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Fear of the dark?
Contrasting impacts of humans *vs* lynx on diel activity of roe deer across Europe

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Abstract

1. Humans, as super predators, can have strong effects on wildlife behaviour, including profound modifications of diel activity patterns. Subsequent to the return of large carnivores to human-modified ecosystems, many prey species have adjusted their *spatial* behaviour to the contrasting landscapes of fear generated by both their natural predators and anthropogenic pressures. The effects of predation risk on *temporal* shifts in diel activity of prey, however, remain largely unexplored in human-dominated landscapes.

2. We investigated the influence of the density of lynx (*Lynx lynx*), a nocturnal predator, on the diel activity patterns of their main prey, the roe deer (*Capreolus capreolus*), across a gradient of human disturbance and hunting at the European scale.

3. Based on 11 million activity records from 431 individually GPS-monitored roe deer in 12 populations within the EURODEER network (http://eurodeer.org), we investigated how lynx predation risk in combination with both lethal and non-lethal human activities affected deer diurnality.

4. We demonstrated marked plasticity in roe deer diel activity patterns in response to spatio-temporal variations in risk, mostly due to human activities. In particular, roe deer decreased their level of diurnality by a factor of 1.37 when the background level of general human disturbance was high. Hunting exacerbated this effect, as during the hunting season deer switched most of their activity to nighttime and, to a lesser extent, to dawn, although this pattern varied noticeably in relation to lynx density. Indeed, in the presence of lynx, their main natural predator, roe deer were relatively more diurnal. Overall, our results revealed a strong influence of human activities and the presence of lynx on diel shifts in roe deer activity.

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

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

Second abstract in native language (French): Résumé

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

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

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

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

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

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

6.

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

Introduction

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

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

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

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

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

Materials and methods

Study areas and data collection

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

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

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

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

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

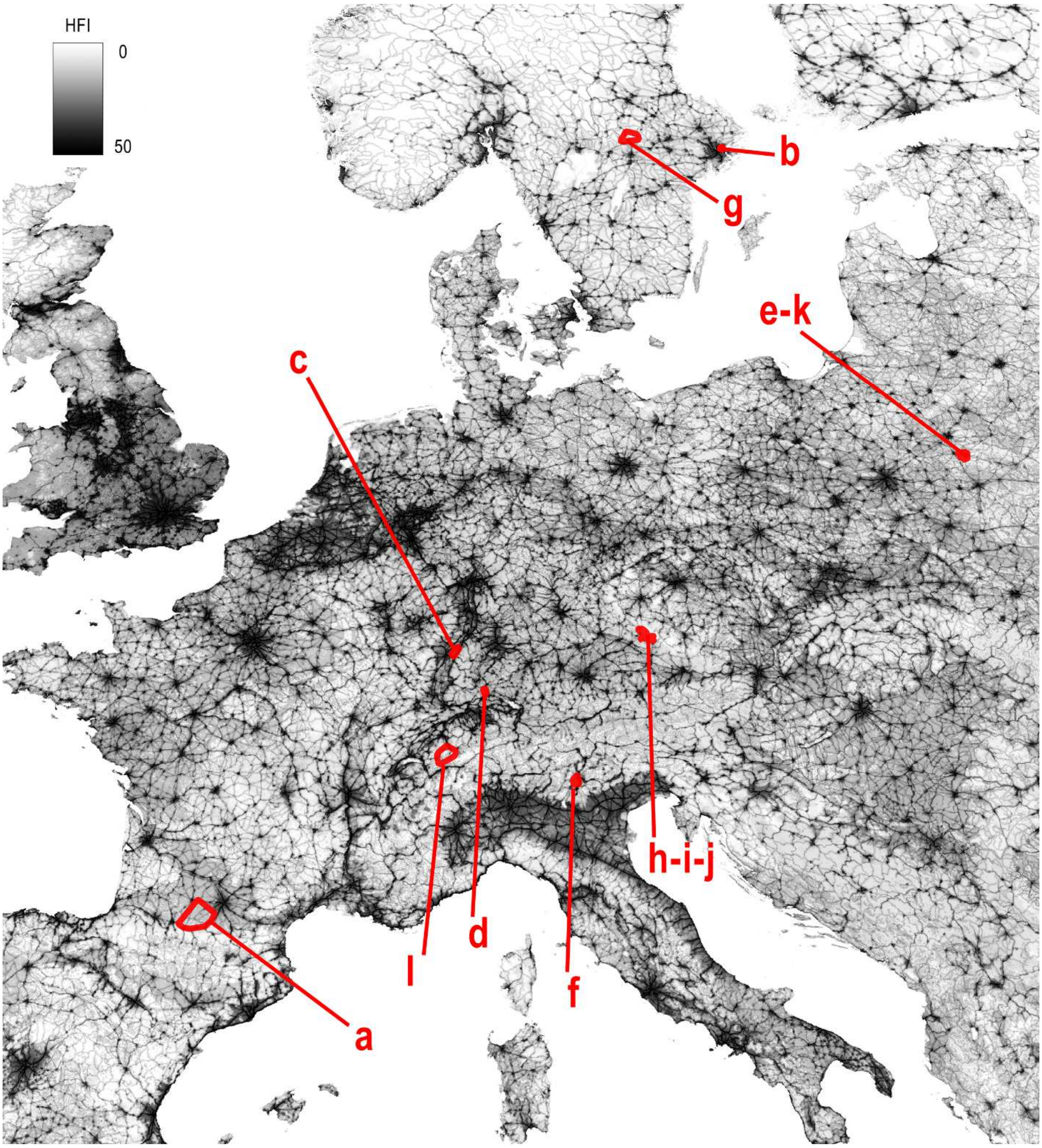


Table 1: Characteristics of the study areas.

Study area id	Study area name	Sample size	Location (average coordinates)	Lynx presence (density in animals/100 km^2)	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

Activity data

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

Diurnality index

To evaluate our first hypotheses, that roe deer would be more nocturnal where human-related disturbance was high but more diurnal where lynx were present, we generated a diurnality index based on the relative level of activity during daylight compared to nighttime for each individual on each given day (Hoogenboom et al. 1984). Because we wished to focus on the shift of activity from daytime to nighttime in this analysis, we removed the twilight periods which we defined here as the period of four hours centered on sunrise (dawn) and sunset (dusk). Date-specific times for sunrise and sunset for each study site were obtained from the National Oceanic & Atmospheric Administration (https://www.noaa.gov/). The diurnality index was calculated as follows (Eqn 1),

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

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

Crepuscularity index

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

$$C_{DAWN_i} = A_{DAWN_i} / (A_{DAY'_i} + A_{NIGHT'_i} + A_{DAWN_i} + A_{DUSK_i}) \qquad \text{(Eqn 2)}$$

$$C_{DUSK_i} = A_{DUSK_i} / (A_{DAY'_i} + A_{NIGHT'_i} + A_{DAWN_i} + A_{DUSK_i}) \qquad \text{(Eqn 3)}$$

where C_{DAWN_i} and C_{DUSK_i} are, respectively, the indices of crepuscularity during dawn and dusk and A_{DAWN_i}, A_{DUSK_i}, $A_{DAY'_i}$ and $A_{NIGHT'_i}$ are, respectively, the mean activity values during dawn, dusk, daytime and nighttime during day i, for a given individual. Crepuscularity indices may range between 0 (when a given deer was strictly inactive during dawn/dusk during day i) and 1 (when a given deer was strictly active during dawn/dusk during day i).

Statistical analyses

Overview

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

$$(Y_i (n - 1) + 0.5) / n \qquad \text{(Eqn 4)}$$

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

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

Diel activity patterns across seasons and lynx densities

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

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

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

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

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

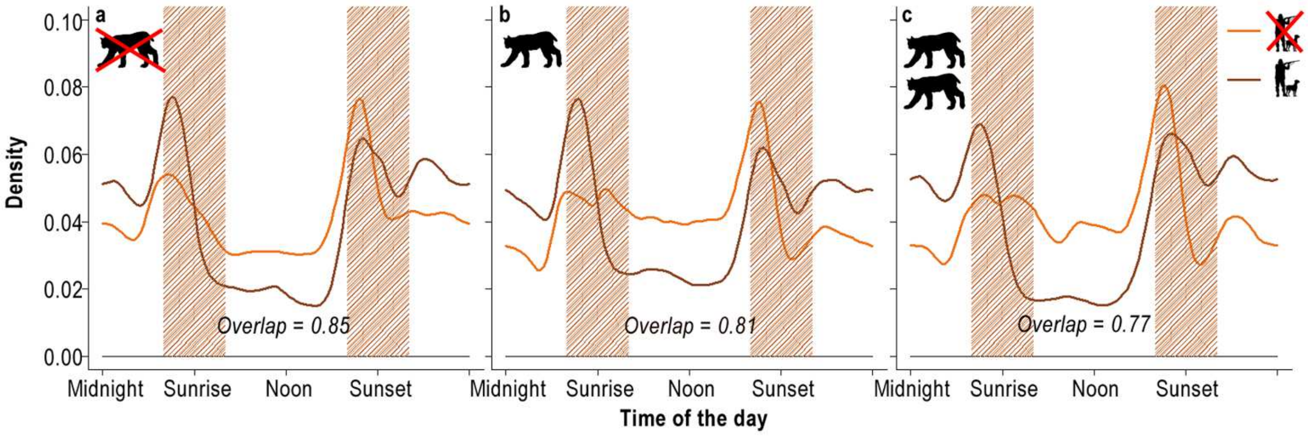
To evaluate our H3 hypotheses concerning the relative level of activity during dawn and dusk compared to the rest of the day, we fitted GLMMs to analyse variation in the crepuscularity index in relation to the HFI, the season and lynx density, but including the crepuscular period (dawn *vs*. dusk) as a binary factor. Because we expected that the influence of both hunting and predation risk would differ between dawn and dusk, and that these sources of risk might be cumulative, the most complex model contained three two-way interactions between lynx density and the crepuscular period, between the season and the crepuscular period, and between lynx density and the season, with the HFI as an additional fixed effect. As before, we included sex as a fixed effect and individual identity as a random effect on the intercept in all models and used AIC criteria for model selection.

Results

Diel activity patterns across seasons and lynx densities

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

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

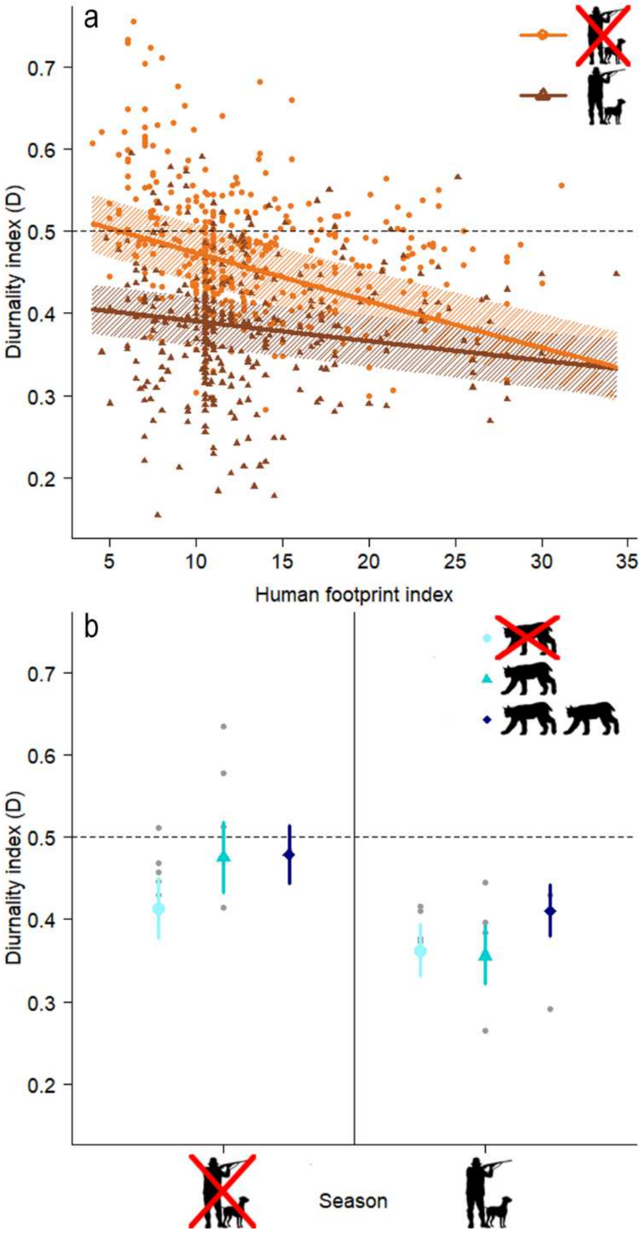


Variation in the level of diurnality

The diurnality index averaged per individual ranged from 0.28 to 0.75 during the non-hunting season, and from 0.15 to 0.59 during the hunting season. Model selection revealed that the diurnality index was best described by two two-way interactions between lynx density and season, and between HFI and season, plus the additive effect of sex (the AIC value was much lower than that of any of the simpler models, i.e. ΔAIC ≥ 240, AIC weight = 1, see Appendix S3). In accordance with our first hypothesis, the level of roe deer diurnality decreased, on average, by a factor of 1.37 over the gradient of HFI (Fig. 3a). Indeed, roe deer were relatively less diurnal when human disturbance was high, particularly during the non-hunting season (mean diurnality estimates ± standard error: D = 0.51 ± 0.01 in areas with low HFI *vs* D = 0.33 ± 0.02 in areas with high HFI). Roe deer were also consistently less diurnal during the hunting season compared to the non-hunting season (Fig. 3), although this difference was not significant in areas with high human disturbance (for HFI > 15).

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

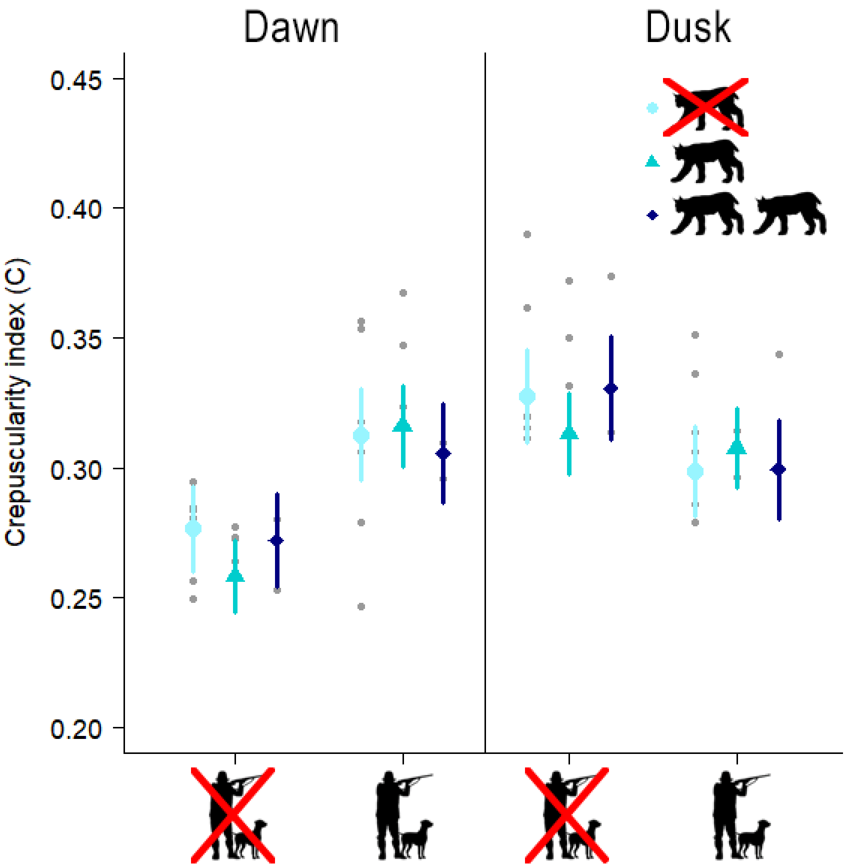
Fig. 3. Graphical representation of the best model describing variation in the level of roe deer diurnality (D) as a function of the two-way interactions between (a) the hunting season and the Human Footprint Index (HFI) and (b) the hunting season and lynx density. The dotted line represents an equivalent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



Variation in the level of crepuscularity

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

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



Discussion

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

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

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

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

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

Impact of a natural predator on diurnality of roe deer

Because large carnivores are predicted to influence the landscape of risk and the landscape of fear of their prey, prey should adjust their behavioural responses to spatial and temporal variation in the risk associated with their natural predators (Lima & Dill 1990; Manning, Gordon & Ripple 2009; Dröge et al. 2017). In support of this hypothesis, we found that roe deer shifted from a predominantly nocturnal activity cycle to a more diurnal rhythm when lynx were present (Fig. 3). In a similar manner, Tambling et al. (2015) showed that African ungulates were more likely to be active during the day when cohabiting with lions (*Panthera leo*) and hyaenas (*Crocuta crocuta*), thereby decreasing activity overlap with these nocturnal predators.

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

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

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

Crepuscularity of roe deer in a multi-predator landscape

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

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

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

Conclusion and perspectives

Our study provides further evidence of the strong behavioural plasticity of large herbivores which allows them to thrive in heavily anthropogenic landscapes. Behavioural plasticity plays a key role in species adjustment to rapid environmental change due to human activities (Sih et al. 2011) and is also likely crucial in the context of the return of large carnivores. Prey may respond in several ways to variations in the level of predation risk: moving to safer habitat during risky times (Godvik et al. 2009), decreasing their movement rate (Picardi et al. 2019), adjusting their levels of vigilance (Dröge et al. 2017) or escape decisions (Bonnot et al. 2015, 2017). With recent advances in biologging, we will soon be able to investigate the fine-scale behavioural responses of prey, as well as their ecological and energetic costs in a dynamic landscape of fear (Brown et al. 2013; Kays et al. 2015; Williams et al. 2017; Kröschel et al. 2017). For example, the observed shift of roe deer to nocturnal activity in response to hunting could result in a higher risk of lynx predation during the hunting season (Gehr et al. 2018), or in lower foraging efficiency due to an increase in alternative anti-predator behaviours such as vigilance (Benhaïem et al. 2008), potentially affecting predator-prey dynamics, ecological communities and ecosystem functioning (Fortin et al. 2005). Indeed, as both prey and consumer of vegetation, large herbivores are key ecosystem engineers with marked impacts on a variety of ecological processes (Côté et al. 2004). Therefore, shifts in the temporal partitioning of their activity in response to predation risk and/or human disturbance likely have knock-on effects on the frequency and spatial distribution of important ecosystem services (e.g. seed and nutrient transfer, biodiversity) and disservices (e.g. road traffic accidents, damage to saplings and crops, parasite abundance). For example, roe deer is one of the main hosts for adult ticks (*Ixodes ricinus*) which are more active during the night (Belozerov 1982; Mejlon 1997). Any shift to diurnal activity in deer populations exposed to nocturnal predators could decrease their level of infestation and, hence, the dispersal of ticks and tick-borne diseases over the landscape (Hofmeester et al. 2017). The modification of the activity patterns of prey species to the contrasting pressures of human activities and large carnivores may therefore result in behaviourally-mediated trophic cascades which urgently require further investigation.

Authors' contributions

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

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Data accessibility

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

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Supporting information provided:

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

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

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

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