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Original Investigation

# Beaver (*Castor fiber*) activity patterns in a predator-free landscape. What is keeping them in the dark?

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ABSTRACT

Activity patterns play an important role in the fitness of animals. Energy conservation, physiological adaptations, prey availability, competition, and predation caused by predators and humans are all important parameters influencing when, and where, animals are active. Over time, however, a change in such external factors can lead to a shift in optimal activity patterns. In this paper, we use camera traps to study the daily activity patterns of Eurasian beavers (*Castor fiber*) reintroduced into an atypical, predator-free landscape. We explore if and how beavers have adjusted their activity patterns in the absence of predators, and whether this varies with day length and moonshine. Our results reveal that beavers in our study area have a mainly crepuscular and nocturnal activity pattern, similar to animals in more natural landscapes with predators. Changes in day length had only a limited effect on the duration of beavers' activity, but, contrary to our expectations, beaver activity increased during bright moonlight. Activity patterns were also clearly bimodal during nights with bright moonlight, but unimodal during dark nights. The shape of their activity pattern did change throughout the year. These results suggest that beavers can alter their activity patterns in response to external cues, but that the current absence of predators has not resulted in a relaxation of their nocturnal activity patterns. We discuss our results in light of historical human persecution and suggest that beaver activity patterns continue to be influenced by ghosts of predators past.

## Introduction

The timing of activity is crucial for most animals. Temporal changes in activity (hereafter activity patterns) are an important adaptation that evolved in response to the time structure of the environment, which changes with a 24 h periodicity. Activity patterns allow an animal to anticipate the right time for a given behaviour or activity (Roll et al., 2006) and are influenced by a number of factors, including an animal's physiological adaptations, prey availability and distribution, competition, and disturbances caused by predators and humans (Kitchen et al., 2000; Yerushalmi and Green, 2009). There is evidence that the evolutionary arms race between predators and prey for temporal niche occupation may have led to considerable adaptive plasticity in temporal niche usage among even the earliest mammals (Hut et al., 2012).

Plasticity in activity patterns has also been observed in a range of modern mammals, often because of changes in the intensity of predation or competition, and over varying time scales. Svalbard reindeer (*Rangifer tarandus platyrhynchus*), isolated from predators for more than 5000 years, have no distinct peaks in activity at sunrise and sunset. This is expected for animals maximizing energy intake rates in predator-free environments (Loe et al., 2007). Changes in behaviour and activity patterns in response to external cues have also been recorded within shorter time spans. A coyote (*Canis latrans*) population that had historically been exposed to human persecution shifted to higher levels of diurnal activity less than eight years after persecution ceased (Kitchen et al., 2000). On an even shorter time scale, Fenn and MacDonald (1995) observed diurnal activity in normally nocturnal wild rats (*Rattus norvegicus*), and found that the rats were active during the day to avoid predation by nocturnal foxes (*Vulpes vulpes*). When rats were placed in a predator-free enclosure, they reverted to their preferred nocturnal activity. Similar temporal shifts have been observed in golden spiny mice (*Acomys russatus*), which appear to have been forced into a diurnal niche under natural conditions, possibly through resource competition with common spiny mice (*Acomys cahirinus*) (Levy et al., 2007). When golden spiny mice are placed under laboratory conditions, they immediately switch back to the nocturnal niche (Hut et al., 2012; Levy et al., 2007).

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Flexible activity patterns are not expected a priori, however, as adaptations to diurnal and nocturnal activity typically require strong exclusive morphological adaptations (Kappeler and Erkert, 2003). Evolutionary plasticity can be limited by phylogenetic constraints, for example, a process that has been proposed to account for the greater similarity of activity patterns between more closely related rodent species than those that are less closely related (Roll et al., 2006). Factors limiting temporal niche switches may therefore be internal, such as an organism's anatomy and/or physiology (e.g. its sensory or thermoregulatory capabilities), or external, for example biotic or abiotic environmental conditions (Hut et al., 2012).

The current phenotype and behaviour expressed by a species or population is not only influenced by the current environment, but also by past selection pressures. Directional selection by predators over many generations can create morphological or behavioural adaptations that remain present long after the selection pressure has relaxed, a concept known as "the ghosts of predators past" (Byers, 1997). The speed and endurance of American pronghorns (*Antilocapra americana*) exceeds that of all their current predators, for example. This anomaly has been attributed to the shaping of the species' morphology by directional selection during the Pleistocene, when the pronghorn's main predators were considerably faster than extant predators (Byers, 1997). Similarly, rodents from a fox containing island, that recently became free of foxes, continue to avoid traps which contained olfactory cues of fox predators, while rodents from a historically fox-free island did not respond to fox cues (Orrock, 2010).

Here, we investigate how contemporary and evolutionary factors shape the activity patterns of a herbivorous, semi-aquatic rodent, the Eurasian beaver (*Castor fiber*) (Herr and Rosell, 2004). Beavers were once widespread across Eurasia, but were nearly extirpated due to overhunting. By the early 20th century, it was estimated that only 1200 individuals remained in eight small populations (Nolet and Rosell, 1998). Increased protection and reintroductions have contributed to widespread population growth, however, and Eurasian beavers currently count over a million individuals (Halley et al., 2012). Beavers feed on aquatic vegetation, ferns, forbs, terrestrial herbs and leaves, shoots and bark of trees (Rosell et al., 2005). The species is highly territorial and lives in family groups consisting of a socially monogamous breeding pair, kits (one to three), yearlings and possibly one or more sub-adults (Crawford et al., 2008; Herr and Rosell, 2004).

Beavers are typically considered nocturnal, active between 17:00 and 08:00 h, and spend the daylight hours in their lodge/burrow (Mott et al., 2011). This activity pattern is somewhat unexpected, and perhaps suboptimal, for a number of reasons. First, the thermo-energetic hypothesis proposes that all endothermic animals in the temperate zone should profit from a diurnal life style, as diurnal-activity is associated with lower energy requirements compared to nocturnal activity (Hut et al., 2012). Second, beavers lack a tapetum lucidum, an intraocular reflective membrane that is considered to be an important adaptation to nocturnal vision (Cullen, 2003; Hut et al., 2012; Rodriguez-Ramos Fernandez and Dubielzig, 2013). And thirdly, as herbivores, beavers are not limited to foraging at particular times of the day by the temporal availability of their food.

Given the possible advantages of diurnal activity for beavers, we suspect that predation pressure has shaped, and continues to shape, the species' nocturnal activity pattern. In Western Europe, Eurasian beavers were once predated upon by three large mammalian predators: the wolf (*Canis lupus*), brown bear (*Ursus arctos*) and lynx (*Lynx lynx*) (Rosell and Czech, 2000). Like beavers, however, these predators were exterminated throughout much of their Western European range, and while predator populations have been expanding in recent years, they remain small and patchily distributed, or even absent in areas with re-establishing beavers (Enserink and Vogel, 2006). Predation by other, smaller predators (e.g. foxes, dogs) is rare (Rosell and Czech, 2000). Historically, however, humans have heavily persecuted beavers. Archaeological evidence indicates that beavers were targeted by prehistoric hunter-gatherers (Nicholas, 2007) and, in more recent times, hunting by humans was responsible for the near extirpation of the species (Nolet and Rosell, 1998). Where beaver hunting or trapping is legal, humans can still be regarded as an important predator (Rosell and Czech, 2000), however beavers are strictly protected in large parts of Western Europe and no hunting or trapping is permitted.

The re-emergence of beaver populations in Western Europe allows us to examine whether the current absence of predators and human persecution (hereafter referred to collectively as predators) influences the activity patterns of free-living beavers. First, we analyzed beaver activity patterns in a predator-free environment throughout the year, and predicted that if darkness were essential for beaver activity, then activity patterns would differ most between the shortest and the longest nights. Second, we examined the effect of moonlight on the activity of beavers. Moonlight influences many species' foraging success, habitat use and vulnerability to predation, and variation in moonlight is often used as a proxy for predation risk (Griffin, 2005; Kotler et al., 1991; Kronfeld-Schor et al., 2013; Prugh and Golden, 2014). Given that predators are absent from our study site, we predicted that the effect of moonlight on beaver activity would depend on whether they are using short- or long-term cues or evolutionary pressures to assess predation risk. If beavers are using short-term cues (the absence of predators), then we predicted that there would be no effect of moonlight on their activity. In contrast, if beavers remain sensitive to the increased predation risks posed by bright moonlight, then we predicted that their activity would be reduced when moonlight is bright. Third, we examined the effect of seasons on the number of beaver recordings. We hypothesized that because there is less food available in winter, this would increase beavers' land-based foraging for remaining woody food sources, resulting in a greater number of beaver recordings during winter.

## Material and methods

### *Study area*

The study was conducted in the densely populated region of Flanders, the most northern region of Belgium (average human population density of 462/km$^2$, Statbel 2010) and the northern part of Wallonia, Belgium. Agriculture comprises 58% of the area, residential areas 17%, nature 9% and parks, recreation, forestry, industry and others the rest (Departement Ruimte Vlaanderen, 2013). After an absence of 150 years, beavers were reintroduced to Flanders in 2003 and the population has continued to grow since then (Verbeylen, 2003; pers. com. KRRS). Beavers are strictly protected in Belgium and are not hunted or trapped. No large predators are currently present in the study area (Enserink and Vogel, 2006). There are no records of domestic dogs targeting beavers in our study area (pers. com. Kristof Baert, Institute for Nature and Forest Research); most domestic dogs are walked within the presence of the owner (on a leash or loose) and spend the rest of their day on their owner's property, while stray dogs are very rare. Red foxes (*Vulpes vulpes*) are present, but predation on beavers is highly unusual (Kile et al., 1996).

Beaver territories were located in nature reserves, but also in agricultural areas and water bodies used for recreation (e.g. fishing, walking, wind/kite surfing) and industrial activity. The average temperature during the study period was 10 °C. The mean