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1 Fear of the dark?

2 Contrasting impacts of humans vs lynx on diel activity
3 of roe deer across Europe
4

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46

47 **Abstract**

- 48 1. Humans, as super predators, can have strong effects on wildlife behaviour, including profound
49 modifications of diel activity patterns. Subsequent to the return of large carnivores to human-
50 modified ecosystems, many prey species have adjusted their *spatial* behaviour to the
51 contrasting landscapes of fear generated by both their natural predators and anthropogenic
52 pressures. The effects of predation risk on *temporal* shifts in diel activity of prey, however,
53 remain largely unexplored in human-dominated landscapes.
- 54 2. We investigated the influence of the density of lynx (*Lynx lynx*), a nocturnal predator, on the
55 diel activity patterns of their main prey, the roe deer (*Capreolus capreolus*), across a gradient
56 of human disturbance and hunting at the European scale.
- 57 3. Based on 11 million activity records from 431 individually GPS-monitored roe deer in 12
58 populations within the EURODEER network (<http://eurodeer.org>), we investigated how lynx
59 predation risk in combination with both lethal and non-lethal human activities affected deer
60 diurnality.
- 61 4. We demonstrated marked plasticity in roe deer diel activity patterns in response to spatio-
62 temporal variations in risk, mostly due to human activities. In particular, roe deer decreased
63 their level of diurnality by a factor of 1.37 when the background level of general human
64 disturbance was high. Hunting exacerbated this effect, as during the hunting season deer
65 switched most of their activity to nighttime and, to a lesser extent, to dawn, although this
66 pattern varied noticeably in relation to lynx density. Indeed, in the presence of lynx, their main
67 natural predator, roe deer were relatively more diurnal. Overall, our results revealed a strong
68 influence of human activities and the presence of lynx on diel shifts in roe deer activity.

69 5. In the context of the recovery of large carnivores across Europe, we provide important insights
70 about the effects of predators on the behavioural responses of their prey in human-dominated
71 ecosystems. Modifications in the temporal partitioning of ungulate activity as a response to
72 human activities may facilitate human-wildlife coexistence, but likely also have knock-on
73 effects for predator-prey interactions, with cascading effects on ecosystem functioning.

74

75 **Key-words:** Accelerometers; Crepuscularity; Diurnality; Human footprint; Hunting;
76 Landscape of fear; Nocturnality; Predator-prey interaction; Temporal partitioning;
77 Urbanization

78

79

80 **Second abstract in native language (French): Résumé**

81 1. Les humains, en tant que “super-prédateurs”, peuvent avoir des effets importants sur le
82 comportement de la faune sauvage, y compris des modifications profondes de leurs rythmes
83 circadiens d’activité. A la suite du retour des grands carnivores dans les écosystèmes
84 anthropisés, de nombreuses espèces proies ont ajusté leur comportement spatial à ces paysages
85 de la peur contrastés, générés à la fois par les pressions liées aux risques anthropiques et à la
86 présence de leurs prédateurs naturels. Les effets du risque de prédation sur les modifications
87 temporelles des rythmes circadiens d’activité des proies restent cependant largement inconnus
88 dans les écosystèmes dominés par l’homme.

89 2. Ici, nous avons étudié l’influence de la densité de lynx (*Lynx lynx*), un prédateur nocturne, sur
90 les rythmes circadiens d’activité de leur proie principale, le chevreuil (*Capreolus capreolus*),
91 à travers un gradient de pressions anthropiques à l’échelle Européenne.

92 3. Sur la base de plus de 11 million de données d’activité issues de 431 suivis individuels de
93 chevreuils équipés de colliers GPS provenant de 12 populations au sein du réseau
94 EURODEER (<http://eurodeer.org>), nous avons analysé comment le risque de prédation par le
95 lynx, associé aux risques létaux et non-létaux des activités humaines, influence la diurnalité
96 des chevreuils.

97 4. Nous avons démontré une forte plasticité des rythmes circadiens d’activité des chevreuils en
98 réponse aux variations spatio-temporelles du risque, et notamment face aux activités
99 humaines. Plus particulièrement, les chevreuils diminuent leur degré de diurnalité d’un facteur
100 de 1.37 lorsque le dérangement humain est important. La chasse accentue cet effet, puisque
101 durant la saison de chasse les chevreuils basculent la plupart de leur activité de nuit, et dans

102 une moindre mesure, durant l'aube également, bien que ce patron soit essentiellement variable
103 en fonction de la densité de lynx. En effet, en présence de lynx, leur principal prédateur, les
104 chevreuils sont relativement plus diurnes. Globalement, nos résultats révèlent une forte
105 influence des activités humaines et de la présence de lynx sur l'ajustement des rythmes
106 circadiens d'activité des chevreuils.

107 5. Dans le contexte du retour des grands carnivores en Europe, notre étude apporte de nouvelles
108 connaissances sur les effets des prédateurs sur la réponse comportementale de leur proie dans
109 des écosystèmes anthropisés. La modification de la répartition temporelle de l'activité des
110 ongulés en réponse aux activités humaines pourrait être un facteur facilitant la coexistence
111 homme-faune sauvage, avec toutefois des conséquences autres sur les interactions prédateurs-
112 proies et leurs effets en cascade sur le fonctionnement des écosystèmes.

113 6.

114 **Mots-clés** : Accéléromètres; Crépuscularité; Diurnalité; Empreinte humaine; Chasse; Paysage
115 de la peur; Nocturnalité; Interaction prédateurs-proies; Répartition temporelle de l'activité;
116 Urbanisation

117

118 **Introduction**

119 Global changes linked to human activity are having increasingly marked impacts on many
120 wildlife populations, influencing their geographical range due to increasing urbanization and
121 landscape fragmentation (Dirzo et al. 2014) and constraining their behavioural repertoire (Sih,
122 Ferrari & Harris 2011). Recently, Tucker et al. (2018) reported a global decrease in the mobility
123 of mammals living in human-disturbed environments. They suggested that animals living in built-
124 up landscapes were confined to smaller ranges due to the prevalence of artificial barriers which
125 reduced the amplitude of their movements, although this may be accentuated by the availability of
126 supplementary food sources in anthropogenic environments. Gaynor et al. (2018) further showed
127 that, irrespective of taxa, habitat or location, mammals were markedly more nocturnal in response
128 to human disturbance. Indeed, wildlife appears to associate anthropogenic activities with a
129 perceived risk of mortality (Frid & Dill 2002). Responses to human activities are particularly
130 common among hunted species (Stillfried et al. 2015), but have been documented even in the
131 absence of real risk (Creel & Christianson 2008; Clinchy et al. 2016).

132 As large carnivores are currently recolonising Europe (Chapron et al. 2014), many game
133 species are faced with the combined risks associated with human hunting and their natural
134 predators. Large carnivores may have significant impact on both the demography (Lehman et al.
135 2018) and behaviour (Lone et al. 2017) of prey populations in areas where they have become re-
136 established. For instance, lynx (*Lynx lynx*) recolonisation lead to a marked fall in population
137 growth rate of roe deer (*Capreolus capreolus*) in Sweden (from $\lambda=1.08$ to 0.94; Andrén & Liberg
138 2015), whereas the presence of olfactory cues for lynx increased the levels of deer vigilance two-
139 fold in Germany (Eccard, Meißner & Heurich 2017). Indeed, prey are expected to adopt
140 behavioural responses to reduce exposure to humans and predators which may be costly (Lima &

141 Dill 1990; Preisser, Bolnick & Benard 2005), generating a complex landscape of fear (Laundré,
142 Hernández & Altendorf 2001).

143 Large herbivores are both primary prey for large carnivores and are widely hunted across
144 Europe. Because prey commonly shift their activity patterns as a strategy to avoid predators
145 (Tambling et al. 2015), we might expect them to adjust their diel activity patterns in relation to
146 variation in these contrasting risk factors (Lone et al. 2017). Indeed, while human hunting and
147 disturbance are concentrated into daylight hours, natural predators are mostly nocturnal or
148 crepuscular (Kusak, Skrbinšek & Huber 2005; Eriksen et al. 2011). The lynx, for instance,
149 primarily hunts during nighttime and twilight, notably during the first part of the night (Schmidt
150 1999; Heurich et al. 2014). Hence, while large herbivores frequently leave refuge habitat to feed
151 at night in human-dominated landscapes (e.g. Graham et al. 2009 on elephants *Loxodonta*
152 *africana*; Tolon et al. 2009 on wild boar *Sus scrofa*; Bonnot et al. 2013 on roe deer; Roberts, Cain
153 III & Cox 2017 on elk *Cervus canadensis*), populations exposed to natural predators might be
154 expected to shift a substantial proportion of their activity to daytime. To minimize exposure to
155 both natural and human risks, we might therefore expect prey to be particularly crepuscular,
156 squeezing as much of their activity as possible into dawn and dusk. Such shifts in diel activity of
157 prey have the potential to mitigate human-wildlife conflicts by lowering the risk of collisions
158 between vehicles and wildlife (e.g. Murray & St Clair 2015), or by attenuating the negative impacts
159 of climate change on water sensitive species (Levy et al. 2019). However, such behavioural
160 alterations may be energetically costly, substantially affecting predator-prey dynamics and,
161 ultimately, prey fitness (Creel & Christianson 2008; Kronfeld-Schor et al. 2017; Levy et al. 2019).
162 With the increasingly widespread cohabitation between large carnivores and human activities, it

163 therefore appears important to better understand how prey species respond behaviourally to the
164 contrasting mortality risks due to hunting and their natural predators.

165 In this study, using a unique data set generated from activity sensors deployed on 431
166 individual roe deer from 12 populations across Europe, we investigated variation in individual diel
167 activity patterns in relation to the landscapes of fear generated by a natural predator and human
168 activities (see Shamooin et al. 2018 for a comparable study at the population-level based on camera
169 traps). We analysed data from populations distributed over a wide gradient of human disturbance,
170 with well-defined hunting seasons, and with contrasting density of lynx, a specialist predator of
171 roe deer (Andersen et al. 2007; Nilsen et al. 2009). We hypothesized that roe deer would adjust
172 their diel activity budgets in relation to variation in the level of human disturbance and lynx
173 predation risk. As human disturbance and hunting are least intense during nighttime, we predicted
174 that: 1/ roe deer would be more nocturnal in areas where human disturbance was higher,
175 particularly during the hunting season. In contrast, we expected 2/ the degree of diurnality would
176 be higher in areas where lynx were present due to the higher risk of predation at night, particularly
177 outside of the hunting season. Finally, although large herbivores are routinely crepuscular, they
178 should partition their activity between dawn and dusk in relation to temporal variations in
179 predation risk. Therefore, we expected 3/ roe deer would be more pronouncedly crepuscular in
180 areas with high levels of both human disturbance (which is most intense during daytime) and lynx
181 predation (which predominantly occurs at night). Notably, we expected roe deer to be particularly
182 crepuscular at dusk during the hunting season (because hunting occurs mainly during daytime),
183 but at dawn where lynx were present (as lynx hunt primarily during the first part of the night;
184 Heurich et al. 2014).

185

186 **Materials and methods**

187 **Study areas and data collection**

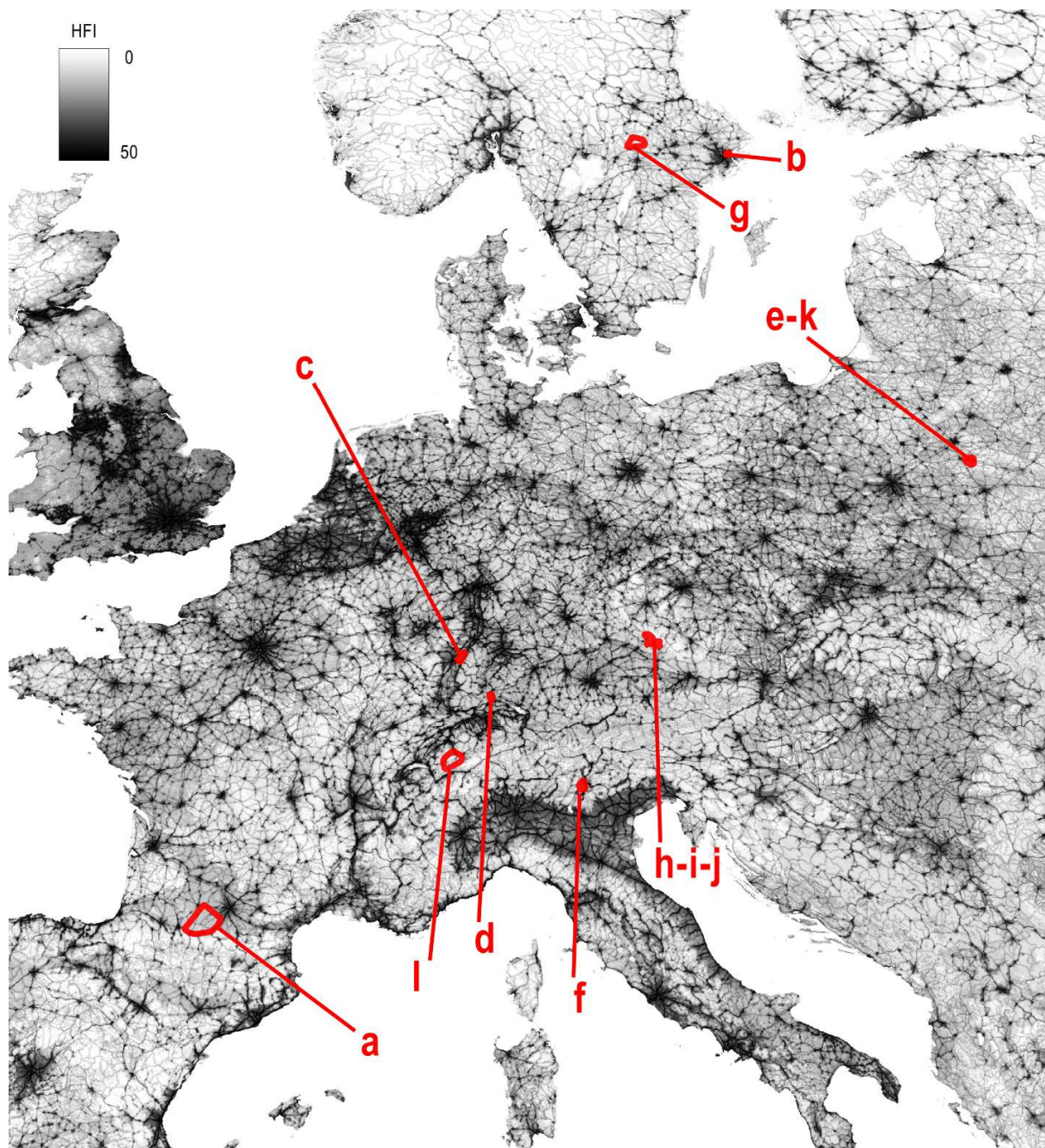
188 To investigate the influence of predation risk and human disturbance on roe deer diel activity
189 patterns, we analysed activity data obtained within the EURODEER project (<http://eurodeer.org>).
190 Data were collected for a period spanning from 2003 to 2015 and included 431 adult roe deer of
191 more than one year old (254 females and 177 males) from 12 contrasted populations located in 9
192 geographical regions across Europe (Fig. 1). At each study site, roe deer were caught during
193 winter, sexed, aged and equipped with GPS collars (Lotek 3300, Lotek Small WildCell, Vectronic
194 GPS Plus or e-obs) carrying activity or acceleration sensors. Collars were programmed to record
195 an activity measurement every 5 min and a GPS fix every 4 to 6 hours (depending on the study
196 areas and the year of monitoring).

197 The studied populations differed in terms of habitats, levels of human disturbance and
198 predation risk (Table 1). Lynx, the main natural predator of roe deer, was present on half of the
199 study sites at densities ranging from 1.0 to 2.5 lynx/100 km² (see Table 1). Wolf (*Canis lupus*) and
200 bear (*Ursus arctos*) are potential predators of roe deer, but were each present on very few study
201 sites (bear: Monte Bondone, Italy; wolf: Białowieża, Poland and Grimsö, Sweden). In contrast,
202 red fox (*Vulpes vulpes*) were widespread across the study sites, but exclusively attack neonates.
203 Therefore, we considered the presence of lynx as the predominant component of variation in
204 predation risk. To account for the presence of lynx, we categorized each study site according to
205 relative lynx density: no lynx, low lynx density (sites with transient lynx and densities of
206 approximately 1 lynx/100 km²) and high lynx density (sites with densities of approximately 2
207 lynx/100 km²; see Table 1 for more details).

208 Roe deer were also hunted in all study areas, most commonly during daytime. Although the
209 start and end of the hunting seasons differed slightly among study sites, we could define a non-
210 hunting season for both sexes ranging from 15th March to 30th April and a hunting season from 1st
211 October to 14th November which were common to all sites. Sit-and-wait hunting occurred on all
212 sites. Drive hunting is also used for roe deer (mainly on three sites: Aurignac, Baden – Rhine
213 valley, Baden – Hegau, but also at Bernese), and for other species (such as wild boar, moose, red
214 deer) almost everywhere during the same period (i.e. Aurignac, Baden – Rhine valley, Baden –
215 Hegau, Bogesund, Grimsö, Bavarian forest).

216 To quantify human disturbance, we used the human footprint index (HFI) which is a reliable
217 proxy of the overall level of human activities (Venter et al. 2016; Tucker et al. 2018). The HFI is
218 generated from nine global data layers related to the level of human pressure which describe spatial
219 variation in population density, built-up areas, nighttime lights, land use/land cover ratio,
220 coastlines, roads, railroads and navigable rivers. At a global scale, values of HFI vary between 0
221 (the least disturbed areas) to 50 (the most disturbed areas). Using the human footprint map of 2009
222 (i.e. the most recent available, <https://wchumanfootprint.org/>, Venter et al. 2016), and based on
223 all pixels (1 km²) within each individual's seasonal home-ranges, we calculated two values of
224 mean HFI for each roe deer, one for the hunting season and one for the non-hunting season.
225 Seasonal home ranges were calculated using the fixed kernel home range method at 95% with an
226 ad hoc factor. The mean HFI values varied substantially across populations (from 6.8 to 25.3).
227 Within populations, the mean HFI values also varied substantially among individuals (see Table
228 1), but not between seasons (15.3 [6.9-24.8] during Spring vs 15.2 [6.2-26.2] during Autumn).

229 **Fig. 1.** Locations of the 12 roe deer populations plotted in red on the European map of the Human Footprint
230 Index (HFI), ranging from 0 (low HFI in white) to 50 (high HFI in black): a: Aurignac; b: Bogesund; c:
231 Baden Rhine Valley; d: Baden Hegau; e: Białowieża – open; f: Monte Bondone; g: Grimsö; h, i, j: Bavarian
232 forest (three populations); k: Białowieża – forest; l: Bernese. The main characteristics of the study sites are
233 reported in Table 1.



234

235 **Table 1: Characteristics of the study areas.**

Study area id	Study area name	Sample size	Location (average coordinates)	Lynx presence (density in animals/100 km²)	Mean individual HFI (range)	Hunting season (both sexes)	Habitat type
a	Aurignac	209	France (43°29'20"N, 00°88'21"E)	-	11 (5–19)	Sep10 - Feb28	Hilly agricultural landscape with forest patches, meadows and croplands
b	Bogesund	5	Sweden (59°39'73"N, 18°19'45"E)	-	18 (16–21)	Oct1 - Jan31	Mixed landscape with forest, bogs and croplands
c	Baden - Rhine Valley	30	Germany (48°63'27"N, 07°97'74"E)	-	19 (13–27)	Sep1 - Jan31	Mixed agricultural landscape with forest patches, meadows and croplands
d	Baden - Hegau	12	Germany (47°88'31"N, 08°72'93"E)	-	19 (16–23)	Sep1 - Jan31	Mixed agricultural landscape with forest patches, meadows and croplands
e	Białowieża - open	4	Poland (52°44'49"N, 23°26'35"E)	-	21 (13–23)	Oct1 - Jan15	Agricultural landscape
f	Monte Bondone	6	Italy (46°02'14"N, 11°01'14"E)	-	25 (13–34)	Sep1 - Oct30	Alpine mountain range
g	Grimsö	9	Sweden (59°68'23"N, 15°40'17"E)	Lynx (1.0)	7 (5–9)	Oct1 - Jan31	Boreal forest
h	Bavarian forest - FRG	22	Germany (49°03'56"N, 13°19'07"E)	Lynx (1.2)	9 (6–19)	Sep1 - Jan15	Mixed mountain forest

i	Bavarian forest - RLG	59	Germany (48°54'40"N, 13°28'09"E)	Lynx (1.2)	10 (6–20)	Sep1 - Jan15	Mixed mountain forest
j	Bavarian forest - PJR	14	Germany (48°54'05"N, 13°15'11"E)	Lynx (transient dispersers)	14 (12–15)	Sep1 - Jan15	Mixed landscape with mountain forests and croplands
k	Białowieża - forest	8	Poland (52°39'22"N, 23°29'12"E)	Lynx (2.5)	10 (6–17)	Oct1 - Jan15	Mixed landscape with forest and croplands
l	Bernese	53	Switzerland (46°33'36"N, 07°30'47"E)	Lynx (2.1)	20 (4–29)	Oct1 - Nov15	Mixed landscape with forest and meadows

237 **Activity data**

238 The activity sensors on the GPS collars measured the overall level of activity by recording
239 forward/backward and sideways motions (Vectronic, e-obs) or up/down and sideways motions
240 (Lotek) on two axes, X and Y. Because activity measured on the third Z-axis was only available
241 for 4 populations (28% of all individuals), we discarded data on this axis prior to analyses. Lotek
242 3300 collars measured activity as the count of contacts along the X- and Y-axes. For each 5-minute
243 interval, the sensors provided the mean value of all activity measurements, indexing the average
244 level of activity associated with the corresponding date and time interval, ranging from 0 to 255
245 for each axis. Lotek Small WildCell and Vectronic collars measured activity based on the true
246 acceleration in the X- and Y-axes by indexing the difference in acceleration between two
247 consecutive measurements and averaging these values within 5-minute intervals ranging from 0 to
248 255 for each axis. E-obs collars sampled acceleration every minute in bursts of 9 seconds and
249 provided raw accelerometer readings for both axes. We calculated activity for e-obs collars as
250 above, by averaging the difference in acceleration between two consecutive measurements within
251 5-minute intervals for each axis. Finally, for all collars, we used the sum of the values for the X-
252 and Y- sensors as our measure of activity per 5-minute interval, with values ranging from 0 (no
253 activity) to 510 (high activity) (see Bonnot et al. 2016). Considering only the two 45-day seasons
254 analysed in this study, we obtained 10,866,096 activity records corresponding to an average of 76
255 \pm 25 days of monitoring per individual.

256

257 **Diurnality index**

258 To evaluate our first hypotheses, that roe deer would be more nocturnal where human-related
259 disturbance was high but more diurnal where lynx were present, we generated a diurnality index

260 based on the relative level of activity during daylight compared to nighttime for each individual
261 on each given day (Hoogenboom et al. 1984). Because we wished to focus on the shift of activity
262 from daytime to nighttime in this analysis, we removed the twilight periods which we defined here
263 as the period of four hours centered on sunrise (dawn) and sunset (dusk). Date-specific times for
264 sunrise and sunset for each study site were obtained from the National Oceanic & Atmospheric
265 Administration (<https://www.noaa.gov/>). The diurnality index was calculated as follows (Eqn 1),

$$266 \quad D_i = A_{DAY_i} / (A_{DAY_i} + A_{NIGHT_i}) \quad (\text{Eqn 1})$$

267 where A_{DAY_i} is the mean activity value during daytime of day i and A_{NIGHT_i} is the mean activity
268 value during nighttime (from midnight to 2 hours before sunrise and from 2 hours after sunset to
269 midnight) of day i for a given individual. D_i ranges between 0 (when a given deer was strictly
270 nocturnal during day i) and 1 (when a given deer was strictly diurnal during day i). By using a
271 diurnality index calculated as the ratio between daytime and nighttime activity levels per 24-h and
272 per individual, we circumvented the need for standardizing the activity data.

273

274 **Crepuscularity index**

275 To evaluate our prediction that roe deer would be more pronouncedly crepuscular in areas
276 with high levels of both human disturbance and predation risk, we calculated a crepuscularity index
277 for both dawn and dusk. In order to restrict this index to the peak crepuscular period, we defined
278 dawn and dusk as periods of two hours, comprising one hour each side of sunrise and sunset,
279 respectively. Thus, the index of crepuscularity is a proxy of the relative level of activity during
280 dawn (or dusk) compared to overall activity recorded during a given 24-hour cycle for each
281 individual (Eqns 2 and 3).

282

283 $C_{DAWNi} = A_{DAWNi} / (A_{DAYi} + A_{NIGHTi} + A_{DAWNi} + A_{DUSKi})$ (Eqn 2)

284 $C_{DUSKi} = A_{DUSKi} / (A_{DAYi} + A_{NIGHTi} + A_{DAWNi} + A_{DUSKi})$ (Eqn 3)

285 where C_{DAWNi} and C_{DUSKi} are, respectively, the indices of crepuscularity during dawn and dusk and
 286 A_{DAWNi} , A_{DUSKi} , A_{DAYi} and A_{NIGHTi} are, respectively, the mean activity values during dawn, dusk,
 287 daytime and nighttime during day i , for a given individual. Crepuscularity indices may range
 288 between 0 (when a given deer was strictly inactive during dawn/dusk during day i) and 1 (when a
 289 given deer was strictly active during dawn/dusk during day i).

290

291 **Statistical analyses**

292 *Overview*

293 In a first step, we explored temporal variation in diel activity in relation to the risk of lynx predation
 294 and hunting using density functions following Ridout & Linkie (2009). We compared diel activity
 295 patterns by quantifying the degree of overlap between seasons (hunting vs. non-hunting) for each
 296 population. In a second step, we analysed variation in the indices of diurnality and crepuscularity
 297 using Generalized Linear Mixed Models (GLMMs). Because the indices ranged within the interval
 298 $[0,1]$, we transformed both metrics using the equation proposed by Cribari-Neto & Zeileis (2010)
 299 (Eqn 4) so that they conformed to a beta distribution (i.e. comprised within the interval $]0,1[$).

300 $(Y_i (n - 1) + 0.5) / n$ (Eqn 4)

301 where Y_i represents the value of a given index (diurnality or crepuscularity) during the day i and
 302 n is the sample size (i.e. the total number of observations for a given index).

303 All analyses were performed in R version 3.3.3 (R Development Core Team 2017). Diel
304 activity patterns and overlaps were estimated using the ‘*overlap*’ package (Ridout & Linkie 2009)
305 and GLMMs were fitted using the ‘*glmmTMB*’ package (Brooks et al. 2017).

306

307 *Diel activity patterns across seasons and lynx densities*

308 We classified activity data into active *vs* inactive behaviour based on the frequency distribution of
309 activity measurements (Gervasi, Brunberg, & Swenson 2006) for each collar type independently
310 (for more details, see Appendix S1 in the Supporting Information file). This method uses a specific
311 threshold to discriminate active and inactive behaviour which is, therefore, insensitive to variation
312 in absolute values of activity among individuals.

313 Using the above mentioned approach, we described deer diel activity patterns for each
314 study site and quantified the degree of overlap between the non-hunting and hunting seasons, based
315 on the observations where a given individual was active. To account for changes in the sun’s
316 position across seasons, instead of using clock time, we first scaled the time of day to sunrise and
317 sunset. We did so by respectively adjusting the time of each sunrise and sunset to $\pi/2$ and $3\pi/2$
318 with the ‘sunTime’ function (see Nouvellet et al. 2012 and ‘*overlap*’ R-package). Once sunset and
319 sunrise times were synchronized across seasons and populations, we then assessed daily activity
320 patterns by fitting circular kernel density functions (Fig. 2 and Appendix S2) and calculated a
321 coefficient of overlap (i.e. the common area under the kernel density curves; Ridout & Linkie
322 2009). The coefficient of overlap ranges from 0, indicating total temporal independence between
323 activity patterns, to 1, indicating perfect synchronization. A high coefficient of overlap between
324 the two seasons indicates that activity patterns are similar.

325

326 ***Variation in diurnality in relation to human disturbance, hunting and lynx***

327 To evaluate our first hypotheses (H1 and H2) concerning the relative level of activity during
328 daytime compared to nighttime, we fitted GLMMs to analyse variation in the diurnality index in
329 relation to i/ the overall level of human disturbance, indexed by the HFI, ii/ the season, as a proxy
330 of hunting activity (non-hunting vs hunting), and iii/ the risk of predation indexed by lynx density
331 (three-modality variable: no-lynx, low lynx density, high lynx density). Because we expected the
332 impact of human disturbance and predation risk on diurnality to differ in relation to hunting
333 activity, the most complex model contained two two-way interactions between the HFI and the
334 season, and between lynx density and the season. Sex was included in all models to control for
335 potential differences in the level of diurnality between males and females (Pagon et al. 2013).
336 However, as we had no a priori reason to expect one sex to respond to risk more strongly than the
337 other in terms of temporal shifts in diel activity, we did not include any interactive effects of sex
338 with other terms in the models. We included individual identity as a random effect on the intercept
339 in all models as we had repeated measures of the diurnality index (one measure per day) for each
340 individual. For model selection, we used Akaike's Information Criterion (AIC, Burnham &
341 Anderson 2002), Akaike weights and the number of parameters to select the most parsimonious
342 model that best described the data.

343

344 ***Variation in crepuscularity in relation to human disturbance, hunting and lynx***

345 To evaluate our H3 hypotheses concerning the relative level of activity during dawn and dusk
346 compared to the rest of the day, we fitted GLMMs to analyse variation in the crepuscularity index
347 in relation to the HFI, the season and lynx density, but including the crepuscular period (dawn vs.
348 dusk) as a binary factor. Because we expected that the influence of both hunting and predation risk

349 would differ between dawn and dusk, and that these sources of risk might be cumulative, the most
350 complex model contained three two-way interactions between lynx density and the crepuscular
351 period, between the season and the crepuscular period, and between lynx density and the season,
352 with the HFI as an additional fixed effect. As before, we included sex as a fixed effect and
353 individual identity as a random effect on the intercept in all models and used AIC criteria for model
354 selection.

355

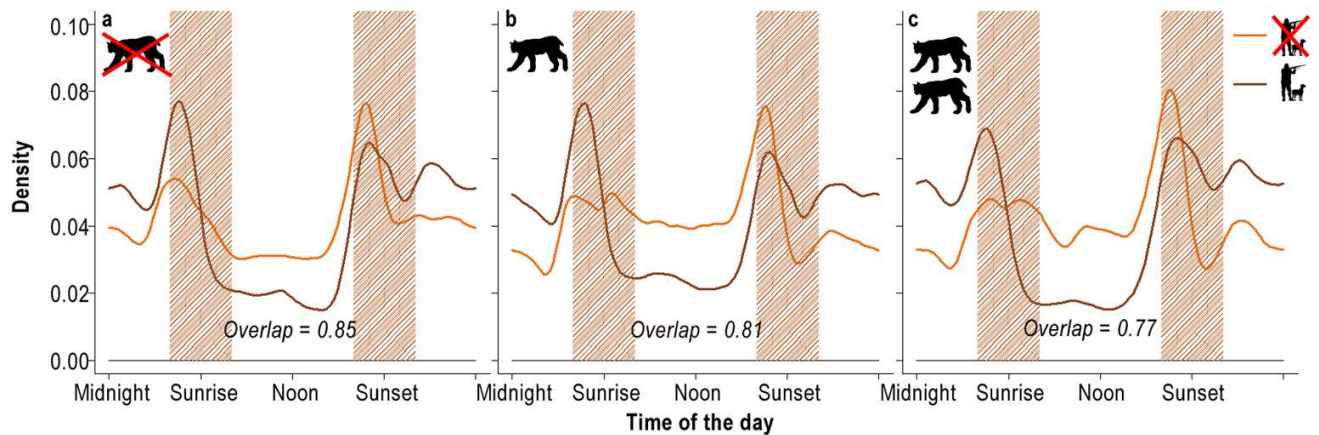
356 **Results**

357 *Diel activity patterns across seasons and lynx densities*

358 In all the 12 studied populations, we observed a clear bimodal diel activity pattern for roe deer
359 which was consistent across seasons (see Fig. 2 for an example of three populations with varying
360 lynx density; see Appendix S2 for the full representation of the 12 populations), as indicated by
361 the high coefficients of overlap between seasons (mean overlap of 0.81 [0.71-0.87]). That is, roe
362 deer expressed marked peaks of activity during the two crepuscular periods, with moderate levels
363 of activity during daytime and nighttime (Fig. 2). As predicted, deer were consistently less diurnal
364 during the hunting season compared to the non-hunting season in all populations (Fig. 2 and
365 Appendix S2). In contrast, during the non-hunting season and where lynx were present, roe deer
366 were more active during daytime (Fig. 2b and c). Note, however, that there was considerable
367 variation among populations in diel activity (see Appendix S2 and the values of HFI on each plot).

368

369 **Fig. 2.** Graphical representation of diel activity patterns during the non-hunting (orange) and hunting
 370 (brown) seasons for three roe deer populations with varying densities of lynx (a: Baden Rhine Valley, n=30,
 371 no lynx; b: Bavarian RLG, n = 59, low lynx density, and c: Białowieża forest, n = 8, high lynx density).
 372 The hatched shading represents the crepuscular periods as defined for the diurnality index.



373

374

375 *Variation in the level of diurnality*

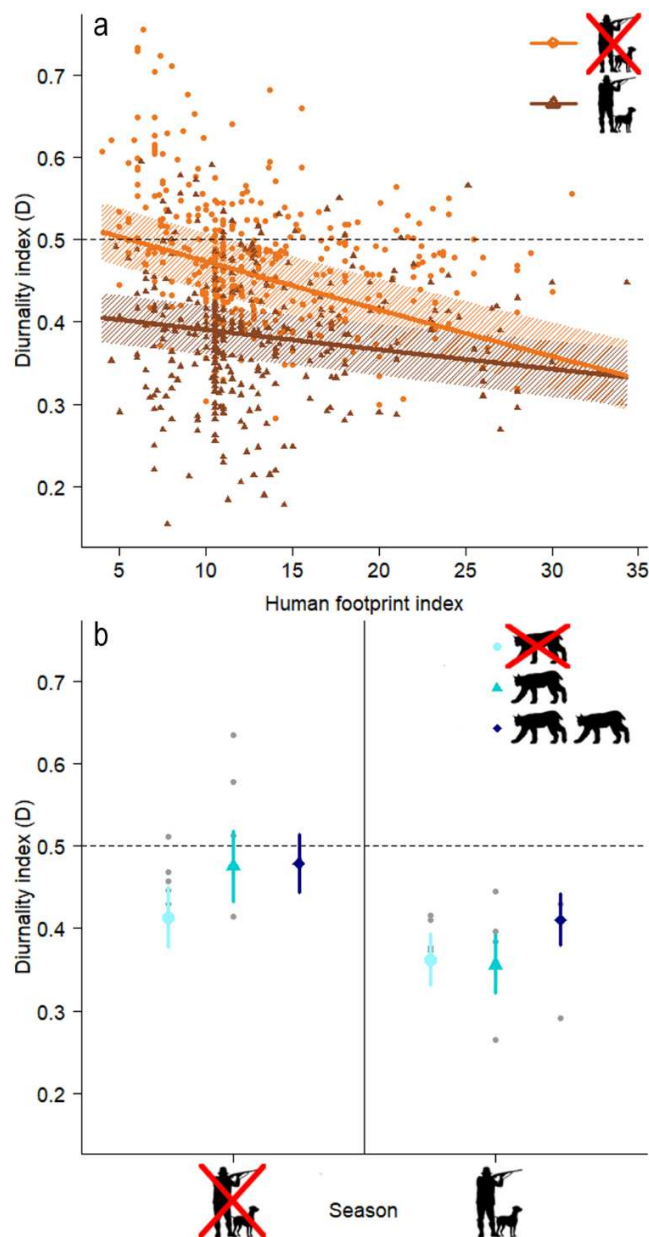
376 The diurnality index averaged per individual ranged from 0.28 to 0.75 during the non-hunting
 377 season, and from 0.15 to 0.59 during the hunting season. Model selection revealed that the
 378 diurnality index was best described by two two-way interactions between lynx density and season,
 379 and between HFI and season, plus the additive effect of sex (the AIC value was much lower than
 380 that of any of the simpler models, i.e. $\Delta AIC \geq 240$, AIC weight = 1, see Appendix S3). In
 381 accordance with our first hypothesis, the level of roe deer diurnality decreased, on average, by a
 382 factor of 1.37 over the gradient of HFI (Fig. 3a). Indeed, roe deer were relatively less diurnal when
 383 human disturbance was high, particularly during the non-hunting season (mean diurnality
 384 estimates \pm standard error: $D = 0.51 \pm 0.01$ in areas with low HFI vs $D = 0.33 \pm 0.02$ in areas with
 385 high HFI). Roe deer were also consistently less diurnal during the hunting season compared to the

386 non-hunting season (Fig. 3), although this difference was not significant in areas with high human
387 disturbance (for HFI > 15).

388 In contrast, as predicted by our second hypothesis, roe deer were relatively more diurnal when
389 lynx were present. On average, the level of diurnality was 1.2 higher where lynx were present at
390 high density compared to areas without lynx ($D = 0.45 \pm 0.02$ and $D = 0.39 \pm 0.02$, respectively
391 Fig. 3b). Interestingly, the effect of lynx density on the level of diurnality was attenuated during
392 the hunting season, particularly where lynx were present at low density. Finally, males were only
393 slightly less diurnal overall than females (see Appendix S3: Figure S3).

394

395 **Fig. 3.** Graphical representation of the best model describing variation in the level of roe deer diurnality
 396 (D) as a function of the two-way interactions between (a) the hunting season and the Human Footprint
 397 Index (HFI) and (b) the hunting season and lynx density. The dotted line represents an equivalent level of
 398 activity during daytime and nighttime (i.e. $D = 0.5$). 95% confidence intervals are represented (a) by the
 399 dashed areas and (b) by bars. The points correspond to the diurnality indices averaged (a) per season and
 400 per individual and (b) per season and per population.



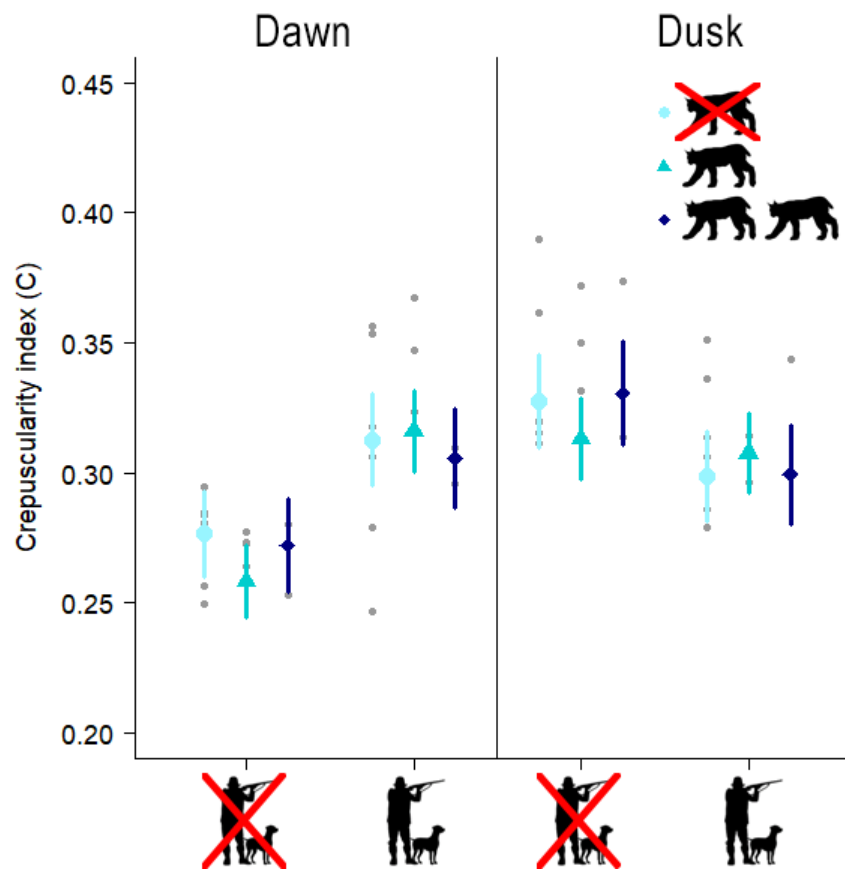
401

402 *Variation in the level of crepuscularity*

403 On average, across all individuals, the crepuscularity index ranged from 0.29 [0.16- 0.61] during
404 dawn to 0.32 [0.18-0.47] during dusk, indicating that roe deer expressed around 60% of their diel
405 activity during twilight periods (Fig. 4). The most parsimonious model that best described variation
406 in the crepuscularity index included the three two-way interactions between lynx density and the
407 crepuscular period, between lynx density and the season, and between the season and the
408 crepuscular period, plus sex (AIC weight = 0.34, Δ AIC = 1.33; see Appendix S4). Contrary to our
409 expectation, we found no marked difference in the global level of crepuscularity between the
410 hunting and non-hunting seasons or among areas with contrasting lynx densities, irrespective of
411 potential differences between dawn and dusk (Fig. 4). However, we found an effect of hunting on
412 how deer partitioned their activity between dawn and dusk. During the hunting season, roe deer
413 shifted their crepuscular activity to become relatively more active at dawn, but slightly less active
414 at dusk. More precisely, they increased their level of crepuscular activity at dawn by a factor of
415 1.19 compared to the non-hunting season (non-hunting: $C_{\text{DAWN}} = 0.26 \pm 0.02$; hunting: $C_{\text{DAWN}} =$
416 0.31 ± 0.02), and decreased their level of crepuscular activity at dusk by a factor of 1.07 (hunting:
417 $C_{\text{DUSK}} = 0.30 \pm 0.02$; non-hunting: $C_{\text{DUSK}} = 0.32 \pm 0.02$). Contrary to our expectations, we did not
418 find a marked effect of lynx density on the partitioning of activity between dawn and dusk (Fig.
419 4). Finally, although both sex and HFI featured in the two best models, there was no obvious
420 relationship with the level of crepuscularity in either case (see Appendix S4: Figures S4).

421

422 **Fig. 4.** Graphical representation of the model describing variation in the level of roe deer crepuscularity (C)
 423 as a function of the three two-way interactions between the hunting season and lynx density, between the
 424 hunting season and the crepuscular period of the day (dawn vs dusk), and between lynx density and the
 425 crepuscular period of the day (dawn vs dusk). The predictions are plotted with their 95% confidence
 426 intervals. The grey points correspond to the crepuscularity indices averaged per season and per population.
 427



428

429

430 **Discussion**

431 In the context of the increasingly widespread coexistence of large carnivores and humans in
432 Europe, our study provides important insights about the contrasting influence of predation risk and
433 anthropogenic activities on temporal partitioning of activity in their ungulate prey. By comparing
434 diel activity patterns among 12 populations of roe deer across Europe, our analyses revealed
435 marked variation in diurnality in response to both lethal and non-lethal human activity and, to a
436 lesser degree, the risk of predation by lynx. These modifications in the temporal partitioning of
437 ungulate activity likely have knock-on effects on a variety of ecological processes. As a
438 perspective to our work, we discuss the implications of our results below, notably in terms of
439 predator-prey interactions and human-wildlife coexistence.

440

441 *Impact of lethal and non-lethal human activities on diurnality of roe deer*

442 First, as expected (H1), the way in which roe deer partitioned their activity over the day was
443 strongly modified by the degree of anthropisation in the surrounding landscape. On average, deer
444 were globally 1.37 times less active during the day in areas with a high human footprint, and up to
445 1.52 times less active outside the hunting season (see Fig. 3a). Moreover, we found an additional
446 effect of hunting such that roe deer shifted their diel activity cycle by, on average, a factor of 1.20
447 to become predominantly nocturnal during the open season (Fig. 3b, Appendix S2). Overall, our
448 results are highly consistent with the recent meta-analysis of Gaynor et al. (2018) who showed that
449 wild mammals increased their degree of nocturnality by a factor of 1.36 in response to human
450 activity.

451 One important novelty of our study is that we were able to disentangle the effects of the
452 general background level of human disturbance on roe deer diurnality from lethal effects due to
453 hunting. In particular, we found that hunting had a greater impact on the level of diurnality for
454 animals living in relatively undisturbed areas (Fig. 3a). Because we evaluated the effect of hunting
455 at the seasonal scale, the observed response reflects behavioural plasticity (i.e. the array of
456 behavioural responses of an individual to variation in the environment, Komers 1997) of
457 individuals to a modification in their landscape of risk (Reebs 2002; Murray & StClair 2015).
458 Behavioural plasticity is likely one of the main keys behind the success of roe deer in human-
459 dominated environments (Andersen, Duncan & Linnell 1998). In these environments, non-lethal
460 human activities are often considered analogous to predation risk (Frid & Dill 2002) so that prey
461 adopt comparable anti-predator responses to disturbance. Whereas plastic behavioural responses
462 are often considered adaptive, responses of prey to non-lethal stimuli could be maladaptive in
463 terms of the loss of time and energy that would otherwise be allocated to fitness-enhancing
464 activities, generating an ecological trap. For instance, roe deer adjust their anti-predator behaviours
465 in relation to proximity to human settlements (e.g. their vigilance levels, see Benhaïem et al. 2008,
466 and flight distances, see Bonnot et al. 2017) which may potentially incur a fitness cost (Bonnot et
467 al. 2018). However, these effects also appear to be highly dependent on the availability of refuge
468 habitat and the period of the day (Benhaïem et al. 2008; Bonnot et al. 2013; Sönnichsen et al.
469 2013), indicating that animals may buffer human disturbance by adjusting both their space use and
470 temporal partitioning of activity.

471 However, the extent of plasticity is finite and our results further suggest that roe deer living in
472 the most human-disturbed areas had reached the upper limit of their potential plasticity with
473 respect to the degree of nocturnality. Indeed, these animals were more nocturnal year round in

474 comparison with roe deer living in relatively undisturbed areas and they did not modify their diel
475 activity patterns further during the hunting season (Fig. 3a). More specifically, at a threshold of
476 approximately 15 for the human footprint index, roe deer diurnality no longer differed between the
477 hunting and non-hunting seasons. On the HFI scale from 0 for wild areas to 50 for very developed
478 areas, this value describes relatively undeveloped environments, with low levels of human
479 pressure. This suggests that, even in areas of relatively low human pressure, anthropogenic
480 activities may substantially modify the degree of nocturnality in prey. However, for the specific
481 case of our study species, we also know that roe deer are constrained to maintain a minimum level
482 of activity to feed during daytime, even in the most human-disturbed landscapes. Indeed, all
483 ruminants must alternate feeding bouts with periods of rest and rumination (Hofmann 1989), but
484 because the roe deer has a particularly small rumen, these cycles are relatively short (Duncan et
485 al. 1998). Roe deer also have highly flexible diets (Abbas et al. 2011), exploiting substantially
486 different foods in spring and autumn, which should affect their spatial behaviour (i.e. habitat
487 selection, Godvik et al. 2009; Bonnot et al. 2018). Although we have no a priori reason why such
488 seasonal differences in the risk-resource trade-off should influence the partitioning of activity
489 between day and night, further work should investigate whether preferred habitat is also associated
490 with higher levels of risk.

491

492 ***Impact of a natural predator on diurnality of roe deer***

493 Because large carnivores are predicted to influence the landscape of risk and the landscape of
494 fear of their prey, prey should adjust their behavioural responses to spatial and temporal variation
495 in the risk associated with their natural predators (Lima & Dill 1990; Manning, Gordon & Ripple
496 2009; Dröge et al. 2017). In support of this hypothesis, we found that roe deer shifted from a

497 predominantly nocturnal activity cycle to a more diurnal rhythm when lynx were present (Fig. 3).
498 In a similar manner, Tambling et al. (2015) showed that African ungulates were more likely to be
499 active during the day when cohabiting with lions (*Panthera leo*) and hyaenas (*Crocuta crocuta*),
500 thereby decreasing activity overlap with these nocturnal predators.

501 In our study, the behavioural modifications associated with the presence of lynx were mainly
502 confined to the spring, when no hunting occurred. During hunting, roe deer became predominantly
503 nocturnal, whether or not lynx were present (Fig. 3b). This result highlights the strong influence
504 of humans as a “super-predator” in shaping the behavioural responses of prey (Ciuti et al. 2012a,
505 b; Clinchy et al. 2016), with potential fitness consequences, notably in multi-predator landscapes
506 (e.g. Gehr et al. 2018). For example, humans kill mesocarnivores at more than four times the rate
507 at which they are killed by non-human predators (Darimont et al. 2015). Moreover, human
508 activities create a well-defined landscape of risk, which is often highly predictable in time and
509 space, provoking direct and immediate behavioural responses of prey (Cromsigt et al. 2013). In
510 contrast, the landscape of risk due to large carnivores may be more difficult for their prey to
511 predict.

512 Besides humans and lynx, wolves were also present in two of our study areas, which likely
513 created even more complex landscapes of risk for roe deer, although they are not their main prey
514 in these ecosystems (see Jędrzejewski et al. 2002; Sand et al. 2005). Wolf can also alter the spatial
515 behaviour of their prey (e.g. Dellinger et al. 2019; Bongi et al. 2008), but there is less evidence
516 that they alter their diel activity patterns (Eriksen et al. 2011 on moose *Alces alces*, but see Kohl
517 et al. 2018 on elk *Cervus elaphus*). One explanation could be that the cues associated with risk of
518 predation by ambush predators, like lynx, are generally more reliable than those for coursing
519 predators, like wolf (Preisser, Orrock & Schmitz 2007; Kohl et al. 2019). Further studies are

520 needed to understand the influence of predator hunting tactics on the activity of their prey, notably
521 in multi-predator environments (see also Kohl et al. 2019).

522 These landscapes of risk are also likely dynamic depending on the degree of interaction
523 between humans and natural predators. For instance, large carnivores generally avoid humans
524 (Oriol-Cotteril et al. 2015; Belotti et al. 2018), which may create a human-shield effect for their
525 prey (Berger 2007), but also may result in higher kill rates (Smith, Wang & Wilmers 2015). Lynx,
526 in particular, must tradeoff avoidance of human activities during daytime against prey availability
527 (Basille et al. 2009; Gehr et al. 2017; Filla et al. 2017), which should accentuate the risk of
528 predation for roe deer during the night.

529

530 *Crepuscularity of roe deer in a multi-predator landscape*

531 Large herbivores are frequently reported to be markedly crepuscular (e.g. Krop-Benesch et al.
532 2013), which has commonly been interpreted as an antipredator strategy (Kamler, Jędrzejewska &
533 Jędrzejewski 2007; Monterroso, Alves & Ferreras 2013; Swinnen, Hughes & Leirs 2015). This is
534 expected to be particularly the case in complex landscapes of risk composed of coexisting
535 predators with contrasting hunting methods and diel activity patterns (Gehr et al. 2018; Lone et al.
536 2014). However, we found little support for this hypothesis here, as the level of crepuscularity did
537 not appear to be linked to variations in either the human- or lynx-induced risk of predation. Overall,
538 roe deer carried out around 60% of their diel activity during dawn and dusk, but, contrary to our
539 expectation, this proportion did not increase when they were exposed simultaneously to both the
540 risk of predation from lynx and hunting (Fig. 4). In line with previous studies, our results rather
541 indicate a strong physiological and/or behavioural constraint promoting the maintenance of
542 crepuscular activity peaks in ungulates, irrespective of the risk context (Kronfeld-Schor et al. 2001;

543 Massé & Côté 2013; Bonnot et al. 2016; but see Loe et al. 2007 and Long et al. 2013). Another
544 explanation could be that any further increase in crepuscular activity would not be an efficient
545 anti-predator strategy (Kronfeld-Schor & Dayan 2003), as both humans and lynx can potentially
546 hunt at twilight.

547 Finally, while markedly crepuscular, we still found that large herbivores may partition their
548 crepuscular activity differently between dusk and dawn, notably depending on hunting risk (Fig.
549 4). Indeed, our results suggest that the risk of predation by lynx did not markedly influence how
550 roe deer partitioned their activity between dawn and dusk, whereas deer became more active at
551 dawn during the hunting season compared to spring. We suggest that, because roe deer were able
552 to feed more during the day when there is no risk of hunting, they were also less constrained to be
553 crepuscular. This could explain why roe deer were markedly less active at dawn during spring,
554 when human daily activities may be prevalent in agro-systems, but maintained their activity peak
555 at dusk when human presence is generally lower (Fig. 4). Although the disturbing effects of
556 hunting on prey behaviour are well-documented (Cromsigt et al. 2013; Gaynor et al. 2018), further
557 work will be required to quantify the variation in how large herbivores respond to varying hunting
558 methods and sources of disturbance, and the cascading effects of their resulting behaviours on
559 ecosystem functioning.

560

561 **Conclusion and perspectives**

562 Our study provides further evidence of the strong behavioural plasticity of large herbivores
563 which allows them to thrive in heavily anthropogenic landscapes. Behavioural plasticity plays a
564 key role in species adjustment to rapid environmental change due to human activities (Sih et al.
565 2011) and is also likely crucial in the context of the return of large carnivores. Prey may respond

566 in several ways to variations in the level of predation risk: moving to safer habitat during risky
567 times (Godvik et al. 2009), decreasing their movement rate (Picardi et al. 2019), adjusting their
568 levels of vigilance (Dröge et al. 2017) or escape decisions (Bonnot et al. 2015, 2017). With recent
569 advances in biologging, we will soon be able to investigate the fine-scale behavioural responses
570 of prey, as well as their ecological and energetic costs in a dynamic landscape of fear (Brown et
571 al. 2013; Kays et al. 2015; Williams et al. 2017; Kröschel et al. 2017). For example, the observed
572 shift of roe deer to nocturnal activity in response to hunting could result in a higher risk of lynx
573 predation during the hunting season (Gehr et al. 2018), or in lower foraging efficiency due to an
574 increase in alternative anti-predator behaviours such as vigilance (Benhaïem et al. 2008),
575 potentially affecting predator-prey dynamics, ecological communities and ecosystem functioning
576 (Fortin et al. 2005). Indeed, as both prey and consumer of vegetation, large herbivores are key
577 ecosystem engineers with marked impacts on a variety of ecological processes (Côté et al. 2004).
578 Therefore, shifts in the temporal partitioning of their activity in response to predation risk and/or
579 human disturbance likely have knock-on effects on the frequency and spatial distribution of
580 important ecosystem services (e.g. seed and nutrient transfer, biodiversity) and disservices (e.g.
581 road traffic accidents, damage to saplings and crops, parasite abundance). For example, roe deer
582 is one of the main hosts for adult ticks (*Ixodes ricinus*) which are more active during the night
583 (Belozarov 1982; Mejlou 1997). Any shift to diurnal activity in deer populations exposed to
584 nocturnal predators could decrease their level of infestation and, hence, the dispersal of ticks and
585 tick-borne diseases over the landscape (Hofmeester et al. 2017). The modification of the activity
586 patterns of prey species to the contrasting pressures of human activities and large carnivores may
587 therefore result in behaviourally-mediated trophic cascades which urgently require further
588 investigation.

589 **Authors' contributions**

590 NCB, PK, MH, AJMH, FC conceived the ideas and designed the study. AJMH, NM, PK, MH, MK, AB,
591 FC, BG, LS provided the data with the critical help of JDG who managed the database. OC and NCB carried
592 out the statistical analyses with the help of AJMH and NM. NCB, OC and AJMH took the lead in writing
593 the manuscript. All authors contributed to the interpretation of the results, provided critical feedback on the
594 manuscript and gave final approval for publication.

595

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606

607 **Data accessibility**

608 Data used in this study are available from the Dryad Digital Repository (Bonnot, Couriot et al. 2019)
609 at <https://doi.org/10.5061/dryad.1zcrjdfnm>. Raw data are also available through the EURODEER platform.
610 Anyone is welcome to join the EURODEER project and obtain an access to the database after contacting
611 the persons in charge (see <https://eurodeer.org/contacts/>).

612

613 **References**

- 614 Abbas, F., Morellet, N., Hewison, A.J.M., Merlet, J., Cargnelutti, B., Lourtet, B., Angibault,
615 J.-M., Daufresne, T., Aulagnier, S. & Verheyden, H. (2011) Landscape fragmentation generates
616 spatial variation of diet composition and quality in a generalist herbivore. *Oecologia*, 167(2), 401-
617 411
- 618 Andersen, R., Duncan, P., & Linnell, J.D.C. (Eds.). (1998). The European roe deer: the
619 biology of success.
- 620 Andersen, R., Karlsen, J., Austmo, L.B., Odden, J., Linnell, J.D.C & Gaillard, J.-M. (2007)
621 Selectivity of Eurasian lynx *Lynx lynx* and recreational hunters for age, sex and body condition in
622 roe deer *Capreolus capreolus*. *Wildlife Biology*, 13(4), 467-474
- 623 Andrén, H. & Liberg, O. (2015) Large impact of Eurasian lynx predation on roe deer
624 population dynamics. *PloS One*, 10(3), e0120570
- 625 Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C, Odden, J., Andersen, R., Høgda,
626 K.A. & Gaillard, J.-M. (2009). What shapes Eurasian lynx distribution in human dominated
627 landscapes: selecting prey or avoiding people? *Ecography*, 32(4), 683-691
- 628 Belotti, E., Mayer, K., Kreisinger, J., Heurich, M., & Bufka, L. (2018). Recreational activities
629 affect resting site selection and foraging time of Eurasian lynx (*Lynx lynx*). *Hystrix*, 29, 181–189
- 630 Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.J.M.,
631 Morellet, N. & Verheyden, H. (2008) Hunting increases vigilance levels in roe deer and modifies
632 feeding site selection. *Animal Behaviour*, 76(3), 611-618
- 633 Belozеров, VN. (1982). Diapause and biological rhythms in ticks. *Physiology of ticks* (eds
634 F.D. Obenchain & R. Galun), pp. 469-500 Oxford: Pergamon Press, Oxford

635 Berger, J. (2007) Fear, human shields and the redistribution of prey and predators in protected
636 areas. *Biology Letters*, 3(6), 620-623

637 Bongi, P., Ciuti, S., Grignolio, S., Del Frate, M., Simi, S., Gandelli, D. & Apollonio, M. (2008)
638 Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning
639 season in a wolf area. *Journal of Zoology*, 276(3), 242-251

640 Bonnot, N.C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J., Gehr, B.,
641 Heurich, M., Kjellander, P., Kröschel, M., Morellet, N., Soennichsen, L. & Hewison, A.J.M.
642 (2019) Data from: Fear of the dark? Contrasting impacts of humans vs lynx on diel activity of roe
643 deer across Europe. *Dryad Digital Repository* <https://doi.org/10.5061/dryad.1zcrjdfnm>

644 Bonnot, N.C., Goulard, M., Hewison, A.J.M., Cargnelutti, B., Lourtet, B., Chaval, Y. &
645 Morellet, N. (2018) Boldness-mediated habitat use tactics and reproductive success in a wild large
646 herbivore. *Animal Behaviour*, 145, 107-115

647 Bonnot, N.C., Hewison, A.J.M., Morellet, N., Gaillard, J.-M., Debeffe, L., Couriot, O.,
648 Cargnelutti, B., Chaval, Y., Lourtet, B., Kjellander, P. & Vanpé, C. (2017) Stick or twist: roe deer
649 adjust their flight behaviour to the perceived trade-off between risk and reward. *Animal*
650 *Behaviour*, 124, 35-46

651 Bonnot, N.C., Morellet, N., Hewison, A.J.M., Martin, J.-L., Benhamou, S. & Chamaillé-
652 Jammes, S. (2016) Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) adjust habitat selection
653 and activity rhythm to the absence of predators. *Canadian Journal of Zoology*, 94(6), 385-394

654 Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F. & Hewison,
655 A.J.M. (2013) Habitat use under predation risk: hunting, roads and human dwellings influence the
656 spatial behaviour of roe deer. *European Journal of Wildlife Research*, 59(2), 185-193

657 Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B., Klein, F.,
658 Hewison, A.J.M. & Morellet, N. (2015) Interindividual variability in habitat use: evidence for a
659 risk management syndrome in roe deer? *Behavioral Ecology*, 26(1), 105-114

660 Brown, D.D., Kays, R., Wikelski, M., Wilson, R., & Klimley, A.P. (2013). Observing the
661 unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry*, 1(1), 20

662 Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A.,
663 Skaug, H.J., Maechler, M. & Bolker, B.M. (2017) glmmTMB balances speed and flexibility
664 among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378-
665 400

666 Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a*
667 *practical information-theoretic approach*. Second edition. Springer-Verlag, New York

668 Chapron, G., Kaczensky, P., Linnell, J. D., von Arx, M., Huber, D., Andrén, H., López-Bao,
669 J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Vaidas Balys, V., Bedő, P., Bego, F.,
670 Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A.,
671 Engleder, T., Fuxjäger, C., Groff, C, Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić,
672 J., Jerina, K., Kluth, G., Knauer, F., Kojola, I, Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak,
673 J., Kutal, M., Liberg, O., Majjić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski,
674 D., Mersini, D., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G.,
675 Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser,
676 A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-
677 Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F.,
678 Zlatanova, D. & Boitani, L. (2014) Recovery of large carnivores in Europe's modern human-
679 dominated landscapes. *Science*, 346(6216), 1517-1519

680 Ciuti, S., Muhly, T.B., Paton, D.G., McDevitt, A.D., Musiani, M. & Boyce, M.S. (2012a)
681 Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society*
682 *of London B: Biological Sciences*, rspb20121483

683 Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A. & Boyce, M.S. (2012b)
684 Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of
685 fear. *PloS one*, 7(11), e50611

686 Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C. &
687 Macdonald, D.W. (2016). Fear of the human “super predator” far exceeds the fear of large
688 carnivores in a model mesocarnivore. *Behavioral Ecology*, 27(6), 1826-1832

689 Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C. & Waller, D.M. (2004) Ecological
690 impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, 35, 113-
691 147

692 Creel, S. & Christianson, D. 2008. Relationships between direct predation and risk effects.
693 *Trends in Ecology and Evolution*, 23, 194-201

694 Cribari-Neto, F. & Zeileis, A. (2010) Beta Regression in R. *Journal of Statistical Software*,
695 34(2), 1–24

696 Cromsigt, J.P.G.M., Kuijper, D.P.J., Adam, M., Beschta, R.L., Churski, M., Eycott, A.,
697 Kerley, G.I.H., Mysterud, A., Schmidt, K. & West, K. (2013) Hunting for fear: innovating
698 management of human–wildlife conflicts. *Journal of Applied Ecology*, 50(3), 544-549

699 Darimont, C.T., Fox, C.H., Bryan, H.M. & Reimchen, T.E. (2015) The unique ecology of
700 human predators. *Science*, 349(6250), 858-860

701 Dellinger, J.A., Shores, C.R., Craig, A., Heithaus, M.R., Ripple, W.J. & Wirsing, A.J. (2019)
702 Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray
703 wolves. *Oecologia*, 189(2), 487-500

704 Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014)
705 Defaunation in the Anthropocene. *Science*, 345(6195), 401-406

706 Dröge, E., Creel, S., Becker, M.S. & M'soka, J. (2017) Risky times and risky places interact
707 to affect prey behaviour. *Nature Ecology & Evolution*, 1(8), 1123

708 Duncan, P., Tixier, H., Hofmann, R.R. & Lechner-Doll, M. (1998) Feeding strategies and the
709 physiology of digestion in roe deer. *The European roe deer: the biology of success* (eds R.
710 Andersen, P. Duncan & J.D.C. Linnell), pp. 91-116. Scandinavian University Press, Oslo

711 Eccard, J.A., Meißner, J.K. & Heurich, M. (2017) European roe deer increase vigilance when
712 faced with immediate predation risk by Eurasian Lynx. *Ethology*, 123(1), 30-40

713 Eriksen, A., Wabakken, P., Zimmermann, B., Andreassen, H.P., Arnemo, J.M., Gundersen,
714 H., Liberg, O., Linnell, J.D.C., Milner, J.M., Pedersen, H.C., Sand, H., Solberg, E.J. & Storaas, T.
715 (2011) Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and
716 moose. *Animal Behaviour*, 81(2), 423-431

717 Filla, M., Premier, J., Magg, N., Dupke, C., Khorozyan, I., Waltert, M., Bufka, L. & Heurich,
718 M. (2017) Habitat selection by Eurasian lynx (*Lynx lynx*) is primarily driven by avoidance of
719 human activity during day and prey availability during night. *Ecology and Evolution*, 7(16), 6367-
720 6381

721 Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves
722 influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park.
723 *Ecology*, 86(5), 1320–1330

724 Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk.
725 *Conservation Ecology*, 6(1), 11

726 Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. (2018) The influence of
727 human disturbance on wildlife nocturnality. *Science*, 360(6394), 1232-1235

728 Gehr, B., Hofer, E.J., Muff, S., Ryser, A., Vimercati, E., Vogt, K. & Keller, L.F. (2017) A
729 landscape of coexistence for a large predator in a human dominated landscape. *Oikos*, 126(10),
730 1389-1399.

731 Gehr, B., Hofer, E.J., Pewsner, M., Ryser, A., Vimercati, E., Vogt, K. & Keller, L.F. (2018)
732 Hunting-mediated predator facilitation and superadditive mortality in a European
733 ungulate. *Ecology and Evolution*, 8(1), 109-119

734 Gervasi, V., Brunberg, S. & Swenson, J. (2006) An individual-based method to measure
735 animal activity levels: a test on brown bears. *Wildlife Society Bulletin*, 34, 1314–1319

736 Godvik, I.M.R., Loe, L.E., Vik, J.O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009)
737 Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology*, 90(3),
738 699-710

739 Graham, M.D., Douglas-Hamilton, I., Adams, W.M. & Lee, P.C. (2009) The movement of
740 African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12(5), 445-455

741 Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattisson, J.,
742 Odden, J., Persson, J., Rauset, G.R., Schmidt, K. & Linnell, J.D.C (2014) Activity patterns of
743 Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range.
744 *PLoS One*, 9(12), e114143

745 Hofmeester, T.R., Jansen, P.A., Wijnen, H.J., Coipan, E.C., Fonville, M., Prins, H.H., Sprong,
746 H. & van Wieren, S.E. (2017) Cascading effects of predator activity on tick-borne disease
747 risk. *Proceedings of the Royal Society B: Biological Sciences*, 284(1859), 20170453

748 Hoogenboom, I., Daan, S., Dallinga, J.H., & Schoenmakers, M. (1984) Seasonal change in
749 the daily timing of behaviour of the common vole, *Microtus arvalis*. *Oecologia*, 61(1), 18-31

750 Hofmann, R.R. (1989) Evolutionary steps of ecophysiological adaptation and diversification
751 of ruminants: a comparative view of their digestive system. *Oecologia*, 78(4), 443-457

752 Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K. &
753 Szymura, L. (2002) Kill rates and predation by wolves on ungulate populations in Białowieża
754 Primeval Forest (Poland). *Ecology*, 83(5), 1341-1356

755 Kamler, J.F., Jędrzejewska, B. & Jędrzejewski, W. (2007) Activity patterns of red deer in
756 Białowieża National Park, Poland. *Journal of Mammalogy*, 88(2), 508-514

757 Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye
758 on life and planet. *Science*, 348(6240), aaa2478

759 Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., White,
760 P.J., Smith, D.W. & MacNulty, D.R. (2018) Diel predator activity drives a dynamic landscape of
761 fear. *Ecological Monographs*, 88(4), 638-652

762 Kohl, M.T., Ruth, T.K., Metz, M.C., Stahler, D.R., Smith, D.W., White, P.J. & MacNulty,
763 D.R. (2019) Do prey select for vacant hunting domains to minimize a multi-predator
764 threat? *Ecology Letters*, 00, 1– 10, <https://doi.org/10.1111/ele.13319>

765 Komers, P.E. (1997) Behavioural plasticity in variable environments. *Canadian Journal of*
766 *Zoology*, 75, 161-169

767 Krop-Benesch, A., Berger, A., Hofer, H. & Heurich, M. (2013) Long-term measurement of
768 roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in
769 GPS-collars. *Italian Journal of Zoology*, 80(1), 69-81

770 Kröschel, M., Reineking, B., Werwie, F., Wildi, F. & Storch, I. (2017) Remote monitoring of
771 vigilance behavior in large herbivores using acceleration data. *Animal Biotelemetry*, 5(1), 10

772 Kronfeld-Schor, N. & Dayan, T. (2003) Partitioning of time as an ecological resource. *Annual*
773 *Review of Ecology, Evolution and Systematics*, 34(1), 153-181

774 Kronfeld-Schor, N., Dayan, T., Elvert, R., Haim, A., Zisapel, N., & Heldmaier, G. (2001) On
775 the use of the time axis for ecological separation: diel rhythms as an evolutionary constraint. *The*
776 *American Naturalist*, 158(4), 451-457

777 Kronfeld-Schor, N., Visser, M.E., Salis, L. & van Gils, J.A. (2017) Chronobiology of
778 interspecific interactions in a changing world. *Philosophical Transactions of the Royal Society B:*
779 *Biological Sciences*, 372(1734), 20160248

780 Kusak, J., Skrbinšek, A.M. & Huber, D. (2005) Home ranges, movements, and activity of
781 wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. *European Journal of Wildlife*
782 *Research*, 51(4), 254-262

783 Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001). Wolves, elk, and bison:
784 reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of*
785 *Zoology*, 79(8), 1401-1409

786 Lehman, C.P., Rota, C.T., Raithel, J.D. & Millspaugh, J.J. (2018) Pumas affect elk dynamics
787 in absence of other large carnivores. *The Journal of Wildlife Management*, 82(2), 344-353

788 Levy, O., Dayan, T., Porter, W.P. & Kronfeld-Schor, N. (2019) Time and ecological
789 resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity?
790 *Ecological Monographs*, 89(1), e01334

791 Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a
792 review and prospectus. *Canadian Journal of Zoology*, 68(4), 619-640

793 Loe, L.E., Bonenfant, C., Mysterud, A., Severinsen, T., Øritsland, N.A., Langvatn, R., Stien,
794 A., Irvine, R.J. & Stenseth, N.C. (2007) Activity pattern of arctic reindeer in a predator-free
795 environment: no need to keep a diel rhythm. *Oecologia*, 152, 617–624

796 Lone, K., Loe, L.E., Gobakken, T., Linnell, J.D.C., Odden, J., Remmen, J. & Mysterud, A.
797 (2014) Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting
798 pattern of predation risk imposed by lynx and humans. *Oikos*, 123(6), 641-651

799 Lone, K., Mysterud, A., Gobakken, T., Odden, J., Linnell, J.D.C. & Loe, L.E. (2017)
800 Temporal variation in habitat selection breaks the catch-22 of spatially contrasting predation risk
801 from multiple predators. *Oikos*, 126(5), 624-632

802 Long, E.S., Jacobsen, T.C., Nelson, B.J. & Steensma, K.M.M. (2013) Conditional diel and
803 seasonal movement strategies of male Columbia black-tailed deer (*Odocoileus hemionus*
804 *columbianus*). *Canadian Journal of Zoology*, 91(10), 679–688

805 Massé, A. & Côté, S.D. (2013) Spatiotemporal variations in resources affect activity and
806 movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density. *Canadian*
807 *Journal of Zoology*, 91(4), 252–263

808 Manning, A.D., Gordon, I.J. & Ripple, W.J. (2009) Restoring landscapes of fear with wolves
809 in the Scottish Highlands. *Biological Conservation*, 142(10), 2314-2321

810 Mejlon, H.A. (1997). Diel activity of *Ixodes ricinus* Acari: Ixodidae at two locations near
811 Stockholm, Sweden. *Experimental & Applied Acarology*, 21(4), 247-256

812 Monterroso, P., Alves, P.C. & Ferreras, P. (2013) Catch me if you can: diel activity patterns
813 of mammalian prey and predators. *Ethology*, 119, 1044-1056

814 Murray, M.H. & St. Clair, C.C. (2015) Individual flexibility in nocturnal activity reduces risk
815 of road mortality for an urban carnivore. *Behavioral Ecology*, 26(6), 1520-1527

816 Nilsen, E.B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., Van Laere, G. & Linnell,
817 J.D.C. (2009) A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe
818 deer populations. *Journal of Animal Ecology*, 78(3), 585-594

819 Nouvellet, P., Rasmussen, G.S.A., Macdonald, D.W. & Courchamp, F. (2012) Noisy clocks
820 and silent sunrises: measurement methods of daily activity pattern. *Journal of Zoology*, 286(3),
821 179-184

822 Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., & Macdonald, D.W. (2015)
823 Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being
824 downgraded from ultimate to penultimate predator by humans. *Oikos*, 124(10), 1263-1273

825 Pagon, N., Grignolio, S., Pipia, A., Bonghi, P., Bertolucci, C. & Apollonio, M. (2013) Seasonal
826 variation of activity patterns in roe deer in a temperate forested area. *Chronobiology*
827 *International*, 30(6), 772-785

828 Picardi, S., Basille, M., Peters, W., Ponciano, J. M., Boitani, L. & Cagnacci, F. (2019)
829 Movement responses of roe deer to hunting risk. *The Journal of Wildlife Management*, 83(1), 43-
830 51

831 Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005) Scared to death? The effects of
832 intimidation and consumption in predator-prey interactions. *Ecology*, 86(2), 501-509

833 Preisser, E.L., Orrock, J.L. & Schmitz, O.J. (2007) Predator hunting mode and habitat domain
834 alter nonconsumptive effects in predator–prey interactions. *Ecology*, 88(11), 2744-2751

835 R Core Team. (2017) R: a language and environment for statistical computing. R Foundation
836 for Statistical Computing, Vienna, Austria. Available from <https://www.r-project.org/>

837 Reeb, S.G. (2002). Plasticity of diel and circadian activity rhythms in fishes. *Reviews in Fish*
838 *Biology and Fisheries*, 12(4), 349-371

839 Roberts, C.P., Cain III, J.W. & Cox, R.D. (2017) Identifying ecologically relevant scales of
840 habitat selection: diel habitat selection in elk. *Ecosphere*, 8(11), e02013

841 Ridout, M. & Linkie M. (2009) Estimating overlap of daily activity patterns from camera trap
842 data. *Journal of Agricultural, Biological and Environmental Statistics*, 14(3), 322-337

843 Sand, H., Zimmermann, B., Wabakken, P., Andr en, H. & Pedersen, H.C. (2005) Using GPS
844 technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife*
845 *Society Bulletin*, 33(3), 914-925

846 Schmidt, K. (1999). Variation in daily activity of the free-living Eurasian lynx (*Lynx lynx*) in
847 Bia owie a Primeval Forest, Poland. *Journal of Zoology*, 249(4), 417-425

848 Shammoun, H., Maor, R., Saltz, D. & Dayan, T. (2018) Increased mammal nocturnality in
849 agricultural landscapes results in fragmentation due to cascading effects. *Biological Conservation*,
850 226, 32-41

851 Sih, A., Ferrari, M.C. & Harris, D.J. (2011) Evolution and behavioural responses to human-
852 induced rapid environmental change. *Evolutionary Applications*, 4(2), 367-387

853 Smith, J.A., Wang, Y. & Wilmers, C.C. (2015) Top carnivores increase their kill rates on prey
854 as a response to human-induced fear. *Proceedings of the Royal Society B: Biological*
855 *Sciences*, 282(1802), 20142711

856 Sönnichsen, L., Bokje, M., Marchal, J., Hofer, H., Jędrzejewska, B., Kramer-Schadt, S. &
857 Ortmann, S. (2013). Behavioural responses of European roe deer to temporal variation in predation
858 risk. *Ethology*, 119(3), 233-243

859 Stillfried, M., Belant, J.L., Svoboda, N.J., Beyer, D.E. & Kramer-Schadt, S. (2015) When top
860 predators become prey: black bears alter movement behaviour in response to hunting pressure.
861 *Behavioural Processes*, 120, 30-39

862 Swinnen, K.R.R., Hughes, N.K. & Leirs, H. (2015) Beaver (*Castor fiber*) activity patterns in
863 a predator-free landscape: what is keeping them in the dark? *Mammalian Biology* 80, 477-483

864 Tambling, C.J., Minnie, L., Meyer, J., Freeman, E.W., Santymire, R.M., Adendorff, J. &
865 Kerley, G.I. (2015) Temporal shifts in activity of prey following large predator reintroductions.
866 *Behavioral Ecology and Sociobiology*, 69(7), 1153-1161

867 Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C.,
868 Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L.,
869 Bertassoni, A., Beyer, D., Bidner, L., van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown,
870 D., de Bruyn, P.J.N., Cagnacci, F., Calabrese, J.M., Camilo-Alves, C., Chamaillé-Jammes, S.,
871 Chiaradia, A., Davidson, S.C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I.,
872 Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C.H., Ford, A.T., Fritz,
873 S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.J.M., Hof,
874 C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M.,
875 Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P.,
876 Linnell, J.D.C., López-López, P., Markham, A.C., Mattisson, J., Medici, E.P., Mellone, U.,
877 Merrill, E., de Miranda Mourão, G., Morato, R.G., Morellet, N, Morrison, T.A., Díaz-Muñoz, S.L.,
878 Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., O'Hara, R.B., Oliveira-Santos,

879 L.G.R., Olson, K.A., Patterson, B.D., de Paula, R.C., Pedrotti, L., Reineking, B., Rimmler, M.,
880 Rogers, T.L., Rolandsen, C.M., Rosenberry, C.S., Rubenstein, D.I., Safi, K., Saïd, S., Sapir, N.,
881 Sawyer, H., Schmidt, N.M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J.P., Singh, N.,
882 Solberg, E.J., Spiegel, O., Strand, O., Sundaresan, S., Ullmann, W., Voigt, U., Wall, J., Wattles,
883 D., Wikelski, M., Wilmers, C.C., Wilson, J.W., Wittemyer, G., Zięba, F., Zwijacz-Kozica, T.,
884 Mueller, T. (2018) Moving in the Anthropocene: Global reductions in terrestrial mammalian
885 movements. *Science*, 359(6374), 466-469

886 Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C. & Baubet, E. (2009) Responding to
887 spatial and temporal variations in predation risk: space use of a game species in a changing
888 landscape of fear. *Canadian Journal of Zoology*, 87(12), 1129-1137

889 Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham,
890 H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A. & Watson, J.E.M. (2016) Global
891 terrestrial Human Footprint maps for 1993 and 2009. *Scientific Data*, 3, 160067

892 Williams, H.J., Holton, M.D., Shepard, E.L., Largey, N., Norman, B., Ryan, P.G., Duriez, O.,
893 Scantlebury, M., Quintana, F., Magowan, E.A., Marks, N.J., Alagaili, A.N., Bennett, N.C. &
894 Wilson, R.P. (2017) Identification of animal movement patterns using tri-axial magnetometry.
895 *Movement ecology*, 5(1), 6

896

897 **Supporting information provided:**

898 **Appendix S1.** Classification of the activity data into active vs inactive behaviour for
899 describing diel activity patterns

900 **Appendix S2.** Graphical representation of the diel activity patterns of roe deer over a 24-h
901 cycle and overlap between the non-hunting and hunting seasons

902 **Appendix S3.** Summary and results of the top-ranked candidate models explaining variation
903 in the level of diurnality (D)

904 **Appendix S4.** Summary and results of the top-ranked candidate models explaining variation
905 in the level of crepuscularity (C)

906