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Research Article

Variability in the movement and foraging behaviour of female Eurasian lynx during the denning season across Europe

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Animal movement and reproductive behaviour are crucial components of ecological and evolutionary processes. After parturition, the behaviour of reproducing females adapts to the needs of their offspring, including thermoregulation, protection and food provisioning. However, little is known about how these adaptations vary across environmental conditions at larger scales in species with large distribution ranges. Here, we explored how female Eurasian lynx *Lynx lynx* movement and predation patterns change during the denning season. We analysed GPS telemetry data from two different climatic regions in Europe, cold and temperate, and evaluated the effect of explanatory variables on movement metrics and kill-to-den distances using generalized additive mixed models. Female lynx moved significantly longer daily distances in the cold region (central and northern Scandinavia) compared to the temperate region (southern Scandinavia and continental Europe) both before and after parturition. Reproducing females in both regions considerably reduced their movement after the start of the denning season. The typical pattern of increasing daily movements and decreasing time spent at the den with time persisted across regions, and the presence of females at the den followed a similar circadian rhythm, regardless of the markedly different daylight period. Only in the cold region females increased the distances of their

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excursions from the den as time passed. The distances between den and kill sites spanned from 1 to 3 km over the latitudinal range. The kill-to-den distances did not increase with time, but in the cold region the larger prey killsites were farther from the den than in the temperate region. Overall, our results show how some behaviours of female lynx during the denning season remain constant over a large latitudinal range, while others vary. This suggests local adaptations to particular environments, and possible increased energetic demands of reproducing females in more extreme environmental conditions.

Keywords: Eurasian lynx, carnivore, Europe, feeding, GPS tracking, *Lynx lynx*, maternal behaviour, reproduction, spatial ecology

Introduction

Movement plays a crucial role in ecological and evolutionary processes (Nathan et al. 2008). Animals move to satisfy their biological needs, such as feeding, resting, predator avoidance and reproduction, all of which directly impact their fitness and survival (Liedvogel et al. 2013).

Reproduction represents an energetic cost that results in a tradeoff between maximising the number of offspring and ensuring their survival (Anderson and Gillooly 2021). While some mammals invest more energy in gestation and give birth to juveniles that are highly mobile, others have altricial non-mobile offspring and must invest more energy in the postnatal care (Royle et al. 2012). For the latter, the initial period after parturition, when offspring are immobile and highly dependent on their mothers' care, is particularly critical, as mortality can be relatively high. This is typically the case for carnivores (Derocher and Stirling 1996, Wolff and Peterson 1998, Mattisson et al. 2022), whose offspring are usually reared in dens, which provide microclimatic stability and protection against predators, during the first weeks after birth (Fernández and Palomares 2000, Szor et al. 2008, Ross et al. 2010). During this period (hereafter, denning season), the spatio-temporal movements of the reproductive female may change considerably (Maehr et al. 1989, Olson et al. 2011, Pomilia et al. 2015, Aronsson et al. 2016, Pålsson 2022), as she adapts her behaviour to the offspring's needs by regularly returning to the den to feed them. Consequently, her energetic expenses increase, which may require a higher hunting effort (Oftedal and Gittleman 1989, Laurenson 1994). Additionally, the need to protect young from predators and aid them with thermoregulation further limits the mother's movements. As such, the mother's behaviour during the denning season has a crucial impact on the survival of the offspring and, therefore, on population dynamics (Oftedal and Gittleman 1989, Engebretsen et al. 2024).

An important and potentially limiting factor in the efficiency of offspring care during the denning season is the availability of food resources in the surrounding landscape (White et al. 2015). When prey is scarce, females may need to travel longer distances and leave their offspring alone for longer, exposing them to a higher risk of starvation, predation or hypothermia. On the other hand, if prey is abundant, females might hunt closer to the den to reduce foraging expenditure, but not too close, as to avoid attracting scavengers or other predators near the den (Krofel et al. 2013). However,

intensively hunting in a smaller area around the den could lead to either prey depletion or increased antipredator behaviours from prey. Consequently, longer periods of time spent at the same den, may result in females hunting farther away from the den (Krofel et al. 2013, Signer 2017). Accordingly, the distance of foraging trips away from the den may be correlated with the level of reproductive success.

The Eurasian lynx *Lynx lynx* (hereafter, lynx) is the most widespread felid in the Palearctic region. It has adapted to various environmental conditions, within a broad climatic gradient, and different levels of prey availability and human disturbance. Therefore, it is an ideal species for studying behavioural adaptations across large environmental gradients. The denning season is particularly important as the female lynx adopt movement patterns that are similar to central place foraging (by returning to the den to feed and protect the kittens; Bell 1990), which imposes constraints on their behaviours. Lynx are seasonal breeders, and their kittens are initially immobile and highly dependent on their mother's care (Chagaeva and Naidenko 2012). Mortality in lynx kittens is relatively high, with only around 50% surviving at the onset of winter (Breitenmoser et al. 1993, Mattisson et al. 2022).

In Europe, several local studies have focused on movement patterns of female lynx during the denning season (Schmidt 1998, Jędrzejewski et al. 2002, Krofel et al. 2013, Van Dalum 2013, Signer 2017). While these studies have significantly increased our understanding of female lynx maternal behaviour, they are limited in their sample sizes and do not account for possible effects of environmental variability at different latitudes. Thus, it remains unclear whether there is variability in denning behaviour across geographical regions which differ in climate and prey availability. Indeed, while the maternal behaviour has been studied in several species of large carnivores with wide distribution ranges (Alfredén 2006, Roffler and Gregovitch 2018, Wiesel et al. 2019, Pålsson 2022, Aronsson et al. 2023,), the spatial aspect of denning behaviour is understudied in solitary felid species, which differ from social carnivores in that, first, they do not transport food back to the den (only in the form of milk) and, second, the female is the only one in charge of raising the offspring. Furthermore, there is still no information regarding the distance of kill sites in relation to the den throughout the denning season (Krofel et al. 2013). The lack of such knowledge narrows our understanding of maternal behaviour during such a constraining and crucial period across the species

range, ultimately limiting the implementation of conservation measures.

The present study aims to fill this knowledge gap and improve our understanding of movement, den use, and predation patterns of female lynx during the denning season across a large latitudinal gradient in Europe, from the Arctic to the Dinaric mountains (Fig. 1). First, we described how their daily movements change across the pre-denning and the denning season, and across the denning season. We hypothesised that females at higher latitudes move longer distances per day, and away from the den, when compared to temperate regions, as prey is more scattered and lynx home ranges are generally larger (H1; Schmidt 2008, Linnell et al. 2021). Next, we hypothesised that females generally spend on average more time at the den during the central hours of the day and mostly leave the den at nighttime following the general activity pattern of this species (H2; Heurich et al. 2014). We also expected the duration of use of each consecutive den to become shorter as time passes, due to increased mobility of the growing kittens, and therefore a higher risk of being detected by predators, or faster accumulation of parasites and waste (H3; Boutros et al. 2007). We hypothesised that the duration of den use is shorter in larger denning home ranges

(H4), as a higher number of shifts in the centres of activity may result in an overall larger area used. Secondly, we investigated foraging behaviour of female lynx while denning, by examining the distances between kill sites and dens across the denning season, comparing two regions at different latitudes. We predicted that, in both regions, the kill sites of larger prey would be located further away from the den compared to smaller prey, as large prey could potentially increase the risk of attracting scavengers near the kittens (H5). We expected the kill-to-den distances to increase with time from parturition, and the increase would be more pronounced at higher latitudes, where prey availability is less predictable in space and may require increased movement rates (H6).

Material and methods

Data description

GPS data

We analysed GPS telemetry data from five study areas across Europe (North Scandinavia, South Scandinavia, Baltic, Alpine and Dinaric; Fig. 1) divided into two regions (Cold

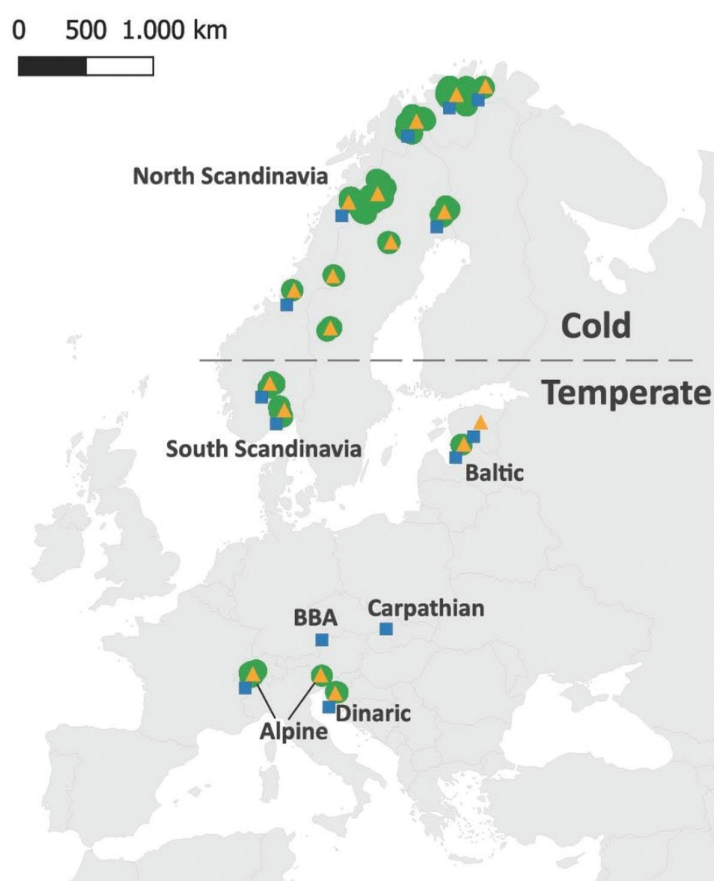


Figure 1. Distribution of the standardized GPS data (green circles), of den sites (orange triangles) used for the analysis of movement patterns and den use of female lynx, and of field-checked kill sites and corresponding dens (blue squares) used to analyse kill site distribution in relation to the den. BBA stands for Bohemian–Bavarian–Austrian.

and Temperate), which differ in daylight period, main prey species for lynx, and climate type. The raw data had a high variability in GPS fix schedules (from 1 to 24 fixes / 24 h cycle). Since the GPS-fix rate strongly determines the scale of the analysis, especially when focusing on movement parameters (Latham et al. 2015), we did not include all GPS data available when calculating movement metrics. To date, there is no specific protocol available indicating what would be the best data resolution to estimate meaningful movement metrics from GPS data (Latham et al. 2015). Since previous studies have used time intervals from one to four hours (Signer 2017), and to avoid discarding too much data from the analyses, we selected periods of GPS data with a resolution between 6 to 24 fixes per 24 h cycle (hereafter, full dataset). Because the GPS-fix schedule variability was still high, which can significantly influence movement metrics, we created a second dataset. This dataset was subsampled from the full dataset so that all data periods would have a resolution of 6 fixes per day, distributed regularly along a 24 h cycle (hereafter, standardized dataset). We used the standardized dataset to test all our hypotheses related to female movement. However, we also compared the results obtained with the two datasets, full and standardised, to understand how using different GPS-fix intervals could affect our results and their interpretations. Furthermore, since the full dataset had a high variability in GPS-fix schedules, we repeated the comparison by selecting only the data with a GPS resolution of 12 fixes / 24 h cycle, and compared it with the corresponding data from the same individuals in the standardized dataset (6 fixes / 24 h cycle). The information regarding lynx captures and permit numbers are provided in Supporting information.

Den site detection

In general, GPS fixes that suggested the presence of a den (i.e. female returning to the same location for at least 5 days, and increased proportion of missing GPS fixes, which indicate her presence at the den; Krofel et al. 2013, Walton and Mattisson 2021) were visited by researchers, who then confirmed the den's location. Each litter was only visited once, generally when kittens were on average three weeks old (Krofel et al. 2013). When field-checked data was not available, the location of the dens was derived from GPS data by analyzing GPS clusters lasting at least five days and looking for a star shaped movement, as described in the Supporting information. The den where the offspring is born will be hereafter referred to as 'natal den'. All other dens to where the kittens were later translocated are referred to as 'secondary dens'.

Kill sites data

GPS location clusters (GLCs) potentially reflecting kill sites during the denning season were identified following standard procedures (Mattisson et al. 2011, Krofel et al. 2013, Vogt et al. 2018) and only those that were confirmed in the field (i.e. prey remains found) were included in the analysis of kill-to-den distances, to be able to include prey size (Supporting information). We considered additional dens compared to those used for the analysis of movement metrics:

we included all dens determined from GPS data with any GPS-fix resolution (i.e. including data less than 6 fixes per day), as they were still sufficient to determine den site locations. Therefore, besides including dens and field-checked kill sites available in the same study areas considered for the movement analyses, we also considered additional data from two additional populations: Carpathian and Bohemian-Bavarian-Austrian (BBA; Fig. 1).

Data analyses

Response variables

We evaluated the following response variables to test our hypotheses (Supporting information): daily distances (i.e. total distances moved per day) and distances from the den (meters, continuous; H1), absence/presence at the den (binary; H2), duration of den use (number of days, continuous; H3, H4) and kill-to-den distances (meters, continuous; H5 and H6).

We obtained daily distances as the sum of Euclidean distances between consecutive GPS fixes (step lengths) within a day. Daily distances were compared between breeding and non-breeding females across the pre-denning period and the denning period. We also looked at how the GPS-fix success rate (i.e. % of successful GPS-fixes) per day changed across the same period, comparing females with and without kittens, as females often show a reduction in fix success rate when they give birth due to lower satellite coverage inside the den, where they spend a large amount of time (Krofel et al. 2007). All other response variables were estimated only for breeding individuals and within the denning period.

We classified female absence/presence at the den as a binary variable, with '1' indicating GPS fixes where the female was > 100 m away from the den, and '0' where the female was within 100 m of the den. For all fixes where the female was absent from the den, we also looked at the Euclidean distances from the den (meters, continuous).

The duration of den use was determined as the number of days between the first and the last fix within a cluster identified as a den site. Those included dens where we were able to determine the date of start and end of use from GPS data with any fix resolution (i.e. including data with less than 6 fixes per day). We considered only non-field checked dens for duration analyses, since a visit from researchers may cause females to move the kittens sooner than they would otherwise (Van Dalum 2013). The kill-to-den distances were determined as the Euclidean distances from each kill site to the den that was being used at the time the kill started.

Explanatory variables

We created the temporal variable 'time' indicating the day within the pre-denning and/or the denning seasons (continuous, H1–H3). We considered the denning season to last for 60 days, after which kittens usually start following their mother (Krofel et al. 2013), and the pre-denning season to be 30 days before parturition, as we assumed that females' movements would not be significantly altered during the first part of the pregnancy. The date of parturition was set as day

'0' for reproducing females. For non-reproducing females, we considered the average date of parturition in the given area (Supporting information). We included the variable 'reproduction status' (binary), indicating whether a given female had kittens, to investigate potential differences in the distances moved per day. The cases that we classified as the female not having kittens are those where we did not detect a parturition event. It is possible that in cases where the female gave birth and kittens died soon after, the parturition event was not detected. The 'hour' of the day was extracted from the timestamp of each fix (H2). The 'den type' variable (binary), indicating whether the den was natal or a secondary, was included in the den duration analysis (H3). For the kill-site analysis, we classified prey into larger prey (ungulates > 7 kg) and smaller prey (ungulate neonates and other small prey < 7 kg; Oliveira et al. 2023) (H5, H6). To analyse how the kill-to-den distances vary after a den is established, we calculated the 'time since the establishment of a den' as the time difference, in days, between the date of the first fix at the start of den use and the date of the first fix at the kill site (H6).

The denning home range (km^2 , continuous) was defined as the 95% isopleth of the autocorrelated kernel density estimation (aKDE; Fleming et al. 2015) with all fixes included within the two months of the denning season (H4). We compared it with the pre-denning home range, calculated with the same method using all GPS fixes included within the 30 days of the pre-denning season, and the total home range, calculated using all GPS data available for each individual in one specific year.

We divided the data into two geographical regions, temperate and cold. We included the populations from central Europe, the Baltic and South Scandinavia, in the 'temperate region'. The population from North Scandinavia, above 62° of latitude, was included in the 'cold region'. We based this division on the different climates (European Environmental Agency, <https://www.eea.europa.eu/>), and on the differences of specific ecological conditions between them. Specifically, the two regions also differ in average summer temperatures (12–15°C in the cold region and 15–20°C in the temperate region; <https://climate-adapt.eea.europa.eu/en/metadata/indicators/mean-temperature>) and in daylight period during the summer (20–24 h long days in the cold region and 16–20 h long days in the temperate region; US Navy Astronomical Applications Department https://aa.usno.navy.mil/data/Dur_OneYear). From an ecological perspective, lynx have markedly different home range sizes in those two regions (i.e. larger in the cold region; Herfindal et al. 2005), as well as different main prey type (i.e. mostly roe deer in the temperate region and semi-domestic reindeer and smaller prey in the cold region; Krofel et al. 2011, Mattisson et al. 2011, Heurich et al. 2016). Since environmental variables such as daylight duration, temperature and prey type do not vary much within each single region, we did not include them as separate variables, to maintain model simplicity.

Modelling approach

We built generalized additive mixed models (GAMM; Wood 2017) to test our hypotheses. Before running the models, we

tested for collinearity between variables using a variance inflation factor (VIF). We excluded covariates from models if the factor value was > 3 (Zuur et al. 2010). When considering the absence/presence at the den as a response variable, we used the binomial distribution family with a logit link. For all other response variables, we fitted the models with a gamma error distribution family with a log link. The model structure for each response variable and a given set of explanatory variables can be found in the Supporting information. We included individual ID as a random intercept in all models, to account for repeated observations of the same individual and the unbalanced data between individuals (Bolker 2008). Additionally, we included the proportion of unsuccessful fixes in a day as a random intercept in the models with daily distances as response variable, as missing locations can influence the calculation of step lengths. We included four explanatory variables as fixed factors to test the different hypotheses: the reproduction status (H1), den type (H3), prey size (H6) and region (cold or temperate). Region was included in all hypotheses, both as a fixed factor and as an interaction with the variables of interest (Supporting information).

The following explanatory variables were added to the models as smooth factors: time (number of days to or from parturition), hour (hour of the day), and time since the establishment of a given den (only in the analysis of kill-to-den distances). The hour of the day was added as a cyclic cubic regression spline smooth ('cc'), reflecting the cyclic nature of this variable. Additionally, for the analysis of duration of den use, we included the denning home range size as a smooth factor (Supporting information).

We retained the covariates that significantly improved the Akaike's information criteria (AIC) when compared to the null model. Specifically, we compared AIC values and calculated each model's difference (Δ) in AIC (lower values indicate a better fit) to evaluate the value of adding these variables. We considered the coefficients from the model(s) with the better fit ($\Delta\text{AIC} \leq 2$; Burnham and Anderson 2004) to evaluate which was the best model to test the hypotheses. Whenever two models had a $\Delta\text{AIC} \leq 2$, we selected the simplest model. Since we proposed two different hypotheses regarding the duration of use of the den, we chose two different best models for this response variable.

All data processing and statistical analyses were conducted using R ver. 4.2.1 (www.r-project.org). We used the 'mgcv' ver. 1.8-42 (Wood 2011) package to build GAMMs, and the 'DHARMa' ver. 0.4.6 (Hartig 2022) and 'gratia' ver. 0.8.1 (Simpson 2024) R packages (www.r-project.org) for model diagnosis. We used the package 'marginaleffects' ver. 0.13.0 (Arel-Bundock et al. 2022) to plot the output of our models as conditional predictions.

Results

Female movement

The standardised dataset used for the analysis of movement patterns included data from 58 GPS-collared female lynx (39 from the 'cold' region and 19 from the 'temperate'

region; Fig. 1) during overall 26 seasons where the female did not reproduce and 59 reproduction events (Supporting information), with 113 dens. The average number of days of GPS data per animal was 54.4 (SE=3.19) over the 90 days taken into consideration (i.e. 30 days pre-denning and 60 days denning season). Animals with and without kittens were tracked for an average of 59.4 days (SE=3.70) and 42.7 days (SE=5.91), respectively. When looking at the duration of den use, we included data from 75 dens in 51 denning seasons from 38 different females (Supporting information).

In both regions the denning home ranges were significantly smaller than the pre-denning home ranges and the total home ranges (Supporting information). In the temperate region the average denning home range was around 4% of the average total home range, which was similar to the average pre-denning home range. In the cold region the average denning home range was around 10% of the average total home range and around 13% of the average pre-denning home range.

The average temperate region denning home range was significantly smaller (16%) than the average denning home range in the cold region (Supporting information). We found a similar pattern for the pre-denning home range and total home ranges (Supporting information).

The model that best explained the variations in daily distances included time, reproductive status and region (Supporting information). Specifically, the daily distances moved by females with kittens showed a significant decrease after parturition (Fig. 2), and then a gradual increase during the denning season. This pattern was observed in both regions, but the daily distances of females both with and

without kittens were overall longer in females in the cold region than in the temperate region (Fig. 2). When the kittens were around 30 days old, daily distances became longer than in the pre-denning period. The daily distances then decreased again at around 40 days after parturition. Daily movements of non-reproducing females did not vary significantly over time (Fig. 2). The overall GPS-fix success rate did not vary significantly between females with and without kittens, but it was possible to observe a localised drop in the GPS-fix success of females with kittens around the date of parturition, in both regions (Supporting information).

The absence of females from the den varied significantly across time (Supporting information). We observed that females were more often present at the den at the beginning of the denning season and, as kittens grew older, females increased their absence from the den (Fig. 3). In the cold region, the distances from the den increased as time passed, a pattern which was not observed in the temperate region (Fig. 4). Furthermore, we observed that females were often present at the den between early morning and early afternoon and absent from the den at night (Fig. 3). There were no significant differences between regions despite markedly different daytime periods (Fig. 3, Supporting information), but females in the temperate region tended to leave the den earlier in the day (Fig. 3).

We compared results related to all movement metrics (daily distances, distances from the den and absence from the den) obtained with the full and the standardized dataset (Supporting information). The general trends were all similar. The daily distances were longer when derived from the full dataset. We observed larger confidence intervals in the

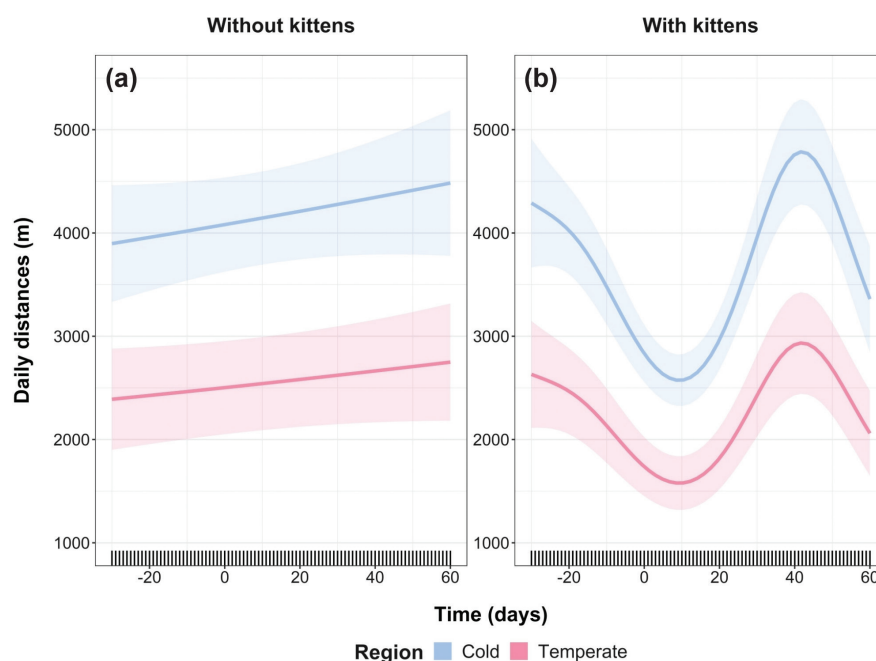


Figure 2. Effect of the time (x-axis) to and from the date of parturition (value of 0) during pre-denning season (negative values) and the denning season (positive values) on the predicted daily distances moved (y-axis) by females without kittens (a) and with kittens (b), in the cold and temperate regions.

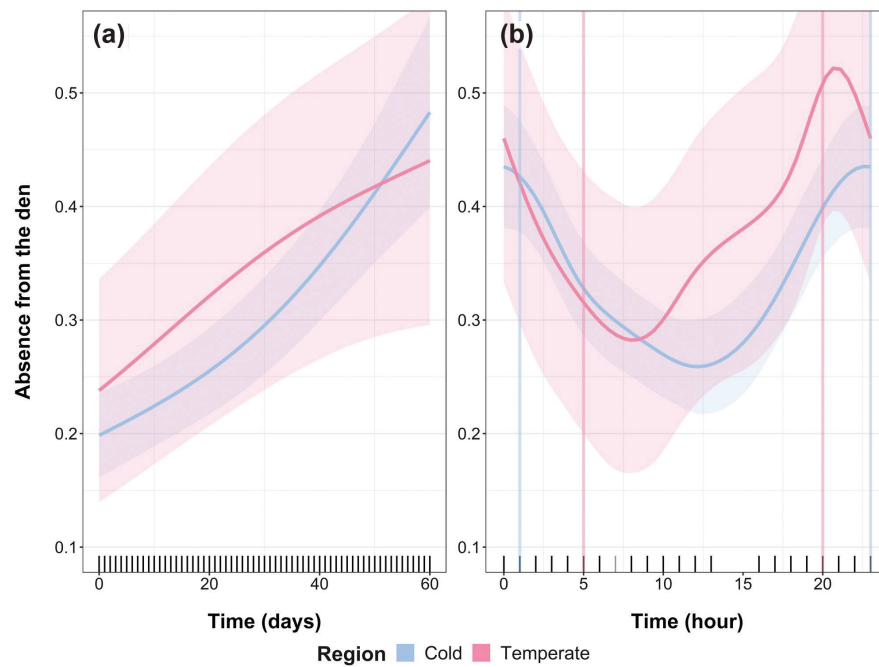


Figure 3. (a) Effect of time elapsed since parturition (days, x-axis) on the proportion of time females are absent from the den, as predicted by the model (y-axis). The 'time' value of 0 indicates the date of parturition. (b) Effect of the time of the day (hour) on the predicted absence from the den over the whole denning period. Values on the y-axis indicate the probability of the mother being absent from the den. The vertical lines indicate the average nautical sunrise and sunset times in the two regions, between the months of May and July (roughly when the lynx denning season happens), as derived from <https://aa.usno.navy.mil>. Sunrise and sunset are conventionally defined as the times when the upper edge of the disk of the sun is on the horizon where there are no visual obstructions and the observer's eye is considered to be on the surface of the Earth, so that the horizon is geometrically 90° from the observer's zenith (https://aa.usno.navy.mil/faq/RST_defs#rise).

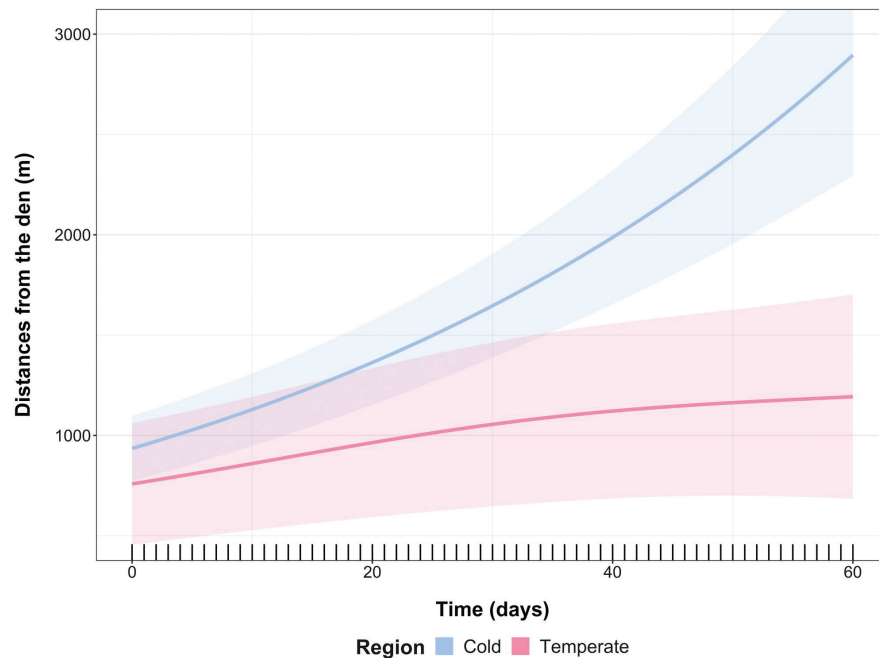


Figure 4. Effect of time elapsed since parturition (days, x-axis) on the distances of the female from the den during excursions (y-axis). The 'time' value of 0 indicates the date of parturition.

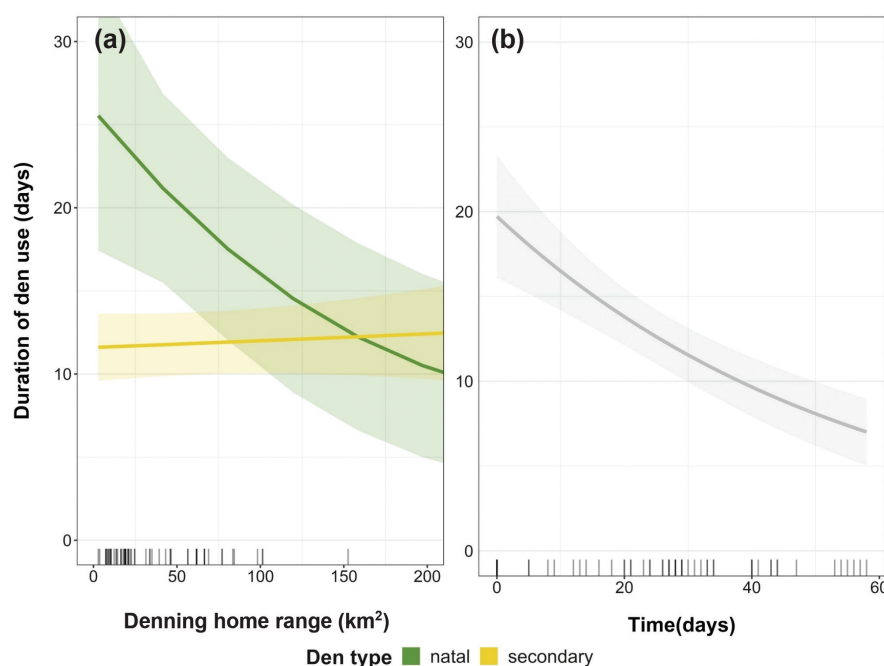


Figure 5. (a) Effect of the denning home-range size on the predicted duration of use of each den. The plot is cut to the 95th percentile of the denning home ranges because there were three extreme outliers that considerably stretched the plot. (b) Effect of time (corresponding to the age, in days, of the kittens when the den starts being used) on the predicted duration of use of the den (i.e. $x=0$ for natal dens, $x > 0$ for secondary dens (min value 5 days)).

distances from the den obtained with the full dataset (i.e. all data) compared to those obtained with standardized dataset (i.e. 6 fixes / 24 h) or with the subsampled datasets (i.e. only 12 fixes / 24 h).

The duration of den use decreased as kittens grew older (Fig. 5, Supporting information), being therefore longest for natal dens. The duration of use of natal dens was shorter when the denning home ranges were larger, while the denning home range size did not affect the duration of use of secondary dens (Fig. 5, Supporting information). We did not find support for differences in the duration of den use between regions (Supporting information). The DHARMA plots for the best model for each hypothesis are provided in the Supporting information.

Distribution of kill sites around the den

For the analysis of kill-to-den distances, we considered a total of 55 dens with at least one associated kill site checked in the field ($n=145$ kills), from 25 females (Supporting information).

The median of all minimum kill-to-den distances was 0.98 km (interquartile range; IQR 1.46 km), while the median of maximum distances was approximately 3.11 km (IQR 4.78 km).

The model that best explained the kill-to-den distance included only region and prey type (Supporting information). Overall kill-to-den distances were not influenced by region. However, females in the cold region killed larger prey further away from the den than in the temperate region and only in the cold region were adult ungulate kill sites located

further from the den than smaller prey (Fig. 6). We found a significant effect of the time passed since the start of den use (Fig. 6, Supporting information). Until around 15 days after the start of den use, the kill-to-den distances increased gradually, and after that time the distances decreased (Fig. 6).

Discussion

Our study provided new insights into the behaviour of female Eurasian lynx during the denning season, showing how some behaviours remain constant at different latitudes while others differ between regions. We found that, at higher latitudes, female lynx moved longer distances per day and away from the den during the denning season compared to lower latitudes (H1) and that, even at higher latitudes, with longer daylight hours, females were present at the den mostly during the central hours of the day (H2). Furthermore, we found that natal dens were used for longer periods than secondary dens (H3), and natal dens in larger denning home ranges (the largest ones were in the cold region) were used for a shorter amount of time compared to natal dens in smaller denning home ranges (H4). We also found that, at higher latitudes, larger prey kill-sites were located farther away from dens compared to smaller prey, whereas they were at similar distances at lower latitudes (H5). We did not find enough evidence to support that the kill-to-den distances increase in time since the establishment of the den (H6). Our results show the importance of incorporating large datasets across multiple environmental conditions to identify potential

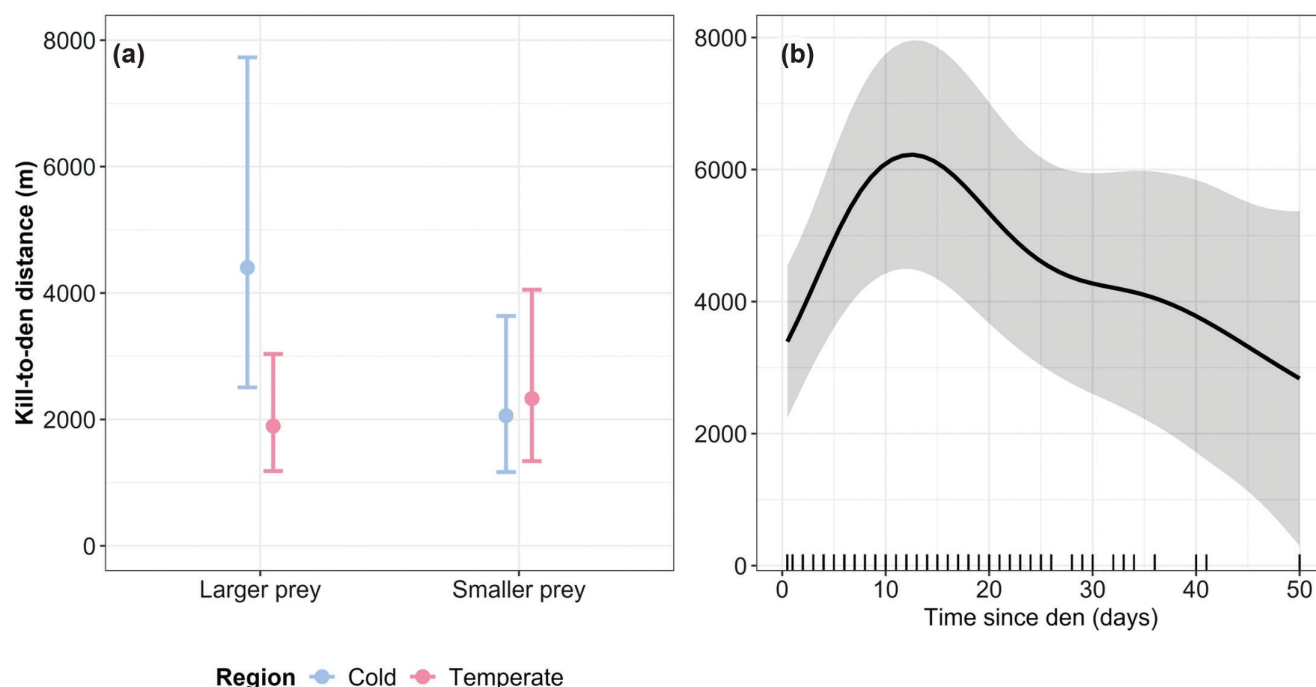


Figure 6. Variation of predicted kill-to-den distances, in meters, in relation to (a) prey type and the region, and (b) with time passed since the start of use of the den. Larger prey include ungulates > 7 kg, while smaller prey includes ungulates and other prey with less than 7 kg.

behavioural differences, local adaptations and constraints imposed in regions with more extreme conditions.

Variation of movement patterns across the latitudinal gradient

The distances moved per day were significantly longer in the cold region compared to the temperate region and the same pattern was observed in both breeding and non-breeding female lynx (consistent with hypothesis H1). This is likely connected to the less predictable distribution of prey in the cold region, requiring lynx to move more to find enough food and sustain their energetic demands (Schmidt 2008, Mattisson et al. 2014, Linnell et al. 2021). This is reflected in overall larger total home ranges (Linnell et al. 2001) and denning home range sizes, as observed in our study. In both regions, the daily distances of non-breeding females were constant over time, while breeding females suddenly became considerably restricted in their movements at the beginning of the denning period when kittens were born. These findings support the hypothesis that females initially need to spend a higher amount of time at the den for nursing and to aid kittens in thermoregulation, regardless of the different environmental factors at different latitudes (Boutros et al. 2007, Ross et al. 2010). A similar pattern was observed locally for lynx in Switzerland (Signer 2017) and Poland (Schmidt 1998, Jędrzejewski et al. 2002). In line with these findings, we observed a clear drop in the GPS fix success rate of breeding females at the beginning of the denning season, indicating that the female suddenly spends a larger amount of time at the den after parturition, as the satellite reception at the location of the den is lower (Krofel et al. 2007, 2013,

Mattisson et al. 2010, Van Dalum 2013). The restriction in movements of breeding female lynx was also reflected by the sizes of the denning home ranges, which were significantly smaller compared to the pre-denning home ranges in both regions. Reduced female home range size after parturition has been reported for lynx in Scandinavia (Aronsson et al. 2016), in Poland (Schmidt 1998) and in the Carpathians (Kubala et al. 2024), as well as in several other carnivores (*Chrysocyon brachyurus*, Bandeira de Melo et al. 2007, *Felis concolor coryi*, Maehr et al. 1989, *Lynx canadensis*, Martinez 2023, *Panthera uncia*, Pålsson 2022, *Canis lupus*, Roffler and Gregovich 2018, *Caracal caracal*, Serieys et al. 2024, *Gulo gulo*, Trydal 2022).

As hypothesised, females were gradually more absent from the den as kittens grew older and could be left alone for longer. With a portion of the same dataset that we used for this study, Van Dalum (2013) observed that female lynx in Norway increased the duration of excursions away from the den as kittens grew older. A similar pattern was also observed in Switzerland (Signer 2017), and is in line with the findings of this study. Larger kittens not only need less protection and thermoregulation but they also have greater energetic requirements, demanding increased foraging efforts from the mother, who needs more energy to feed them through nursing (Jobin et al. 2000, Krofel et al. 2014, Belotti et al. 2015). Indeed, coinciding with their increasing absence from the den, the daily distances travelled by breeding females steadily increased during the first weeks after parturition and this pattern was consistent across the two contrasting regions. Similar results were also observed locally in Switzerland (Signer 2017) as well as in other carnivores such as Canada lynx (Moen et al.

2008, Olson et al. 2011), snow leopards (Pålsson 2022), wolverines (Trydal 2022, Aronsson et al. 2023), brown hyena (Wiesel et al. 2019), and wolves (Alfredeén 2006). Starting from around 30 days after parturition, the daily distances became even longer than during the pre-denning period, despite the denning home range being smaller than the pre-denning home range. Jędrzejewski et al. (2002) found that female lynx increased movement by 43% during denning, while remaining restricted to the denning home range, which indicates more intensive but concentrated movements. Similarly, Signer (2017) and Heurich et al. (2014), showed increasing movements of female lynx during the period of intensive care of kittens.

While there was no significant difference in the absence from the den between regions, which may be due to the kittens needing the presence of their mother for similar amounts of time irrespective of the climate, the distances from the den increased much more steeply in the cold region than in the temperate region. Such a pattern shows that females in Scandinavia, where prey is less evenly distributed, while still being limited by the need to return to the den often, must travel longer distances during their excursions, possibly to find enough prey. We observed that the daily distances decrease between 40 and 50 days after parturition, presumably around the time when the kittens start leaving the den and following their mother (Krofel et al. 2013, Van Dalum 2013). When the kittens start following the female, her movements are slowed down since the kittens are still very young to walk long distances. As the denning season progresses dens are used for shorter periods, which may be connected to kittens becoming more mobile (Ewer 1985) or to the faster accumulation of ectoparasites in the den (Kitchener 1991, consistent with hypothesis H3). Towards the end of the denning season there are no longer stable dens, but only temporary lairs. The frequency of den shifts has similarly been observed to increase as time progresses in wolverines as well (Aronsson et al. 2023).

As we hypothesised, the duration of use of natal dens decreased with increasing denning home ranges (consistent with hypothesis H4). Naturally, if the female changes the den location more often, the overall area used during the denning season might become larger, as the centre of activity shifts between places. There may be several reasons for den shifts, such as flooding, need for more space, disturbance, or the accumulation of ectoparasites (Boutros et al. 2007). Another explanation could be prey depletion around the den, as time passes (Boutros et al. 2007, Krofel et al. 2013). Females may be then forced to move sooner if prey availability around the den is lower, which is often correlated with larger home ranges (Herfindal et al. 2005, Schmidt 2008). However, in case of the prey depletion hypothesis (H6), we would have expected an increase of distances between dens and ungulate kills as time passed, which we did not observe.

We observed that females attend the den mainly during the day and are mostly absent from the den between late afternoon and early morning (consistent with hypothesis H2), which is in accordance with previous local studies in the Dinaric

Mountains and Scandinavia (Krofel et al. 2013, Van Dalum 2013). Lynx usually rest during the daytime (Hočevár et al. 2021), while twilight and nighttime is when they mostly hunt or feed, as their activity is synchronised with that of their main prey (Podolski et al. 2013, Heurich et al. 2014). We did not detect any statistical difference between regions in the temporal pattern of female's absence from the den during the 24 h cycle, despite the considerable differences in the day length across the latitudinal gradient. This indicates that the bimodal activity of reproducing female lynx is not influenced by the different daylight duration or by the different prey type. We observed that in the cold region females spend more time at the den later in the day, which may be connected to longer days at higher latitudes, however this difference was not significant as the variability in the temperate region is relatively high (larger confidence interval). Our results are in contrast with what was observed in female Canada lynx, which spend similar proportions of time active during dusk, day and dawn, while denning (Olson et al. 2011). This may be connected to the fact that, unlike the Eurasian lynx, Canada lynx is a predator specialized on smaller prey species compared to the Eurasian lynx. Usually they mainly prey on the snowshoe hare *Lepus americanus*, which are crepuscular (Foresman and Pearson 1999) but while denning they may adjust their prey type and depend more on the Columbian ground squirrels *Spermophilus columbianus* (Olson et al. 2011), which are diurnal (Elliott and Flinders 1991).

Distances of the kill sites from the dens

The kill site that was the closest to each den was located at a median of approximately one kilometre. This may suggest that females avoid hunting prey in the immediate proximity of the den, which could be a strategy to avoid attracting scavengers that could put the kittens at risk (Krofel et al. 2013). The median maximum distance between den and kill site was around three km. This suggests that females most likely aim at minimising their energetic expenses when going back and forth between den and kill sites. While smaller prey were located at a similar distance from the den in both cold and temperate region, in the cold region larger prey kill sites were generally farther from the den compared to smaller prey kill sites (partly consistent with hypothesis H5). We expected larger prey to be found farther from the den in both regions compared to smaller prey, for two main reasons: lynx may avoid killing large prey close to the den to avoid attracting scavengers near the kittens, whereas small prey is consumed faster and is less likely to attract scavengers; and larger prey may avoid areas where the dens are as it has been suggested that ungulates can use scent to avoid predation risk (Kuijper et al. 2014) and their larger home ranges and movement capacity can allow more for predator avoidance compared to smaller prey. However, small prey were found at similar distance from the den compared to larger prey in the temperate region. At higher latitudes the main ungulate prey for lynx are reindeer, which are more unevenly scattered and less predictable than roe deer in the temperate region, therefore requiring longer foraging trips. In this case, small

prey may be an important alternative source of energy during a period where the energetic demands are higher than usual. We must bear in mind that smaller prey is harder to detect in the field (due to shorter handling times; Oliveira et al. 2023), and for this study we only considered field-confirmed kill sites. In the temperate region, where the field effort for checking kill sites was generally lower than in the cold region, some of the smaller prey kill sites may not have been found by the researchers. We found a significant effect of time passed since the start of den use in the kill-to-den distances. However, the pattern is not clear; besides the relatively large confidence interval, there is an increase in the kill-to-den distances up to approximately 15 days after the start of den use, but then these distances decreased to similar values at the beginning of den use. A possible explanation is that most kills monitored after 25–30 days are from the temperate region, which are closer to den, than those in the cold region. However, to provide sound conclusions regarding the influence of this covariate, we would need a larger sample size in both regions.

Methodological limitations and recommendations for future studies

Although the large sample size across multiple populations is an important advantage of this study, a limitation is the disparity of the number of individuals considered between the different populations and regions. The largest portion of the data came from the cold region (~70%), and, to enhance the reliability of our results, we should strive for a more balanced sample size across populations. This approach would ensure a fair representation of diverse environmental conditions among and within populations while accounting for potential variations in behaviour and adaptability among individual lynx.

Furthermore, the GPS-fix schedules had a high variability. When comparing results obtained with the full and the standardized dataset, the general trends for all movement metrics were similar, and there were only differences in the length of daily distances, which were longer in the full dataset (Supporting information). The length of the same track is inevitably longer and more precise (closer to the actual length moved) if calculated from more GPS fixes, so a higher resolution is more appropriate to conduct accurate movement analyses. However, standardization of the data is also important. When we compared results obtained with the full (i.e. all data) and standardized datasets (i.e. 6 fixes / 24 h) with those obtained with subsampled datasets (i.e. only 12 fixes / 24 h), we observed large confidence intervals for the distances from the den with the full dataset (i.e. all data). Thus, these results are more challenging to interpret compared to those obtained with a single resolution of 12 fixes / 24 h cycle or 6 fixes / 24 h cycle (Supporting information). Therefore, regular intervals of GPS data with 4 h or less, are recommended when studying movement patterns during the denning period. Higher resolutions also allow for analysis at a finer scale (Olson et al. 2011) and consideration of different behavioural states (e.g. hidden Markov models; Glennie et al. 2023).

Additionally, our interpretations of our results on kill-to-den distances are based on the assumption that the distribution of prey within a lynx territory would be homogenous, which may not necessarily be the case. Unfortunately, we were unable to include prey availability as a variable in our models, because it was not possible to obtain this information in a standardized way over all of the study areas.

Conclusion

Our large-scale analyses of movement patterns and foraging behaviour of female Eurasian lynx demonstrated variable responses of lynx maternal behaviour to contrasting environmental conditions. While some behaviours remained constant despite different environmental conditions (e.g. daily presence at the den), while others (e.g. distances of foraging forays from the den) varied significantly with different conditions. These results suggest that some intrinsic behaviours remain constant, while others are adapted to meet the needs of the females and the offspring in different environments. Furthermore, we showed that including datasets from contrasting regions is crucial and might reveal nuanced behavioural responses, which are missed when analyses are limited to a smaller spatial scale. Such deeper understanding of behaviours during the denning season, especially across a large environmental gradient, is particularly relevant since female lynx adopt a similar strategy to central place foragers during this period, which constrains their movements.

Our insights from a large latitudinal gradient also highlight possible increased energetic demands imposed on reproducing females in the more extreme environments. Because of the higher movement rates, which must be maintained also during the denning period, the energetic demands of female lynx in the cold region appear considerably higher than those of female lynx in the temperate region. This could potentially result in lower fitness, as was already documented in grey wolves *Canis lupus* (Mahoney et al. 2020). Therefore, future studies should focus on the energetic demands of female lynx during this critical period for offspring survival, and its implications for Eurasian lynx conservation. This might be especially relevant in areas with increasing human pressure, as females with higher energetic expenses during the denning season could be less resilient to additional constraints, such as human disturbance at dens or kill sites. Therefore, future studies should investigate how the behaviour of breeding female lynx is influenced by human disturbance, inter- and intraspecific competition and kleptoparasitism, and how this can affect litter size and kitten survival, especially in extreme environments.

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Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9kd51c5wx> (Dalpiaz et al. 2025).

Supporting information

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

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