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

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.

© 2016 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour.

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

* 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).

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