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Martin Mayer

Territoriality and life history strategies of the Eurasian beaver

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Preface

When I was in primary school, I had a nickname. Biber (beaver; it does not mean the same thing in German than in English). That name stuck with me throughout high school and even today, some of my old school friends call me Biber. Now maybe they can call me Dr. Biber. Funny how things pan out sometimes…

Acknowledgements

First, I want to thank my amazing supervisors, Frank Rosell and Andreas Zedrosser. You put trust in me from the beginning and let me develop my own projects, giving me lots of freedom with my work. I think you two function quite well as a team, with Frank always being enthusiastic and throwing in lots of ideas, and with Andreas helping to keep me on track and advising on the statistics. Thank you for all the discussions, ideas, help and support! It was great to work with you, and I hope that our paths cross again in the not too far future.

During my PhD, I conducted quite some fieldwork, and I want to thank all the people involved, namely Frank, Joar, Patricia, Boris, Alina, Jon Martin, Julia, Hannah, Fabian, Katrin, Elena, Richard, Lia, Claudia, and Laura. And Christian. Without you, nothing would have happened. You are the best boat driver and I think we were an incredible team, capturing over 200 beavers together. We had some amazing nights out catching beavers both on the river and in the bar, together with Patricia et al. I will never forget that one night when we tried to get Moritz, and legendarily failed.

Although I really like fieldwork, the reality is that I spent most of my time in the office. An amazing office. With Shane, who was incredibly helpful with statistical advice and in general with discussing all kinds of stuff, Priyank and Jean-Marc, our geneticists and beer brewing experts, and Patricia and Hannah, who introduced me to the beaver team and to the nightlife in Bø. A special thanks here to Patricia; we were a really good team, both when collaborating on our PhDs and when going out. Thanks to the whole LEBE team for all the fruitful discussions and the fun we had! Moreover, I would like to thank the students I had the pleasure to supervise: Katrin, Elena, Lia, Claudia, Fabian, and Richard. You were all amazing and motivated students and I learned at least as much from supervising you guys than the other way around. And a special thanks here to you Katrin, for all the sport sessions you dragged me to and all the good times we had. I have met many very nice people during my stay in Norway. Thank you all for making this time unforgettable.

Last, and maybe most importantly, I would like to thank my parents. You triggered my deep interest for nature by bringing me outdoors as soon as I could walk. First, I joined my mom

controlling fences and making feeding stations, and a little later, my dad took me out hunting around Feldstetten and then to Slovenia and Austria. You always supported me in my decision to study biology, endured my snake obsession, and sustained my adventures in Russia and Australia (which must have been quite hard for my mom at times). Thank you for your everlasting support, without you I would not be where I am today!

Abstract

We studied life history strategies in the Eurasian beaver (*Castor fiber*), a territorial, monogamous, long-lived mammal, to increase our understanding of the mechanisms and trade-offs affecting the onset of natal dispersal, mate change, spatial movement patterns, and the duration of territory occupancy.

The mean age at dispersal in our study area was 3.5 years, with some individuals remaining within their natal family group until age 7. Subordinates delayed dispersal with increasing age of the same-sex parent. This suggests that either parents are more tolerant towards their offspring at an increasing age, or that subordinates can perceive senescence and thus ”queue” in the natal territory to take it over after the death of the parents. In addition, individuals were more likely to disperse with increasing age and at lower population densities. This suggests that subordinates gain competitive abilities with increasing age, and that they can perceive changes in population density. We found that subordinates often conducted extra-territorial movements, which lasted longer compared to extra-territorial movements by territory holders (dominants), and they usually intruded into multiple territories, which likely is a mechanism to detect a suitable timing for dispersal by gaining knowledge on available territories and population density fluctuations.

Further, we found that mate change in beavers was non-adaptive, most likely caused by the intrusion of a younger, incoming individual replacing the same-sex territory holder, and to a lower degree by the accidental loss of a partner. We then investigated spatial movement patterns of dominant beavers, and found that there was a territory size-dependent trade-off between patrolling and foraging: beavers in smaller territories had reduced costs of patrolling (they travelled at lower speed), but stayed further from the shore when foraging, possibly due to resource depletion. Beavers in smaller territories also conducted more extra-territorial movements, likely to assess possibilities for territory expansion. Additionally, older beavers spent more time on land and close to territory borders suggesting a behavioral change with age due to senescence or experience.

The duration of territory occupancy ranged between 1 and 11 years (mean ± SD: 6.2 ± 2.8 years), and was a predictor for the lifetime reproductive success of an individual. Beavers that delayed dispersal and established in intermediate-sized territories occupied them for longer compared to younger dispersers and individuals establishing in smaller or larger territories. This suggests that an individual should await its physical and behavioral maturation before the acquisition of a territory, and demonstrates that intermediate-sized territories follow the optimization criterion, ensuring sufficient resource availability and decreased costs of territorial defense at the same time.

The high population density in our study area is likely a major factor affecting many of the observed patterns, leading to an intense competition for territories, in effect causing delayed dispersal, non-adaptive mate change, and is driving spatial movement patterns related to patrolling and resource availability.

Keywords: Behavioral ecology, dispersal, *Castor fiber*, life history, mate change, movement ecology, territoriality.

List of papers

Paper I

Mayer, M., Zedrosser, A., & Rosell, F. (2017). Beyond the border: The role of extra-territorial movements in a large, monogamous rodent. Submitted to Scientific Reports.

Paper II

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

Paper III

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

Paper IV

Graf, P. M., Mayer, M., Zedrosser, A., Hackländer, K., & Rosell, F. (2016). Territory size and age explain movement patterns in the Eurasian beaver. Mammalian Biology-Zeitschrift für Säugetierkunde 81: 587-594.

Paper V

Mayer, M., Zedrosser, A., & Rosell, F. (2017). Couch potatoes do better: Delayed dispersal and territory size affect the duration of territory occupancy in a monogamous mammal. Ecology and Evolution 00: 1-10. https://doi.org/10.1002/ece3.2988

Abbreviations

AIC	Akaike's Information Criterion
DTO	Duration of territory occupancy
ETM	Extra-territorial movement
EPC	Extra-pair copulation
GLM	Generalized linear model
GLMM	Generalized linear mixed model
ITM	Intra-territorial movement
LRS	Lifetime reproductive success
MCP	Minimum convex polygon
NA beaver	North American beaver

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1 Introduction

Life history strategies and the role of behavior

The life of an organism can be broken down into two main purposes, survival and reproduction, which ultimately means to maximize fitness (Rolandsen et al. 2016). An animal's life history can be defined as its lifetime pattern of growth, reproduction, and mortality, which are driven by long-term evolutionary processes, but also by direct changes of the environment an individual lives in (Begon and Harper 1990). Life history evolution makes the simplifying claim that the phenotype, expressed by a certain genotype, consists of demographic traits that are connected by constraining relationships (Stearns 1992). Such life history traits are the size at birth and maturity, growth patterns, the number, size and sex ratio of offspring, age- and size specific reproductive investments and mortality schedules, and the length of life. Trade-offs between those traits include those between current reproduction and survival, current and future reproduction, and the number, size and sex of offspring (Stearns 1992, Brommer et al. 1998).

Behavior plays an important role when studying life history strategies, because it is potentially unique in the respect that it can be a 'choice' per se (Sih et al. 2010). While animals naturally display a wide range of responses that enable them to cope with their environment, behavior is a response that gives individuals flexibility to adjust to the various environmental conditions they live in (Sih et al. 2010). The decision to invest into a specific activity is usually traded-off with other activities, e.g. foraging and predator avoidance (Hebblewhite and Merrill 2009) or scent marking and hunting (Vogt et al. 2016), and can affect the fitness and survival of an individual (Stearns 1992).

Territoriality

Animals compete for different resources, such as food, mating partners, shelter and breeding sites. Competition can be indirect, e.g. by the exploitation of a limited food resource (Petren and Case 1996, Balfour et al. 2015) or direct via interference (Hersteinsson and Macdonald 1992, Bleach et al. 2015). A way to ensure access to resources is to defend them against conspecifics, i.e. being territorial. Territoriality has been shown to regulate animal populations

(Wolff 1997, López-Sepulcre and Kokko 2005), and can be defined as the defense of a fixed area by an individual or a group of mutually tolerant individuals in order to exclude competitors and to ensure exclusive resource use (Maher and Lott 1995). Territoriality and territorial behaviors can be limited to a certain time of the year (Fuxjager et al. 2017) or to one sex (Webb et al. 2015); this is often the case in polygamous and promiscuous mating systems (Clutton-Brock 1989). Generally, the occurrence and degree of territoriality has been shown to depend on resource availability (Schradin and Pillay 2004, 2006). In some ungulate species, males defend feeding or mating territories during the reproductive season (Clutton-Brock 1989, Ofstad et al. 2016), and in some rodents females establish territories during the reproductive season, which they defend against conspecific females (Wolff and Peterson 1998).

Monogamous mating systems occur in only 3-5% of all mammalian species including canids, some primates, mustelids, viverrids, artiodactyls, insectivores and rodents (Kleiman 1977b, Moehlmann 2014, Rood 2014). In such species, a male-female pair usually defends a fixed territory throughout the year. The increase in relative fitness via a higher reproductive success, the avoidance of predation or diseases, exclusive access to limiting resources, and the availability of mating partners have been used to explain the evolution of territoriality (Riechert 1981).

Dispersal and territory acquisition

In monogamous, territorial animals, offspring can acquire breeding status in three ways: 1) dispersal and territory establishment (Bowler and Benton 2005), 2) awaiting the disappearance of the parents to take over the breeding position in the natal territory (Ekman et al. 2001), or 3) conducting extra-territorial movements (ETM) to seek breeding opportunities outside the natal area without having to disperse (Young et al. 2007). The first and last possibilities are not mutually exclusive; for example, an individual could initially increase its reproductive success via ETMs, and then disperse later in life when environmental conditions are more favorable. Dispersal is possibly the most common mechanism to acquire a breeding position/territory, and can have large consequences on the demography and genetic structure of a population (Le Galliard and Clobert 2003, Bowler and Benton 2005). The ultimate cause of dispersal is to avoid inbreeding with closely related individuals (Wolff 1994), to decrease competition for mates (Dobson 1982), and to gain access to environmental resources (Greenwood 1980). Generally, dispersal is a dangerous period in the life of an animal and can result in high mortalities (Bonnet et al. 1999). Thus, the timing of natal dispersal is important to increase the probability of successful territory establishment, and consequently, reproductive success. The timing of dispersal has been connected to kin competition (Ronce et al. 1998, Bowler and Benton 2005) and population dynamics (Matthysen 2005). Although the probability of dispersal is well covered in the ecological literature (Zedrosser et al. 2007, Armitage et al. 2011, Saino et al. 2014), there are still knowledge gaps concerning the onset of natal dispersal, especially in large, long-lived mammals (Sarno et al. 2003, Sparkman et al. 2010).

Mate change

The final process of dispersal is to establish in a new area. An individual can establish in a previously unoccupied area, or it can take over an existing territory by challenging its current owner. In addition, an individual has to find a mate during or after dispersal. Mate choice is an important factor for an individual's reproductive success, especially in obligate monogamous species that rely on a partner for the successful raising of their offspring (Kleiman 1977a). Individuals cannot always pair with an optimal mate, due to competition for high quality mates that is costly and limited in time. To adjust for initial mate choice, individuals may try to obtain extra-pair copulations to increase their reproductive success (Griffith et al. 2002, Westneat and Stewart 2003, Forstmeier et al. 2014), or they can divorce their current partner and find a new partner that is more compatible, i.e., adaptive mate change (divorce) (Moody et al. 2005, Dreiss and Roulin 2014). In species that are territorial throughout the year, there are two main hypothesis explaining adaptive mate change. 1) The 'better option' hypothesis states that one partner of the mated pair initiates a divorce, and that this individual will improve its reproductive success after re-pairing with a higher quality mate (Ens et al. 1993, Choudhury 1995). 2) the 'incompatibility' hypothesis states that the divorce is initiated by both members of the pair due to a poor genetic or behavioral compatibility (Choudhury 1995). However, mate change can also be non-adaptive, i.e., caused by an incoming individual that outcompetes and replaces the same-sex member of the mated pair, which is termed the ‘forced divorce’ hypothesis (Taborsky and Taborsky 1999, Lardy et al. 2011). Another cause for non-adaptive mate change can be the accidental loss of a partner, for example due to hunting (Milleret et al. 2017), i.e., the ‘obligate mate change’ hypothesis (Lardy et al. 2011). Although numerous studies exist on adaptive mate change in invertebrates (Beltran and Boissier 2008), fish (van Breukelen and Draud 2005), and birds (Heg et al. 2003, Jeschke et al. 2007, Dreiss and Roulin 2014), little is known about divorce in mammals (Palombit 1994), and especially about non-adaptive mate change in general (Jeschke et al. 2007, Lardy et al. 2011).

Spatial movement patterns

Once an individual has established in a territory, it has to make the best out of the available resources. Further, territorial animals have to advertise territory occupancy, e.g. via visual or acoustic signals (Gardner and Graves 2005, Van Dyk and Evans 2007). In species that advertise territory occupancy via scent marking (Sillero-Zubiri and Macdonald 1998, Gosling and Roberts 2001, Wise et al. 2004), territory patrolling is an important driver of spatial movements (Moorcroft et al. 2006, Fagan et al. 2013). Patrolling and scent marking might be traded-off with other important activities, such as foraging (Amsler 2010, Vogt et al. 2016). In general, the costs of territoriality increase with territory size, i.e., larger areas are more costly to defend (Righton et al. 1998). However, estimating the costs and benefits of different territory sizes can be difficult (Kacelnik et al. 1981, Ydenberg and Krebs 1987, López-Sepulcre and Kokko 2005). Many studies have investigated habitat selection and space use patterns in animals (Rettie and Messier 2000, Matthiopoulos et al. 2015, Cristescu et al. 2016), but little attention has been paid to the trade-off between foraging and territorial behaviors (Ydenberg and Krebs 1987, Vogt et al. 2016). The optimization criterion for territory size is defined as insuring sufficient resource availability and low costs of territorial defense at the same time (Adams 2001). Further, individual differences in movement patterns might be related to age. For example, older male moose (*Alces alces*) had larger home ranges compared to younger ones, possibly caused by differences in nutritional demands and social activities, such as rutting behavior (Cederlund and Sand 1994).

Duration of territory occupancy and lifetime reproductive success

For individuals of monogamous species that occupy territories year round and stay with their partners until they die or are replaced (e.g. by takeover of an intruder) the duration of territory occupancy (DTO), should be a predictor for their fitness, i.e., lifetime reproductive success (LRS). The best-quality individuals should occupy the best-quality territories according to the ideal despotic model (Fretwell and Lucas 1970), suggesting that both the quality of the territory holder and the quality of the territory itself should be a predictor for the DTO (Sergio and Newton 2003). These predictions have rarely been tested in long-lived monogamous mammals (Sparkman et al. 2010). However, individual-based long-term studies are necessary to answer important questions in ecology and evolution (Clutton-Brock and Sheldon 2010). An animal can improve its competitive ability (which should be a predictor for quality) by awaiting physical and behavioural maturity before the acquisition of a territory according to the maturation hypothesis (Weimerskirch 1992, Piper et al. 2015). In addition, the size of the established territory should be a predictor for its quality, and consequently of DTO, as patrolling activities are traded off with foraging activities (Ydenberg and Krebs 1987, Amsler 2010). Both, the territory size and DTO, might depend on competition with conspecifics, resource availability, and population density.

Study species

We used the Eurasian beaver (*Castor fiber*, hereafter beaver) as a model species to study life history strategies in large, long-lived, monogamous mammals (Rosell and Pedersen 1999, Campbell et al. 2005, Rosell and Thomsen 2006). The beaver is, together with the North American beaver (*C. canadensis*, hereafter NA beaver), the second largest rodent in the world (Macdonald 2001). After being hunted to near extinction during the 19th century, it is now recovering in Europe and Asia, and occurs in large parts of its former range (Nolet and Rosell 1998, Halley et al. 2012). Both species have a very similar biology and ecology, and can live up to 20 years (Gorbunova et al. 2008). Beavers are sexually monomorphic and live in family groups consisting of the dominant breeding pair, their kits of the year, and often non-breeding offspring ≥ 1 year old (Wilsson 1971, Campbell et al. 2005). Mating in both species takes place in January and February (Wilsson 1971), and extra-pair copulation (EPC) has been recorded in a NA beaver population (Crawford et al. 2008), suggesting that extra-territorial movements

(ETM) occur during the mating season. In Eurasian beavers, there is little evidence for EPC (Syrůčková et al. 2015), and Tinnesand (2017) found that EPC was responsible for only 5.4% of the offspring in our study population. One to five kits are born in mid-May (Parker and Rosell 2001, Campbell et al. 2005). Beavers display a high degree of biparental care (Wilsson 1971), and hence, are considered obligate monogamous (Kleiman 1977a). Kits are fully weaned at about two months of age and emerge from the lodge during July when they start feeding on their own (Wilsson 1971). Before they emerge from the lodge, family members provide them with twigs and leaves of deciduous trees (Wilsson 1971, Zurowski et al. 1974), on which beavers predominantly feed (Wilsson 1971, Campbell et al. 2005). Generally, beavers are central-place foragers and foraging mostly occurs within 40 m from the shore (Fryxell and Doucet 1991, Haarberg and Rosell 2006).

Both beaver species are highly territorial and defend territories year-round against conspecifics via scent-marking (Rosell et al. 1998, Müller-Schwarze and Sun 2003). Intruders are treated aggressively and territorial combat can result in serious or even fatal injuries (Nolet and Rosell 1994, Crawford et al. 2015). Beavers typically disperse at around 2 years of age (Hartman 1997, Sun et al. 2000) to establish a territory of their own. Dispersal occurs alone (M. Mayer, pers. obs.). Two studies on dispersal in NA beavers gave an annual proportion of dispersers for different age cohorts (McNew and Woolf 2005, Havens 2006), and another study reported that all individuals dispersed latest at age 3 years (Sun et al. 2000). Hartman (1997) and Sun et al. (2000) suggested density dependency in beaver dispersal onset (both species), with individuals in denser populations dispersing at older ages; however, this has never been tested. ETMs may be a mechanism to evaluate population density levels, and there is evidence for pre-dispersal ETMs in beavers. For example, 3 of 8 subordinates made ETMs before dispersal in a NA beaver population (Havens 2006), and 3 of 9 subordinates made pre-dispersal forays ranging between 1.5 and 15 km in a Swedish beaver population (Hartman 1997). However, there is no information about ETMs of dominant individuals or spatial movement patterns during ETMs. Beavers form pairs year round, but pair formation was shown to peak (56% of all known pairs) in September, October, and November in a NA beaver population (Svendsen 1989). Further, pair formation is thought to occur when a single territory owner is joined by an incoming individual (Svendsen 1989). Once paired, beavers remain together for long periods (Wilsson 1971, Sun 2003).

2 Objectives

The aim of this thesis was to investigate different aspects of the life history strategies of a territorial and monogamous large mammal, using the beaver as a model species. We investigated life history strategies representing sequential stages in the life of a beaver, specifically the patterns of dispersal from the natal territory, territory acquisition, mate change, and territory occupancy.

Pre-dispersal ETMs and the timing of dispersal (paper I and II)

We investigated patterns of ETMs in 10 subordinate and 46 dominant beavers using GPS tags (paper I). We hypothesized that ETM patterns would be related to an individual’s social status, and predicted that subordinates would conduct more and longer ETMs compared to dominants to gain pre-dispersal information. Further, we predicted that subordinates would conduct more ETMs during spring when beavers typically disperse.

We then investigated the timing of dispersal, i.e., in which year an individual initiated dispersal, and the variation in dispersal age to test the proximate causes of dispersal onset (paper II). We tested whether the timing of dispersal and variation in dispersal age were related to the competitive ability of the disperser, population density, group size, the presence of a new, unrelated dominant individual in the natal family group, and the parental age.

Mate change (paper III)

We tested four hypotheses to investigate mate change in beavers. For the ‘incompatibility’ hypothesis, we predicted that a mate change would occur early in a partnership and depends upon the mated pair’s previous reproductive success. Hence, we expected the reproductive success in pairs where no mate change occurs to be higher than in pairs that later experienced a mate change. For the ‘better option’ hypothesis, we predicted an improved reproductive success of the resident after re-pairing with a new mate. For the ‘forced divorce’ hypothesis, we predicted that the mate change is independent of the reproductive success, and that the incoming individual would be of similar or greater body mass than the replaced individual. For the ‘obligate mate change’ hypothesis, we predicted that the body mass of the incoming individual would be independent of that of the replaced individual, and that the mate change would be independent of the reproductive success.

Spatial movement patterns in the established territory (paper I and IV)

We deployed GPS units on dominant, territory-holding beavers to analyze intra-territorial terrestrial and aquatic movement patterns in relation to environmental and demographic factors. We hypothesized that spatial movement patterns would depend on territory size, resource availability, season, intruder pressure, and age. We predicted that owners of larger territories trade-off increased foraging opportunities close to the shoreline (due to higher resource availability) with a greater patrolling effort compared to owners of smaller territories. Further, we predicted that beavers would patrol more in spring, when subordinates are dispersing, and that beavers would generally increase patrolling activities when facing higher intruder pressure (measured as the number of individuals in neighboring colonies). Finally, we hypothesized that movement patterns would change with increasing age due to increased experience or senescence.

We then investigated ETMs (paper I), and hypothesized that spatial movement patterns would differ between intra-territorial movements (ITM) and ETMs. We predicted that individuals would travel at a greater speed and spend less time on land when on an ETM compared to ITMs to minimize the risk of being detected by a neighbor and to decrease the chances of a physical dispute.

The duration of territory occupancy (paper V)

Finally, we investigated the factors affecting the DTO and LRS in beavers. We hypothesized that DTO would be affected by the age at dispersal, and predicted that individuals that delayed dispersal would occupy a territory longer due to an increased competitive ability in comparison to younger dispersers. Further, we hypothesized that DTO would be related to the size of the established territory, as well as to the resource availability in the territory. We predicted that individuals in smaller territories had an increased DTO compared to individuals in larger territories due to decreased patrolling efforts (Graf et al. 2016b). However, smaller territories potentially had fewer resources (Campbell et al. 2005). We further hypothesized that DTO would be related to population density, and predicted that individuals living at lower population densities face fewer intruders in comparison to higher densities, thus holding a territory longer. Finally, we tested the prediction that the LRS of beavers would increase with increasing DTO, while controlling for the effects of territory size, resource availability, and population density.

3 Material and Methods

3.1 Study area

Our study area was located in Telemark county, southeast Norway, and consisted of three rivers, the Gvarv, Sauar and Straumen (59° 23′ N, 09°09′ E), covering ~32 km river length (Figure 1 and 2). The rivers vary in width between 20 and 150 m (Campbell et al. 2012), and all empty into Lake Norsjø. The average annual temperature is 4.6 °C, and the average annual precipitation is around 790 mm (Campbell et al. 2012). Most parts of the rivers do not freeze during winter, because lakes (in Sauar an Straumen) and weirs (in Straumen) keep them open (Webb and Walling 1996). The land use type in the area is semi-agricultural (Figure 2), with farms, fields and small towns being interspersed with riparian woodland (Campbell 2010, Steyaert et al. 2015), and the main forest type is mixed-deciduous, dominated by Norway spruce (*Picea abies*) and to a lesser degree Scots pine (*Pinus sylvestris*) (Haarberg and Rosell 2006). The most common deciduous tree species along the shore of the rivers are grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), bird cherry (*Prunus padus*), birch (*Betula spp.*), and willow (*Salix spp.*) (Haarberg and Rosell 2006). Beavers do not build dams in the large rivers in our study area, because they are wide and deep enough (Hartman and Törnlöv 2006); however, they do so in smaller streams at the periphery of our study area (pers. obs.).

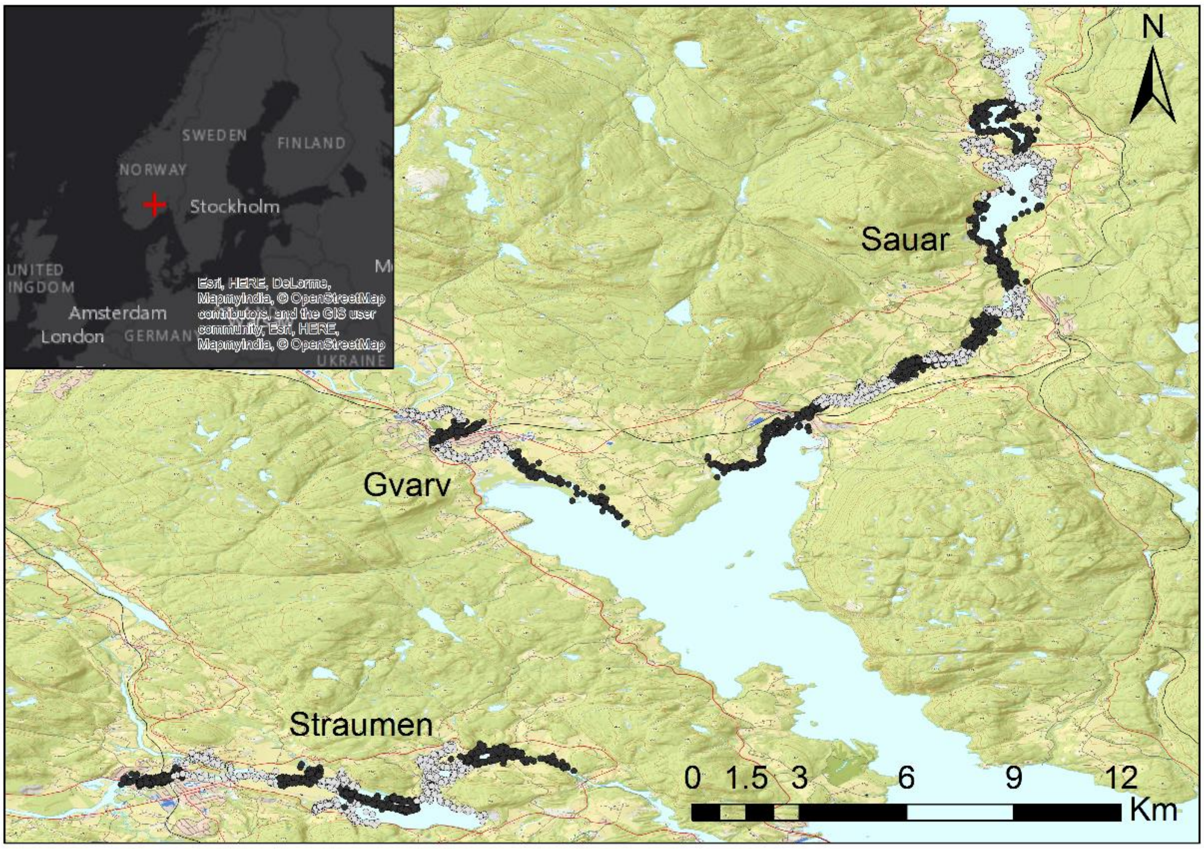

Figure 1: Map of the study area in southeast Norway (red cross). Light and dark grey dots are GPS positions of beavers in the different territories on the three rivers Gvarv, Sauar, and Straumen.

3.2 Study population

Beavers have occurred in the study area since at least the 1920s (Olstad 1937). Between 11 and 27 family groups were monitored annually (Gvarv and Straumen were monitored since 1998 and Sauar since 2004) via an extensive live-trapping program. The population was considered saturated for the last 12 years (Campbell et al. 2005), because territories directly bordered each other, and there were no unoccupied stretches of river in the study area (Figure 1). Hunting pressure was low to moderate, with 0-12% (mean ± SD: 3.9 ± 3.3%) of the population harvested annually (unpubl. results). Overall 54 (12%) of 454 live-captured individuals were hunter harvested during the study period. The predation pressure in the study area was also low, because wolves (*Canis lupus*) and bears (*Ursus arctos*) were functionally extinct in the area, and lynx (*Lynx lynx*) occurred in low densities (Rosell and Sanda 2006). Red foxes (*Vulpes vulpes*) occurred along the rivers (pers. obs.), and there is limited evidence that they occasionally prey on beaver kits (Kile et al. 1996).

3.3 Capture, handling, and collection of demographic data

Beavers were captured every year in spring (March-June) and fall (August-November) as part of a long-term monitoring program (Campbell et al. 2005). Over the 20 years of the study, 454 individual beavers were live-captured. Captures were conducted during the night from a motor boat. Beavers were spotted using searchlights, and captured using large landing nets either in shallow water (Figure 2 and 3) or on land (Rosell and Hovde 2001). They were then transferred into cloth sacks, enabling easy handling without having to anesthetize the animals. Newly captured individuals were sexed based on the color of their anal gland secretion (Rosell and Sun 1999), and aged based on body mass (Rosell et al. 2010). Individuals that were captured for the first time as kit or one-year old were assigned an exact age based on their body mass, and older individuals captured for the first time with a body mass ≥17 kg and ≤19.5 kg were assigned a minimum age of 2 years. Individuals captured for the first time with a body mass >19.5 kg were assigned a minimum age of 3 years (Rosell et al. 2010). Further, all beavers were individually marked with a microchip and a unique combination of ear tags (Sharpe and Rosell 2003), weighed to the nearest 0.2 kg, and measured (body length, tail length and tail width). Each individual was assigned a social status. Breeder (hereafter dominant) status was assigned based on multiple capture and sighting events within the same territory, and lactation in females (Campbell et al. 2013), and was confirmed via genetic paternity tests (Tinnesand 2017). Non-breeders (hereafter subordinates) were subdivided into sexually non-mature kits and yearlings, and mature ≥2 year old individuals. We counted the number of individuals per family group and aimed to capture all kits every year after they emerged from the lodge (usually at the end of July) to estimate reproductive success and group size for each family group in the study area.

Figure 2: Images of the study area, the rivers Sauar (top left), Straumen (top right), and Gvarv (bottom left), and the capture of a beaver with a landing net (bottom right, © Floris Smeets).

3.4 GPS tagging

To study spatial movement patterns, we GPS-tagged 25 (paper IV) and 54 (paper I) beavers, respectively, from 2009-2016. Tag units consisted of a VHF transmitter (Reptile glue-on, series R1910; Advanced Telemetry Systems, Isanti MN, USA) and a GPS receiver (model G1G 134A; Sir-track, Havelock North, New Zealand or TGB-317/315GX; Telenax, Playa del Carmen, Mexico). The unit was glued on the lower back (Figure 3) using a two-component epoxy resin (System Three Resins, Auburn WA, USA) (paper IV). This position was chosen to minimize the drag, but also to allow for obtaining GPS positions while the animal was swimming as the tag was above water level. GPS units recorded GPS positions every 15 min from 1900-0700 h, the beavers' active time, and were set to sleep during the day when beavers were not active (Sharpe and Rosell 2003). Beavers rarely dive for long periods (typically <2 min (Graf et al.

2015)). Hence, diving was unlikely to influence the number of successful GPS fixes, because GPS transmitters attempted to acquire a GPS position for 3 min. The total handling time (from capture to release) for GPS attachment ranged between 20 and 50 min. The total weight of the tags did not exceed 1% of the beaver's body weight. For retrieval, we re-trapped the beavers after two to six weeks, and removed the unit from the fur using a scalpel. GPS units recorded between 4 and 22 days of data (10.3 ± 3.9 days) and from 102 to 816 GPS positions.

3.5 Ethical statement

All trapping and handling procedures were approved by the Norwegian Experimental Animal Board (FOTS id 742, id 2170, 2579, 4384, 6282, 8687) and the Norwegian Directorate for Nature Management (2008/14367 ART-VI-ID, archive code 444.5, 446.15/3, 14415), which also granted permission to conduct fieldwork in our study area. Our study met the guidelines of the American Society of Mammalogists (Sikes 2016). None of the captured beavers were injured during capture and handling, and all were successfully released at the site of capture after handling (Figure 3). No subsequent long-term effects of capture and tagging were observed.

Figure 3: Images showing the search for beavers with spotlights (top left, © Rolf Øhman), a beaver with a GPS tag on its back (top right), a swimming beaver with a GPS tag (bottom left), and the release of a beaver after handling (bottom right, © Floris Smeets).

3.6 Data preparation

3.6.1 GPS data

For the analyses using GPS data (paper I and IV), we removed the capture night from the analysis to remove possible short-term effects of capture (Graf et al. 2016a). To correct for imprecise locations, we removed GPS positions with a horizontal dilution of precision (HDOP) value > 5 and < 4 available satellites (Lewis et al. 2007). We calculated territory size (paper I, IV, V) based on the river bank length that was extracted from 95% minimum convex polygons (MCP) of individual GPS positions in ArcMap 10.1 (Esri, Redlands, CA, USA), but excluding ETMs, and confirmed territory borders in the field based on scent mounds (Nolet and Rosell

1994). This estimate of territory size was chosen, because beavers spend most of their time close to the shore (on average <20 m), both when being on land and in water (paper IV), making a linear measure the most sensible. Other methods, such as MCP or kernel, would have overestimated territory sizes in meandering stretches of river. An ETM (paper I) was defined when ≥ 1 GPS position was outside an individual's territory and inside a neighboring or distant family groups' territory. For each individual, we counted the number of ETMs, and we calculated the duration and distance of individual ETMs. Further, we counted the number of territories a beaver intruded into during individual ETMs. To analyze spatial movement patterns (paper I and IV), we defined GPS positions as being in water and on land, respectively, in ArcMap 10.1. Probably, we incorrectly assigned a number of GPS positions to land or water, respectively, due to GPS inaccuracy, erroneous maps and varying water levels. However, we assume that this was a systematic error, that is, we wrongly assigned a similar proportion of GPS positions to land and water, respectively. To calculate travel speed (separately for land and water positions), we calculated the direct line distance between consecutive GPS positions, averaged per hour. For each individual, we calculated the average perpendicular distance to the shoreline separately for land and water positions (paper IV). In addition, we investigated relative and absolute patrolling effort in paper IV. Relative patrolling effort was estimated as the time a beaver spent within the territorial borders, defined as the proportion of GPS positions inside the upper (upstream) and lower (downstream) 5% zones of the total territory size. Absolute patrolling effort was defined as how much time a beaver spent at the actual territory borders, which we assumed to be independent of territory size. Absolute border zones were defined as the last 75 m on each side of the river on the upstream and downstream side of each individual territory. This zone was chosen because Rosell et al. (1998) found that the majority of scent mounds were located within 150 m between bordering territories (i.e., 75 m border zone per territory). For both relative and absolute patrolling effort, we only used GPS positions inside water and within two meters from the shoreline on land, because scent marking activity is limited to close proximity to water and because positions further inland most likely are foraging sites (Rosell and Nolet 1997).

3.6.2 Demographic data

For paper II and V, we defined the status of an individual as a disperser, if it left its natal family group and never returned, and as a successful disperser if it established itself in a new territory as dominant individual. If an individual was last observed in the natal family group during the first 6 months of the year, its dispersal age was assigned to that respective year, and to the next year if it was last observed in the natal family group in the latter 6 months of a year, because of the low dispersal probability in the second half of the year (beavers mainly disperse between March and June (Sun et al. 2000)). We categorized 1-3 year old beavers as normal dispersers and ≥4 year olds as delayed dispersers.

Individuals were defined as philopatric when they remained in their natal family group and established themselves as dominant individual after the disappearance of their parents. Beavers that disappeared from their natal family, but were never observed again, were defined as unknown fate individuals (paper II). The duration of territory occupancy (DTO) was defined as the total number of years a dominant individual occupied a territory (paper V). The end of territory occupancy was verified either by the death of the individual or via the presence of a new dominant beaver of the same sex in the territory.

For paper III, we defined mate change as when one of the dominant individuals (hereafter the replaced) was no longer observed in the territory or was found dead and another individual of the same sex (the successor) had obtained the dominant breeding position together with the remaining individual (the resident). We defined the timing of mate change as the year *t* when the replaced was last observed in its territory and the start of the new pair bond between the successor and the resident in the year when the successor was first observed.

3.7 Statistical analyses

In paper I, we analyzed the factors affecting extraterritorial movements (ETM). We analyzed the number of ETMs, differences of the time spent on land and travel speed between ITMs and ETMs, and the distance moved, duration, and number of intruded territories during individual ETMs. Independent variables for these analyses included sex, age, status (dominant versus subordinate), season (spring versus fall), and home territory size. In paper II, we investigated the timing of dispersal and the variation in dispersal age. Independent variables were age, family group size, population density, parental age, parental replacement, sex and status. In paper III, we investigated mate change by testing four hypothesis, namely the 'incompatibility' hypothesis, the 'better option' hypothesis, the 'forced divorce' hypothesis, and the 'obligate mate change' hypothesis. In paper IV, we investigated spatial movement patterns separately for land (average distance from the shoreline, time spent on land, and travel speed) and water (travel speed, relative patrolling effort, and absolute patrolling effort). Independent variables were territory size, resource availability, number of neighbors, season, and individual age. For paper V, we investigated the factors affecting the duration of territory occupancy and lifetime reproductive success. Independent variables were dispersal age, territory size, resource availability, and population density.

Where required, we log-transformed variables to satisfy the assumptions of normality and variance homogeneity. We used generalized linear models (GLM) with different distributions (normal, Bernoulli, binomial, or poisson) depending on the data for analyses with one observation per individual. For analyses including multiple observations of individuals, we used generalized linear mixed models (GLMM), and included the beaver ID as random effect. For all analyses, we used a set of candidate models to find the most parsimonious model. Model selection was based on Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham et al. 2011). In papers I, II and V, we performed model averaging if ΔAIC_c was < 4 in two or more of the most parsimonious models (Anderson 2008). Parameters that included zero within their 95% CI were considered uninformative (Arnold 2010). All statistical analyses were performed in R 3.2.1 (R Development Core Team 2015).

4 Results and discussion

Pre-dispersal movements and the timing of dispersal (paper I and II)

We investigated ETMs in 54 GPS-tagged beavers, and found that they spent between 0.00 and 10.63% of their active time on ETMs. Individuals conducted between zero and five ETMs during the GPS sampling period. When conducting ETMs, subordinate individuals (n = 10) intruded into more territories and moved greater distances compared to dominant territory holders (n = 46), suggesting that the purpose of these movements was to gain pre-dispersal information, e.g. concerning population density and vacant territories. Other mammal (Messier 1985, Doolan and Macdonald 1996) and bird (Kesler et al. 2007) species also conduct pre-dispersal ETMs to gain information on territory occupancy, mate availability, and habitat quality.

We then investigated the onset of dispersal in 39 beavers. In general, the dispersal age ranged between 1 and 7 years; 23 beavers (59%) were normal dispersers (1–3 years old) and 16 (41%) delayed dispersal (4–7 years old). We found that individuals were more likely to disperse with increasing age and decreasing population density. Individuals that dispersed at an older age had a greater body mass compared to younger dispersers, which likely gave them a competitive advantage in order to successfully take over or establish a new territory (Sun et al. 2000). Our findings are in line with the maturation hypothesis, which states that an individual should await physical and behavioral maturity before acquiring a territory (Weimerskirch 1992, Piper et al. 2015). The result that the onset of dispersal was related to population density suggests that subordinates can perceive changes in the population density. ETMs are likely to be the mechanism allowing subordinates to detect such changes before dispersal (Hartman 1997, Havens 2006).

Further, the variation in dispersal age was best explained by the parental age, that is, individuals dispersed later when their parent of the same sex was older (Figure 4). In paper IV, we found that dominant individuals changed their behavior with increasing age (they spend more time on land), indicating senescence or possibly increased experience. In effect, senescing territory holders might be more tolerant towards philopatric offspring, allowing them to queue in the natal territory to increase their competitive ability before dispersal (Ekman et al. 2001). Further, subordinates were shown to contribute towards the territorial defense (Tinnesand et al. 2013) and the provisioning of the kits before they emerge from the lodge (Müller-Schwarze and Sun 2003), which could be an important help for their senescing parents and an experience gain for the subordinates. Alternatively, subordinates might detect parental senescence and hence, queue to take over the natal territory.

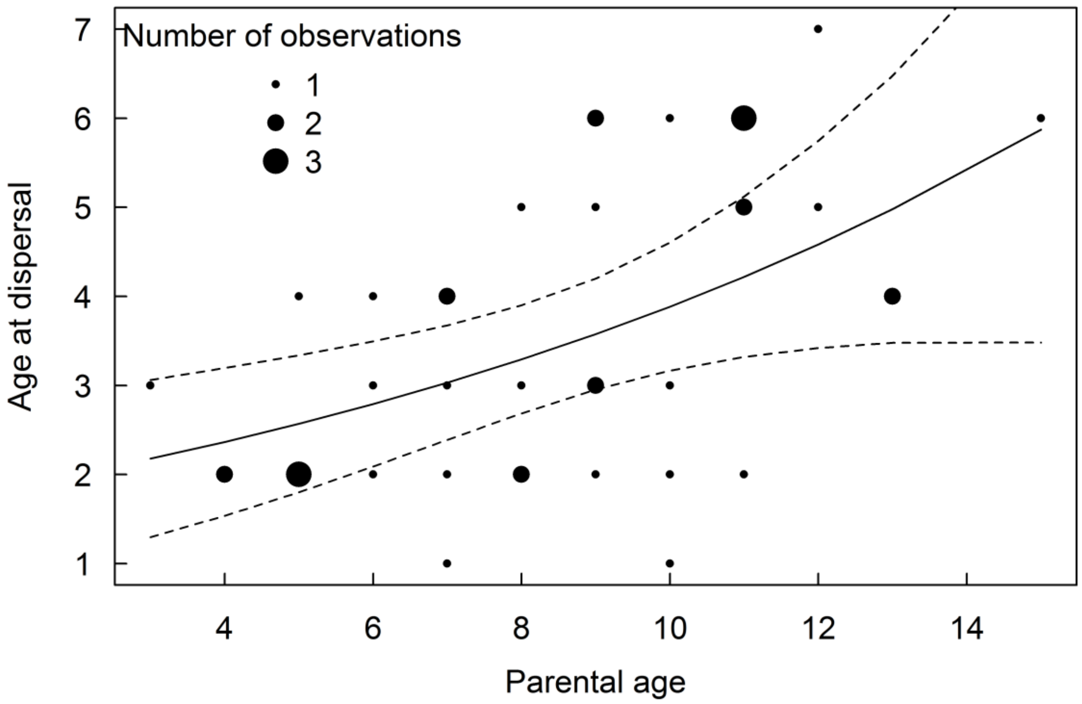

Figure 4: Predicted relationship (solid line) between the age of the parent (of the same sex) and the dispersal age of 37 dispersing Eurasian beavers from data collected between 1998 and 2015 in southeast Norway. Dashed lines present the upper and lower 95% confidence intervals, and dot sizes indicate the number of observations.

Individuals of unknown fate (n = 75) were significantly younger at the time of disappearance compared to known dispersers (2.1 ± 1.4 versus 3.5 ± 1.6 years), and they were more likely to disappear with increasing age and when a parental replacement occurred. Hence, (younger) unknown-fate individuals might have been forced to disperse by a new dominant incomer, as shown in lions (*Panthera leo*) (Pusey and Packer 1987) and white-faced capuchins (*Cebus* *capucinus*) (Jack and Fedigan 2004). Expelled subordinates might have died during the dispersal process or they might have established in an area with a lower population density outside our study area where competition is reduced.

Mate change (paper III)

Between 1998 and 2014, we observed 62 beaver pairs consisting of 101 dominant individuals in 30 territories. Forty-four partnerships were terminated at this time. The partnership ended in a mate change for 25 pairs, 19 pairs were still together at the end of the study, both members of the pair were replaced by a new dominant pair in 11 cases, and 7 cases were uncertain due to incomplete information.

The occurrence of a mate change was not related to the annual reproductive success, the age difference within pairs or the pair bond length, but was best explained by the intercept alone model (n = 26 pairs, 154 pair years). Further, the annual reproductive success decreased with increasing age of the resident, but was independent from the mate order, the age difference between the original and the new pair, the pair bond length and the sex of the resident (n = 19 mate changes, 38 pairs, 166 pair years). This suggests that mate change was not caused by divorce, that is, the adaptive ‘incompatibility’ and ‘better option’ hypotheses.

Year-round territorial species by definition exhibit a strong site fidelity, and the benefits of holding a territory are expected to exceed the costs of being paired with a low-quality mate (Morton et al. 2000). Saturated populations like ours with very few available territories intensify the competition for territories, suggesting that deserting a territory would be very costly for a dominant individual (Lardy et al. 2011). Hence, we consider it unlikely that a one or both members of the pair initiated the partner change and left its territory. Another reason making adaptive mate change unlikely in our population, is that the genetic variation between individuals is very small (Ellegren et al. 1993, Durka et al. 2005), and generally, the reproductive success in our population is lower as compared to German and Russian beaver populations with greater genetic diversity (Heidecke 1984, Saveljev and Milishnikov 2002, Halley 2011). Thus, reproductive benefits achieved by a mate change might be low due to genetic causes.

Replaced individuals were significantly older than successors in the year the mate change occurred (10.21 ± 2.70 vs. 6.00 ± 3.43 years, $n = 20$, $p < 0.001$), but there was no significant difference in body mass (replaced = 21.43 ± 2.52 kg vs. successor = 19.44 ± 3.35 kg, $n = 11$ mate changes, $p = 0.240$). This suggests, together with the finding that the reproductive success was independent of the mate order, that mate change is non-adaptive, i.e., not initiated by a member of the mated pair, but rather by the intrusion of a younger, incoming individual of similar body mass as suggested by the ‘forced divorce’ hypothesis (Lardy et al. 2011). In our study population, body mass gain levelled off at around age six in both sexes and decreased in males around age eight (but not in females), indicating senescence (replaced individuals were on average ten years old). Further, in paper IV we could show that older individuals spent more time on land, which also indicates senescence. In male crab spiders (*Misumena vatia*) of similar body mass, young individuals were more successful in encounters than old ones (Hu and Morse 2004), and middle aged male song sparrows (*Melospiza melodia*) were more successful in expanding and regaining territories compared to younger or older individuals (Arcese 1989). This suggests that competitive ability decreases with increasing age after a certain point, resulting in competitive advantages for incoming younger individuals. Finally, hunting and car accidents were the cause of death for 20% of the replaced individuals leading to an accidental mate change, i.e., the ‘obligate mate change’ hypothesis.

Spatial movement patterns in the established territory (paper I and IV)

We investigated intra-territorial spatial movement patterns of 25 territory-holding dominant beavers (paper IV). Spatial movement patterns in water were related to the territory size with individuals in larger territories travelling faster (Figure 5a) and spending more time in the up- and downstream 5% border zones compared to smaller territories. This suggests that beavers in larger territories face higher patrolling costs for three reasons: swimming has been shown to decrease the body temperature compared to being on land, especially during winter and early spring (Nolet and Rosell 1994), an increased patrolling effort constrains the time that an animal can spend foraging (Amsler 2010), and faster spatial movements entail energetic costs (Halsey et al. 2008). Further, older individuals spend more time on land and in the absolute border zones, that is, the up- and downstream 75 m of the territory, compared to younger individuals. Spending more time at territory borders may allow beavers to spend more time on land instead of swimming between up- and downstream borders, that is, patrolling via presence. The change in spatial movement patterns with age could be either explained by increased individual experience over the time of territory occupancy or senescence. We now compiled more evidence that beavers start to senesce after age 8, because males lose body mass then (paper III), and because the reproductive success of individuals decreases with increasing age (paper III and V).

When on land, beavers stayed on average 16 ± 8 m from the shore. In smaller territories, individuals were further from the water compared to larger territories (Figure 5b). Travelling on land is considered to be costly due to increased energetic demands and time constrains (Belovsky 1984, Haarberg and Rosell 2006), and an increased predation risk (Basey and Jenkins 1995). This suggests resource depletion in smaller territories, in effect forcing beavers to forage further from the shore (Goryainova et al. 2014). In addition, beavers travelled faster on land in spring compared to fall. This could be a strategy to compensate for body mass loss after the winter by foraging in high-quality food patches that possibly lie further apart from each other. For example, NA beavers were shown to forage on different plant species in different seasons (Svendsen 1980, Milligan and Humphries 2010), which may lead to different spatial movement patterns throughout the year. In conclusion, we found a trade-of concerning the size of the established territory, with beavers in smaller territories trading-off reduced costs of travelling and patrolling with increased foraging costs.

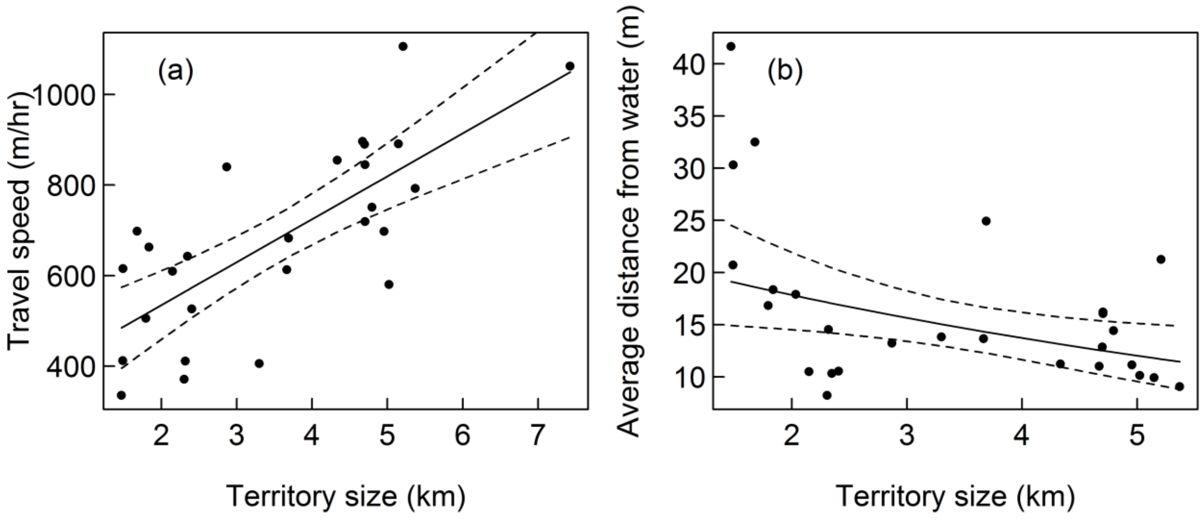

Figure 5: Predicted relationship (solid line) between (a) the territory size and the average travel speed in water (m/h), and (b) the territory size and the average distance from the shoreline for GPS positions on land for 25 GPS tagged beavers in southeast Norway. Dashed lines present the upper and lower 95% confidence intervals.

We then examined ETMs (paper I). The number of ETMs was related to an individual's territory size, and beavers in smaller territories conducted more ETMs compared to individuals in larger territories. Possibly, individuals in smaller territories assessed opportunities for territory expansion, because they did not have sufficient food resources as indicated in paper IV, where we found that beavers in smaller territories forage further from the shore. Gosling and McKay (1990) showed that male house mice (*Mus domesticus*) delayed fighting if scent between opponents matched, indicating that scent marking is used for competitor assessment (Gosling and McKay 1990). Consequently, ETMs could provide an additional mechanism to assess neighbors and to decrease the costs of territory defense, e.g. physical disputes (Crawford et al. 2015). Compared to ITMs, we found that beavers spent less time on land and travelled faster when conducting ETMs. Faster spatial movements are associated with reduced vigilance to detect predators (McAdam and Kramer 1998) or conspecifics (Christensen et al. 2016), and entail energetic costs (Halsey et al. 2008). The low proportion of ETMs conducted (on average < 2% of an individuals' activity time) and the little time spent on land during ETMs (compared to ITMs) also indicate that ETMs could be costly, e.g., being detected by a conspecific and risking a physical dispute (Crawford et al. 2015).

The duration of territory occupancy and lifetime reproductive success (paper V)

We obtained data of 25 individuals from 16 different territories with known and finished duration of territory occupancy (DTO). Two individuals remained philopatric and established as dominant individual after the disappearance of their parents. The DTO ranged from 1-11 years (mean ± SD: 6.2 ± 2.8 years). Individuals that dispersed at an older age and established in an intermediate-sized territory occupied their territory longer than younger dispersers and individuals that established in smaller or larger territories (Figure 6). Populations at carrying capacity likely exert a strong selection on the competitive ability of dispersers that try to acquire and defend a territory. Delayed dispersers had a greater body mass at the time of dispersal, which likely resulted in such an advantage compared to younger dispersers (Ekman et al. 1999). Generally, beavers in our study area reach their maximum body mass around age six (paper II). Thus, individuals establishing at younger ages were probably more likely to lose their territory to larger intruders before reaching their maximum body mass. Apart from a body mass gain, delayed dispersers might gain parenting experience via helper behavior (Cockburn 1998), e.g. by provisioning kits with food before they emerge from the lodge (Müller-Schwarze and Sun 2003) and territorial defense (Wilsson 1971, Tinnesand et al. 2013). Our results support the maturation hypothesis stating that an animal should await physical and behavioral maturity before the acquisition of a territory (Weimerskirch 1992, Piper et al. 2015). The finding that the DTO was longer in intermediate territories suggests that they follow the optimization criterion (Adams 2001), ensuring sufficient resource availability and decreased costs of territorial defense at the same time.

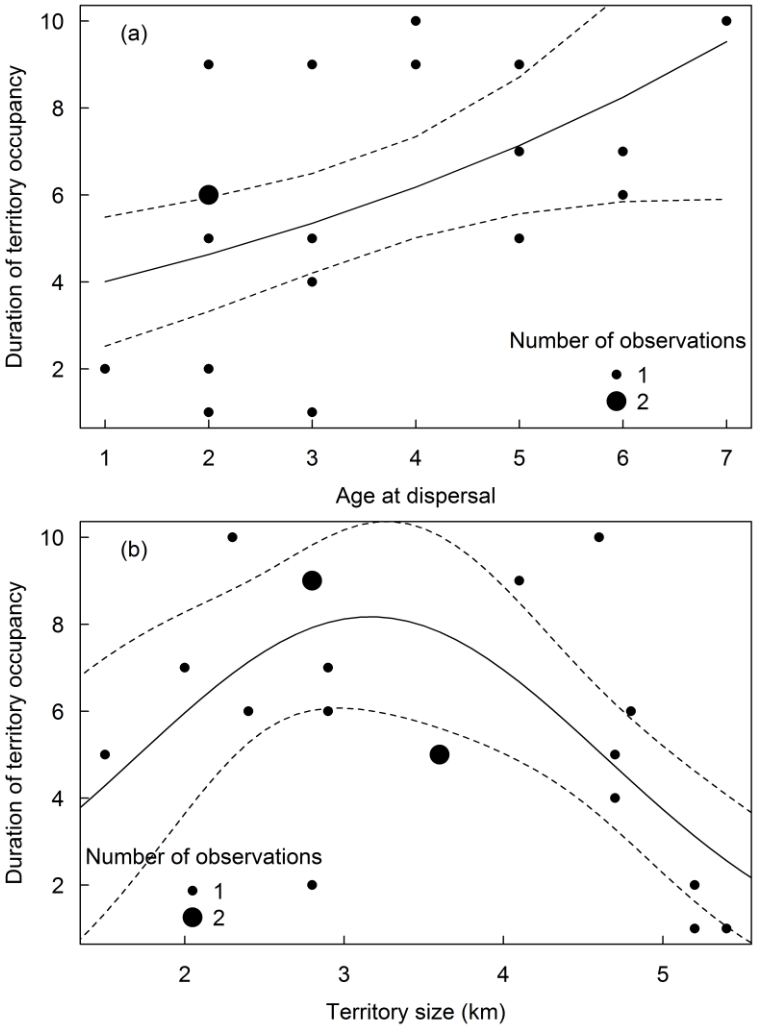

Figure 6: The predicted relationship (solid line) between (a) the age at dispersal (in years) and the duration of territory occupancy (DTO, in years), and (b) the territory size and DTO for 19 Eurasian beavers in southeast Norway. Dashed lines present the upper and lower 95% confidence intervals.

The annual reproductive success of territory holders ranged from zero to four kits (0.63 ± 0.97) and decreased with the age, that is, older individuals produced fewer kits suggesting senescence. Individuals that dispersed at an older age were also older when reproducing for the first time. Importantly, there was a general positive relationship between an individual's DTO and lifetime reproductive success (LRS), although LRS leveled off in individuals that held a territory for more than 9 years. We could show that the costs of an older age at first reproduction were offset by an increased DTO in delayed dispersers, resulting in a greater LRS. Similarly, delayed dispersal led to an increased LRS in male Siberian jays (*Perisoreus infaustus*) (Ekman et al. 1999), and an increased probability of reproduction in male red wolves (*Canis rufus*) (Sparkman et al. 2010).

5 Conclusions and future perspectives

This thesis investigated life history strategies of the Eurasian beaver and sheds light on the mechanisms affecting the onset of dispersal, mate change, spatial movement patterns, and duration of territory occupancy. We found that beavers in our high-density study population dispersed later compared to other beaver populations (Hartman 1997, Sun et al. 2000, McNew and Woolf 2005), with some individuals remaining in the natal family group until age 7. Also, subordinates dispersed at an older age with increasing age of their same-sex parent. Older parents might be more tolerant towards their offspring, or alternatively, subordinates might detect senescence and thus await the disappearance of their parents. Further, subordinates were more likely to disperse with increasing age, a measure of competitive ability, and with decreasing population density. The fact that dispersal onset was more likely at lower population densities suggests that individuals can perceive fluctuations in population density. We found that subordinates carried out longer ETMs compared to dominant individuals, and intruded into more territories, which likely is the mechanism how they detect changes in population densities. The question arises whether pre-dispersal ETMs increase the chances for subordinate individuals to successfully establish a territory and consequently, affect their DTO and LRS. For example, in northern wheatears (*Oenanthe oenanthe*), a seasonally territorial bird, individuals that established territories at their previous year's prospecting sites, had a higher reproductive success compared to other individuals of the same age (Pärt et al. 2011), demonstrating that familiarity with an area can be advantageous. Further, in roe deer (*Capreolus capreolus*) individuals that conducted pre-dispersal ETMs were more likely to disperse compared to individuals that did not conduct ETMs. In addition, individuals were more likely to disperse in the direction in which they conducted the majority of their pre-dispersal forays (Debeffe et al. 2013). This suggests that dispersal is facilitated by pre-dispersal ETMs. Future studies in beavers should investigate the success of establishment and reproductive success in relation to pre-dispersal ETMs.

The observed movement patterns during ETMs (higher travel speed and more time spent in water compared to ITMs) suggest that ETMs are costly and stressful. In general, it would be interesting to investigate the role of stress in beavers in more detail. We routinely collect fecal samples during fieldwork, which would enable us to analyze fecal steroid hormone metabolites for a very large sample of individuals over long periods of time. We could use such corticosterone analyses to investigate stress levels during ETMs, as shown in meerkats (*Suricata suricatta*) (Young and Monfort 2009). However, this method could have a much greater applicability, such as to investigate the stress-related suppression hypothesis, which predicts that dominant females suppress subordinate reproduction by inducing chronic physiological stress (Young et al. 2006). Further, we could compare corticosterone levels of floaters compared to subordinates that are still in their natal family group, to increase our understanding of dispersal decisions and the costs of solitary living in highly social animals. More generally, we could compare stress levels between different demographic groups (dominants versus subordinates, young versus old individuals, males versus females) to study the effects of stress on the fitness of individuals and ultimately, the role of stress on population dynamics in long-lived monogamous species.

Because the population was considered saturated, with territories directly bordering each other and no unoccupied areas, there was factually no possibility for subordinate individuals to establish a new territory that had not been occupied previously within our study area. Thus, subordinates had three options to acquire a territory. 1) They could remain within the natal family group to await the disappearance of their parents in order to take over the natal territory, or until a dominant individual in the surrounding territories disappeared due to an accident ('obligate mate change' hypothesis). 2) They could disperse and challenge a territory owner to take over its territory, i.e., the 'forced divorce' hypothesis. Or 3) they could disperse into lower density areas (outside our study area) to acquire a territory that had not been occupied previously. We found evidence for both the 'obligate mate change' and the 'forced divorce' hypotheses, and rejected the adaptive 'obligate mate change' and 'incompatibility' hypotheses, because it is unlikely that an individual initiated a divorce that would cause the loss of its territory, being the limiting factor in our saturated study area. However, it could be possible that an individual of the mated pair 'forces' a divorce with its current mate in order to get access to a better quality mate. We could not address the third possibility of territory acquisition (dispersing outside our study area), because we could not distinguish between mortality and dispersal for individuals of unknown fate. To resolve this issue, we would have to increase the sampling duration of our GPS tags substantially. GPS units that are glued on the lower back usually fall off after one month, often even earlier in spring when beavers are molting their guard hair (unpubl. results). Therefore, we are planning to change the GPS attachment method. New GPS tags will be attached at the base of a beaver's tail using an elastic rubber band. That way GPS tags should remain attached for a long period of time (months or years rather than weeks) without impeding the tagged individual physically or behaviorally. We consider this method less invasive than the currently used gluing method, because the beavers do not lose any guard hair with the new method. For a study investigating long-distance dispersal, GPS units could be programmed to take one or two positions per day, thereby considerably increasing the sampling duration.

GPS technology enabled us to obtain fine-scale spatial data without introducing an observer bias. We could show that also dominant individuals conduct ETMs, possibly to assess possibilities for territory expansion. Further, we found that territory size and individual age affected spatial movement patterns. Beavers in smaller territories had lower costs of patrolling, but foraged further from the shore, possibly due to resource depletion. We showed that spatial movement patterns changed with individual age, with older individuals spending more time on land and at territory borders. This change might be induced by senescence or increased experience, or both. Although, GPS technology enables us to get a better idea of spatial animal movements than ever before, there are technological limitations. For example, we did not obtain exact information on the accuracy of our GPS units. To study the reliability of the GPS units, we conducted a study (manuscript in preparation) investigating the location error, defined as the distance of a GPS position from the true location, of the GPS units in 25 test locations within our study area. Preliminary results suggest that the GPS units had an average location error of 14.14 ± 17.84 m (mean ± SD). The location error increased with increasing HDOP and decreasing number of satellites, and removing GPS positions with HDOP values > 5 and < 4 available satellites (Lewis et al. 2007) improved the location error to 12.58 ± 14.71 m. Nevertheless, this method did not remove the largest outliers stressing the need to develop another method to screen the GPS data for imprecise locations. Further, the location error decreased with increasing vegetation closure and slope.

Another limitation of our study was that resource availability was measured as the area of mixed-deciduous forest based on land cover maps from the year 2014 (Bjørkelo et al. 2014), which only provided a snapshot of the resource availability to that time. Resource availability is a crucial part when looking at the habitat use of animals (Manly et al. 2007, Matthiopoulos et al. 2015), and we included resource availability when investigating spatial movement patterns of dominant beavers (paper IV) and factors affecting the duration of territory occupancy (paper V). Thus, the next step would be to obtain more detailed habitat data. We initiated a project in spring 2017 to map all the riverbanks of our study area, using a drone, and to obtain precise information about resource availability, both on land (proportion of coniferous and deciduous forest, shrub, and other vegetation) and water (aquatic vegetation). This will help our understanding of the role of resource availability on movement patterns, reproductive success, and ultimately, population dynamics. The individual-based, long-term data collection design of the beaver project would further allow for an experimental approach to investigate the influence of environmental stochasticity on the fitness of individuals/family groups. Specifically, we could alter resource availability via food supplementation in some territories over one or multiple seasons to test how environmental stochasticity affects the reproductive success of family groups, and how variation in resource availability shapes the future life history of individuals.

We found that delayed dispersers (that established in intermediate-sized territories) had an increased DTO, leading to a higher LRS. This raises the question whether individuals gain other advantages (apart from an increased body weight) from remaining in the natal family group, such as increased experience with territorial defense and raising of offspring. We therefore conducted a study, investigating the contribution of subordinate family group members towards territorial defense conducting scent experiments, and we tested whether the number of subordinates present in a family group affected the body mass of kits (Hohwieler et al. 2017, in revision). The presence of subordinates had no effect on the body mass of kits, but subordinates reacted towards simulated intruders as expected by their proportion in the family group, suggesting that they learned territorial behaviors and possibly helped with the territory defense. The ultimate reason why individuals in our study area delay dispersal is probably the high population density, however, the proximate reason for remaining in the natal family group for a longer time, might be that individuals gain both physical (body mass) and behavioral (territory defense) advantages.

In paper V, we found that individuals in large territories had a shorter DTO compared to individuals in medium-sized territories, suggesting that territory patrolling is costly. This raises the question how territory holders respond towards intruders. While many studies focus on the strength or mode of the behavioral response, like the inspection or destruction of intruder scent marks (Cross et al. 2014), little research has been conducted on longer-term and spatial responses towards simulated intruders. For example, dwarf mongooses (*Helogale parvula*) decreased their travel speed after a simulated intrusion, possibly due to increased vigilance behavior after the perceived threat (Christensen et al. 2016), and male red foxes (*Vulpes vulpes*) spent more time patrolling in areas with artificial scent mounds suggesting an increased effort to defend their territory (Arnold et al. 2011). We currently investigate the spatial response of beavers (manuscript in preparation) towards a simulated intruder. Rosell and Nolet (1997) suggested that the construction of scent mounds is relatively uncostly. Therefore, the real costs of territorial defense might be an increased patrolling effort, leading to an increased energy expenditure and a reduction in the time spend on foraging, as suggested in paper IV. We conducted a scent experiment in the territories of GPS-tagged beavers, comparing movement patterns of tagged beavers in periods where no simulated intruder was present (control) and periods when we simulated a territory intruder, and to beavers where we did not simulate an intruder. Preliminary results suggest that spatial movement patterns did not change after we had simulated a territorial intruder. Contrary to our predictions, individuals did not spend more time in water, nor did they travel faster in water. This might suggest that beavers patrol territories at their maximum capacity in our saturated population, therefore not allowing for an increase in patrolling activity. Alternatively, the presence of only one simulated intruder might not trigger a visible spatial response in territory owners, as there were presumably real dispersers present in many experiments (which we unfortunately could not measure).

In this thesis, we mainly focused on life history strategies of individuals. However, obligate monogamous mammals live as a pair for most of their life. Consequently, it would be sensible to look at the pair as a unit (what we partly did when looking at mate change). A good start would be to look at spatial movement patterns of the breeding pair within their territory to gain further insight into topics like territoriality, mate guarding and foraging strategies. Since 2015, we generally tried to equip the dominant pair at the same time. However, the sample size was too small to be included in this thesis. Sharpe and Rosell (2003) investigated time budgets of the mated pair and found no differences apart from the result that males spent more time travelling than females. Generally, the cohesiveness between the members of a pair, and especially the underlying spatial movement patterns, have not received much attention. For example, pair partners of klipspringers (*Oreotragus oreotragus*) remain within 5 m throughout their life (Dunbar 1984), and in fork-marked lemurs (*Phaner furcifer*), the cohesiveness of pairs is extremely low even though pairs are stable over several years and their territories overlap almost completely (Schülke and Kappeler 2003).

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Paper I

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Beyond the border: The role of extra-territorial movements in a large, monogamous rodent

Martin Mayer *, [1], Andreas Zedrosser [1, 2], Frank Rosell [1]

[1] Department of Natural Sciences and Environmental Health, University College of Southeast Norway, Bø i Telemark, Norway

[2] Department of Integrative Biology, Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Austria

* Correspondence: M. Mayer, Department of Natural Sciences and Environmental Health, University College of Southeast Norway, 3800 Bø i Telemark, Norway.
Email: martin.mayer@usn.no

Abstract

Territorial animals carry out extra-territorial movements (ETM) to obtain pre-dispersal information or to increase reproductive success via extra-pair copulation. However, little is known about other purposes and spatial movement patterns of ETMs. In this study, we GPS-tagged 54 Eurasian beavers (*Castor fiber*), a year-round territorial, monogamous mammal, during the non-mating season. We investigated ETMs in territory holding breeders (dominants) and non-breeding (subordinate) family members. Twenty of 46 dominant individuals (44%), and 6 of 10 subordinates (60%) conducted ETMs. Generally, beavers spent between 0 and 11% of their active time on ETMs, travelled faster and spend more time in water when on ETMs compared to intra-territorial movements, suggesting that ETMs are energetically costly. Further, beavers in smaller territories conducted more ETMs. Possibly, smaller territories might not have sufficient resources and thus, dominant individuals might conduct ETMs to assess possibilities for territory expansion. Generally, besides territory advertisement (e.g. via scent marking), ETMs might serve as additional mechanism for territory owners to assess neighbours. Subordinates spent more time on ETMs, moved greater distances, and intruded into more territories than dominant individuals did, suggesting that they conduct ETMs as pre-dispersal forays to gain information on the population density and available mates.

Key words. Eurasian beaver, *Castor fiber*, dispersal, GPS, prospecting, territoriality.

Introduction

Animals are territorial when the benefits of holding a territory, i.e. exclusive access to limited resources such as food, mating partners and shelter, exceed the costs of territory defence (Brown 1964). Spatio-temporal movements outside of an animals' or a breeding pairs' territory are defined as extra-territorial movements (ETM) (Bartels 1984, Soulsbury et al. 2011). ETMs are important for ecological processes, such as gene flow (Dugdale et al. 2007, Suter et al. 2007) and dispersal (Young and Monfort 2009), and are common in vertebrates, including fish (Bartels 1984), birds (Naguib et al. 2001, Norris and Stutchbury 2001, Williams and Rabenold 2005), and mammals (Woodroffe et al. 1995, Teichroeb et al. 2011, Debeffe et al. 2014). Generally, three types of ETMs are distinguished: 1) ETMs by adults seeking extra-pair copulations (EPC) (White et al. 2000, Iossa et al. 2008, Debeffe et al. 2014). This type of ETM relies on information about neighbours (Naguib et al. 2004) and habitat structure (Norris and Stutchbury 2001), and is usually limited to the reproductive season (Kesler et al. 2007). 2) ETMs by subordinate individuals (non-breeders) to gain experience and information about dispersal opportunities (Messier 1985, Doolan and Macdonald 1996, Kesler et al. 2007, Debeffe et al. 2013). 3) ETMs to increase foraging success. For example, wolves (*Canis lupus*) conducted ETMs during periods of low food availability (Messier 1985), and feral cats (*Felis catus*) in Australia carried out ETMs into recently burned areas, probably providing them with foraging opportunities due to the availability of vulnerable prey (McGregor et al. 2016). However, apart from gaining foraging opportunities, little is known about the role of ETMs of year-round territory holders outside of the mating season, and especially about the movement patterns during ETMs in general (e.g. Soulsbury et al. 2011).

The frequency of ETMs can vary with demographic parameters. In birds, ETMs are often skewed towards males (Yezerinac et al. 1995, Norris and Stutchbury 2001), and in song sparrows (*Spizella pusilla*) and reed buntings (*Emberiza schoeniclus*) older males conducted more ETMs than younger ones (Kleven et al. 2006, Celis-Murillo et al. 2017). Because ETMs generally have other purposes than intra-territorial movements (ITM), e.g. prospecting for EPC, their movement patterns can also differ. For example, dispersing red foxes (*Vulpes vulpes*) moved faster and straighter when outside of their own territory and avoided contact with territorial adults; and adult territory owners often intruded into neighbouring core areas during ETMs (Soulsbury et al. 2011).

In this study, we investigated ETMs outside the mating season in a large, monogamous, semi-aquatic rodent, the Eurasian beaver (*Castor fiber*). Both the Eurasian beaver (hereafter beaver) and the North American beaver (*C. canadensis*; hereafter NA beaver) are nocturnal, live in family groups, and have a very similar ecology (Wilsson 1971, Müller-Schwarze and Sun 2003). They are highly territorial and defend territories year-round against conspecifics (Rosell et al. 1998). Territory occupancy is advertised at the territory borders via scent marking (Rosell et al. 1998). Mating in both species takes place in January and February (Wilsson 1971). EPC have been recorded in a NA beaver population (Crawford et al. 2008), suggesting that ETMs occur during the mating season, whereas there is little evidence for EPC in Eurasian beavers (Syrůčková et al. 2015, Tinnesand 2017). Non-breeding family members of ≥ 1 year old (hereafter subordinates) typically disperse at age 1.5 (Hartman 1997) to 3.5 years old (Mayer et al. 2017b), but can delay dispersal up to age 7 (Mayer et al. 2017b). An increased age at dispersal has been related to high population densities (Hodgdon and Lancia 1983, Hartman 1997), and Mayer et al. (2017b) suggested that individuals can perceive changes in population density before initiating dispersal. ETMs may be the mechanism to evaluate population density levels, and there is evidence for pre-dispersal ETMs in beavers. For example, 3 of 8 subordinates made ETMs before dispersal in a NA beaver population (Havens 2006), and 3 of 9 subordinates carried out pre-dispersal forays ranging between 1.5 and 15 km in a Swedish beaver population (Hartman 1997). However, to our knowledge there is no information available about ETMs of territory-holding breeders (hereafter dominants) or movement patterns during ETMs in general.

Here we investigated patterns of ETMs conducted by dominant and subordinate beavers during the non-mating season in a beaver population in southeast Norway (we could not investigate ETMs during the mating season in winter, due to difficulties in observing and attaching GPSs to beavers at this time of the year). We hypothesized that patterns of ETMs are related to an individuals' social status. We predicted a) that dominant territory owners would conduct ETMs only into adjacent neighbouring territories to assess the potential of territory expansion, and b) that subordinates would conduct more and longer ETMs compared to dominants to gain pre-dispersal information. Further, we hypothesized that movement patterns would differ between ITMs and ETMs, and c) predicted that individuals would travel at a greater speed and spend less time on land during ETMs compared to ITMs.

Material and methods

Study area and data collection

Our study area was located in Telemark county, southeast Norway (Figure 1), and consisted of 3 rivers (Sauar, Straumen and Gvarv) (Herr and Rosell 2004). The population was at carrying capacity and territories directly bordered each other (Campbell et al. 2005, Graf et al. 2016b). Beavers were captured every year since 1998 in spring (March-June) and autumn (August-November), individually marked with a microchip and ear tags (Rosell and Hovde 2001, Sharpe and Rosell 2003), and assigned a social status (dominant, subordinate, kit) (Campbell et al. 2012). Individuals that were captured for the first time as kit or one-year old could be assigned an exact age based on their body mass (Rosell et al. 2010). Older individuals were assigned a minimum age of 2 years old when captured for the first time with a body mass ≥17 kg and ≤19.5 kg, and a minimum age of 3 years old with a body mass >19.5 kg (Rosell et al. 2010).
From 2009-2016, we equipped 54 individual beavers (15 individuals were tagged multiple times) with a unit consisting of a VHF transmitter (Reptile glue-on, series R1910; Advanced Telemetry Systems, Isanti MN, USA) and a GPS receiver (model G1G 134A; Sir-track, Havelock North, New Zealand or TGB-317/315GX; Telenax, Playa del Carmen, Mexico). The unit was glued on the lower back (Figure 1) using a two-component epoxy resin (System Three Resins, Auburn WA, USA) (Graf et al. 2016b). GPS units recorded GPS positions every 15 min from 1900-0700 h, the beavers' active time, and were set to sleep during the day when beavers were not active (Sharpe and Rosell 2003). GPS units recorded between 4 and 22 days of data (mean ± SD: 10.3 ± 3.9 days) and between 102 and 816 GPS positions.

Ethical note

All trapping and handling procedures were approved by the Norwegian Experimental Animal Board (FOTS id 742, id 2170, 2579, 4384, 6282, 8687) and the Norwegian Directorate for Nature Management (2008/14367 ART-VI-ID, archive code 444.5, 446.15/3, 14415), which also granted permission to conduct fieldwork in our study area. Our study met the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching (ASAB/ABS, 2016). We captured a total of 54 individuals for this study. None of these individuals were injured during capture and handling, and all were successfully released at the site of capture after handling. No subsequent long-term effects of capture and tagging were observed.

Data preparation

The capture night was excluded from the analysis to remove possible effects of capture (Graf et al. 2016a). To correct for imprecise locations, we removed GPS positions with a horizontal dilution of precision (HDOP) value > 5 and < 4 available satellites (2,537 (10.1%) of 25,000 positions) (Lewis et al. 2007). We calculated individual territory sizes as river bank length (in km) that was extracted from 95% minimum convex polygons (MCP) of individual GPS positions in ArcMap 10.1 (Esri, Redlands, CA, USA) (Graf et al. 2016b), but excluding ETMs as their inclusion would have resulted in a large overestimation of the territory size in some cases. We confirmed territory borders in the field based on the presence of scent mounds (Nolet and Rosell 1994). Bank length was chosen as measure of territory size, because beavers typically stay close to the shoreline (both when being on land and in water), and because other methods, like MCP or kernel, could have resulted in an overestimation of territory size due to the inclusion of unused habitat in meandering rivers (Graf et al. 2016b). An ETM was defined as ≥ 1 GPS position outside of an individual's territory, if the GPS position(s) was/were 1) > 100 m from the individuals' territory border to account for possible territory overlap as found by Nolet and Rosell (1994) and for GPS inaccuracy, and 2) inside a neighbouring or distant family groups' territory, which was also known from GPS data and from personal observations. Hence, if a GPS position was outside the 95% MCP, but within 100 m from the territory border and not inside a neighbour's territory it was not assigned as ETM. For each individual, we counted the number of ETMs, and we calculated the ETM frequency as the number of ETMs per week. The duration of individual ETMs was defined from the first to the last consecutive GPS position outside the beavers' territory. The distance moved (in m) during individual ETMs was calculated as straight line distance between consecutive ETM-GPS positions plus adding the distance between the territory border and the first and last ETM-GPS position, respectively. Further, we counted the number of territories a beaver intruded into during individual ETMs as measure for intruder extent. We defined GPS positions as being in water and on land, respectively, in ArcMap 10.1. Possibly, we wrongly assigned a number of GPS positions to land or water, respectively, due to GPS inaccuracy, erroneous maps and varying water levels. We assume that this was a systematic error, i.e., we erroneously assigned the same proportion of GPS positions to land and water, respectively. To calculate travel speed, we calculated the direct line distance between consecutive GPS positions per hour (Graf et al. 2016b). There were too few consecutive GPS positions during ETMs to calculate the travel speed separately for land and water positions (to investigate differences between land and water), however this calculation was possible for ITMs, because beavers travel faster in water compared to land (Graf et al. 2016b).

Statistical analysis

We investigated the number of ETMs conducted during the GPS sampling period (dependent variable, n = 54 individuals) using zero-inflated mixed models with a negative-binomial distribution and a logit link using the R package glmmADMB (Bolker et al. 2012) to account for zero-inflation and overdispersion of the count data. Independent variables were sex, (minimum) age, status (dominant versus subordinate), season (spring versus autumn), the territory size, the total number of GPS positions (to account for different GPS sampling durations). No interactions were included to avoid overfitting the model. The beaver ID was included as random effect to control for multiple observations.

To investigate if movement patterns differed between ETMs and ITMs, we conducted 2 separate analyses investigating 1) the proportion of time spent in water, i.e., water versus land GPS positions (1 = in water, 0 = on land) using a generalized linear mixed model (GLMM) with Bernoulli distribution and a logit link, and 2) the travel speed using a linear mixed model (LMM) with a Gaussian distribution and an identity link. In both analyses, the beaver ID was included as random effect, and fixed effects were the movement type (ITM versus ETM), sex, age, status, season, and territory size (no interactions were included to avoid overfitting the models, n = 27 beavers).

To examine individual ETMs, we conducted 3 separate analyses investigating 1) the distance moved during individual ETMs using a LMM with a Gaussian distribution and an identity link, 2) the duration of individual ETMs using a LMM with an identity link, and 3) the number of intruded territories during individual ETMs using a GLMM with a Poisson distribution and a log link. Independent variables in all analyses were sex, age, status, season, territory size, and the beaver ID as random effect (no interactions were included to avoid overfitting the models). During the study period, we additionally conducted scent experiments, simulating a territorial intruder via experimental scent mounds (Hohwieler et al. 2017, in revision), in the territories of 30 GPS tagged beavers included in the present study. Initially, we included the scent experiment (simulated intruder present versus absent) as independent variable, but did not find an effect in any analysis, and thus excluded it from the main analyses to avoid overfitting the models.

For all analyses, we used a set of candidate models including all possible combinations of the fixed effects. We found no collinearity among independent variables ($r < 0.6$ in all cases), and variance inflation factors were < 3 (Zuur et al. 2010). Model selection was based on Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham et al. 2011), and was carried out using the R package MuMIn (Barton 2013). If ΔAIC_c was < 4 in two or more of the most parsimonious models, we performed model averaging (Anderson 2008). Parameters that included zero within their 95% CI were considered uninformative (Arnold 2010). All statistical analyses were performed in R 3.2.1 (R Core Team 2015).

Results

We GPS tagged a total of 54 individuals: 46 dominant individuals consisting of 23 females (7 were tagged multiple times) and 24 males (6 were tagged multiple times), and 10 subordinate (4 females and 6 males) beavers. Two individuals were trapped first as subordinate and then as dominant individual. Of the 54 GPS tagged individuals, 25 (46.3%) carried out ETMs; 20 of 46 (43.5%) dominant beavers carried out ETMs, and 6 of 10 (60%) subordinates conducted ETMs. Beavers spent between 0.00 and 10.63% of their active time on ETMs (mean ± SD: 1.47 ± 2.76%, median: 0%). They carried out between zero and five ETMs during the GPS sampling period (mean ± SD: 0.71 ± 1.22 ETMs, median: 0); on average 0.59 ± 0.97 ETMs (median: 0, range: 0-4.4) per week. The number of ETMs was best explained by the territory size (Table 1, S1) with individuals in smaller territories conducting more ETMs compared to larger ones (Figure 2).

Differences between ETMs and ITMs

Movement patterns differed between ITMs and ETMs (Table 2, S1). Beavers spent a larger proportion of time in water when conducting ETMs compared to ITMs (Figure 3a) and during spring compared to autumn (Table 2). Because beavers spend more time in water when on ETMs, we calculated travel speed for ITMs only from consecutive water positions, because beavers travel faster in water (Graf et al. 2016b). Beavers travelled considerably faster during ETMs compared to ITMs (Table 2), both when travel speed of ITMs was calculated from water GPS positions only (Figure 3b) or from all GPS positions (Table S1). Additionally, beavers travelled at a greater speed in larger territories, and dominant individuals travelled faster than subordinates (Table 2).

Individual ETMs

We observed 51 individual ETMs (43 ETMs by 20 dominant individuals and 8 ETMs by 6 subordinates) that ranged between 0.25 and 8.75 hrs (mean ± SD: 1.63 ± 1.62 hrs, median: 1 hr) of an individuals' active time (between 1900 and 0700 h). Four individuals (2 dominant females and 2 subordinate males) conducted ETMs that lasted longer than one night, i.e., they spanned over two activity periods (i.e., they spent the daytime away from their own territory). In total (including daytime), these ETMs lasted between 14.50 and 20.25 hrs (mean ± SD: 16.69 ± 2.61 hrs).

The distance moved on individual ETMs ranged between 298 and 11,237 m (mean ± SD: 2278.80 ± 2212.62 m, median: 1349.07 m), and beavers intruded into 1-5 different territories while conducting ETMs (mean ± SD: 1.61 ± 1.04, median: 1). The distance moved, duration, and number of intruded territories during individual ETMs were highly correlated with each other ($r > 0.75$, $p < 0.001$), and were best explained by the status of an individual (Table 3, S2). Subordinates moved greater distances during ETMs compared to dominant individuals (4756.33 ± 3862.56 versus 1817.87 ± 1398.19 m, Figure 4), and subordinate ETMs lasted longer compared to ETMs by dominant individuals (189.38 ± 162.93 versus 80.93 ± 69.99 min). Further, subordinates intruded into more territories while on ETMs compared to dominants that mainly intruded only into the adjacent territory (2.75 ± 1.91 versus 1.40 ± 0.62 territories). Of the 10 subordinates, 5 were still present in their natal family group when we drafted this manuscript, 3 had dispersed and established a territory, 1 established in its natal territory after the disappearance of its parents, and 1 disappeared for reasons unknown.

Discussion

We investigated extra-territorial movements (ETM) of beavers in southeast Norway. Individuals conducted fewer ETMs when occupying larger territories, and they spend more time in water and travelled faster when conducting ETMs compared to intra-territorial movements (ITM). Fewer dominant than subordinate individuals made ETMs (33% versus 60% of the GPS tagged individuals). Subordinates generally intruded into multiple territories and moved greater distances during ETMs, suggesting that the purpose of these forays is to gain pre-dispersal information as shown in other mammals (Messier 1985, Gese et al. 1996, Soulsbury et al. 2011).

ETM as means of neighbor and area assessment

Independent of their social status, beavers conducted more ETMs in smaller compared to larger territories, and dominant individuals mostly carried out ETMs into adjacent territories. Possibly, the resource availability in small territories was not sufficient and thus, dominant individuals might have assessed opportunities for territory expansion. In the same population, Graf et al. (2016b) reported that beavers in smaller territories stayed further from the shore when on land (i.e., when foraging), possibly due to resource depletion. In addition, Mayer et al. (2017a) showed that the duration of territory occupancy was shorter in small (and large) territories compared to intermediate ones, suggesting that suboptimal sized territories entail costs. In 4 instances, we observed that an individual/pair expanded their territory after the disappearance of one or both dominant individuals of an adjacent territory (unpublished results). Hence, ETMs might serve as an additional mechanism (apart from scent marking) to rapidly detect changes in neighbouring family groups.

Gosling and McKay (1990) proposed that mammals assess their opponents (or neighbours) by scent matching, i.e., comparing neighbouring scent marks with their own odour. They showed that male house mice (*Mus domesticus*) delayed fighting if scent between opponents matched, indicating that scent marking is used for competitor assessment (Gosling and McKay 1990). Further, Rosell and Bjørkøyli (2002) showed that when beavers were presented with experimental scent mounds of neighbours and strangers, they reacted less strong to the neighbouring individuals, known as the dear enemy phenomenon (Temeles 1994). Consequently, ETMs could provide an additional mechanism to assess neighbours and to decrease the costs of territory defence, e.g. physical disputes (Crawford et al. 2015). Additionally, prospecting could serve to assess future breeding opportunities. In northern wheatears (*Oenanthe oenanthe*), a seasonally territorial bird, individuals that established territories at their previous years prospecting sites, had an increased reproductive success compared to other individuals of the same age (Pärt et al. 2011), demonstrating that familiarity with an area can be advantageous. Similarly, field sparrows (*Spizella pusilla*) might conduct ETMs to gain information on future breeding habitat or nest site selection (Celis-Murillo et al. 2017).

Extra-territorial versus intra-territorial movements

In accordance with evidence from Nolet and Rosell (1994), we found that beavers spent less time on land and travelled faster when conducting ETMs in comparison to ITMs. This suggests that ETMs likely did not serve as foraging opportunities; however, we are not able to support this with visual observations. Also red foxes moved faster during ETMs (Soulsbury et al. 2011). Faster spatial movements are associated with reduced vigilance to detect predators (McAdam and Kramer 1998) or conspecifics (Christensen et al. 2016), and entail energetic costs (Halsey et al. 2008). Hence, ETMs might be costly as suggested by Young and Monfort (2009). In contrast, wolf packs in Canada conducted more ETMs when prey densities were lower, in order to hunt for deer outside their territory boundaries (Messier 1985), and female song sparrows (*Melospiza melodia*) likely conducted ETMs for foraging purposes (Akçay et al. 2011). The low proportion of ETMs carried out in our study (on average < 2% of an individuals' activity time) and the little time spent on land during ETMs (compared to ITMs) also indicate that ETMs could be costly, e.g., being detected by a conspecific and risking a physical dispute. A study in NA beavers showed that conspecific aggression is common in NA beavers with one third of all investigated individuals having injuries (Crawford et al. 2015). Young and Monfort (2009) reported that male subordinate meerkats had elevated stress levels in periods when they conducting ETMs. This might result in a trade-off between the information and experience gain before dispersal (or the benefits of EPC) and the costs of a decreased health or even fitness due to stress; and could explain why ETMs often make up a small proportion of an individuals' total time budget (Kesler et al. 2007).

Apart from differences between ETMs and ITMs, we found that beavers spent more time on land during spring, possibly to compensate for the loss of body mass during winter (Campbell et al. 2013). Further, in line with Herr and Rosell (2004) and Graf et al. (2016b), we found that beavers travelled faster in larger compared to smaller territories, possibly to be able to patrol the whole territory. Patrolling might also explain why dominants travelled faster compared to subordinates, as they are typically the ones defending the territory (Rosell et al. 1998, Tinnesand et al. 2013).

ETM to obtain pre-dispersal information

Six of the 10 of the subordinates conducted ETMs. They intruded into a larger number of territories and moved greater distances during ETMs compared to dominant individuals, indicating that these ETMs were prospecting movements possibly to investigate population density and vacant territories. Mayer et al. (2017b) found that subordinate beavers in this study population were more likely to disperse at low population densities. Pre-dispersal ETMs might provide individuals with information on population density, vacant territories and/or the condition of territory owners while they profit from remaining safely in the natal family group, i.e. a stay-and-foray tactic rather than becoming a floater (Brown 1987, Walters et al. 1992). Beavers that delayed dispersal had an increased lifetime reproductive success compared to younger dispersers, possibly because they gained information via ETMs (e.g. on population density (Mayer et al. 2017b)) and because they gained body mass (i.e., competitive ability) while remaining in their natal family group (Mayer et al. 2017a).

Pre-dispersal ETMs of subordinates have been shown in other mammal (Messier 1985, Doolan and Macdonald 1996) and bird (Kesler et al. 2007) species, and it was suggested that individuals conduct ETMs in order to gain information on territory occupancy, mate availability, and habitat quality. Debeffe et al. (2013) could in fact show that explorative trips prior to dispersal were more common in future dispersers compared to future philopatric individuals in roe deer (*Capreolus capreolus*), and dispersers were more likely to disperse in the direction they had previously conducted ETMs. This suggests that dispersal was facilitated by pre-dispersal ETMs (Debeffe et al. 2013).

In contrast to our prediction, subordinates did not conduct more ETMs in spring when beavers typically disperse (Wilsson 1971, Sun et al. 2000). It is likely that beavers in our high-density study population also disperse during autumn due to the high competition for available territories.

Conclusions

In this study, we provide novel evidence that ETMs by dominant territory owners can also be carried out for reasons other than EPC or foraging, likely to assess their neighbours and possibilities for territory expansion. For dominant territory owners, neighbour assessment could be used to increase their territory size and/or to reduce conflict potential and the costs of territoriality, whereas subordinates possibly use ETMs to gain pre-dispersal information to ultimately increase their dispersal success. As shown by Pärt et al. (2011), ETMs might have important consequences on the fitness of an individual. However, a direct link between ETMs and reproductive success remains to be shown in year-round territorial animals.

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Author contributions

MM, AZ and FR developed the design of the work, MM and FR contributed to the data collection, MM and AZ performed the statistical analyses, and MM wrote the manuscript. The authors declare no competing financial interests.

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Tables

Table 1: Effect size (β), standard error (SE), and lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables for the number of extra-territorial movements (ETM) of 73 GPS-tagged Eurasian beavers in southeast Norway (2009-2016). We performed model averaging of best models ($\Delta AIC_c < 4$) to estimate the effect size of each variable. Informative parameters are presented in bold.

Variable	Estimate	SE	LCI	UCI
Territory size (km)	**-0.390**	**0.146**	**-0.681**	**-0.100**
Age	-0.155	0.086	-0.326	0.016
Sex (male)	0.749	0.490	-0.226	1.725
Season (spring)	-0.380	0.340	-1.058	0.298
GPS positions	0.001	0.001	-0.002	0.003
Status (subordinate)	-0.251	0.559	-1.363	0.861

Table 2: Effect size (β), standard error (SE), and lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables for (a) the proportion of time spent in water and (b) distance moved per hour (m) from 28 GPS-tagged Eurasian beavers in southeast Norway (2009-2016). We performed model averaging of best models ($\Delta AIC_c < 4$) to estimate the effect size of each variable. Informative parameters are presented in bold.

Variable	Estimate	SE	LCI	UCI
(a) Proportion of GPS positions in water				
Movement type (ITM)	**-0.667**	**0.133**	**-0.928**	**-0.405**
Season (spring)	**-0.394**	**0.146**	**-0.681**	**-0.107**
Status (subordinate)	-0.262	0.230	-0.738	0.011
Territory size (km)	0.041	0.059	-0.031	0.203
Sex (male)	-0.053	0.114	-0.438	0.151
Age	-0.002	0.019	-0.077	0.062
(b) Travel speed (m/hr)				
Movement type (ITM)	**-185.782**	**9.645**	**-204.690**	**-166.873**
Status (subordinate)	**-36.109**	**13.713**	**-62.991**	**-9.227**
Territory size (km)	**23.195**	**2.452**	**18.387**	**28.002**
Age	-2.081	1.288	-4.605	0.444
Season (spring)	-9.055	8.555	-25.827	7.716
Sex (male)	14.838	8.193	-1.224	30.900

* For extra-territorial movements (ETM) the distance moved per hour was calculated based on all available GPS positions (there were too few positions to separate for land and water positions); for intra-territorial movements we only used water positions to be conservative (beavers move faster in water and individuals spend more time in water when conducting ETMs).

Table 3: Effect size (β), standard error (SE), and lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables for 1) the distance moved, 2) the duration, and 3) the number of intruded territories during individual extra-territorial movements (ETM) from 27 GPS-tagged Eurasian beavers in southeast Norway (2009-2016). Informative parameters are presented in bold.

Variable	Estimate	SE	LCI	UCI
1) Distance moved (m)				
Status (subordinate)	**2755.600**	**1163.690**	**491.937**	**4337.225**
Age	-75.880	175.270	-373.976	142.633
Territory size (km)	312.710	326.940	-200.425	801.162
Season (spring)	-891.010	723.770	-1488.494	707.096
Sex (male)	-395.850	867.570	-1763.220	870.568
2) Duration (min)				
Status (subordinate)	**142.003**	**54.632**	**34.927**	**249.080**
Age	8.425	8.635	-8.500	25.349
Territory size (km)	9.864	16.080	-21.652	41.380
Season (spring)	-41.064	34.595	-108.869	26.741
Sex (male)	-45.404	42.879	-129.445	38.636
3) Number of intruded territories				
Status (subordinate)	**0.635**	**0.284**	**0.065**	**1.204**
Territory size (km)	0.132	0.097	-0.063	0.327
Age	-0.033	0.055	-0.142	0.076
Season (spring)	-0.120	0.225	-0.572	0.331
Sex (male)	-0.201	0.238	-0.680	0.278

Figures

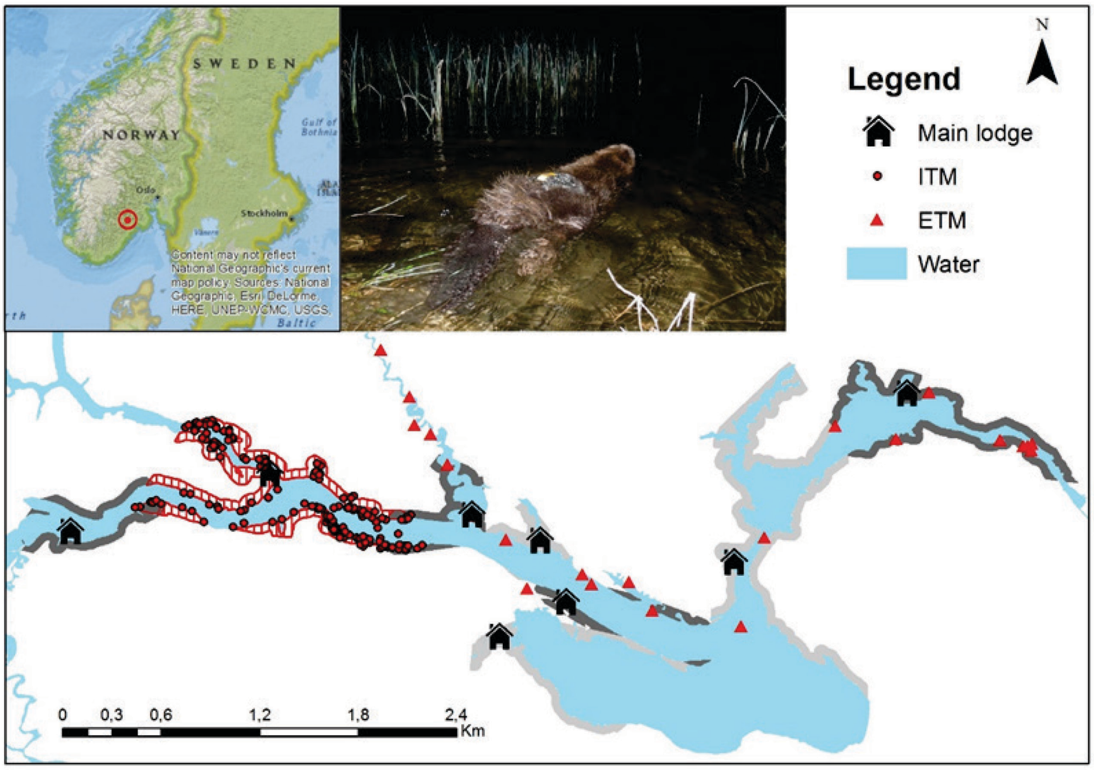

Figure 1: The location of our study area in southeast Norway (top right), and our study species, the Eurasian beaver, with a GPS on its back (top middle). The main map shows exemplary GPS data from a subordinate individual who conducted extra-territorial movements (ETM, triangles) through five different territories (shown with grey shadings). The territory is shown in red hatching.

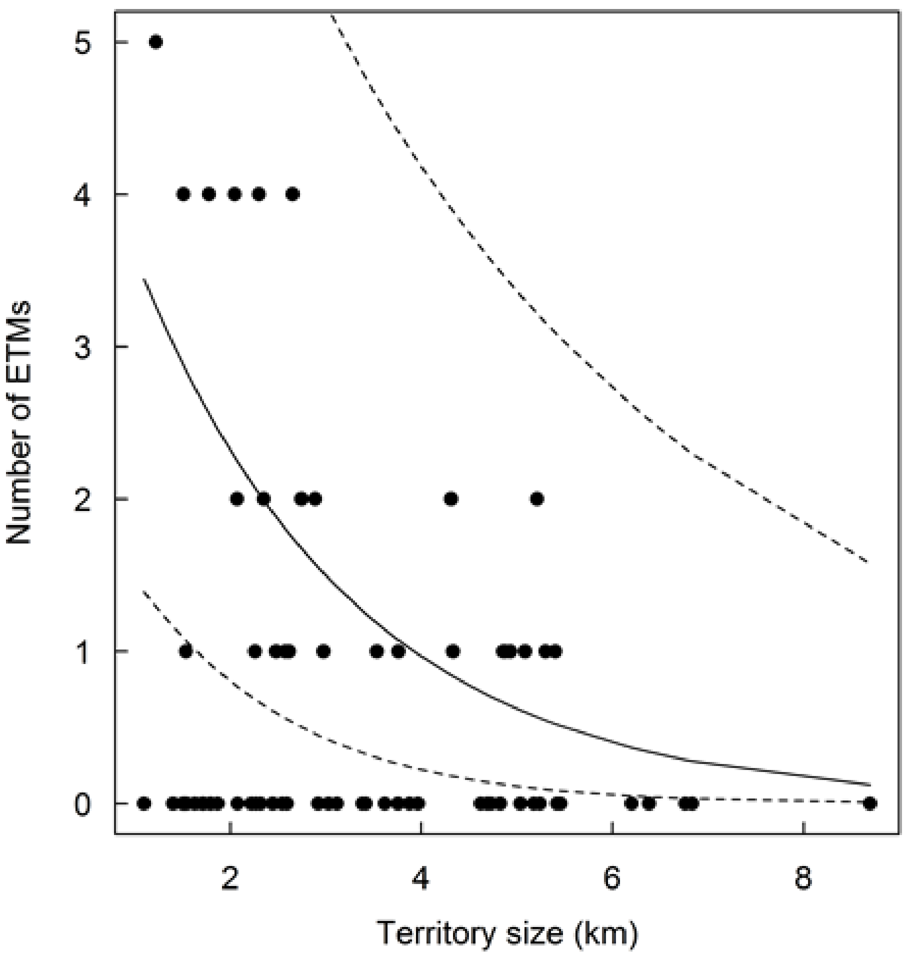

Figure 2: Predicted relationship (solid line) between the territory size and the number of ETMs of 54 GPS-tagged Eurasian beavers in southeast Norway (2009-2016). Dashed lines represent upper and lower confidence intervals.

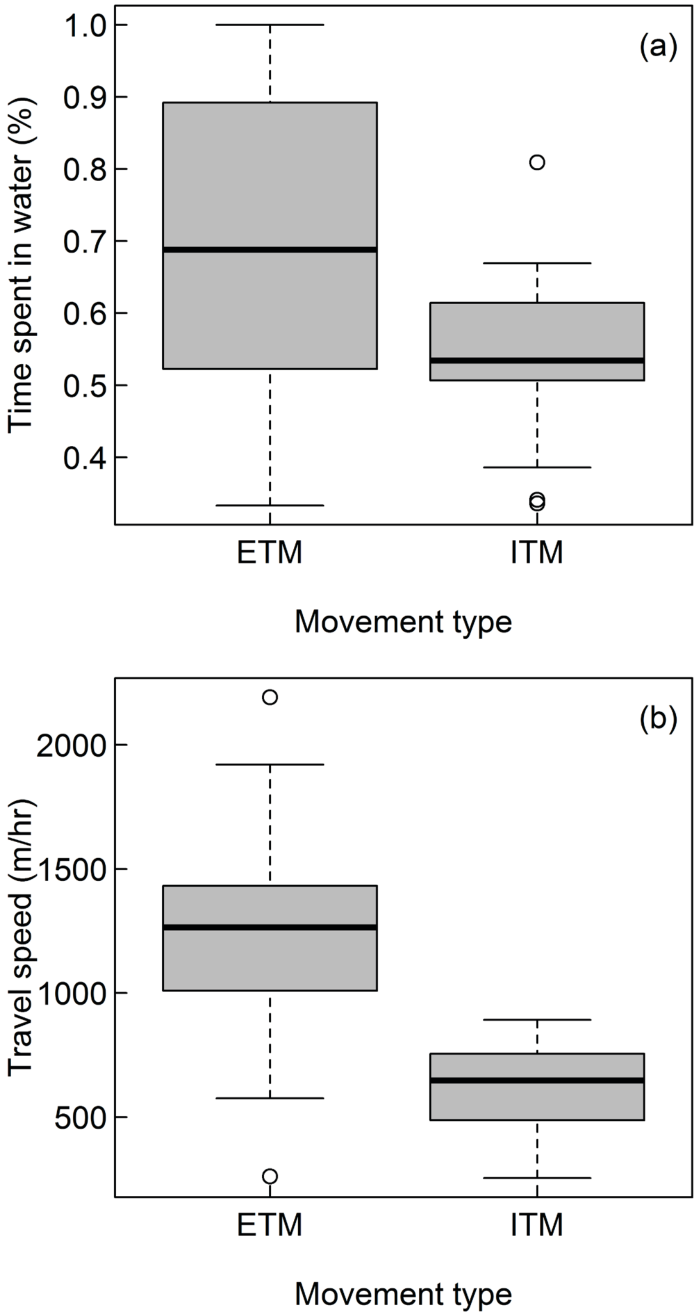

Figure 3: Box plots showing (a) the proportion of time spent in water and (b) the travel speed (m/hr) for extra-territorial movements (ETM) and intra-territorial movements (ITM) of 54 GPS-tagged Eurasian beavers in southeast Norway (2009-2016). The box plots show the median, 25th and 75th percentile, the range of the data and outliers (dots).

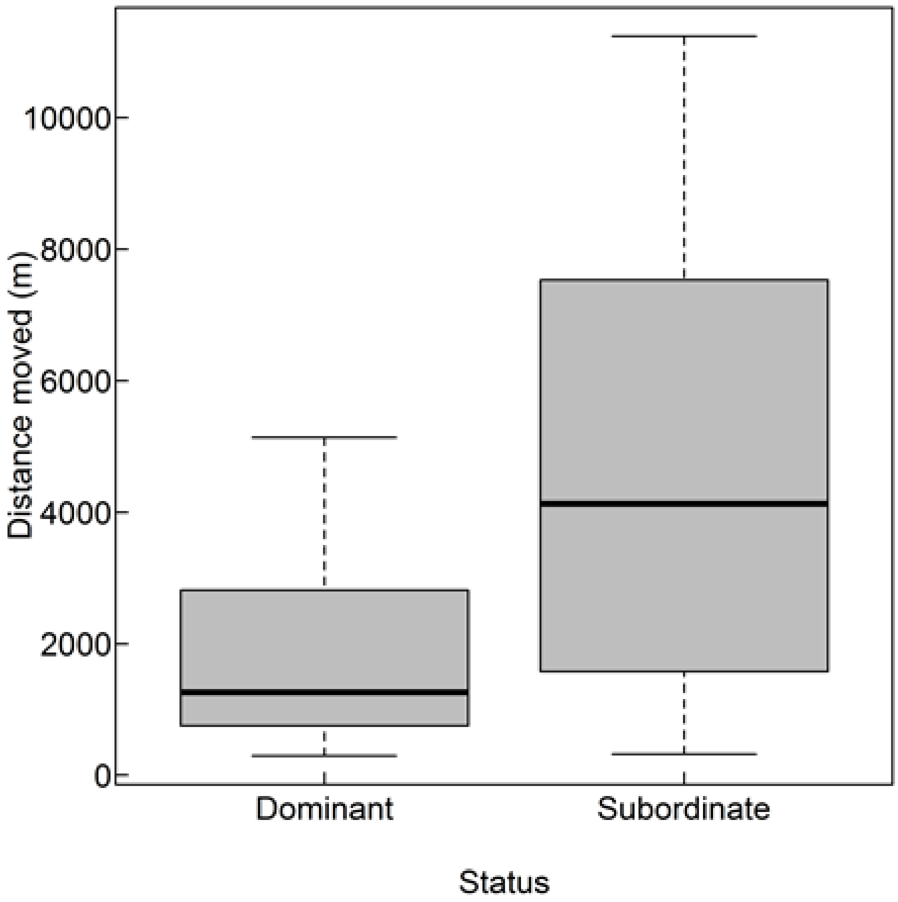

Figure 4: Box plot showing the distance moved (in m) on individual extra-territorial movements (ETM) separately for dominant (n = 20 individuals, 43 ETMs) and subordinate (n = 6 individuals, 8 ETMs) GPS-tagged Eurasian beavers in southeast Norway (2009-2016). Box plots show median values, 25th and 75th percentile, the range of the data and outliers (dot).

Supplementary tables

Table S1: The most parsimonious models within $\Delta AIC_c < 4$ for the analysis of 1) the number of extra-territorial movements (ETM), 2) the proportion GPS positions on land versus water, and 3) the travel speed (calculated from all GPS positions and water positions only, respectively) in the Eurasian beaver based on data collected between 2009 and 2016 in southeast Norway. Beaver ID was included as random effect in all analyses.

Model	df	logLik	AICc	delta AIC	AIC weight
Number of ETMs					
Age + Territory size + Sex	7	-76.63	169.0	0.00	0.134
Territory size	5	-79.11	169.1	0.15	0.125
Territory size + Season	6	-78.38	170.0	1.07	0.079
Territory size + Sex	6	-78.60	170.5	1.50	0.063
Age + Sex	6	-78.62	170.5	1.54	0.062
Territory size + Season + Sex	7	-77.60	170.9	1.95	0.051
Territory size + Number of GPS positions	6	-78.97	171.2	2.24	0.044
Territory size + Number of GPS positions + Sex	7	-77.84	171.4	2.42	0.040
Territory size + Status	6	-79.11	171.5	2.52	0.038
Age + Territory size + Sex + Status	8	-76.62	171.5	2.52	0.038
Age + Territory size + Season + Sex +	8	-76.68	171.6	2.63	0.036
Age + Season + Sex +	7	-78.05	171.8	2.84	0.032
Age + Territory size + Season	7	-78.13	172.0	3.00	0.030
Age + Territory size + Number of GPS positions + Sex	8	-76.92	172.1	3.11	0.028
Age + Sex + Status	7	-78.20	172.1	3.15	0.028
Age	5	-80.70	172.3	3.32	0.026
Territory size + Number of GPS positions + Season	7	-78.37	172.5	3.48	0.024
Territory size + Season + Status	7	-78.38	172.5	3.50	0.023
Age + Territory size + Status	7	-78.46	172.6	3.66	0.022

Territory size + Number of GPS positions + Season + Sex	8	-77.22	172.7	3.71	0.021
Territory size + Sex + Status	7	-78.56	172.8	3.86	0.019
Age + Territory size + Number of GPS positions	7	-78.58	172.9	3.91	0.019
Age + + Number of GPS positions + Sex	7	-78.62	173.0	3.99	0.018
Proportion of GPS positions in water versus on land					
Territory size + Movement type + Season + Status	6	-5869.99	11752.0	0.00	0.171
Movement type + Season + Status	5	-5871.13	11752.3	0.28	0.149
Territory size + Movement type + Season + Sex + Status	7	-5869.52	11753.0	1.06	0.101
Age + Territory size + Movement type + Season + + Status	7	-5869.63	11753.3	1.28	0.090
Movement type + Season	4	-5872.68	11753.4	1.37	0.086
Movement type + Season + Sex + Status	6	-5870.75	11753.5	1.52	0.080
Age + Movement type + Season + Status	6	-5871.13	11754.3	2.27	0.055
Movement type + Season + Sex	5	-5872.14	11754.3	2.29	0.054
Age + Territory size + Movement type + Season + Sex + Status	8	-5869.30	11754.6	2.62	0.046
Territory size + Movement type + Season	5	-5872.42	11754.8	2.85	0.041
Age + Movement type + Season	5	-5872.45	11754.9	2.91	0.040
Age + Movement type + Season + Sex + Status	7	-5870.75	11755.5	3.52	0.029
Age + Movement type + Season + Sex	6	-5871.79	11755.6	3.60	0.028
Territory size + Movement type + Season + Sex	6	-5871.80	11755.6	3.63	0.028
Travel speed (distance moved/hr) calculated from all GPS positions					
Age + Movement type + Sex + Status + Season + Territory size	9	-107341.00	214700.0	0.00	1.000

Travel speed (distance moved/hr) calculated from water GPS positions only					
Age + Movement type + Sex + Status + Season + Territory size	9	-35194.00	70406.0	0.00	0.813
Movement type + Sex + Status + Season + Territory size	8	-35196.47	70409.0	2.94	0.187

Table S2: The most parsimonious models within $\Delta AIC_c < 4$ for the analysis of 1) the distance moved during individual extra-territorial movements (ETM), 2) the duration of individual ETMs, and 3) the number of territories intruded into during individual ETMs in the Eurasian beaver based on data collected between 2009 and 2016 in southeast Norway. Beaver ID was included as random effect in all analyses.

Model	df	logLik	AICc	delta AIC	AIC weight
Distance moved during individual ETMs					
Status + Age + Territory size + Season + Sex	8	-414.197	847.8	0.00	1.000
Duration of individual ETMs					
Status + Age + Territory size + Season + Sex	8	-274.37	568.2	0.00	1.000
Number of territories intruded into during individual ETMs					
Status	3	-68.51	143.5	0.00	0.257
Status + Territory size	4	-67.91	144.7	1.17	0.143
Status + Sex	4	-68.14	145.1	1.63	0.114
Status + Season	4	-68.38	145.6	2.10	0.090
Territory size	3	-69.62	145.7	2.23	0.084
Age + Status	4	-68.50	145.9	2.34	0.080
Age + Territory size	4	-68.52	145.9	2.40	0.077
Status + Sex + Territory size	5	-67.58	146.5	2.98	0.058
Status + Season + Territory size	5	-67.74	146.8	3.28	0.050
Age + Status + Territory size	5	-67.77	146.9	3.35	0.048

Paper II

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When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver

Martin Mayer [a], [*], Andreas Zedrosser [a], [b], Frank Rosell [a]

[a] *Department of Environmental and Health Studies, Faculty of Arts and Sciences, University College of Southeast Norway, Bø i Telemark, Norway*
[b] *Department of Integrative Biology, Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Austria*

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monogamy
territoriality

As dispersal is a dangerous part of an individual's life, its timing is important to increase the chances of survival and successful establishment of a territory. We investigated factors affecting the timing of natal dispersal in the Eurasian beaver, *Castor fiber*, a territorial, monogamous, long-lived mammal, using data from an 18-year individual-based study (1998–2015). We tested hypotheses about the causes of dispersal onset, namely competitive ability, kin competition (sibling competition and offspring–parent competition), population density and intolerance by an incoming, unrelated dominant individual. Only 9% of individuals remained philopatric and became dominant after both of their parents disappeared. Average age at dispersal was 3.5 years, with some individuals delaying dispersal up to age 7 years. Beavers dispersed more frequently with increasing age (i.e. with increasing competitive ability and possibly experience) and when population density was lower. Further, both females and males delayed dispersal with increasing same-sex parental age. Older parents were either more tolerant towards philopatric subordinates, or subordinates awaited the disappearance of their senescing parents to take over the natal territory. From comparisons with other populations, we conclude that the high population density in our area was possibly the ultimate driver of dispersal with individuals delaying dispersal to increase their competitive ability.

Natal dispersal has important consequences for the demography and genetic structure of populations (Bowler & Benton, 2005). Therefore, understanding the selective drivers of natal dispersal strategies is an important subject in behavioural ecology (Le Galliard & Clobert, 2003). Natal dispersal can be divided into three stages: emigration from the natal area, search for a new area and, if dispersal is successful, immigration and establishment in a new area (Ims & Yoccoz, 1997).

Although numerous studies have investigated the probability of dispersal in birds (Negro, Hiraldo, & Donázar, 1997; Saino et al., 2014) and mammals (Armitage, Vuren, Ozgul, & Oli, 2011; Le Galliard, Gundersen, Andreassen, & Stenseth, 2006; Swilling & Wooten, 2002; Zedrosser, Støen, Sæbø, & Swenson, 2007), i.e. comparing dispersers and philopatric individuals, less attention has been given to the timing of dispersal, i.e. when an animal initiates dispersal (Lens & Dhondt, 1994; Nunes & Holekamp, 1996), especially in large, long-lived mammals (Sarno, Bank, Stern, & Franklin, 2003; Sparkman, Adams, Steury, Waits, & Murray, 2010). As dispersal is a dangerous period during the life of an animal (Lucas, Waser, & Creel, 1994), and can result in high mortality (Bonnet, Naulleau, & Shine, 1999), the timing of dispersal is crucial to increase the probability of survival and establishment of a new territory.

The onset of natal dispersal can be affected by intragroup dynamics such as kin competition, i.e. the competition between siblings or between parent and offspring (Ronce, Clobert, & Massot, 1998). Smaller siblings might be forced to disperse earlier as larger siblings are competitively superior. On the other hand, larger siblings might disperse earlier because they are in better condition and may be better at finding and establishing a new territory (Bowler & Benton, 2005; Nunes & Holekamp, 1996). Competition between offspring and parent was found in lizards, *Lacerta vivipara*, where the female offspring dispersal rate decreased with increasing maternal age (Ronce et al., 1998). A driver for parent–offspring competition can be competition for resources. For example, juvenile guanacos, *Lama guanicoe*, were forced to disperse by territorial males, probably to increase resource availability for younger offspring (Sarno et al., 2003). In territorial species, an

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[*] Correspondence: M. Mayer, Faculty of Arts and Sciences, Department of Environmental and Health Studies, University College of Southeast Norway, 3800 Bø i Telemark, Norway.
E-mail address: martin.mayer@hit.no (M. Mayer).

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incoming unrelated individual replacing the previous parent can be intolerant towards previous offspring and, in effect, force dispersal, as shown in mantled howler monkeys, *Alouatta palliata* (Glander, 1992) and Siberian jays, *Perisoreus infaustus* (Ekman & Griesser, 2002). Another driver of dispersal onset can be population dynamics, i.e. density-dependent dispersal (Matthysen, 2005). When population densities are high, delayed dispersers might queue either to take over the natal territory or to await better dispersal opportunities to ultimately establish a territory and breed in high-quality habitat (Ekman, Eggers, Griesser, & Tegelström, 2001; Kokko & Johnstone, 1999) and/or to increase their competitive ability. Conversely, high population densities can lead to increased dispersal rates as individuals have better fitness perspectives by moving to lower density areas to reduce competition (Matthysen, 2005).

Ultimately, individuals disperse to avoid inbreeding with close relatives (Gundersen & Andreassen, 1998; Wolff, 1994), to evade competition for mates (Dobson, 1982), or to gain access to environmental resources, such as food and shelter (Greenwood, 1980). Such constraints can lead to sex-specific dispersal distances as shown in eastern chipmunks, *Tamias striatus*, where males dispersed further than females to avoid competition with resident males and inbreeding with closely related females (Loew, 1999).

Here we investigated the factors affecting the timing of dispersal in a large, monogamous mammal, the Eurasian beaver, *Castor fiber*. Both the Eurasian beaver and the North American beaver, *Castor canadensis*, live in family groups consisting of the dominant pair, the young of the year, yearlings and subordinates, i.e. nondominant individuals of 2 years or older (Busher, Wolff, & Sherman, 2007; Wilsson, 1971). Group sizes generally range between two and six individuals in Eurasian beavers (Rosell, Parker, & Steifetten, 2006), and both species are strictly territorial with both sexes defending their territory via scent marking (Müller-Schwarze & Sun, 2003; Rosell, Bergan, & Parker, 1998). The two beaver species are long lived, sometimes reaching an age of over 20 years (Gorbunova, Bozzella, & Seluanov, 2008), and typically disperse around 2 years of age (Hartman, 1997; Sun, Müller-Schwarze, & Schulte, 2000) during which individuals try to establish a territory of their own. Dispersal occurs alone (M. Mayer & F. Rosell, personal observations). Two studies on dispersal in North American beavers gave an annual proportion of dispersers for different cohorts (Havens, 2006; McNew, Lance, & Woolf, 2005), and another study reported that all individuals dispersed at the latest at age 3 years (Sun et al., 2000). However, none of these studies investigated the factors affecting the timing of natal dispersal. Hartman (1997) and Sun et al. (2000) suggested density dependency in beaver dispersal onset (both species), with individuals in denser populations dispersing at older ages, but whether individuals can perceive changes in population density has not been tested. Some studies have investigated the distance of dispersal, with inconsistent results. Sun et al. (2000) found that in North American beavers females dispersed further from their natal colonies than males, whereas a study on Eurasian beavers found that males dispersed further (Saveljev, Stubbe, Stubbe, Unzhakov, & Kononov, 2002).

In this study, we investigated (1) the timing of dispersal, i.e. in which year a disperser emigrates, and (2) the variation in dispersal age in order to test five hypotheses about the proximate causes of dispersal onset. (1) If the timing of dispersal is related to the competitive ability of the disperser, it should increase with the disperser's age (due to an increase in body mass) as beavers are then more able to compete for territories. (2) If dispersal onset is density dependent it should increase with decreasing population density as competition for available territories is expected to decrease. (3) If dispersal occurs to avoid sibling competition and inbreeding it should increase with family group size, i.e. with increasing sibling competition. (4) Dispersal is forced by the presence of a new, unrelated dominant individual in the natal family group. (5) If dispersal onset is related to parental age it should decrease with increasing parental age as older parents might be more tolerant towards their offspring or because offspring await the disappearance of their parents.

METHODS

General Methods

Data were collected from 1998 to 2015 as part of a long-term study on three rivers (the Saua, Gvarv and Straumen which all flow into Lake Norsjø) in Telemark County, southeast Norway. The landscape along the rivers was a mix of agricultural lands and mixed forest (Steyaert, Zedrosser, & Rosell, 2015). Beavers were captured every year during spring (March–June) and autumn (August–November) at night from a boat. We individually marked all beavers with ear tags and microchips, weighed them, and determined their age and social status (dominant, subordinate, yearling, kit). To facilitate handling and tagging, beavers were placed in a cloth sack and restrained while applying ear tags. No beaver responded aggressively while kept in the sack; individuals tended to remain comparatively calm and docile (Sharpe & Rosell, 2003). For detailed description of capture and handling procedures see Rosell and Hovde (2001) and Campbell, Nouvellet, Newman, Macdonald, and Rosell (2012). The group size and number of kits produced were recorded annually for each family group between August and November (after the kits emerged from the lodge).

Dominance was determined by lactation in females, multiple recapture events and the absence of the previous dominant same-sex individual (parent; Campbell et al., 2012). An individual was defined as a disperser if it left its natal area and never returned, and established itself in a new territory as dominant individual ($N = 36$) or was found dead in a different area ($N = 3$). Between dispersal and successful establishment in a new territory individuals were defined as floaters. We calculated the dispersal distance in ArcMap 10.3 (Esri, Redlands, CA, U.S.A.) along the course of the waterbody from the natal lodge to the lodge in the new territory. Beavers mainly disperse between March and June (Sun et al., 2000). Thus, the dispersal age of an individual during the first 6 months of a year was assigned to that respective year. If individuals were last observed in their natal family group in the latter 6 months of a year, their dispersal age was assigned to the next year due to the low dispersal probability in the second half of the year. Because beavers were previously reported to disperse no later than 3 years old (Hartman, 1997; Sun et al., 2000), we categorized 1–3 year olds as normal dispersers and 4 year olds or older as delayed dispersers. Beavers that disappeared from the natal family group, but were never seen again, were defined as individuals of unknown fate ($N = 75$). The age of all dispersing and disappearing individuals was known as they were first captured as kit or yearling (Rosell, Zedrosser, & Parker, 2010). Because measurements were taken at different times of the year and beavers gain mass from spring to autumn (Campbell, Newman, Macdonald, & Rosell, 2013), we standardized the body mass of dispersers to a hypothetical dispersal date of 1 June (as we did not obtain the actual dispersal date of the beavers) assuming beavers gain 0.021 kg/day (95% confidence interval, CI: 0.015 kg/day; 0.030 kg/day) following Campbell (2010). Parental age was defined as the minimum age of the same-sex parent in the year an individual dispersed or disappeared. As the age determination of beavers captured for the first time as adults is difficult, for individuals ≥ 2 years, a minimum age was assigned when first captured based on body mass (Rosell et al., 2010): beavers were classified as at least 2 years old when they had a mass ≥ 17 kg and ≤ 19.5 kg, or at least 3 years when > 19.5 kg at the time of first capture (e.g. a beaver captured for the first time in 2000 at 18 kg was classified as at least 2 years old and therefore, when captured again in 2003, it was classified as at least 5 years old). A parental replacement was defined as the replacement (0 = no replacement, 1 = replacement) of one or both parents by a new dominant individual in the natal family group in a given year.

The population was considered saturated as territories directly bordered each other (Campbell, Rosell, Nolet, & Dijkstra, 2005). We calculated the population density as the average number of individuals per family group separately for the three rivers and for each year. Group size and number of kits were highly correlated ($r = 0.915$, $P < 0.001$). Therefore, we removed the number of kits from the analyses based on a variance inflation factor >3 (Zuur, Ieno, & Elphick, 2010), and used group size as a measure of sibling competition. Our study may be biased towards short-distance dispersers (<10 km), because we were not able to track individuals that emigrated outside of our study area.

Ethical Note

All trapping and handling procedures were approved by the Norwegian Experimental Animal Board (id 742, id 2170) and the Norwegian Directorate for Nature Management (2008/14367 ART-VI-ID), which also granted permission to conduct fieldwork in our study area. Our study met the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching (ASAB/ABS, 2016). We caught a total of 118 individuals for this study. None of them were injured and all were successfully released at the site of capture after handling. No subsequent long-term effects of capture were observed.

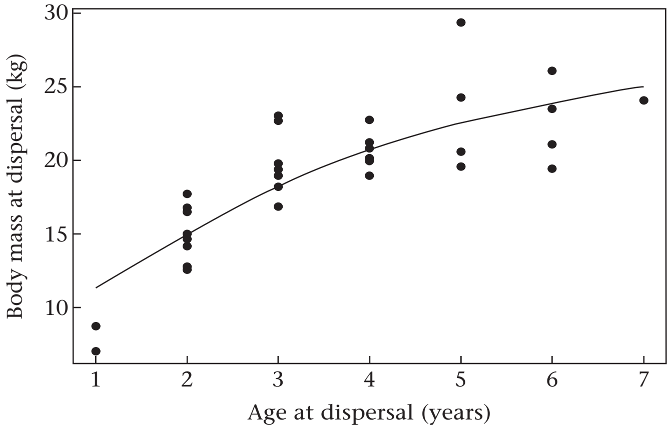

Figure 1. The relationship between age at dispersal and body mass at dispersal in Eurasian beavers from data collected between 1998 and 2015 in southeast Norway ($N = 33$).

Statistical Analyses

To test whether individuals of unknown fate were disappearing due to dispersal (in which case we would predict that they would show the same patterns as known dispersers) or due to mortality (or a mix), we included them in our analyses together with the known dispersers as the categorical variable ‘status’ (disperser versus individual of unknown fate). The analysis was divided into two parts (1) the timing of dispersal and disappearance (unknown fate individuals) and (2) the variation in dispersal age and age at disappearance (unknown fate individuals). To model the timing of dispersal/disappearance, i.e. in which year an individual initiated dispersal (or disappeared from the natal family group for individuals of unknown fate), we compared the year of dispersal or disappearance, respectively, to all the previous years an individual could have left the natal territory running a generalized linear mixed model using the R package lme4 (Bates et al., 2015) with a logit link and the individual ID and the year as random effects ($N = 110$, 386 observation years). Year was included as a random effect to account for possible conditional effects, e.g. interannual variation in environmental factors or cohort effects. We used the dependent binomial variable ‘presence in natal family group’ (present in a given year versus left (dispersed or disappeared) in a given year) to investigate whether an individual had dispersed or disappeared in a given year or not. The fixed effects were age, group size, population density, parental age, parental replacement, sex and status. Age was used instead of body mass, because we did not weigh all individuals in every year. Dispersal age and body mass at dispersal were highly correlated ($r = 0.789$, $\beta = 2.329 \pm 0.326$, $P < 0.001$, $N = 33$; Fig. 1). Generally, body mass and age were highly correlated in the beavers in our study area ($r = 0.737$, $N = 347$ observations of 136 individuals), and individuals reached their maximum body mass around age 6 years (Mayer, Kuenzel, Zedrosser, & Rosell, 2016). We used a set of candidate models including all possible combinations of the fixed effects, but did not include two-way interactions due to convergence issues (which could not be resolved by standardizing the variables around their mean). After we found an effect of status, we ran two separate analyses (same model as before) for the timing of known dispersers (not dispersed in a given year versus dispersed in a given year), and for individuals of unknown fate (present in a given year in the natal family group versus disappeared in a given year) to be able to clearly distinguish between the two groups.

To investigate the variation in dispersal age/age at disappearance (dependent variable), we used a general linear model with a log link. Independent variables were group size in the year of dispersal/disappearance, population density, parental age, parental replacement, sex and status. We used a set of candidate models with all possible combinations of the single independent variables, and included the two-way interactions of status and the other independent variables to test for differences between known dispersers and individuals of unknown fate (no convergence issues were detected in this analysis). For all analyses we created single-effect models for all independent variables (apart from the categorical variables parental replacement and status) to test whether their relationship with the dependent variable was linear or quadratic, based on Akaike's information criterion corrected for small sample size (AIC_c) (Burnham & Anderson, 2002), and found that the linear relationship fitted better in all cases. The independent variables used in all analyses were not correlated ($r < 0.6$ in all cases), and variance inflation factors were <3 (Zuur et al., 2010). Model selection was based on AIC_c values (Arnold, 2010), and was carried out using the R package MuMIn (Barton, 2013). If ΔAIC_c was <4 in two or more of the most parsimonious models, we performed model averaging (Anderson, 2008). Parameters that included zero within their 95% CI were considered as uninformative (Arnold, 2010). All statistical analyses were performed in R 3.2.1 (R Core Team, 2015).

RESULTS

The average annual population densities varied between 2.7 and 7 individuals per group (mean ± SD: 4.3 ± 0.9). Over the 18 years of the study, we recorded 39 dispersers (19 females, 20 males) from 21 territories that were born inside our study area (Table A1). Another 75 individuals (36 females, 39 males) disappeared without information on their fate (dispersal or mortality). Known dispersers were significantly older than individuals of unknown fate (in the year of dispersal or disappearance, respectively: 3.5 ± 1.6 versus

2.1 ± 1.4 years; *t* test: $P < 0.001$). The dispersers' age ranged between 1 and 7 years (Fig. 2a); 23 beavers (59%) were normal dispersers (1–3 years old) and 16 (41%) delayed dispersal (4–7 years old). The average weight at dispersal was 18.8 ± 4.7 kg (range 7.1–29.4 kg) and was positively related to the dispersal age (Fig. 1). The average dispersal distance was 4.5 ± 5.4 km (median = 3.0 km; range 0.5–27.5 km; Fig. 2b), and there was no sex difference in dispersal distance (*t* test: $P = 0.861$). Four individuals did not disperse (out of 43 with known fate; 9%), but stayed within their natal family group and became dominant after their parent of the same sex disappeared. The beavers all paired up with an immigrant mate (born in another territory).

The timing of dispersal and disappearance (global model) was best explained by an individual's age, the population density, parental replacement and status (Tables 1, A2): beavers were more likely to disperse or disappear with increasing age, when there was a parental replacement and when population density was lower (Table 1). Individuals of unknown fate disappeared earlier from the natal family group than known dispersers. When analysed separately, known dispersers ($N = 36$, 160 individual years) were more likely to disperse with increasing age and decreasing population density (Tables 2, A2). Individuals of unknown fate ($N = 74$, 226 individual years) were more likely to disappear with increasing age and when a parental replacement occurred (Tables 2, A2). Population density appeared in the most parsimonious model, but was considered uninformative because its 95% CI included zero.

Figure 2. Frequency histogram of (a) dispersal age and (b) dispersal distance from data collected between 1998 and 2015 in southeast Norway ($N = 39$ Eurasian beavers).

Table 1

Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables for the timing of dispersal/disappearance (unknown fate individuals)

Variable	β	SE	LCI	UCI
Age	**1.469**	**0.380**	**0.722**	**2.215**
Population density	**−0.442**	**0.197**	**−0.829**	**−0.055**
Parental replacement (yes)	**1.509**	**0.508**	**0.511**	**2.507**
Status (unknown fate)	**1.472**	**0.460**	**0.567**	**2.377**
Sex (male)	0.161	0.344	−0.514	0.837
Group size	0.047	0.209	−0.363	0.457
Parental age	0.005	0.193	−0.374	0.384

We performed model averaging of best models ($\Delta AIC_c < 4$) to estimate the effect size of each variable. Informative parameters are given in bold. Data were obtained from Eurasian beavers in southeast Norway (1998–2015).

Table 2

Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables separately for the timing of dispersal and timing of disappearance (unknown fate individuals)

Variable	β	SE	LCI	UCI
Timing of dispersal				
Age	**1.710**	**0.751**	**0.227**	**3.194**
Population density	**−0.803**	**0.398**	**−1.588**	**−0.018**
Parental replacement (yes)	1.196	0.910	−0.602	2.993
Sex (male)	0.549	0.640	−0.716	1.813
Group size	0.312	0.400	−0.477	1.101
Parental age	0.126	0.395	−0.656	0.907
Timing of disappearance (individuals of unknown fate)				
Parental replacement (yes)	**1.648**	**0.602**	**0.462**	**2.834**
Age	**1.197**	**0.461**	**0.288**	**2.106**
Population density	−0.311	0.222	−0.748	0.127
Group size	−0.120	0.221	−0.555	0.316
Parental age	−0.118	0.220	−0.551	0.316
Sex (male)	0.026	0.399	−0.760	0.812

We performed model averaging of best models ($\Delta AIC_c < 4$) to estimate the effect size of each variable. Informative parameters are given in bold. Data were obtained from Eurasian beavers in southeast Norway (1998–2015).

The variation in dispersal age and age at disappearance was best explained by the parental age and status (Table A3), with beavers dispersing and disappearing later when the parent of the same sex was older (Table 3, Fig. 3 for known dispersers), and known dispersers were older when leaving the natal colony than individuals of unknown fate (Table 3).

Table 3

Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables for variation in dispersal age/age at disappearance (unknown fate individuals)

Variable	β	SE	LCI	UCI
Parental age	**0.240**	**0.067**	**0.107**	**0.372**
Status (unknown fate)	**−0.473**	**0.127**	**−0.725**	**−0.221**
Population density	0.094	0.079	−0.062	0.250
Sex (male)	0.080	0.133	−0.183	0.343
Parental replacement (yes)	−0.092	0.175	−0.439	0.254
Group size	0.035	0.066	−0.096	0.166
Population density ∗ Status	−0.119	0.132	−0.381	0.142
Parental age ∗ Status	−0.035	0.121	−0.274	0.205
Sex ∗ Status	0.128	0.240	−0.347	0.603
Parental replacement ∗ Status	−0.102	0.326	−0.748	0.543
Group size ∗ Status	−0.016	0.119	−0.252	0.220

We performed model averaging of best models ($\Delta AIC_c < 4$) to estimate the effect size of each variable. Informative parameters are given in bold. Data were obtained from Eurasian beavers in southeast Norway (1998–2015).

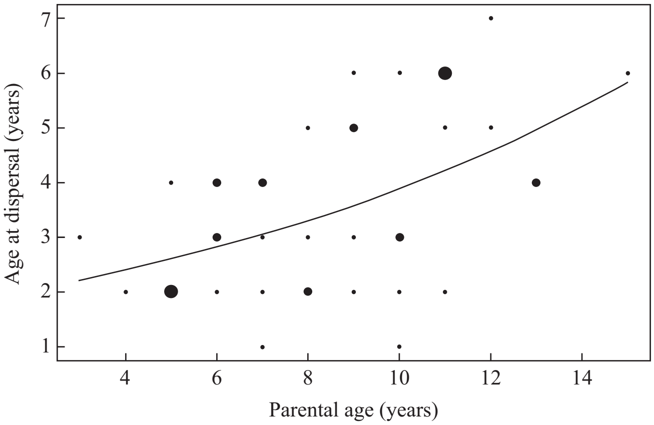

Figure 3. Predicted relationship between age of the parent (of the same sex) and dispersal age of 37 dispersing Eurasian beavers from data collected between 1998 and 2015 in southeast Norway. Dot sizes indicate the number of observations.

DISCUSSION

This study investigated five hypotheses concerning the timing of natal dispersal. We found that a high competitive ability (i.e. body mass) and a low population density were the variables most affecting the timing of natal dispersal. Further, individuals that had older parents (of the same sex) dispersed at older ages, delaying dispersal up to age 7 years. Density dependence and parent–offspring competition were also found to be drivers of dispersal in other mammals (Andreassen & Ims, 2001; Støen, Zedrosser, Sæbø, & Swenson, 2006; Zedrosser et al., 2007). Our findings suggest that the timing of dispersal in beavers is driven by changes in population density and the age of their parents, i.e. beavers delay dispersal with increasing parental age at high population densities.

Philopatric Individuals

Four beavers in our study area did not disperse (9% versus 91% dispersers) but established themselves as dominants within their natal family group. The prerequisite of becoming dominant in the natal territory was the disappearance of the parent of the same sex. It is unlikely that there were physical disputes between dominant parent and subordinate offspring, as we never observed this during the 18 years of our study (F. Rosell, personal observation), and there is also no such evidence in North American beavers (Crawford, Bluett, & Schauber, 2015). Also, we did not have any evidence for inbreeding between parent and offspring (or between siblings). Easy access to resources and possibly the takeover of the breeding position could be the benefits from remaining in the natal territory.

Timing of Dispersal

Beavers dispersed when annual population densities were lower than in the previous years, indicating that a higher population density hampered the chances of successfully dispersing and establishing a territory. Density-dependent dispersal has also been described in brown bears, *Ursus arctos* (Støen et al., 2006), ungulates (Matthysen, 2005) and small rodents; for example, root voles, *Microtus oeconomus*, had low emigration rates when densities were high and immigrated to low-density patches (Andreassen & Ims, 2001). This demonstrates the constraints of habitat saturation on dispersal patterns, possibly masking other factors, such as inbreeding avoidance (Moore & Ali, 1984). Our findings suggest that individuals can perceive annual changes in population densities. This might be possible as subordinate beavers were shown to make exploratory movements to neighbouring and distant territories before they actually dispersed from their natal family group (Hartman, 1997; Havens, 2006). Birds (e.g. Kesler, Haig, & Brittingham, 2007), meerkats, *Suricata suricatta* (Doolan & Macdonald, 1996) and wolves, *Canis lupus* (Messier, 1985) have also been reported to make extraterritorial predispersal forays to gain information on dispersal opportunities. The information and experience gained by an individual may increase with its age.

In an expanding beaver population in Sweden at low population density (0.13 colonies/km shoreline) the average age at dispersal was 1.4 years (Hartman, 1997) compared to 3.5 years in our saturated study area in Norway (0.64 colonies/km shoreline, no unoccupied areas between territories). We are the first to report delayed natal dispersal (later than age 3 years) in beavers. Individuals dispersing at an older age had a greater body mass at the time of dispersal. This finding suggests that high population density exerts strong selection on delayed dispersal, possibly because older individuals with greater body mass and experience are more competitive and likely to successfully take over or establish a new territory. Sun et al. (2000) found that older dispersing North American beavers were more successful at establishing neighbouring territories suggesting that they have a competitive advantage. In the three-spined stickleback, *Gasterosteus aculeatus*, larger males were more successful in gaining and defending a territory, and a 15% disparity in body mass was sufficient to give a competitive advantage to the heavier male (Rowland, 1989). Similarly, in striped mice, *Rhabdomys pumilio*, individuals were more likely to attack a conspecific that had a lower body mass than themselves (Schradin, 2004). The range in body weight at dispersal in our study was wide, with delayed dispersers being on average 31% heavier as 1–3 year olds at the time of dispersal. These results support the maturation hypothesis stating that an animal awaits physical and behavioural maturity before acquiring a territory, as found in long-lived bird species (Piper et al., 2015; Weimerskirch, 1992). Further, this is in line with the queuing hypothesis stating that individuals queue for the possibility to disperse to high-quality habitat or to take over the natal territory (Kokko & Johnstone, 1999).

Similar to studies in common lizards and brown bears which found that the probability of female dispersal decreased with maternal age (Ronce et al., 1998; Zedrosser et al., 2007), we found that both sexes delayed dispersal with increasing same-sex parental age in beavers. In brown bears, this pattern was suggested to be caused by the formation of matrilineal assemblages with related females being more tolerant of each other, in effect leading to a decreased dispersal probability with increasing maternal age (Støen et al., 2006; Zedrosser et al., 2007). Senescing parents might be more tolerant of their offspring possibly because subordinates older than 2 years were observed to help with the territorial defence (Tinnesand, Jojola, Zedrosser, & Rosell, 2013) and because they might help with the provisioning of the kits before they emerge from the lodge (Müller-Schwarze & Sun, 2003). Graf, Mayer, Zedrosser, Hackländer, and Rosell (2016) found that dominant beavers change their behaviour with increasing age, i.e. they spend more time on land. This shows that a behavioural change with age is plausible, strengthening our suggestion that senescing beavers become more tolerant towards philopatric offspring, allowing them to queue in the natal territory to increase their competitive ability before dispersal as suggested by Ekman et al. (2001). Alternatively, subordinates might be able to detect senescence in their parents and await their disappearance in order to take over the natal territory. In wolves, a territorial, monogamous mammal in which helping behaviour is common, subordinates have also been reported to delay dispersal up to 5 years (Mech & Boitani, 2010).

Unknown Cases, Direction and Distance of Dispersal

Of 120 beavers, we had information on the fate of 45 (37.5%) dispersers and philopatric individuals. The fate of the remaining beavers was unknown, and they were significantly younger at the time of disappearance than the dispersers (when dispersing). Also, individuals of unknown fate were more likely to disappear after one or both parents were replaced. Possibly, younger individuals (i.e. beavers with a lower body mass) were more affected by a new incoming dominant beaver that was not tolerant towards the offspring of the previous dominant territory holder of the same sex. In effect, this could lead to forced dispersal, as shown in male lions, *Panthera leo* (Pusey & Packer, 1987) and white-faced capuchins, *Cebus capucinus* (Jack & Fedigan, 2004), or mortality, either via infanticide as is common in bears and voles (Andreassen & Gundersen, 2006; Bellemain et al., 2006) or during the dispersal process. However, we could not disentangle dispersal and mortality, and hence could not assess the causes of disappearance in the individuals of unknown fate. The variation in age at disappearance was positively related to the parental age, which is in line with the findings on the variation in dispersal age of known fate individuals, strengthening our results.

We have evidence for long-distance dispersal (>10 km) of two individuals that dispersed 23 and 27 km, respectively, making it likely that several beavers dispersed outside our study area. Dispersal distances reported here are similar to those in a study on North American beavers which found mean distances of 5.9 km in streams and no sex differences (McNew et al., 2005). However, another study on North American beavers reported that females dispersed significantly further than males (10.2 versus 3.5 km; Sun et al., 2000). These differing findings reflect the inconsistencies in the existing literature on dispersal patterns in monogamous mammals. For example, Dobson (1982) reported predominantly female-biased dispersal (92% of studied species), whereas Lawson Handley and Perrin (2007) reported this in only 60% of the species they studied. The different findings within the two beaver species suggest that sex-biased dispersal is not necessarily a species-specific trait, but may also be an adaptive strategy depending on other factors, such as population density.

Conclusions

We found evidence that the high population density in our beaver population in southeast Norway was the ultimate cause of delayed natal dispersal, resulting in high competition for resources and a low probability of successfully establishing a territory outside the natal area. Thus, subordinates remain within their natal territory to increase their competitive ability (via an increased body mass and possibly experience) and to await a promising time to initiate dispersal, i.e. lower population densities. Further, senescing parents are possibly more tolerant towards philopatric subordinates as they might help with territorial defence and offspring care, thereby increasing their indirect fitness (or subordinates await the disappearance of their senescing parents to take over the natal territory). Our findings suggest that natal dispersal onset in beavers is driven by changing environmental and social conditions as suggested by Bowler and Benton (2005). It remains to be answered whether these dispersal strategies affect the fitness of an individual.

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APPENDIX

Table A1
Overview of the 39 dispersing beavers in our study area in southeast Norway observed between 1998 and 2015

Name	Sex	Dispersal age (years)	Dispersal distance (km)	Dispersal direction	Group size	Change in dominance structure	Parental age (years)	Population density
141	M	3	5.6	Downstream	5	Yes	7	3.6
Adrian	M	3	3.1	Upstream	4	No	6	4.7
Alasdair	M	5	4.7	Upstream	5	No	9	5.0
Alfhild	F	2	4.7	Upstream	9	No	5	3.4
Andreas	M	3	2.5	Upstream	6	No	8	3.7
Anette	F	6	23.7	Upstream	13	No	9	7.0
Anne Lise	F	2	1.3	Downstream	4	Na	4	NA
Baktus	M	2	4.3	Upstream	4	No	5	5.1
Billy	M	2	7.8	Upstream	3	No	4	3.1
Bram	M	7	3.2	Downstream	4	Yes	12	3.9
Daiya	F	4	3.5	Upstream	5	No	13	3.8
Darwin	M	2	2.8	Downstream	7	No	8	3.1
Demi	F	3	3.0	Upstream	5	No	3	5.0

(*continued on next page*)

Table A1 (*continued*)

Name	Sex	Dispersal age (years)	Dispersal distance (km)	Dispersal direction	Group size	Change in dominance structure	Parental age (years)	Population density
Easy	M	6	2.8	Downstream	7	No	10	3.9
Fiona	F	5	3.0	Upstream	11	No	11	5.0
Gabi	F	5	2.2	Upstream	8	No	12	4.8
Greg burly	M	4	1.7	Downstream	4	No	5	5.0
Gunn Rita	F	2	0.7	Downstream	3	Yes	11	2.8
Hanna Christi	F	2	0.8	Upstream	4	Yes	10	3.9
Ida	F	3	5.8	Upstream	6	No	9	3.7
Ivo	M	4	2.7	Downstream	6	Yes	7	4.6
Karin	F	2	9.3	Upstream	8	No	7	4.4
Kolbjørn	M	2	5.6	Downstream	4	No	5	4.4
Konrad	M	2	27.5	Upstream	7	No	9	4.7
Lasse	M	1	2.7	Downstream	7	No	10	3.9
Laurits	M	4	1.7	Upstream	3	No	13	3.6
Leigh	F	5	1.8	Upstream	5	No	11	3.3
Lona	F	4	3.7	Upstream	3	No	6	4.4
Loran	M	5	1.5	Downstream	7	No	9	4.7
Maerta	F	6	4.1	Upstream	4	No	11	2.8
Montana	M	1	1.5	Upstream	5	No	7	3.1
Morten	M	3	1.4	Upstream	5	No	7	3.3
Paddy	M	3	0.5	Downstream	11	No	10	5.0
Pam	F	6	3.0	Upstream	5	No	15	3.8
Sara	F	2	2.2	Downstream	4	No	6	3.6
Stina	F	4	1.8	Downstream	8	No	6	4.7
Suzanne	F	3	4.0	Downstream	NA	NA	NA	2.8
Terje	M	5	9.5	Upstream	5	No	8	3.0
Yasmin	F	2	4.1	Upstream	4	No	8	3.0

F: female; M: male. NA: not available. Group size, change in dominance structure, parental age and population density are given in the year of dispersal.

Table A2

The most parsimonious models within $\Delta AIC_c < 4$ for the analysis of the timing of dispersal separately for the global model, known dispersers and unknown fate individuals in the Eurasian beaver based on data collected between 1998 and 2015 in southeast Norway

Variables	*df*	Log likelihood	AIC_c	ΔAIC_c	AIC weight
Timing of dispersal/disappearance (global model)					
1/3/5/7	7	−189.850	394.000	0.000	0.414
1/3/5/6/7	8	−189.748	395.900	1.880	0.162
1/2/3/5/7	8	−189.771	395.900	1.930	0.158
1/3/4/5/7	8	−189.850	396.100	2.090	0.146
1/2/3/5/6/7	9	−189.629	397.700	3.740	0.064
1/3/4/5/6/7	9	−189.746	398.000	3.980	0.057
Timing of dispersal					
1/3	5	−64.702	139.800	0.000	0.201
1/3/5	6	−63.880	140.300	0.520	0.155
1/3/6	6	−64.366	141.300	1.490	0.095
1/2/3	6	−64.442	141.400	1.640	0.089
1/3/5/6	7	−63.522	141.800	1.990	0.074
1/2/3/5	7	−63.542	141.800	2.030	0.073
1/3/4	6	−64.658	141.900	2.070	0.071
1/3/4/5	7	−63.849	142.400	2.640	0.054
1/2/3/6	7	−63.915	142.600	2.770	0.050
1/2/3/5/6	8	−62.941	142.800	3.040	0.044
1/3/4/6	7	−64.239	143.200	3.420	0.036
1/2/3/4	7	−64.427	143.600	3.800	0.030
1/3/4/5/6	8	−63.410	143.800	3.980	0.027
Timing of disappearance (individuals of unknown fate)					
1/3/5	6	−123.825	260.000	0.000	0.228
1/5	5	−125.001	260.300	0.240	0.202
1/2/5	6	−124.677	261.700	1.700	0.097
1/3/4/5	7	−123.722	262.000	1.930	0.087
1/4/5	6	−124.831	262.000	2.010	0.083
1/2/3/5	7	−123.816	262.100	2.110	0.079
1/3/5/6	7	−123.824	262.200	2.130	0.079
1/5/6	6	−124.992	262.400	2.340	0.071
1/2/4/5	7	−124.498	263.500	3.480	0.040
1/2/5/6	7	−124.677	263.900	3.830	0.034

Variables: age = 1, group size = 2, population density = 3, parental age = 4, parental replacement = 5, sex = 6, status = 7.

Table A3

The most parsimonious models within $\Delta AIC_c < 4$ for the analysis of the variation in dispersal age/age at disappearance (unknown fate individuals) in the Eurasian beaver based on data collected between 1998 and 2015 in southeast Norway

Variables	*df*	Log likelihood	AIC_c	ΔAIC_c	AIC weight
3/6	3	−182.28	370.8	0	0.158
2/3/6	4	−181.55	371.5	0.71	0.111
3/5/6	4	−182.04	372.5	1.69	0.068
3/4/6	4	−182.05	372.5	1.71	0.067
1/3/6	4	−182.06	372.5	1.72	0.067
2/3/6/2×6	5	−181.14	372.9	2.08	0.056
3/6/3×6	4	−182.24	372.9	2.09	0.056
2/3/5/6	5	−181.29	373.2	2.38	0.048
2/3/4/6	5	−181.41	373.4	2.63	0.042
2/3/6/3×6	5	−181.48	373.5	2.76	0.04
1/2/3/6	5	−181.55	373.7	2.9	0.037
1/3/5/6	5	−181.71	374	3.22	0.032
3/4/5/6	5	−181.82	374.2	3.45	0.028
3/5/6/5×6	5	−181.9	374.4	3.6	0.026
1/3/4/6	5	−181.91	374.4	3.61	0.026
3/5/6/3×6	5	−182	374.6	3.79	0.024
3/4/6/4×6	5	−182	374.6	3.8	0.024
2/3/5/6/2×6	6	−180.9	374.6	3.83	0.023
3/4/6/3×6	5	−182.02	374.6	3.84	0.023
1/3/6/3×6	5	−182.03	374.6	3.87	0.023
1/3/6/1×6	5	−182.05	374.7	3.9	0.023

Variables: group size = 1, population density = 2, parental age = 3, parental replacement = 4, sex = 5, status = 6.

Paper III

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ORIGINAL ARTICLE

The 7-year itch: non-adaptive mate change in the Eurasian beaver

Martin Mayer[1] · **Fabian Künzel**[1,2] · **Andreas Zedrosser**[1,3] · **Frank Rosell**[1]

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Abstract

Mate change in socially monogamous species can be explained by adaptive and non-adaptive hypotheses. Adaptive hypotheses describe a mate change as a strategy to correct for initial mate choice and to improve reproductive success: the 'incompatibility' hypothesis states that mate change is initiated by both mates, whereas in the 'better option' hypothesis, one partner initiates the mate change. In contrast, non-adaptive hypotheses predict mate change to be independent from previous reproduction: the 'forced divorce' hypothesis suggests that mate change is initiated by an incoming individual and the 'obligate mate change' hypothesis states that the mate change occurs after the accidental death of a partner. We investigated these hypotheses in the socially monogamous Eurasian beaver (*Castor fiber*), using data from a long-term study in southeast Norway between 1998 and 2014. Generally, the mate change occurred in the seventh year of a partnership and the staying individual repaired with a younger, incoming individual. The fate of the replaced individual was mostly unknown. Resident individuals had a decreased reproductive success with increasing age but gained no benefits from a mate change in terms of reproduction. Thus, we reject the adaptive hypotheses as cause of mate change. Our results support non-adaptive mate change hypotheses, most likely the 'forced divorce' hypothesis and to a lower degree the 'obligate mate change' hypothesis.

Significance statement

We investigated the causes of mate change in the Eurasian beaver, a long-lived, monogamous mammal living in family groups. We found that mate change was not initiated by a member of the mated couple but rather by the intrusion of an incoming individual as suggested by the 'forced divorce' hypothesis. Additionally, mate change was partly caused by the accidental loss of a partner. Mean reproductive success did not change after a mate change but with increasing age of the resident individual suggesting senescence. Together with a study on Alpine marmots, this is one of the first studies investigating mate change in mammals.

Keywords Forced divorce · Mammals · Monogamy · Pair bond · Reproductive success

Introduction

A mating system is defined as socially monogamous when females and males form exclusive pairs for at least one reproductive event or breeding season and as genetically monogamous when the members of a pair share exclusive parentage (Reichard and Boesch 2003). Only a minority of socially monogamous animal species have a unique, holistic, monogamous lifetime partnership, and generally individuals will accept a new mate if the first mate dies or is lost

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Martin Mayer and Fabian Künzel contributed equally to this work.

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✉ Martin Mayer
martin.mayer@usn.no

[1] Department of Environmental and Health Studies, Faculty of Arts and Sciences, University College of Southeast Norway, 3800 Bø i Telemark, Norway

[2] Faculty of Mathematics and Natural Science, Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany

[3] Department of Integrative Biology, Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Austria

otherwise, i.e. serial or sequential social monogamy (Wickler and Seibt 1983).

Mate choice is a critical factor for an individual's reproductive success, especially in monogamous species. However, individuals may be forced to pair with a suboptimal mate because the process of mate selection is competitive and limited in time (Luttbeg 2002). Behavioural strategies to adjust for initial mate choice are extra-pair copulation (EPC) (Møller 1988; Forstmeier et al. 2014) or adaptive mate change, i.e. divorce. Hypotheses regarding the cause of divorce (Table 1) have been investigated particularly in birds (Choudhury 1995). The 'incompatibility' hypothesis suggests that a pair with poor genetic or behavioural compatibility divorces to pair with more compatible mates. The decision to divorce is assumed to be mutual by both sexes, and divorce is more likely to occur early in a partnership and in pairs with low reproductive success (Choudhury 1995). As a consequence of mating with a new mate, both members of the original pair should increase their reproductive success after divorce (Choudhury 1995; Ens et al. 1996). In contrast, the 'better option' hypothesis states that only one partner initiates a divorce, and only this individual will improve its reproductive success after re-pairing with a higher quality mate (Ens et al. 1993; Choudhury 1995). Both hypotheses suggest that divorce is an adaptive strategy to correct for initial mate choice. However, Taborsky and Taborsky (1999) introduced a non-adaptive hypothesis, the 'forced divorce' hypothesis, where divorce is proposed to be the outcome of intra-sexual competition. The divorce is caused by the intrusion of a third individual who outcompetes the same-sex member of a pair. This process is independent of previous reproductive success, which should not improve for the resident after pairing with the new mate (Taborsky and Taborsky 1999). Studies in birds suggest that 'forced divorce' is most common in populations at or close to carrying capacity when competition for mates increases (Taborsky and Taborsky 1999; Heg et al. 2003; Jeschke et al. 2007). Another non-adaptive hypothesis, the 'obligate mate change' hypothesis, states that the accidental death of a partner, i.e. widowing (e.g. due to hunting), leads to a divorce (Lardy et al. 2011).

Divorce in monogamous species has been reported for invertebrates (Beltran et al. 2008), fish (van Breukelen and Draud 2005), birds (Heg et al. 2003; Jeschke et al. 2007; Dreiss and Roulin 2014), rodents (Svendsen 1989) and primates (Palombit 1994). However, to our knowledge, the only study testing hypotheses about the causes of mate change in mammals was carried out on the Alpine marmot (*Marmota marmota*) finding evidence for the 'forced divorce' hypothesis (Lardy et al. 2011).

Here, we investigated the causes of mate change in a socially monogamous mammal, the Eurasian beaver (*Castor fiber*), by comparing the 'incompatibility', the 'better option', the 'forced divorce' and the 'obligate mate change' hypotheses (Table 1) using data from a long-term study in southeast Norway. For the 'incompatibility' hypothesis, we predicted that a mate change occurs early in a partnership and is dependent on previous reproductive success. Therefore, reproductive success in pairs where no mate change occurs was expected to be higher than in pairs that later experienced a mate change. In addition, we tested whether the age difference between the members of the dominant pair affected the probability of a mate change, predicting that pairs with a larger age difference were more likely to divorce as shown in humans (Kalmijn and Poortman 2006). For the 'better option' hypothesis, we predicted an improved reproductive success of the resident after re-pairing with a new mate. For the 'forced divorce' hypothesis, we predicted that the mate change is independent of reproductive success and will not increase after re-pairing. In order to successfully challenge a resident dominant beaver, we also expected the incoming individual to be of similar or greater body mass than the individual replaced by the divorce. For the 'obligate mate change' hypothesis, we predicted that the body mass of the incoming individual would be independent of replaced individual's mass and that the mate change would be independent of the reproductive success. Further, we hypothesised

Table 1 Hypotheses and their predictions regarding mate change in socially monogamous species

Hypothesis	Definition	Predictions
'Better option'	Mate change is initiated by one pair member	Mate change is beneficial (better mate, better territory, improved reproduction) only for the individual initiating the mate change
'Incompatibility'	Mate change is initiated by both pair members and dependent on previous reproductive success	Mate change occurs early in the partnership, and reproductive success improves for both individuals after the mate change
'Forced divorce'	Mate change is independent from previous reproductive success and initiated by an intruder	No improvement of reproductive success after the mate change
'Obligate mate change'	Mate change is caused by the accidental death of the replaced individual and is independent from previous reproductive success	No improvement of reproductive success after the mate change

that the mate change rate (i.e. the proportion of mate change in a population) would be related to a fluctuating population density.

Material and methods

Study species

The Eurasian beaver is a large, socially monogamous rodent. It is similar to the North American beaver (*Castor canadensis*); both species live in family groups consisting of the dominant pair and offspring from the current and previous years (Sun 2003). Beavers are considered obligate monogamous as they exhibit a high degree of biparental care (Wilsson 1971; Kleiman 1977; Sharpe and Rosell 2003). Juvenile beavers stay in their natal territory until they reach sexual maturity and usually disperse thereafter to establish a territory of their own (Svendsen 1989; Hartman 1997; McNew et al. 2005) but may remain within the natal territory as old as 7 years (Mayer et al. 2016). Only the dominant pair reproduces with copulation taking place between late January and February and one to four kits usually born around mid-May (Parker and Rosell 2001; Sun 2003). Pairs form year round, but pair formation was shown to peak (56 % of all known pairs) in September, October and November in a population of North American beavers (Svendsen 1989). Once paired, beavers remain a couple for long periods (Wilsson 1971; Svendsen 1989; Sun 2003). Due to this behaviour, beavers are assumed to be genetically monogamous (Sun 2003; Busher 2007). However, the first molecular study investigating paternity in North American beavers revealed the presence of EPC (Crawford et al. 2008). In contrast, Syrůčková et al. (2015) did not find any evidence of EPC in a Eurasian beaver population. Dominant adults are highly territorial and both sexes participate in scent marking and territorial defence (Jenkins and Busher 1979; Rosell and Nolet 1997). Intruders are treated aggressively and territorial combat can result in serious or even fatal injuries (Nolet and Rosell 1994; Crawford et al. 2015).

Study area and data collection

The study area consisted of the three rivers Straumen (59° 29′ N, 09° 153′ E), Gvarv (59° 386′ N, 09° 179′ E) and Sauar (59° 444′ N, 09° 307′ E) in Telemark County, southeast Norway (Campbell et al. 2012). The population density was saturated in all three rivers (Campbell et al. 2012) with adjacent territories and no unoccupied stretch of river in between (Herr and Rosell 2004). Hunting pressure in the study area was considered to be low (Campbell et al. 2012). Because wolves (*Canis lupus*) and bears (*Ursus arctos*) were functionally absent, and lynx (*Lynx lynx*) occurred in low densities, predation pressure was also considered to be low (Rosell and Sanda 2006).

Beavers were monitored since 1998 via an extensive live-trapping program during spring (March–June) and fall (August–October) each year (Steyaert et al. 2015). Capture took place at night from a motor boat with a landing net, and beavers were immobilized in a cloth sack during handling without medical sedation (Rosell and Hovde 2001). The colour of the anal gland secretion was used to determine the sex of individuals (Rosell and Sun 1999), and beavers were weighed to the nearest 500 g. For individual identification, all beavers were tagged with a microchip and a unique combination of plastic or metal ear tags (Campbell et al. 2012). Individuals were confirmed as dominant (being the reproducing individual) from genetic paternity tests (FR, unpublished data) and via multiple capture and sighting events and lactation in females. Unless dominant individuals disappeared or died, they were assumed to maintain their status (most individuals were captured annually). Individuals that had newly dispersed into a territory were considered as dominant if the previously dominant territory holder of the same sex disappeared at the same time (Campbell et al. 2012) and based on positive paternity tests. Annual reproductive success was defined as the number of kits in a given year and was based on the number of trapped and observed kits plus the number of unmarked yearlings captured in the following year (i.e. kits missed the previous year) (Campbell et al. 2013). Also, we recorded family group sizes every year (after the kits had emerged from the lodge) based on captures and observations. It was not possible to record data blind because our study involved focal animals in the field.

Data preparation

We defined mate change as when one of the dominant individuals (hereafter the replaced) was no longer observed in the territory or was found dead and another individual of the same sex (the successor) had obtained the dominant breeding position together with the remaining individual (the resident). We defined the timing of mate change as the year t when the replaced was last observed in its territory and the start of the new pair bond between the successor and the resident in the year when the successor was first observed (which could be either year t (4 cases) or $t + 1$ (21 cases)).

For individuals first trapped as kit or yearling, exact age determination was possible. For older individuals (≥2 years), a minimum age was assigned when first captured based on body mass (Rosell et al. 2010) with beavers being classified as minimum 2-year-olds when they had a mass ≥17 and ≤19.5 kg or as minimum 3 years when >19.5 kg at the time of first capture (e.g. a beaver captured for the first time in 1999 with 18 kg was classified as minimum 2 years old and therefore, when captured again in 2002, it was classified as minimum 5 years old). We tested if the assigned age was a good estimate for individuals of uncertain age (replaced = 15, residents = 15, successor = 6) and compared them with individuals of known age (replaced = 5, residents = 5, successor = 14) separately for each group using a Mann-Whitney U test. There was no difference between the age of replaced individuals (9.66 ± 3.39 (mean ± standard error) years vs. 9.40 ± 4.22, $p = 0.965$), residents (8.93 ± 3.71 vs. 8.00 ± 2.00 years, $p = 0.597$) and successors (4.67 ± 4.18 vs. 4.43 ± 2.77 years, $p = 0.802$). Therefore, we considered the assigned age as a good estimate and used it for further analyses. To test for age differences, the age of all groups (replaced, resident and successor) was assigned to year t.

The mass measurements were taken in either year t or $t-1$ for the replaced and year t or $t+1$ for the successor but with a maximum difference of 1 year between replaced and successor. To correct for the year difference (if captured in different years), we estimated mean annual growth increments separately for male and female beavers using a generalized linear mixed model (GLMM) using the package *lme4* (Bates et al. 2015) following Campbell (2010). Both models were based on mass measurements from beavers of known ages (males = 210 observations, females = 137 observations, Fig. S1). The models were carried out with an identity link, mass as dependent variable, age and age^2 as fixed effects and the individual ID as random effect. We then used these mean growth increments (Fig. S1) to correct the mass of the replaced or the resident to the year t, based on the estimates of the models. Because beavers gain mass during summer (Smith and Jenkins 1997), all measurements were additionally adjusted to the same day of the year (Julian day 182, first of July), using an estimated daily growth rate of 0.012 kg for adults and 0.021 kg for subordinates (Campbell 2010). Population density was measured annually as the mean number of individuals per family group separately for each study site.

Data analysis

For our analyses, we only used individuals of known and finished duration of territory occupation. To test the 'incompatibility' hypothesis, we compared the annual reproductive success of pairs that experienced a mate change only using the original pair (i.e. the resident with the replaced, $n = 19$ pairs, 108 pair years) with the annual reproductive success of pairs that remained together for their whole life ($n = 7$ pairs, 46 pair years). We used a GLMM with the occurrence of mate change in a given year (yes vs. no) as dependent variable and the pair as random effect to account for multiple observations. We included as fixed effects the annual reproductive success (as measure of compatibility), the age difference between the male and female of the dominant pair (as another measure of compatibility, predicting that pairs with a greater age difference would be less compatible) and the pair bond length (to test the prediction that a mate change should occur early in a partnership).

To test the 'better option' and 'forced divorce' hypotheses, we tested if the annual reproductive success of the resident increased ('better option') or was unchanged ('forced divorce') when mated with the first (the replaced) and the second partner (the successor) in pairs that experienced a mate change ($n = 19$ mate changes and 38 pairs (18 residents, from which one had three mates), 166 pair years). We used a GLMM with a negative binomial error distribution of the response variable, using the R package *glmmADMB* (Bolker et al. 2012) in order to correct for a non-normal distribution of the annual reproductive success and to correct for zero inflation (O'hara and Kotze 2010). The annual reproductive success was the dependent variable, and the resident was used as the random effect. The mate order (mate 1 vs. mate 2), the age difference within the pair (for the original and the new pair, respectively), the pair bond length, the age of the resident individual (to control for possible age effects) and the interaction between the mate order and the sex of the resident (to test if the mate change only had advantages for one sex) were included as fixed effects.

To further test the 'forced divorce' hypothesis, we compared the body mass between the successor and the replaced (which was known in 11 cases) using a paired Mann-Whitney U test; and we investigated whether replaced individuals disappeared due to conspecific aggression ('forced divorce') or accidents ('obligate mate change').

We calculated the annual mate change rate for each year and study site by dividing the number of mate changes by the number of observed pairs. To check if the mate change rate (dependent variable) was related to the adult population density (independent variable, kits and yearlings were excluded assuming that they would not challenge a resident), we used a linear mixed-effect model (LME) using the R package *lmerTest* (Kuznetsova et al. 2013) with the study site as random effect. The mate change rate was square-root transformed to meet assumptions of normality and homogeneity of variance (Hu 2007).

The fixed effects/independent variables used in all analyses were not correlated (all Pearson r coefficient < 0.6) and variance inflation factor values were <3 (Zuur et al. 2010). Model selection was carried out using Akaike's Information Criterion (AIC$_c$ values) (Burnham and Anderson 2002; Arnold, 2010). We used the dredge function in the R package *MuMIn* (Barton 2013) to create candidate models including all possible combinations of fixed effects (no interactions were included due to the small sample sizes). Parameters that included zero within their 95 % confidence interval (CI) were considered as uninformative (Arnold 2010). All analyses were conducted in R 3.1.1 (R Core Team 2015). Mean values are given with standard error (SE).

Results

Sixty-two beaver pairs consisting of 101 dominant individuals were observed in 30 territories from 1998 to 2014 (44 partnerships were terminated at this time). During this period, 73 individuals had one mate, 16 individuals had two mates, for eight individuals the number of mates was uncertain and four individuals had more than two mates with a maximum of four mates.

For 25 pairs the partnership ended in a mate change, 19 pairs were still together at the end of this study, in 11 cases both members of the pair were replaced by a new dominant pair (of these replaced pairs, seven pairs stayed together for life, i.e. had only one partner, and four had had another partner previously) and seven cases were uncertain due to a lack of information on the end of the partnership or the new mate. Human-caused mortality (hunting and car accidents) accounted for 20 % of the mate changes (five cases out of 25). These cases, uncertain cases and cases with incomplete information, were not used for further analyses. The average annual mate change rate was 7.03 ± 10.35 % and tended to decrease negatively with increasing adult population density ($\beta \pm \mathrm{SE} = -1.093 \pm 0.546$, $p = 0.056$). When including kits and yearlings in the calculation of the population density, this trend became significant ($\beta \pm \mathrm{SE} = -0.743 \pm 0.326$, $p = 0.030$, Fig. 1).

The average pair bond length of all terminated partnerships in the study area was 4.73 ± 3.04 years (range = 1–14 years, $n = 44$). Pairs that remained together for life had an average pair bond length of 6.57 ± 2.07 years (range = 4–9 years, $n = 7$). In pairs that experienced a mate change, the partnership with the first mate lasted on average significantly longer than with the second mate (paired Mann-Whitney U test = 6.25 ± 3.53 vs. 3.06 ± 1.84 years, $n = 19$, $p = 0.007$, Fig. 2).

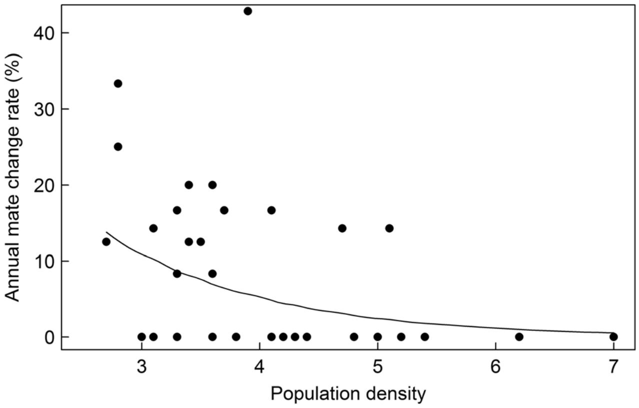

Fig. 1 Predicted relationship between the population density (measured as the annual average number of individuals per family group including kits and yearlings separately for each river) and the annual mate change rate (%) for our Eurasian beaver population in southeast Norway, 1998–2014

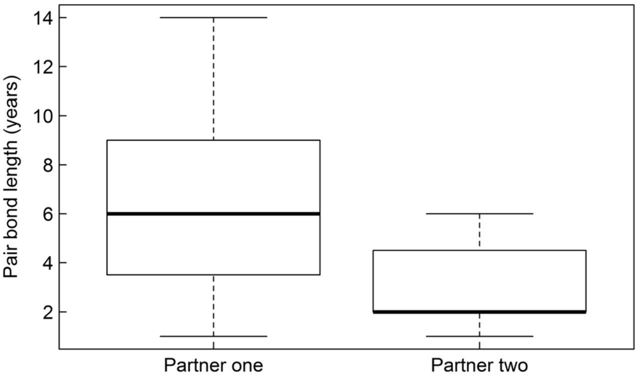

Fig. 2 Box plot showing the pair bond length (in years) with the first and the second partner ($n = 19$ pairs) for data of Eurasian beavers in southeast Norway, 1998–2014. The box plots show median values, 25th and 75th percentile and the range of the data

For pairs that stayed together for life ($n = 7$), the average annual probability to reproduce was 0.39 ± 0.49 and they had on average 0.59 ± 0.86 kits per year (median = 0). In pairs that experienced a mate change and where we had information on annual reproductive success ($n = 19$ mate changes), the average annual probability to reproduce was 0.38 ± 0.49 with the first mate (on average 0.60 ± 0.86 kits per year, median = 0) and 0.28 ± 0.45 with the second mate (on average 0.45 ± 0.86 kits per year, median = 0).

In the 20 mate changes (that were not human-caused), nine males and 11 females were replaced. The fate of the replaced was unknown in 17 cases, in two cases the replaced was found dead and in one case it established a new territory and re-paired with a new individual (Table 2). From the 20 successors, 11 were subdominant before intruding the new territory, two were previously dominant and seven came from outside the study area (Table 2). No successor was born in the same family group as the replaced individual.

Testing the ‘incompatibility’ hypothesis

There was no age difference (in the year the partnership ended) between individuals of pairs where both partners were simultaneously replaced as compared to individuals of pairs that later experienced a mate change (9.00 ± 2.63 vs. 9.61 ± 2.90 years, Mann-Whitney U test: $p = 0.412$). The occurrence of a mate change was not related to the annual reproductive success, the age difference within pairs or the pair bond length but was best explained by the intercept alone model ($n = 26$ pairs, 154 pair years, Table 3).

Testing the ‘better option’ and ‘forced divorce’ hypotheses

The age difference between the male and the female of the original pair was significantly smaller than the age difference

Table 2 Overview of male and female replaced individuals and incoming individuals (successors) involved in mate change in a Eurasian beaver population in southeast Norway, 1998–2014

	Male	Female	Total
Replaced	9	11	20
Fate			
Unknown	8	9	17
Dead	1	1	2
Re-paired	0	1	1
Successor	9	11	20
Status			
Unknown	3	4	7
Subdominant	5	6	11
Dominant	1	1	2

For the replaced individuals, the fate is shown after the mate change. For the successors, the social status before intruding is shown

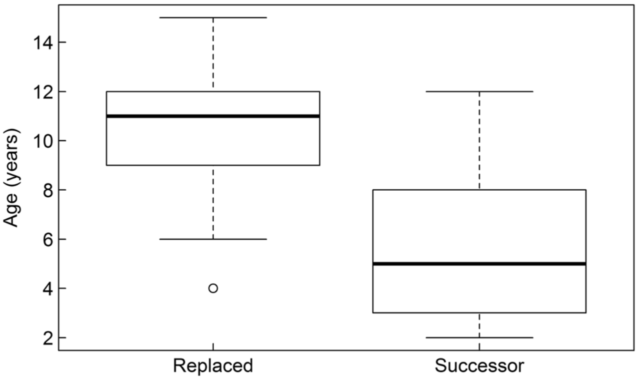

Fig. 3 Box plot showing the age (in years) of the replaced and the successor (n = 38 individuals) in the year the mate change occurred for data of Eurasian beavers in southeast Norway, 1998–2014. The box plots show median values, 25th and 75th percentile and the range of the data including an outlier (*dot*)

between the remaining individual of the original pair and its second mate (1.63 ± 2.34 vs. 4.74 ± 4.07 years, Mann-Whitney U test: $p = 0.005$). Annual reproductive success decreased with increasing age of the resident but was independent from the mate order, the age difference between the original and the new pair, the pair bond length and the sex of the resident (n = 19 mate changes, 38 pairs, 166 pair years, Table 3). Replaced individuals were significantly older than successors in the year the mate change occurred (10.21 ± 2.70 vs. 6.00 ± 3.43 years, $n = 20$, $p < 0.001$, Fig. 3), but there was no significant difference in body mass (replaced = 21.43 ± 2.52 kg vs. successor = 19.44 ± 3.35 kg, n = 11 mate changes, $p = 0.240$).

Discussion

Our study showed that mate change in the Eurasian beaver was independent of previous reproductive success and that reproductive success did not increase after a mate change. Therefore, we reject the adaptive 'incompatibility' and 'better option' hypotheses. Our results support the non-adaptive

Table 3 The five most parsimonious and the full model (based on AIC weights) for the analysis of the probability of mate change and the variation in annual reproductive success in the Eurasian beaver based on data collected between 1998 and 2014 in southeast Norway

Probability of mate change								
Model	Fixed effects	Estimate ± SE	LCI	UCI	*df*	AIC_c	ΔAIC	AIC weight
1	Intercept	14.09 ± 2.57	NA	NA	152	26.90	0.00	0.399
2	Age difference				151	28.90	1.99	0.147
3	Pair bond length				151	29.00	2.06	0.142
4	Annual reproductive success				151	29.00	2.08	0.141
5	Age difference + pair bond length				150	31.00	4.05	0.053
Full	Age difference + pair bond length + annual reproductive success				148	33.10	6.19	0.018
Annual reproductive success								
Model	Fixed effects	Estimate ± SE	LCI	UCI	*df*	AIC_c	ΔAIC	AIC weight
1	Resident age	−0.12 ± 0.04	−0.20	−0.04	162	328.40	0.00	0.299
2	Age difference + resident age				161	330.10	1.70	0.128
3	Partner + resident age				161	330.40	2.04	0.108
4	Pair bond length + resident age				161	330.50	2.12	0.104
5	Partner + resident age + partner × resident sex				159	331.00	2.68	0.078
Full	Age difference + pair bond length + partner + resident age + partner × resident sex				157	334.60	6.24	0.013

The remaining degrees of freedom (*df*), the AIC_c and ΔAIC are given for all models. For the best model (model 1), parameters are given with estimates (β), standard error (SE) and lower (LCI) and upper (UCI) 95 % confidence intervals hypotheses, i.e. the 'forced divorce', and to a lesser degree the 'obligate mate change' hypotheses.

Adaptive hypotheses

When evaluating the causes of mate change, it is crucial to identify which mate initiated the mate change. We only had data on the reproductive success after a mate change for residents, however never for the replaced, because in most cases the replaced was assumed to be dead or to have dispersed outside the study area.

The 'incompatibility' hypothesis predicts that in cases when both partners initiate a mate change simultaneously, then such a change should occur early in a partnership and should be more likely for pairs with low reproductive success (Ens et al. 1996). In our study, mate change occurred on average in the seventh year of a partnership and was independent from previous annual reproductive success. The average pair bond length in our study was 4.95 years as compared to 2.5 years in a North American beaver population (Svendsen 1989). These differences might be due to different population densities or environmental factors in the respective populations.

Year-round territorial species are generally assumed to exhibit strong site fidelity, as the benefits of holding a territory are expected to be greater than the costs of being paired with a low-quality or incompatible mate (Morton et al. 2000). For example, buff-breasted wrens (*Thryothorus leucotis*) were more faithful to their territories than to their mates (Gill and Stutchbury 2006). This might be especially the case in saturated populations with only very few available territories and a high intruder pressure, such as our study population (Mayer et al. 2016), and is also in line with Lardy et al. (2011) who suggested that deserting a territory would be very costly for a dominant individual. Hence, we consider it unlikely that a one or both members of the pair initiated the partner change and left its territory. Nevertheless, secondary dispersal might occur as shown in a North American beaver population (Sun et al. 2000) but is considered unlikely as only one dominant individual (replaced) re-established after a mate change and because of the high population density in our area.

If the resident initiated the mate change, it presumably would gain some benefits (e.g. an improved reproductive success) according to the 'better option' hypothesis (Ens et al. 1993; Choudhury 1995). As residents in our study were never observed changing their territory, the benefits should be directly related to the quality of the new mate. For example, in the endoparasite *Schistosoma mansoni*, the divorce rate increased when females were given the chance to increase genetic dissimilarity through re-pairing (Beltran et al. 2008). However, the mitochondrial DNA haplotype variation is zero in beavers from southeast Norway (Durka et al. 2005), and there is also little variation in nuclear fingerprinting profiles (Ellegren et al. 1993). In addition, the reproductive success in our population is lower as compared to German and Russian beaver populations with greater genetic diversity (Heidecke 1984; Saveljev and Milishnikov 2002; Halley 2011). This suggests that reproductive benefits achieved by a mate change may be low due to genetic causes.

Non-adaptive hypotheses

Our results show that mate change was not due to low reproductive success with the initial partner, and it did not increase after mating with a new partner. This suggests that mate change in the Eurasian beaver is non-adaptive, similar to alpine marmots (*M. marmota*) (Lardy et al. 2011) and common guillemots (*Uria aalge*) (Jeschke et al. 2007).

The reproductive success decreased with increasing age of the resident suggesting senescence.

We found no difference in body mass between the replaced and the successor. In our study population, mass gain stagnated approximately at age 6 in both sexes and decreased in males around age 8 (but not in females), indicating senescence (replaced individuals were on average 10 years old). Moreover, movement patterns of dominant beavers in our study area changed over time, with older individuals spending more time on land (Graf et al. 2016), which might also indicate senescence. Hu and Morse (2004) showed that in male crab spiders (*Misumena vatia*) of similar body mass, young individuals were more successful in encounters than old ones. Also, middle-aged male song sparrows (*Melospiza melodia*) were more successful in expanding and regaining territories as compared to younger or older individuals (Arcese 1989). This indicates that, after a certain point, competitive ability decreases with increasing age, which may result in competitive advantages for incoming younger successors. We found two dead individuals with bite marks and captured four injured individuals with bite marks suggesting territorial fights between replaced and successor. Moreover, most of the adult beavers we captured had tail scars, indicating frequent conspecific disputes (MM, unpublished result), which is in line with Crawford et al. (2015) who showed that conspecific aggression is widespread in North American beavers. Additionally, the population densities in our area were very high (Campbell et al. 2012) possibly leading to a high intruder pressure. Combined, these findings support the 'forced divorce' hypothesis suggesting that younger beavers intrude a territory and take it over after a physical dispute.

We found some evidence that the mate change rate increased with decreasing population density. A reduction in the population density was likely caused by increased mortality, either via intraspecific competition in line with the 'forced divorce' hypothesis or via other causes of mortality (e.g., hunting, accidents), resulting in the widowing of the resident, i.e. the 'obligate mate change' hypothesis. Although considered low (Campbell et al. 2012), the hunting pressure in our area might be higher than suspected as cryptic hunting was reported in many wildlife species (Gavin et al. 2010; Liberg et al. 2012) and might be in fact a driver of the beaver population in Telemark. This is partly supported by the high number of unknown fates of replaced beavers (which likely did not undergo secondary dispersal (Campbell et al. 2005)) and because 20 % of all mate changes were due to legal hunting. Population densities would be expected to decrease with increasing hunting pressure, and Parker et al. (2002) showed that adult and pregnant beavers were more likely to be shot. Consequently, the mate change rate could increase with increasing hunting pressure due to widowing, supporting the 'obligate mate change' hypothesis. In wolves (*Canis lupus*), Milleret et al. (2016) showed that the majority of pair dissolutions were related to human-caused mortalities, such as legal control actions and cryptic hunting. Also, Forslund and Larsson (1991) found that mate change in barnacle geese (*Branta leucopsis*) was the consequence of the (likely accidental) loss of one partner.

In conclusion, we found support for the prediction of Lardy et al. (2011) that adaptive hypothesis of mate change should be poorly supported in monogamous long-lived species that hold a territory year-round. Our study adds to the small number of studies suggesting non-adaptive hypotheses as the cause of mate change in monogamous mammals.

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Conflict of interest The authors declare that they have no conflict of interest.

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Supplementary material

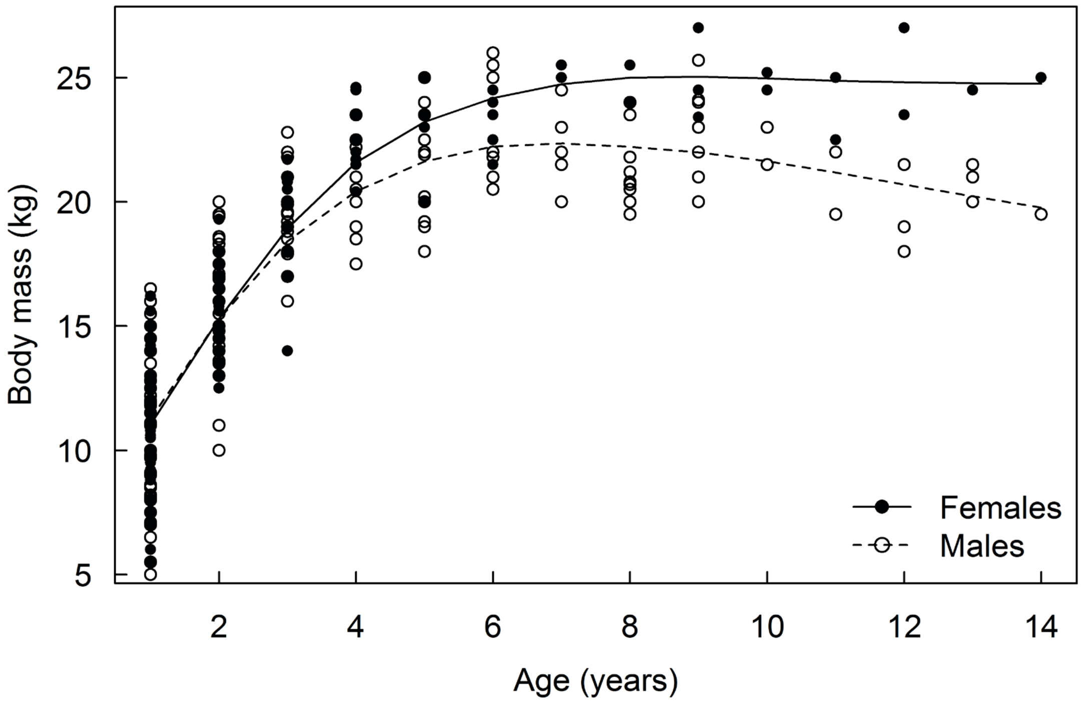

Figure S1 Body mass (kg) of male and female Eurasian beavers in relation to their known age, based on 347 observations (males = 210; females = 137) in southeast Norway, 1998 - 2014

Paper IV

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Original investigation

Territory size and age explain movement patterns in the Eurasian beaver

Patricia M. Graf[a,b,1], Martin Mayer[a,*,1], Andreas Zedrosser[a,b], Klaus Hackländer[b], Frank Rosell[a]

[a] Department of Environmental and Health Studies, Faculty of Arts and Sciences, University College of Southeast Norway, Bø i Telemark, Norway
[b] Department of Integrative Biology and Biodiversity Research, Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Austria

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ABSTRACT

Territoriality is only profitable when the benefits gained from territory exploitation exceed the costs of defence, and territory sizes are usually optimized by time constraints related to resource defence (e.g. patrolling) and exploitation. In this study, we equipped 25 dominant Eurasian beavers (*Castor fiber*) with GPS units to study spatial movement patterns both on land and in water in relation to territory size, resource availability, the number of neighbours, season, and the beavers' age. We show a territory size-dependent trade-off between territorial behaviours and foraging distances: Beavers in larger territories moved greater distances each night, thereby spending more time patrolling, and stayed closer to the shoreline when being on land (i.e. when foraging). Inversely, in smaller territories beavers patrolled less and foraged further away from the shoreline. These results suggest that individuals trade-off the costs of patrolling larger territories against the benefits of foraging closer towards the shoreline. Smaller territories might be more prone to resource depletion, thus, making foraging further from the shoreline a strategy to ensure sustainable resource use. Further, older beavers spent more time on land and close to territory borders compared to younger ones, suggesting a behavioural change with age possibly due to increased experience and boldness.

Introduction

Territoriality is linked to the defence of a fixed area by an individual or a group of mutually tolerant individuals (Maher and Lott, 1995). Animals typically occupy territories when resources, such as food, cover, shelter, and mating partners, are scarce (Brown, 1969; Davies and Houston, 1984; Maher and Lott, 1995). Territorial behaviour is expected to evolve when the benefits gained from the exclusive use of essential and restricted resources exceed the costs of defence (Brown, 1964; Stamps, 1994). Defence mechanisms are diverse and may include aggressive, physical disputes with intruders, which generally impose significant metabolic costs (Parker, 1974; Viera et al., 2011), and advertisement of territory ownership by chemical (e.g. scent-marking) (Gosling and Roberts, 2001; Roberts and Dunbar, 2000), acoustic (Bee et al., 2000; McGregor, 1993), or visual signals (Burst and Pelton, 1983; Penteriani and del Mar Delgado, 2008). Patrolling territory borders is essential for effectively advertising territory occupation (Sillero-Zubiri and Macdonald, 1998) and is, besides foraging, an important driver of spatial movement behaviour in territorial species (Fagan et al., 2013; Ims, 1995).

Animals are continually subject to multiple decisions regarding energy investment and thus need to trade-off which activity to adopt at any time (Mangel and Clark, 1986). Such trade-offs may impact an animal's fitness and survival (Ohgushi, 1996; Stearns, 1989) and have been a research area of interest for decades. The literature in this field is extensive, however, most studies focus on the trade-offs between offspring size and offspring number (e.g. Charnov and Ernest, 2006; Fleming and Gross, 1990), foraging and predation risk (e.g. Lima et al., 1985; Sih, 1980; Verdolin, 2006), or growth and reproduction (e.g. Kozłowski, 1992; Roff, 1983). Studies investigating the trade-off between foraging and territorial behaviours are comparatively rare. For example, great tits (*Parus major*) traded off food intake for territory defence in the presence of an intruder (Kacelnik et al., 1981; Ydenberg and Krebs,

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* Corresponding author at: Faculty of Arts and Sciences, Department of Environmental and Health Studies, University College of Southeast Norway, 3800 Bø i Telemark, Norway.
E-mail addresses: martin.mayer@hit.no, m.mayer89@web.de (M. Mayer).

[1] These authors contributed equally to this work.

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1987). Jaeger et al. (1983) found that red-backed salamanders (*Plethodon cinereus*) decreased foraging time and devoted more time to territory defence when potential competitors intruded. Wild chimpanzees (*Pan troglodytes*) reduced their feeding time by at least 50% when on patrolling trips (Amsler, 2010).

Generally, the costs of territoriality are positively correlated with territory size, because larger areas are more costly to defend (Righton et al., 1998; Schoener, 1983). Determining the costs and benefits of different territory sizes in a species is difficult (Jaeger et al., 1983) and has been subject to a range of modelling approaches (e.g. Adams, 2001; Dill, 1978; Schoener, 1983). The optimization criterion for territory size is usually related to time constraints between resource defence and exploitation (Adams, 2001; Kacelnik et al., 1981), and has been described as the minimum economically defensible area (Gill and Wolf, 1975; Pyke et al., 1977). Adams (2001) suggested two additional factors that may influence territory sizes, i.e. interactions among neighbours and interactions between established residents and potential settlers. Such interactions may be especially important in high-density populations with contiguous territory borders (Adams, 2001), and may result in territory sizes smaller or larger than the minimum economically defensible area. Further, individual differences in movement patterns might be related to age: e.g. Cederlund and Sand (1994) found that older male moose (*Alces alces*) had larger home ranges than younger ones, which may be caused by differences in nutritional demands and social activities like rutting behaviour. Similarly, in tailed frogs (*Ascaphus truei*) (Daugherty and Sheldon, 1982) and pinnipeds (Baker et al., 1995; Cameron et al., 2007), older individuals exhibited greater site fidelity than younger ones, which was suggested to be related to sexual maturation, age-specific variation in ecological requirements and accumulated knowledge on breeding site characteristics.

We used the Eurasian beaver (*Castor fiber*) to investigate factors affecting spatial movement patterns in a long-lived, territorial animal. Beavers (both the Eurasian and the North American beaver (*Castor canadensis*)) are semi-aquatic, nocturnal rodents that are socially monogamous and live in family groups consisting of the dominant pair, the young of the year, yearlings, and subadults, i.e., non-dominant individuals of two years or older (Campbell et al., 2005; Wilsson, 1971). The two beaver species are in the small percentage of mammals (3–5%) that form monogamous pair bonds (Kleiman, 1977) with complex social behaviours including male parental care and shared territorial defence (Busher, 2007). Beavers build lodges or bank dens and are central-place foragers with a preference for poplars (*Populus* sp.) and willows (*Salix* sp.) (Haarberg and Rosell, 2006; Vorel et al., 2015). They move relatively close to the shoreline and feed within approx. 40 m from the water's edge (Barnes and Dibble, 1988; Parker et al., 2001). The beavers' fusiform body with short limbs and webbed hindfeet make them good, enduring swimmers, but constrain their agility in terrestrial environments (Allers and Culik, 1997). Beavers hold larger territories during initial settlement, whereas in populations at carrying-capacity territories of various sizes are occupied (Campbell et al., 2005). To advertise territory occupation, both sexes deposit scent-marks within their territories, especially along up- and downstream borders (Hodgdon, 1978; Rosell et al., 1998; Sun and Müller-Schwarze, 1999). Scent-marking activity increases during spring when subadults disperse from their natal colony (Rosell et al., 1998). Territorial behaviour by both sexes is suggested to have evolved from a mate-guarding strategy and/or a resource defence strategy (both food and the physical family area, Busher, 2007). In autumn, beavers prepare food caches in front of their lodges to sustain the family during the cold months (Busher, 1996; Hartman and Axelsson, 2004). The dominant pair exhibits similar space use and movement behaviour, and does not reduce their patrolling activity in the presence of an increasing number of subordinate helpers in the colony (Herr and Rosell, 2004).

We deployed GPS units on dominant, territory-holding beavers to analyse terrestrial and aquatic movement patterns in relation to environmental and demographic factors. We hypothesized that terrestrial and aquatic movement patterns would depend on 1) territory size, 2) resource availability, 3) season, 4) intruder pressure (number of neighbours), and 5) age. We predicted that 1) owners of larger territories would move greater distances in water (i.e., have a higher relative patrolling effort), but 2) also have more opportunities to forage closer to the shoreline due to higher resource availability than owners of smaller territories. Third, we predicted that beavers would patrol more in spring when subadults are dispersing, and spent more time on land in autumn to prepare for winter, i.e., to build food caches and repair lodges. Fourth, we predicted that beavers would generally increase patrolling activities when facing higher intruder pressure as determined by the number of individuals in neighbouring colonies. And 5), we hypothesized that movement patterns would change with increasing age due to a shift in behavioural traits such as dominance and experience.

Material and methods

Study area, animals and capture

Our study was conducted between 2009 and 2014 in Telemark county, southeast Norway (Fig. 1). Data were collected in three connected rivers, the Straumen, Gvarv, and Saua, which flow through a semi-cultural and mixed forest landscape, and empty into Lake Norsjø. The rivers are mostly slow flowing and between 10 and 100 m wide with stable water levels, making it unnecessary for beavers to build dams. Woody vegetation along the rivers mostly consists of grey alder (*Alnus incana*), willow (*Salix* spp.), bird cherry (*Prunus padus*), common ash (*Fraxinus excelsior*), rowan (*Sorbus aucuparia*), birch (*Betula* spp.), and Norway spruce (*Picea abies*) (Haarberg and Rosell, 2006). The proportion of deciduous habitat was similar between the rivers in our study area (ANOVA: $F = 0.544$, $p = 0.586$) (Campbell et al., 2005). Hunting pressure in the area was presumably low (Rosell et al., 2000) with eight known cases of hunted beavers (4.6% of the known population) between 2009 and 2014 (unpublished results). Natural predators, predominantly Eurasian lynx (*Lynx lynx*), were present in low densities in our area (Herfindal et al., 2005). Red fox (*Vulpes vulpes*), which is known to occasionally predate on beaver kits (Kile et al., 1996), was also present.

Dominant Eurasian beavers were captured at night from a motorboat using landing nets from March to June (spring), and August to October (autumn) each year as part of a long term study (Steyaert et al., 2015). Dominance status (i.e., being the reproductive individual) had previously been assigned by multiple capture and sighting events in the same territory, body weight, lactation in females, and evidence indicating the disappearance of the previous dominant same-sex individual in that territory (Campbell et al., 2012). All individuals had been previously marked and were sex-determined based on the colour of the anal gland secretion (Rosell and Hovde, 2001; Rosell and Sun, 1999). The exact age was known for 13 individuals as they were captured as kits or yearlings; for the other 12 individuals age was determined as minimum age based on body weight (Rosell et al., 2010). There was no difference between individuals of known age and ones of uncertain age suggesting that our age determination worked reliably (8.72 ± 3.44 vs. 7.0 ± 3.19 years, $p = 0.820$). At capture, beavers were transferred into a cloth sac where they were immobilized and easier to handle (no anaesthesia was administered). We measured body mass and length, and attached a unit consisting of a VHF transmitter

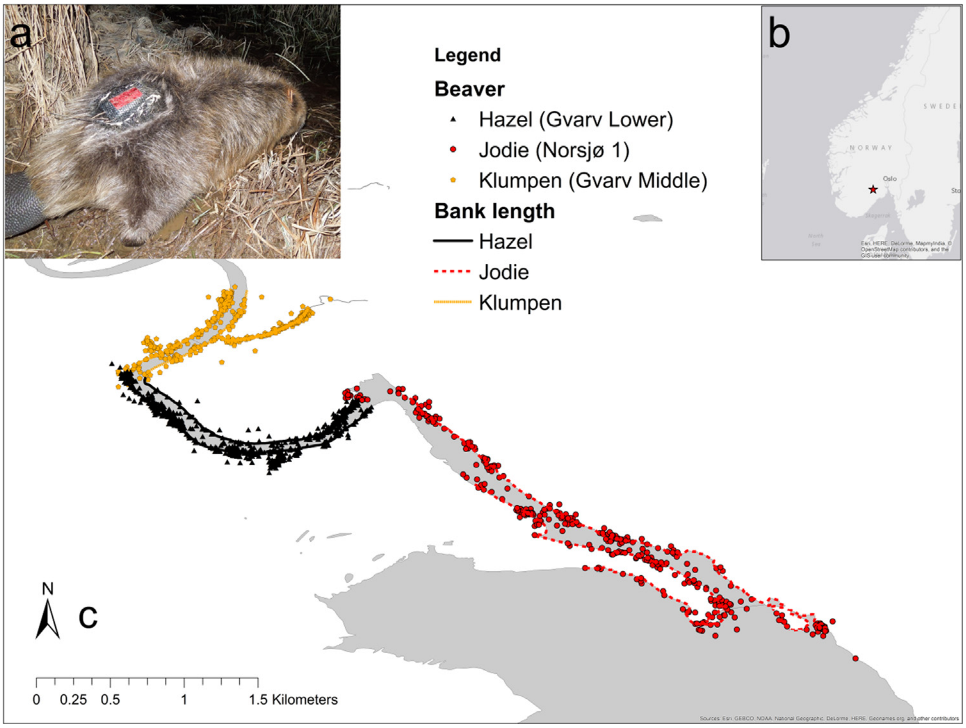

Fig. 1. A Eurasian beaver (*Castor fiber*) with a GPS unit glued onto its lower back (a) in our study area in southeast Norway (b). The main map (c) shows data examples of GPS positions and calculated territory size (measured as bank length) for three beavers in Gvarv River.

(10 g, Reptile glue-on, series R1910; Advanced Telemetry Systems, Isanti MN, USA) and a µGPS transmitter (24 g, model G1G 134A; Sirtrack, Havelock North, NZ). The unit was glued on the lower back (ca. 15 cm from the base of the tail, Fig. 1) using a two-component epoxy resin (System Three Resins, Auburn WA, USA). This position was chosen to minimize drag and potential effects on the animal, respectively, but also allowed for obtaining GPS positions while the animal was swimming as the tag was above water level. GPS transmitters were programmed to take a position every 15 min between 1900 and 0700 h and were set to sleep during the day as beavers are not active then (Sharpe and Rosell, 2003). In contrast to fully aquatic endotherms, beavers rarely dive for long periods (typically <3 min, (Graf et al., 2012)), thus, diving events were unlikely to influence the number of successful GPS fixes in water as transmitters were programmed to acquire a position for 3 min. Handling time of captured animals ranged between 20 and 50 min. The total weight of the glued-on unit did not exceed 1% of the beavers' body weight. For retrieval, animals were re-trapped after two to six weeks and the unit was cut off the fur with a scalpel. All animal handling procedures were approved by the Norwegian Directorate for Nature Management and the Norwegian Animal Research Authority.

Data preparation

Due to our long-term individual-based monitoring program, we had information on the number of individuals per colony, allowing us to estimate the number of adjacent neighbours. For adjacent colonies in which we did not obtain the number of individuals (i.e., in territories located at the edge of our study area), we used the average annual number of individuals per colony as an estimate. Kits were not included in this estimate, because they do not present an intruder threat.

The capture night and the following night were removed from the analysis to correct for possible effects of capture (Graf et al., 2016, in prep.). GPS positions with horizontal dilution of precision (HDOP) values of ≥ 5 and ≤ 4 available satellites were removed from the analysis (8.5% of the raw data), to correct for imprecise locations (Lewis et al., 2007). As a measure for distance from the shoreline (separately for land and water positions), we calculated the average perpendicular distance of GPS positions to the shoreline using the join tool in ArcMap 10.1 (Esri, Redlands, CA, USA).

We used bank length as a measure of territory size, because the beavers in our study area generally stayed close to the shoreline (on average <20 m), both when being on land and in water (see Results, Fig. 1). Other measures of territory size, such as minimum convex polygon (MCP) or kernel methods, would have resulted in an overestimation of territory size due to the inclusion of unused habitat, for example in meandering rivers. To obtain accurate estimates of bank length, we calculated the 95% MCP based on each individuals' GPS relocations in ArcMap 10.1, and then extracted bank length (from now on referred to as territory size) for each individual from the MCPs. Explorative trips (defined as a one-time movement outside the territory lasting less than 4 h) were removed when calculating territory sizes, as they were visibly outside the territorial borders (and within the neighbours' territory). Land cover data was derived from a digital topographic map (Felles KartDatabase, FKB data Geovekst, http://www.kartverket.no/). The amount of mixed and deciduous forested area within a buffer of 50 m from the shoreline was calculated to obtain a measure for resource availability (measured in ha). A buffer of 50 m was chosen because 95% of all land positions were located within this buffer (see Results).

Time spent on land was determined by the proportion of land positions. The distance between GPS positions was calculated as direct line distance between two consecutive GPS positions separately for land and water, and was averaged per hour. Beavers typically travel in water, thus, this method may have resulted in an overestimation of the average distance moved per hour on land, as it is possible that beavers swam in between two consecutive land positions. Consequently, instead of using this estimate as measure for actual movement on land, it should be interpreted as an estimate for different foraging tactics, i.e. foraging more selectively between multiple patches versus less selective foraging within the same or

Table 1
Overview of 25 Eurasian beavers (*Castor fiber*) equipped with a GPS unit between 2009 and 2014 in southeast Norway. A = autumn, S = spring.

Territory	Beaver	Sex	Year and Season	# GPS Days	# GPS Positions	Group Size	# of Kits	Banklength (km)	Time on land (%)	Absolute patrolling (%)
Bråfjorden a	Andreas	M	2010S	7	252	2	0	4.70	36.4	15.8
Bråfjorden a	Leslie	F	2010S	17	747	2	0	4.80	41.0	11.2
Bråfjorden a	Leslie	F	2014A	10	400	8	3	5.21	43.6	6.6
Bråfjorden b	Moritz	M	2010A	6	159	2	0	2.87	43.0	4.6
Gvarv_Lower	Hazel	F	2010S	22	722	8	0	2.41	46.3	15.0
Gvarv_Lower	Paddy	M	2012S	11	425	6	3	2.35	37.8	10.4
Gvarv_Middle	Klumpen	M	2014S	11	427	9	1	2.15	56.7	15.0
Lille Patmos	Ida	F	2010A	13	421	5	2	4.70	63.6	10.5
Lille Patmos	Kjartan	M	2010A	8	242	5	2	4.96	54.6	20.3
Lunde 2	Lasse	M	2011S	9	327	5	1	5.37	31.1	25.5
Lunde 4a	Loran	M	2009A	10	400	3	0	2.31	45.5	56.5
Lunde 4a	Malena	F	2014S	8	254	3	0	7.42	42.6	12.2
Lunde 6a	Bram	M	2011S	6	181	3	0	3.67	45.8	18.0
Lunde 6a	Maud	F	2009A	10	414	2	0	3.30	44.6	6.1
Norsjø 1	Jodie	F	2012S	11	407	5	1	5.02	52.6	22.1
Patmos 0	Hanne	F	2010A	10	271	4	1	4.33	34.0	8.2
Patmos 0	Jan Marc	M	2010A	14	461	4	1	4.70	32.7	14.6
Patmos 1	Live	F	2013A	18	247	5	2	2.32	34.8	9.3
Patmos 2a	Apple	F	2013A	16	709	5	0	1.80	44.7	9.1
Patmos 2b	Moses	M	2010A	14	340	5	2	1.84	48.9	48.8
Patmos 3a	Christina	F	2010A	18	539	3	0	1.68	43.4	51.4
Patmos 3b	Erlend	M	2010S	12	470	3	1	1.49	45.6	18.3
Patmos 3b	Erlend	M	2013A	15	448	3	1	1.47	68.4	36.9
Patmos 4	Horst	M	2010A	5	152	3	1	1.49	62.9	7.4
Patmos 5	Tanja	F	2014S	5	102	5	0	3.69	68.5	29.0
Patmos 6	Ase	F	2014S	10	370	4	0	4.67	37.0	14.5
Patmos 6	Edwin	M	2014S	5	182	4	0	5.15	37.7	15.6

fewer patches. Similarly, this uncertainty may have resulted in an underestimate of the average distance moved per hour in water since beavers could have been on land in between two consecutive water positions. By choosing a GPS sampling interval of 15 min, we attempted to minimize such effects. Moreover, we assume that uncertainties were consistent among individuals, thereby not or only marginally influencing our analysis.

Relative patrolling effort was estimated as the time a beaver spent inside the border zones of its territory, defined as the proportion of GPS positions inside the upper (upstream) and lower (downstream) 5% zones (ranging from 74 to 371 m) of the overall territory size. To obtain a measure of absolute patrolling effort, i.e., how much time a beaver spent at the actual territory borders, we assumed borders as independent of territory size and defined them as the last 75 m on each side of the river on the upper and lower side of each individual territory. This 75 m buffer was chosen because Rosell et al. (1998) found that the majority of scent mounds were clumped within 150 m between bordering territories (i.e., 75 m border zone per territory). For both relative and absolute patrolling effort, we only used GPS positions inside water and within two meters from the shoreline on land, because scent marking activity is limited to close proximity to water and because positions further inland most likely were foraging sites (Rosell and Nolet, 1997).

Statistical analysis

We used generalized linear models (GLM) to investigate movement patterns separately for water and land positions, as the mode and purpose of movement differs on land in comparison to water (swimming vs. walking, and patrolling vs. foraging). Initially, we also tested generalized linear mixed models (GLMM) as two beavers were equipped with a GPS twice; however, the results were not different and thus, we chose the simpler GLMs. The dependent variables for movement patterns in water were average distance moved/h, relative patrolling effort (measured as the proportion of all positions in water and within 2 m on land within 5% border zones), and absolute patrolling effort (proportion of all positions in water and within 2 m on land within 75 m from the borders; three separate analyses). The dependent variables for movement patterns on land were average distance from the shoreline, time spent on land and average distance between GPS positions/h (three separate analyses). Average distance from shoreline was ln-transformed to normalize residuals of the statistical models and one outlier was excluded based on Cook's distance (Cook, 1977).

The independent variables used in all six analyses were territory size, resource availability (i.e., area of mixed-deciduous forest in ha), number of neighbours, season (spring vs. autumn), and the beaver's age. No correlations between the independent variables were detected ($r < 0.6$ in all cases), and variance inflation factors (VIF) were <3 (see Zuur et al., 2010). To avoid overfitting the models we initially tested for an effect of sex and group size in all analyses, but removed these variables as there was no effect. For the analysis of each dependent variable, we selected 12 explanatory models *a priori* based on biological knowledge. These models included the full model (all independent variables, no interactions due to small sample size and to avoid overfitting the model); the five independent variables in separate models; and six models with a two-way interaction: 1) number of neighbours and season; 2) resource availability and season; 3) territory size and resource availability; 4) territory size and season, 5) number of neighbours and age, and 6) season and age. Model selection was based on Akaike weights (Table S1) (Wagenmakers and Farrell, 2004), i.e., the model with the highest conditional probability was chosen, and parameters that included zero within their 95% confidence interval (CI) were considered as uninformative (Arnold, 2010) as their estimated coefficients could not be reliably interpreted. All statistical analyses were performed using the software R 3.1.1 (R Core Team, 2015).

Results

Twenty-five dominant beavers (13 males and 12 females) of 17 different territories, and ranging between 3 and 14 years of age (mean ± SD: 7.3 ± 3.2 years) were equipped with a GPS (two individuals were tagged twice, Table 1). Thirteen beavers were captured in spring and 14 in autumn. On average, the GPS units delivered 11 nights of data (range: 5–22) and 356 GPS positions (range:

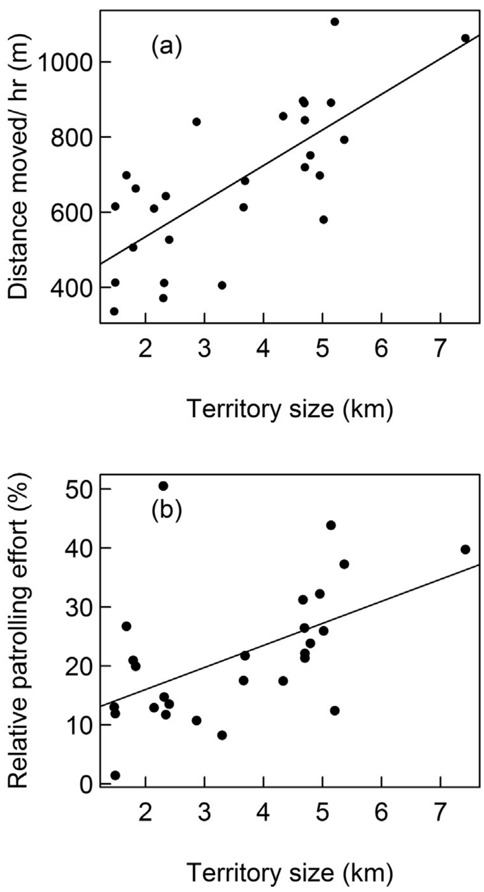

Fig. 2. Predicted relationship between territory size (given as bank length in km) and (a) average distance moved/h (in m) in water, and (b) relative patrolling effort defined as the proportion of GPS positions close to the territory borders (within the lower and upper 5% of the territory) for 25 Eurasian beavers (*Castor fiber*) in southeast Norway.

102–747) per individual. The number of neighbouring colonies varied between two (n = 13 territories) and three (n = 4 territories) with the number of neighbours varying between 4 and 16 individuals (7.1 ± 2.8). Territory sizes varied between 1472 and 7425 m bank length (3550 ± 1591 m, Table 1). Four beavers (one female and three males) made explorative trips into neighbouring territories; two individuals did three and two individuals did one explorative trip. These trips lasted on average 1.9 ± 1.1 h (range: 0.5–3.5 h).

Movement patterns in water

When in water, beavers stayed on average 14 ± 5 m (range: 0–255 m) from the shoreline, and moved on average 682 ± 204 m/h (individual range: 335–1106 m/h). The average distance moved/h was best explained by territory size (Tables 2 and S1), with beavers in larger territories moving greater distances (Fig. 2a). Relative patrolling effort varied between 1.4 and 50.5% (21.8 ± 11.5%) and was best explained by territory size (Tables 2 and S1, Fig. 2b), with beavers in larger territories spending more time patrolling. On average, beavers visited at least one territory border in 81.5 ± 20.7% of the recorded days. The absolute patrolling effort varied between 4.6 and 56.6% (19.0 ± 14.1%) and was best explained by the age of an individual (Tables 2 and S1); older beavers were spending more time at the border.

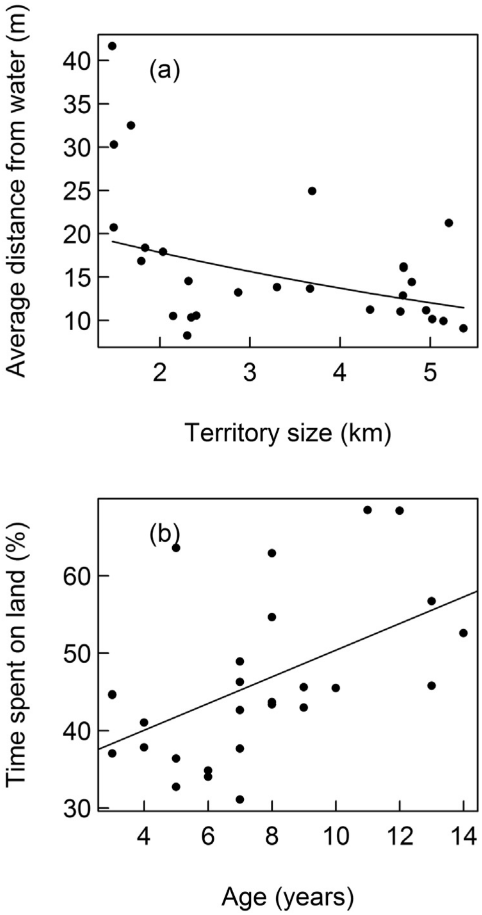

Fig. 3. Back-transformed prediction (solid line) between territory size (measured as bank length) and average distance from the shoreline for all land positions (a), and predicted relationship between the age of an individual and the time spent on land (b) for 25 Eurasian beavers (*Castor fiber*) in southeast Norway.

Movement patterns on land

When being on land, beavers stayed on average 16 ± 8 m (range: 0–201 m) from the shoreline. The average distance from the shoreline was best explained by territory size (Table 2, Fig. 3a), i.e., beavers in larger territories stayed closer to the water. Beavers spent between 31.1 and 68.5% of their active time on land (46.1 ± 10.5%). Time spent on land was best explained by the age of an individual (Tables 2, S1), with older beavers spending more time on land (Fig. 3b). The distance between GPS positions on land was on average 355 ± 121 m/h (individual range: 165–641 m/h), and was best explained by season (Table 2), i.e., beavers moved greater distances on land in spring compared to autumn.

Discussion

We found that beavers adjusted their movement patterns in water and on land in relation to territory size and age. Beavers in larger territories moved greater distances in water and spent more time within relative territory borders, thereby indicating that they patrolled more. Further, individuals in larger territories stayed closer to the shoreline when on land, i.e., when foraging. In contrast, beavers in smaller territories had a lower relative patrolling effort and foraged further away from the shoreline. Age also affected movement patterns with older beavers spending more time on land and at territory borders. In addition, we also found that beavers generally moved greater distances between land positions during spring.

Table 2
Results of the model selection showing the best model based on Akaike weight for the six dependent variables for 25 Eurasian beavers (*Castor fiber*) that were equipped with a GPS between 2009 and 2014 in southeast Norway. Number of observations = 27, β = estimated coefficient, SE = standard error, LCI = lower limit of the 95% confidence interval, UCI = upper limit of the 95% confidence interval.

Dependent variable	AICc	Akaike weight	Predictor	β	SE	LCI	UCI	R^2
Movement patterns in water								
Average distance moved/h	348.3	0.77	Territory size	94.820	17.200	61.111	128.535	0.55
Relative patrolling effort	206.3	0.55	Territory size	3.739	1.242	1.304	6.173	0.27
Absolute patrolling effort	221.4	0.34	Age	1.655	0.832	0.025	3.285	0.14
Movement patterns on land								
Average distance from shoreline	27.2	0.46	Territory size	−0.132	0.052	−0.233	−0.030	0.21
Time spent on land	201.5	0.55	Age	1.723	0.575	0.596	2.849	0.26
Average distance moved/h	327.5	0.43	Season Spring	151.390	36.590	79.664	223.113	0.41

Territory sizes found in this study are comparable with radio-tracking derived territory sizes for beavers in the same study area (Campbell et al., 2005; Herr and Rosell, 2004), as well as territory sizes of Eurasian beavers in general (Heidecke, 1986; Nolet and Rosell, 1994). Our results suggest that individuals may trade-off the costs of patrolling larger territories against the benefits of foraging closer towards the shoreline.

Changing movement patterns with age

Interestingly, we found that older beavers spent more time within the 75 m border zones than younger ones and, thus, had a greater absolute patrolling effort. However, the distance moved in water was not explained by age, suggesting that older beavers spent more time per visit at a border. Further, we found that older beavers spent more time on land. Spending more time at territory borders (patrolling via presence) may in effect allow beavers to spend more time on land instead of swimming between up- and downstream borders. Beavers can reach 20 years of age (Gorbunova et al., 2008) and only five beavers in this study were older than 10 years, suggesting that the observed pattern was rather related to a change in personality than senescence. Other studies reported changing movement patterns in relation to sex or social status, e.g. Sollmann et al. (2011) found that female jaguars (*Panthera onca*) both had smaller home ranges and moved less than males, and Messier (1985) found different amounts of extraterritorial movements between adult and yearling wolves (*Canis lupus*). However, to our knowledge we are the first to report changing movement patterns in relation to age within individuals of the same social status (dominant territory holders).

Beavers possibly gain experience over the years as a territory holder, leading to enhanced boldness and dominance. Moreover, experiencing a low abundance of natural predators coupled with a relatively low hunting pressure in the area may lead to increased boldness of older individuals explaining the higher proportion of time spent on land. Plasticity in behavioural traits related to (social) learning allows for adjusting behaviour based on environmental conditions, which is important for individual fitness (Dingemanse et al., 2010; Frost et al., 2007). An increase in boldness with age was shown in perch (*Perca fluviatilis*) (Magnhagen and Borcherding, 2008), and a shift in behavioural traits with age has also been shown in humans (Martin et al., 2002; Wilson et al., 1994). Body mass was shown to influence the boldness of fish and reptiles (Brown and Braithwaite, 2004; Mayer et al., 2016); this could also partly explain an increasing boldness with age in beavers as they reach their maximum body mass around age seven (Mayer et al., unpubl. results).

Movement in water and patrolling effort

Beavers typically disperse along watersheds; therefore intrusion by dispersers is most likely to occur at the up- or downstream borders of a territory (Herr and Rosell, 2004; Rosell et al., 1998). Thus, scent-marking activity is highest within border zones (Rosell and Thomsen, 2006), and border visits are crucial for beavers, particularly in saturated populations. Holders of larger territories showed a higher relative patrolling effort (as determined by the presence within 5% border zones) and thus swam greater distances. This suggests that beavers in larger territories generally spent more time patrolling territory borders. As beavers in larger territories have to cover greater distances to reach the borders, they face higher patrolling costs for two reasons: swimming has been shown to decrease the body temperature compared to being on land, especially during winter and early spring (Nolet and Rosell, 1994). In addition, an increased patrolling effort constrains the time that beavers can spend foraging. Similarly, wild chimpanzees (*Pan troglodytes*) reduced their feeding time from 33% to 10% during patrolling trips (Amsler, 2010), which demonstrates the trade-off between foraging and patrolling.

Foraging distance from the shoreline and distance between land positions

As central place foragers, beavers should deplete foraging patches close to the water before exploiting patches further away (Orians and Pearson, 1979). However, beavers need to forage further inland once the majority of food plants close to the shoreline are depleted. Beavers in smaller territories were found to move farther away from the shoreline when on land, which suggests resource depletion along the shoreline. However, travelling on land to forage is also considered to be costly both energetically and in time (Belovsky, 1984; Haarberg and Rosell, 2006), as terrestrial forays enhance predation risk (Basey and Jenkins, 1995). In addition, transporting food items on land is an arduous task compared to the efficient, buoyancy-supported transport in water (Novak, 1987). Several studies found beavers to be more selective (both in food item size and species) when foraging at greater distances from the shore (Fryxell and Doucet, 1991; Haarberg and Rosell, 2006; Jenkins, 1980), however, this selectivity diminished in low quality habitats (Gallant et al., 2004). Unfortunately, the resource availability in our study area was not measured on the ground, but based on land cover data. This relatively poor temporal and spatial resolution did not allow us to measure changes in resource availability over the years, and we cannot exclude the possibility that it did influence the observed movement patterns.

Contrary to our prediction, we found that beavers moved greater distances between land positions in spring, independent of territory size. This could be a strategy to compensate for winter weight loss via more selective foraging (in patches further apart from each other) during the spring green-up when food quality is higher. For example, North American beavers were shown to utilize different resources in different seasons (Milligan and Humphries, 2010; Svendsen, 1980), which may result in different movement patterns when foraging. Similarly, a study on food-caching behaviour of

North American beavers describes higher selectivity of tree species early in autumn compared to later in the caching season, suggesting that beavers appear to balance energy content and nutritional diversity of the food cache (Busher, 1996). Another semi-aquatic rodent, the capybara (*Hydrochaeris hydrochaeris*), also displayed different seasonal foraging patterns, spending more time for foraging during the dry season, but being more selective during the rainy season when food quality was higher (Barreto and Herrera, 1998).

The trade-off between patrolling and foraging distance

In general, food abundance has been shown to affect the intensity of territorial defence in animals, resulting in smaller territories (Carpenter, 1987; Simon, 1975) or even non-territorial behaviour (Davies and Houston, 1984) during high food availability. Beavers, however, show a strong, year-round territorial defence (Nolet and Rosell, 1994), which may reduce the rate of resource depletion and increases food availability during the cold months when vegetation is scarce. Because the study population is at carrying-capacity for the last ten years (Campbell et al., 2005; Steyaert et al., 2015), likely all territories in our study area are affected by resource depletion along the shoreline. Resource depletion forces beavers to forage further inland (Goryainova et al., 2014) and, in combination with male feeding territory defence, has been suggested to have triggered the evolution of social monogamy in beavers (Busher, 2007; Sun, 2003). These findings could explain the trade-off we observed in this study: In larger territories beavers have to invest more time in patrolling activities, but can forage closer to the shoreline. In smaller territories beavers moved greater distances on land, possibly as a consequence of resource depletion along the shoreline. However, the short distance between the up- and downstream border reduces patrolling costs and results in greater efficiency in territorial defence, thus, compensating for increased foraging costs in smaller territories.

Territory size seems to act as a counterbalancing factor for patrolling and foraging, making both owning larger and smaller territories a viable strategy in beaver populations at high densities. This is supported by the findings of Campbell et al. (2005), who found that beaver territories are not configured to a minimum economically defensible area: they rather seem to occupy larger territories to reduce the rate of resource depletion during initial settlements in an area, whereas in populations at or near carrying-capacity, territories that become vacant are conquered independent of size. Our findings stress the need for further investigations on whether constraints in foraging or constraints in territorial defence have greater impact on the length of territory occupation and long-term life history parameters such as life-time reproductive success.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2016.07.046.

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Supplementary material

Table S1: Model selection results showing the five best models for all six dependent variables with the AICc, delta AICc and Akaike weight values based on data from 25 Eurasian beavers (*Castor fiber*) that were equipped with a GPS between 2009 and 2014 in southeast Norway. Models were sorted after the Akaike weight from highest to lowest.

Models	AICc	delta AICc	Akaike weight	Models	AICc	delta AICc	Akaike weight
Average distance moved/hr (water)				Average distance from shoreline			
TS	348.3	0.00	0.772	TS	28.3	0.00	0.464
TS + RA + TS x RA	351.3	3.00	0.173	S	30.0	1.73	0.195
TS + S + TS x S	353.8	5.52	0.049	TS + S + TS x S	31.0	2.70	0.120
TS + NN + RA + S + A	359.2	10.92	0.003	TS + RA + TS x RA	32.6	4.27	0.055
RA	359.8	11.56	0.002	NN	33.4	5.09	0.036
Relative patrolling effort				Time spent on land			
TS	206.3	0.00	0.554	A	201.5	0.00	0.548
TS + S + TS x S	207.4	1.10	0.320	A + NN + A x NN	202.8	1.33	0.282
TS + RA + TS x RA	211.0	4.67	0.054	A + S + A x S	205.3	3.82	0.081
RA	212.6	6.25	0.024	TS	207.2	5.73	0.031
S	213.3	6.99	0.017	TS + RA + TS x RA	208.6	7.08	0.016
Absolute patrolling effort				Average distance between land positions/hr			
A	221.4	0.00	0.336	S	327.5	0.00	0.430
A + S + A x S	222.5	1.12	0.192	A + S + A x S	329.0	1.48	0.205
TS	222.6	1.19	0.186	TS + S + TS x S	329.7	2.20	0.143
RA	224.8	3.40	0.061	RA + S + RA x S	329.8	2.32	0.135
S	224.9	3.51	0.058	TS + NN + RA + S + A	331.9	4.37	0.049

The independent variables were: TS = territory size, NN = number of neighbours, RA = resource availability, S = season, and A = age.

Paper V

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ORIGINAL RESEARCH

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Couch potatoes do better: Delayed dispersal and territory size affect the duration of territory occupancy in a monogamous mammal

Martin Mayer[1] | **Andreas Zedrosser**[1,2] | **Frank Rosell**[1]

[1]Faculty of Technology, Natural Sciences and Maritime Sciences, Department of Natural Sciences and Environmental Health, University College of Southeast Norway, Bø i Telemark, Norway

[2]Department of Integrative Biology, Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Austria

Correspondence
Martin Mayer, Faculty of Technology, Natural Sciences and Maritime Sciences, Department of Natural Sciences and Environmental Health, University College of Southeast Norway, Bø i Telemark, Norway.
Email: martin.mayer@usn.no

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Abstract

In territorial, socially monogamous species, the establishment and defense of a territory are an important strategy to maximize individual fitness, but the factors responsible for the duration of territory occupancy are rarely studied, especially in long-lived mammals. A long-term monitoring program in southeast Norway spanning over 18 years allowed us to follow the individual life histories of Eurasian beavers (*Castor fiber*) from adolescence in their natal family group to dispersal and territory establishment until the end of territory occupancy. We investigated whether territory size, resource availability, population density, and dispersal age could explain the duration of territory occupancy, which ranged from 1 to 11 years. The duration of territory occupancy was positively related to dispersal age, suggesting that individuals that delayed dispersal had a competitive advantage due to a larger body mass. This is in support with the maturation hypothesis, which states that an animal should await its physical and behavioral maturation before the acquisition of a territory. Further, we found that individuals that established in medium-sized territories occupied them longer as compared to individuals in small or large territories. This suggests that large territories are more costly to defend due to an increased patrolling effort, and small territories might not have sufficient resources. The lifetime reproductive success ranged from zero to six kits and generally increased with an increasing duration of territory occupancy. Our findings show the importance of holding a territory and demonstrate that dispersal decisions and territory selection have important consequences for the fitness of an individual.

KEYWORDS

Castor fiber, dispersal, Eurasian beaver, fitness, life history, territoriality

1 | INTRODUCTION

Animals have to compete for different resources, such as food, mating partners, shelter, and breeding sites, throughout their life. One way to insure access to these resources is to defend them against conspecifics, that is, being territorial (Maher & Lott, 1995). In many species with polygynous or facultative monogamous mating systems, the defense of territories is restricted to males during the reproductive season (Emlen & Oring, 1977; Hau, Wikelski, Soma, & Wingfield, 2000; Kleiman, 1977). In contrast, individuals of obligate monogamous species that

FIGURE 1 Our study species, the Eurasian beaver (*Castor fiber*) in southeast Norway

rely on a partner to successfully raise offspring (Kleiman, 1977) often occupy territories year round and stay with their partners until they die or are replaced, for example, by takeover of an intruder (e.g., Lardy, Cohas, Figueroa, & Allainé, 2011; Raemaekers & Raemaekers, 1985). Here, we investigated the factors affecting the duration of territory occupancy (DTO), defined as how long (i.e., from establishment to loss of the territory) an individual is holding a territory in a large, monogamous rodent, the Eurasian beaver (*Castor fiber*, Figure 1).

The ideal despotic model predicts that the best quality individuals should monopolize the best quality territories (Fretwell & Lucas, 1970). This in turn suggests that both the quality (e.g., body size or mass) of the territory holder and the quality of the territory itself should be a predictor for the DTO (Sergio & Newton, 2003). An animal can increase its competitive ability (e.g., body mass and experience) by awaiting physical and behavioral maturity before the acquisition of a territory, that is, the maturation hypothesis (Piper et al., 2015; Weimerskirch, 1992). For example, male Siberian jays (*Perisoreus infaustus*) that delayed dispersal had more breeding events as compared to early dispersers (Ekman, Bylin, & Tegelstrîm, 1999), indicating a fitness benefit of delayed dispersal. Similarly, delayed dispersal increased the probability of survival and reproduction in red wolves (*Canis rufus*) (Sparkman, Adams, Steury, Waits, & Murray, 2010). Further, the territory size should be a predictor for the quality of the territory, and consequently the DTO, as patrolling activities are traded off with foraging activities, as shown in great tits (*Parus major*) (Ydenberg & Krebs, 1987) and chimpanzees (*Pan troglodytes*) (Amsler, 2010). Additionally, both the territory size and DTO might depend on competition with conspecifics and population density. For example, intraspecific competition influenced territory occupancy in booted eagles (*Hieraaetus pennatus*) (Martinez, Pagan, & Calvo, 2006), and in male red foxes (*Vulpes vulpes*), individuals with greater body mass held larger territories and had a higher reproductive success (Iossa, Soulsbury, Baker, & Harris, 2008) demonstrating the advantages of an increased competitive ability. Although some studies in birds investigated territory occupancy, that is, whether a territory is occupied versus unoccupied (Korpimaki, 1988; Martinez et al., 2006; Sergio & Newton, 2003), little is known about the factors affecting the DTO, especially for obligate monogamous mammals (e.g., Sparkman et al., 2010).

We used data collected from an individual-based long-term study of Eurasian beavers in southeast Norway to investigate the factors and mechanisms affecting the DTO. Further, we tested if DTO was a predictor for the lifetime reproductive success (LRS) of an individual, here defined as the total number of offspring produced during its lifetime. Beavers (both the Eurasian and the North American beaver [*C. canadensis*]) are large, long-lived (up to 20 years: Gorbunova, Bozzella, and Seluanov (2008)), socially monogamous rodents that live in family groups (Jenkins & Busher, 1979; Wilsson, 1971). Both Eurasian and North American beavers typically disperse at about 2 years of age (Hartman, 1997; Sun, Müller-Schwarze, & Schulte, 2000), but individuals were found to delay dispersal up to age seven when population densities are high (Mayer, Zedrosser, & Rosell, 2017b). Once established in an area, beavers are highly territorial (Campbell, Rosell, Nolet, & Dijkstra, 2005) and defend their territory via scent marking (Rosell, Bergan, & Parker, 1998; Rosell & Sun, 1999). Both sexes participate in territorial defense (Rosell & Nolet, 1997). Pairs remain together until the loss of a partner, either by death or emigration (Svendsen, 1989) or via replacement by a new individual (Mayer, Küenzel, Zedrosser, & Rosell, 2017a). Movement patterns of Eurasian beavers change with territory size (Herr & Rosell, 2004), and individuals trade off the costs of patrolling large territories by foraging closer to the shore (Graf, Mayer, Zedrosser, Hackländer, & Rosell, 2016). Although observed in North American beavers (Crawford, Liu, Nelson, Nielsen, & Bloomquist, 2008), there is little evidence that extrapair copulation occurs in Eurasian beavers (Syrůčková et al., 2015; Tinnesand, 2017). Thus, it is crucial for an individual's fitness, that is, its LRS, to establish and retain a territory, because only the dominant pair is reproducing in beavers (Sun, 2003).

We hypothesized that DTO in Eurasian beavers would be affected by (1) the age at dispersal and predicted that individuals that delayed dispersal would occupy a territory longer due to an increased competitive ability in comparison to younger dispersers [i.e., the maturation hypothesis: Piper et al. (2015)]. Further, we hypothesized that DTO would be related to (2) the size of the established territory, and to (3) the resource availability in the territory. We predicted that individuals in smaller territories had an increased DTO compared to individuals in larger territories due to decreased patrolling efforts (Graf et al., 2016), but only to some degree as smaller territories potentially had fewer resources (Campbell et al., 2005). We further hypothesized that (4) DTO is related to population density and predicted that individuals living at lower population densities face fewer intruders in comparison to higher densities, thus holding a territory longer. Finally, we tested the prediction that the LRS of beavers would increase with increasing DTO, while controlling for the effects of territory size, resource availability, and population density.

2 | METHODS

2.1 | Data collection and preparation

Data were collected as part of an individual-based long-term study of Eurasian beavers at the rivers Straumen, Gvarv, and Saua (all emptying

TABLE 1 Candidate models used to investigate the size of the established territory of 27 Eurasian beavers based on data collected in a population in southeast Norway between 1998 and 2015. Models were ranked based on AIC weights

Model	Variables	*df*	logLik	AIC_c	Delta AIC	AIC weight
Size of the established territory						
1	Resource availability	24	−225.47	458.0	0.00	0.628
2	Dispersal age + Resource availability	23	−224.94	459.7	1.72	0.266
3	Dispersal age + Resource availability + Dispersal age × Resource availability	22	−224.88	462.6	4.63	0.062
4	Dispersal age	24	−228.13	463.3	5.32	0.044

into Lake Norsjø) in Telemark County, southeast Norway, from 1998 to 2015. Beavers were captured annually in spring (March–June) and autumn (August–November) at night from a motor boat (Rosell & Hovde, 2001). They were individually marked with ear tags and a microchip, weighed to the closest 0.2 kg, and sex, age, and social status (dominant, subordinate [i.e., nondominant individuals ≥2 years], yearling, kit) were determined (Campbell, Nouvellet, Newman, Macdonald, & Rosell, 2012). For a detailed description of capture and handling procedures see Campbell, Newman, Macdonald, and Rosell (2013) and Rosell and Hovde (2001). Hunting pressure was considered low in all three rivers (between 1.8 and 3.3% of the population was harvested annually; FR unpublished results).

We only included individuals in this study that were captured for the first time as kit or yearling, thus, allowing exact age determination (Rosell, Zedrosser, & Parker, 2010). An individual was defined as philopatric if it remained within its natal family group for its lifetime and became dominant after the disappearance of its parents. An individual was defined as successful disperser if it left its natal territory, never returned, and established a family group outside its natal territory. We excluded individuals of unknown fate from this study. We categorized individuals that dispersed at age one to three as normal dispersers, and four years or older as delayed dispersers, based on Mayer et al. (2017b). Individuals were defined as floaters from the onset of dispersal until the establishment of a territory. Territory occupancy and dominance were determined by multiple captures and sightings in the same territory, evidence indicating the disappearance of the previous dominant individual of the same sex, lactation in females (Campbell et al., 2012), and positive paternity tests (FR, unpublished results). DTO was defined as the total number of years a dominant individual occupied a territory. The end of territory occupancy was verified either by death of the individual or via the presence of a new dominant beaver of the same sex in the territory. Apart from one exception, where a dominant beaver moved away from its original territory and occupied a new territory together with its original partner, we never observed that an individual that lost its territory established a new territory.

Territory borders were recorded based on visual observations of patrolling beavers, the presence of scent mounds (Rosell et al., 1998), and from individuals equipped with radio tags (Campbell et al., 2005) or global positioning system (GPS) (Graf et al., 2016; Steyaert, Zedrosser, & Rosell, 2015). Territory size was defined as river bank length based on territory borders determined with radio tag/GPS data in ArcMap 10.3 (Esri Redlands, CA) (Graf et al., 2016). Borders between neighboring territories were well established and barely changed over time (Campbell et al., 2005). Resource availability was calculated separately for each territory from land cover data (Felles KartDatabase, FKB data Geovekst, http://www.kartverket.no/) as the amount of mixed and deciduous forest within 50 m from the shore, following Graf et al. (2016). The annual population density was calculated as the mean number of individuals per family group separately for each river. The number of family groups per km bank length (calculated for the exact course of the bank length in ArcMap 10.3) was high in all three rivers (on average 0.64 family groups/km) with territories directly bordering each other and mostly no unoccupied areas, suggesting a saturated population (Campbell et al., 2005). The family group size and number of kits produced were recorded annually between August and October (after the kits emerged from the lodge) as part of the general population monitoring. We determined LRS by annual capture and marking of kits and positive genetic parentage analysis (FR, unpublished results). Our study might be biased toward short-distance dispersers (<10 km) as we could not assess the DTO and reproductive success of individuals immigrating from outside our study area, because we did not know their exact age.

2.2 | Statistical analysis

Philopatric individuals were removed from the analysis as no statistical comparison was possible due to the low sample size ($N = 2$). Initially, we tested whether the size of the established territory (dependent variable) was related to its quality, that is, resource availability, an individual's age at dispersal (as a measure for the individual's quality) (independent variables), and the interaction of these variables using a general linear model (Table 1).

To analyze which factors affect the DTO (in years, dependent variable, Poisson-distributed), we used a generalized linear model (GLM) with a log link. As independent variables we used dispersal age, territory size (of the established territory), resource availability, and population density (averaged over the years of territory occupancy). No correlations between the independent variables were detected (all $r < .6$). Body mass and age at dispersal age were highly correlated ($r = .76$, $p < .001$, $N = 26$), thus, age at dispersal was used as measure for body mass (age was used, because we did not obtain the body mass of all the individuals in the year of their dispersal, but we always knew their age) and therefore also competitive ability (Mayer et al., 2017b). Initially, we created single-effect models for the independent variables

TABLE 2 Candidate models for the analysis of the duration of territory occupancy of Eurasian beavers based on data collected in a population in southeast Norway between 1998 and 2015 (*N* = 19 individuals). Models were ranked based on AIC weights

Model	Variables	*df*	logLik	AICc	Delta AIC	AIC weight
Duration of territory occupancy						
1	Dispersal age + Territory size + Territory size^2	15	−39.66	90.2	0.00	0.623
2	Territory size + Territory size^2	16	−42.90	93.4	3.22	0.124
3	Dispersal age	17	−45.18	95.1	4.93	0.053
4	Dispersal age + Territory size + Dispersal age × Territory size	15	−42.25	95.4	5.17	0.047
5	Resource availability + Territory size + Territory size^2	15	−42.51	95.9	5.70	0.036
6	Population density + Territory size + Territory size^2	15	−42.82	96.5	6.31	0.027
7	Dispersal age + Population density + Resource availability + Territory size + Territory size^2	13	−38.84	96.7	6.49	0.024
8	Dispersal age + Resource availability + Dispersal age × Resource availability	15	−43.17	97.2	7.03	0.019
9	Dispersal age + Population density	16	−44.86	97.3	7.14	0.018
10	Dispersal age + Resource availability	16	−45.11	97.8	7.65	0.014
11	Dispersal age + Population density + Dispersal age × Population density	15	−44.30	99.5	9.28	0.006
12	Resource availability	17	−47.36	99.5	9.30	0.006
13	Population density	17	−48.52	101.8	11.61	0.002
14	Population density + Resource availability	16	−47.14	101.9	11.71	0.002

to test if their relationship with the dependent variable was linear or quadratic, based on Akaike's Information Criterion corrected for small sample size (AIC_c) (Hu, 2007), and found that linear function better described dispersal age, resource availability, and average population density, but that a squared function better described territory size. We then created 14 candidate models to test our hypotheses: a full model including all four independent variables without interactions, four single-effect models for each independent variable separately, six models including the combination of two independent variables without interactions, and three models including a two-way interaction (Table 2). The two-way interactions were (1) territory size × dispersal age, to test whether delayed dispersers establish in smaller territories; (2) resource availability × dispersal age, to test whether delayed dispersers establish in territories with more resources; and (3) dispersal age × population density, to test if delayed dispersers had a competitive advantage when population densities were high.

We used a generalized linear mixed model (GLMM) to test whether the annual reproductive success changed with the age of the territory holder (and therefore over the time of territory occupancy). We used the number of kits produced annually as the dependent variable, the individual's age was the fixed effect (linear function fitted better), and the beaver ID was used as random effect. We used a negative binomial response distribution in the R package *glmmADMB* (Bolker, Skaug, Magnusson, & Nielsen, 2012). To analyze LRS (dependent variable, Poisson-distributed), we used a GLM with a log link. Independent variables were the quadratic function of DTO, resource availability, mean population density, and the quadratic function of territory size; the variables were not correlated with each other (all $r < .6$). We then created a set of 11 candidate models (Table 3).

Model selection of all analyses was based on AIC_c and Akaike weights (Wagenmakers & Farrell, 2004), and parameter estimates that included zero within their 95% confidence interval (CI) were considered as uninformative (Arnold, 2010). If ΔAIC_c was <4 in two or more of the most parsimonious models, we performed model averaging (Anderson, 2008). Sample sizes in the different analyses vary because we did not always have complete information for all individuals (Table S1). All statistical analyses were performed in R 3.2.1 (R Core Team, 2015).

3 | RESULTS

Annual population density varied between 3.1 and 5.1 individuals per family group (mean ± SD = 3.7 ± 0.6) and territory sizes varied between 1.4 and 5.6 km bank length (3.6 ± 1.2 km). Normal dispersers (*N* = 23) dispersed at a mean age of 2.35 ± 0.71 years old and delayed dispersers at a mean age of 5.06 ± 0.93 years (*N* = 16); the average age at dispersal for both groups combined was 3.5 ± 1.6 years. Delayed dispersers (*N* = 14) had a significantly greater body mass than normal dispersers (*N* = 20) in the year of dispersal (22.1 ± 3.0 vs. 16.8 ± 4.5 kg, *t* test: $p < .001$, Figure 2). The size of the established territory was positively related to the amount of mixed and deciduous forest (*N* = 27, Tables 1 and 4).

3.1 | Duration of territory occupancy

We had data of 25 individuals from 16 different territories with known and finished DTO (Table S1). Two individuals remained philopatric

TABLE 3 Candidate models used for the analysis of the lifetime reproductive success of Eurasian beaver in a population in southeast Norway between 1998 and 2015 (*N* = 25 individuals). Models were ranked based on AIC weights

Model	Variables	*df*	logLik	AICc	Delta AIC	AIC weight
Lifetime reproductive success						
1	DTO + DTO^2	3	−44.31	95.8	0.00	0.466
2	DTO + DTO^2 + Resource availability	4	−43.44	96.9	1.12	0.267
3	Population density + DTO + DTO^2	4	−43.72	97.4	1.68	0.201
4	DTO + DTO^2 + Territory size + Territory size^2	5	−43.35	99.9	4.09	0.060
5	DTO + DTO^2 + Population density + Resource availability + Territory size + Territory size^2	7	−42.18	104.9	9.19	0.005
6	Territory size + Territory size^2	3	−52.36	111.9	16.11	0.000
7	Resource availability	2	−53.77	112.1	16.32	0.000
8	Population density	2	−53.77	112.1	16.33	0.000
9	Resource availability + Territory size + Territory size^2	4	−52.26	114.5	18.75	0.000
10	Population density + Resource availability	3	−53.76	114.7	18.91	0.000
11	Population density + Territory size + Territory size^2	4	−52.35	114.7	18.94	0.000

DTO, duration of territory occupancy.

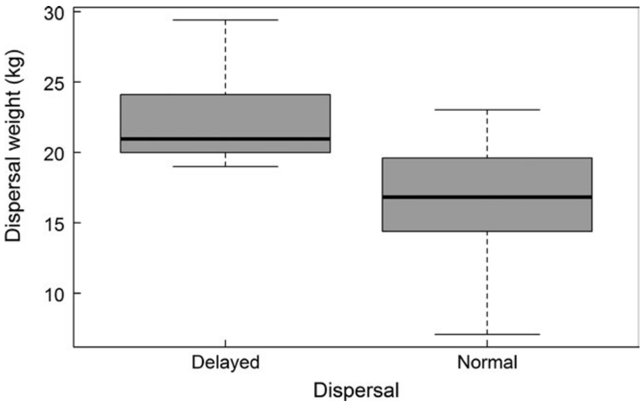

FIGURE 2 Boxplot of the body mass of Eurasian beavers in the year of dispersal for delayed (≥4 years old, *N* = 14) and normal (1–3 year old, *N* = 20) dispersers in southeast Norway. The boxplot shows median values, and 25th and 75th percentile and 95% confidence intervals

and became dominant in their natal territory after their parents had disappeared; the remaining 23 beavers dispersed and established in a new territory. Of the dispersers, 11 individuals were normal dispersers (1–3 years old) and eight were delayed dispersers (≥4 years old) (the dispersal age of the remaining four beavers was unknown). DTO ranged from one to eleven years, and mean DTO was not significantly different between females (6.3 ± 2.5 years, *N* = 12) and males (6.1 ± 3.2 years, *N* = 13, *t* test: *p* = .948). Two individuals (8%) were killed by a vehicle, seven (28%) were killed by hunters, and the cause of disappearance in the remaining 16 beavers was unknown (64%). There was no significant difference in DTO between individuals that died due to human-caused mortalities and ones with unknown causes of disappearance (5.7 ± 2.7 vs. 6.5 ± 2.9 years, *t* test: *p* = .485). DTO was best explained by the territory size and age at dispersal (Tables 2 and 4): Beavers that delayed dispersal and established in medium-sized territories occupied their territory longer than normal dispersers and individuals in smaller or larger territories (Figure 3).

3.2 | Annual reproduction and lifetime reproductive success

Of 35 dominant individuals (of which 10 were still alive when we drafted this manuscript), 25 produced offspring. Individuals that dispersed at older ages were also older when reproducing for the first time (β = 1.537 ± 0.404, 95% CI: 0.745; 2.329, *N* = 18, Figure 4). The annual reproductive success ranged from zero to four kits (0.63 ± 0.97, median = 0) and decreased with the age of the territory holder (β = −0.10 ± 0.04, 95% CI: −0.18; −0.02, *N* = 25, 163 individual years) with older individuals producing fewer kits. The LRS was known for 25 individuals and ranged from zero to six kits (2.2 ± 2.1, median = 2). LRS was best explained by the squared function of DTO (Tables 3 and 4). The LRS increased with increasing DTO, but then leveled off in individuals that held a territory for more than 9 years (Figure 5).

4 | DISCUSSION

We investigated the factors best explaining the duration of territory occupancy (DTO) and lifetime reproductive success (LRS) in the Eurasian beaver and found that there was a positive relationship between these two measures, with individuals holding a territory longer also having a higher LRS. This is in line with Sergio and Newton (2003) who suggest that territory occupancy is a measure for territory quality and thus also individual fitness. DTO was longer for individuals dispersing at an older age, indicating that delayed dispersal may be a strategy to increase individual fitness, similar to findings in red wolves (Sparkman et al., 2010) and Siberian jays (Ekman et al., 1999). Further,

Parameter	Estimate	*SE*	LCI	UCI
Size of the established territory				
Resource availability	**0.015**	**0.005**	**0.005**	**0.026**
Dispersal age	−141.500	144.700	−440.273	157.184
Duration of territory occupancy				
Dispersal age	**0.147**	**0.057**	**0.026**	**0.268**
Territory size	**1.827**	**0.713**	**0.315**	**3.339**
Territory size^2	**−0.275**	**0.099**	**−0.486**	**−0.065**
Lifetime reproductive success				
Duration of territory occupancy	**1.013**	**0.399**	**0.185**	**1.841**
Duration of territory occupancy^2	**−0.060**	**0.027**	**−0.117**	**−0.003**
Population density	−0.234	0.220	−0.692	0.224
Resource availability	0.000	0.000	0.000	0.000

TABLE 4 Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analyses of the size of the established territory, the duration of territory occupancy, and the lifetime reproductive success in a Eurasian beaver population in southeast Norway between 1998 and 2015. We performed model averaging of best models ($\Delta AIC_c < 4$) to estimate the effect size of each variable. Informative parameters are given in bold

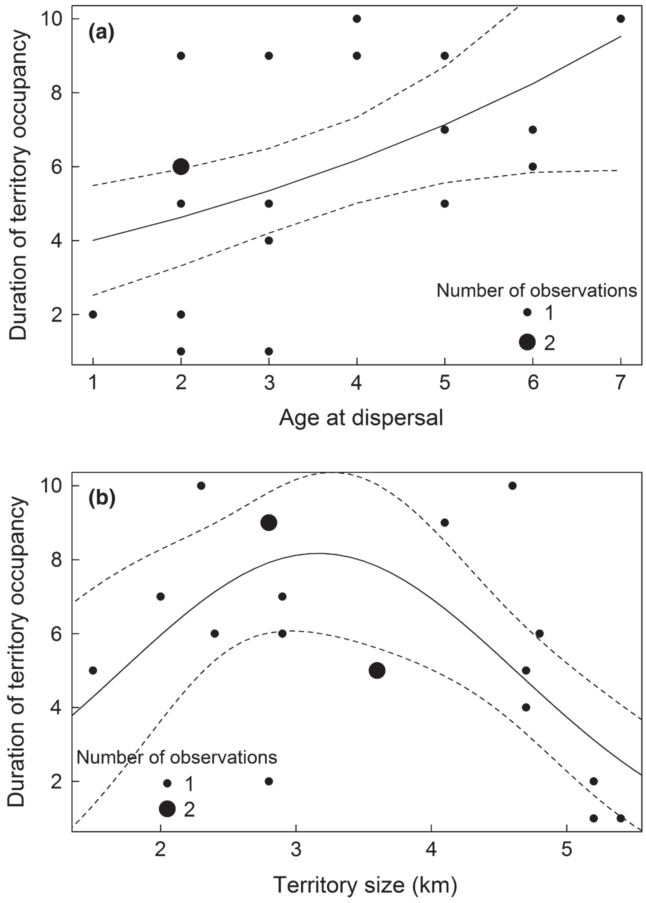

FIGURE 3 The predicted relationship (solid line) between (a) the age at dispersal (in years) and the duration of territory occupancy (DTO, in years), and (b) the territory size and DTO for 19 Eurasian beavers in southeast Norway (1998–2015). Dashed lines present the upper and lower 95% confidence interval

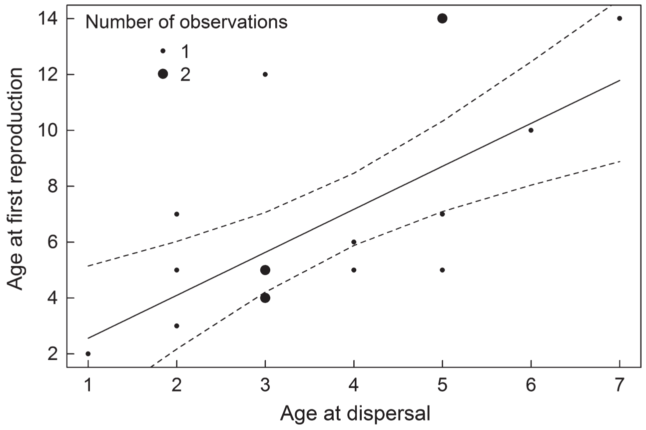

FIGURE 4 The predicted relationship (solid line) between the age at dispersal (in years) and the age at first reproduction (in years) for 18 Eurasian beavers in southeast Norway (1998–2015). Dashed lines present the upper and lower 95% confidence interval

the DTO was affected by the size of the established territory, indicating a trade-off between the costs of patrolling larger territories and possibly limited resource availability in smaller territories. This is in line with the optimization criterion that predicts a time constraint between foraging and territory defense (Adams, 2001). Consequently, this trade-off should result in a minimum economically defensible area (Adams, 2001).

4.1 | The duration of territory occupancy

4.1.1 | Dispersal age

In populations below carrying capacity, dispersal at a young age is presumably the best strategy as competition is low, and the chances to establish an own territory are high. For example, prairie voles (*Microtus ochrogaster*) dispersed at younger ages when population densities were lower (McGuire, Getz, Hofmann, Pizzuto, & Frase, 1993). In contrast, high-density populations likely exert a strong selection on the competitive ability (e.g., body condition and perhaps experience) (Mueller, 1988) of dispersers that try to establish and defend a territory, and Ekman et al. (1999) suggested that there should be a competitive advantage for individuals that delay dispersal.

In our saturated population (Campbell et al., 2005), 41% of the beavers delayed dispersal, and individuals that were older at dispersal

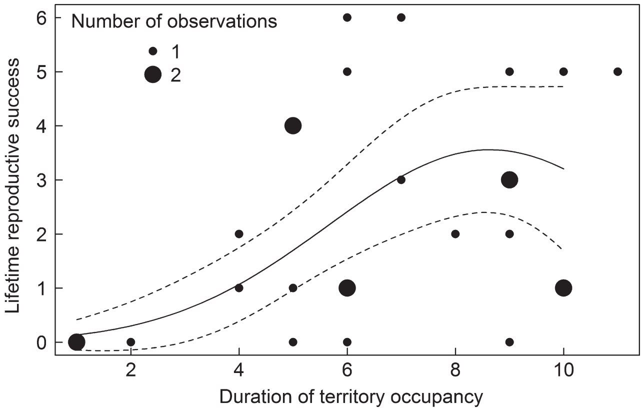

FIGURE 5 The predicted relationship (solid line) between the duration of territory occupancy (in years) and the lifetime reproductive success (measured as total number of kits produced in a lifetime) for 25 Eurasian beavers in southeast Norway (1998–2015). Dashed lines present the upper and lower 95% confidence interval

had a greater DTO in comparison to younger dispersers. Beavers that spent a longer period within their natal family group had a greater body mass at the time of dispersal, and delayed dispersers were on average 31% heavier than normal dispersers. This likely resulted in a competitive advantage to establish and retain a territory. Generally, beavers in our study area do not reach their maximum body mass before age six (Mayer et al., 2017a). Hence, individuals that established at younger ages were probably more prone to lose their territory to larger individuals before reaching their maximum body mass. In the three-spined stickleback (*Gasterosteus aculeatus*), larger males were more successful in obtaining and defending a territory (Rowland, 1989), and in Common loons (*Gavia immer*), larger individuals held mating territories longer, possibly due to an increased fighting ability (Piper, Tischler, & Klich, 2000). Additionally, by remaining longer in the natal family group, an individual might gain parenting experience, for example, via helper behavior (Cockburn, 1998) as subordinate North American beavers were shown to provision kits with food before they emerge from the lodge (Müller-Schwarze & Sun, 2003). Further, subordinates might gain experience in patrolling and defending the territory (subordinates were occasionally shown to overmark scent mounds [Tinnesand, Jojola, Zedrosser, & Rosell, 2013; Wilsson, 1971)], and they might gain experience in lodge building and food caching. Our findings are in support of the maturation hypothesis which states that an animal should await physical and behavioral maturity before the acquisition of a territory (Piper et al., 2015; Weimerskirch, 1992).

If there is a fitness benefit for delayed dispersers, the question arises why not all individuals delay dispersal. Parental tolerance toward the offspring is assumed to be a driver for the evolution of delayed dispersal (Ekman, Sklepkovych, & Tegelstrom, 1994), and the age at dispersal in our study area was positively related to the parental age (Mayer et al., 2017b). Older parents might be more tolerant toward their offspring (Graf et al., 2016; Mayer et al., 2017b), whereas younger parents might force their offspring to disperse earlier. Alternatively, individuals might perceive senescence in their parents and await their disappearance in order to take over the natal territory as shown in female common lizards (*Lacerta vivipara*) (Ronce, Clobert, & Massot, 1998).

4.1.2 | Territory size

Apart from the dispersal age, DTO was related to territory size, with individuals establishing in medium-sized territories having a greater DTO as individuals in smaller and larger territories. This indicates that medium-sized territories were of better quality, either via a higher resource availability (compared to smaller territories) or a decreased patrolling effort (compared to larger territories), or both. In a beaver population in southern France, smaller territories had a higher willow (*Salix* sp.) grove cover as compared to larger ones (however, these results must be treated with caution, because there were substantial limitations to the estimation of territory sizes) (Fustec, Lodé, le Jacques, & Cormier, 2001). However, two other studies (of which one was conducted in our study area) found that larger territories had a higher percentage of deciduous habitat, implying that larger territories were of better habitat quality (Campbell et al., 2005; McClintic, Taylor, Jones, Singleton, & Wang, 2014). The important question is which parameters are in fact decisive for the quality of a territory? The above-mentioned studies (and the current study) only used mixed and deciduous woody plants as measure for quality. However, especially from late spring to early fall, grass, herbs, and aquatic plants can play an important dietary role, as shown in North American beavers (Milligan & Humphries, 2010), and Fryxell (2001) showed that beaver density was positively related to aquatic biomass. Unfortunately, we did not have a reliable measure for non-woody plants, especially over the long time scale of the study, and resource availability could change over time, for example, due to resource depletion (Beier & Barrett, 1987; Fryxell, 2001). Due to these difficulties, the measure of territory size might provide a possibility to potentially bypass arduous habitat studies (Sergio & Newton, 2003). We did not have evidence that delayed dispersers, which are larger and heavier than normal dispersers, established in smaller territories. The reason could be, because in saturated populations, territories that become vacant, will be re-occupied independently of their size (Campbell et al., 2005).

Apart from being an estimate for resource availability, the territory size can entail a trade-off between foraging and territorial defense. For example, in red-backed salamanders (*Plethodon cinereus*), territorial defense constrained the time spent foraging and the quality of food items consumed, independent of resource availability (Jaeger, Nishikawa, & Barnard, 1983), and male chimpanzees spent more time traveling and less time foraging when on patrolling trips (Amsler, 2010). However, these studies did not provide information on long-term or fitness effects of territorial defense. In our study area, beavers were foraging closer to the shore when occupying larger territories as compared to smaller ones, suggesting sufficient resource availability in larger territories (Graf et al., 2016). It was shown that beavers in larger territories were moving greater distances in water and spent more time patrolling, indicating that they used more energy due to swimming effort and temperature constrains (being in cold water) (Graf et al., 2016; Herr & Rosell, 2004). Hence, there is evidence that the defense of larger territories is constrained by an increased patrolling effort, which in effect leads to a reduced DTO and LRS. In line with our findings, a study in sanderlings (*Calidris alba*) found that territories with better resource (prey) availability had increased intruder frequencies, consequently leading to smaller territory sizes due to the high costs of territorial defense (Myers, Connors, & Pitelka, 1979). After controlling for the interaction of prey density and intruder pressure, prey density had no effect on the territory size, emphasizing the importance of territorial defense for the optimal territory size (Myers et al., 1979). In conclusion, it appears that the intermediate territory sizes follow the optimization criterion stating that there is a time constraint between foraging and territory defense resulting in a minimum economically defensible area (Adams, 2001; Gill & Wolf, 1975).

4.1.3 | The end of territory occupancy

Although having a low effect at the population level (between 2% and 3% annually), hunting mortality might play an important role for individual dominant territory holders, as 28% of all mortalities in this study were caused by hunting, and because there appears to be a selection for adults and pregnant females (Parker, Rosell, Hermansen, Sørløkk, & Stærk, 2002). However, there was no difference in DTO between individuals that died due to human causes and individuals of unknown disappearance, but these results must be treated with caution due to our small sample size. We have evidence that individuals of unknown fate were forced out by an intruding individual of the same sex that took over the territory (Mayer et al., 2017a). Alternatively, human-caused mortality might be more common as observed, due to unreported cases of hunting or poaching, for example, shown in wolves (*Canis lupus*) (Liberg et al., 2012; Milleret et al., 2016). After the loss of its territory, an individual could have died, it could have become a floater, or it could have managed to establish in a new territory with a new mate. The first two possibilities would not increase the individuals' fitness, whereas secondary dispersal and territory occupancy could increase the total DTO and LRS. Although secondary dispersal was found in 39% of all dispersal events in a study of North American beavers (Sun et al., 2000), we observed secondary dispersal in only one case (both members of a pair moved to a new territory). Generally, secondary dispersal seems very unlikely in our study area due to the saturated population with few unoccupied territories available (Campbell et al., 2005). Nevertheless, we cannot exclude that beavers were establishing outside our study area.

4.2 | Lifetime reproductive success

Dispersal at an older age may be costly in terms of lifetime reproductive success as it represents a trade-off with an increased age at first reproduction. Additionally, the reproductive success decreased with increasing age of the territory holder, indicating senescence. However, these costs were offset by an increased DTO in delayed dispersers, resulting in a greater LRS. Apart from increasing their body mass and thus, competitive ability, delayed dispersers might additionally gain parenting skills that later increase their reproductive success (Cockburn, 1998). Our finding that senescing beavers produce fewer offspring could explain why the LRS leveled off after a certain time of territory occupancy. Further, territories that had been occupied for a longer time might have suffered from a greater resource depletion, which could result in a lower reproductive success. Finally, there is natural variation in the reproductive success between individuals (Kruuk, Clutton-Brock, Rose, & Guinness, 1999; Pelletier, Clutton-Brock, Pemberton, Tuljapurkar, & Coulson, 2007), suggesting that some beavers may have contributed more to population growth despite having a shorter DTO. Similar to our study, it was shown that delayed dispersal could lead to an increased LRS in male Siberian jays (Ekman et al., 1999) and to an increased probability of reproduction in male red wolves (Sparkman et al., 2010). Generally, the annual reproductive success in our study area was very low compared to other Eurasian beaver populations (Halley, 2011; Saveljev & Milishnikov, 2002). This might be due to resource depletion as beavers inhabited the area at least since 1920 (Olstad, 1937) and because the population is saturated (Campbell et al., 2012; Steyaert et al., 2015). Alternatively, the low reproductive success might be caused by an inbreeding depression, because the genetic diversity in our population is lower as compared to other populations (Durka et al., 2005).

5 | CONCLUSION

Studies investigating factors affecting DTO in long-lived mammals are rare (e.g., Sparkman et al., 2010), possibly due to the challenge of compiling detailed long-term individual-based data sets. Nevertheless, such data are necessary to answer important questions in ecology and evolution (Clutton-Brock & Sheldon, 2010). Here, we show evidence that delayed dispersal and the establishment in intermediate sized territories provided fitness benefits in beavers, such as increased DTO and LRS. Intermediate territories follow the optimization criterion (Adams, 2001), insuring sufficient resource availability and decreased costs of territorial defense at the same time. Further, we could demonstrate a competitive benefit of delayed dispersal due to increased body mass, as suggested by Ekman et al. (1999).

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

MM, AZ and FR developed the design of the work, MM and FR contributed to the data collection, MM and AZ performed the statistical analyses, and MM wrote the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Supplementary material

Table S1: Overview of the 35 Eurasian beavers (25 with complete life history) in a population in southeast Norway between 1998 and 2015 that we used for our analyses.

Name	Sex	DTO*	LRS**	Age at dispersal	Status	Age at fist reproduction	Average population density (individuals per colony)	Body mass at dispersal (kg)	Average colony size	Territory size (km)
Alfhild	F	1	0	2	Normal disperser		3.5	14.9	2.0	5.4
Andreas	M	1	0	3	Normal disperser		3.6	19.8	2.0	5.2
Anne Lise	F	9	5	2	Normal disperser	5	3.7	17.7	3.3	4.1
Bram	M	10	1	7	Delayed disperser	14	3.3	24.1	3.2	4.6
Chris	M	4	1		Philopatric	11	3.2		3.5	2.4
Demi	F	9	2	3	Normal disperser	12	4	22.7	2.3	2.8
Easy	M	7	3	6	Delayed disperser	10	3.2	21.1	3.0	2.0
Greg burly	M	9	0	4	Delayed disperser		4	22.8	2.3	2.8
Hanna Christi	F	5	0	2	Normal disperser		3.2	12.8	2.0	3.6
Hanne	F	7	3		Philopatric	6	3.8		3.7	4.3
Homer	M	6	1	NA	Unknown	5	4.6	NA	3.2	1.5
Ida	F	4	2	3	Normal disperser	5	3.6	19	4.3	4.7
Karin	F	6	6	2	Normal disperser	3	3.5	14.2	3.8	4.8
Kathrin	F	8	2	NA	Unknown	5	5.2	NA	2.8	1.5
Kolbjørn	M	2	0	2	Normal disperser		3.5	16.5	2.0	5.2
Konrad	M	6	5	2	Normal disperser	7	5.1	15	5.0	2.9
Linn	F	6	0	NA	Unknown		4.9	NA	2.3	2.8
Loran	M	7	6	5	Delayed disperser	7	3.2	24.3	3.1	2.9

Maerta	F	6	1	6	Delayed disperser	10	3.2	26.1	4.0	2.4
Montana	M	2	0	1	Normal disperser		3.1	8.7	2.0	2.8
Oddi	M	5	1	5	Delayed disperser	14	5.1	NA	2.2	1.5
Ola By	M	11	5	NA	Unknown	7	4	NA	4.3	1.9
Stina	F	10	5	4	Delayed disperser	5	3.6	20.2	4.7	2.3
Suzanne	F	5	4	3	Normal disperser	5	3.3	18.2	3.4	4.7
Terje	M	9	3	5	Delayed disperser	5	3.7	19.6	3.3	4.1
Darwin	M	NA	NA	2	Normal disperser		3.1	14.8	2.0	4.8
Jodie	F	NA	NA		Philopatric	8	5		5.2	4.3
Lasse	M	NA	NA	1	Normal disperser	2	3.3	7.1	4.8	5.4
Laurits	M	NA	NA	4	Delayed disperser	6	4.1	19	5.8	4.8
Leigh	F	NA	NA	5	Delayed disperser		4.1	29.4	2.6	1.8
Live	F	NA	NA		Philopatric	4	4.3		5.0	2.3
Lona	F	NA	NA	4	Delayed disperser	5	3.9	20	3.1	4.3
Morten	M	NA	NA	3	Normal disperser	4	4.3	19.8	5.0	5.7
Paddy	M	NA	NA	3	Normal disperser	4	4.7	23	6.3	2.4
Sara	F	NA	NA	2	Normal disperser		3.4	23	2.0	2.4

* DTO = duration of territory occupancy

** LRS = lifetime reproductive success

Errata:

Page IV, line 6: ‘3.4 years’ was changed to ‘3.5 years’

Page 9, line 8 : ‘43 dominant beavers’ was changed to ‘46 dominant beavers’

Page 14, line 12: ‘73’ was changed to ‘54’

Page 23, line 3: ‘73’ was changed to ‘54’

Page 23, line 7: ‘63’ was changed to ‘46’

Page 39 , line 26: Beltran and Boissier 2008 citation was added in the references

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