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



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Keywords: density dependence kin competition mammals 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.

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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 (Ronce et al., 1998). Α driver for age parentoffspring 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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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 samesex 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 \geq 17 kg and \leq 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, leno, & 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.

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



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).

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 \pm SD: 4.3 \pm 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 (Δ AlC_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 (ind	ividuals of u	nknown fa	te)	
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 (Δ AlC_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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Table A1

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

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APPENDIX

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

Table A1 (continued)

Name	Sex	Dispersal age	Dispersal distance (km)	Dispersal	Group	Change in dominance	Parental age (years)	Population density
		(years)			3120			
Easy	М	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	Μ	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	М	4	2.7	Downstream	6	Yes	7	4.6
Karin	F	2	9.3	Upstream	8	No	7	4.4
Kolbjørn	М	2	5.6	Downstream	4	No	5	4.4
Konrad	М	2	27.5	Upstream	7	No	9	4.7
Lasse	М	1	2.7	Downstream	7	No	10	3.9
Laurits	М	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	М	5	1.5	Downstream	7	No	9	4.7
Maerta	F	6	4.1	Upstream	4	No	11	2.8
Montana	М	1	1.5	Upstream	5	No	7	3.1
Morten	М	3	1.4	Upstream	5	No	7	3.3
Paddy	М	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	М	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

Table A3

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 dis	persal					
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 dis	appear	ance (individuals o	of unknown f	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.

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.

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