ARTICLE

Mammal responses to predator scents across multiple study areas

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Abstract

Antipredator behaviors allow prey to mitigate the impacts of their predators. We investigated antipredator responses of two herbivore species, roe deer and European hare, and one mesopredator, red fox, toward predation risk imposed by lynx and wolf. We collected data (using camera traps) on visitation frequency and vigilance behavior to olfactory predator stimuli during 158 standardized scent trials in five areas across Europe, where lynx and wolves either occurred or had been absent for centuries. After a period without scent, trial sites were either marked with lynx or wolf urine, or butyric acid (unspecific scent used to contrast species-specific scent responses). We expected the two herbivores to respond aversively (reduced visitation frequency, and increased vigilance) to predator urine, while red foxes (scavengers) might adopt a risk-sensitive exploration strategy by increasing vigilance near predator urine without reducing visitation frequency. For all species, we expected stronger responses toward the ambush predator lynx than to the pursue predator wolf (cryptic predator hypothesis). If prey responds more strongly to predator stimuli when coexisting with the predator, we expected stronger reactions to predator urine in areas where predators occurred (naïve prey hypothesis). Roe deer significantly avoided lynx urine and butyric acid, but not wolf urine. However, roe deer visitation frequency did not differ between scent treatment with large

carnivore urine and butyric acid (suggesting that roe deer generally avoid areas with unfamiliar scent), or between areas where large carnivores were present and absent. Hares did not significantly avoid predator urine. Red foxes were attracted to lynx urine in sympatry, but not in allopatry with large carnivores. They increased vigilance rates in the presence of lynx urine independent of sympatry/allopatry with large carnivores. These findings generally confirm our expectations of predator avoidance by herbivores, and attraction combined with increased vigilance of mesopredators. In all species, lynx urine elicited stronger responses than wolf urine (although not significantly different), which to some extent conforms to the cryptic predator hypothesis. We found no support for the naïve prey hypothesis. However, higher attraction of red foxes to lynx urine in sympatric situations might indicate that positive responses by scavengers are learning based.

KEYWORDS

antipredator behavior, avoidance, *Canis lupus*, *Capreolus capreolus*, intra-guild predation, landscapes of fear, *Lepus europaeus*, *Lynx lynx*, odor, risk-sensitive foraging, vigilance, *Vulpes vulpes*

INTRODUCTION

Animals navigating through heterogeneous landscapes experience varying levels of predation risk (Laundré et al., 2010). Theoretical and experimental research has revealed that predation risk can strongly shape the behavior of their prey (Gaynor et al., 2019). Studies on the "ecology of fear" have linked antipredator responses to changes in spatio-temporal distribution (Kuijper et al., 2013; Latombe et al., 2014; Lima & Dill, 1990) or an increase in vigilance behavior (Brown, 1999; Delm, 1990), which can result in an impaired energy balance for the individual and reduced carrying capacity at the population level (Brown et al., 1999; Lima & Bednekoff, 1999; Lima & Dill, 1990).

Prey responses toward their predators depend on the sensory ability of prey to recognize the threat and the strength and reliability of cues (Gaynor et al., 2019). Olfactory cues differ between visual and acoustic cues, because they provide information about the time elapsed since the predator has left (Apfelbach et al., 2005; Kats & Dill, 1998). Prey species react to a variety of chemical compounds present in carnivore urine, feces, or skin (Apfelbach et al., 2015; Kats & Dill, 1998; Muller-Schwarze, 2006), some of which are metabolic waste products that carry information about the diet of the producer (Berton et al., 1998; Nolte et al., 1994) and others are taxon specific (Hendriks et al., 1995; Osada et al., 2015). By the ability to relate these direct cues to predator type, prey can determine the spatial variation of predation risk or the likelihood of a predation event from predators differing in hunting mode (Gaynor et al., 2019; Kuijper et al., 2014; Wikenros et al., 2015), which consequently influences the behavioral reaction of prey. In this light, some studies have argued that prey may perceive greater risk from cryptic ambush predators (like solitary felids) than from pursuing predators (like wolves *Canis lupus*), because the presence of olfactory cues suggests proximity of the predator (Preisser et al., 2007; Thaker et al., 2011).

Behavioral responses to predator stimuli can be either innate properties, that is, genetically based through generations of past selection, or acquired through individual or socially transferred experience, or a combination thereof (Cox & Lima, 2006; Griffin, 2004; Sih et al., 2010). Examples of innate anti-predator behaviors observed in areas where the predation threat has disappeared include avoidance of areas marked with brown bear (*Ursus arctos*) feces by fallow deer (*Dama dama*) (Sahlén et al., 2016) and avoidance of wolf urine by black-tailed deer (*Odocoilus hemionus*) (Chamaille-Jammes et al., 2014). On the other hand, multiple examples also exist of weakened anti-predator behaviors in predator-relieved populations (Blumstein & Daniel, 2005; Bonnot et al., 2016). Understanding variation in anti-predator behavioral responses of prey whose geographical ranges overlap with their predators (sympatry) or that are physically isolated from their predators (allopatry) is essential to develop a predictive understanding of the conditions that affect prey populations.

Antipredator responses might differ between prey species. For example, herbivores generally adapt different strategies to minimize predation risk (Creel et al., 2005). Mesopredators can also be suppressed by large carnivores on a landscape scale but might locally profit from the presence of large predators, because they can scavenge on their kills (Prugh & Sivy, 2020; Sivy et al., 2017; Wikenros

et al., 2013). Consequently, for mesopredators, responses to the threat of predation risk are likely more complex than fear alone (Wooster et al., 2021). For instance, despite Eurasian lynx (*Lynx lynx*) kill red foxes (*Vulpes vulpes*) and can limit their density (Helldin et al., 2006), red foxes have been found to be attracted to lynx feces as a possible risk-sensitive foraging strategy (Wikenros et al., 2017).

In large parts of Europe, all mammalian apex carnivores were exterminated centuries ago. This long-lasting disturbance of natural predator–prey relationships in mammal communities, followed by the recent re-establishment of large carnivore populations, especially Eurasian lynx and wolf (Chapron et al., 2014), makes Europe interesting for studies on the effects of re-establishing top predators on antipredator behaviors of herbivores and mesopredators. Both lynx and wolves prey on ungulates, as well as smaller prey, such as leporids and rodents, and on mesopredators (Valdmann et al., 2005), with prey choice depending on availability (Jędrzejewski et al., 2012).

In this paper, we investigated how two herbivores, the roe deer (*Capreolus capreolus*) and European hare (*Lepus europaeus*), and one mesopredator, the red fox, react to olfactory predator cues (lynx and wolf urine) across multiple study areas. To do so, we conducted scent trials and measured the visitation frequency and vigilance behavior of these species. We hypothesized that (1) antipredator responses depend on the prey type. Specifically, we predicted that roe deer and hares reduced their visitation frequency

and increased vigilance in response to predator scents, compared with red foxes that might use predator scent as cue for scavenging opportunities. Moreover, we hypothesized that (2) cues of a cryptic predator caused stronger antipredator responses than a more conspicuous pursue predator, termed the cryptic predator hypothesis (Preisser et al., 2007; Thaker et al., 2011), predicting that visitation frequency decreased more and vigilance increased more in the presence of lynx scent compared with wolf scent. Finally, we hypothesized (3) prey species to be less sensitive to predator cues in areas where large predators were absent, termed the naïve prey hypothesis (Berger, 2007), predicting that visitation frequency was higher and change in vigilance in response to predator scents was lower in areas where prey was allopatric with large predators than in areas where prey and large predators occurred in sympatry.

MATERIALS AND METHODS

Study areas, experimental setup, and data registration

Between September 2013 and October 2014, we conducted 158 scent trials with either lynx urine, wolf urine, or butyric acid as scent treatment. The trials were conducted in forest habitats in five different study areas in Europe (Table 1, Figure 1). In three study areas

TABLE 1 Number of experiments with observations per study area divided by scent treatment and species.

| Study area | Location | Large carnivore presence[a] | Study period | No. scent experiments[b] | | | | No. experiments with species observations | | |
				Lynx urine	Wolf urine	Butyric acid	Sum	Roe deer	Red fox	Eurasian hare
Jutland, Denmark (DK)	56.29° N, 10.49° E	...	16 Sep 2013–7 Oct 2014	19	22	17	58	56	16	23
Bavarian Forest, Germany (BAF)	48.96° N, 13.39° E	L	18 Jan–25 Oct 2014	17	16	18	51	44	42	15
Black Forest, Germany (BLF)	48.31° N, 08.15° E	...	24 Jan–14 Apr 2014	7	9	8	24	21	11	1
Grimsö, Sweden (GR)	59.72° N, 15.47° E	LW	8 Jul–26 Sep 2014	5	5	6	16	15	4	...
Danube-Zahorie, Slovakia (DZ)	48.59° N, 17.11° E	...	9 Jul–25 Oct 2014	5	3	1	9	8	3	2
No. experiments				53	55	50	158	144	76	41
No. survey days								3636	2018	946
No. count observations								717	402	151
No. count observations that could be coded as vigilant/not vigilant								586	358	89

[a]Permanent presence of large carnivores: L, lynx; W, wolf.

[b]Number of experiments resulting in ≥1 observation of one of the three species.
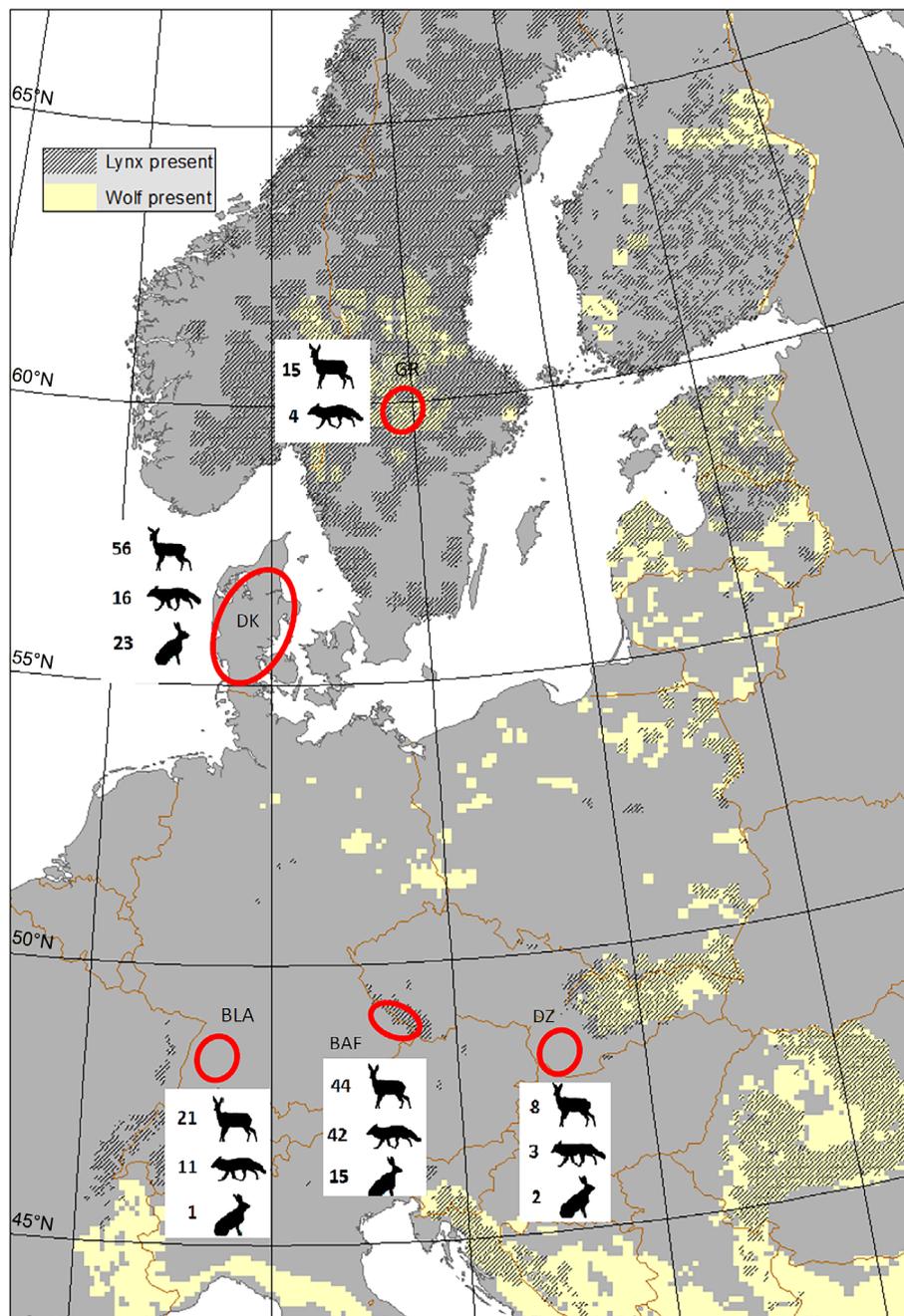
FIGURE 1 Location of the experimental study sites and the geographical distribution of Eurasian lynx and gray wolf as of 2014 (Chapron et al., 2014). The number of scent experiments that resulted in observations of roe deer, red fox, and European hare is indicated for each study area. BAF, Bavarian Forest National Park, Germany; BLA, Black Forest, Germany; DK, Jutland, Denmark; DZ, Danube-Zahore National Park, Slovakia; GR, Grimsö, Sweden.

(Jutland, Denmark [DK], Black Forest, Germany [BLA], and Danube-Zahore National Park, Slovakia [DZ]), all large carnivores had been absent for >160 years, while in two (Bavarian Forest National Park, Germany [BAF] and Grimsö, Sweden [GR]), lynx had been permanently present for >20 years. Furthermore, in GR, wolves had been present for 15 years. A detailed description of the study areas and experimental protocol can be found in Appendix S1.

Urine from wolf and bobcat (*Lynx rufus*; used as a substitute for Eurasian lynx) fed on meat was obtained from Wildlife Control Suppliers (East Granby, CT, USA). Each urine type was a mixture of urine from different individuals conserved with small amounts of sodium benzoate. We are aware that using mixed urine from a supplier might have resulted in unnatural scent cues and caused pseudoreplication (Kroodsma et al., 2001), but

argue that these potential issues were outweighed by the benefit of being able to use the same scent type across study areas. Butyric acid is a fatty acid that occurs in carrion (Dekeirsschieter et al., 2009; Forbes et al., 2014), mammalian secretions, and carnivore feces (Arnould et al., 1998; Verbrugghe et al., 2010) to which many animals respond (Muller-Schwarze, 2006) and was thus considered as a taxonomically non-specific olfactory cue of a carnivore. We considered butyric acid as an extended control in the sense that a response to a given predator scent (lynx or wolf urine) would only be considered as genuinely species-specific if it was significantly stronger than the response to the taxonomically neutral scent.

Each scent trial consisted of five sponges placed at 0.5–1 m height on sticks or twigs, forming a 30–50 m quadrat with a sponge placed in the center, 4–5 m in front of an infrared, motion-sensitive wildlife camera (Figure 2). We used this design to increase the area covered by the scent cue, informing passing mammals about the presence of the scent cue before entering the central observation point (camera). To each of the five sponges within each scent trial, we added a minimum of 2 ml of lynx urine, wolf urine, and 1 ml of butyric acid (33% dilution), which was sufficient to be detected by humans at a minimum of 20 m distance. As previous studies showed that wolf scent-marking under natural conditions contains approximately 5 ml of urine, Peters and Mech (1975) and Eccard et al. (2017) found an effect on roe deer vigilance behavior using 7 ml of urine, we believe adding 10+ ml of urine within each scent trial was enough to trigger a response. Each scent trial consisted of an initial period with no scent ("no-scent period"), followed by a treatment period with scent addition. This split-plot design with a no-scent period within each experiment ensured that spatial variation between observation sites and study areas with regard to baseline observation frequency and behavior was accounted for in relation to scent/no-scent comparisons. Within each trial, the no-scent and treatment periods were of approximately equal length (median = 12 days, range: 6–48 days, 90th percentile: 7–27 days). In trials where the treatment periods lasted longer than 10 days, we usually renewed scents every 7–10 days. As the number of observations per day varied grossly between experiments, we defined no upper limit for the duration of the trials. By the end of the trials, all scent types were still detectable by human observers from >1 m distance. Whenever possible, we placed experimental sites >1 km apart to avoid possible interference between adjacent experimental sites. We allocated an equal number of scent types to the experiments, with the scent type being assigned randomly to each trial. However, as the number of observations of a
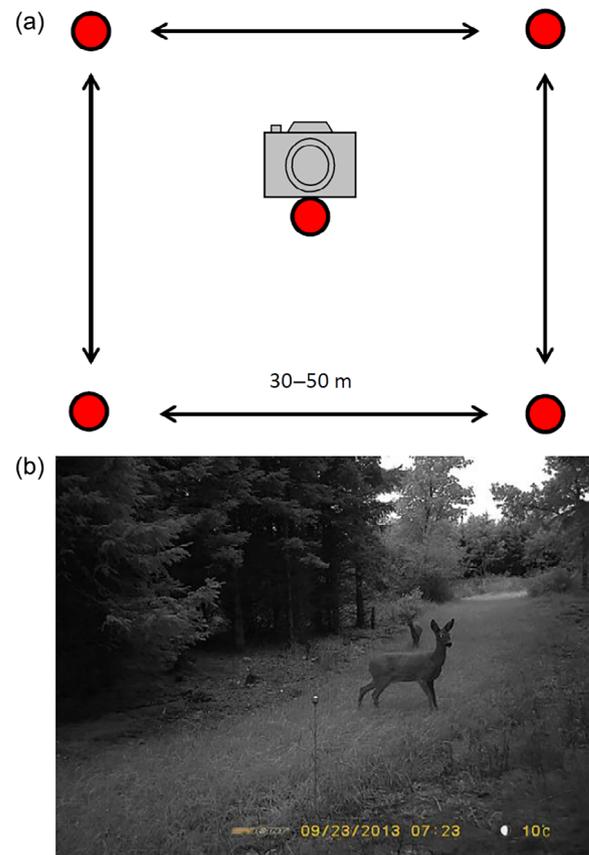

FIGURE 2 (a) Experimental field design. Four sponges were placed on sticks or twigs in the corners of a quadrat and one sponge was placed in the center, in front of a wildlife camera. An experiment consisted of a period with no scent and a treatment period with scent (butyric acid, lynx urine, or wolf urine) added to each sponge. (b) Example of roe deer observation, with behavior coded as "vigilant" and diurnal period coded as "day."

given species varied between experiments, and not all experiments resulted in observations, it was impossible to achieve a perfect balance between scent treatments in the number of experiments and animal observations in the final data. In DK, BAF, GR, and DZ, we conducted consecutive scent trials with different scent types (the order of scent types was randomized) at the same sites, separated by ≥10 days from the end of the treatment period of the first trial to the start of the no-scent period of the subsequent trial to allow animal activity and behavior to return to baseline levels (in agreement with Kuijper et al., 2014; van Beeck Calkoen et al., 2021; Wikenros et al., 2015).

Camera models, settings, and images (photos or video sequences lasting 3–10 s) varied between the study areas, but this spatial variation is not important since our analyses compared differences between scent and no-scent situations within the same experiment (see below).

Photographs and videos from all locations except BAF were analyzed and coded by the same person, recording the species, date, time, and animal behavior. Additionally, we coded the dominating behavior (if identifiable; if more than one individual appeared on the image, the one nearest the camera was selected) for each individual recorded following Kuijper et al. (2014). Behavior was quantified as either "walking," "running," "foraging" (grazing, browsing, and chewing), "vigilant" (animal stood still with its head held at body height or higher or was looking around), "sudden rush" (animal went from standing still to running: only observable from videos), "sniffing/exploring" (animal explored or sniffed the scent sponges), "checking camera," and "other behavior" (e.g., resting, rubbing, or scratching).

Analyses of visitation frequency as response to scent addition

As a measure of visitation frequency, we counted the number of observations (multiple individuals within the same picture were counted as one observation) for the separate species. Observations were defined as independent when photographs or videos of animals were separated by ≥ 60 min (to lower potential effects of pseudoreplication of the same individuals), unless the images showed clearly different individuals.

For each species, we modeled visitation frequency as the number of independent observations per time unit with generalized linear mixed models (GLIMMIX procedure in SAS 9.4, SAS Institute) with a logit-link function and binomially distributed errors. To ensure an event/trial ratio (p) close to 0 (hence, the binomial distribution approaching a Poisson distribution, and the logit scale a log-scale), the response variable was the number of observations within a treatment or no-scent period divided by the number of days multiplied by 100 ($p = n/[\text{days} \times 100]$). Hence, if an experiment consisted of a 10-day no-scent and a 9-day scent treatment period within which four and two independent observations were registered, the number of events/trials for the two phases entered into the logistic regression model were 4/1000 and 2/900, respectively. On an arithmetic scale, the scent response was expressed as the odds ratio of the observation frequency during the scent period (p_{scent}) relative to the no-scent period ($p_{\text{no-scent}}$). In the example, $p_{\text{scent}}:p_{\text{no-scent}} = [2/900]:[4/1000] = 0.556$, equivalent to a 44.4% reduction (1–0.556) in visitation frequency in the presence of scents. In the output from logistic regression, the scent response coefficients was defined as $B = \ln(p_{\text{scent}}/[1 - p_{\text{scent}}]) - \ln(p_{\text{no-scent}}/[1 - p_{\text{no-scent}}])$. In practice, this could be simplified to $B = \ln(p_{\text{scent}}) - \ln(p_{\text{no-scent}}) \Leftrightarrow B = \ln(p_{\text{scent}}:p_{\text{no-scent}})$ as all $p \to 0$. Hence, in

the aforementioned example, the log-odds ratio, modeled with logistic regression, would be $B = 0.590$ ($B = \ln[(2/900)/(1–2/900)] - \ln[(4/1000)/(1–4/1000)]$), equaling a back-transformed odds ratio at $\exp(B) = 0.555$. We accounted for random variation in visitation frequency between the experimental units by including scent trial ID nested within observation site, observation site nested within study area, and study area as random intercepts. If the generalized χ^2/df ratio was larger than 1 (overdispersed residuals, which indicate the dependency of observations not accounted for in the model structure), we adjusted the models for variance inflation ("random_residual_;" statement in the script provided).

For each species, we obtained and tested for differential responses to different scent types either as a four-level categorical variable (lynx urine, wolf urine, butyric acid, and no scent) or as an interactive effect of scent type and scent presence (absent/present). The two model structures produced similar predictions: we used the first (and simplest) model type to derive pairwise scent effect estimates (scent treatment A vs. no-scent; scent treatment A vs. scent treatment B) as least-square means and the latter model type to obtain overall model tests (F statistics) for whether different scents elicited differential responses in visitation frequency.

We separated the analyses into four steps. First, we estimated changes in visitation frequency as a response to scent addition for all scent trials combined from all observation sites and study areas (random intercepts model). From these models, we estimated the basic response in visitation frequency to scent addition as compared to the no-scent (no-scent) situation, as well as the difference in responses between scents. Second, we contrasted scent response estimates between areas where large carnivores were present (either only lynx or both lynx and wolves) and absent (both species absent). Third, to explore whether responses varied between study areas, we also split the analyses and estimates into as many study areas as data permitted. Fourth, we ran models that included an interaction term between scent type and study area type (random slopes model), hence allowing us to test for differential scent responses between study areas and to produce mean responses that accounted for heterogeneity in scent responses between study areas, which provided the most rigorous, universal scent response estimates.

Initially, we also tested for seasonal effects (October–March vs. April–September; problems with model convergence prevented finer divisions) on scent responses and effects of days since last human visit on the number of animal observations per day. As we found no indications of these predictors influencing our estimates,

these potential nuisance variables were not considered in the subsequent models.

Analysis of vigilance rates in response to scent presence

For the analysis of vigilance frequency, we compared the number of times the respective species was recorded "vigilant" opposed to non-alert behaviors ("walking," "foraging," and "other behaviors") as a logistic regression function (logit link and binomial error distribution) with scent type (no-scent, lynx urine, wolf urine, and butyric acid), day-or-night and presence-or-absence of large carnivores as fixed effects, and (if estimable) study area and experimental site nested within study area as random effects. We furthermore split the analysis between areas with and without large carnivores and tested for differences in odor-specific responses. As foxes were significantly more alert by night than by day, day versus night was included as a nuisance variable for this species.

RESULTS

Roe deer

Compared with the no-scent period, roe deer visitation frequencies significantly declined upon addition of lynx urine and butyric acid, but not wolf urine (Figure 3a). However, visitation frequencies did not differ significantly between the three scent types (overall difference: $F_{2,141} = 0.62$, $p = 0.54$; for pairwise comparisons, see Figure 3b). Moreover, the changes in visitation frequencies upon scent addition did not differ between areas where large carnivores were present and absent (Table 2). When analyzed separately by study area, scent response coefficients were negative in DK, BLF, and BAF ($p < 0.05$ for lynx urine and butyric acid in DK, $p < 0.10$ for lynx urine in BLF and BAF), and inconclusive in GR and DA (Figure 4a). The random slope model estimated roe deer to significantly avoid lynx urine and tended to avoid butyric acid ($B = -0.31$, $SE_{12} = 0.14$, $p = 0.0501$), but not wolf urine (Figure 4a).
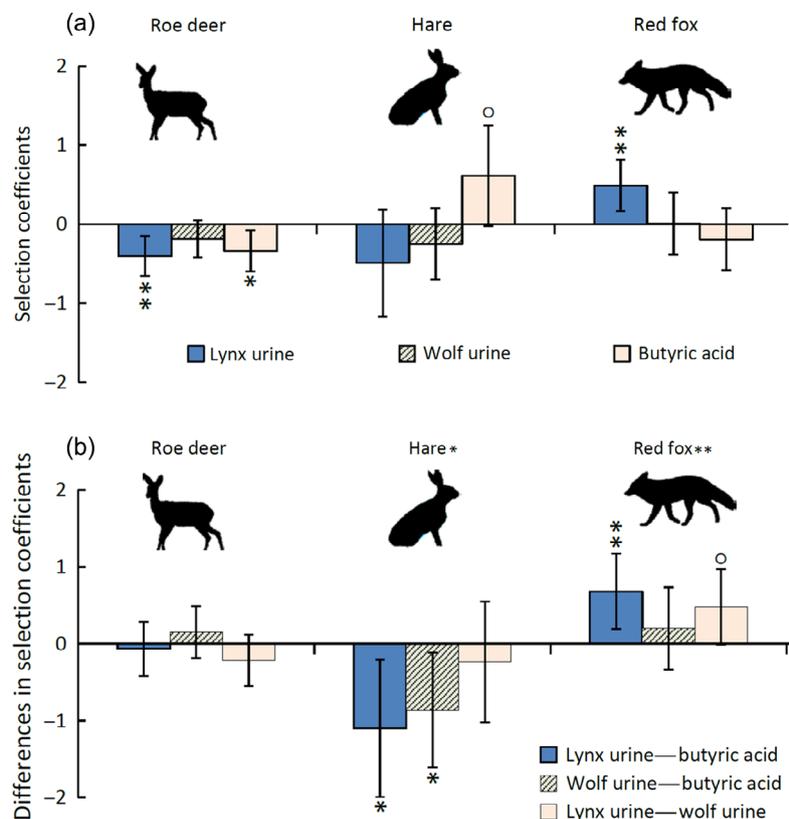

FIGURE 3 (a) Selection coefficients (95% CIs) for difference in visitation frequencies upon scent placement. A selection coefficient of 1 indicates that a site is observed $\exp(1) = 2.718$ times more often per time unit after scent has been added than before scent was added, while a selection coefficient of -1 indicates that a site is visited 2.718 times less often ($\exp[-1] = 1/2.718$) upon scent addition. (b) Differences in selection coefficients between scent types. Statistical significances (symbols under species names indicate significances for the entire species model, symbols over or beneath error bars indicate significance of the specific response): $°p < 0.1$; $*p < 0.05$; $**p < 0.01$.

TABLE 2   Selection coefficients (study area and experimental sites nested within the study area as random intercepts) for change in visitation frequency after scent addition (negative values indicate avoidance, positive values attraction: Selection ratio = e^B).

Scent type	LC status	B	SE	df	t	p
Roe deer						
Lynx urine	LCs absent	−0.42	0.15	82	−2.72	**0.008**
	LCs present	−0.33	0.24	56	−1.37	0.18
	Difference	−0.09	0.28	138	−0.31	0.76
Wolf urine	LCs absent	−0.22	0.14	82	−1.61	0.11
	LCs present	−0.07	0.24	56	−0.27	0.79
	Difference	−0.16	0.28	138	−0.56	0.57
Butyric acid	LCs absent	−0.44	0.17	82	−2.68	**0.009**
	LCs present	−0.19	0.23	56	−0.84	0.41
	Difference	−0.25	0.28	138	−0.89	0.37
Hare[a]						
Lynx urine	LCs absent	−0.30	0.41	23	−0.74	0.47
	LCs present	−0.98	0.64	12	−1.53	0.15
	Difference	0.68	0.76	35	0.89	0.38
Wolf urine	LCs absent	−0.30	0.27	23	−1.09	0.29
	LCs present	−0.10	0.44	12	−0.24	0.82
	Difference	−0.19	0.52	35	−0.37	0.71
Butyric acid	LCs absent	0.66	0.43	23	1.55	0.14
	LCs present	0.64	0.49	12	1.29	0.22
	Difference	0.02	0.65	35	0.04	0.97
Red fox						
Lynx urine	LCs absent	−0.86	0.5	27	−1.71	0.10
	LCs present	0.65	0.19	43	3.41	**0.001**
	Difference	−1.51	0.54	70	−2.81	**0.006**
Wolf urine	LCs absent	0.09	0.33	27	0.26	0.79
	LCs present	−0.02	0.25	43	−0.06	0.95
	Difference	0.10	0.42	70	0.25	0.81
Butyric acid	LCs absent	−0.27	0.38	27	−0.71	0.49
	LCs present	−0.18	0.24	43	−0.74	0.46
	Difference	−0.09	0.45	70	−0.20	0.84

Note: Different models are established for all observations and for study areas where large carnivores (LC) were absent and present (*t* statistics for difference: $t_{df1+df2} = [B_1 − B_2]/[SE(B_1)^2 + SE(B_2)^2]^{0.5}$). Statistically significant *p*-values (< 0.05) are boldfaced.
[a]Hares also have natural enemies where large carnivores are absent.

Vigilance rates in roe deer were not affected by scent presence in any situation (Table 3).

Hares

Hares showed no significant changes in visitation frequency upon addition of any of the scent types, although visitation rates tended to decrease in the presence of lynx urine and wolf urine, but increase upon addition of butyric acid (Figure 3a). As a consequence, the direction of the responses differed significantly between the scent types (overall difference: $F_{2,38} = 3.85$, $p = 0.03$), with the positive response to butyric acid differing significantly from the negative responses to lynx and wolf urine (Figure 3b). There was no difference in scent response patterns between areas where large carnivores were absent and present (Table 2), or between the two study areas for which study-area-based estimates could be established (DK and BAF; Figure 4b). Consequently, the random slope model estimated the study-area-by-scent covariance parameter to 0
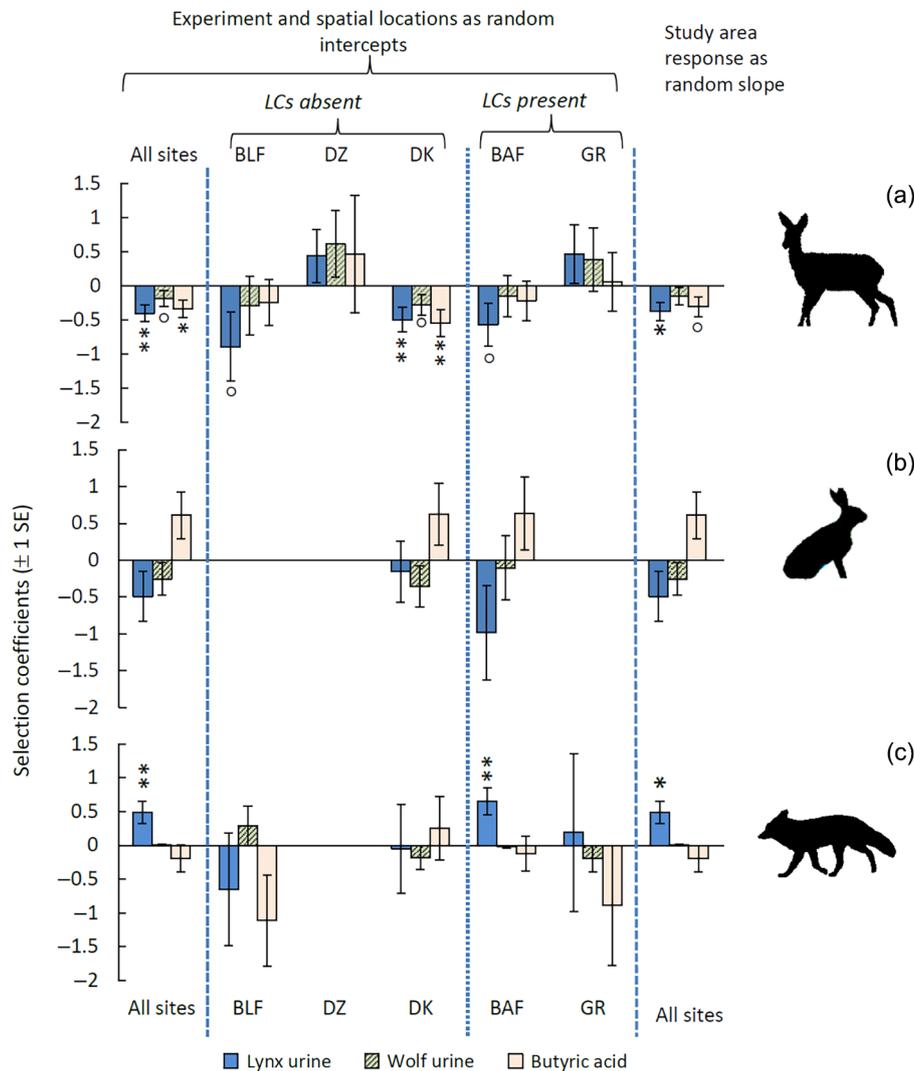
FIGURE 4 Scent responses (selection coefficients [log-odds ratios; scent: no scent] ± 1 SE) for (a) roe deer, (b) hare, and (c) red fox to lynx urine, wolf urine, and butyric acid estimated for all sites, separated on study area (if estimable) and as mean responses averaged across study areas (models with study area in interaction with scent response as random slope). The figures shown in the "All sites" panel are the same as those shown in Figure 3a. LCs, large carnivores. Statistical significances: °$p < 0.1$; *$p < 0.05$; **$p < 0.01$. BAF, Bavarian Forest National Park, Germany; BLA, Black Forest, Germany; DK, Jutland, Denmark; DZ, Danube-Zahore National Park, Slovakia; GR, Grimsö, Sweden.

(no heterogeneity in scent responses between study areas), providing similar estimates as the random intercept model (Figure 4b).

Hare vigilance rates were not affected by scent presence in any situation (Table 3).

Red foxes

Compared with the no-scent period, red fox visitation frequency significantly increased upon addition of lynx urine (Figure 3a), but not during wolf urine and butyric acid treatment (Figure 3a). Overall visitation frequency differed between scent types ($F_{2,73} = 6.73$, $p = 0.002$), with visitation frequency increasing significantly more during lynx urine treatment compared with butyric acid treatment and wolf urine (the latter being a trend only; Figure 3b).

When comparing areas where large carnivores were present and absent, red foxes were only attracted to lynx urine in areas where they were sympatric with large carnivores (Table 2). Divided by study area, red foxes significantly increased visitation frequency during lynx urine treatment in BAF, which was the study area that contributed with most fox observations to the analysis, whereas no significant deviations from 0 were registered in any of the other study areas (Figure 4c). The random slope model estimated the study-area-by-scent covariance parameter to 0 (no heterogeneity in scent responses between study areas could be established),

TABLE 3 Mixed model logistic regression equations for the probability of roe deer, hares, and red foxes being vigilant as opposed to "foraging," "walking," or "other behaviors" as functions of the presence of scent treatment (relative to no scents) and diel variation (only significant in red fox).

LC status	Parameter	B	SE (B)	df	t	p
Roe deer						
All	Intercept	−1.28	0.2			
	Lynx urine	−0.50	0.38	475	−1.32	0.19
	Wolf urine	0.34	0.29	475	1.18	0.24
	Butyric acid	−0.01	0.34	475	−0.02	0.99
	Study area	*0.51*	*0.25*			
	Site	*0.05*	*0.13*			
LCs absent	Intercept	−1.49	0.38			
	Lynx urine	−0.98	0.53	372	−1.86	0.06
	Wolf urine	0.27	0.33	372	0.82	0.42
	Butyric acid	0.15	0.42	372	0.37	0.71
	Study area	*0.44*	*0.27*			
	Site	*0.25*	*0.37*			
LCs present	Intercept	−1.25	0.3			
	Lynx urine	0.30	0.62	100	0.48	0.63
	Wolf urine	0.55	0.6	100	0.93	0.36
	Butyric acid	−0.18	0.61	100	−0.30	0.77
	Study area	*0.60*	*0.47*			
	Site	*0.00*				
Difference	Lynx urine	−1.28	0.82	472	−1.56	0.12
	Wolf urine	−0.28	0.68	472	−0.42	0.67
	Butyric acid	0.33	0.74	472	0.45	0.65
Hare						
All	Intercept	−0.66	0.3	79		
	Lynx urine	−0.03	0.92	79	−0.03	0.97
	Wolf urine	−0.15	0.67	79	−0.22	0.83
	Butyric acid	−13.9	389	79	−0.04	0.97
LCs absent	Intercept	−0.24	0.35	49		
	Lynx urine	−0.46	1.27	49	−0.36	0.72
	Wolf urine	−0.61	0.77	49	−0.79	0.43
	Butyric acid	−13.33	360	49	−0.04	0.97
LCs present	Intercept	−1.95	0.76	26		
	Lynx urine	1.25	1.44	26	0.87	0.39
	Wolf urine	1.25	1.44	26	0.87	0.39
	Butyric acid	−12.6	515	26	−0.02	0.98
Difference	Lynx urine	−1.71	1.92	75	−0.89	0.38
	Wolf urine	−1.86	1.63	75	−1.14	0.26
	Butyric acid	−0.73	628	75	0.00	1.00
Red fox						
All	Intercept	−2.52	0.57			
	Lynx urine	1.64	0.62	294	2.66	**0.008**

(Continues)

T A B L E   3 (Continued)

LC status	Parameter	B	SE (B)	df	t	p
	Wolf urine	0.6	0.67	294	0.89	0.38
	Day versus night	−1.33	0.56	294	−2.38	**0.02**
	Butyric acid	1.26	0.66	294	1.90	0.06
	Study area	*1.34*	*0.76*			
	Site	*0.40*	*1.04*			
LCs absent	Intercept	−3.24	1.02			
	Lynx urine	3.52	1.6	26	2.15	**0.04**
	Wolf urine	1.78	1.3	26	1.38	0.18
	Butyric acid	−16.9	9341	26	0.00	1.00
	Day versus night	−0.56	1.66	26	−0.34	0.74
	Study area					
	Site	*0.00*				
LCs present	Intercept	−3.22	0.74			
	Lynx urine	1.59	0.82	264	1.92	0.055
	Wolf urine	0.10	0.92	264	0.11	0.91
	Butyric acid	2.10	0.95	264	2.21	**0.03**
	Day versus night	−1.68	0.65	264	−2.59	**0.01**
	Study area					
	Site	*2.67*	*2.09*			
Difference	Lynx urine	1.93	1.80	290	1.05	0.29
	Wolf urine	1.68	1.59	290	1.06	0.29
	Butyric acid	−19	9341	290	0.00	1.00

Note: Different models are established for all observations and for study areas where large carnivores (LCs) were absent and present. The *t* statistics for difference in scent response between areas where large carnivores were absent and present (diff. = $B_{\text{LCs present}} - B_{\text{LCs present}} = B_1 - B_2$) is calculated as $t_{\text{df1+df2}} = ([B_1 - B_2]/[\text{SE}(B_1)^2 + \text{SE}(B_2)^2]^{0.5}$. In italics are shown covariance parameters for the random effects of the study area and observation site nested within the study area, if estimable. Statistically significant *p*-values (< 0.05) are boldfaced.

yielding similar estimates as the random intercepts model, hence a significant preference for lynx urine (Figure 4c).

Red foxes increased vigilance rates more than three-fold after lynx urine had been added (Table 3), independent of large carnivore presence (Table 3). Vigilance rates also tended to increase in the presence of butyric acid ($p = 0.06$), but not in the presence of wolf urine ($p = 0.38$; Table 3). Even though red foxes were nearly three times more vigilant when lynx urine was added compared with situations where wolf urine was added, this difference was not significant (lynx–wolf difference: $B = 1.04$, $\text{SE}_{294} = 0.78$, $p = 0.18$).

DISCUSSION

Our experimental approach over multiple study areas demonstrated different reactions to scent cues for different species, some of which were consistent across study areas, while others varied spatially. Roe deer avoided olfactory stimuli in general (significant deviations from no-scent situations for lynx urine and butyric acid, but no significant discriminations between scent types), whereas red foxes behaved ambivalently to lynx urine treatment, increasing visitation frequencies while increasing vigilance. Results from hares (no significant deviations from no-scent situations, but preferred butyric acid relative to carnivore urine) were less clear, possibly because of fewer observations, and thus less statistical power.

No species responded significantly more aversively to lynx urine than to wolf urine when the two responses (visitation frequency and vigilance) could be contrasted, albeit the direction of the responses pointed toward stronger responses to lynx urine than to wolf urine. Hence, the cryptic predator hypothesis (Preisser et al., 2007; Thaker et al., 2011) predicting stronger negative responses to lynx than to wolf urine was not supported when tested explicitly.

Finally, we found no support for the naïve prey hypothesis (Berger, 2007), as there were no significant differences in visitation frequencies (of any species) when predators were present versus absent.

Species-specific responses to scent types

Roe deer avoided lynx urine and butyric acid, but not wolf urine, and scent did not affect vigilance rates. These results are in line with studies from Bialowieza, Poland, where roe deer avoided lynx scent without showing increased vigilance (Kuijper et al., 2014; Wikenros et al., 2015). In comparison, GPS-tagged roe deer in DK and GR avoided all three scent types when placed within their home ranges, with no changes in movement or activity patterns (Jensen, 2014). Nonsignificant responses to wolf urine conform to an experimental study, showing no significant effect of the presence of wolf urine on the visitation frequency by roe deer in Denmark (Elmeros et al., 2011). In contrast, another experimental study found substantially increased vigilance by roe deer (registered by direct observations) as response to administration of lynx urine in two study areas inside and few kilometers outside BAF, where large carnivores were present and absent, respectively (Eccard et al., 2017). A potential explanation for these contrasting findings might be different observation methodologies (direct observations vs. camera trap recordings) or differences in local ecological settings, such as habitat type and structure. Hence, heterogeneity between study areas and camera trap location can affect the visitation rate in response to scent addition, which underlines the importance of obtaining results from multiple study areas before a firm, general conclusion can be drawn about a species' response behavior to olfactory predator cues. Our results indicate an unspecific avoidance-based antipredator strategy in roe deer, primarily based on minimizing encounters with predators in the first place by avoiding potentially risky places, as assessed from suspicious scents, rather than by increasing vigilance in such sites. However, despite the fact that lynx predation is the main mortality cause in BAF (Heurich et al., 2012) and GR (Andrén & Liberg, 2015; Davis et al., 2016), it seems that lynx have only a limited impact on deer habitat selection (Samelius et al., 2013). This suggests that roe deer may have more difficulties coping with the risk of lynx predation than with wolf predation (Davis et al., 2016).

The results for hares were ambiguous as no-scent type was significantly avoided or preferred compared with the no-scent period. Nevertheless, the direction of the responses significantly differed between scent types, with butyric acid being selected relative to predator urine. Although this result does not justify bold conclusions, it might be worth noting that attraction by hares to sites marked with butyric acid was shown previously (Mayer et al., 2020). A possible explanation why hares (unexpectedly) might appear to be attracted to butyric acid could be that they associated it with plants of high fat content that are strongly selected for by hares (Schai-Braun et al., 2015). Because hares previously have been shown to avoid sites marked with fox scent (Mayer et al., 2020), we also expected avoidance of large predator scents in our experiments. A possible reason why we did not register significant avoidance of lynx and wolf urine by hares could perhaps be that large carnivores are not responsible for a large proportion of hare mortality; that is, there might be too little selection for large carnivore avoidance.

In red foxes, attraction to lynx urine, and increased vigilance in the presence of lynx urine, conforms to results from Bialowieza, where red foxes visited sites marked with lynx feces more often than control sites, and were more vigilant than at control sites, apparently as a risk-sensitive foraging strategy (Wikenros et al., 2017). The increase in vigilance in the presence of lynx urine was statistically significant both in areas where lynx were present or had been absent for centuries. This may suggest that awareness to olfactory cues from this powerful predator on red foxes (Helldin et al., 2006) has a genetic link. In contrast, increased visitation frequency of foxes at sites marked with lynx urine where both species were sympatric (but not where lynx were absent) indicates that foxes learn that lynx presence provides opportunities via carrion provisioning (Prugh & Sivy, 2020; Sivy et al., 2017) and adjust their exploitation effort accordingly. Red foxes did not react to wolf urine, which is partly contrary to a study by Haswell et al. (2018), who found red foxes in Croatia (wolves present) exploited food resources less and spend more time vigilant on bait stations if marked with wolf urine. This discrepancy could be due to differences in experimental setup or because our experiments only included seven fox observations from a study area where wolves occurred. If responses to wolf scent by red foxes are learning based, it would probably not be expressed in our investigation.

Cryptic predator hypothesis

Our study produced mixed evidence regarding the general validity of the cryptic predator hypothesis (Preisser et al., 2007; Thaker et al., 2011) that predicted more aversive responses to lynx than to wolf urine. As stated in the hypothesis, two species responded significantly aversive

to lynx urine (lower visitation frequency by roe deer and increased vigilance by red foxes) but not to wolf urine. On the other hand, aversive responses to lynx urine were not significantly stronger than responses to wolf urine.

To our knowledge, just two previous studies (Jensen, 2014; van Beeck Calkoen et al., 2021) have explicitly tested responses to both wolf and lynx scent using the same experimental setup. In DK and GR, GPS-tagged roe deer also tended to avoid areas marked with lynx urine more than areas marked with wolf urine, but without the difference in response being statistically significant (Jensen, 2014). In a study on captive red deer (*Cervus elaphus*) in BAF exploiting food items (saplings), the duration of the visits (and consequently browsing intensity) was significantly reduced for sites marked with urine from wolves as well as lynx, with slightly higher reductions in response to wolf urine than lynx urine, although the two predator responses did not differ significantly (van Beeck Calkoen et al., 2021).

Naïve prey hypothesis

For all three species, we found no evidence for the naïve prey hypothesis (Berger, 2007), as there were no differences in aversive response patterns in areas where lynx and other large predators were present versus absent. At least for roe deer (avoidance) and red foxes (vigilance), this suggests that antipredator responses are innate, which also suggests that these species probably could adjust rapidly to the presence of re-establishing large carnivores. No conclusions can be drawn for hares, as they are heavily preyed upon by foxes and other mesopredators in all study areas. Furthermore, natural selection may have favored constantly high vigilance levels and fast escape behaviors of hares (Mayer et al., 2020, 2021). Similar vigilance but different (positive) responses to lynx scent in red foxes indicate that antipredator responses by foxes were a combination of innate and acquired behaviors. Our overall result is in concurrence with several other studies, which found that the current absence of predators did not result in a relaxation of antipredator behaviors, such as nocturnal activity patterns in beavers (Rosell & Sanda, 2006; Swinnen et al., 2015) or where captive red deer still showed antipredator responses even though they never faced a direct risk of predation (van Beeck Calkoen et al., 2021). This might be the result of long periods during which large carnivores exerted a strong population control on their prey, leading to a natural selection for innate antipredator behaviors (Sinclair, 2003). However, other studies have shown that prey can lose important antipredator behaviors when released from predation pressure (Jolly et al., 2021).

Methodological considerations

This study was conducted as a joint effort by several research groups to obtain standardized, experimentally based behavioral data of wild mammals from multiple study areas based on a simple but rigorous experimental protocol (Appendix S1). We acknowledge that starting the no-scent period at the same time when cameras and sticks with sponges were deployed did not allow for a true conditioning period before the recordings started. If wild animals reacted aversively to the appearance of such new objects, this setup might be biased with respect to detecting differences between the initial no-scent and the subsequent scent-addition period. On the contrary, if wildlife reacted to new human objects with curiosity, more observations would appear during the no-scent period. However, since initial analyses indicated no effect of time since last human visit in observation frequency, we consider these potential biases as negligible.

In those cases where the same observation site was used for repeated experiments (new scents at each trial), the protocol prescribed an interim period of minimum 14 days between the termination of the first experiment (scent removed) before commencing the next one (start of the no-scent period). As most experiments lasted for more than 2 weeks, most interim periods were longer than 2 weeks. Nevertheless, if wildlife avoided scent-treated places for more than 2 weeks after the scent had been removed, the baseline observation frequency in the subsequent experiment would be lower. Since none of the three species reduced their observation frequency by more than 50% upon scent addition, we presume that a local condition period of >14 days was sufficient for most subjects to resume their baseline behavior if affected by scent treatments.

As follows from the different biomes (from boreal to nemoral forest), seasons and technical equipment used in the different areas, considerable spatial variation was expected. This baseline spatial variation was accounted for in the experimental design (no scent vs. scent A, B, or C) and analyses that strictly contrasts differences between different scent treatments, equaling out any spatial component of variation. The design was still open for spatial variation in scent responsiveness caused by differences in habitat constitution and other environmental factors, such as population density, as they were previously shown to affect antipredator behaviors (Burger et al., 2000; Watson et al., 2007). We have addressed this by contrasting study areas with and without large carnivores, providing estimates per study area and by accounting for possible differences in responses between study areas when possible. Additionally, behavioral responses to olfactory cues in experimental studies might be

conditional to the type of olfactory cue (e.g., excrement, urine, or tissue), the experimental setup by which study subjects are confronted with scent stimuli, and how the response is measured. For instance, the observed reaction patterns may depend on whether a scent cue is located on a single point to which a passing subject is reacting in front of the camera or observer (Eccard et al., 2017; Kuijper et al., 2014; van Beeck Calkoen et al., 2021; Wikenros et al., 2015, 2017) or has also been allocated to a wider area around the observation point (this study; Mayer et al., 2020). Compared with studies measuring responses to single-point cues, subjects observed within a scent-treated zone are probably more likely to have taken an active decision to move into the scent-marked area and react with less surprise when passing the observation field. Placement of food to which the study subjects are attracted (Haswell et al., 2018; van Beeck Calkoen et al., 2021) is also likely to affect risk-taking decisions compared with setups with fewer rewards for visiting the observation field. Apparent differences in scent responses measured in this study compared with other studies may be rooted in such methodological differences.

Finally, "only" two of the five study areas contributed with >15 experiments of each scent, distributed over more than 9 months of the year, so our study was not exhaustive in its ability to capture all systematic and study-area-based variation with reasonable statistical power. Nevertheless, our results give an initial assessment of the extent to which antipredator behavior responses vary across study areas and in the presence/absence of natural predators. To obtain even more robust assessments of anti-predator responses of wild animals across ecological gradients that account for possible local variation, we advocate for the usage of standardized, easy-to-use experimental approaches (like this one: Appendix S1), across multiple study areas, analytically addressing systematic and random spatial variation.

CONCLUSIONS

We tested behavioral responses of wild terrestrial mammals to predator scents across multiple populations by means of a standardized, experiment-based method. Antipredator responses differed between herbivores and a mesopredator. Our findings might have implications for predicting how the current expansion of large carnivore populations (Chapron et al., 2014) will affect behavioral adjustments of both ungulate prey and mesopredators, which could affect the population dynamics of these species beyond a numerical response to predation alone. The innate avoidance of lynx scent by roe deer suggests that prey can adapt to large carnivore presence and might

adjust its habitat use, avoiding areas of high predation risk, as shown for other systems (Creel et al., 2005). However, future studies are required to quantify the extent to which predators affect antipredator responses in human-managed landscapes. Studies so far suggest that predator-induced effects might play a smaller role in driving habitat selection and foraging behavior of their ungulate prey as compared with human activities (Loosen et al., 2021; van Beeck Calkoen et al., 2022). Red fox antipredator responses appeared to be partly innate (vigilance response to lynx urine) and partly acquired (preference for lynx urine), likely via individual plasticity (phenotypic flexibility) to exploit resources provided by large carnivores. These findings emphasize the behavioral flexibility of red foxes, allowing them to persist in different landscapes and predator guilds (Reshamwala et al., 2021). Overall, our study contributes to our understanding of the complex effects that large carnivores can have on other species across multiple populations.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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