Prey attracting but not repelled by predators suggests an asymmetric investment in the encounter-avoid-escape sequence.

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Abstract

Understanding predator-prey interactions, particularly how species use space and time to influence encounter rates, is crucial in ecology. Camera traps, while not being able to directly measure encounters of large free-roaming species, can help estimating how species tolerate or avoid proximity with eachother. We used data from a one-year study in four German protected areas used 283 camera traps and applied recurrent event analysis to explore interactions among three prey species (red deer, roe deer, wild boar) and two predators (grey wolf, Eurasian lynx). Prey visitation rates were unaffected by predators, but wolves showed a strong attraction to prey, with visitation rates approximatively seven times higher right after prey occurrence. Insufficient data hindered robust pattern estimation regarding the Eurasian lynx. This suggests an asymmetry where predators need to succeed at every stage of the encounter sequence, while prey can disrupt the process at any stage to avoid being caught.

Introduction

Understanding predator-prey interactions is fundamental to ecology, with implications for individual fitness, population dynamics, community structure, and ecosystem functions (Sih et al. 1985; Krebs et al. 1995). Predation is one possible outcome of the encounter sequence (*sensu* Lima & Dill, 1990), with mutual ignorance, prey avoidance or escape (Lima & Dill, 1990). Encounters occur at a certain rate (Holling, 1959) when the predator or prey detection radius exceeds the distance between them (Lima & Dill, 1990). Predators aim to maximize this rate, while prey aim to minimize it. Estimating this encounter rate is challenging, especially for large free-ranging animals (Hebblewhite et al., 2005). Estimating this encounter rate, depicting the predator-prey “space race” (Sih, 1984) is challenging, especially for large free-ranging animals (Hebblewhite et al., 2005).

Traditionally, spatial overlap has been the primary metric used (e.g., occupancy, MacKenzie et al., 2004; resource selection probability, Hebblewhite et al., 2005; habitat use similarity, Smith et al., 2019a). However, space overlap solely is insufficient to estimate the encounter rate (Suraci et al. 2022), which depends on predator and prey biology (e.g., population density, foraging tactic, locomotion, sensory abilities) as well as environmental conditions (Sih, 1984; Lima & Dill, 1990). Even with complete spatial overlap, low population densities (Travis & Palmer, 2005; Sims et al., 2006) or slower movement speeds (Sih, 1984) can reduce encounter rates. Additionally, predators and prey must co-occur in both space and time for encounters to happen (Sih, 1984; Minta, 1992; Caro, 2005; Sih, 2005; Suraci et al.,

2022). Temporal overlap within cycles (e.g., circadian) can serve as a proxy for encounter rates, facilitated by analytical advancements (e.g., diel activity pattern overlap, Ridout & Linkie, 2009) and technologies (e.g., GPS collars, Eriksen et al., 2011; camera traps, Harmsen et al., 2009). However, summarizing linear time in a circular pattern (yearly or daily) only provides a partial view. High temporal and spatial overlap may occur, but individuals can avoid encounters by consistently being out of sync by a day or more. Thus, considering spatial and temporal overlaps separately is insufficient for understanding how predators and prey aim to maximize and minimize encounter rates.

Telemetry is the most accurate method for estimating encounter rates and attraction/repulsion processes (e.g., Li et al., 2013). However, there are few empirical studies on this topic (e.g., Courbin et al., 2013; Middleton et al., 2013; Isbell et al., 2018; Tallian et al., 2023; Elbroch et al., 2017; Rafiq et al., 2020). This scarcity is likely due to the difficulty of simultaneously monitoring two large free-roaming species with sufficient sample sizes and defining an adequate detection radius to identify encounters (Lynch et al., 2015). Stationary monitoring devices, like camera traps, cannot accurately estimate encounter rates because they rarely capture direct encounters (Suraci et al., 2022). However, they can assess proximate co-occurrence, or the likelihood of one species being detected after another at a location within a certain time frame, indicating whether species tolerate or avoid each other (Schliep et al., 2018). Thus, camera traps can help bridge the gap between spatial/temporal overlaps and encounter rates (Suraci et al., 2022).

Grey wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) populations are recovering in western and central Europe after near-extinction (Chapron et al., 2014). As a consequence, larger herbivores, including red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), face an increasing risk of non-human predation, providing opportunities to examine predator-prey interactions in European ecosystems. Apart from human-induced mortality, wolf predation is the main cause of death for red deer while lynx predation is less significant, and only for calves and hinds (Kamler et al., 2007; Okarma et al., 1995; Belotti et al., 2015). Both lynx and wolves threaten roe deer, whereas wild boar is primarily predated by wolves and almost never by lynx (Okarma et al., 1995). Wolves are cursorial predators, relying on long-distance movements (Mech, 1970; Peterson & Ciucci, 2003), for which these three herbivores are a significant part of its diet (Newsome et al., 2016). Lynx are ambush predators, mainly preying on roe deer, occasionally on red deer and rarely on wild boar (Khorozian & Heurich, 2023; Okarma et al., 1997; Molinari-Jobin et al., 2007; Krofel et al., 2011; Heurich et al., 2016).

In this study, we used camera traps to investigate the proximate co-occurrence between these two predators and three herbivores. Following Ferry et al. (2024), three different patterns of visitation rate over time of a species after the occurrence of another scenarios could be distinguished: i) a flat rate (neutral), ii) first low and increasing until reaching a plateau (avoidance) or iii) first high and decreasing until reaching a plateau (attraction). Based on prey prevalence, predator impact on prey mortality, and prey responses to hunting strategies (cursorial vs. ambush, Kuijper et al., 2014; Sunde et al., 2022), we hypothesized various scenarios:

(H1). Red deer show avoidance towards wolves and, to a lesser extent, towards lynx.

(H2). Roe deer show avoidance towards both wolves or lynx.

(H3). Wild boars show avoidance towards wolves and remain neutral towards lynx.

(H4). Wolves are attracted to all three herbivores.

(H5). Lynx are attracted to roe deer, somewhat attracted to red deer, and neutral towards wild boars.

The physical landscape affects predator and prey spatial and temporal use (Lone et al., 2014). Prey may choose habitats to reduce encounter rates with predators or lower death probabilities upon encounters (Heithaus et al., 2009). Cover can either provide safety or act as an obstacle, depending on context and species (Hernandez & Laundré, 2005; Ordiz et al., 2011; Camp et al., 2013). We hypothesize that:

(H6). Prey avoidance will be higher towards wolves in open areas and towards lynx in closed areas.

(H7). Predator attraction will be higher towards prey in open areas for wolves and in closed areas for lynx.

Information on previous species presence is mandatory for observing a repulsion or attraction effect. Olfactory clues like fur, skin, feces, or urine, are recognized as important signals for heterospecific local presence (Kuijper et al., 2014; Parsons et al., 2018) and are assumed to diminish over a few days or a week (Lima, 1998; Parsons et al., 2018; Prat-Guitart et al., 2020). Consequently, we anticipate that all visitation rates will return to baseline levels after a few days (H8).

Methods

Study sites

Camera-trap data was collected from four large protected areas in Germany: Bavarian Forest National Park, Müritz National Park, Harz National Park, and Königsbrücker Heide wilderness area. These areas were sampled in the "Ungulate Monitoring in German National Parks" project from 2019 to 2020. Eurasian lynx were present only in Bavarian Forest and Harz National Parks, while grey wolves were found in all four areas. Camera traps were set up within a grid of 1 km² cells, covering at least 50 percent of the cells and a minimum of 55 cells (Fig. 1). Grid cells for camera traps were selected randomly, with traps placed within 25 meters of the cell center, facing north. Due to the large size of Harz and Müritz National Parks, only sub-areas were sampled: the northern part of Müritz and the Lower Saxony part of Harz (Fig. 1).

Figure 1: Map of the four protected areas monitored in Germany from October 2019 to October 2020. The number of camera traps deployed in each area is specified next to the area's name (N). Black dots indicate camera trap locations. The number of independent wolf and lynx events is provided for each area (N_{events}).

Vegetation density

In August 2019, vegetation density around each camera trap was measured. Four photos were taken facing north, west, south, and east from the camera trap's center, each facing a red blanket 4 meters away. Pictures were cropped to the extend of the red blanket and converted to black and white using the image processing software Gimp2. cropped to the blanket's extent and converted to black and white using Gimp2. Vegetation density was calculated as the ratio of black to white pixels, averaged across all four photos (0 = completely open, 1 = completely closed).

Camera trap data preparation and analyses

All data preparations and analyses were done using R 4.3.0 open-source software (R Core Team, 2023). Each event was a detection of either a single individual or a cluster of individuals. Multiple detections of the same species and at the same location less than five minutes apart were considered as a single independent event (Heinrich et al., 2022). Following Ferry et al. (2024) approach, we tested the effect of a primary species on a secondary species, e.g. wolf on red deer, while considering the confounding effect of tertiary species, e.g. lynx and human. We created surveys starting after a primary event, considering all following secondary events, and ending when: i) another primary or tertiary species was observed, ii) prolonged camera trap inactivity occured, iii) the survey reached a 30-day duration threshold or iv) study's ended (see Supplementary Material 1 for survey definition and data formatting details). We then applied the Piece-wised Additive Mixed Model (PAMM, Bender & Scheipl, 2018; Ramjith

et al. 2022) to estimate the temporal dynamics of the secondary species event rate after the passage of the primary species and tested an effect of the vegetation density on this dynamics (see Supplementary Material 1 for models details).

Results

Red deer were most frequently observed, followed by wild boar and roe deer. Survey numbers were primarily constrained by predator events (Supplementary Material 2). Wolves were the most prevalent predators in the four protected areas, while lynx were only observed in two (Figure 1). This led to fewer post-lynx surveys and limited lynx recurrent events (Supplementary Material 2). In contrast, there was ample information on post-wolf surveys and wolf recurrent events. The limited data on combinations involving roe deer, lynx, and wolves, and wild-boar/lynx, prevented testing the effect of vegetation density (Table 1, Supplementary Material 3).

The prey response to predators showed notable changes only for red deer following lynx occurrences (Table 1). Red deer exhibited avoidance behavior, with a slight increase in visitation rate after twenty days, though variability was substantial (Figure 2), and surveys after twenty days were limited (Supplementary Material 2). No patterns were observed for wild boar or roe deer (Table 1, Figure 2), and no interaction effect with vegetation density was found (Table 1).

Lynx showed no clear response to prey, except for a slight decrease in visitation rate over time after red deer occurrences, suggesting attraction (Table 1, Figure 3). Wolves exhibited visitation rates 6.6, 7, and 7 times higher immediately after encountering red deer, roe deer, and wild boar, respectively, indicating strong initial attraction to all prey (Table 1, Figure 3). The variability in wolf visitation rate after fifteen days, particularly following red deer and roe deer encounters, was due to limited surveys and few wolf recurrent events (Supplementary Material 2). No wolf recurrent events occurred after fourteen days following wild boar encounters, precluding further trend estimation (Figure 3). No interaction effect with vegetation density was observed (Table 1).

Table 1: PAMM results for each primary-secondary combination include the estimated degrees of freedom (EDF), indicating the polynomial degree required to describe curvature. EDF is not indicative of effect size or direction (e.g., positive). The associated p-value tests for non-linear effect of time, i.e. whether the smooth function significantly differs from a flat line.

Primary	Secondary	Variable	EDF	Chi^2	p-value
Lynx	Red Deer	Time	3.25	26.56	**<0.001**

		Time*Vegetation density	2.23	2.14	0.34
	Roe Deer	Time	1.15	0.06	0.86
	Wild Boar	Time	2.4	6.26	0.1
Wolf	Red Deer	Time	1.86	2.45	0.41
		Time*Vegetation density	1	0.01	0.91
	Roe Deer	Time	1	0.01	0.97
	Wild Boar	Time	2.92	8.56	0.05
		Time*Vegetation density	3.64	7.31	0.15
Red deer	Lynx	Time	1	2.07	0.15
	Wolf	Time	2.45	47.46	**<0.001**
		Time*Vegetation density	1	0.05	0.82
Roe Deer	Lynx	Time	1.01	0.75	0.39
	Wolf	Time	2.49	9.83	**0.02**
Wild Boar	Lynx	Time	1.75	2.06	0.392
	Wolf	Time	1	9.8	**0.001**
		Time*Vegetation density	2.77	6.48	**0.1**

Figure 2: Estimated prey visitation rate over 30 days after predator occurrence. Columns represent prey species (red deer, roe deer, wild boar), and rows depict predators (Eurasian lynx, wolf).

Figure 3: Estimated predator visitation rate over 30 days after prey occurrence. Columns represent predator species (Eurasian lynx, wolf); rows depict prey species (red deer, roe deer, wild boar). Horizontal dashed lines in the right column compare wolf visitation rates at t = 0 and t = 10 days. High variability after fifteen days in wolf estimates is due to limited surveys (Supplementary Material 2).

Discussion

Our findings did not support the hypotheses of deterrence effects by grey wolves on all three prey species or by Eurasian lynx on roe deer and wild boar (H1, H2, H3). Only red deer showed a slight, enduring avoidance. Conversely, our results supported the hypothesis that wolves respond to prey presence with a significant increase in visitation rates (H4). Lynx showed only a slight attraction to red deer (H5) but not to roe deer or wild boar. The limited number of post-roe deer surveys and lynx events may explain the lack of response to roe deer. Placing camera traps on trails (Filla et al. 2017), where lynx are more active at night (Heurich et al. 2014), could improve sample size. Consequently, our discussion will focus on the wolves' response. Finally, no effect of vegetation density was observed for either prey (H6) or predators (H7).

The encounter sequence

The study aimed to assess proximate co-occurrence through a novel statistical approach using camera trap data, with an emphasis on understanding predator-prey interactions. While the focus was not on providing a complete approximation of encounter rates, by considering also spatial and temporal overlaps, some interesting conclusions can nonetheless already be drawn. Wolves showed expected attraction patterns towards prey, supporting the hypothesis of encounter rate maximization. However, prey did not show the anticipated avoidance patterns. This aligns with Sunde et al. (2022), who found no change in prey visitation after predator urine was deposited. This asymmetry in predation interactions may be due to the different pressures faced by predators and prey. Among all components of the encounter sequence (spatial and temporal overlap, proximity, avoidance post-encounter, capture or escape from attack), prey can optimize specific components of their response to avoid predation, such as reducing capture probability through behaviors like mobbing (Crofoot, 2013), without necessarily addressing all the other components to avoid predation. Predators, however, must achieve a minimul success probability in each component to complete the encounter sequence. Thus, prey responses may seem counterintuitive (e.g., Hebblewhite et al., 2005; Kauffman et al., 2007; Cuzack et al. 2017; Prat-Guitart et al., 2020; Sunde et al., 2022) but would reflect this flexibility of managing predation risks, showcasing the complexity of predator-prey interactions.

Proximate co-occurrence on unmarked species

Studies using unmarked species and camera traps face a limitation: the absence of individual-level data. For example, when observing a flat visitation rate of red deer after wolf occurrences, it’s hard to distinguish between (i) the same individual repeatedly visiting or (ii) several individuals appearing once and not returning. The first scenario suggests no response, while the second indicates repulsion. The reality is likely a mix of both, but distinguishing them is currently impossible. However, some signs can help infer the more likely scenario. Lower population density and smaller home ranges increase the likelihood of observing the same individual. For instance, given the red deer's population density (2 indiv.km², Tourani et al., 2023), monthly home range (around 4.7 km²), and camera trap spacing (max. 1 trap.km²) in the Bavarian Forest National Park, observing dozens of different individuals at a site during a 30-day survey is unlikely, suggesting the first scenario of absence of response. The low density of predators compared to prey, especially for gregarious species like wolves (e.g., Mech & Peterson, 2003), makes it more likely to observe the same individual or group.

The effect of the environment

Dormann et al. (2018) stressed the importance of considering underlying processes and confounding factors when interpreting species interactions from co-occurrence data. Multi-Species Occupancy Models (MacKenzie et al. 2004) and joint Species Distribution Models (Pollock et al. 2014) can help by accounting for covariate effects on species occurrence. In spatio-temporal analyses, issues like a carcass causing apparent attraction between scavengers or herbivores gathering at waterholes during the dry season (Ferry et al. 2016) can lead to misinterpretations. Time-to-event analyses often struggle to incorporate covariates, but Prat-Guitart et al. (2020) used a survival framework as an exception. PAMM, given enough data, allowed us to examine vegetation density as a proxy for perceived predation risk and its impact on species interaction. Unfortunately, our analysis found no influence of this parameter on interactions. This may be due to the limited scope of our measurement, confined to a 4m radius around camera traps, covering about 64 m². Additionally, camera trap placement often avoids dense vegetation to maximize detection probability, which might not accurately reflect the broader habitat context, hindering precise assessment of vegetation density effects.

Conclusion

Our study delved into the spatio-temporal dynamics of interactions among three herbivore species (red deer, roe deer, and wild boar) and two carnivores (wolf and lynx) using camera trap data collected across four protected areas. Leveraging PAMM, we precisely estimated the temporal patterns of visitation rates for each species following occurence of another. Contrary to our initial expectations, none of the herbivores exhibited discernible reactions to the presence of predators. Conversely, we observed a notable attraction of wolves to all three prey species, with lynxes showing a slight degree of attraction towards red deer. This stark contrast suggests an inherent asymmetry in predator-prey interactions: while predators must navigate through all stages of the encounter sequence to successfully achieve a predation event, prey species have the flexibility to evade predation by succeeding either in all or only a portion of these stages. These intriguing findings highlight the potential existence of asymmetry in predator-prey interactions, warranting further investigation.

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Statement of authorship

NF conceived this idea; NF led the writing of the manuscript; NF led analyses; CF, AB carried out the investigations, CF and MH acquired fundings and conceived the data collection design. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility statement

R scripts and data are available from the Zenodo Digital Repository https://doi.org/10.5281/zenodo.13911909.

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

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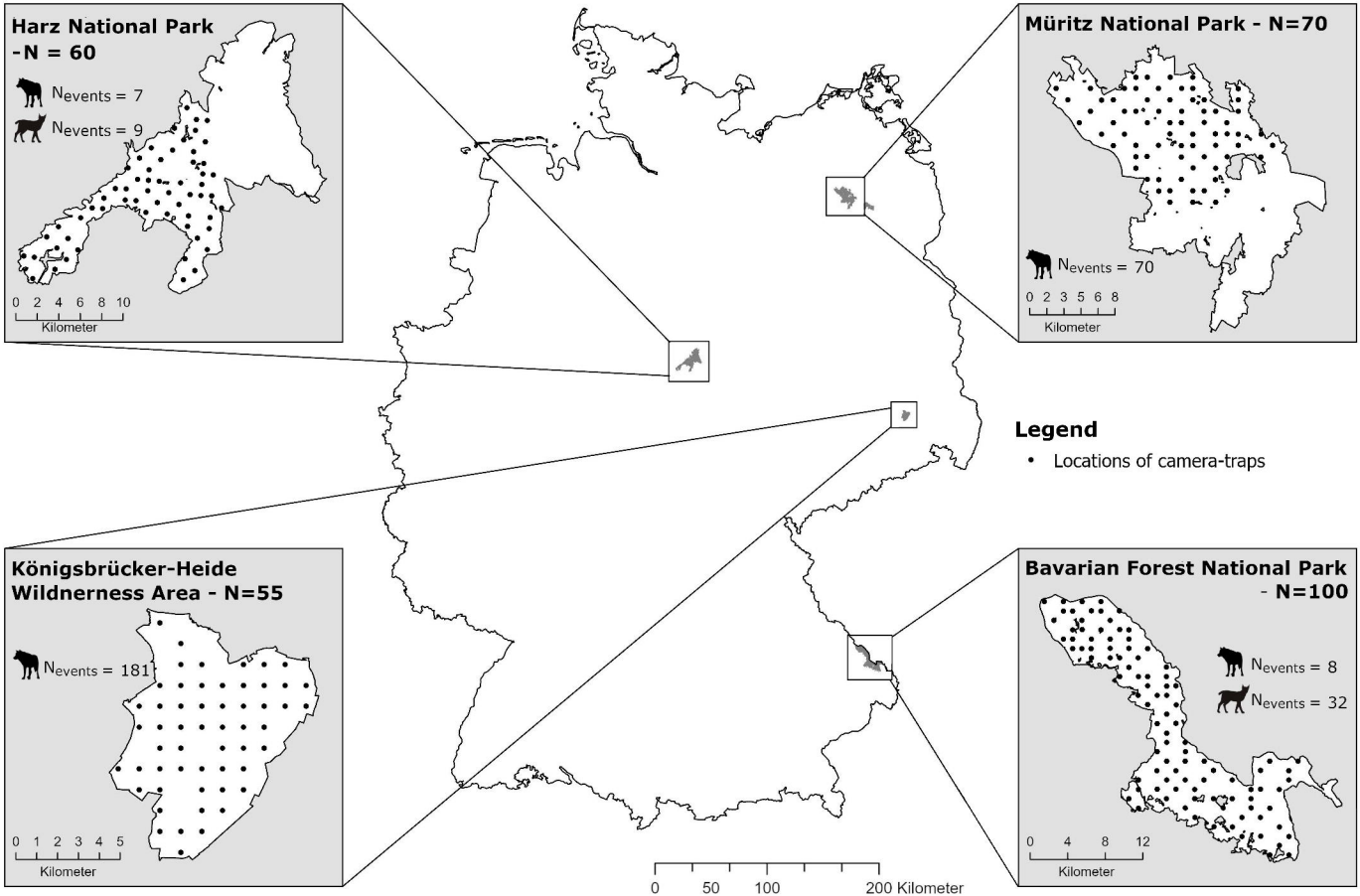
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Königsbrücker-Heide
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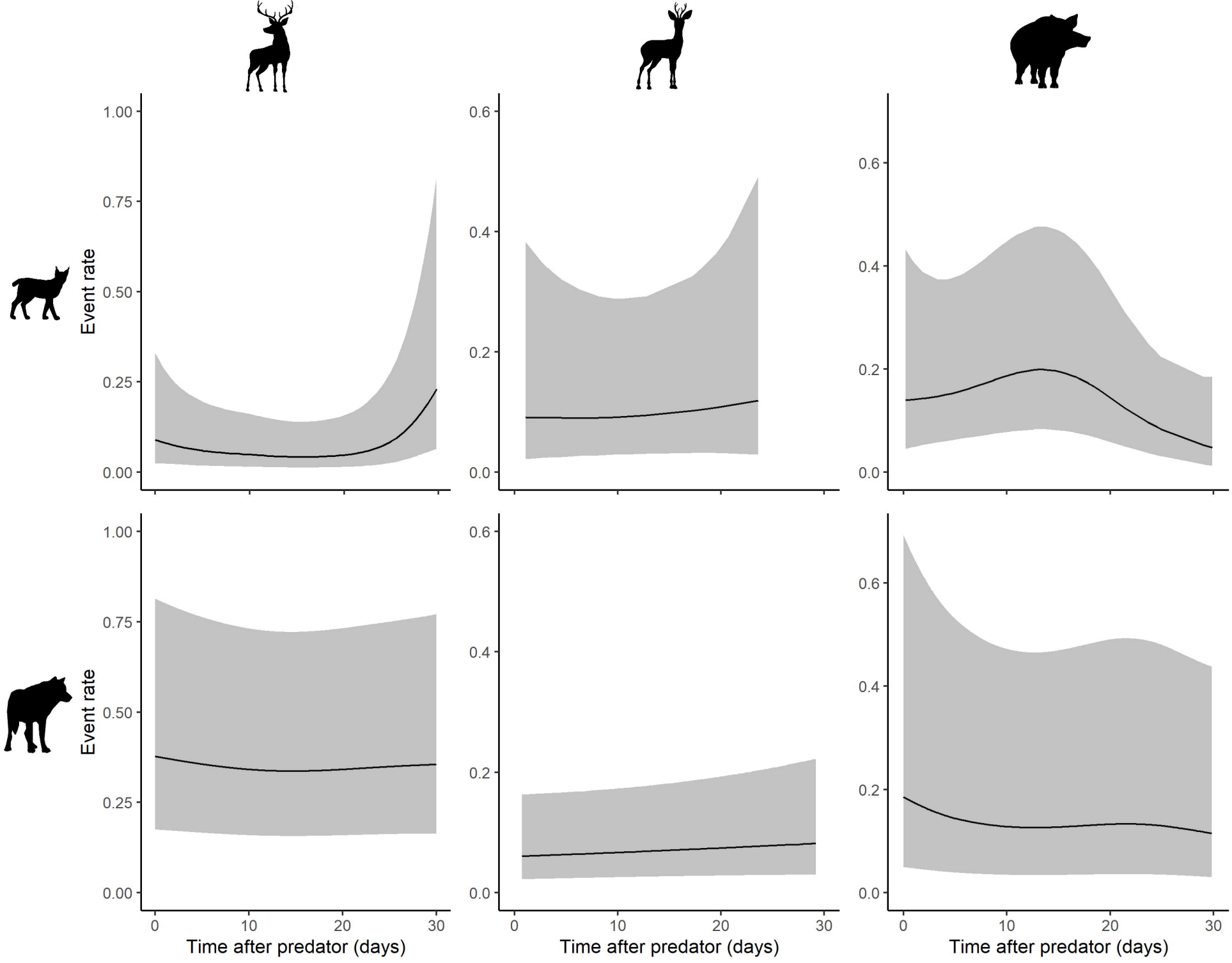
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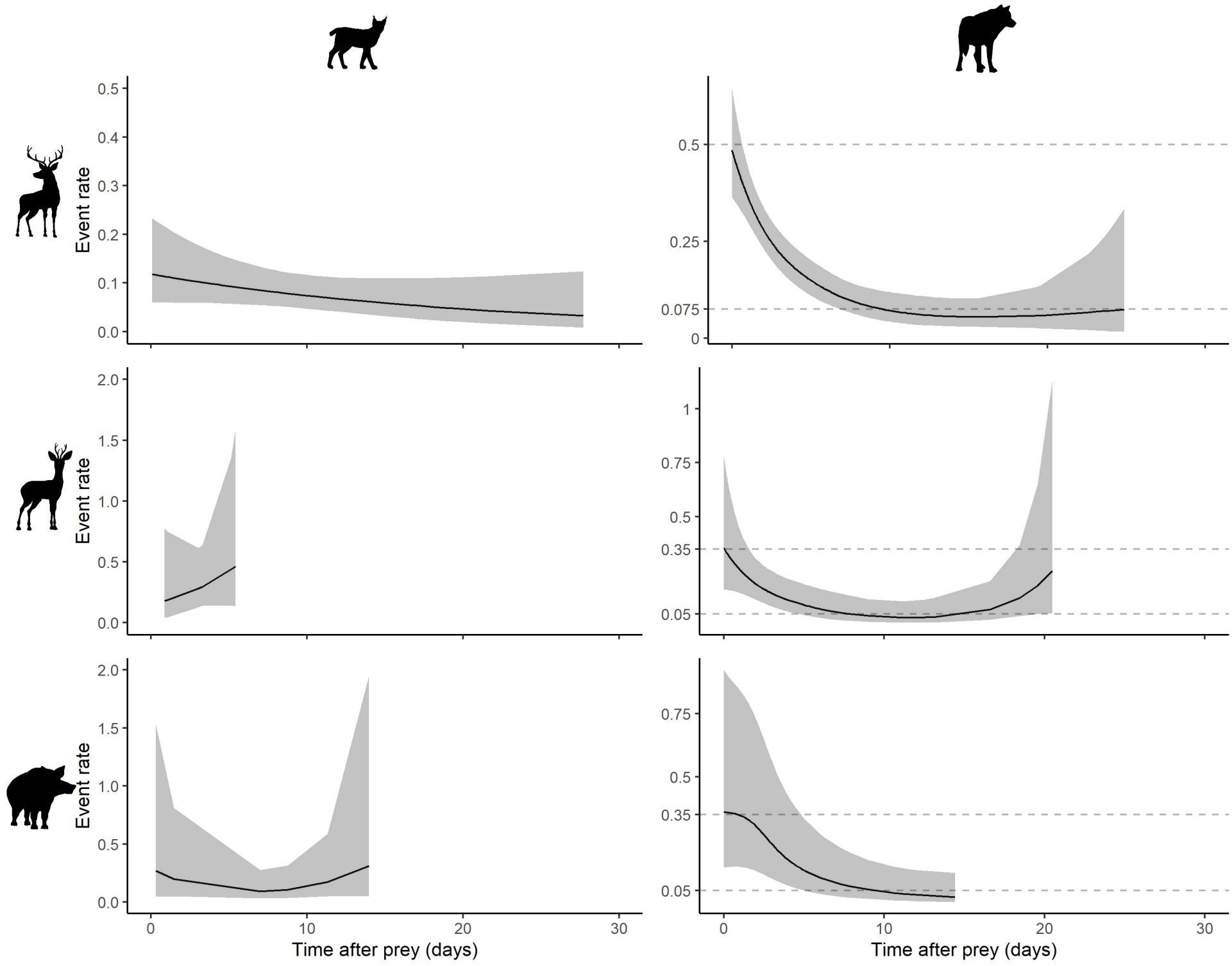
30
Time after predator (days)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0
10
20
30
Time after prey (days)
0
10
20
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Time after prey (days)