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

3

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13

14 **ABSTRACT**

15 Activity patterns play an important role in the fitness of animals. Energy conservation,
16 physiological adaptations, prey availability, competition, and predation caused by predators
17 and humans are all important parameters influencing when, and where, animals are active.
18 Over time, however, a change in such external factors can lead to a shift in optimal activity
19 patterns. In this paper, we use camera traps to study the daily activity patterns of Eurasian
20 beavers (*Castor fiber*) reintroduced into an atypical, predator-free landscape. We explore if
21 and how beavers have adjusted their activity patterns in the absence of predators, and whether
22 this varies with day length and moonshine. Our results reveal that beavers in our study area
23 have a mainly crepuscular and nocturnal activity pattern, similar to animals in more natural
24 landscapes with predators. Changes in day length had only a limited effect on the duration of
25 beavers' activity, but, contrary to our expectations, beaver activity increased during bright

26 moonlight. Activity patterns were also clearly bimodal during nights with bright moonlight,
27 but unimodal during dark nights. The shape of their activity pattern did change throughout the
28 year. These results suggest that beavers can alter their activity patterns in response to external
29 cues, but that the current absence of predators has not resulted in a relaxation of their
30 nocturnal activity patterns. We discuss our results in light of historical human persecution and
31 suggest that beaver activity patterns continue to be influenced by ghosts of predators past.

32

33 KEYWORDS

34 activity pattern, camera trap, lunarphilia, moonlight, semi-aquatic mammal, predator-free
35 environment, ghosts of predators past

36

37 INTRODUCTION

38 The timing of activity is crucial for most animals. Temporal changes in activity (hereafter
39 activity patterns) are an important adaptation that evolved in response to the time structure of
40 the environment, which changes with a 24 h periodicity. Activity patterns allow an animal to
41 anticipate the right time for a given behaviour or activity (Roll et al., 2006) and are influenced
42 by a number of factors, including an animal's physiological adaptations, prey availability and
43 distribution, competition, and disturbances caused by predators and humans (Kitchen et al.,
44 2000; Yerushalmi and Green, 2009). There is evidence that the evolutionary arms race
45 between predators and prey for temporal niche occupation may have led to considerable
46 adaptive plasticity in temporal niche usage among even the earliest mammals (Hut et al.,
47 2012).

48

49 Plasticity in activity patterns has also been observed in a range of modern mammals, often
50 because of changes in the intensity of predation or competition, and over varying time scales.
51 Svalbard reindeer (*Rangifer tarandus platyrhynchus*), isolated from predators for more than
52 5000 years, have no distinct peaks in activity at sunrise and sunset. This is expected for
53 animals maximizing energy intake rates in predator-free environments (Loe et al., 2007).
54 Changes in behaviour and activity patterns in response to external cues have also been
55 recorded within shorter time spans. A coyote (*Canis latrans*) population that had historically
56 been exposed to human persecution shifted to higher levels of diurnal activity less than eight
57 years after persecution ceased (Kitchen et al., 2000). On an even shorter time scale, Fenn and
58 MacDonald (1995) observed diurnal activity in normally nocturnal wild rats (*Rattus*
59 *norvegicus*), and found that the rats were active during the day to avoid predation by
60 nocturnal foxes (*Vulpes vulpes*). When rats were placed in a predator-free enclosure, they
61 reverted to their preferred nocturnal activity. Similar temporal shifts have been observed in

62 golden spiny mice (*Acomys russatus*), which appear to have been forced into a diurnal niche
63 under natural conditions, possibly through resource competition with common spiny mice
64 (*Acomys cahirinus*) (Levy et al., 2007). When golden spiny mice are placed under laboratory
65 conditions, they immediately switch back to the nocturnal niche (Hut et al., 2012; Levy et al.,
66 2007).

67
68 Flexible activity patterns are not expected *a priori*, however, as adaptations to diurnal and
69 nocturnal activity typically require strong exclusive morphological adaptations (Kappeler and
70 Erkert, 2003). Evolutionary plasticity can be limited by phylogenetic constraints, for example,
71 a process that has been proposed to account for the greater similarity of activity patterns
72 between more closely related rodent species than those that are less closely related (Roll et al.,
73 2006). Factors limiting temporal niche switches may therefore be internal, such as an
74 organism's anatomy and/or physiology (e.g. its sensory or thermoregulatory capabilities), or
75 external, for example biotic or abiotic environmental conditions (Hut et al., 2012).

76
77 The current phenotype and behaviour expressed by a species or population is not only
78 influenced by the current environment, but also by past selection pressures. Directional
79 selection by predators over many generations can create morphological or behavioural
80 adaptations that remain present long after the selection pressure has relaxed, a concept known
81 as “the ghosts of predators past” (Byers, 1997). The speed and endurance of American
82 pronghorns (*Antilocapra americana*) exceeds that of all their current predators, for example.
83 This anomaly has been attributed to the shaping of the species’ morphology by directional
84 selection during the Pleistocene, when the pronghorn’s main predators were considerably
85 faster than extant predators (Byers, 1997). Similarly, rodents from a fox containing island,
86 that recently became free of foxes, continue to avoid traps which contained olfactory cues of

87 fox predators, while rodents from a historically fox-free island did not respond to fox cues
88 (Orrock, 2010).

89

90 Here, we investigate how contemporary and evolutionary factors shape the activity patterns of
91 a herbivorous, semi-aquatic rodent, the Eurasian beaver (*Castor fiber*) (Herr and Rosell,
92 2004). Beavers were once widespread across Eurasia, but were nearly extirpated due to
93 overhunting. By the early 20th century, it was estimated that only 1200 individuals remained
94 in eight small populations (Nolet and Rosell, 1998). Increased protection and reintroductions
95 have contributed to widespread population growth, however, and Eurasian beavers currently
96 count over a million individuals (Halley et al., 2012). Beavers feed on aquatic vegetation,
97 ferns, forbs, terrestrial herbs and leaves, shoots and bark of trees (Rosell et al., 2005). The
98 species is highly territorial and lives in family groups consisting of a socially monogamous
99 breeding pair, kits (one to three), yearlings and possibly one or more sub-adults (Crawford et
100 al., 2008; Herr and Rosell, 2004).

101

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

112

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

128

129 The re-emergence of beaver populations in Western Europe allows us to examine whether the
130 current absence of predators and human persecution (hereafter referred to collectively as
131 predators) influences the activity patterns of free-living beavers. First, we analysed beaver
132 activity patterns in a predator-free environment throughout the year, and predicted that if
133 darkness were essential for beaver activity, then activity patterns would differ most between
134 the shortest and the longest nights. Second, we examined the effect of moonlight on the
135 activity of beavers. Moonlight influences many species' foraging success, habitat use and
136 vulnerability to predation, and variation in moonlight is often used as a proxy for predation

137 risk (Griffin, 2005; Kotler et al., 1991; Kronfeld-Schor et al., 2013; Prugh and Golden, 2014).
138 Given that predators are absent from our study site, we predicted that the effect of moonlight
139 on beaver activity would depend on whether they are using short- or long-term cues or
140 evolutionary pressures to assess predation risk. If beavers are using short-term cues (the
141 absence of predators), then we predicted that there would be no effect of moonlight on their
142 activity. In contrast, if beavers remain sensitive to the increased predation risks posed by
143 bright moonlight, then we predicted that their activity would be reduced when moonlight is
144 bright. Third, we examined the effect of seasons on the number of beaver recordings. We
145 hypothesised that because there is less food available in winter, this would increase beavers'
146 land-based foraging for remaining woody food sources, resulting in a greater number of
147 beaver recordings during winter.

148

149

150 MATERIAL AND METHODS

151 *Study area.*— The study was conducted in the densely populated region of Flanders, the most
152 northern region of Belgium (average human population density of 462/km², Statbel 2010) and
153 the northern part of Wallonia, Belgium. Agriculture comprises 58% of the area, residential
154 areas 17%, nature 9% and parks, recreation, forestry, industry and others the rest
155 (Departement Ruimte Vlaanderen, 2013). After an absence of 150 years, beavers were
156 reintroduced to Flanders in 2003 and the population has continued to grow since then
157 (Verbeylen, 2003; pers. com. KRRS). Beavers are strictly protected in Belgium and are not
158 hunted or trapped. No large predators are currently present in the study area (Enserink and
159 Vogel, 2006). There are no records of domestic dogs targeting beavers in our study area (pers.
160 com. Kristof Baert, Institute for Nature and Forest Research); most domestic dogs are walked
161 within the presence of the owner (on a leash or loose) and spend the rest of their day on their

162 owner's property, while stray dogs are very rare. Red foxes (*Vulpes vulpes*) are present, but
163 predation on beavers is highly unusual (Kile et al., 1996).

164

165 Beaver territories were located in nature reserves, but also in agricultural areas and water
166 bodies used for recreation (e.g. fishing, walking, wind/kite surfing) and industrial activity.

167 The average temperature during the study period was 10°C. The mean daily temperature was
168 below 0°C on 32 days, however there were only two periods longer than seven days during
169 which temperatures were low enough to potentially cause difficulties for beavers to break
170 through ice (30/1/2012 - 12/2/2012, average -5.5°C (range -0.6°C to -9.1°C) and 12/1/2013 -
171 26/1/2013, average -3.0°C (range -1.6°C to -4.6°C), location: Hove, Antwerp, Belgium, 10-
172 100 km from study territories). Not all territories with cameras were visited to assess the
173 effect of frost during this period, but we suspect no beavers were restricted to their
174 lodge/burrows (pers. obs. (KRRS) of broken ice in a number of territories near lodges). Data
175 from these periods was therefore included in the analysis. Precipitation was on average 847
176 mm per year (2012-2013, location: Hove, Antwerp, Belgium).

177

178 *Camera traps.*— Twelve Bushnell Trophy Cam cameras (Bushnell Outdoor Products, 9200
179 Cody, Overland Park, Kansas 66214, Model 119436c) were rotated at 97 different locations in
180 34 different beaver territories, for an average of 48 days per location (SD = 36.3), from
181 January 2012 until October 2013. Signs of presence were used to determine beaver territories
182 (according to Dewas et al. 2012). No animal ethics or conservation permits were necessary to
183 deploy camera traps during this study as camera traps are considered non-invasive (Gert Van
184 Hoydonck, Agency for Nature and Forest). Cameras were deployed at seven different types of
185 locations (Table 1) and camera settings were standardized over all cameras. The video length
186 was set at 15 sec, with a 1s interval between recordings. Videos were filmed with 720 x 480

187 resolution with sound, and all videos were time stamped. Cameras detect animals by means of
188 a passive infrared sensor, which detects the difference between the ambient temperature and
189 the animal's body temperature, and activates the camera based on a combination of movement
190 and heat (Meek et al., 2012). The sensitivity of the sensor was set to low, medium or high
191 according to local circumstances. The medium sensitivity was used in most environmental
192 settings, but was reduced to low when cameras were directed towards highly dynamic
193 streams, as camera traps were otherwise triggered by the water movement. High sensitivity
194 was used when vegetation was limited and beavers were expected to pass farther from the
195 camera. All sensitivities were suitable to detect beavers because of their size and slow speed,
196 and we expect no substantial influence of sensitivity on the results. Cameras were
197 programmed to record day and night. Cameras were attached to a robust tree at a height of 20
198 to 60 cm. Trap shyness was not expected because cameras used an infrared illumination and
199 no flash (Schipper, 2007; Wegge et al., 2004). We assume that beavers cannot become "trap-
200 happy" as we did not use a reward (e.g. a bait or lure) to attract them.

201

202 The time of placement and GPS coordinates of each trap location were recorded. Camera
203 failure caused by technical problems, filled memory card or empty batteries, was handled by
204 considering the date and time of the last correct recording to be the end of the sampling at this
205 location. Time of recording was corrected for daylight saving time when necessary. We
206 defined independent recordings as two recordings of the same species in the same territory
207 being at least one hour apart (Ridout and Linkie, 2009; Tobler et al., 2009). We used
208 independent recordings in the analyses unless stated otherwise.

209

210 *Beaver activity.*— The activity pattern was estimated by using a kernel density analysis. In
211 this non parametric method, the probability density function of a random variable (time) is

212 estimated (Ridout and Linkie 2009; Figure 1). As just six camera locations contributed 43.3 %
213 of independent recordings (>100 independent recordings), we used a Chi^2 test to determine
214 whether this biased the results for beaver activity patterns. For this, beaver observations were
215 grouped per hour, and the distribution of activity from the six high-activity locations was
216 compared with the general activity pattern of all other locations.

217

218 We determined the effect of day length on beaver activity patterns via pairwise comparisons
219 of activity during periods of very different day length, to periods of similar day length. To do
220 so, we buffered the shortest day (21 December), the longest day (21 June) and the spring and
221 autumn equinox (12h day and night; 21 March and 21 September) with a one-month period
222 before and after that date. We calculated the coefficient of overlap ($\hat{\Delta}_4$ for large sample sizes,
223 Monterroso et al., 2013; Ridout and Linkie, 2009) for the period of shortest days, 21
224 November – 21 January, (average day length = time between sunset and sunrise: 8 h 12 min)
225 and the period with the longest days, 21 May – 21 July (average day length = 16 h 16 min).
226 This overlap was compared to the overlap between two periods in the year with an
227 intermediate day length, 21 February – 21 April and 21 August – 21 October (average day
228 length for both periods is = 12 h 18 min). The coefficient of overlap can vary from 0 (no
229 overlap) to 1 (complete overlap) (Ridout and Linkie, 2009). Thus, we expect that the periods
230 with a similar day length have a higher degree of overlap. This method was originally
231 developed to study overlap between prey and predators or males and females of the same
232 species (Ridout and Linkie, 2009) but to our knowledge, it has not been used before to
233 compare seasonal differences in activity. Statistical analysis was performed by using the R
234 package ‘overlap’ and by adapting the R script provided by Linkie and Ridout (2011),
235 available at <http://www.kent.ac.uk/ims/personal/msr/overlap>. The 95% confidence intervals of
236 the overlap were calculated based on 10,000 bootstrapped samples.

237 The effect of moon illumination on activity patterns was examined by calculating the
238 illumination index per night by adjusting the methods of Norris et al. (2010). The illumination
239 index is the duration (in minutes) of moonshine between the end and start of civil twilight
240 (when the sun is 6° below the horizon), multiplied by the illuminated fraction of the moon (in
241 percentage), multiplied by the cloud cover ranging from 0 (completely overcast) to 1
242 (completely clear), with intermediate steps of 1/8th. Data on cloud cover was recorded at
243 Brussels Airport, Zaventem, Belgium, situated in the centre of Flanders with study territories
244 5 to 100 km from this location, and provided by the Royal Meteorological Institute, Belgium.
245 The illumination index was normalized by dividing the daily value by the average
246 illumination index of the complete study length resulting in the normalized illumination index
247 (hereafter NII). This NII ranged from 0 (no light) to 8.25 (brightest night) (median 0.53).

248

249 To categorize illumination during the study period, we listed all daily NII from January 2012
250 to October 2013. We classified the lowest 25% of NII values (0 - 0.08) as “Dark” and the
251 highest 25% of NII values (1.55 - 8.25) as “Light”; intermediate values were classified as
252 “Medium”. All independent beaver recordings were allocated to 1 of these 3 categories,
253 except for 1 recording for which no cloud coverage data was available. This recording was
254 excluded from the analysis. A Chi² test was used in order to detect preference or avoidance
255 for Dark, Medium or Light circumstances. Overlap between Light and Dark circumstances
256 was calculated comparable with the overlap between seasons.

257

258 For every camera location the season (spring: 1 April-30 June; summer: 1 July-30 September;
259 autumn: 1 October-31 December; and winter: 1 January-31 March) and the type of location
260 (seven categories; see Table 1) at which the camera was directed were recorded. Because the
261 locations of “Dam”, “Feeding location”, “Water”, and “Frequently flooded running tract”

262 represented only a small number of recordings, they were combined in the category “Other”.
263 A linear mixed-effects model was fitted with the logarithmically transformed average number
264 of independent beaver recordings per 10 days, per camera location as the response variable.
265 “Season” and “Type” (i.e. location type) were fixed effects and beaver territory was added as
266 a random effect. No interactions were considered as the sample size was too small (97
267 locations). Results were Holms corrected for multiple testing (Holm, 1979). When camera
268 traps were present at a site in more than one season, only data from the longest-sampled
269 season was considered. All statistical analyses were performed in R (The R Foundation for
270 Statistical Computing, Vienna, Austria).

271

272 RESULTS

273 We obtained 1889 independent beaver recordings during 4,019 full recording days. The
274 cameras revealed that beavers had a mainly crepuscular and nocturnal activity pattern, with a
275 rapidly increasing probability of recording beavers starting between 18:00 h and 22:00 h, a
276 peak around 02:00 h, and few recordings later than 07:00 h (Figure 1). There were no
277 differences in the general activity patterns when comparing the six high-activity locations
278 with all the other locations ($\chi^2_{18} = 14.31$, $p = 0.7084$).

279

280 The activity peak was from 23:00 h to 03:00 h during the shortest nights (21 May – 21 July),
281 and tended to be wider than the peak around 02:00 h during the longest nights (21 November
282 – 21 January) (Figure 2A). Activity before 18:00 h was more common during the shortest
283 nights, and from 18:00 h to 21:00 h during the longest nights. After 03:00 h patterns were
284 largely similar during periods of short and long nights (Figure 2A). The activity patterns in
285 both periods with intermediate-length nights (21 February – 21 April and 21 August – 21
286 October) look very similar, although the clear bimodal peak in activity appears to have shifted

287 one hour during the autumn equinox period, resulting in a later increase and decrease in
288 activity (Figure 2B). The amount of overlap in activity between the shortest and the longest
289 nights was high $\hat{\Delta}_4 = 0.90$ (95% confidence interval: 0.86-0.95; Figure 2A) and very similar to
290 the amount of overlap between the two periods with intermediate nights, $\hat{\Delta}_4 = 0.91$ (95%
291 confidence interval: 0.90-0.96; Figure 2B), indicating that differences in activity patterns
292 between shortest and longest nights are not larger compared to the differences in activity
293 patterns between intermediate nights. The activity patterns of short and long nights were
294 wider compared to activity patterns of intermediate nights.

295

296 Nocturnal illumination influenced the activity of beavers. We recorded 24.5% (463 videos) of
297 beavers during the Dark nights (27.6% of nights), 48.7% (920 videos) during Medium nights
298 (49.6% of nights) and 26.8% (505 videos) of beavers during the Light nights (22.8% of
299 nights). Significantly more recordings were registered during Light nights than expected
300 based on the sampling effort ($\chi^2_2 = 19.67$, $p < 0.001$). Although there was a high level of overlap
301 $\hat{\Delta}_4 = 0.91$ (0.87-0.96) between activity on Dark (N= 463) and Light (N= 505) nights, there
302 were also differences: activity patterns on Dark nights showed two clear peaks (around 22:00
303 h and 03:00 h) and a reduction in activity around midnight, while there was a single main
304 peak around 02:00 h on Light nights. Activity on Light nights also began slightly later in the
305 evening than on Dark nights (Figure 3).

306

307 The average capture frequency was 3.6 independent beaver recordings per location per 10
308 days (± 6.0 , range 0-34.7). The linear mixed model indicated that there were no significant
309 seasonal effects on beaver activity patterns (summer – winter, $p = 0.163$, spring – summer, p
310 $= 0.462$, other seasonal comparisons, $p = 1$). The camera trap location “Other” registered
311 significantly fewer beaver recordings per 10 days than “Tree” ($p < 0.01$), “Running track”

312 ($p < 0.05$) and “Burrow” ($p < 0.001$). No other significant differences between camera trap
313 locations were present.

314

315 DISCUSSION

316 Our results demonstrate that beaver activity patterns in a predator-free landscape resemble
317 those of beaver populations in more natural ecosystems with predators. This suggests that it is
318 not current predation pressure that causes beavers to remain crepuscular and nocturnal.
319 Instead, we suggest that the activity patterns we observed in this study are an example of “the
320 ghosts of predators past” (Byers, 1997). Beavers have been targeted by hunter-gatherers since
321 the Pleistocene (Nicholas, 2007), and more recent human persecution almost caused the
322 extinction of the Eurasian beaver. Although beavers are currently not hunted in our study
323 area, we propose that the effects of human persecution remain evident in their activity
324 patterns. Our study highlights the importance of not only considering current environmental
325 influences, but also previous selection pressures, in order to understand current behaviour.

326

327 Apart from predation pressure, other selective forces such as competition, disturbance or food
328 availability can influence activity patterns, but we do not believe that any of these factors are
329 responsible for the activity patterns that we observed. First, competition is unlikely to affect
330 beavers’ temporal niche in our study area, as no other species occupy a similar niche. Second,
331 while it is possible that disturbance by predators, domestic dogs, or humans could alter beaver
332 activity patterns, traditional predators are absent from the study site, and the rare cases of
333 diurnal activity that we recorded did not exclusively occur in locations without human or dog
334 disturbance. Similarly, beavers in disturbance free enclosures (by humans, dogs, or other
335 predators) in Great Britain also show activity from early evening to early morning, without
336 any real diurnal activity (pers. com.: Derek Gow). Finally, because the food utilised by

337 beavers does not change during the day, food availability is also unable to explain beavers'
338 nocturnal pattern of activity.

339

340 Traps were used to catch beavers in more recent times: these function independent of time and
341 consequently should not select for changes in activity patterns. In earlier times, however,
342 hand-held weapons would have been used to hunt beavers. Given the extent of human
343 persecution throughout history, we suggest that diurnal hunters would have placed strong
344 selection pressure on beavers, possibly more so than natural predators, resulting in the
345 evolution of crepuscular/nocturnal activity patterns to reduce their probability of encountering
346 humans. Indeed, rapid and large phenotypic changes have been recorded in a number of
347 species subjected to strong human harvest selection (Darimont et al., 2009). For example,
348 brown bears from populations subjected to long-term persecution have altered life history
349 traits and produce larger litters compared to populations that were less persecuted (Zedrosser
350 et al., 2011). Thus, while hunting pressure is currently absent from the beaver population
351 studied here, we suggest that the temporal activity patterns that developed under past selection
352 pressures are still present.

353

354 The degree of overlap in activity between periods of nights with very different lengths (short
355 and long) was very similar to the overlap in activity during periods with similar night lengths.
356 These similarities suggest that day length has a limited effect on activity, even though there is
357 a substantial variation in the timing of sunrise (04:29 h - 08:45 h) and sunset (16:37 h - 21:00
358 h) throughout the year. Bimodal activity was clearly present during the spring equinox period
359 (Figure 2B) and during Dark nights (Figure 3).

360

361 Unexpectedly, more beavers were recorded during Light nights than Dark nights. This is in
362 contrast with the most frequently described pattern of reduced activity during bright
363 moonlight for mammals, because of increased predation risk (Daly et al., 1992; Griffin, 2005;
364 Meyer et al., 2004). However, not all animals avoid moonlight. For example, nocturnal
365 primates and kangaroo rats (*Dipodomys* sp.) increase activity during moonlit nights, possibly
366 due to increased foraging success outweighing predation risk, or as a result of increased light
367 levels facilitating predator detection (Bouskila, 1995; Gursky, 2003; Prugh and Brashares,
368 2010; Prugh and Golden, 2014). We suspect that beavers, whose eyes might not be optimally
369 adapted to vision in the dark (Cullen, 2003; Hut et al., 2012), have higher foraging success
370 during bright moonlight, and this benefit outweighed a possible increased predation risk by
371 humans. Whether beavers behave similarly in environments where natural predators are still
372 present remains to be investigated.

373

374 We had predicted that the reduced availability of food during winter would drive beavers to
375 access a limited amount of remnant (woody) food sources located along fixed trails,
376 increasing the number of winter recordings relative to recordings in other seasons. Contrary to
377 our expectations, we did not find an effect of season on beaver recordings. This result might
378 stem from beavers collecting, and subsequently feeding from, partially submerged winter food
379 caches. Previous studies suggest that food caches are infrequently constructed in mild
380 climates (Hartman and Axelsson, 2004), which is consistent with our observations (pers. obs.
381 KRRS). Alternatively, it is possible that our methods were not suitable to detect seasonal
382 differences in activity: although beavers may have spent more time on land during winter, the
383 effect of this on the number of recordings may have been counterbalanced by the greater
384 absolute number of beavers in summer, when juveniles have left the lodge and the size of
385 family groups is at their maximum.

386

387 Our results show that, in the current absence of predators, beavers remain primarily nocturnal.

388 We suggest that it is likely that selection by human persecution in earlier times has shaped

389 beaver activity patterns. Although this hunting pressure is currently absent in our study area,

390 we propose that the behaviour developed under this past selection is still present. We suggest

391 that future research should examine the activity of beavers during high and low moon

392 illumination, and in populations with (natural) predators, in order to better understand the

393 effect of predators on the activity patterns of beavers.

394

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406

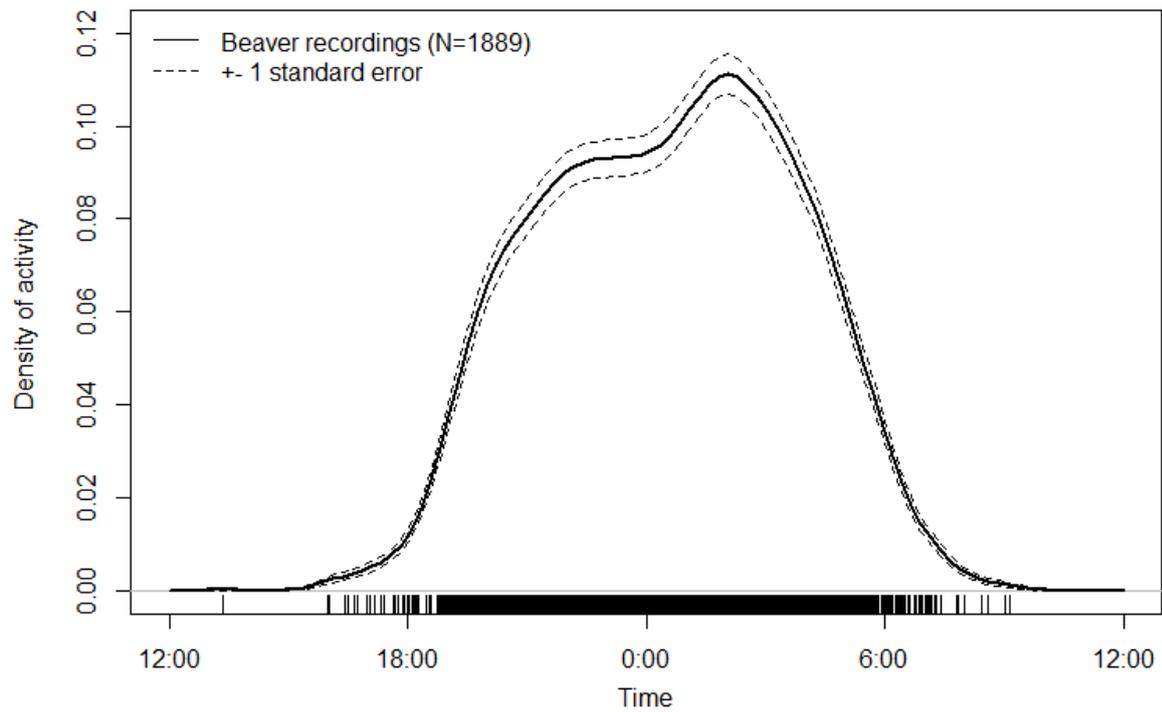
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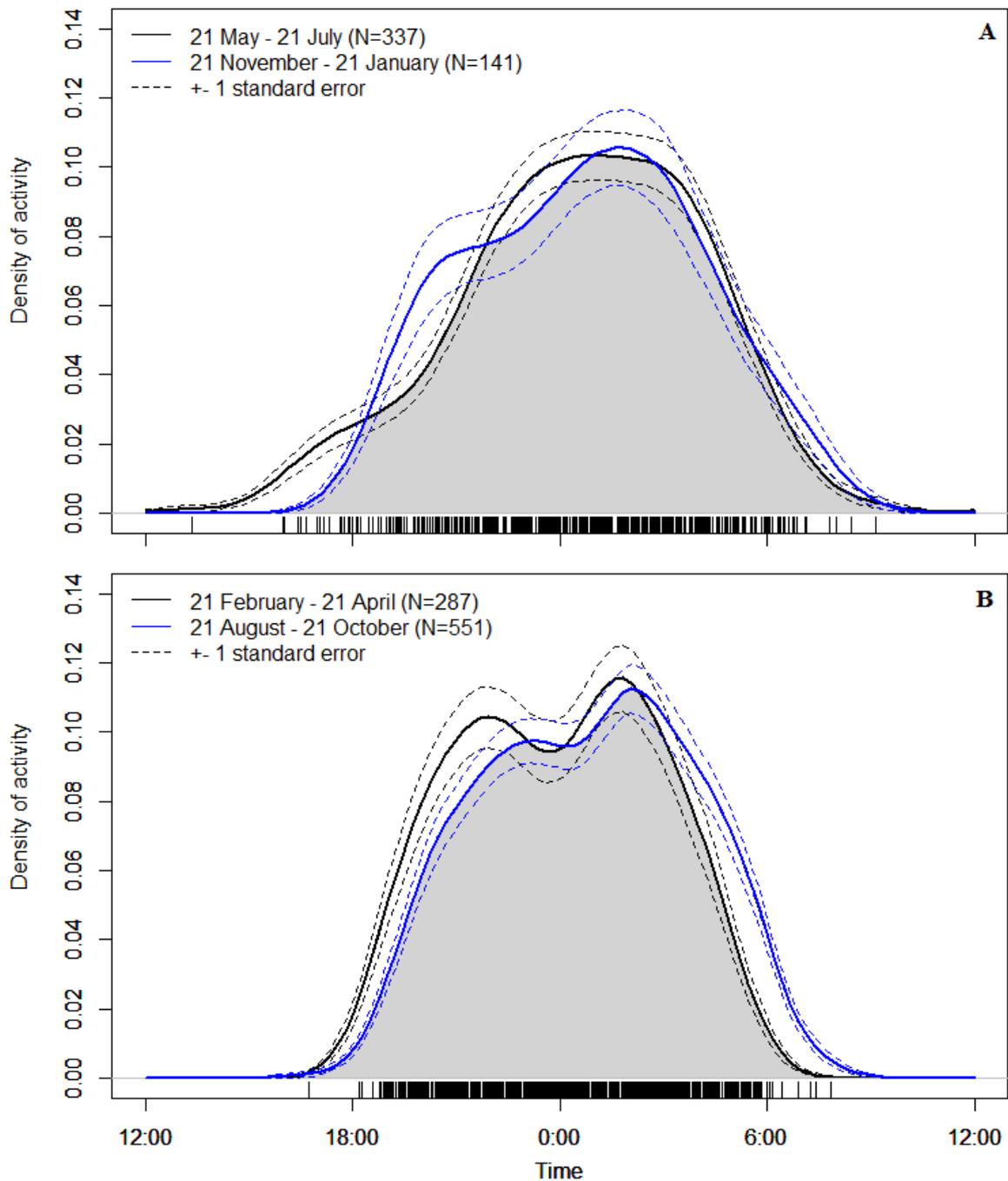
538 Figure 1: General activity pattern of beavers based on 1889 independent beaver recordings.

539 The standard errors are based on 10,000 bootstrapped samples. Each recording is represented

540 by a vertical black lines above the x-axis.

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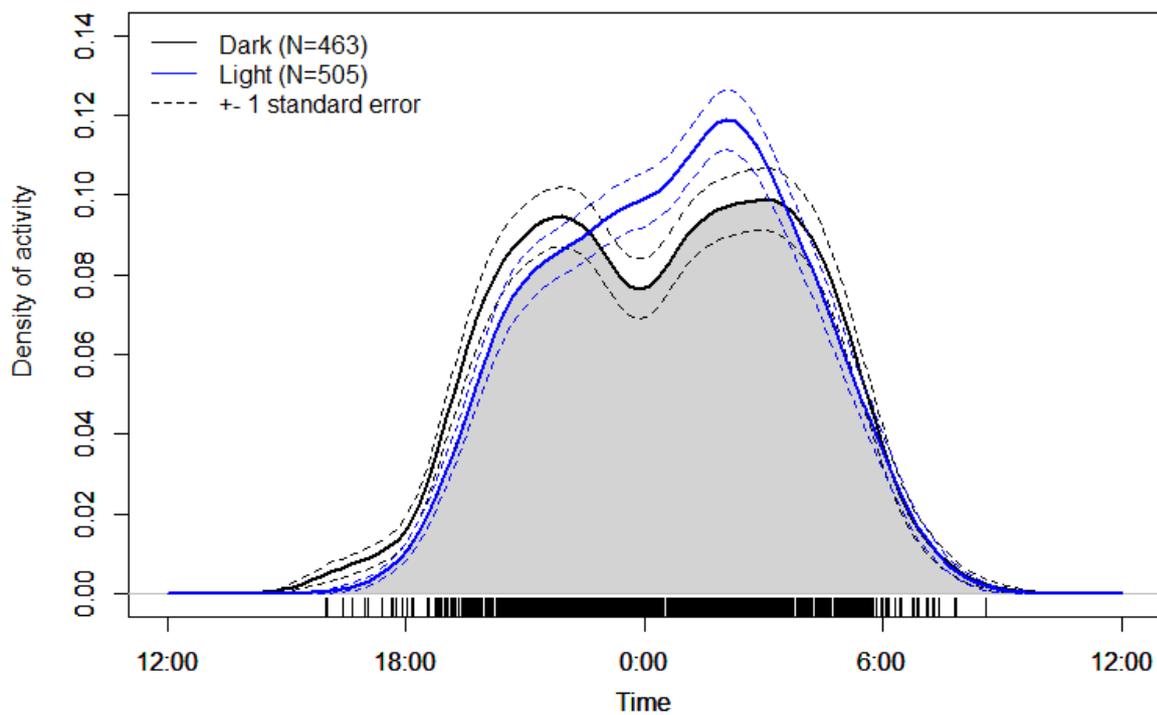
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544 Figure 2: A comparison between the activity patterns of beavers during (A) the shortest nights
 545 (21 May – 21 July) and the longest nights (21 November – 21 January) (B) both periods with
 546 intermediate night length (21 February – 21 April and 21 August – 21 October). The overlap
 547 between activity patterns is shaded grey and the standard errors for each activity pattern are

548 based on 10,000 bootstrapped samples. Each recording is represented by a vertical black lines
549 above the x-axis.
550



551
552 Figure 3: Beaver activity patterns on nights classified as Dark and Light, based on the
553 normalized nocturnal illumination (NII). The overlap between activity patterns is shaded grey
554 and the standard errors for each activity pattern are based on 10,000 bootstrapped samples.
555 Each recording is represented by a vertical black lines above the x-axis.
556

557 Table 1: A description of the locations at which camera traps were directed, including the
558 number of locations and the number of beaver recordings per location.

Type of location	# locations	# beaver recordings
Tree (beavers started but did not yet cut it down)	25	465
Burrow (running tract on burrow)	9	394
Dam	2	0
Feeding location (with non woody vegetation)	8	16
Water (near entrance of lodge or directed on a small passage)	11	19
Running tract	39	627
Frequently flooded running tract	3	14

559

560