Original investigation

Territory size and age explain movement patterns in the Eurasian beaver

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A B S T R A C T

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.

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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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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