




The best defence is not being there: avoidance of larger carnivores is not driven by risk intensity

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Abstract

Species interactions are key factors determining the distribution and structure of species assemblages. Owing to their central positions, mid-ranking mammalian carnivores are involved in interactions with numerous species, including competition for resources and instances of killing by higher ranking predators. Lethal interactions can directly influence species' demography. However, the fear of lethal interactions, competition or both may also affect when and where individuals are active (i.e. non-lethal interactions). Although differences in body-size and trophic overlap are known predictors of the frequency of lethal interactions, their influence on non-lethal interactions is uncertain. Through camera trapping, we studied non-lethal interactions between a small mesocarnivore (pine marten), a potential killer and intense competitor (red fox) and a moderate competitor and unlikely killer (Eurasian badger). We determined overlap and differences in their diel activity patterns and the degree of spatial overlap in two seasons with contrasting resource availability. Additionally, we estimated the effect of larger carnivore detection rates on pine marten detection rates. We also compared time intervals between pine marten visits to baited stations in the absence and presence of either or both larger carnivores. Our results are consistent with pine martens distributing their daily activity to maximize overlap with prey and to minimize competition and risk of aggression over the spatial scale. Pine martens also responded to the immediate threat of larger carnivores irrespective of the threat they pose by taking 4–7 days longer to re-visit a station. Small-scale non-lethal interactions such as these may enable pine martens to coexist closely with two larger carnivores, yet it remains uncertain whether their population incurs a demographic cost through restricted access to resources. Carnivore's risk-avoidance strategies could be harnessed to protect prey species of interest. However, our results suggest avoidance is short-lived and recurrent stimuli would be necessary.

Introduction

The distribution of species at geographic, regional and local scales is governed by numerous biotic and abiotic factors (Dunson & Travis, 1991; Kneitel & Chase, 2004; Wisz *et al.*, 2013; García-Girón *et al.*, 2020). Among these, species interactions are central to the composition of vertebrate communities across scales (Brown *et al.*, 2001; Wilson *et al.*, 2003). Competitive and predatory interactions have understandably received much attention given their prevalence and significance across ecosystems (Schoener, 1983; Fryxell & Lundberg, 1994; Amarasekare, 2003; Pettorelli *et al.*, 2011). Remarkably, mid-ranking predators (i.e. mesopredators; *sensu* Prugh *et al.*, 2009) can be subject to both, where interference competition can take the form of interspecific killing, or one predator can

be prey to another (Sunde, Overskaug & Kvam, 1999; Arim & Marquet, 2004). In mammalian carnivore assemblages, lethal interactions can influence species' demography and cause population suppression of the victim (Lindström *et al.*, 1995; Prugh *et al.*, 2009; Prugh & Sivy, 2020; Wagnershauser *et al.*, 2021). Moreover, whether as a result of (the fear of) lethal interactions, competition or both, subordinate carnivores may change aspects of their use of space, time or resources (Linnell & Strand, 2000; Letnic *et al.*, 2009; Newsome *et al.*, 2017; Ferretti *et al.*, 2020). Indeed, sympatric competing species are expected to segregate along these or other axes of their ecological niches to coexist (MacArthur & Levins, 1967). Two known predictors of the intensity of lethal interactions are body-size differences and trophic overlap, where killings peak at size ratios of 2–5.4, and competition for prey provides a motivation

for killing (Palomares & Caro, 1999; Donadio & Buskirk, 2006). However, whether these factors are transferable to the strength of non-lethal interactions (i.e. spatial or temporal segregation and reactive behaviours) remains uncertain (Monterroso *et al.*, 2020).

At small scales, individuals are expected to utilize feeding sites according to the energetic gain and the risk incurred in doing so (Charnov, 1976; Berger-Tal *et al.*, 2009). Hence, we expect them to adjust their activity to maximize their access to prey while minimizing encounters with potential enemies (Penteriani *et al.*, 2013; Edwards, Gange & Wiesel, 2015; Pudyatmoko, 2019). Changes towards these ends can occur over multiple scales, including temporal, where an individual entrains its activity to that of its prey or to avoid activity peaks of larger carnivores (Dröge *et al.*, 2017; Botts *et al.*, 2020; Mori *et al.*, 2020), and spatial, where their activity is centred around prey-rich patches or sites exploited by larger carnivores are underused (Viota *et al.*, 2012; Guerisoli *et al.*, 2019; Mori & Menchetti, 2019). Instead, individuals can exhibit fine-scale reactive behaviours to immediate risks, avoiding sites only when the risk of encountering an enemy is high (hereafter spatiotemporal interactions; Barrull *et al.*, 2014; Torretta *et al.*, 2016; Karanth *et al.*, 2017; Prat-Guitart *et al.*, 2020). Multiple strategies may operate complementarily according to seasonal and geographical changes in predator and prey diversity and activity (Barrull *et al.*, 2014; Monterroso, Alves & Ferreras, 2014; Vilella, Ferrandiz-Rovira & Sayol, 2020). In this study, we addressed non-lethal interactions at feeding-site level over the temporal, spatial and spatiotemporal scales in a simplified carnivore community of north-western Europe.

Throughout most of Scotland, the largest mammalian carnivores are the Eurasian badger (*Meles meles* L.; badger hereafter; body weight 12 kg; Kruuk, 1989), the red fox (*Vulpes vulpes* L.; fox hereafter; body weight 6.4 kg; Kolb & Hewson, 1974) and the pine marten (*Martes martes* L.; marten hereafter; body weight 1.9 kg; Balharry, 1993). In Scotland, badgers feed mostly on earthworms (*Lumbricus terrestris* L.) year-round (Kruuk & Parish, 1981). Unlike their European counterparts whose main prey are mostly forest-dwelling bank voles, Scottish martens rely predominantly on short-tailed field voles (*Microtus agrestis* L.; Balharry, 1993; Zalewski, 2004; Caryl *et al.*, 2012b). Field voles (and other *Microtus* spp.) are also a major prey species for foxes across much of their range, including Britain (O'Mahony, Lambin, & MacKinnon, 1999; Webbon *et al.*, 2006; Kidawa & Kowalczyk, 2011; Meisner *et al.*, 2014). Martens are 3.4 and 6.3 times smaller than foxes and badgers, respectively. Therefore, given their higher trophic overlap and intermediate size ratio, lethal interactions are predicted to be most frequent between martens and foxes. This prediction is supported by the literature. Instances of martens killed by foxes and even of demographic suppression (or release) are well documented, while analogous cases with badger attackers are not (Storch, Lindström & Dejoune, 1990; Lindström *et al.*, 1995; Palomares & Caro, 1999; Waggershauser *et al.*, 2021). Hence, we take advantage of this simplified predator community to address the role of trophic overlap and size differences in determining the intensity of small-scale non-lethal interactions among

sympatric predators in the absence of interfering interactions with other carnivores.

Species' characteristics intersect with our hypothesis for this system. We could expect stronger segregation between martens and foxes across all scales due to intense competition and risk of aggression. However, badgers are reportedly nocturnal while foxes and martens are flexible in their use of time (Monterroso *et al.*, 2014; Torretta *et al.*, 2017). Therefore, we hypothesize that temporal partitioning will be consistently higher between martens and badgers owing to inherently different uses of time (Mori & Menchetti, 2019). In contrast, martens will not be able to temporally segregate with foxes as well due to their similar food habits (Mori & Menchetti, 2019; Botts *et al.*, 2020). Conversely, we predict that martens will show stronger spatial partitioning with foxes than with badgers to minimize competition and agonistic encounters (Viota *et al.*, 2012; Mori & Menchetti, 2019). Alternatively, spatiotemporal interactions could mitigate the need for segregation over either scale (Swanson *et al.*, 2016; Karanth *et al.*, 2017). Given the threat foxes represent to martens, if spatiotemporal interactions are detected, we expect foxes will prompt stronger reactions than badgers. We also hypothesize that seasonal variation in prey diversity and availability will influence the two main competitors more strongly, relaxing segregation during periods with abundant and diverse prey (e.g. spring; Vanak *et al.*, 2013; Barrull *et al.*, 2014). Instead, seasonality should have little effect on the marten–badger pair.

Using camera traps, we studied non-lethal interactions between martens, badgers and foxes in two seasons. We describe their seasonal diel activity patterns, test for significant differences and quantify temporal overlap. We also estimate spatial overlap in their use of baited stations and test the effect of increasing detection rates of the larger two carnivores on marten detection rates. Lastly, we investigate spatiotemporal interactions by comparing time intervals between consecutive marten visits to a station to time intervals when fox, badger or both were present at the station in-between marten visits.

Materials and methods

Study area

The study area was located in Strathspey (57°09'34"N, 03°51'40"W), a wide valley along the river Spey, Scotland. This region has a temperate oceanic climate. Average monthly temperatures for the study period (2018–2019) ranged from 1 to 7.8°C between February and April and from 8.3 to 15.9°C between May and July. Annual rainfall was 503.8 mm in 2018 and 1005.5 mm in 2019 (Cuthbert, 2021). The study focussed on a ca. 180 km² area of continuous seminatural (Caledonian) forest and forestry plantations of Scots pine (*Pinus sylvestris* L.) on the north-western slopes of the Cairngorms National Park. The area is surrounded by floodplains, grassland and arable lands in the valley bottom to the east, and heath, peats and bogs in the high ground to the west (NatureScot, 2018). Camera stations were set between 250 and 500 m a.s.l. Study sites differed in their forest composition. Semi-natural forest was restricted mostly to Abernethy and Rothiemurchus Pinewood

(henceforth referred to as Rothiemurchus), while Glenmore and Inshriach were forestry plantations with clear-felled areas rich in herbaceous plants. Glenfeshie is situated in a narrow valley to the south. The valley bottom is mostly herbaceous, and the slopes are a mosaic of Scottish pine and broadleaf (*Betula* spp.) plantations, heath scattered with old pine trees and thickets of saplings. Martens were re-sighted in the area in the mid-1990s and are now widespread (Summers, 2018). Badgers have been continuously present in the area, with some suggestions of increasing abundances (NESBReC, 2017). Although year-round culling of foxes is legal in Scotland, predator control has not been systematic throughout the area since the mid-2000s. However, fox population trends are unknown. Other mammalian carnivores present are weasels (*Mustela nivalis* L.) and stoats (*Mustela erminea* L.). European otters (*Lutra lutra* L.) and wildcats (*Felis silvestris* Schreb.) are present but rare with no detections in this survey (Table S1).

Data collection

Images were collected in three camera-trapping sessions: one from late-winter to early-spring in 2019 (February 2nd–April 16th) and two from mid-spring to early-summer in 2018 and 2019 (May 21st–July 4th and May 17th–July 11th, respectively). They are referred to as winter and spring hereafter (Table 1).

Five sites of approximately 8 km² were selected across the study area, and 6–8 camera traps were deployed at fixed locations. These locations were selected using the ‘Random points’ tool in QGIS and adjusting for accessibility (QGIS.org, 2018). The camera trap stations were approximately 1 km apart. Cameras were attached to trees at 30–40 cm from the ground and oriented to maximize visibility and reduce glare and false triggers from sunlight. Stations were baited with a quail carcass (c. 200 g), feathers and dried valerian root (*Valeriana officinalis* L.; 100 g, placed in canvass cloth bag) to increase detectability (Saunders & Harris, 2000; Ferreras, Diaz-Ruiz & Monterroso, 2018). The quail was fixed to a tree or wooden post 2–3 m from the camera at a height of no more than 1 m. Bait was replaced after approximately 3 weeks; once in the 2018 session and twice in the 2019 sessions. In the first session, 15 cameras (out of 38) were only deployed during rebait due to logistical constraints. These were distributed equally across sites and randomly within sites. We assume bait did not

affect the behaviour of our target species as the amount provided would only support an individual for a short period and was likely detected by already foraging individuals (Braczkowski *et al.*, 2016).

Two camera models were used: Bushnell NatureViewHD (119439) and Browning Strike Force HD Pro (BTC-5HDP). The two were distributed equally across sites, randomly within sites and swapped between seasons to minimize bias. The cameras were set to take three photographs per trigger, with a one-second delay before the next trigger. A total of 5572 trapping nights were surveyed; 1311 in spring 2018, and 2099 and 2162 in winter and spring 2019, respectively. Effort ranged between 922 and 1190 trapping nights across sites and from 50 to 157 nights between stations.

Data extraction

Using *digiKam* 6.3.0 (Digikam Team, 2019), KZ assigned every image recorded with a metadata tag from each of the three tag categories: species (fox, badger, marten), number of individuals present (1–10) and bait (visibly present and absent, NA). Uncertain detections were assigned ‘NA’ tags. Bait was considered absent after being visibly removed by an animal and ‘NA’ when absent but an animal was not observed removing it. The images’ metadata were extracted using ‘*camtrapR*’ package (Niedballa *et al.*, 2016) and ExifTool (Harvey, 2019) in R 3.5.1 software (R Core Team, 2018). Detections within 30 min of each other were removed to reduce temporal autocorrelation (e.g. Torretta *et al.*, 2016; Curveira-Santos *et al.*, 2017).

Statistical analyses

We analysed the daily activity patterns of the three species. For this, we assumed individuals were active if detected at a station. The frequency distribution of the species’ activity during the day was plotted and compared using a von Mises kernel for circular data (smoothing parameter of 0.8) from the ‘*overlap*’ package (Ridout & Linkie, 2009; Meredith & Ridout, 2018). A Hermans–Rasson test was applied using the ‘*CircMLE*’ package (Fitak & Johnsen, 2017) to check for uniformity in the distributions of their activity (Landler, Ruxton & Malkemper, 2019; Table S2). The coefficient of overlap between the species’ temporal activity was calculated (Δ ;

Table 1 Number of camera trap stations, the survey period, length and effort, the overall number of images collected, as well as the number of images of the three predators, for each season of the study

Season	Spring 2018	Winter 2019	Spring 2019
Number of camera trap stations	38	40	40
Survey period	21/05–04/07/2018	15/02–16/04/2019	17/05–11/07/2019
Survey duration (days)	45	61	56
Effort (trapping nights)	1311	2099	2162
Visits	Setup, rebait, pickup	Setup, 2x rebait, pickup	Setup, 2x rebait, pickup
Number of images	159 952	24 686	24 674
Number of images with predators	2819	10 368	7229

We refer to trapping sessions as spring or winter though they overlap the start of the following season (i.e. spring and summer).

values from 0 = no overlap; to 1 = complete overlap), for each species pair and season. Two equivalent overlap coefficients were estimated depending on the number of detections: Δ_1 was calculated for each pairing with fox due to their small sample size ($N_{\text{fox}} < 75$), and Δ_4 for all other pairings (Meredith & Ridout, 2018). The *'bootCIlogit'* function was used to calculate the bootstrapped 95% confidence intervals (95% CI) with 10 000 resamples. Wald tests were applied using the function *'compareAct'* from the package *'activity'* to test for significant differences in the activity distributions of each pair (Rowcliffe, 2021). Additionally, we estimated the proportion of detections over four different times of the day for each season and carnivore: night (1 h after sunset to 1 h before sunrise), day (1 h after sunrise to 1 h before sunset) and twilight (1 h before and after sunrise and sunset; Lucherini *et al.*, 2009; Monterroso *et al.*, 2014). Average time of sunrise and sunset for each season were obtained from timeanddate.com (Time & Date AS, 2021).

The degree of spatial overlap between the three carnivores was estimated in each season with Pianka's index of niche overlap with the *'spaa'* package (Pianka, 1974; Zhang, 2016) and the number of detections per trapping night at each station. We report bootstrapped means and standard deviations with 10 000 iterations. The effect of the number of detections of both larger carnivores on the number of marten detections was tested by means of a Generalized Linear Model (GLM). The GLM was fitted with a negative binomial distribution through the *'MASS'* package to account for overdispersion (Venables & Ripley, 2002). The number of marten detections offset by trapping nights was regressed against the number of badger and fox detections per trapping night (DPTN). The percentage of forest cover at 1000-m radius around each station was included in the model as a second-degree polynomial to account for the effect of habitat on the activity of martens and the non-linear relationship between marten abundance and forest cover observed in Scotland (Caryl, Quin & Park, 2012a). Forest cover percentage was obtained from the National Forest Inventory (Forest Research, 2018) and included mature (>20 years) and young stands of plantation, conifer, broadleaf, and mixed forest and natural regeneration. Observations between stations were assumed to be independent based on the exploration of spatial correlograms (Fig. S1). Additionally, study site, season and year were fitted as categorical variables to account for the structure of the data and relax assumptions of independence. Scaled residuals were simulated and visualized, and uniformity and overdispersion tested using *'DHARMA'* (Hartig, 2020).

To detect spatiotemporal interactions between martens and the two larger carnivores, the time interval between consecutive visits of martens to the same station was calculated when either or both larger carnivores were present between marten visits, and when no other carnivores were detected between marten visits (Parsons *et al.*, 2016). The same analysis was done on badgers, the largest carnivores, as a methodological control. Only time intervals longer than the shortest interval with presence of another carnivore (875 min) were used to avoid biases caused by intervals too short for another species to visit. Time intervals were natural log-transformed to normalize the residuals and regressed in a Linear Mixed Effects

Model (LMM) using the *'lme4'* package (Bates *et al.*, 2015). A base model was fitted with the type of interval (no carnivore present, badger/marten, fox or both present), bait (present, absent) and season (winter, spring) as explanatory variables. Station was fitted as a random effect. The function *'dredge'* from the *'MuMIn'* package was used to generate the full set of models from the base model, ranked by their Akaike's information criterion (AIC; Bartoń, 2016). Nested models were excluded and models within $\Delta\text{AIC} < 2$ were assumed as equally parsimonious (Richards, 2008; Harrison *et al.*, 2018). Model predictions are reported with their 95% confidence intervals.

Results

In total, 209 312 photographs were collected, of which 32 616 photographs contained an individual of an identifiable species. Thirty-one species of birds and mammals were recorded across all seasons (Table S1). A total of 1183 independent detections were obtained of our three focal carnivores: 532 marten, 577 badger and 74 fox. Across stations, marten detections per trapping night ranged from 0 to 0.75 DPTN, fox from 0 to 0.25 DPTN and badger from 0 to 1.18 DPTN. The three species were never detected using a station at the same time.

Daily activity pattern overlap between carnivores

None of the species used time uniformly (Table S2). In winter, all three carnivores were mostly nocturnal. Particularly badgers, with 87.2% detections at night-time, and 1.1% during the day (Table S5). Their peak of activity was shortly before midnight, but they remained active through the night (Fig. 1). Night-time detections of marten in winter accounted for 77%, and twilight detections for 20.1%. Martens had three main peaks of activity, one at dusk, one around midnight and a third one before dawn. Foxes were the least active during the night with 65.2% of their detections during this period, while the rest were equally spread between day and twilight (17.4%). The foxes' main peak of activity was after dusk, with a smaller second peak before dawn and a dip around midnight. In spring, the proportion of night-time detections declined for all three carnivores. It remained highest for badgers at 54.7%, which were now active during twilight (32.2%) and daytime (13.2%) as well. Detections of both martens and foxes were most frequent during daytime, 42% and 35.7%, respectively, compared to 32.8% and 28.6% during night-time. Fox detections were equally frequent during twilight and daytime, but marten detections were the least frequent during twilight with 25.3% of detections. Martens showed two peaks of activity, the first around dusk and the second shortly before dawn, while foxes had a single peak of activity shortly after dusk.

The only significant contrast of daily activity distributions was between martens and badgers in spring ($\Delta = 0.62$, $P < 0.001$, Fig. 1, Table S3). However, overlap between the two in winter was high ($\Delta = 0.86$). The second lowest overlap was between foxes and badgers in spring ($\Delta = 0.64$). Here, too overlap was higher in winter ($\Delta = 0.71$). Instead, marten and

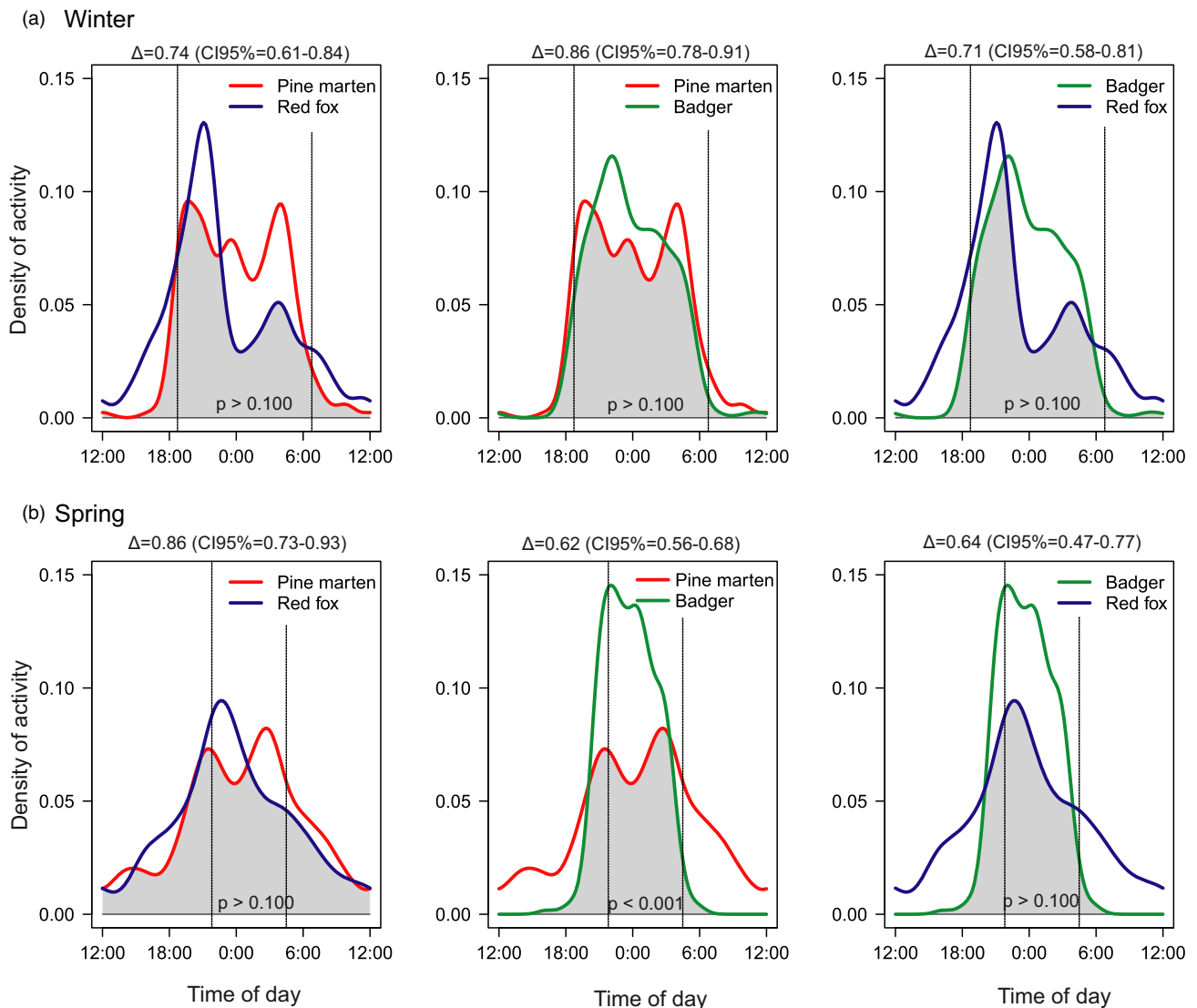


Figure 1 Daily activity pattern contrasts between pine martens (red), Eurasian badgers (green), and red foxes (blue), for winter (a) and spring (b). Grey area represents overlap of temporal activity between the species. Vertical lines show average time of sunrise and sunset for each season (obtained from: timeanddate.com). Δ value above each panel corresponds to the coefficient of overlap with 95% confidence intervals for each species pairing. P -values from Wald test are included in each panel. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

fox overlap were higher in spring than in winter ($\Delta = 0.86$ and 0.74 , respectively).

Spatial overlap between carnivores

Spatial overlap was low among all three carnivores, ranging between 0.15 and 0.43 (Fig. 3a). Standard deviations largely overlapped between seasons for all pairs. Overlap was lowest between martens and badgers and similar between the two seasons at $0.17 (\pm 0.06)$ and $0.15 (\pm 0.05)$ in winter and spring, respectively. Marten detections were roughly complementary to badger detections and highest in their absence (Fig. 2). Spatial overlap was highest between fox and badger in winter at 0.43

(± 0.14) though it was lower in spring at $0.31 (\pm 0.13)$. Overlap between marten and fox was intermediate, with $0.25 (\pm 0.08)$ in winter and $0.36 (\pm 0.11)$ in spring. Stations used by fox largely coincided with those frequently used by either marten or badger (Fig. 2).

Only the number of badger DPTN and the contrasts between sites had significant effects on marten detections rates ($P < 0.05$; Table 2). Keeping all other factors constant at average or intercept conditions (forest cover = 67.9%, fox DPTN = 0.01, season = spring, year = 2018), average marten detections declined by a factor of 7.8 across sites, from 0.23 and 0.10 DPTN (0.14–0.38 and 0.05–0.17, respectively) in the absence of badgers, down to 0.03 and 0.01 DPTN (0.01–0.13

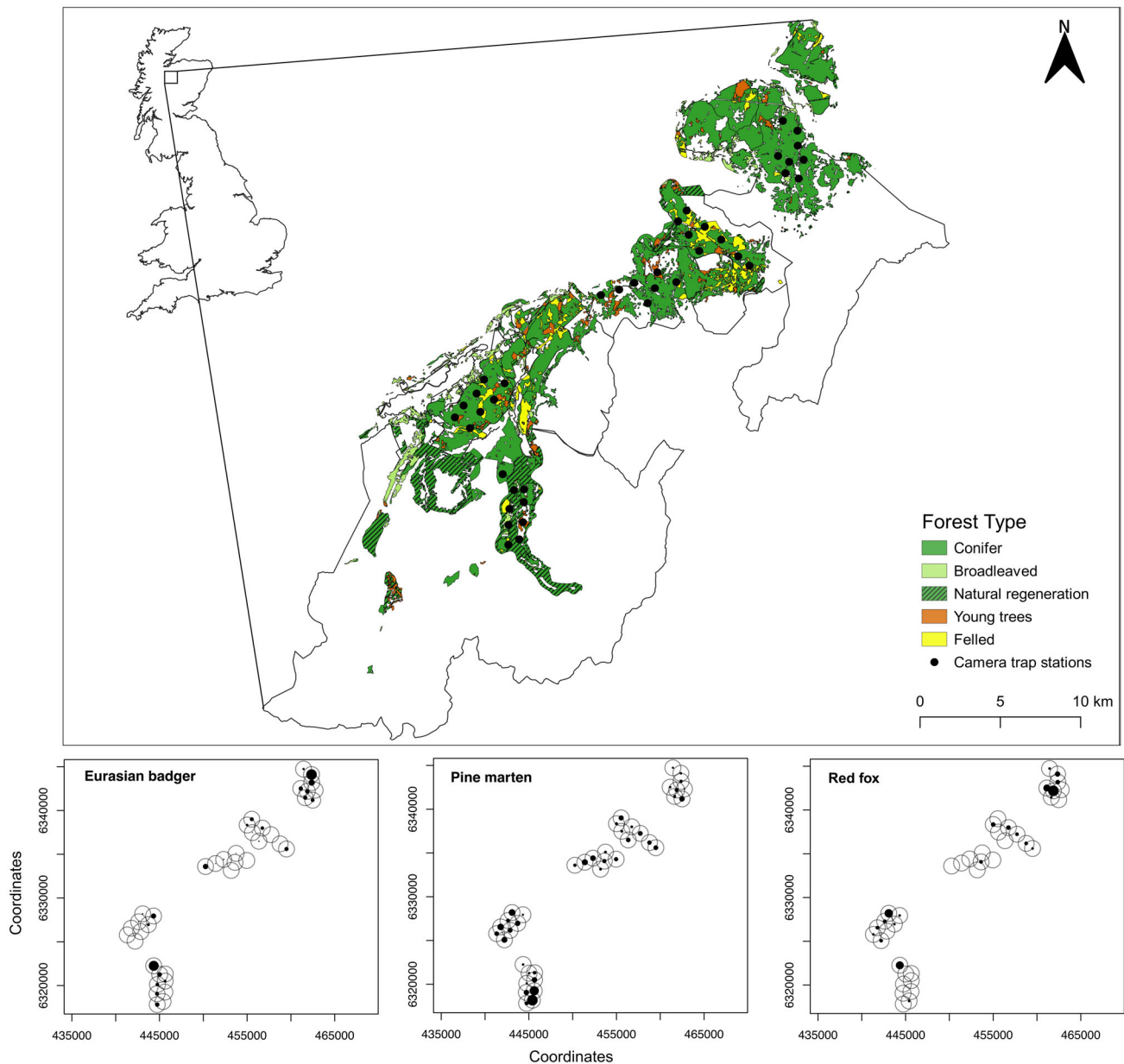


Figure 2 Top panel: Map of the estate boundaries of the study area and the distribution forest types and camera trap stations (black circles) within. Bottom panels: maps showing the distribution of stations (empty circles) and the number of detections of each carnivore (black circles; size relative to number of detections) throughout the study. European badger (left), pine marten (centre) and red fox (right). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

and 0.002–0.06, respectively) at high badger detection rates (1.18 DPTN; Fig. 3b). Forest cover, season and year had only marginally significant and weak effects on the detection rate of martens ($P < 0.1$; Fig. S2).

Time intervals—spatiotemporal interactions

The top model explaining variation in the time intervals between consecutive visits of martens included the type of

interval and presence of bait (Table 3). The time interval between consecutive marten visits was the shortest (66.9 h, 58.6–75.9) when there were no other carnivores at the cameras between marten visits, and longest when a larger carnivore was present between the marten visits (Table 4): 181.6 h (141.2–235.1) when badgers had visited the station; 221.4 h (111.1–441.4) when both a badger and a fox had visited the station; and 214.9 h (134.3–347.2) when a fox had visited the station (Fig. 4). Martens took almost 32 h longer to revisit

Table 2 Parameter estimates from the Generalized Linear Model explaining the variation in the number of pine marten detections per trapping night as a function of Eurasian badger and red fox detection rates, a second-degree polynomial of forest cover percentage in a 1000-m radius around each station, site, season and year

Factors	Estimate	SE	z-value	P-value
Intercept	-1.646	0.249	-6.620	<0.0001
Badger detections	-1.746	0.639	-2.734	0.00625
Fox detections	4.184	3.102	1.349	0.17742
% forest cover ²	-2.159	1.147	-1.883	0.05974
Site (Abernethy)	-0.827	0.338	-2.443	0.01455
Site (Glenmore)	-0.904	0.315	-2.868	0.00413
Site (Inshriach)	-0.272	0.302	-0.900	0.36808
Site (Rothiemurchus)	-0.647	0.317	-2.042	0.04117
Season (Winter)	0.394	0.233	1.687	0.09153
Year (2019)	-0.441	0.241	-1.828	0.06748

The intercept is estimated for the site Glenfeshie, Spring season and year 2018.

Significant effects ($P < 0.05$) are highlighted in bold.

stations in the presence of bait compared to when bait was absent: 98.5 h (86.5–114.4) and 66.7 h (56.8–78.3), respectively.

The top model explaining the time interval between badger visits only included the presence of bait (Table S4). When there was no bait at the station, the average time interval between visits of badgers (63.4 h; 95% CI: 50.9–79.8) was shorter than when there was bait present (115.6 h; 95% CI: 90.9–245.5; Table 4).

Discussion

This study suggests that martens distribute their activity throughout the day to maximize access to prey, and instead use the spatial axis together with small-scale spatiotemporal mechanisms to minimize interactions with larger carnivores. The observed close temporal coexistence might be enabled by reactive behaviours at feeding-site level. Interestingly and contrary to our predictions, natural cues of past visits by badger, fox or both triggered similar reactions by marten. This may indicate that, at this scale, martens have a response tuned to the presence of risk rather than to its intensity. Risk-avoidance strategies might allow resource exploitation at minimal risk or instead limit the access to resources, such that the net outcome for the population of martens is uncertain.

Using camera traps, we collected a large amount of data of non-lethal interactions between three sympatric predators with minimal human interference. However, despite the large number of images, only 74 independent fox visits (and 1095 photos) were recorded. While this could reflect a lower density of foxes, we do not have the data to corroborate this. Low fox detection rates could also be the result of avoidance of camera stations due to light or sound produced by the cameras, or avoidance of human smell, as they remain a widely culled species in Scotland (Aebischer *et al.*, 2011; Meek *et al.*, 2014, 2016). For instance, (re-)baiting the stations prompted weak spatiotemporal responses by martens and badgers, which took an additional 1–2 days before another visit despite the presence of food. Furthermore, no fox was recorded physically interacting with the bait. Human avoidance may thus be an important driver of carnivore activity (Clinchy *et al.*, 2016; Suraci *et al.*,

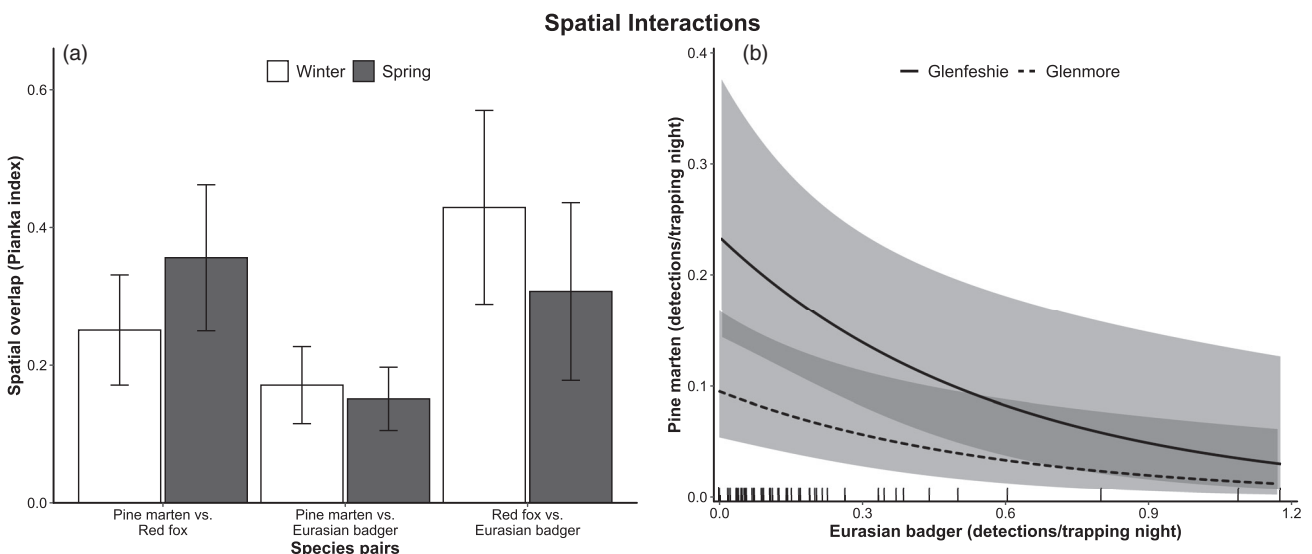


Figure 3 (a) Spatial overlap based on Pianka's index of niche overlap for each species pair in winter (white) and spring (dark grey). Arrows represent standard deviations. (b) Predicted lines from generalized mixed model of pine marten detection rates over Eurasian badger detection rates at average conditions of red fox and forest cover and intercept conditions of year (2018) and season (spring). Lines represent the sites with the highest (Glenfeshie; solid line) and lowest (Glenmore; dashed line) detection rates of pine marten. Grey areas represent 95% confidence intervals; bounded at zero.

Table 3 Results of model selection for models comparing time intervals between pine marten visits

Intercept	Species	Bait	season	d.f.	logLik	AIC	Delta	Weight
4.39	+	+		7.00	−413.00	840.01	0.00	0.99
4.24	+			6.00	−419.29	850.57	10.56	0.01
4.62		+		4.00	−445.17	898.34	58.33	0.00
4.50				3.00	−447.14	900.28	60.27	0.00

Models are listed by row, and the explanatory variables included in each model, degrees of freedom (d.f.), log likelihood (logLik), AIC, AIC difference from top model (Δ AIC) and AIC weight (Weight) are presented.

The number of time intervals when no predator visited the station between the marten visits it was 232, when a badger visited between marten visits was 20, when a fox visited it was 8, and when both a fox and a badger visited it was 6.

Table 4 Parameter estimates from top Linear Mixed-Effects Models comparing intervals between pine marten and Eurasian badger visits

Fixed effects	Estimate	SE	d.f.	t-value	P-value
Pine marten (model 1)					
Intercept	4.391	0.077	49.144	56.929	<0.0001
M-M vs. M-B-M	0.998	0.139	246.396	7.191	<0.0001
M-M vs. M-B&F-M	1.198	0.358	191.422	3.345	0.001
M-M vs. M-F-M	1.170	0.244	330.249	4.803	<0.0001
No Bait	−0.392	0.099	216.658	−3.959	0.0001
European badger (model 2)					
Intercept	4.748	0.119	30.047	39.944	<0.0001
No Bait	−0.593	0.084	385.022	−0.704	<0.0001

Model 1: shows the influence of predator and bait presence-absence on the log-time interval between consecutive visits by pine martens. Model 2: shows the influence of bait absence (bait present = intercept) on the log time interval between consecutive visits by European badgers. M-M – interval between marten visits without predator (intercept), M-B-M – interval between marten visit separated by badger visits, M-B&F-M – interval between marten visits separated badger and fox visits, M-F-M – interval between marten visits separated by fox visits.

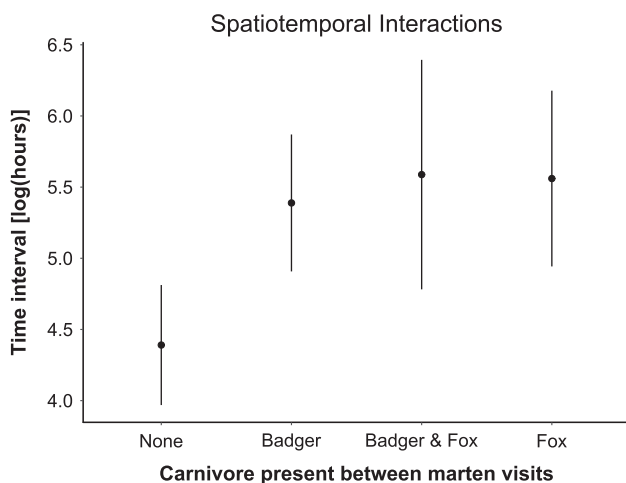


Figure 4 Predicted values from the linear mixed effects model of time intervals (natural log-transformed hours) between pine marten visits when, respectively, no carnivore, badgers, foxes and badgers, and foxes, were present. Lines show 95% confidence intervals.

2019). The subsequent small range of fox detection rates at stations, nearly fivefold smaller than badger's, could be a contributing factor to the weaker evidence of spatial avoidance of foxes by martens (but see below).

Niedballa *et al.*, (2019) concluded that the analysis of time intervals between visits of different carnivore species at camera stations was the most effective method to detect spatiotemporal interactions (e.g. Barrull *et al.*, 2014). However, this method would underestimate the time during which the station was avoided by the smaller carnivore if the larger one continuously visited the cameras for a long time, as was often the case for badgers in our study (e.g. up to 14 badger detections between two marten visits). Hence, the intervals used here following Parsons *et al.* (2016) were well-suited for this group of meso-carnivores and allowed the detection of spatiotemporal interactions between martens and both larger carnivores. Additionally, this approach was validated using badgers as a methodological control, finding no avoidance of the smaller carnivores as expected.

Following our expectations, badgers were largely nocturnal in both seasons, while foxes and martens showed flexibility in their use of time (Monterroso *et al.*, 2014; Torretta *et al.*, 2017). However, the hypothesis that temporal segregation between martens and badgers would be high due to inherent differences in their use of time was only partially supported. Temporal overlap was low and the use of time significantly different in spring, but overlap was high in winter. The pattern was analogous, albeit weaker, for the fox–badger pair, and opposite for martens and foxes. Collectively, these findings may reflect the trophic plasticity (or lack thereof) of the three carnivores. Badgers, which in Scotland rely mostly on

earthworms year-round, would be restricted to periods of lower radiation when their prey are more accessible (Kruuk & Parish, 1981; Duriez, Ferrand & Binet, 2006). Instead, generalist martens and foxes could tune their activity to maximize access to prey and, as the nights shorten and the prey base diversifies in spring, remain active during light hours (Jędrzejewski & Jędrzejewska, 1992; Caryl *et al.*, 2012b). High temporal overlaps relative to earlier studies could be attributed partly to the low diversity of the predator guild, reducing the need for temporal partitioning (Monterroso *et al.*, 2014). Although we lacked data on the temporal activity of prey species and predator diet, our results are consistent with prey being an important driver of the carnivores' daily activity patterns, rather than competition or the risk of agonistic encounters (Dias *et al.*, 2019; Botts *et al.*, 2020). Other factors such as human disturbance may also be shaping their use of time on account of the study area being a popular destination (Gaynor *et al.*, 2018).

Seasonal differences in spatial overlap offered some support to the hypothesis that seasonal changes in prey availability would affect the two main competing species more strongly, as marten and fox spatial segregation relaxed in spring (Vanak *et al.*, 2013; Barrull *et al.*, 2014). However, overlap across all three pairs of carnivores was low (0.22–0.43; Mori & Menchetti, 2019). While this was expected in the absence of temporal partitioning, martens' spatial overlap was lower with badgers than with foxes, their main competitor and potential killer, contradicting our prediction (Lindström *et al.*, 1995; Webbon *et al.*, 2006; Caryl *et al.*, 2012b). These results concurred with the negative binomial regression, where the detection rate of badgers had a significant and negative effect on the detection rate of martens, but the detection rate of foxes did not. However, caution should be exercised when interpreting the latter results. The distribution of sightings was left-skewed and with large proportions of zeroes (marten 16.7%, badger 49.2% and fox 71.7%). This implies that our surveying effort took place mostly in the absence or at low detection rates of fox and badger. Consequently, randomly high marten detection rates were inherently more likely to occur at stations with low visitation rates of larger carnivores, which could lead to spurious relationships (Cook, 1979; Zuur, Ieno & Elphick, 2010). In conclusion, regressions of multiple variables with negative binomial distributions should be interpreted carefully. Despite these caveats, our results support the notion that martens can adjust their space-use to minimize competition and/or encounters with larger carnivores, particularly badgers, though their absence does not ensure marten activity.

Due to the limitations described above, we could not evaluate the interaction between spatial and spatiotemporal mechanisms. However, the avoidance of locations during periods of high risk could contribute to the close temporal coexistence observed, such that to avoid risks, martens would not change the time at which they are active but the location (Swanson *et al.*, 2016; Karanth *et al.*, 2017). Contrary to our hypothesis, the reactions prompted by cues of both larger carnivores were not significantly different (6.2 days fox, 4.8 days badger). Furthermore, the combined presence of foxes and badgers did not significantly lengthen the delay (6.5 days). In another interval-based study between fox, badger and stone marten (*Martes*

foina Erxleben), Barrull *et al.*, (2014) also found largely similar responses of the smaller carnivore to the odour paths of the larger two. Additionally, in their comprehensive study, Monterroso *et al.*, (2020) found only weak associations between body–size ratio and trophic niche overlap and larger scale spatial co-occurrence in the carnivore community of south-western Europe. Therefore, at feeding-site level, spatiotemporal interactions may respond to the presence of risk more than to its intensity. However, further work should address small-scale interactions across a wider range of predator size ratios and trophic overlaps (generalists vs. specialists) to determine the existence of interaction thresholds (Edwards, *et al.*, 2015).

This study highlights the importance of considering multiple dimensions across which carnivores can interact (Barrull *et al.*, 2014; Karanth *et al.*, 2017; Vilella *et al.*, 2020). Martens seemingly use multiple overlapping strategies to maximize access to resources (i.e. seasonal changes in time-use) while minimizing the risks of exploiting them (i.e. spatial partitioning and spatiotemporal interactions) as would be expected from foraging theory (Berger-Tal *et al.*, 2009). However, we are unable to determine whether these mechanisms impart a net benefit to the marten population through a reduction of competition and agonistic encounters or a net impact through reduced access to resources. In addition to the potential demographic impacts of predatory interactions among carnivores (Wagershauser *et al.*, 2021), those of non-lethal interactions (also known as sub-lethal or non-consumptive effects) have been theorized to exceed the impacts of lethal interactions through stress-mediated responses (e.g. Creel & Christianson, 2008; McCauley, Rowe & Fortin, 2011; Clinchy, Sheriff & Zanette, 2013). However, the evidence that non-lethal interactions alone can reduce population densities of wild animals is scarce and arguably absent for terrestrial vertebrates (Sheriff *et al.*, 2020). Certainly, martens have thrived in our study area since their recolonization in the 1990s (Summers, 2018). Simultaneous tracking of multiple carnivores would contribute to clarify whether a significant proportion of the landscape is unavailable to subordinate carnivores at any one time due to the continuous movement of larger carnivores or if they are able to exploit largely the same resources (Vanak *et al.*, 2013).

Concluding remarks

We have seen how martens operate under a low-risk tolerance strategy where they respond to the presence of risk rather than to its intensity. This enables close coexistence with two medium carnivores, foxes and badgers. Larger carnivore-avoidance strategies such as the one identified here may be harnessed for the protection of prey species of conservation or economic value. However, our results highlight that the effects of larger carnivore cues on the targeted carnivore species may be short-lived and recurrent stimuli necessary to replicate their presence and offer lasting protection.

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Author contributions

Karolina Zalewska involved in conceptualization, software, methodology, formal analysis, data curation, writing the original draft and writing, reviewing and editing; Cristian Navarro Wagershauser involved in conceptualization, software, methodology, formal analysis, investigation and writing reviewing and editing; Kenny Kortland involved in resources, writing, reviewing and editing, and funding acquisition; Xavier Lambin involved in conceptualization, methodology, writing, reviewing and editing, supervision, project administration and funding acquisition.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Table S1. The number of images of all species detected during the three seasons of the study.

Table S2. Hermans-Rasson tests of the distribution of observations of pine marten, European badger, and red fox throughout the day (H0: distributions are uniform).

Table S3. Pairwise differences and standard errors (SE) between estimated kernel activity of pine marten, European badger, and red fox, Wald test statistic (W) and associated p-value (H0: differences in activity are zero). Significant contrasts are highlighted in bold.

Table S4. Results of nested model selection for models determining the time interval between European badger visits. Models are listed by row, and the explanatory variables included in each model, degrees of freedom (d.f.), log likelihood (logLik), AIC, AIC difference from top model (Δ AIC), and AIC weight (Weight) are presented. The number of time intervals when no other species were present between badger visits was 272, 20 with fox visits between badger visits and 32 with marten visits.

Table S5. Proportion of independent detections of Eurasian badger, pine marten and red fox at different times of the day and each season. Day: 1 h after sunrise and 1 h before sunset; Night: 1 h after sunset and 1 h before sunrise; Twilight: 1 h before and after sunrise and sunset. Average times of sunset and sunrise obtained from: timeanddate.com.

Figure S1. Isotropic spatial correlograms of pine marten detections per trapping night at each station. Panels (a–c): univariate (one observation per station) spline correlograms for spring 2018 (a), winter 2019 (b) and spring 2019 (c). Y-axis represents similarity between two points at a given distance in kilometres (x-axis). Zero line represents region-wide similarity (i.e., if the line overlaps zero, any two locations at that distance are no more similar than expected by chance). Panel (d): multivariate (timeseries) non-parametric correlation function. Y axis represents correlation over distance, dotted line is regional average correlation (0.06), and zero line is true zero. Grey areas represent the 2.5th and 97.5th quantiles of the bootstrapping distribution. Correlograms were produced with the ‘nfc’ package (Bjornstad, 2020).

Figure S2. Predicted values of pine marten detections per trapping night over percentage of forest cover (a), season (b) and year (c) controlling for all other factors (kept at average or intercept conditions). Grey areas and arrows represent 95% confidence interval.