar in Vestfold and Telemark County, south-eastern Norway. The river sections are generally slow flowing with stable water levels, have similar depth structure and are 20–150 m wide[96]. All rivers contain natural lakes and man-made impoundments along part of their length, resulting in only limited water temperature fluctuations along the main river channels[96]. The rivers flow through small towns, farms and fields interspersed with riparian woodland[44,45].

Beavers have inhabited the rivers since the 1920s where they recolonized the rivers. The population is at carrying capacity, as territories of various sizes border each other directly[94]. Territory borders are identified based on scent mound concentrations, sight observations of patrolling known beavers and GPS data.

Capture protocol.

Since 1997, beavers in the area have been monitored through an extensive live-trapping program (the Norwegian Beaver Project, NBP). The long-term monitoring project aims to annually capture all newcomers (kits and dispersers from outside the study site) to enable identification at later encounters, as well as annually record family group sizes.

Captures were conducted at night. Individuals were detected from a motorboat using searchlights and captured using large landing-nets in shallow water or on land[97]. Captured individuals were immobilized in cloth sacks, enabling easy handling without anaesthesia. Beavers were weighed to the nearest 100 g. Body length was

Variables	**Estimate**	**SE**	**LCI**	**UCI**	**$R^2_{marginal}$**	**$R^2_{conditional}$**
Probability of reproducing						
Intercept	**– 0.669**	**0.309**	**– 1.274**	**– 0.063**	0.08	0.14
Captures	– 0.100	0.056	– 0.210	0.010		
Years of monitoring	0.018	0.034	– 0.049	0.085		
Carried telemetry device (yes)	0.232	0.335	– 0.425	0.889		
Log (age)	– 0.072	0.233	– 0.530	0.385		
Origin (resident)	– 0.083	0.227	– 0.528	0.363		
Log (territory size)	0.399	0.263	– 0.117	0.914		
Family group size	0.019	0.047	– 0.074	0.111		
Reproduced previous year (yes)	0.131	0.232	– 0.325	0.586		
Captures: years of monitoring	**0.026**	**0.009**	**0.009**	**0.043**		
Captures: log(age)	– 0.060	0.095	– 0.247	0.127		
Annual litter size						
Intercept	**– 0.620**	**0.225**	**– 1.062**	**– 0.179**	0.09	0.21
Captures	– 0.007	0.040	– 0.084	0.071		
Years of monitoring	0.004	0.025	– 0.045	0.053		
Carried telemetry device (yes)	0.049	0.143	– 0.231	0.329		
Log (age)	– 0.041	0.030	– 0.099	0.017		
Origin (resident)	– 0.185	0.250	– 0.674	0.305		
Log (territory size)	0.196	0.179	– 0.155	0.548		
Family group size	0.007	0.023	– 0.039	0.053		
Reproduced previous year (yes)	0.046	0.108	– 0.167	0.259		
Captures: years of monitoring	**0.021**	**0.006**	**0.010**	**0.032**		
Captures: log(age)	**– 0.019**	**0.007**	**– 0.034**	**– 0.005**		

Table 4. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of reproduction in a Eurasian beaver population in south-eastern Norway between 1998 and 2018 (n = 388). Beaver ID, monitoring year and river were included as random effects. We performed model averaging of best models (ΔAICc < 4) to estimate the effect size of each variable. Informative parameters are given in bold. Reference level of carried telemetry device: no. Reference level of origin: immigrant. Reference level of reproduced previous year: no.

measured following the curvature of the spine from nose tip to the base of the tail. Tail length was measured from the base to the tip of the tail and tail width was measured from edge to edge of the dorsal surface at the midpoint between tail base and tip.

When encountering individuals, samples of castoreum and anal gland secretion were obtained. Hair samples from the lower back were obtained at an individual's first encounter. Furthermore, some adults participated in short-term experiments involving deployment of various data-loggers and transmitters. Unfamiliar individuals were sexed based on the colour of their anal gland secretion[98], and tagged with microchips and unique combinations of plastic and metal ear-tags. Individuals first captured as kit or yearling were given an exact age. Older individuals (≥ 2 years) were assigned a minimum age based on body mass when first captured[99]; minimum 2 years (subadult) when ≥ 17 and ≤ 19.5 kg and minimum 3 years (adult) when > 19.5 kg. Dominance was in most cases attributed to adult territorial residents of each sex. Dominance was otherwise verified by eventual dispersal of the alternative candidate, greatest body weight among same-sex group members or lactation in females (large nipples). Individuals dispersing into a territory were posited to have achieved the dominant breeding position when the previous dominant of the same sex had disappeared or evidence outlined above were applicable. Unless proven otherwise, dominant individuals were assumed to maintain their status until they disappeared or died[100]. Captured beavers were released near capture site within their territory after 20–40 min of handling time[97].

Ethical note. All capture and handling procedures were approved by the Norwegian Experimental Animal Board (Most recent authorization: FOTS ID15947) and by the Norwegian Directorate for Nature Management (Most recent authorization: 2014/14415). Our study met the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching[101]. No captured individuals were injured during capture and handling, and all were successfully released afterwards. All methods were performed in accordance with the relevant guidelines and regulations.

Body condition indices. The beaver tail functions as fat storage[102]. Tail size (length × width) varies with season and is positively correlated with body mass[56]. Using the ratio of the tail size (seasonally variable) to body length (seasonally stable) as an index of tail fat content, tail size has been used as proxy for body condition[37,103]. Larger tail fat index thus indicates higher tail fat content and better body condition.

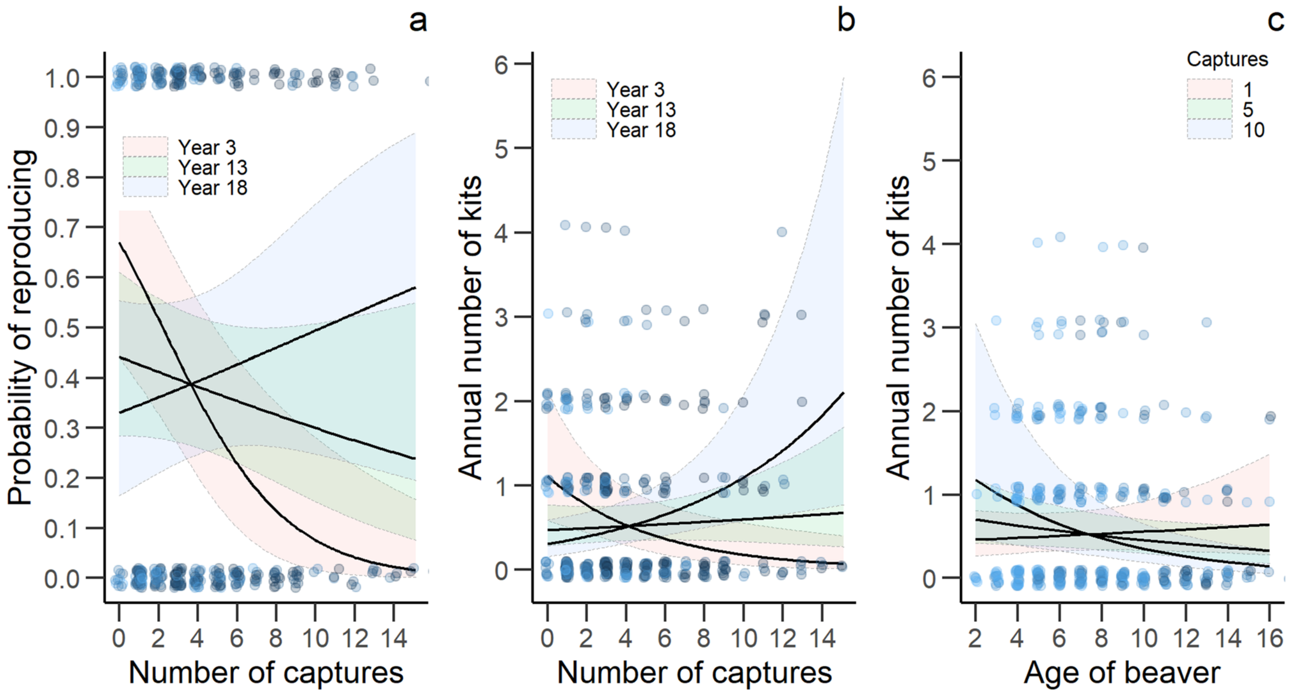

Figure 4. The predicted relationship ± 95% confidence interval between number of captures, years of monitoring and probability of reproducing (**a**) and annual litter size (**b**), and between number of captures, age and probability of reproducing (**c**) in a Eurasian beaver population in south-eastern Norway between 1998 and 2018. Points represent the actual observations with small random variation for better visualisation. Darker colours increase with (**a**,**b**) increasing years of monitoring and (**c**) increasing number of captures.

Variables	Estimate	SE	LCI	UCI	Tjur's R^2
Probability of survival					
Intercept	**– 2.372**	**0.200**	**– 2.765**	**– 1.980**	0.07
Age	**0.111**	**0.039**	**0.035**	**0.187**	
Social status (subordinate)	**0.857**	**0.230**	**0.407**	**1.307**	
Family group size	**– 0.091**	**0.035**	**– 0.159**	**– 0.022**	
Social status (subordinate): age	**– 0.201**	**0.054**	**– 0.307**	**– 0.094**	

Table 5. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the continuous time capture-recapture analysis of annual survival in a Eurasian beaver population in south-eastern Norway between 1998 and 2018 (n = 1145). Informative parameters are given in bold. Reference level of Social status: Dominant.

However, body mass and body length may vary differently than tail fat in relation to long-term capture and handling effects. Body length was not recorded in a few capturing events (21 individuals), but tail size was measured. In those cases, we interpolated body length between measures within the individual in an age group (i.e., kit, yearling, subadult and adult) and excluded observations if interpolation was not possible within the age group.

Since young and adults are not treated equally in our protocol and may be affected by different ecological factors, we chose to divide our analyses on body condition indices into young (kits and yearlings) and adults (subadults and adults) to balance the data set.

Reproduction. Each year we aimed to capture all kits and yearlings not captured during their first year. We recorded annual reproductive success for breeding pairs in each territory as the number of kits in a given year, based on the number of captured and observed kits plus unmarked yearlings captured the following year.

Survival. Using observations from the capture protocol in a capture-mark-recapture (CMR) framework, we can estimate apparent survival in the population, which may reflect actual survival, but also emigration from the study area[104–106].

As dispersal is a dangerous period during the life of an animal, which may result in high mortality[107,108], territory occupancy of dominant individuals may be used as proxy for survival assuming dominant individuals perished when they lost territory occupancy and did not overtake a new territory[83].

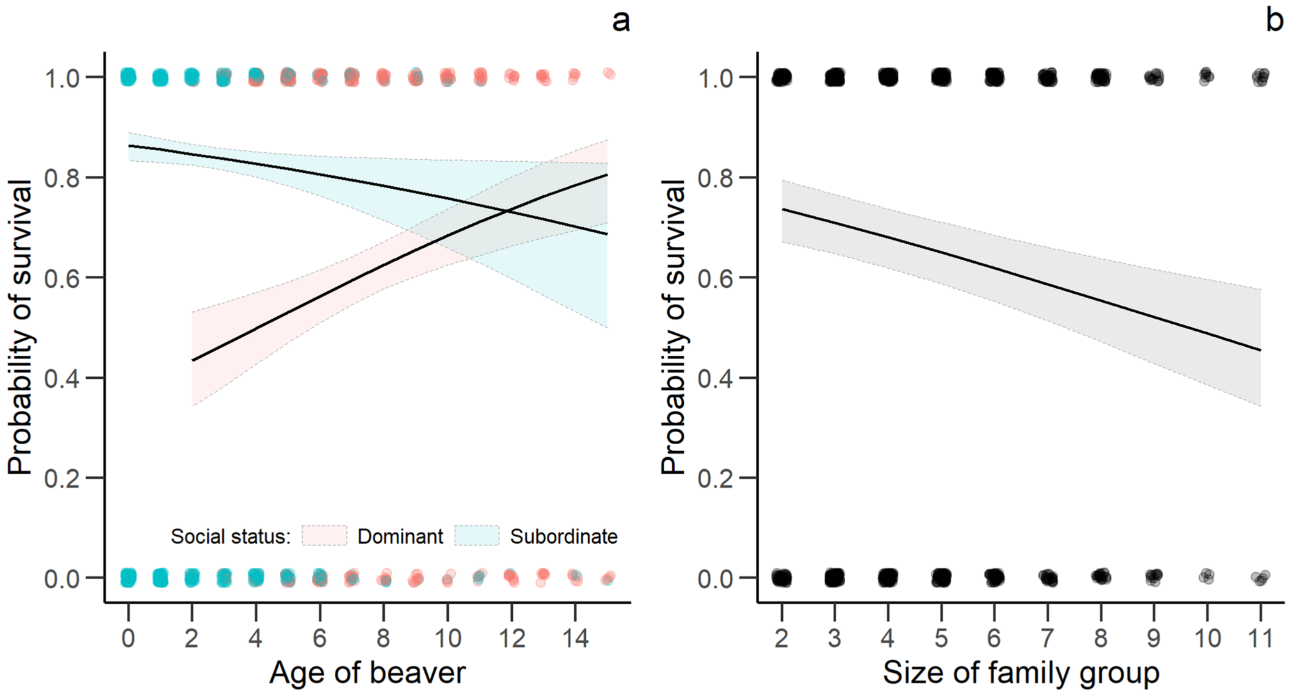

Figure 5. The predicted relationship ± 95% confidence interval between age, social status and survival probability (**a**) and between family group size and survival probability (**b**) in a Eurasian beaver population in south-eastern Norway between 1998 and 2018. Points represent the actual observations with small random variation for better visualisation.

Variables	Estimate	SE	LCI	UCI	R^2_{marginal}	$R^2_{\text{conditional}}$
Probability of staying dominant the following year						
Intercept	**3.637**	**0.428**	**2.797**	**4.476**	0.19	0.25
Captures	0.020	0.059	− 0.095	0.136		
Years of monitoring	− 0.062	0.040	− 0.140	0.016		
Carried telemetry device (yes)	− 0.054	0.195	− 0.436	0.328		
Sex (male)	0.017	0.101	− 0.181	0.215		
Age	**− 0.164**	**0.037**	**− 0.236**	**− 0.091**		
Origin (resident)	− 0.101	0.216	− 0.523	0.322		
log(territory size)	− 0.441	0.251	− 0.932	0.050		
Family group size	**0.291**	**0.085**	**0.124**	**0.458**		
Captures: years of monitoring	0.001	0.004	− 0.007	0.008		
Captures: carried telemetry device (yes)	0.004	0.031	− 0.058	0.065		
Captures: age	− 0.002	0.005	− 0.012	0.009		

Table 6. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analysis of staying dominant the following year in a Eurasian beaver population in south-eastern Norway between 1998 and 2018 (n = 773). Beaver ID, monitoring year and river were included as random effects. We performed model averaging of best models (ΔAICc < 4) to estimate the effect size of each variable. Informative parameters are given in bold. Reference level of sex: Female. Reference level of carried telemetry device: No. Reference level of origin: Immigrant.

Statistical analysis. For all analyses on body condition, reproduction and dominance status we used linear mixed-effects models (LMM) and generalized linear mixed-effects models (GLMM) with capture year, beaver ID and study river as random effects to account for variability between years, individuals and study sites that might be caused by climatic differences, habitat quality or sampling frequency.

We investigated how capture and handling affected tail fat index, body mass and body length using LMMs for young and adult individuals, respectively. For young individuals we analysed how the number of capture and handling events and years of monitoring (years since 1997) affected the tail fat index, body mass and body length of individuals. Capture season (spring: March–May, summer: June–August, autumn: September–November), sex, age, territory size (km bank length) and family group size were included to account for important ecological factors. Similar LMMs were built for adults, additionally analysing the effect of carrying a telemetry device (yes/

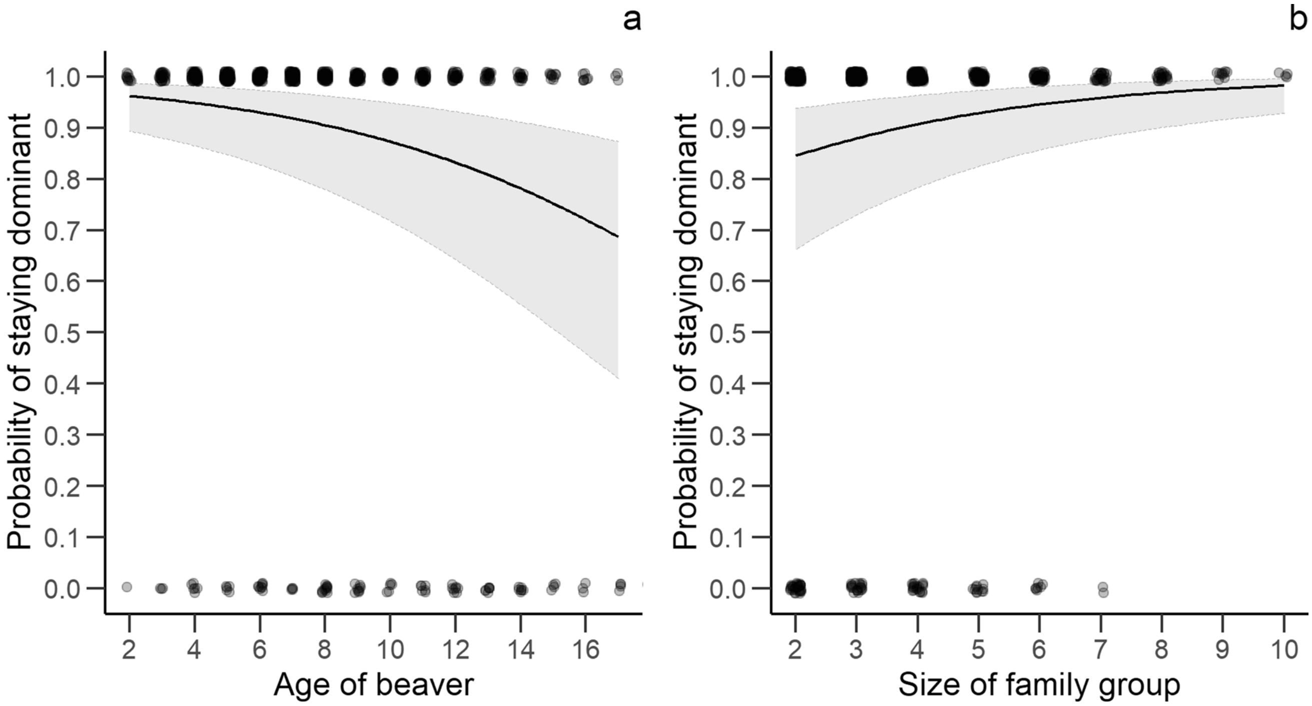

Figure 6. The predicted relationship ± 95% confidence interval between age (**a**), family group size (**b**) and probability of keeping dominance in a Eurasian beaver population in south-eastern Norway between 1998 and 2018. Points represent the actual observations with small random variation for better visualisation.

no) in its lifetime up to the given capture event, accounting for social status of the beaver (dominant/subordinate) at the capture event and the individual's family origin (immigrant or resident).

To investigate effects of long-term capture and handling on annual reproduction, we used a GLMM with binomial distribution and logit link (1 = reproducing dominant females, 0 = non-reproducing dominant females), analysing the relative importance of number of capture and handling events, years of monitoring and whether the animal had carried a telemetry device in its life time. We included age of the beaver, whether the female reproduced the previous year, territory size family origin and size of family group. The same covariates were included in a GLMM with Poisson distribution and log link to analyse the effect of long-term captures and handling on annual reproductive success (i.e. litter size).

To investigate effects of long-term capture and handling on dominance status, we used a GLMM with binomial distribution and logit link (1 = individuals that kept dominance in the following year, 0 = individuals that lost dominance in the following year), analysing the relative importance of number of capture and handling events, years of monitoring and whether the animal had carried a telemetry device in its life time for keeping dominance status the following year, including effects of sex, age, territory size, family origin and family group size.

The fixed effects used in all analyses were not correlated (Pearson r coefficient < 0.6) and variance inflation factor values were < 3[109].

A list of candidate models was created using ecologically relevant combinations of fixed effects. Variables were included to account for variability in endogenous (such as sex, age and social status) and exogenous factors (such as territory size, family group size, family origin and season) that are important for describing the ecology of the beaver. Years since 1997 (years of monitoring) were included to capture the long-term effects of our capture protocol, as the monitoring may not only affect individuals that are monitored at a given time but may also affect future generations. Years of monitoring for a given individual at a given time is implicitly within the age of the beaver (r = 0.9) and in the number of captures (r = 0.7). Linearity of variables were tested in univariable mixed-effect models with either linear or squared variables. We included interactions to capture the variability in how the beavers reacts to capture and handling events on a long term (Captures × Years of monitoring), and the variability in how males, females, dominants and subordinates, young and old may react to repeated capture and handling events (Captures × Sex, Captures × Social status, Capture × Age, respectively). Furthermore, we included interactions to account for ecological differences between males and females over the year (Season × Sex) and the variability for social status at different ages (Social status × Age), as there is a higher degree of subordinates among young individuals and a higher degree of dominants among older individuals.

Model selection was based on Akaike's Information Criterion corrected for small sample size[110], and carried out using the R packages glmmTMB[111] and MuMIn[112]. If ΔAICc was < 4 in two or more of the most parsimonious models, we performed model averaging[110,113]. Parameters that included zero within their 95% confidence interval (CI) were considered uninformative[113]. The most parsimonious models were visually validated using the R package DHARMa[114] to plot standardised model residuals against the fitted values[109]. Models for reproduction and dominance status were furthermore checked for zero-inflation using DHARMa. Top candidate models for all analyses can be found in the supporting material.

Survival probability was modeled in a CMR framework. Since classical CMR models require discrete-time assumptions[106] that introduce constraints in CMR protocols that are not always compatible with the reality[104,105], we chose to fit our survival model in a continuous time capture-recapture model using the R-package CMRCT [104], enabling us to estimate the apparent annual survival in our population. We modeled how the importance of repeated capture and handling events, years of monitoring and carrying a telemetry device in its lifetime affected apparent survival. Capture season, sex, age, territory size and family group size were included to account for important ecological factors. Furthermore we included interactions described above (Supplementary information S1).

As CMRCT currently does not offer any model selection, we fitted all variables and interactions in a global model and removed uninformative parameters by backwards selection until the model consisted only of informative parameters. Parameters that included zero within their 95% confidence interval (CI) were considered uninformative[113].

All analyses were conducted in R 3.6.3[115].

Data availability

Data is available at https://doi.org/10.23642/usn.13083782.

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Author contributions

F.R. founded the NBP, F.R. and R.M.M. contributed to the data collection, R.M.M. performed the statistical analyses, R.M.M. and F.R. wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Long-term capture and handling effects on body condition, reproduction and survival in a semi-aquatic mammal

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Supplemental material

S1. The model selection result for the candidate models investigating the tail fat index in young individuals in a Eurasian beaver population in south-eastern Norway between 1998 and 2019. Beaver ID, capture year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	deltaAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
1/4/6	9	-153.26	325.08	0.00	0.18	0.56	0.73
1/4/5/6	10	-152.69	326.05	0.97	0.11	0.56	0.73
1/4/6/7	10	-152.77	326.22	1.14	0.10	0.56	0.73
1/3/4/6	10	-152.88	326.45	1.37	0.09	0.56	0.74
1/3/4/5/6	11	-152.18	327.19	2.10	0.06	0.56	0.74
1/2/4/6	10	-153.26	327.20	2.12	0.06	0.56	0.73
1/4/5/6/7	11	-152.23	327.27	2.19	0.06	0.56	0.73
1/3/4/6/7	11	-152.41	327.65	2.57	0.05	0.56	0.74
1/4	8	-155.65	327.75	2.67	0.05	0.55	0.73
1/2/4/5/6	11	-152.68	328.19	3.11	0.04	0.56	0.73
1/4/5	9	-154.85	328.26	3.18	0.04	0.56	0.73
1/2/4/6/7	11	-152.76	328.35	3.26	0.04	0.56	0.73
1/3/4/5/6/7	12	-151.75	328.47	3.39	0.03	0.56	0.74
1/2/3/4/6	11	-152.85	328.51	3.43	0.03	0.56	0.74
1/4/7	9	-155.17	328.90	3.82	0.03	0.55	0.73
1/3/4	9	-155.17	328.90	3.82	0.03	0.55	0.74

1 = Age, 2 = Captures, 3 = Family group size, 4 = Season, 5 = Sex, 6 = log(Territory size), 7 = Years of monitoring

S2. The model selection result for the candidate models investigating the tail fat index in adult individuals in a Eurasian beaver population in south-eastern Norway between 1998 and 2019. Beaver ID, capture year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	ΔAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
1/2/4/8/9/12/14	15	-229.32	489.24	0.00	0.04	0.12	0.48
1/2/4/8/9/12	13	-231.44	489.32	0.08	0.04	0.12	0.48
1/4/8/9/12/14	14	-230.63	489.78	0.54	0.03	0.12	0.48
1/4/8/9/12	12	-232.79	489.95	0.72	0.03	0.11	0.48

1/2/4/8/9/10/12/14	16	-228.88	490.44	1.20	0.02	0.13	0.48
1/3/4/8/9/12	13	-232.05	490.54	1.30	0.02	0.12	0.48
1/2/4/8/9/10/12	14	-231.03	490.58	1.34	0.02	0.12	0.47
1/3/4/8/9/12/14	15	-230.03	490.65	1.41	0.02	0.12	0.48
1/4/8/9/10/12/14	15	-230.06	490.70	1.46	0.02	0.12	0.48
1/2/4/5/8/9/12/14	16	-229.05	490.78	1.54	0.02	0.13	0.48
1/2/4/5/8/9/12	14	-231.17	490.85	1.61	0.02	0.12	0.48
1/4/8/9/10/12	13	-232.25	490.94	1.71	0.02	0.12	0.48
1/2/4/8/9/11/12	14	-231.29	491.10	1.86	0.02	0.12	0.48
1/4/8/9/11/12/14	15	-230.26	491.12	1.88	0.02	0.12	0.48
1/2/3/4/8/9/12	14	-231.33	491.18	1.94	0.02	0.12	0.48
1/2/3/4/8/9/12/14	16	-229.27	491.21	1.97	0.02	0.12	0.48
1/2/4/8/9/12/13/14	16	-229.27	491.21	1.97	0.02	0.12	0.48
1/2/8/9/14	13	-232.41	491.26	2.03	0.02	0.12	0.48
1/2/4/7/8/9/12/14	16	-229.30	491.27	2.03	0.02	0.12	0.48
1/2/4/8/9/12/13	14	-231.41	491.33	2.09	0.02	0.12	0.48
1/4/8/9/11/12	13	-232.45	491.35	2.11	0.02	0.12	0.48
1/2/4/7/8/9/12	14	-231.42	491.36	2.12	0.02	0.12	0.48
1/2/8/9	11	-234.57	491.47	2.23	0.01	0.12	0.47
1/4/5/8/9/12/14	15	-230.44	491.47	2.23	0.01	0.12	0.49
1/3/4/8/9/10/12	14	-231.53	491.58	2.34	0.01	0.12	0.47
1/4/7/8/9/12/14	15	-230.50	491.59	2.36	0.01	0.12	0.49
1/3/4/8/9/10/12/14	16	-229.47	491.62	2.38	0.01	0.12	0.48
1/4/5/8/9/12	13	-232.60	491.64	2.40	0.01	0.12	0.48
1/4/7/8/9/12	13	-232.62	491.70	2.46	0.01	0.12	0.48
1/2/4/5/8/9/10/12/14	17	-228.50	491.76	2.52	0.01	0.13	0.48
1/2/4/8/9	12	-233.69	491.76	2.52	0.01	0.12	0.47
1/2/4/8/9/13/14	15	-230.65	491.89	2.65	0.01	0.12	0.48
1/2/4/5/8/9/10/12	15	-230.66	491.90	2.66	0.01	0.13	0.47
1/4/8/9/10/11/12/14	16	-229.71	492.09	2.85	0.01	0.12	0.48
1/3/4/5/8/9/12	14	-231.82	492.16	2.92	0.01	0.12	0.48
1/4/5/8/9/10/12/14	16	-229.75	492.18	2.94	0.01	0.12	0.48
1/2/4/8/9/10/11/12/14	17	-228.72	492.19	2.95	0.01	0.13	0.48
1/3/4/8/9/11/12	14	-231.87	492.25	3.01	0.01	0.12	0.48
1/3/4/5/8/9/12/14	16	-229.80	492.28	3.04	0.01	0.12	0.48
1/3/4/8/9/11/12/14	16	-229.81	492.29	3.05	0.01	0.12	0.48
1/2/4/8/9/13	13	-232.94	492.33	3.10	0.01	0.12	0.48
1/2/8/9/10/14	14	-231.93	492.37	3.13	0.01	0.12	0.47
1/4/8/9/10/11/12	14	-231.93	492.38	3.15	0.01	0.12	0.48
1/2/3/4/8/9/10/12/14	17	-228.82	492.39	3.15	0.01	0.13	0.48
1/2/3/4/8/9/10/12	15	-230.91	492.42	3.18	0.01	0.12	0.47
1/4/5/8/9/10/12	14	-231.95	492.42	3.19	0.01	0.12	0.48
1/2/4/8/9/10/12/13/14	17	-228.84	492.43	3.19	0.01	0.13	0.48
1/2/4/7/8/9/10/12/14	17	-228.85	492.46	3.22	0.01	0.13	0.48
1/2/4/8/9/10/14	15	-230.95	492.49	3.25	0.01	0.12	0.47
1/3/4/7/8/9/12	14	-231.99	492.51	3.27	0.01	0.12	0.48

1/4/8/9/14	13	-233.05	492.54	3.30	0.01	0.11	0.48
1/8/9/14	12	-234.08	492.55	3.31	0.01	0.11	0.48
1/4/7/8/9/10/12/14	16	-229.96	492.58	3.34	0.01	0.12	0.48
1/2/4/8/9/10/12/13	15	-231.01	492.61	3.37	0.01	0.12	0.47
1/2/4/7/8/9/10/12	15	-231.01	492.62	3.38	0.01	0.12	0.47
1/2/8/9/10	12	-234.13	492.63	3.40	0.01	0.12	0.47
1/3/4/7/8/9/12/14	16	-229.99	492.65	3.41	0.01	0.12	0.48
1/2/3/4/5/8/9/12	15	-231.06	492.70	3.47	0.01	0.12	0.48
1/2/3/4/5/8/9/12/14	17	-228.99	492.74	3.50	0.01	0.13	0.48
1/4/7/8/9/10/12	14	-232.12	492.76	3.52	0.01	0.12	0.48
1/4/5/8/9/11/12/14	16	-230.05	492.77	3.53	0.01	0.12	0.49
1/2/4/5/7/8/9/12/14	17	-229.03	492.81	3.57	0.01	0.13	0.48
1/2/4/5/8/9/12/13/14	17	-229.03	492.82	3.58	0.01	0.13	0.48
1/8/9	10	-236.30	492.87	3.63	0.01	0.11	0.47
1/2/4/5/7/8/9/12	15	-231.15	492.89	3.65	0.01	0.12	0.48
1/2/4/5/8/9/12/13	15	-231.16	492.91	3.67	0.01	0.12	0.48
1/3/4/5/8/9/10/12	15	-231.19	492.97	3.73	0.01	0.12	0.47
1/4/8/9	11	-235.33	492.99	3.75	0.01	0.11	0.48
1/4/7/8/9/11/12/14	16	-230.16	493.00	3.76	0.01	0.12	0.49
1/4/5/8/9/11/12	14	-232.24	493.00	3.76	0.01	0.12	0.48
1/3/4/5/8/9/10/12/14	17	-229.13	493.01	3.77	0.01	0.12	0.48
1/2/3/4/8/9/11/12	15	-231.21	493.02	3.78	0.01	0.12	0.48
1/2/4/7/8/9/11/12/14	17	-229.13	493.02	3.78	0.01	0.13	0.48
1/2/4/8/9/10/13/14	16	-230.19	493.05	3.81	0.01	0.12	0.48
1/2/4/8/9/11/12/13	15	-231.26	493.11	3.87	0.01	0.12	0.48
1/2/4/8/9/10/11/12	15	-231.27	493.14	3.90	0.01	0.13	0.47
1/2/8/9/11/14	14	-232.32	493.15	3.91	0.01	0.12	0.48
1/4/7/8/9/11/12	14	-232.32	493.16	3.92	0.01	0.12	0.48
1/2/3/4/8/9/12/13/14	17	-229.22	493.19	3.95	0.01	0.12	0.48
1/2/3/4/8/9/12/13	15	-231.31	493.20	3.96	0.01	0.12	0.48
1/2/3/4/7/8/9/12	15	-231.32	493.23	3.99	0.01	0.12	0.48

1 = Age+Age^2, 2 = Captures, 3 = Carried telemetry device, 4 = Social status, 5 = Family group size, 7 = Origin, 8 = Season, 9 = Sex, 10 = log(Territory size), 11 = Years of monitoring, 12 = Social status:Age, 13 = Captures:Social status, 14 = Season:Sex

S3. The model selection result for the candidate models investigating the body mass in young individuals in a Eurasian beaver population in south-eastern Norway between 1998 and 2019. Beaver ID, capture year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	ΔAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
1/2/3/4/6	11	-561.97	1146.75	0.00	0.20	0.87	0.93
1/3/4/6/	10	-563.12	1146.92	0.17	0.18	0.87	0.93
1/2/3/4/6/7	12	-561.24	1147.43	0.68	0.14	0.87	0.93
1/3/4/6/7	11	-562.42	1147.64	0.89	0.13	0.87	0.93

1/2/3/4/5/6	12	-561.93	1148.81	2.06	0.07	0.87	0.93
1/3/4/5/6	11	-563.08	1148.97	2.22	0.07	0.87	0.93
1/2/3/4/5/6/7	13	-561.20	1149.52	2.77	0.05	0.87	0.93
1/3/4/5/6/7	12	-562.39	1149.72	2.98	0.05	0.87	0.93
1/4/6	9	-565.60	1149.75	3.00	0.04	0.87	0.93
1/4/6/7	10	-564.81	1150.29	3.54	0.03	0.87	0.93
1/2/4/6	10	-564.99	1150.65	3.90	0.03	0.87	0.93

1 = Age, 2 = Captures, 3 = Family group size, 4 = Season, 5 = Sex, 6 = log(Territory size), 7 = Years of monitoring

S4. The model selection result for the candidate models investigating the body mass in adult individuals in a Eurasian beaver population in south-eastern Norway between 1998 and 2019. Beaver ID, capture year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	ΔAICc	weight	$\mathbf{R^2}_{\mathbf{marginal}}$	$\mathbf{R^2}_{\mathbf{conditional}}$
1/2/4/5/8/9/11/12/14/15/16	19	-1854.13	3747.10	0.00	0.22	0.48	0.78
1/2/4/5/8/9/11/12/13/14/15/16	20	-1853.94	3748.82	1.72	0.09	0.48	0.78
1/2/4/5/8/9/10/11/12/14/15/16	20	-1854.10	3749.13	2.03	0.08	0.48	0.78
1/2/4/8/9/11/12/14/15/16	18	-1856.20	3749.16	2.06	0.08	0.48	0.78
1/2/3/4/5/8/9/11/12/14/15/16	20	-1854.12	3749.17	2.07	0.08	0.48	0.78
1/2/4/5/7/8/9/11/12/14/15/16	20	-1854.13	3749.19	2.09	0.08	0.48	0.78
1/2/4/8/9/11/12/13/14/15/16	19	-1855.69	3750.23	3.13	0.05	0.48	0.78
1/2/4/5/8/9/12/14/16	17	-1857.83	3750.34	3.24	0.04	0.47	0.78
1/2/4/5/8/9/11/12/14/15	17	-1857.92	3750.53	3.43	0.04	0.48	0.78
1/2/4/5/8/9/14/16	16	-1858.97	3750.54	3.44	0.04	0.48	0.78
1/2/4/5/8/9/10/11/12/13/14/15/16	21	-1853.91	3750.85	3.75	0.03	0.48	0.78
1/2/4/5/8/9/11/12/14/16	18	-1857.06	3750.89	3.79	0.03	0.48	0.78
1/2/3/4/5/8/9/11/12/13/14/15/16	21	-1853.94	3750.91	3.81	0.03	0.48	0.78
1/2/4/5/7/8/9/11/12/13/14/15/16	21	-1853.94	3750.91	3.81	0.03	0.48	0.78
1/2/4/5/8/9/11/14/15/16	18	-1857.09	3750.95	3.85	0.03	0.49	0.78
1/2/4/8/9/10/11/12/14/15/16	19	-1856.10	3751.05	3.95	0.03	0.48	0.78

1 = Age+Age^2, 2 = Captures, 3 = Carried telemetry device, 4 = Social status, 5 = Family group size, 7 = Origin, 8 = Season, 9 = Sex, 10 = log(Territory size), 11 = Years of monitoring, 12 = Captures:Age, 13 = Social status:Age, 14 = Captures:Social status, 15 = Captures:Years of monitoring, 16 = Season sex

S5. The model selection result for the candidate models investigating the body size in young individuals in a Eurasian beaver population in south-eastern Norway between 1998 and 2019. Beaver ID, capture year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	ΔAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
1/3/4/6	10	-964.75	1950.19	0.00	0.17	0.78	0.84
1/4/6/7	10	-964.81	1950.30	0.11	0.16	0.78	0.83
1/3/4/6/7	11	-963.87	1950.57	0.38	0.14	0.78	0.84
1/4/5/6	10	-965.55	1951.79	1.60	0.08	0.77	0.84
1/2/4/6	10	-965.65	1951.99	1.80	0.07	0.77	0.84
1/4/5/6/7	11	-964.69	1952.21	2.02	0.06	0.78	0.83
1/2/3/4/6	11	-964.70	1952.23	2.04	0.06	0.78	0.84
1/3/4/5/6	11	-964.71	1952.23	2.05	0.06	0.78	0.84
1/2/4/6/7	11	-964.80	1952.42	2.24	0.06	0.78	0.83
1/2/3/4/6/7	12	-963.81	1952.60	2.41	0.05	0.78	0.84
1/3/4/5/6/7	12	-963.82	1952.61	2.43	0.05	0.78	0.84
1/2/4/5/6	11	-965.55	1953.93	3.74	0.03	0.77	0.84

1 = Age, 2 = Captures, 3 = Family group size, 4 = Season, 5 = Sex, 6 = log(Territory size), 7 = Years of monitoring

S6. The model selection result for the candidate models investigating the body size in adult individuals in a Eurasian beaver population in south-eastern Norway between 1998 and 2019. Beaver ID, capture year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	ΔAICc	Weight	$R^2_{marginal}$	$R^2_{conditional}$
1/3/4/5/8/12	13	-2160.49	4347.43	0.00	0.04	0.35	0.57
1/3/4/5/8/11/12	14	-2159.53	4347.58	0.15	0.04	0.35	0.56
1/3/4/8/12	12	-2161.87	4348.12	0.69	0.03	0.35	0.57
1/3/4/8/11/12	13	-2160.94	4348.33	0.90	0.03	0.35	0.56
1/3/4/5/8/9/12	14	-2159.98	4348.47	1.04	0.03	0.35	0.57
1/3/4/5/7/8/12	14	-2160.03	4348.58	1.15	0.02	0.35	0.57
1/3/4/5/7/8/11/12	15	-2159.01	4348.61	1.18	0.02	0.35	0.56
1/3/4/5/8/9/11/12	15	-2159.02	4348.63	1.20	0.02	0.35	0.56
1/3/4/5/8/10/12	14	-2160.22	4348.96	1.53	0.02	0.35	0.57
1/3/4/5/8/10/11/12	15	-2159.26	4349.10	1.67	0.02	0.35	0.56
1/3/4/8/9/12	13	-2161.36	4349.18	1.75	0.02	0.35	0.57
1/4/5/8/12	12	-2162.47	4349.33	1.90	0.02	0.34	0.56
1/3/4/8/9/11/12	14	-2160.44	4349.39	1.96	0.02	0.35	0.56
1/3/4/8/10/12	13	-2161.48	4349.42	1.99	0.02	0.35	0.57
1/3/4/7/8/12	13	-2161.49	4349.43	2.01	0.02	0.34	0.57
1/3/4/5/7/8/9/12	15	-2159.44	4349.47	2.04	0.02	0.35	0.57
1/2/3/4/5/8/12	14	-2160.49	4349.50	2.07	0.02	0.35	0.57
1/3/4/5/7/8/9/11/12	16	-2158.41	4349.50	2.07	0.02	0.35	0.56
1/3/4/7/8/11/12	14	-2160.51	4349.54	2.11	0.02	0.34	0.56
1/3/4/8/10/11/12	14	-2160.55	4349.61	2.18	0.01	0.35	0.56

1/2/3/4/5/8/11/12	15	-2159.52	4349.63	2.20	0.01	0.35	0.56
1/2/3/4/5/8/12/13	15	-2159.56	4349.70	2.27	0.01	0.35	0.57
1/2/3/4/5/8/11/12/13	16	-2158.66	4349.99	2.56	0.01	0.35	0.57
1/3/4/5/8/9/10/12	15	-2159.70	4349.99	2.56	0.01	0.35	0.57
1/3/5/8/11	12	-2162.82	4350.02	2.59	0.01	0.34	0.56
1/3/4/5/7/8/10/12	15	-2159.75	4350.09	2.66	0.01	0.35	0.57
1/3/4/5/7/8/10/11/12	16	-2158.72	4350.11	2.68	0.01	0.35	0.56
1/3/5/8	11	-2163.91	4350.13	2.71	0.01	0.34	0.56
1/3/4/5/8/9/10/11/12	16	-2158.74	4350.14	2.72	0.01	0.35	0.56
1/2/3/4/8/12	13	-2161.87	4350.18	2.75	0.01	0.35	0.57
1/2/3/4/5/8/13	14	-2160.84	4350.20	2.77	0.01	0.35	0.57
1/4/5/8/9/12	13	-2161.89	4350.23	2.80	0.01	0.34	0.56
1/4/8/12	11	-2163.96	4350.25	2.82	0.01	0.34	0.56
1/2/4/5/8/12/13	14	-2160.88	4350.28	2.86	0.01	0.35	0.57
1/2/3/4/5/7/8/11/12	16	-2158.83	4350.33	2.91	0.01	0.35	0.56
1/2/4/5/8/12	13	-2161.95	4350.34	2.91	0.01	0.34	0.57
1/2/3/4/8/11/12	14	-2160.92	4350.35	2.92	0.01	0.35	0.56
1/3/4/7/8/9/12	14	-2160.92	4350.36	2.93	0.01	0.34	0.57
1/2/3/4/5/8/11/13	15	-2159.91	4350.40	2.98	0.01	0.35	0.57
1/2/4/5/8/13	13	-2161.99	4350.44	3.01	0.01	0.34	0.57
1/4/5/8/11/12	13	-2162.00	4350.46	3.03	0.01	0.34	0.56
1/3/4/7/8/9/11/12	15	-2159.93	4350.46	3.03	0.01	0.35	0.56
1/3/4/8/9/10/12	14	-2160.97	4350.46	3.03	0.01	0.35	0.57
1/2/3/4/5/7/8/12	15	-2159.95	4350.48	3.06	0.01	0.35	0.57
1/2/3/4/5/8/9/12	15	-2159.98	4350.55	3.12	0.01	0.35	0.57
1/2/3/4/5/8/9/12/13	16	-2158.99	4350.65	3.22	0.01	0.35	0.57
1/3/4/8/9/10/11/12	15	-2160.04	4350.67	3.24	0.01	0.35	0.56
1/2/3/4/5/8/9/11/12	16	-2159.01	4350.69	3.27	0.01	0.35	0.56
1/3/4/7/8/10/12	14	-2161.09	4350.70	3.27	0.01	0.34	0.57
1/4/5/8/10/12	13	-2162.15	4350.75	3.32	0.01	0.34	0.56
1/3/4/7/8/10/11/12	15	-2160.10	4350.79	3.36	0.01	0.34	0.56
1/3/5/8/9/11	13	-2162.22	4350.88	3.45	0.01	0.35	0.56
1/2/3/4/5/7/8/12/13	16	-2159.12	4350.91	3.48	0.01	0.35	0.57
1/2/3/4/5/7/8/11/12/13	17	-2158.10	4350.96	3.53	0.01	0.35	0.56
1/2/3/4/5/8/9/11/12/13	17	-2158.10	4350.96	3.54	0.01	0.35	0.57
1/3/4/5/7/8/9/10/12	16	-2159.15	4350.97	3.54	0.01	0.35	0.57
1/3/5/8/9	12	-2163.30	4350.98	3.55	0.01	0.34	0.56
1/2/3/4/5/8/9/13	15	-2160.20	4350.99	3.56	0.01	0.35	0.57
1/3/4/5/7/8/9/10/11/12	17	-2158.12	4350.99	3.56	0.01	0.35	0.56
1/2/4/5/8/11/12	14	-2161.25	4351.03	3.60	0.01	0.35	0.56
1/4/5/7/8/12	13	-2162.29	4351.03	3.60	0.01	0.34	0.56
1/2/3/4/5/8/10/12	15	-2160.22	4351.03	3.60	0.01	0.35	0.57
1/2/3/4/8/12/13	14	-2161.28	4351.07	3.64	0.01	0.35	0.57
1/2/4/5/8/11/12/13	15	-2160.25	4351.09	3.66	0.01	0.35	0.57
1/2/4/8/12	12	-2163.36	4351.10	3.67	0.01	0.34	0.57
1/2/4/5/8/11/13	14	-2161.31	4351.14	3.71	0.01	0.35	0.56

1/4/8/9/12	12	-2163.39	4351.17	3.74	0.01	0.34	0.56
1/2/3/4/5/8/10/11/12	16	-2159.25	4351.17	3.75	0.01	0.35	0.56
1/2/4/5/7/8/12	14	-2161.33	4351.18	3.76	0.01	0.34	0.56
1/3/5/7/8/11	13	-2162.38	4351.20	3.77	0.01	0.34	0.55
1/2/4/5/8/9/12/13	15	-2160.31	4351.20	3.78	0.01	0.35	0.57
1/2/4/5/8/9/13	14	-2161.34	4351.20	3.78	0.01	0.35	0.57
1/2/3/4/5/8/9/11/13	16	-2159.27	4351.22	3.79	0.01	0.35	0.57
1/2/3/4/8/9/12	14	-2161.36	4351.24	3.82	0.01	0.35	0.57
1/2/3/4/7/8/11/12	15	-2160.33	4351.24	3.82	0.01	0.34	0.56
1/2/3/4/5/7/8/9/11/12	17	-2158.25	4351.26	3.83	0.01	0.35	0.56
1/2/3/4/5/8/10/12/13	16	-2159.32	4351.31	3.89	0.01	0.35	0.57
1/2/3/4/7/8/12	14	-2161.40	4351.32	3.89	0.01	0.34	0.57
1/4/5/8/9/11/12	14	-2161.42	4351.35	3.93	0.01	0.34	0.56
1/2/4/5/8/9/12	14	-2161.42	4351.36	3.93	0.01	0.35	0.57
1/2/3/4/8/11/12/13	15	-2160.39	4351.37	3.95	0.01	0.35	0.57
1/2/4/5/7/8/12/13	15	-2160.40	4351.39	3.96	0.01	0.34	0.57
1/2/3/4/5/7/8/9/12	16	-2159.36	4351.40	3.97	0.01	0.35	0.57
1/4/8/10/12	12	-2163.51	4351.41	3.98	0.01	0.34	0.56

1 = Age+Age^2, 2 = Captures, 3 = Carried telemetry device, 4 = Social status, 5 = Family group size, 7 = Origin, 8 = Season, 9 = Sex, 10 = log(Territory size), 11 = Years of monitoring, 12 = Social status:Age, 13 = Captures:Social status

S7. The model selection result for the candidate models investigating the annual reproduction in a Eurasian beaver population in south-eastern Norway between 1998 and 2018. Beaver ID, monitoring year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	ΔAICc	weight	$R^2_{marginal}$	$R^2_{conditional}$
2/6/7/8/10	9	-249.90	518.27	0.00	0.06	0.07	0.14
2/5/6/7/8/10	10	-248.94	518.47	0.20	0.05	0.08	0.13
6/7/8/10	8	-251.13	518.64	0.37	0.05	0.06	0.14
1/6/7/8/9/10	10	-249.04	518.66	0.39	0.05	0.09	0.17
5/6/7/8/10	9	-250.12	518.73	0.46	0.04	0.07	0.13
1/4/6/7/8/9/10	11	-248.09	518.88	0.61	0.04	0.09	0.16
2/3/6/7/8/10	10	-249.27	519.13	0.86	0.04	0.08	0.13
1/2/6/7/8/9/10	11	-248.31	519.32	1.05	0.03	0.09	0.16
1/5/6/7/8/9/10	11	-248.40	519.51	1.24	0.03	0.09	0.15
3/6/7/8/10	9	-250.58	519.64	1.37	0.03	0.07	0.14
1/2/4/6/7/8/9/10	12	-247.52	519.88	1.61	0.02	0.09	0.16
1/4/5/6/7/8/9/10	12	-247.55	519.94	1.67	0.02	0.09	0.15
2/4/6/7/8/10	10	-249.73	520.04	1.77	0.02	0.07	0.13
1/3/6/7/8/9/10	11	-248.69	520.08	1.81	0.02	0.09	0.16
2/3/5/6/7/8/10	11	-248.72	520.14	1.87	0.02	0.08	0.13
1/2/5/6/7/8/9/10	12	-247.68	520.18	1.91	0.02	0.09	0.15
2/4/5/6/7/8/10	11	-248.80	520.30	2.03	0.02	0.08	0.12
4/6/7/8/10	9	-250.93	520.33	2.06	0.02	0.06	0.14
1/2/6/7/8/10	10	-249.90	520.38	2.11	0.02	0.07	0.14

4/5/6/7/8/10	10	-249.94	520.47	2.20	0.02	0.07	0.12
3/5/6/7/8/10	10	-249.95	520.49	2.22	0.02	0.07	0.13
1/2/5/6/7/8/10	11	-248.91	520.52	2.25	0.02	0.08	0.13
1/3/4/6/7/8/9/10	12	-247.88	520.59	2.32	0.02	0.09	0.16
1/2/3/6/7/8/9/10	12	-247.90	520.63	2.36	0.02	0.09	0.16
5/7/8/10	8	-252.13	520.64	2.37	0.02	0.05	0.12
1/5/6/7/8/10	10	-250.08	520.74	2.47	0.02	0.07	0.13
1/6/7/8/10	9	-251.13	520.74	2.47	0.02	0.06	0.14
7/8/10	7	-253.23	520.76	2.49	0.02	0.04	0.14
2/5/7/8/10	9	-251.17	520.82	2.55	0.02	0.06	0.12
2/7/8/10	8	-252.26	520.89	2.62	0.01	0.05	0.13
1/2/4/5/6/7/8/9/10	13	-246.99	520.95	2.68	0.01	0.10	0.15
2/3/4/6/7/8/10	11	-249.17	521.05	2.78	0.01	0.08	0.13
1/7/8/9/10	9	-251.35	521.17	2.90	0.01	0.07	0.17
1/2/3/6/7/8/10	11	-249.24	521.18	2.91	0.01	0.08	0.13
2/3/7/8/10	9	-251.36	521.19	2.92	0.01	0.06	0.13
3/7/8/10	8	-252.44	521.26	2.99	0.01	0.05	0.13
1/3/5/6/7/8/9/10	12	-248.27	521.38	3.11	0.01	0.09	0.15
3/4/6/7/8/10	10	-250.44	521.47	3.20	0.01	0.07	0.13
1/2/3/4/6/7/8/9/10	13	-247.26	521.50	3.23	0.01	0.10	0.15
1/3/6/7/8/10	10	-250.54	521.66	3.39	0.01	0.07	0.13
1/5/7/8/9/10	10	-250.57	521.73	3.46	0.01	0.07	0.15
1/3/4/5/6/7/8/9/10	13	-247.49	521.96	3.69	0.01	0.09	0.15
1/2/3/5/6/7/8/9/10	13	-247.50	521.98	3.71	0.01	0.09	0.15
1/3/7/8/9/10	10	-250.74	522.06	3.79	0.01	0.07	0.16
2/3/4/5/6/7/8/10	12	-248.61	522.06	3.79	0.01	0.08	0.12
1/2/3/5/6/7/8/10	12	-248.65	522.13	3.86	0.01	0.08	0.12
3/5/7/8/10	9	-251.83	522.13	3.86	0.01	0.06	0.12
1/2/4/6/7/8/10	11	-249.73	522.16	3.89	0.01	0.07	0.13
2/3/5/7/8/10	10	-250.79	522.17	3.90	0.01	0.07	0.12
1/2/7/8/9/10	10	-250.81	522.20	3.93	0.01	0.07	0.16

1 = log(Age), 2 = Carried telemetry device, 3 = Family group size, 4 = Origin, 5 = Reproduced previous year, 6 = log(Territory size), 7 = Captures, 8 = Years of monitoring, 9 = Captures:log(Age), 10 = Captures:Years of monitoring

S8. The model selection result for the candidate models investigating the annual litter size in a Eurasian beaver population in south-eastern Norway between 1998 and 2018. Beaver ID, monitoring year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	ΔAICc	weight	**R$^2_{marginal}$**	**R$^2_{conditional}$**
1/4/6/7/8/9/10	11	-415.22	853.15	0.00	0.12	0.09	0.21
1/6/7/8/9/10	10	-416.57	853.72	0.57	0.09	0.08	0.22
1/4/5/6/7/8/9/10	12	-414.74	854.31	1.17	0.07	0.09	0.20
1/7/8/9/10	9	-418.03	854.54	1.40	0.06	0.08	0.23
1/5/6/7/8/9/10	11	-416.01	854.71	1.57	0.06	0.09	0.21

1/3/4/6/7/8/9/10	12	-414.96	854.74	1.60	0.06	0.09	0.20
1/2/4/6/7/8/9/10	12	-414.96	854.75	1.60	0.06	0.09	0.21
1/4/7/8/9/10	10	-417.15	854.89	1.74	0.05	0.08	0.22
1/3/6/7/8/9/10	11	-416.19	855.09	1.94	0.05	0.09	0.21
1/2/6/7/8/9/10	11	-416.20	855.10	1.95	0.05	0.09	0.22
1/5/7/8/9/10	10	-417.47	855.53	2.38	0.04	0.08	0.21
1/3/7/8/9/10	10	-417.66	855.90	2.75	0.03	0.08	0.22
1/2/4/5/6/7/8/9/10	13	-414.49	855.95	2.80	0.03	0.09	0.20
1/4/5/7/8/9/10	11	-416.67	856.05	2.90	0.03	0.08	0.21
1/2/7/8/9/10	10	-417.73	856.05	2.91	0.03	0.08	0.23
1/2/5/6/7/8/9/10	12	-415.65	856.13	2.98	0.03	0.09	0.20
1/2/3/4/6/7/8/9/10	13	-414.65	856.27	3.13	0.03	0.10	0.20
1/3/4/5/6/7/8/9/10	13	-414.66	856.30	3.15	0.03	0.09	0.19
1/2/3/6/7/8/9/10	12	-415.76	856.36	3.21	0.02	0.09	0.21
1/3/4/7/8/9/10	11	-416.87	856.44	3.29	0.02	0.08	0.21
1/2/4/7/8/9/10	11	-416.93	856.57	3.42	0.02	0.08	0.22
1/3/5/6/7/8/9/10	12	-415.88	856.59	3.44	0.02	0.09	0.20
1/2/5/7/8/9/10	11	-417.18	857.06	3.91	0.02	0.08	0.21

1 = log(Age), 2 = Carried telemetry device, 3 = Family group size, 4 = Origin, 5 = Reproduced previous year, 6 = log(Territory size), 7 = Captures, 8 = Years of monitoring, 9 = Captures:log(Age), 10 = Captures:Years of monitoring

S9. The model structure for the global model investigating the annual survival in a Eurasian beaver population in south-eastern Norway between 1998 and 2018 using a continuous time capture-recapture model (Fouchet et al. 2016):

Survival ~ Captures + Years of monitoring + Carried telemetry device + Season + Sex + Social status + log(Territory size) + Family group size + Age + Immigrant + Captures:Years of monitoring + Captures:Sex + Captures:Social status + Captures:Age + Season:Sex + Social status:Age

Model terms were removed by backwards selection until the model only consisted of informative parameters:

Survival ~ Age + Social status + Family group size + Social status:Age

S10. The model selection result for the candidate models investigating the probability of staying dominant in a Eurasian beaver population in south-eastern Norway between 1998 and 2018. Beaver ID, monitoring year and river were included as random effects. Models were ranked based on AICc.

Variables	df	log likelihood	AICc	ΔAICc	weight	$\mathbf{R^2_{marginal}}$	$\mathbf{R^2_{conditional}}$
1/3/6/8	8	-260.70	537.59	0.00	0.15	0.20	0.24
1/3/4/6/8	9	-260.28	538.80	1.20	0.08	0.20	0.25
1/3/6/7/8	9	-260.56	539.36	1.77	0.06	0.20	0.24
1/3/5/6/8	9	-260.59	539.42	1.83	0.06	0.20	0.24
1/2/3/6/8	9	-260.60	539.43	1.84	0.06	0.20	0.25
1/3/6	7	-262.79	539.73	2.14	0.05	0.16	0.24
1/3/4/6/7/8	10	-259.84	539.97	2.37	0.04	0.20	0.24
1/2/3/6	8	-261.99	540.16	2.57	0.04	0.17	0.25
1/3/8	7	-263.08	540.30	2.71	0.04	0.17	0.22
1/3/4/8	8	-262.15	540.49	2.90	0.03	0.18	0.22
1/3/4/5/6/8	10	-260.13	540.54	2.95	0.03	0.20	0.25
1/3/6/7/8/11	10	-260.17	540.63	3.03	0.03	0.20	0.26
1/3/4/6/7/8/9	11	-259.16	540.66	3.07	0.03	0.19	0.23
1/2/3/4/6/8	10	-260.20	540.70	3.10	0.03	0.20	0.25
1/3/6/7/8/9	10	-260.25	540.79	3.19	0.03	0.19	0.23
1/2/3/6/7/8	10	-260.31	540.92	3.32	0.03	0.20	0.25
1/3/4/6/7/8/9/11	12	-258.33	541.06	3.47	0.03	0.20	0.25
1/3/6/7/8/9/11	11	-259.41	541.16	3.57	0.02	0.20	0.25
1/3/5/6/7/8	10	-260.48	541.26	3.66	0.02	0.20	0.24
1/2/3/5/6/8	10	-260.50	541.29	3.70	0.02	0.20	0.25
1/2/3/4/6/7/8	11	-259.53	541.41	3.81	0.02	0.20	0.25
1/3/4/6/7/8/11	11	-259.53	541.41	3.81	0.02	0.21	0.26
1/2/3/6/7/8/9/10	12	-258.54	541.49	3.90	0.02	0.22	0.32
1/3/5/6	8	-262.68	541.54	3.95	0.02	0.16	0.24
1/2/3/6/7	9	-261.66	541.56	3.96	0.02	0.17	0.25

1 = Age, 2 = Carried telemetry device, 3 = Family, 4 = Origin, 5 = Sex, 6 = log(Territory size), 7 = Captures, 8 = Years of monitoring, 9 = Captures:Age, 10 = Captures:Carried telemetry device, 11 = Captures:Years of monitoring

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