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Research article

The wolf is back! Non-consumptive effects of the return of a large carnivore on the use of supplementary feeding sites by roe deer

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Understanding how prey species tradeoff predation risk and resource acquisition is particularly important for advancing our knowledge of predator–prey relationships. We investigated this by studying the use of concentrated anthropogenic resources, namely supplementary feeding sites, by roe deer *Capreolus capreolus* before and after grey wolf *Canis lupus* recolonisation in an area of the eastern Italian Alps. We used camera traps to monitor roe deer visits to feeding sites, where ad libitum food was provided, before and after wolf recolonisation, in winter and spring, to control for seasonal effects. First, we compared the daily cycle of visits using circular statistics. We then used generalised linear mixed models to assess roe deer, duration of visits, and tendency to congregate at feeding sites as a function of wolf presence and season. Roe deer became more diurnal after wolf recolonisation, particularly in winter, while in spring they tended to concentrate their visits around dusk and dawn. Roe deer visits to feeding sites decreased from winter to spring, but only after wolf recolonisation, while their duration was shorter in spring when wolves were absent than in any other period. Roe deer grouping at feeding sites decreased from winter to spring, especially after wolf recolonisation. These results show that roe deer have changed their resource use behaviour following wolf recolonisation, adopting a range of behavioural tactics that could mitigate predation risk, while maintaining resource acquisition when more profitable. The increase in diurnality may reduce the temporal overlap with wolves' predominantly nocturnal activity; access to the resource-rich, but fairly exposed sites mainly occurred during the most limiting season, or with solitary visits. We call for further research to understand whether other unmeasured processes contribute to shaping the observed patterns, such as demographic decline and fine-scale behavioural adjustments (e.g. increased vigilance).

Keywords: camera-trapping, consumptive versus non-consumptive effects, generalized linear mixed models, grey wolf, roe deer, supplemental feeding

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Introduction

Predators have important consumptive and non-consumptive effects on prey species, both in terms of their demography (e.g. by reducing the abundance of local populations; Schoener and Spiller 1996) and their behaviour. Specifically, fear of predation leads prey species to adopt anti-predator behaviours (Caro and Girling 2005). These include diel adjustment of activity patterns, e.g. by increasing diurnal behaviour in the presence of nocturnal predators to reduce temporal overlap of activity with them (Tambling et al. 2015, Dolapchiev et al. 2023), or spatial modification of habitat use, e.g. by shifting nesting sites to areas with lower predator densities (Clermont et al. 2021). In addition, prey may modify their social behaviour, either by increasing group size to dilute individual predation risk, or by decreasing group size to reduce the risk of encountering a predator (Hebblewhite and Pletscher 2002). Collectively, such individual or group tactics allow prey to navigate a spatiotemporal dynamic landscape of fear (Palmer et al. 2022), which changes according to the perceived risk of predation (Gaynor et al. 2019).

Within the landscape of fear, highly profitable resource patches are particularly risky hotspots because predators tend to focus their search for prey around these sites, especially if prey tend to congregate there (e.g. water holes: Valeix et al. 2010; supplementary feeding sites: Woodruff et al. 2018). However, such sites are also key for resource acquisition and individual energetic balance (Parker et al. 2009). Therefore, when prey use these patches, they face a fitness tradeoff between minimising predation risk and gaining energy. Investigating whether and how prey trade off risk and resource acquisition by adopting specific behavioural tactics is of particular interest to improve our ecological understanding of predator–prey relationships. This can be achieved either by comparing prey behaviour at sites with and without predator presence (i.e. a spatial control-treatment experiment; e.g. Tambling et al. 2015) or by analysing temporal variation in behavioural tactics when the prey is exposed to the return of a predator (i.e. a temporal control-treatment experiment; e.g. Ruble et al. 2022). In both cases, the emergence of such behavioural differences in space or time is conditioned by the behavioural plasticity of the prey (Meuthen et al. 2019) and mediated by the cultural legacy of predation risk (Griffin 2004).

Here, we conducted a temporal control-treatment study of the non-consumptive effects of the recolonisation of a large carnivore, the grey wolf *Canis lupus*, on the patterns of use of highly profitable resource patches, namely supplementary feeding sites, by one of its main prey, roe deer *Capreolus capreolus* (Meriggi et al. 2011). We carried out this work in Trentino, in the eastern Italian Alps, which has experienced rapid recolonisation by wolves in a little more than a decade, favoured by the adoption of conservation measures, the increase in natural prey, and the abandonment of rural areas by humans (Passoni et al. 2024). In this Alpine region, as in several other parts of Europe and North America, feeding sites are used to manage roe deer and other ungulate species (Putman and Staines 2004, Ossi et al. 2017). These concentrated anthropogenic resources provide roe deer with the opportunity to consume food ad libitum when natural resources are scarce (Ossi et al. 2020). At the same time, feeding sites are perceived as risky hotspots within the landscape of fear, as roe deer are shot there by hunters (Ossi et al. 2020). Although wolves are not ambush predators like the Eurasian lynx *Lynx lynx* (Vogt et al. 2016) their recolonisation may increase the perception of risk in the whole landscape used by roe deer, and in these sites in particular. This ecological context therefore provides an ideal setting to study the proactive behavioural response of a prey species to the return of its main predator (Creel 2018), and the possible occurrence of a tradeoff between reducing predation risk and obtaining high-value energy resources.

To this end, we took advantage of a relatively long-term study (2017–present) investigating the ecological consequences of supplemental feeding on the ecology of roe deer (Ossi et al. 2020, Ranc et al. 2020, 2021) to conduct a camera trap-based assessment of the use of feeding sites by this ungulate before and after wolf return. Camera trapping is a non-invasive monitoring technique that allows undisturbed observation of wildlife (Rovero and Kays 2021). As a result, camera trapping is increasingly being used by ecologists to investigate a variety of ecological aspects, such as community diversity (Hedwig et al. 2018), population abundance (e.g. density estimation; Palencia et al. 2021), activity patterns (Iannino et al. 2025), and the study of intra- and interspecific relationships (Salvatori et al. 2022). In this specific case, we relied on camera traps to study the use of concentrated resources within the landscape. We collected roe deer observations at feeding sites before and after wolf recolonisation, both in winter and in spring. This allowed us to compare the behaviour of roe deer in relation to the potential predation pressure they were exposed to, while taking into account their use of feeding sites (Ossi et al. 2020). We first hypothesised that roe deer would have responded to the presence of wolves by changing their diel pattern, frequency, and intensity of visits to feeding sites. In particular, we expected that roe deer, which were previously recorded as more likely to visit feeding sites at dusk and dawn (Ossi et al. 2020), would have shifted to a more diurnal pattern of visits to reduce overlap with the activity pattern of wolves, which are typically nocturnal (Merrill and Mech 2003) (Prediction P1: from here below 'P1'). We also expected roe deer to reduce the number of visits to feeding sites (Prediction P2: from here below 'P2') and their duration (Prediction P3: from here below 'P3') after wolf recolonisation to minimise predation risk, especially in spring when natural food resources are more available (Ossi et al. 2020). We also investigated whether the presence of wolves affected the social behaviour of roe deer by comparing the tendency to visit feeding sites in groups or alone between the period before and after wolf recolonisation. In general, group size in roe deer, as in other ungulate species, is larger in open habitats than in forests because hiding opportunities are limited and therefore individual predation risk can be diluted by the formation of larger herds (Pays et al. 2007). In forested areas, group size is smaller, with animals tending to form small family groups in winter, but social aggregation is limited otherwise (Hewison et al. 1998). In our context, where the landscape is mostly forested, we expected roe deer to form small groups, with a decline following wolf recolonisation, to reduce the probability of detection, especially in spring when this small ungulate tends to be more solitary (Prediction P4: from here below 'P4').

Material and methods

Study area

The study area is located in the eastern Italian Alps, specifically in the southern part of the Cembra Valley (Autonomous Province of Trento, Italy). The area, which covers about 20 km^2, is hilly, with altitudes ranging from 600 to 1000 m a.s.l. The territory is mainly covered by deciduous and coniferous forests (80%), with interspersed meadows and a few swamps. The climate is continental (966 mm annual rainfall), with sporadic snow cover in winter and average temperatures ranging from 1.0°C in January to 21°C in July (source: Meteotrentino, www.meteotrentino.it). Ungulates include mainly roe deer and red deer *Cervus elaphus*, with occasional wild boar *Sus scrofa* and chamois *Rupicapra rupicapra*. Other terrestrial mammals include the European badger *Meles meles*, European hare *Lepus europaeus*, red squirrel *Sciurus vulgaris*, red fox *Vulpes vulpes*, beech marten *Martes foina*, and rodents (*Myodes glareolus*, *Apodemus* spp.). Since 2021, the grey wolf has recolonised the area, with the formation of a stable pair in 2022 and a pack in 2023 and 2024 whose territory covers the whole study area and beyond (Groff et al. 2024).

There are several feeding sites in the area (hereafter referred to as FS). The FS are supplied with maize by hunters throughout the year to comply with a hunting management plan registered in 2013 (Resolution of the Trento Provincial Government no. 2852/2013). This intensive supplementary feeding programme is aimed at roe deer, which are hunted in the autumn (officially from the first week of September to the end of December, but most of the hunting pressure occurs until November at the latest) from hunting stands near the FS. Several other non-target species have also been recorded near or at the FS, ranging from other ungulates to birds and small mammals (Supporting information).

Experimental design

We continuously monitored eight FS across the central part of the study area (Fig. 1) since the onset of the study, ensuring that food was always present in the FS through regular field visits. For the monitoring, we used three different camera trap models, namely Browning BTC-8A, StealthCam STC-G45NG, and IcuCam4. We set each camera trap to take one image, with a trigger interval of 30 seconds. We set the timestamp of the camera traps on solar time throughout the study. As our overall aim was to compare roe deer behaviour in the FS in relation to wolf recolonisation, we kept the data collected in 2017, 2018, and 2019 as the 'No wolf' period and in 2022, 2023, and 2024 as the 'Wolf' period (Supporting information). We excluded the data collected in 2020 and 2021 because the presence of wolves in this period was sporadic (Groff et al. 2024), and therefore, we could not clearly associate the data collected with the certainty of wolf presence or absence. In addition, the reduction in human activity in the area due to COVID19 pandemic restrictions may have altered deer behaviour during this time window, as has been observed elsewhere (Wilmers et al. 2021).

Within each retained year, we defined a spring and a winter window of analysis to control for any seasonal effect in the observed pattern. These windows were comprised between 20 March and 19 April (Spring) and between 8 December and 7 January of the following year (Winter) (Supporting information). We chose these windows because 1) they cover periods when hunting is either absent (Spring) or almost over (Winter), and 2) the baseline use of FS is not biased by the life history of roe deer (males: territorial behaviour, peaking in late spring and summer (Linnell and Andersen 1998); females: late gestation and birth events, May–June (Andersen and Linnell 1996)).

Data processing

We processed the camera trap images using TimeLapse software (https://timelapse.ucalgary.ca; Greenberg et al. 2019) to create the structure of the dataset we needed for the analyses. For each image, we automatically extracted the timestamp from TimeLapse. We then visually inspected each picture within Timelapse to annotate the species, sex, number of individuals, FS where the picture was taken, period ('No wolf'/'Wolf'), and season ('Spring'/'Winter'). We did not annotate age because the physical appearance of roe deer in the images does not allow for accurate age classification. We thus obtained a compiled dataset of 27 571 roe deer observations, which we processed to obtain independent events (i.e. roe deer visits to FS). To do this, we applied the method outlined by Vanderlocht et al. (2025), determining the interval between two independent events using a data-driven maximum likelihood approach (Luque and Guinet 2007), separately for each category season*period ('Spring No Wolf'; 'Spring Wolf'; 'Winter No Wolf'; 'Winter Wolf') (Supporting information). We thus obtained 3379 independent events, which we used to determine three metrics describing roe deer visits to FS. First, we counted the daily number of visits in each category season*period, grouped by FS. Then we calculated the duration of each visit by subtracting the timestamp of the first image of an event from the timestamp of the last image of that event. Finally, we obtained the number of individuals detected in a given visit as the sum of the maximum specific number of males and females that we counted in the set of images forming a given event.

Statistical analyses

We tested the effect of wolf presence on the diel pattern of visits to FS in spring and winter (P1) using circular statistics. For each season × period category, we extracted the hourly frequency of visits to FS and visualised the 24-hour

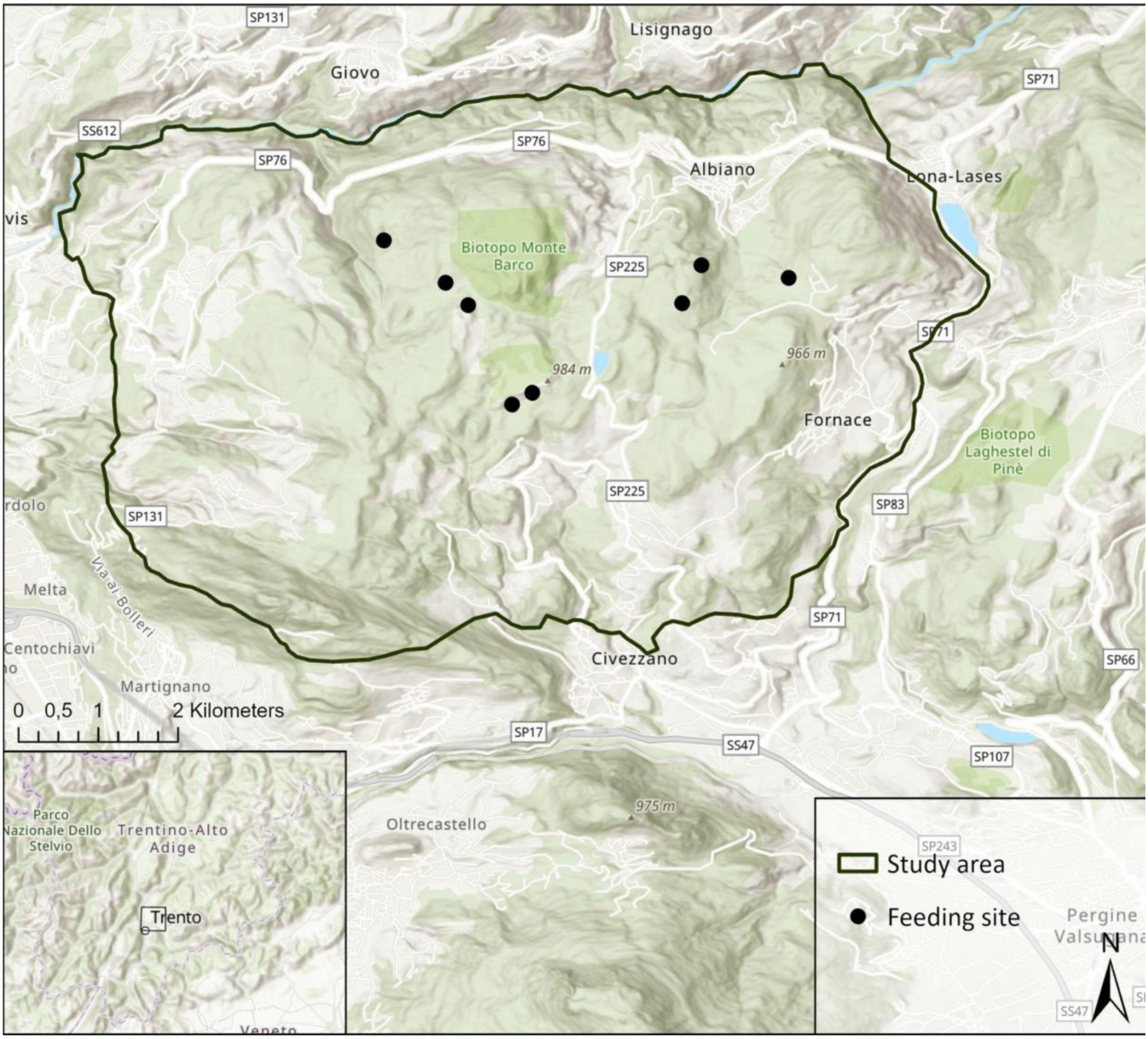

Figure 1. Map of the study area. The eight feeding sites (FS) monitored for this analysis are shown as black dots.

distribution by plotting rose diagrams. We then performed a nonparametric Hermans–Rasson test (Landler et al. 2019) to assess whether each of these four circular distributions deviated from uniformity. Finally, we applied a two-sample Watson test (Zar 1976) to pairwise compare the homogeneity of the circular distributions of visits to FS between 'No wolf' and 'Wolf' periods, for winter and spring separately.

We used generalised linear mixed models (GLMMs) to test the effect of wolf presence on the number of daily visits to FS (P2), their duration (P3) and group size (P4). Specifically, we fitted three GLMMs on 1) the daily number of visits to FS, 2) the duration of visits to FS, and 3) a reclassified dummy for group size ('solitary' versus 'group'; the reclassification was done to account for the unbalanced contingencies of group size in visits to FS; see the Supporting information), with a negative binomial distribution (nbinom2 family), a gamma distribution, and a binomial distribution, respectively. In each model, we included a four-level covariate ('Spring No Wolf'; 'Spring Wolf'; 'Winter No Wolf'; 'Winter Wolf') as an explanatory variable, combining the presence of wolves with the season. We did this because we wanted to test for a potential tradeoff between risk avoidance and food resource gain in the observed patterns. In the model that accounted for the duration of visits to FS, we also fitted the additive effect of group size (i.e. the maximum specific number of roe deer recorded in a given visit to FS), which could influence the time spent at an FS (Ossi et al. 2020). Finally, in each model, we fitted FS and year of observation as random effects to account for pseudoreplication between FS and inter-annual differences in environmental conditions that may influence roe deer visits to FS, respectively. For each model, we performed an AIC score model selection, keeping those with $\Delta AIC \leq 2$ from the best model, and selecting among them the one that allowed us to better test our predictions (Burnham and Anderson 2004; Supporting information). We estimated the proportion of variance explained by each model by calculating the coefficient of determination R^2 (Nakagawa et al. 2017).

Statistical analyses were performed using R ver. 4.4.3 (www.r-project.org). In particular, we relied on the packages 'chron' (James and Hornik 2024), 'circular' (Agostinelli and Lund 2024), and 'CircStats' (Lund and Agostinelli 2018) to fit circular statistics; 'glmmTMB' (Brooks et al. 2017) to run the generalised linear mixed models; and 'MuMIn' (Barton 2024) for model selection via the *dredge* function and for calculating R^2.

Results

Diel pattern of visits to FS by roe deer (P1)

Each distribution of visits to FS was found to deviate from uniformity (Hermans–Rasson test: $p < 0.001$ for each distribution). When comparing the distributions between 'No wolf' and 'Wolf' periods, we found a significant difference both in winter ($p < 0.001$) and, more marginally, in spring ($p < 0.05$). Specifically, in winter, roe deer maintained crepuscular peaks of visits to FS in the late afternoon (around 16:00–17:00 h) and early morning (around 06:00–07:00 h) but increased the frequency of visits during the daytime hours after the return of wolves, with a concomitant decrease in nighttime visits to FS (Fig. 2). In spring, crepuscular peaks (18:00–19:00; 05:00–06:00 h) were accentuated after wolf recolonisation, with a lower frequency of visits especially in the first part of the night, while daily visits remained low in both periods (Fig. 2). The patterns observed were not distorted by potential competition with red deer for access to these sites (Franchini et al. 2023; Supporting information).

Daily visits to FS by roe deer (P2)

The percentage of days with at least one visit to FS was lower in the 'Spring Wolf' category (56%, 227/403 total days) than in the other three categories ('Spring No Wolf': 85%, 185/217 total days; 'Winter No Wolf': 83%, 262/316 total days; 'Winter Wolf': 79%, 268/341 total days). Accordingly, the predicted daily number of visits to FS was significantly lower in 'Spring Wolf' ($\beta = -0.44 \pm 0.21$; $p < 0.05$) than in 'Spring No Wolf' (reference category), while there was no significant difference between the latter and any winter category (Fig. 3). The model explained 14.2% of the total variance (fixed components: 2.3%; random component: 11.9%).

Duration of visits to FS (P3)

The observed duration of visits to FS varied between the four season × period categories, being lower in 'Spring No Wolf' (728.05 ± 25.76 s) than in 'Spring Wolf' (952.38 ± 21.03 s) and in winter periods ('Winter No Wolf': 1072.08 ± 30.72 s; 'Winter Wolf': 1162.98 ± 30.17 s). Correspondingly, the predicted duration of visits to FS was significantly higher for all tested categories compared to 'Spring No Wolf' ('Winter Wolf': $\beta = 0.38 \pm 0.07$, $p < 0.001$; 'Spring Wolf': $\beta = 0.34 \pm 0.08$, $p < 0.001$; 'Winter No Wolf: 0.40 ± 0.07, $p < 0.001$; Fig. 4A). The duration of visits to FS was significantly higher when deer visited these sites in groups than when they visited alone ($\beta = 1.03 \pm 0.05$, $p < 0.001$; reference category: 'alone'; Fig. 4B). The fitted model accounted for 19.2% of the total variance (fixed component: 7.3%; random component: 11.9%).

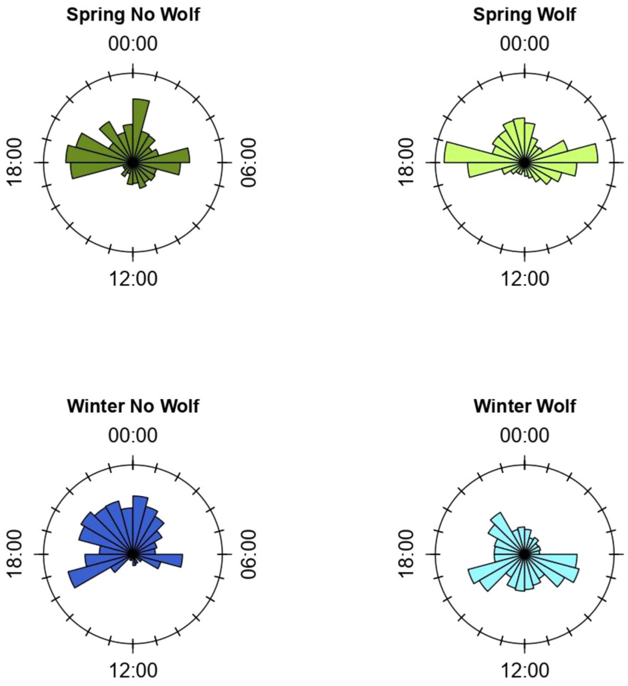

Figure 2. Rose diagram of the diel pattern of roe deer visits to feeding sites (FS) for each category period × season.

Grouping behaviour at FS (P4)

The probability of roe deer visiting FS in a group was significantly lower in 'Spring Wolf' than in 'Spring No Wolf' ($\beta = -0.65 \pm 0.17$; $p < 0.001$; reference category: 'Spring No Wolf'; Fig. 5), whereas it was higher in both winter categories ('Winter Wolf': $\beta = 0.35 \pm 0.11$; $p < 0.01$; 'Winter No Wolf': $\beta = 0.40 \pm 0.15$; $p < 0.01$; reference category: 'Spring No Wolf'; Fig. 5). The model explained 7.5% of the total variance (fixed component: 4.7%; random component: 2.9%).

Discussion

This work contributes to the large body of evidence on the non-consumptive effects of large carnivore occurrence on prey behaviour (Say-Sallaz et al. 2019, Gerber et al. 2024), by providing semi-experimental evidence of plastic response to the return of grey wolves. Overall, our results support that

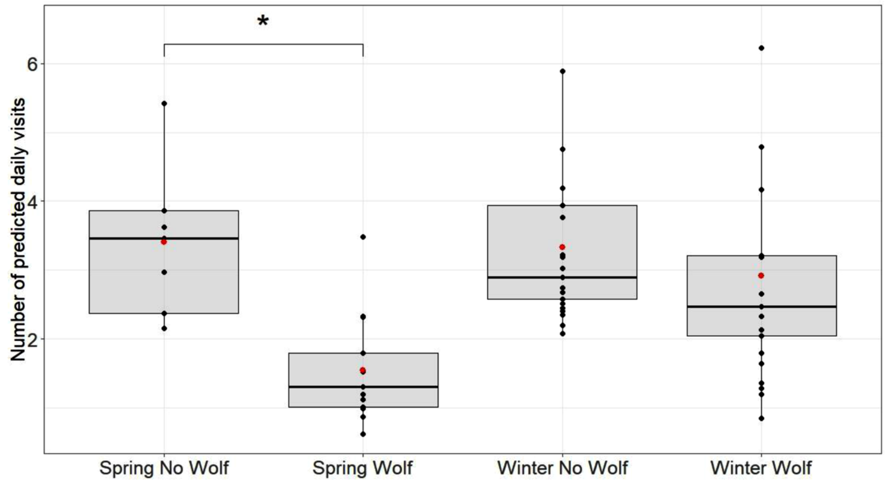

Figure 3. Predictive boxplot of the number of daily visits to feeding sites (FS) as a function of each category season × period. Red dots represent the predicted means. Stars indicate significant pairwise comparisons between levels of the fitted covariate (* $p < 0.05$; ** p 0.001 < 0.01; *** $p < 0.001$).

a tradeoff between predation risk reduction and food acquisition may be at work (Creel 2018), although we cannot exclude that other processes, such as demographic decline, may interact with proactive behavioural responses to shape the patterns found.

In partial agreement with our first prediction (P1), roe deer showed a temporal change in visits to FS in response to wolf recolonisation, but it differed in winter and spring. In both seasons, roe deer maintained the typical bimodal pattern of visits previously observed (Ossi et al. 2020), which

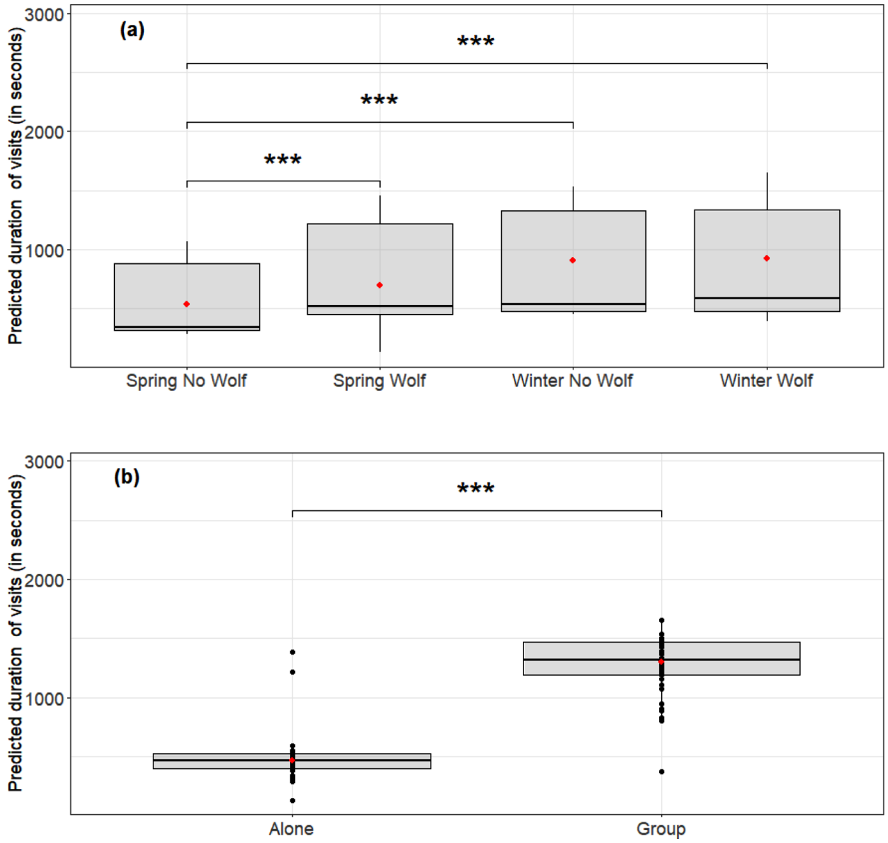

Figure 4. Predictive box plots of the duration of a visit to feeding sites (FS) as a function of (a) the four categories season × period and (b) the presence of conspecifics. Red dots represent the predicted means. Stars indicate significant pairwise comparisons between levels of the fitted covariates (* $p < 0.05$; ** p 0.001 < 0.01; *** $p < 0.001$).

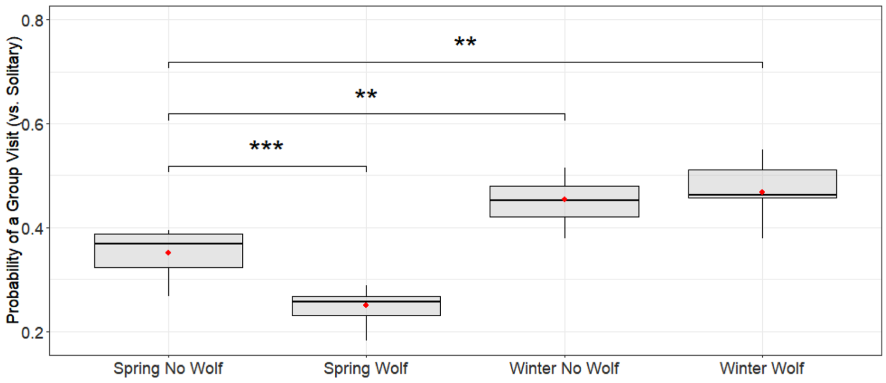

Figure 5. Predictive box plot describing the probability of a group visit of roe deer compared to a solitary visit of roe deer as a function of the four categories season × period. Red dots represent the predicted means. Stars indicate significant pairwise comparisons between levels of the fitted covariate (* $p < 0.05$; ** p $0.001 < 0.01$; *** $p < 0.001$).

is consistent with the known diel pattern of activity of this small ungulate (Pagon et al. 2013). However, while in winter roe deer clearly shifted their overall diel pattern of visits in response to wolves towards diurnality, this was not the case in spring, when we observed a tendency to squeeze the visits in crepuscular windows, while maintaining a certain degree of nocturnality. The winter diel pattern fits within the temporal niche partitioning framework, which establishes a reduction in activity overlap between prey and predator as an anti-predator tactic (Khan et al. 2025). When exposed to the presence of nocturnal predators, roe deer tend therefore to become more diurnal, a proactive response to predation risk that has also been observed in other taxa (European rabbit *Oryctolagus cuniculus*: Bakker et al. 2005; African large herbivores: Tambling et al. 2015). Instead, the pattern we observed in spring may be the result of the simultaneous effect of two pressures, a nocturnal one caused by wolf activity and a diurnal one caused by human activity. Although lethal human pressure (i.e. hunting) does not occur in spring, it is possible that other non-lethal human disturbances such as work (e.g. forest logging) and recreational activities (e.g. cycling, running), which increase in spring in the study area as elsewhere (Shephard and Aoyagi 2009), exert pressure on roe deer that limits their shift towards diurnality. Similarly, Bonnot et al. (2020) found that roe deer, when exposed to the double pressure of diurnal human disturbance and nocturnal lynx predation, reduced their diurnal activity and reallocated their activity budget to the night. Our results suggest that roe deer adopt an intermediate tactic of avoiding the time when human disturbance most likely occurs, while attempting to reduce temporal overlap with predators to minimise predation risk. Ultimately, we believe that our results denote a proactive plastic response by roe deer, confirming the high flexibility that this species exhibits to cope with multiple predator contexts (Sönnichsen et al. 2013, Lone et al. 2014).

A second facet of behavioural responses to wolves' return comes from the analysis of the actual use of FS. In other contexts, it has been observed that the presence of predators influences the spatial behaviour and therefore resources use of prey (roe deer: Bonnot et al. 2013; red deer Kuijper et al. 2014; white-tailed deer *Odocoileus virginianus* and mule deer *Odocoileus hemionus*: Dellinger et al. 2019). Our results demonstrate this non-consumptive effect of predators on prey behaviour with the use of controlled and resource-rich sites, in partial agreement with the second prediction (P2). The observed responses strongly support a tradeoff between reducing predation risk and food acquisition, which is consistent with the risk control hypothesis predicting that proactive responses to foreseeable risk may have food-mediated costs (Creel 2018). Indeed, the number of daily visits to FS decreased between winter and spring, but only after the recolonisation by wolves. This indicates that roe deer plastically reduce their usage of these sites when the risk perception is higher (i.e. after wolf recolonisation), but only in spring when the environmental conditions are more favourable, including natural food availability (Parker et al. 2009, Ossi et al. 2020). We expected this seasonal reduction to be detected even before wolf recolonisation, in line with what previously observed (Ossi et al. 2020), but our findings do not support a decrease of visits to FS from winter to spring when risk perception is low. We believe that the lack of consistency between our results and Ossi et al. (2020) lies in the fact that in the latter analysis the monitoring period was extended until the end of May, thus allowing a better comparison between the winter and spring situation in terms of natural resources. In this work, instead, the choice of the spring window fell on an earlier period (March–April), when the availability of alternative food is certainly higher than in wintertime but not yet as abundant as in late spring. Winter severity, which is known to affect roe deer use of FS (Ossi et al. 2017, 2020) does not influence the observed patterns because it has remained essentially unchanged over the years covered by the study (Supporting information).

In the overall context of these analyses, we expected that the duration of visits to FS, which measures a complementary aspect of resource use to the number of daily visits, would yield similar results. This was not the case (P3 not supported), with an opposite trend to that expected. While we observed a decrease in visit duration from winter to spring in the period prior to wolf recolonisation, in line with previous findings (Ossi et al. 2020), we did not observe a seasonal difference in this pattern in the period following wolf recolonisation. We speculate that this is related to the fact that roe deer have increased their vigilance following wolf recolonisation, which is indeed dependent on risk perception (Sirot and Pays 2011). In other contexts, roe deer have been found to increase their vigilance when exposed to the olfactory stimulus of a predator urine (Eccard et al. 2017). It is therefore plausible that when visiting FS, roe deer have to alternate between feeding and vigilance, thus increasing the total duration of visits. If this hypothesis were correct, the duration of visits should also be longer in winter after recolonisation by the wolf than in the winter before wolf return, because a longer baseline duration of visits in winter is added to the time spent on vigilance. However, this was not the case. We speculate that the observed tendency of roe deer to gather in winter and be more solitary in spring, especially after wolf recolonisation, may explain this. When visiting FS in groups in winter, roe deer may benefit from the vigilance of other conspecifics during feeding (Schmidt et al. 2008), whereas in spring, when they are mostly alone, they need to devote time to vigilance when perceiving the risk of predation. We acknowledge that these hypotheses are speculative. We suggest a camera trap-based analysis of roe deer behaviour at FS, e.g. through video recording and subsequent ethogram analysis (MacNulty et al. 2007, Ghaskadbi et al. 2016), to classify behaviour at FS also in relation to the size of the group of animals visiting them.

The observed tendency to visit FS more individually than in groups, especially after wolf recolonisation as expected (P4 confirmed), could support the hypothesis of reduced detectability risk (Hebblewhite and Pletscher 2002). Indeed, while in open areas roe deer tend to gather in larger groups to dilute individual predation risk (Gerard et al. 1995), in forested areas roe deer naturally tend to form smaller groups (Barja and Rosellini 2008). In such contexts, when exposed to predation risk, roe deer may move solitarily to reduce the risk of being detected by the predator. However, we cannot exclude the possibility that the tendency for solitary visits could be caused by a demographic decline in the population following the return of a large predator, as has been observed elsewhere (Schoener and Spiller 1996). Anecdotally, we report that in three years since wolf recolonisation (2022–2024), 42% (n = 9) of 21 roe deer tracked with GPS radio collars during this period in the project were predated by wolves (Ossi unpubl.), although none of the killing events of these individuals occurred in the immediate proximity of FS.

Understanding the extent to which behavioural and demographic processes interact in shaping the observed patterns is not trivial, yet fundamental to fully understanding the non-consumptive effects of wolf recolonisation on the ecology of their prey (Say-Sallaz et al. 2019). We propose several directions of work to address this issue, even beyond the context of this specific study. First, a demographic analysis of the roe deer population should be carried out, starting with an assessment of density by using a systematic random grid of camera-traps (Palencia et al. 2022) and repeating the survey at regular intervals (Macaulay et al. 2020). Second, it would certainly be interesting to assess whether the use of FS varies between the sexes and age classes, while controlling for winter severity and natural resources productivity. For example, this could be related to intra-specific competition, which seems to be limited in this species anyway (Ossi et al. 2020), or to different levels of vigilance between the sexes, which could be related to the presence of fawns, for example. This has not been covered in this paper due to the difficulty of identifying the sex and age class of individuals with certainty from the collected photos. We suggest that an ethological approach based on video analysis could facilitate the analysis of such aspects. Third, camera trapping should also be used to assess the actual distribution of the carnivore in a given study area through the use of ad hoc opportunistic grids (Sollmann et al. 2013). Fourth, it would be important to assess the body condition (e.g. by measuring kidney fat and bone marrow index) and stress level (Creel 2018) of prey, relying on their faecal samples (Biró et al. 2024). Last, a better understanding of the behavioural response of prey to recolonisation by a predator could come from the analysis of GPS and activity telemetry data (Bonnot et al. 2020) collected by radio collars deployed on both prey and predator. Investigating such aspects would have important implications, not only for improving our understanding of prey–predator relationships, but also for providing management guidance in a historical period of natural (Di Bernardi et al. 2025) or human-induced (Lee et al. 2021) large carnivore return to different parts of the world.

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Supporting information

The Supporting information associated with this article is available with the online version.

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