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Neonatal antipredator tactics shape female movement patterns in large herbivores

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Caring for newborn offspring hampers resource acquisition of mammalian females, curbing their ability to meet the high energy expenditure of early lactation. Newborns are particularly vulnerable, and, among the large herbivores, ungulates have evolved a continuum of neonatal antipredator tactics, ranging from immobile hider (such as roe deer fawns or impala calves) to highly mobile follower offspring (such as reindeer calves or chamois kids). How these tactics constrain female movements around parturition is unknown, particularly within the current context of increasing habitat fragmentation and earlier plant phenology caused by global warming. Here, using a comparative analysis across 54 populations of 23 species of large herbivores from 5 ungulate families (Bovidae, Cervidae, Equidae, Antilocapridae and Giraffidae), we show that mothers adjust their movements to variation in resource productivity and heterogeneity according to their offspring's neonatal tactic. Mothers with hider offspring are unable to exploit environments where the variability of resources occurs at a broad scale, which might alter resource allocation compared with mothers with follower offspring. Our findings reveal that the overlooked neonatal tactic plays a key role for predicting how species are coping with environmental variation.

Mammalian females that provide extensive maternal care need access to high-quality or abundant food resources to meet the marked increase in energetic demands of late gestation and early lactation[1,2]. Many species synchronize births with the seasonal flush of resources[3,4]. At that time, reproductive females often move to track the best food resources[5–8]. Following parturition, the movement of mothers should, however, be restricted by the limited mobility of their newborn, even when precocial. In the absence of any protection provided by a nest or burrow, such as observed in large herbivores, predation threatens offspring survival. Parturient females should, hence, trade resource acquisition against resource provision (lactation) and protection of their offspring[9]. Evolved behavioural adaptations to this trade-off include neonatal antipredator tactics, which range along a continuum from immobile and concealed offspring ('hider' tactic[10]) to mobile offspring that follow their mother ('follower' tactic[10]). Having hider or follower offspring imposes different constraints on mothers' movements (Fig. 1). The bed sites of immobile hider offspring correspond to central places to which the mother has to return at regular intervals to provide care[5,9,11]. Meanwhile, mothers of follower offspring have to adjust their daily ranging behaviour to the movement capacity of their offspring to keep in contact with them[12,13]. Surprisingly, we currently lack a comprehensive understanding of how offspring's antipredator tactics interplay with environmental conditions to shape fine- and large-scale movements of reproductive females in a dynamic landscape.

We aim to fill this knowledge gap by investigating how neonatal tactics affect female movement patterns of large herbivores around parturition, across gradients of resource productivity and spatial scales of resource variation[8]. We performed a comparative analysis across 54 populations of 23 species distributed worldwide, which displayed contrasting neonatal antipredator tactics (Fig. 2). Using continuous-time stochastic movement models (CTMMs)[14,15], we overcame the methodological hurdles of heterogeneous sets of global positioning system (GPS) locations and propose insightful ecological interpretations of three main statistical properties of individual trajectories, namely,

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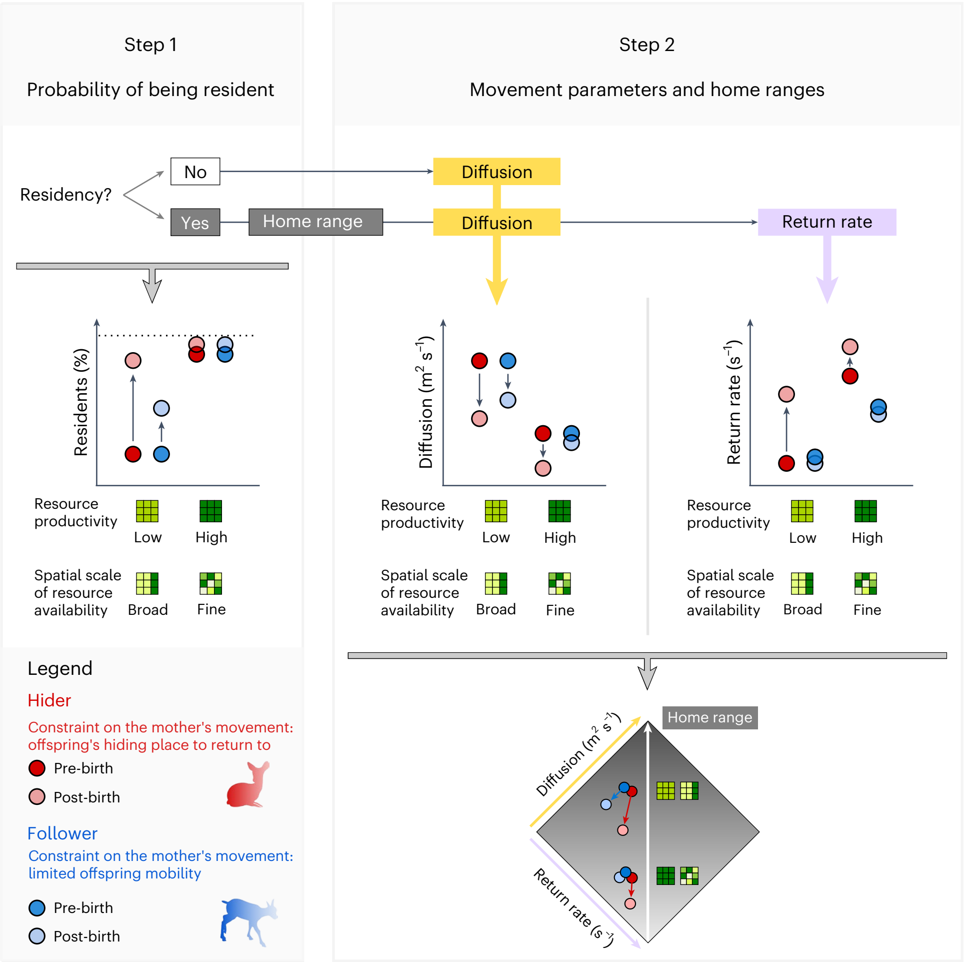

Fig. 1 | Conceptual framework and analytical steps for studying the interplay of neonatal tactics (hider versus follower offspring) and environmental context (resource productivity and spatial scale of resource variation[8]) on residency level, movement metrics and the resulting home range of females before and after giving birth. Step 1 classifies female movement as fitting a Brownian or an Ornstein–Uhlenbeck (OU) type of movement model (see Methods and glossary in Table 1). A female is defined as 'resident' if her movement is best described by an OU model. The figure in the step 1 panel displays how the proportion of residents in a population is expected to vary pre- and post-birth in species with hider and follower offspring, across gradients of resource productivity or spatial scale of resource variation. Step 2 corresponds to the predictions for how the two movement metrics (diffusion in orange and return rate in purple) and the resulting home range size (in black) should respond pre- and post-birth to the same environmental variables depending on neonatal tactics. Note that, when a movement is best described by a Brownian model (no 'residency'), only diffusion (hence, neither return rate nor home range size) can be estimated.

the stationarity, the diffusion and the return rate to a central place (glossary in Table 1). This led us to delve into the interplay of resources and neonatal tactics on residency and movement components. Where resource productivity is high and resource variation occurs at a fine scale, females should manage to fulfil their energetic requirements both before and after parturition in the same area, without having any incentive to leave[16]. Hence, in such environments, we expected high levels of residency, irrespective of the neonatal tactic (Fig. 1, step 1). In contrast, where resource productivity is low and spatial scale of resource variation occurs at a broad scale, neonatal tactics should influence the level of female residency after parturition[17]: mothers with hider offspring that need to be fed regularly should be more resident than mothers with follower offspring. Likewise, after parturition, we expected differences between neonatal tactics in movement metrics (Fig. 1, step 2): only mothers of hider offspring should increase their return rate to places in their home range where offspring hide, while mothers of follower species may only reduce diffusion to cope with the limited movements of their offspring. This influence of neonatal tactics on movement metrics after parturition should be more acute where resource productivity is low and spatial scale of resource variation is broad, that is, in environments that require females to explore a larger range to allow their resource intake[18]. Overall, female movements should be more constrained by resource dynamics in time and across spatial scales, when they have hider rather than follower offspring, leading neonatal tactics to play a key role in female movements.

Results

Neonatal tactics and residency in relation to parturition

The two neonatal tactics were equally represented among the 23 species we studied (11 followers and 12 hiders; Fig. 2). Across species, most females were resident (79 ± 11% and 83 ± 11% before and following parturition, respectively), but, as expected, females with hider offspring were more often resident (81% before and 88% after parturition) than females with follower offspring (76% before and 77% after parturition; Extended Data Fig. 1).

Contrary to our expectation, irrespective of the neonatal tactic, there was no relationship between resource productivity and residency, either before or following parturition (Extended Data Fig. 2). Meanwhile, in support of our expectation, when the spatial scale of resource variation increased, the propensity to be resident decreased, and more strongly so in females with hider than with follower offspring (Fig. 3a,b). However, this difference among neonatal tactics occurred only before parturition (estimated slope with 95% credibility intervals as subscripts; hiders: $_{-2.786}-2.530_{-2.272}$; followers: $_{-1.540}-1.276_{-1.037}$),

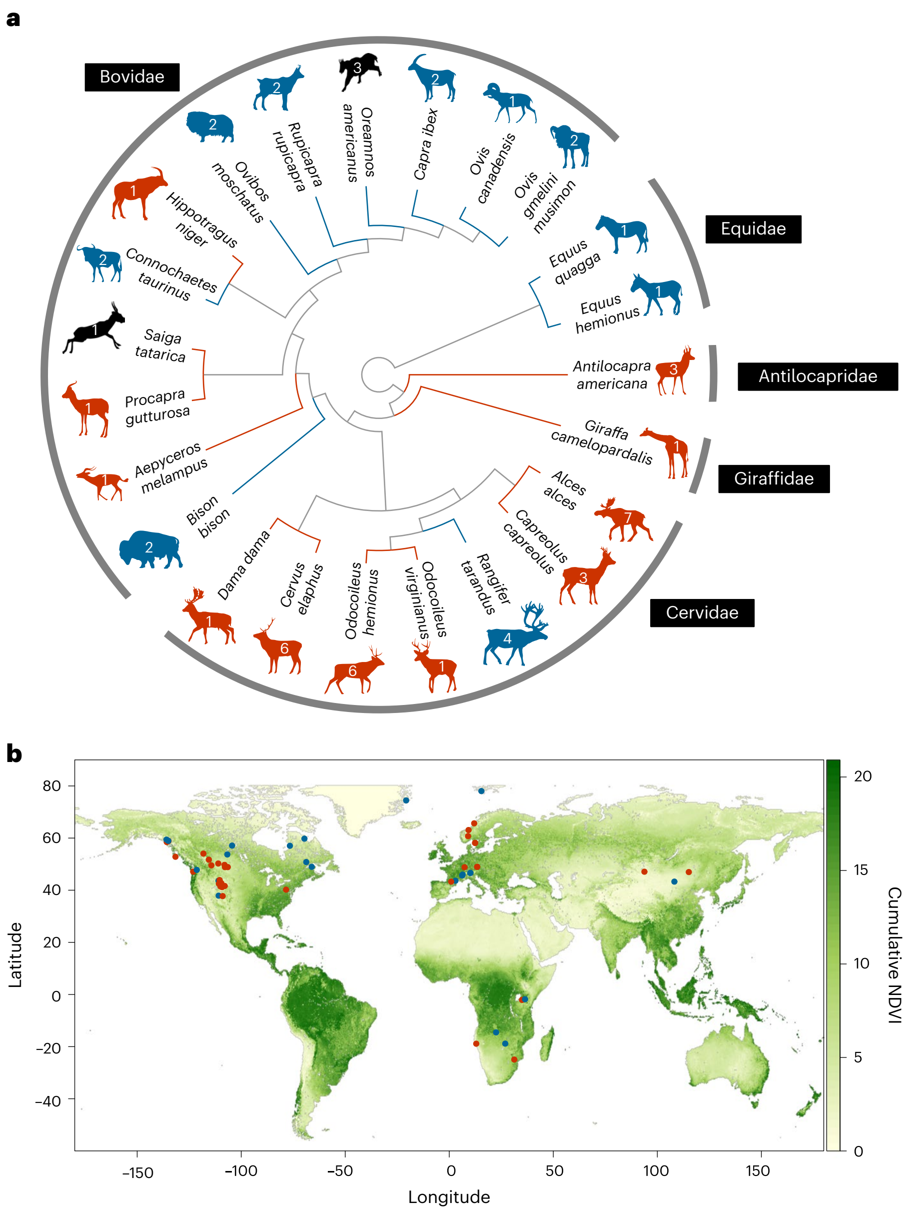

Fig. 2 | Overview of the species and populations. a, The phylogenetic tree of the 23 species of large herbivores included in this study (see 'Phylogenetic analysis' section in Supplementary Table 2). The number of populations for each species is indicated on each pictogram (downloaded from http://www.phylopic.org or from the personal collection of the authors). Blue and red represent follower and hider neonatal antipredator strategies, respectively. **b**, The average location of each population (Supplementary Table 1) on a composite map of cumulative Normalized Difference Vegetation Index (NDVI) values, retrieved from ref. 76 and used solely for presentation purposes. Credit: **a**, Silhouettes adapted from PhyloPic under a Creative Commons license.

and declined after (hiders: $_{-1.149}{-0.926}_{-0.696}$; followers: $_{-1.030}{-0.771}_{-0.524}$) (Extended Data Fig. 2). When resource variation varied at a broad spatial scale (SS_{NDVI} >56 km), females with hider offspring were almost four times more likely to be resident following parturition than before it, whereas the magnitude of this change was less than two in followers (Fig. 3a,b). When resource variation occurred at this broad spatial scale, a substantial proportion of females was not resident after parturition, even with hider offspring (for example, up to 20% of pronghorn in the Northern Sagebrush Steppe and of mule deer in Wyoming's Red Desert, United States and western Washington, United States).

Neonatal tactics and shift in female movements

Before parturition, the diffusion was similar for females with hider and follower offspring, irrespective of resource productivity (difference between tactics: $_{-0.102}{-0.018}_{0.068}$, model output in Extended Data Figs. 3 and 4; Fig. 4a,b and Extended Data Fig. 5). Following parturition, as expected, the diffusion decreased more in females with hider than follower offspring (difference between tactics: $_{-0.517}{-0.426}_{-0.325}$; Fig. 4a,b). This impact of parturition on the mother's diffusion varied with resource productivity, but there was no difference between neonatal tactics (Fig. 4a,b) in how diffusion decreased with increasing resource productivity ($_{-0.277}{-0.194}_{-0.106}$; Extended Data Figs. 3–5). Overall, the change in diffusion post-parturition was lower when productivity was low (4% increase in followers, 26% decrease in hiders) than when productivity was high (38% decrease in followers, 56% in hiders) (Fig. 4a). The spatial scale of resource variation influenced the diffusion more than the resource productivity (Extended Data Fig. 5; model output in Extended Data Figs. 3 and 4). Before parturition, the diffusion increased more strongly with spatial scale of resource

Table 1 | Glossary of parameters and movement processes of interest, adapted from ref. 74

Parameters and models	Notations and acronyms	Biological meaning
Brownian motion	BM	An endlessly diffusing movement process described simply by the instantaneous diffusion parameter (D) and representing non-stationarity.
Ornstein–Uhlenbeck position movement process	OU	A stationary home range-bounded movement process described by two parameters (Ornstein–Uhlenbeck or OU: D and τ_p)[15]. Individuals with OU movement patterns are called 'resident' in the main text.
Movement process variance	σ^2 (m^2)	The non-random movement magnitude of the movement process, representing a proxy of home range size.
Instantaneous diffusion	D (m^{2}s^{-1})	The area covered by an animal per unit of time, with rate representing the area covered when an animal roams away from its position, per time unit. 'Diffusion' in the main text.
Position autocorrelation time[15]	τ_p (s)	Time necessary for an animal to revert back to its expected path after a random deviation. Its inverse represents the frequency of return to a central place and is called 'return rate' in the main text.
Normalized difference vegetation index	NDVI	The mean NDVI is a proxy of vegetation productivity for large herbivores at large spatial scales[75].
Spatial scale of NDVI variation	SS_{NDVI}	Represents 'the distance necessary to travel until NDVI values are uncorrelated'[8].

variation for females with hider (${}_{0.938}0.996_{1.054}$) than with follower (${}_{0.731}0.807_{0.889}$; Extended Data Fig. 5) offspring. However, the same relationship did not differ between neonatal tactics following parturition (${}_{0.273}0.330_{0.385}$ and ${}_{0.291}0.369_{0.448}$ for females with hider and follower offspring, respectively). When the spatial scale of resource variation was low, the diffusion actually increased following parturition in both hiders (by 41%) and followers (by 30%). In contrast, when the spatial scale of resource variation was intermediate or high, the diffusion decreased after parturition, especially in hiders (Fig. 4b).

As expected, females with hider offspring had a consistently higher return rate than females with follower offspring (Fig. 4c,d and Extended Data Figs. 3 and 4). The return rate increased with resource productivity irrespective of the neonatal tactic (difference between tactics: ${}_{-0.027}0.022_{0.060}$) before parturition, and only in females with follower offspring after parturition (Extended Data Fig. 5). Indeed, following parturition, the return rate of females with follower offspring increased by 12% regardless of resource productivity. In contrast, the return rate of females with hider offspring markedly increased after parturition, at values that remained similar across the whole range of resource productivity (slope: ${}_{-0.089}0.005_{0.085}$; Extended Data Fig. 3). To reach this high return rate following parturition, the return rate of females with hider offspring increased by 61% in an environment with poor resource productivity but only by 1% when in an environment with high resource productivity (Fig. 4c).

Spatial scale of resource variation also had a strong impact on return rate. Return rate peaked when spatial scale of resource variation was low, especially for females with hider offspring (Fig. 4). Overall, return rate decreased with increasing spatial scale of resource variation, with a steeper slope for females with hider than follower offspring (before parturition: ${}_{-0.791}-0.724_{-0.659}$ versus ${}_{-0.680}-0.588_{-0.494}$; after parturition: ${}_{-0.646}-0.584_{-0.521}$ versus ${}_{-0.543}-0.458_{0.358}$, respectively; Extended Data Figs. 6 and 7). Noticeably, the impact of the spatial scale of resource variation on return rate was attenuated following parturition irrespective of the neonatal tactics (see slope estimates above). Hence, when the spatial scale of resource variation was high, the difference in return rates between neonatal tactics dampened (Fig. 4). In summary, the consequences of parturition on return rates differed between neonatal tactics and depended on the spatial scale of resource variation: it respectively increased by 11%, 31% and 53% for low, intermediate and high values of spatial scale of resource variation for females with hider offspring, and it decreased by 5% for low values, and then increased by 12% and 31% for intermediate and high values of spatial scale of resource variation, for females with follower offspring (Fig. 4d).

Irrespective of the neonatal tactic, resource productivity impacted home range sizes mostly through its effect on return rate, while the spatial scale of resource variation influenced the size of home ranges through both diffusion and return rates (Fig. 5). Regardless of the resource variable considered (resource productivity (Fig. 5a) or spatial scale of resource variation (Fig. 5b)), females with hider offspring altered their movement after parturition, which explains marked changes in resulting home ranges (decrease by 54%, 55% and 58% following parturition in low-, medium- and high-productivity areas, and increase by 20% and decrease by 55% and 82% in areas with low, medium and high spatial scale of resource variation, respectively; Fig. 5a). The presence of an offspring at heel also impacted females of follower offspring and, thereafter, the size of their home ranges, but to a lesser extent, and mostly when resource productivity was high and spatially variable at a broad scale (decrease by 20%, 36% and 45% following parturition in low-, medium- and high-productivity areas, and increase by 49% and then decrease by 36% and 61% in areas with low, medium and high spatial scale of resource variation, respectively; Fig. 5).

Discussion

Life history variation across species is highly structured by differences in body size[19], phylogenetic relatedness[20], habitat features[21] and lifestyle[22] along a slow–fast continuum[23,24]. However, most studies have been performed on traits that directly describe the life cycle[25], which limits the focus on resource allocation. Up to now, very few comparative studies across species have investigated the consequences of life history on the movement ecology of animals, besides the well-established allometry of home range size[26] and of large-scale movements such as dispersal or migration (for example, ref. 27). One main limitation for conducting comparative analyses of movement was the highly variable sampling designs to collect data locations, which affects the estimation of movement parameters (see ref. 28 for an example on speed). The CTMM framework accommodates this limitation and decomposes home range size into two movement components, namely, the frequency of return to a central place (called return rate here) and the diffusion[14]. We propose here a first behavioural interpretation of these statistical parameters and highlight the contrasting responses of the movement components to ecological and evolutionary drivers. For instance, the well-documented home range size decrease with increasing plant productivity[18,29] mostly results from a decrease in diffusion, while the return rate remains largely unchanged. Indeed, the comparison of return rate and diffusion across populations of 23 species of large herbivores (Fig. 2) that lived in highly diverse ecosystems reveals the complex interaction between a life history trait (here, the tactics of maternal care) and the dynamics of food resource distribution on the different facets of the spatial behaviour of mothers during the critical period of maternal care[1].

The antipredator neonatal tactics are crucial life history traits for the reproductive success of female large herbivores[10]. Our findings demonstrate that these tactics deeply shape movement and habitat use by females around parturition (Fig. 5). Across-species differences and

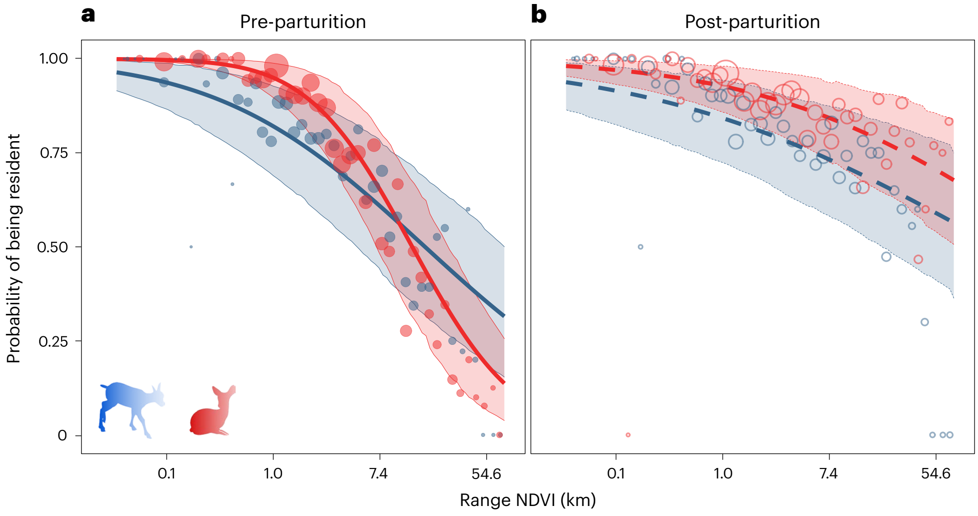

Fig. 3 | Changes in ranging behaviour of females before and after parturition according to the antipredator strategy of their offspring, and the mean quantity and spatial distribution of food resources. a,**b**, Changes in the propensity for a female to be resident across populations of 23 species of large herbivores in the pre-parturition period (**a**) and in the post-parturition period (**b**), in relation to increasing spatial scale of resource variation (measured by SS_{NDVI}) with follower (in blue) and hider (in red) offspring. Points, lines and shading represent mean probability, model fit and its associated 95% credible intervals, respectively. The point size is proportional to the number of females.

similarities we report from our comparative analysis[30] inform about the past selective pressures on the movement behaviour of females in response to the limited mobility (follower) and spatial constraints (hider) imposed by the presence of their newborns. Females with hider offspring such as in roe deer, pronghorns or giraffes are resident to a larger extent, display higher return rate and have a lower diffusion than females with follower offspring such as reindeer, chamois or ibex (Figs. 2–4). This pattern is consistent before and after parturition (Fig. 3), making the requirement of regular visits to immobile hider offspring only a partial explanation. Presumably, the combination of a high propensity for residency, a high return rate and a low diffusion of mothers with hider offspring has been selected to improve their overall reproductive success. However, it might also constrain female movements both within and outside the breeding season, leading them to occupy small home ranges (Figs. 1 and 5). To compensate for the potential loss of food resources induced by restricted movement and foraging areas, females with hider offspring should be more selective in terms of habitat quality[31] or have a more specialized diet[32] to improve energy acquisition and raise their hider offspring successfully, without compromising their own survival. These constraints can explain the tight association between habitat quality and reproductive success in females with hider offspring (see ref. 33 on roe deer). Meanwhile, females with follower offspring are less limited in their movement by their young at heel and can adopt different tactics to secure enough energy to raise offspring successfully, such as surfing the green wave[34,35].

While both return rate and diffusion are under differential selection depending on the antipredator tactics displayed by offspring, these movement metrics exhibit a substantial amount of variation within species among large herbivores (Fig. 4e). Movement is the quickest and most efficient behaviour for most animals to cope with environmental variation and unpredictability in food resources[36]. At the same time, moving is energetically costly[37,38], and mothers seem to trade return rate for diffusion (Fig. 5) to increase home range size in the landscapes with the broadest scale of resource variation. Accordingly, the probability of being resident and the two movement components change depending on the spatial and temporal distribution of resources at the time of parturition; however, this occurs differently before and after parturition and according to whether offspring

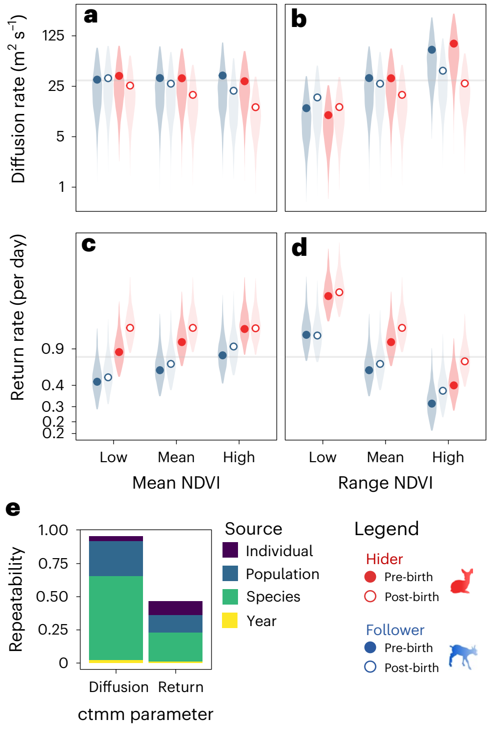

Fig. 4 | Changes in two movement components (diffusion and frequency of return rates) of females before and after parturition according to the antipredator strategy of their offspring, and the mean quantity and spatial distribution of food resources. a–**d**, Changes in expected values of diffusion (**a** and **b**) and return rates (**c** and **d**) for females across 23 species of large herbivores in relation to mean resource productivity (**a** and **c**, measured by mean NDVI) and spatial scale of resource variation (**b** and **d**, measured by SS_{NDVI}) before (dark shading) and following (light shading) parturition with hider (red roe deer fawn) and follower (blue chamois kid) offspring. Low, mean and high categories represent the 10%, mean and 90% quantiles of each environmental variable. **e**, A histogram showing the repeatability of diffusion and return rates, two components of continuous time stochastic movement models (CTMMs), according to the different levels of observation (individual, population and species) and time in years.

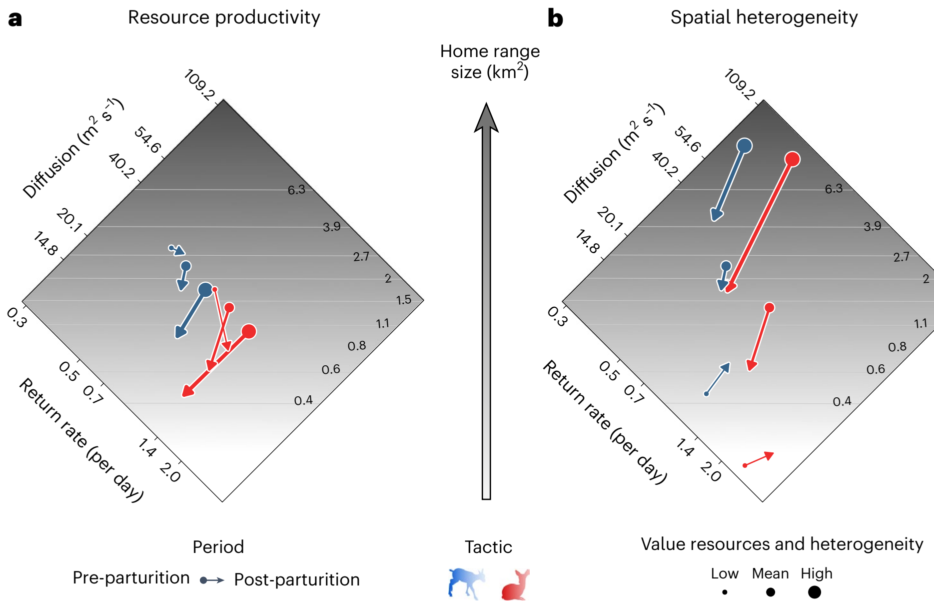

Fig. 5 | Contribution of two movement components (diffusion and frequency of return rates) on the change in home range size of females before and after parturition according to the antipredator strategy of their offspring, and the mean quantity and spatial distribution of food resources. a,**b**, Expected mean values of diffusion and return rates of adult females across populations of 23 species of large terrestrial herbivores in relation to mean resource productivity (measured as mean NDVI) (**a**) and spatial scale of resource variation (measured by SS_{NDVI}) (**b**) before (start of arrow) and following (arrow tip) parturition with hider (in red with a deer fawn symbol) and follower (in blue with a chamois kid symbol) offspring. 'Low', 'mean' and 'high' represent the 10%, 50% and 90% quantiles of each environmental factor (0.18, 0.41 and 0.72 for mean NDVI, and 0.25, 1.33 and 6.5 km for SS_{NDVI}), respectively. Home range size (horizontal dotted grey lines) increases with increasing diffusion and decreasing return rate, the two components of continuous time stochastic movement models (CTMMs).

are hider or follower (Fig. 3). As the size of a home range should be as small as possible to avoid movement costs[39], it should decrease with increasing plant productivity around the time of parturition (Fig. 5), as previously reported in other mammals (for example, ref. 40). Yet, the magnitude of the influence of the spatial distribution of food resources on movement during the most critical time for female fitness has remained underappreciated up to now, and the fact that it could be tactic dependent has not been envisioned so far. Accordingly, the return rate displayed as much as a 3-fold decrease between an environment with a fine grain variation in food resources and an environment where food is fragmented into larger, distant vegetation patches (Fig. 4).

Including an influential life history tactic, the neonatal antipredator tactic, into studies of movement improves the understanding of the spatial distribution of species and their response to future changes in resource variation in space and time[41]. For species with hider offspring, the drop in return rate after parturition increases with the scale of resource variation, while the change is negligible for species with follower offspring (Figs. 4 and 5). Hence, raising a hider offspring emerges as a great constraint for the movement of females in less productive and very patchy environments. In some extreme situations, females with hider offspring may entail too high energetic costs of movement for breeding, making the environment unsuitable for the long-term viability of local populations. This framework opens new avenues of research to delve into other structuring life history traits on movement such as diet[42], the degree of gregarity[43] or the level of sociality[44].

Methods

Study sites and GPS data

We collected datasets either through the Movebank animal tracking database and repository available online (https://www.movebank.org) or by direct contact with the co-authors and data providers (Supplementary Table 1). Because we were focusing on movement before and following parturition, we only included adult females that reproduced and removed individuals with no monitoring covering the entire reproductive period as well as individuals known to be non-reproductive. Survival of newborn over that period was unknown because only the mothers were monitored. We therefore assumed that the initial status of a female—with or without a young at heel—remained unchanged over time.

We excluded GPS location outliers using the method proposed by Bjørneraas et al.[45]. Following this selection procedure, our dataset contained 3,907,880 GPS locations (when considering only the 2 months centred around parturition) in 54 populations of 23 large herbivore species (11 classified as followers and 12 as hiders) worldwide distributed along longitudinal and latitudinal gradients (Fig. 2), including 2,386 individuals monitored from 1997 to 2019, thus representing a total of 3,942 individual-years.

Defining reproductive periods

Because we investigated changes in movement before and following parturition, we defined time frames that best capture the pre- and post-parturition periods, while accounting for methodological constraints of having a long-enough period of monitoring for fitting continuous-time movement models (see 'CTMMs and model fitting' section). We choose a 1-month window pre- and post-parturition that allowed us to cover the last third of the gestation and the first part of the lactation, which are the most demanding periods in terms of energetic intake for females[46]. Gestation length ranges from 140 to 450 days, so the last month is within the last third of the gestation for all species (it represents between 20% and 60% of the last third of the gestation for the largest to the smallest species respectively; Extended Data Table 1). In addition, 1 month after parturition allows for a time frame that ensures that offspring, even from the smallest species, are still fed almost exclusively by their mother. Hence, we position ourselves in the period where changes in movement, whatever the species, are most likely to be influenced by the need for a female to frequently care for her offspring, even though the duration of these interactions varies across species.

When precise information on reproduction was available (12 populations), we used individual parturition dates to divide the data into a 1 month pre-parturition period (parturition date − 30 days) and 1 month post-parturition period (parturition date + 30 days). This was the case for 27% of the follower species and 26% of the hider species. In the remaining 42 populations (half of which were follower species and half of which were hider species), individual parturition dates were unavailable. However, most large herbivores exhibit markedly pulsed breeding[3,4,47], yielding a normal or log-normal distribution of birth dates. We therefore defined a population-based cutoff date, corresponding to 5% of birth events (Extended Data Fig. 8), using data previously published or a best-informed guesstimate provided by data owners (Supplementary Table 2). With a 5% cutoff date, we made sure that most females did not give birth preceding that date but would eventually do so afterward, thus leaving a small margin of error with the presumably 5% of females who had already given birth. This method was applied to females with unknown parturition dates (representing 2,906 or 73.72% of individual-years). In populations where individual parturition dates were available for a only proportion of females (10 out of 12 populations), we used the on-hand available individual parturition dates to compute the 5% cutoff. We repeated our analyses including a factor indicating whether the date of parturition was known at the individual or population level, and this led to results qualitatively similar to the ones presented in detail in Results, but with an enlarged effect size for the neonatal tactics, meaning that our results based on the whole dataset were conservative.

CTMMs and model fitting

In modern telemetry data, CTMMs offer more robust statistical approaches than discrete-time models by accounting for temporal autocorrelation[14,15,48]. They describe movement as continuous through time, with a relatively stable process mean accompanied by random deviations from the expected path (that is, stochasticity). While being the simplest of CTMM classes, the Brownian motion (BM) model fails to account for the emergence of home ranges given its assumption of an infinite diffusion process[49] (Table 1). Other classes of CTMM do actually lead to bounded home ranges, such as Ornstein–Uhlenbeck (OU) models[50]. This class of models is especially attractive because the movement variance (usually denoted σ^2) can be decomposed into the contribution of diffusion (D) and position autocorrelation time[14] (that is, time in autocorrelation of positions) (τ_p), two parameters of biological and ecological interest (Table 1). The diffusion coefficient determines how an animal moves away from its expected path while being constantly attracted back to it at a rate defined by the position autocorrelation time, thus leading to a range-defined movement process. As a consequence, the net squared displacement[51,52] (that is, squared Euclidean distance between start and end point of a trajectory) and the semivariogram of the location time series reach an asymptote that scales to the home range size[15] (Extended Data Fig. 9). In fact, the asymptotic value of the Gaussian distribution of the movement process represents σ^2, which is a proxy of home range size, and the rate of increase of the semivariance with time before it reaches σ^2 represents τ_p, whose inverse represents the return rate to a central point.

Given that the low number of parameters of OU models do not reconcile complex animal movement patterns at fine time scales, further classes of models have been introduced (for example, OU foraging (OUF) model[15]) and incorporate temporal autocorrelation in position (τ_p) and velocity (τ_v). τ_v quantifies the intensity of persistence in the direction and speed of movement. Using these models and parameters, we tested biological hypotheses about stationarity (stationary OU versus non-stationary BM), diffusion and return rate (inverse of τ_p).

For each period (that is, before/after parturition), we first determined whether the individual was stationary or not using empirical semivariograms (Extended Data Fig. 9). The semivariance is a measure of the similarity in distance between two recorded locations, as a function of the time lag between them[15]. The semivariogram is a useful diagnosis tool to categorize movement types. If the semivariance increases monotonically with the time lag, the movement is endlessly diffusive, like a BM. By contrast, if the semivariance exhibits an inflexion point and reaches an asymptote for large time lags, the animal is stationary or home-range-bounded, like an OU process[14,15,50].

Given the heterogeneity in frequency of location records and the duration of the monitoring among individuals and species, we applied a decision rule about the inclusion of an individual in the analysed dataset. We selected only tracks with a median sampling interval not longer than 6 h, with at least 14 days of data and a minimum of 60 locations per period. This rule offered the best compromise between the number of different individuals retained and the minimum number of locations to fit statistical models (using the rule of thumb of at least 30 observations per estimated parameter). We followed Bunnefeld et al.[16] and fitted competing models (linear versus exponential functions of lag τ) to the empirical semivariograms, selecting the best model using the Akaike information criterion. In practice, we fitted the BM and OU models, each having a well-established formalization when working with semivariance[15]. We fitted the OU process to the stationary tracks using the ctmm.fit routine in the ctmm package[14] available in R[53]. Given that velocity autocorrelation can bias the estimation of the movement magnitude[15], we first fitted an OUF (includes velocity autocorrelation time τ_v) model to extract the diffusion parameter (D), position autocorrelation time (τ_p) and movement variance (σ^2). In some cases (1.6% of analysed tracks), our data did not support the OUF model, probably because the velocity autocorrelation time was smaller or of the same order of magnitude as the sampling interval; thus, we fitted the OU model and extracted the same focal parameters. For tracks identified as non-stationary BM, we only extracted the diffusion parameter D from fitting a theoretical semivariogram to the empirical one. All values were $\log_{10}$ transformed. To remove potential outliers, we computed Z scores for each population:

$$Z = \frac{x_{ip} - \mu_{ip}}{\sigma_{ip}},$$

where x_{ip} is the parameter's i value in the period p, μ_{ip} is the mean of all the parameter's i values in period p, and σ_{ip} (not to be confounded with σ of the OU movement model) is the standard deviation of all the parameter's i values in period p. We removed scores that were <3 or >3, which represented 1.14% ($N = 90$ out of 7,884) of all tracks and 0.2% ($N = 8$ out of 3,942) of all individual-years[54]. If an OU track was identified as an outlier for a certain parameter, all parameters of that track were subsequently removed because we were interested in (co-)variation of both diffusion and return rate. Some individual-years had only one of their periods removed as outliers. In these cases, we ended up removing all the individual-years ($N = 74$ out of 3,934) since analysing changes in movement required both tracks. For BM models, only the diffusion coefficient D was used to compare changes between pre- and post-parturition periods.

Following all the above-mentioned criteria, our extensive final dataset included 2,342 reproductive females (Supplementary Table 1) with 3,860 female-years covering the pre- and post-parturition periods (that is, 7,720 tracks). The data covered one to seven populations in 23 species, located in a wide range of ecosystems, from the low-productivity biomes of the Mongolian steppes to the high-productivity systems found in the temperate regions of Europe (Fig. 2b).

Covariates

Resource availability and spatial distribution are known to influence animal movement, where individuals in low-productivity and highly heterogeneous environments move longer distances[8,55], seeking necessary resources to satisfy their energetic needs. To evaluate the effect of resource productivity and spatial distribution on movement, we used the normalized difference vegetation index (NDVI) MOD13Q1 v.006 images with a 250 m resolution at a 16-day interval, derived from Moderate-Resolution Imaging Spectroradiometer (MODIS) satellite imagery and available online from 2000 (https://search.earthdata.nasa.gov/search?q=C194001241-LPDAAC_ECS). NDVI is an index of primary productivity measuring the green biomass of the canopy and grasslands[56,57], although previous studies[58] also found a correlation between understory biomass and NDVI values in forest habitats. Note that only the study of bison in Prince Albert National Park started before 2000. For the two individuals monitored before 2000 (one in 1997, the other in 1997 and 1998), we used the NDVI images from 2000.

We retrieved NDVI composite images spanning from February 2000 to December 2019, which correspond to the year NDVI 250 m was first available and the last year of monitoring in our dataset, respectively. We rescaled NDVI values to vary between −1 and 1, and modified and removed values on the basis of pixel reliability provided with MOD13Q1. Pixels with reliability values of −1 (no data) and 3 (cloudy) were removed, and those of 2 (snow/ice) were assigned to a NDVI value of 0. Following Teitelbaum et al.[8], we set a minimum threshold of 0.05 to all NDVI values below this threshold that do not reflect resource availability for ungulates.

We computed, for each individual-year, the 95% minimum convex polygon of all GPS locations from both periods using the adehabitatHR package[59] in R. Afterwards, we extracted, for each polygon, the mean annual NDVI for the corresponding year of monitoring as a proxy of resource availability. We also measured the spatial range of variation of resources by extracting, for each polygon, the mean annual NDVI (mean interval, derived from MODIS satellite imagery and available online NDVI) values of each pixel for the corresponding year of monitoring and subsequently calculating the spatial range (m) of the autocorrelation in NDVI (range NDVI) values using the variofit function from the geoR package[60] available in R. High values of the spatial range of NDVI represent broad-scale variation in resources, whereas low values represent fine-scale variation[61]. For 421 out of the 3,860 individual-years, we randomly subsampled 6,000 of the 534, 250 × 250 m cells, following Teitelbaum et al.[8], to avoid computational limitations due to the high number of cells retrieved in their polygons. Finally, using published papers, we retrieved the mean body mass of adult females for each species in our dataset (Supplementary Table 1) to take into account the allometry of movement, since larger animals have larger range movement and cover larger areas[62].

Statistical analysis

For all our analyses, we used Bayesian phylogenetic mixed-effect models (BPMMs), which are appropriate to perform phylogenetic analyses on large datasets with multiple measurements per species and implemented in the MCMCglmm package[63] for R. It was essential to control for phylogeny as a way to correct for non-independence between species-specific data points that may arise from relatedness among species sharing common traits. We constructed our own phylogenetic tree using full mitogenome sequences retrieved from GenBank[64] (see 'Phylogenetic analysis' section in Supplementary Table 2 for full details).

We first tested the effect of neonatal tactic (hider versus follower), resource availability and spatial variation, and period (pre-parturition versus post-parturition) on the probability of being stationary. We ran BPMMs with a binomial distribution specified with the argument family = categorical using the function MCMCglmm to investigate the probability of being stationary in each track, defined as a binary response variable (0 = non-stationary BM and 1 = stationary OU/OUF). We included phylogeny (to which we attributed the variance–covariance matrix), species (since multiple measurements for a given species can share biological traits that do not arise from phylogenetic relatedness), population nested in species, year nested in population, and individual nested in population and species as random factors. We added two three-way interactions in the model as two fixed effects: the first between neonatal tactics, mean NDVI and period, and the second one with the log-transformed spatial range NDVI instead of the mean NDVI. The log-transformed body mass was added as an additive fixed effect to account for the allometric relation of movement[62], along with the monitoring duration of the track (days) and number of locations since a finer and longer sampling procedure has a higher chance of detecting a stationary behaviour. Both variables were also log transformed. We first used a non-informative inverse Wishart prior ($\nu = 0.02$ and $V = 1$) with a fixed residual variance ($V = 1$ and fix = 1). As a second step, we conducted a sensitivity analysis to verify that the prior did not impact our results and reran the model using a parameter extended prior ($\nu = 1$, $V = 1$, alpha.mu = 0, alpha. $V = 1{,}000$). We observed no difference between the results from each prior. We ran the model three times with 550,000 iterations (burn-in = 50,000 and thinning = 100) and conducted the Gelman–Rubin diagnostic[65] using the gelman.diag function from the package coda[66] to confirm the convergence of the model. If any difference is observed between the three Markov chains Monte Carlo (MCMC), the diagnostic concludes that the model did not converge. In our case, we did not detect any difference between our chains.

To assess the effect of parturition and the environment on movement parameters in relation to neonatal tactic, we ran similar BPMMs, in terms of random and fixed effects, but with diffusion and return rates as continuous response variables and a Gaussian distribution for the data. In the models on diffusion, we added the attributed model (BM or OU/OUF) as an additive fixed effect to control for differences in diffusion values between BM and OU, the former expressing larger diffusion than the latter. For models on return rate, we only included individuals with tracks identified as stationary OU during both periods. This led to the removal of Mongolian gazelles from the analyses since all individuals were non-stationary during the post-parturition period. We also added, as a statistical weight and for all models, the inverse of the error variance for each data point. We used the non-informative inverse Wishart prior ($\nu = 0.02$ and $V = 1$) with no fixed residual variance and ran the model with 550,000 iterations (burn-in = 50,000 and thinning = 100). We also conducted a sensitivity analysis with an extended prior ($\nu = 1$, $V = 1$, alpha.mu = 0, alpha.$V = 1{,}000$) and found no difference in our results from both priors. We ran the Gelman–Rubin diagnostic and found that our models did converge. To prepare Figs. 4 and 5, we predicted values for each parameter in relation to the 10%, mean and 90% quantiles of every environmental variable (mean and spatial range NDVI) using individuals that were stationary (OU/OUF) during both periods. When predicting values for one environmental variable, we fixed the other at its mean. We fixed the body mass at 60 kg, representing the mean body mass of large herbivores[67], and log-transformed it.

We calculated the phylogenetic heritability[68] H^2 for each model mentioned above, which can be interpreted similarly as Pagel's phylogenetic signal λ (ref. 69). A phylogenetic heritability of $H^2 = 0$ indicates that no phylogenetic relatedness is detected among effect sizes, while $H^2 = 1$ indicates an exact proportional relationship between effect sizes among species and their phylogenetic relatedness[70]. We reported the mean of the posterior distribution for each effect along with its 95% credible interval of the highest posterior density distribution. The significance of an effect was determined by the exclusion of 0 from its credible interval.

Finally, we estimated the consistency of movement parameters at the species, population and individual levels of biological organization by calculating repeatability (R, see ref. 71 for a review). We also computed the repeatability of diffusion and return rates across years. We estimated Rs according to ref. 72 from the estimated variances associated to the nested random effects of species σ^2_{sp}, population σ^2_{pop}, individual σ^2_{id} and time σ^2_{t} in the Generalized Linear Mixed Models (GLMMs) fitted to individual estimations of movement parameters

(σ^2 and τ_p). We extracted inter-individual variance from the residual variance (σ^2_e) and then obtained *R*s by dividing one variance component by the sum of all components ($\sigma^2_{sp} + \sigma^2_{pop} + \sigma^2_{id} + \sigma^2_t + \sigma^2_e$). For instance, we calculated repeatability for τ at the species level as

$$R_{\tau_p} = \frac{\sigma^2_{sp}}{\sigma^2_{sp} + \sigma^2_{pop} + \sigma^2_{id} + \sigma^2_t + \sigma^2_e}.$$

We report all statistics and estimated parameters as the mean and associated 95% credible intervals following ref. 73, in the format $_{95\%\ \text{lowerlimit}}\text{point estimate}_{95\%\ \text{upperlimit}}$.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The computer code and data used in this paper are available at https://gitlab.in2p3.fr/christophe.bonenfant/neonatal-tactics.

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Author contributions

A.L. and G.P. conceived the project, and A.L., C.B. and J.M.G. supervised the revision of the Article up to its acceptance. A.L., G.P. and K.A. assembled existing data that were primary collected and managed by all co-authors. K.A. performed the statistical analyses, under the supervision of A.L., G.P., C.B. and J.M.G. K.A. and A.L. wrote the first draft of the manuscript. C.B., J.M.G., M.G., A.J.M.H., P.M. and N.M. made substantial contributions to the intellectual content of the Article, and A.L., C.B. and J.M.G. revised the Article. All co-authors revised critically, approved the first and revised drafts, and gave their final approval of the version to be published.

Competing interests

The authors declare no competing interests.

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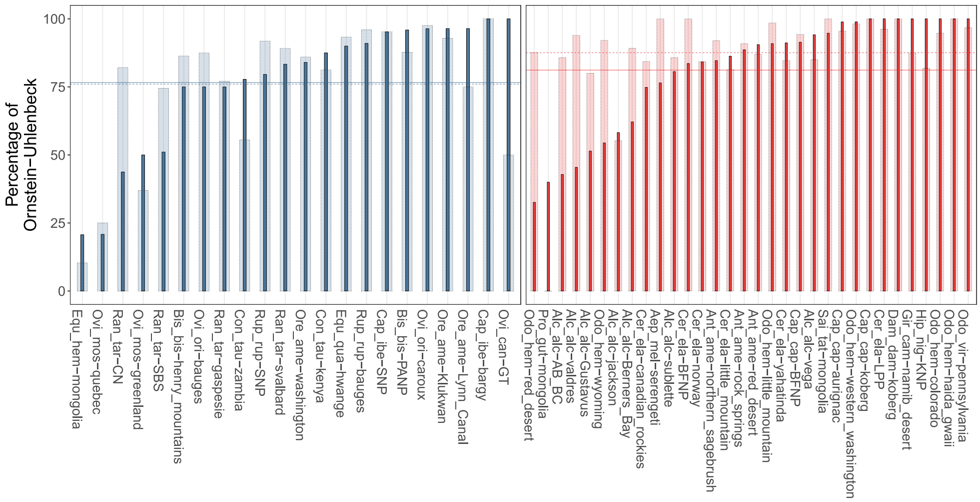
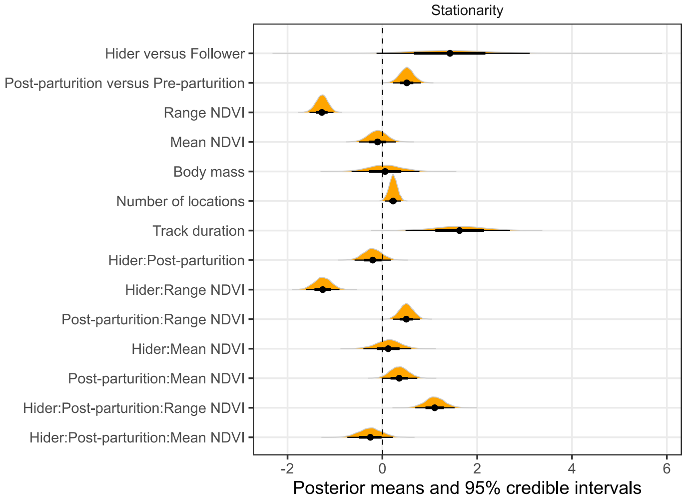
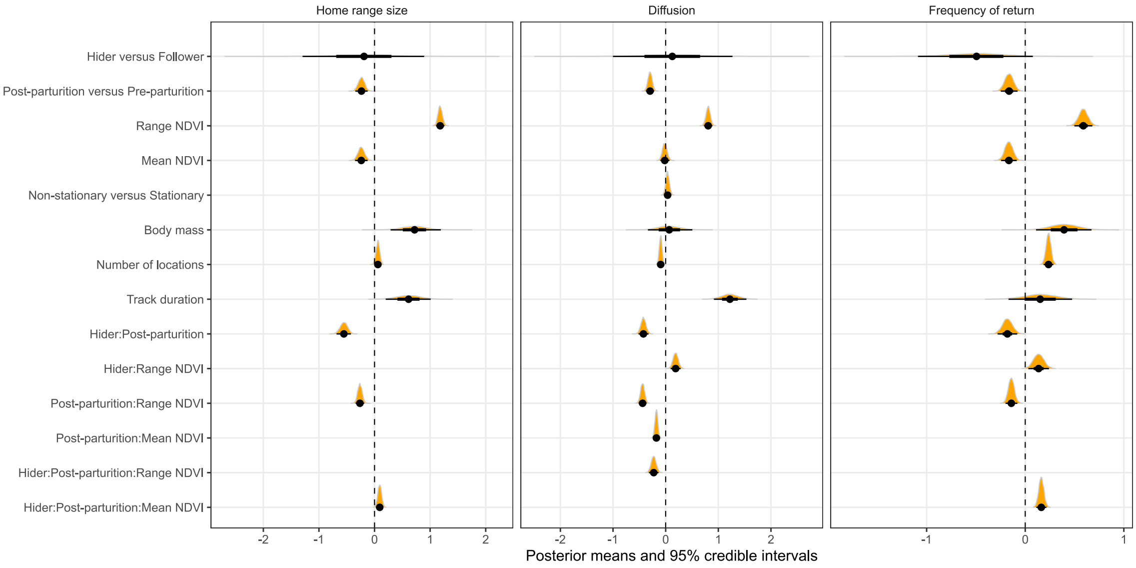


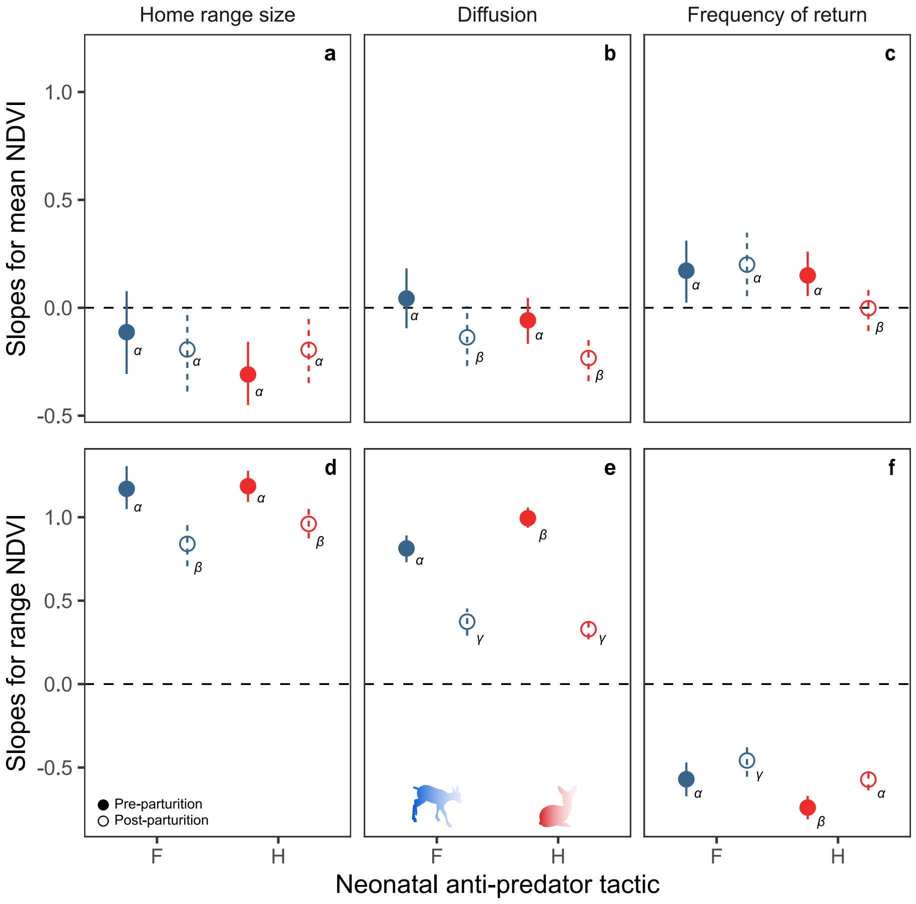
Extended Data Fig. 1 | Percentage of Ornstein-Uhlenbeck models (stationarity) for pre-parturition (plain bars) and post-parturition (dashed bars) for each studied population. Horizontal lines represent the mean percentage of stationarity for each tactic and period. Blue and red represent followers and hiders, respectively. BIS: American bison; BGS: Bighorn sheep; CA: Caribou; CH: Alpine chamois; ELK: Elk; FD: Fallow deer; GI: Giraffe; IB; Alpine ibex; IMP: Impala; KL: Khulan; MG: Mountain goat; MK: Muskox; MOG: Mongolian gazelle; MOU: European mouflon; MS: Moose; MUL: Mule deer; PG: Pronghorn; RD: Red deer; RN: Svalbard reindeer; ROE: Roe deer; SA: Saiga antelope; SAB: Sable antelope; WIL: Wildebeest; WTD: White-tailed deer; ZR: Plains zebra.



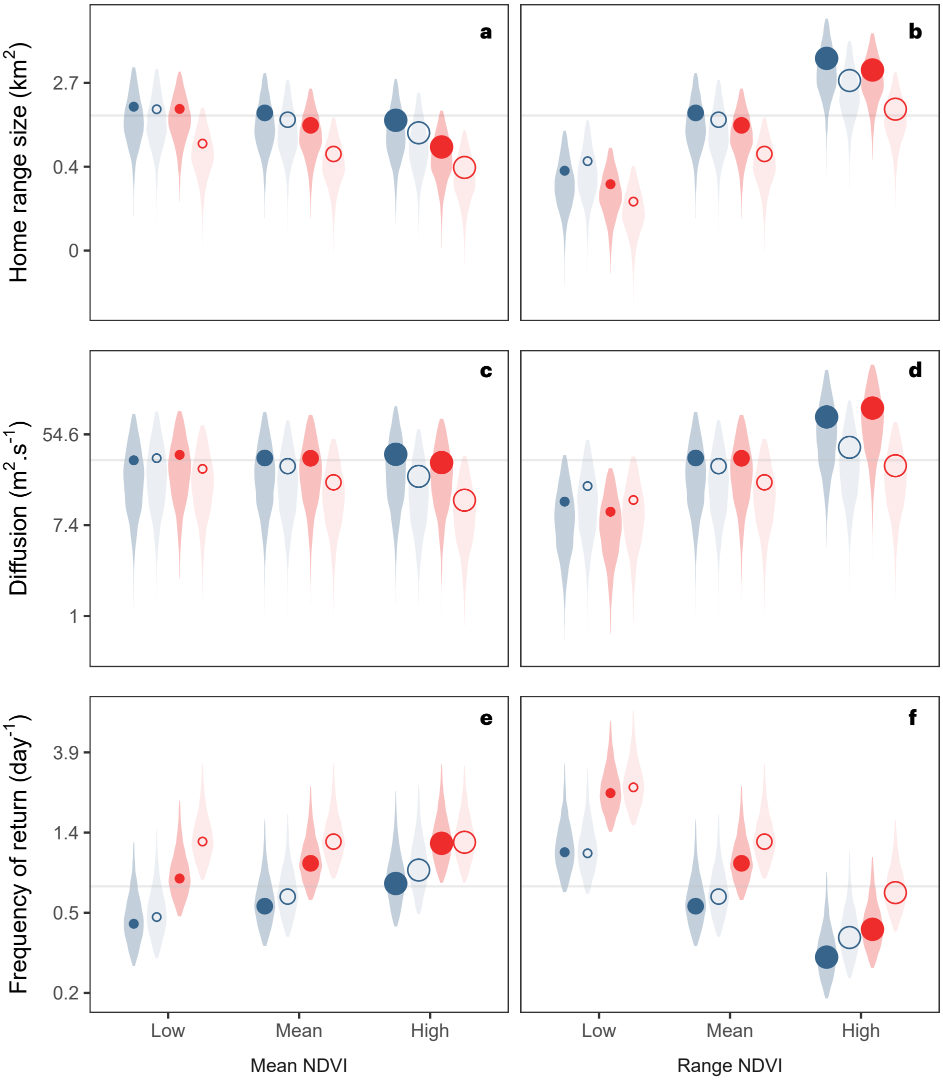
Extended Data Fig. 2 | Posterior distribution for the Bayesian estimation of phylogenetic heritability. Means of the posterior distribution for phylogenetic heritability H^2 and fixed effects, along with their 95% highest posterior density intervals (HPDI), extracted from Bayesian Phylogenetic Mixed Models assessing the relationship between neonatal tactic, reproductive period, seasonality, and the probability of being stationary. Values excluding 0 are statistically significant. We estimated the parameters from a dataset of 23 species and N = 2 386 monitored individuals.



Extended Data Fig. 3 | Posterior distribution and 95% highest posterior density intervals (HPDI) of the fixed effects estimated from them best Bayesian Phylogenetic Mixed Models. Means of the posterior distribution and 95% highest posterior density intervals (HPDI) of the fixed effects retrieved from the most parsimonious Bayesian Phylogenetic Mixed Models determining factors impacting the variation of home range size, diffusion, and the frequency of return to a central place. Values excluding 0 are statistically significant. We estimated the parameters from a dataset of 23 species and N = 2 386 monitored individuals.



Extended Data Fig. 4 | Partial effects of mean and range NDVI on movements parameters of females of large herbivores around the time of parturition. Reconstructed slopes for mean (**a**-**b**-**c**) and range (**d**-**e**-**f**) NDVI from the most parsimonious Bayesian Phylogenetic Mixed models for home range size, diffusion, and frequency of return for each neonatal anti-predator tactic and period. Bars associated to point estimates are the 95% credible intervals. Blue chamois kid and red roe deer fawn represent followers and hiders, respectively. Greek letters (α, β and γ) highlight statistically different parameters at the 5% risk (parameters with the same letter are not distinguishable). We estimated those parameters from a dataset of 23 species and N = 2 386 monitored individuals.



Extended Data Fig. 5 | Predicted values of the home range size, diffusion, and frequency of return female of large herbivores estimated from the most parsimonious Bayesian phylogenetic mixed models. Predicted values of the three movement components (home range size [**a**-**b**], diffusion [**c**-**d**], and frequency of return [**e**-**f**]) of 23 species of large herbivores (N = 2 386), retrieved from the most parsimonious Bayesian phylogenetic mixed models depicting the effect of the interplay between neonatal anti-predator tactic, pre- and post-parturition, productivity (mean NDVI; left panels) and spatial range of resource variation (range NDVI; right panels). Low, mean, and high classes represent the 10%, mean and 90% quantiles of each environmental variable (0.18, 0.41 and 0.72 for mean NDVI, and 0.25, 1.33 and 6.5 km for range NDVI). Predicted values for each parameter were computed for an animal of 60 kg, and the mean value of one environmental variable was fixed when predicting the effect of the other environmental variable for each class. Solid and blank points represent mean predicted values for pre- and post-parturition, respectively. Dark and light shadings represent pre- and post-parturition, respectively. Red roe deer fawn and blue chamois kid represent hider and follower species, respectively. The increase in the size of points represent higher values of environmental variables.

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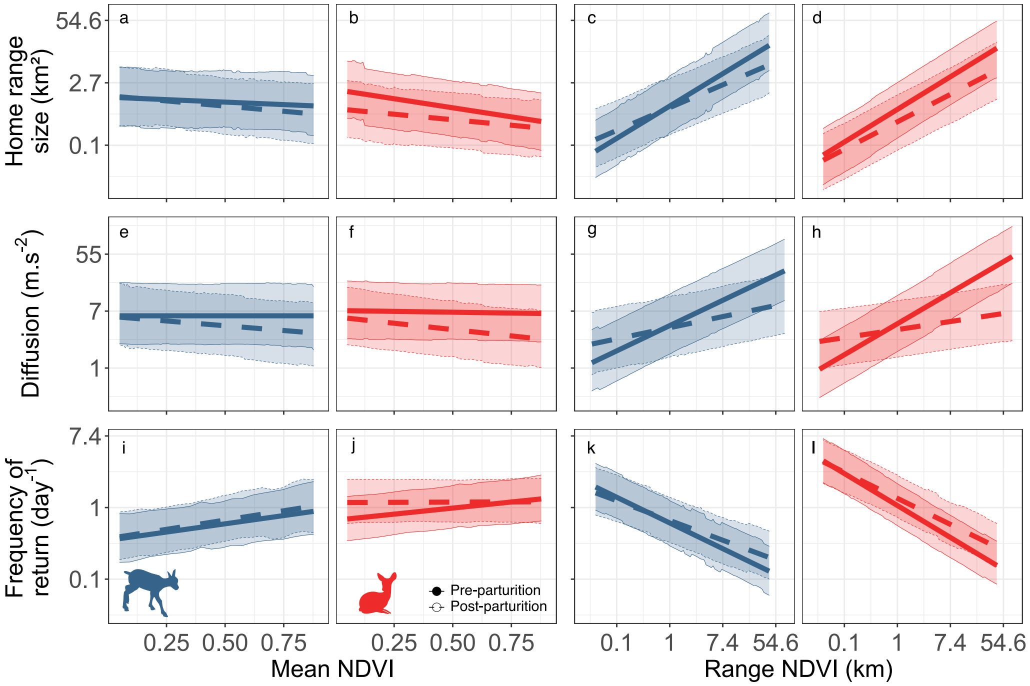

Extended Data Fig. 6 | Predicted relationships between proxies of primary production and its spatial distribution, and the home range size, diffusion, and frequency of return rates of female of large herbivores, as estimated from the most parsimonious Bayesian phylogenetic mixed models. Predicted values of the three movement components (home range [**a**, **b**, **c**, **d**], diffusion [**e**, **f**, **g**, **h**], and frequency of return [**i**, **j** **k**, **l**]) of 23 species of large herbivores, retrieved from Bayesian phylogenetic mixed models depicting the effect of the interplay between neonatal anti-predator tactic (blue vs. red plots), reproductive period (plain vs. dashed line), productivity [**a**-**j**], and spatial range of resource variation [**c**-**l**]. Points and shades represent mean predicted values and 95% credible intervals, respectively. Blue and red represent followers and hiders, respectively, also represented by chamois kid and roe deer fawn silhouettes.

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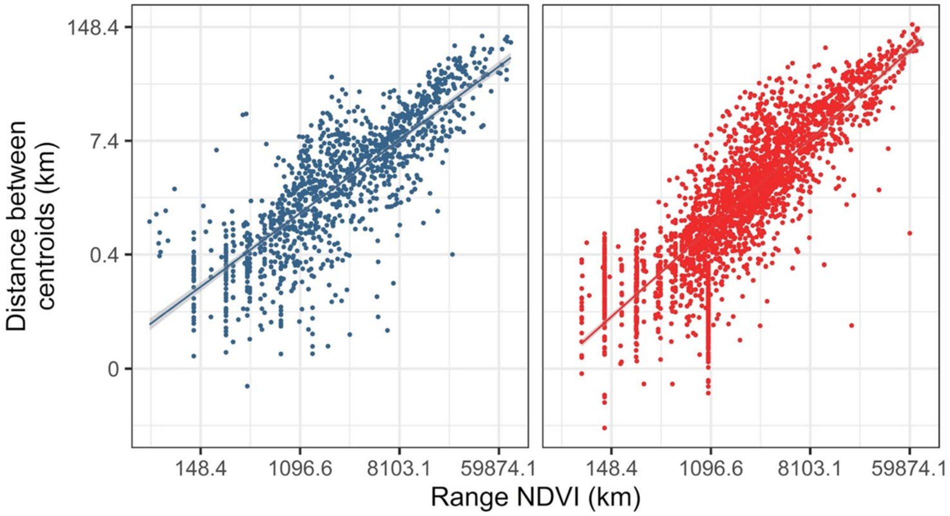
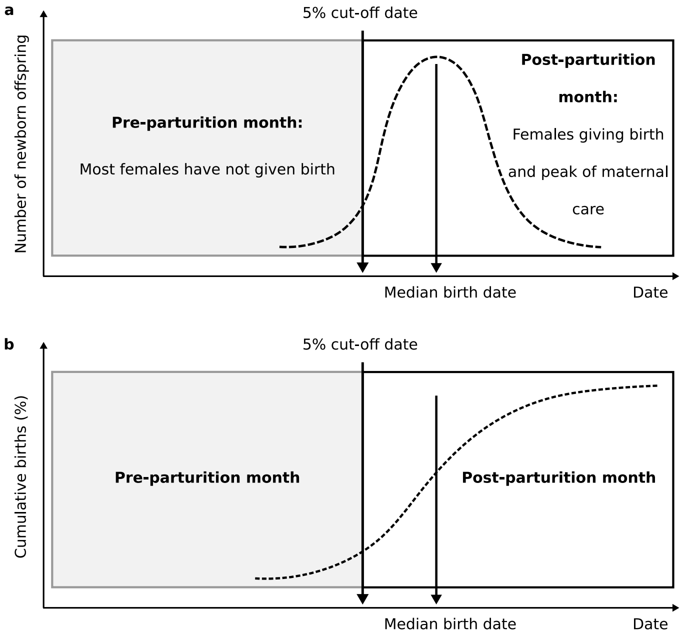
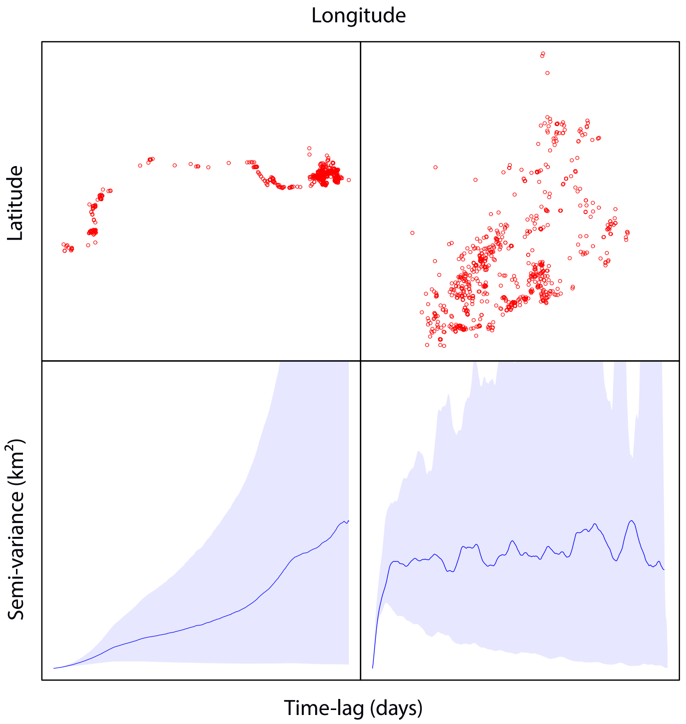


Extended Data Fig. 7 | Relationship between the range NDVI observed at the population level and the Euclidean distance between centroids of locations before and after parturition in female large herbivores. Linear regression between the range of NDVI and the euclidean distance between the centroïds of the locations of each period for every individual year. Plain colored lines are the predicted values from the regression model, and the shaded area covers the 95% credible intervals of the predictions. Blue and red represent followers and hiders respectively.



Extended Data Fig. 8 | Graphical representation of the different methods used to estimate cut-off dates for start and end of parturition periods. Representing the 5% cut-off date from (**a**) the distribution of numbers of newborn offspring or from (**b**) cumulative percentage of birth events to determine pre- and post-parturition periods. The shape of both curves is hypothetical.



Extended Data Fig. 9 | GPS location (points) and semivariograms of Brownian Motion and Ornstein-Uhlenbeck movement behavior of female large herbivores. GPS location (points) and semivariograms of Brownian Motion and Ornstein-Uhlenbeck movement behavior. Only the diffusion coefficient can be estimated from BM tracks. Ornstein-Uhlenbeck leads to a home range with spatially bounded movements where $\sigma 2$ represents the asymptotic movement variance scaling to home range size, τp represents the home range crossing time or the time needed to reach the asymptote, and the diffusion coefficient D represents the rate of increase in the Mean Squared Displacement.

Extended Data Table 1 | Duration of the hiding phase period of newborns in large herbivores retrieved from the literature for each of the studied species

Species	BM (kg)	GL (d)	D (w)	Polytocous	Reference
Aepyceros melampus	44	196	1	m	Mooring & Rubin (1991)
Alces alces	365	240	3	p	Altman(1958)
Antilocapra americana	47	250	3	p	Byers (1997)
Bison bison	275	278	—	m	—
Capreolus capreolus	26	144	8	p	Linnell et al. (1998)
Capra ibex	49	167	—	m	—
Cervus elaphus	239	255	2.5	m	Altman (1963)
Cervus elaphus	125	235	3	m	Clutton-Brock & Guinness (1975)
Connochaetes taurinus	185	250	—	m	—
Dama dama	44	236	1	m	San Jose & Braza (1992)
Equus hemionus	230	406	—	m	—
Equus quagga	322	371	—	m	—
Giraffa camelopardalis	700	450	2	m	Pratt & Anderson (1979)
Hippotragus niger	216	270	2.5	m	Thompson (1998)
Odocoileus hemionus	56	205	6	p	Riley & Dood (1984)
Odocoileus virginianus	68	200	8	p	Schwede et al. (1994)
Oreamnos americanus	61	186	—	m	—
Ovis canadensis	58	180	—	m	—
Ovibis moschatus	246	250	—	m	—
Ovis ?	37	150	—	m	—
Rangifer tarandus	132	210	—	m	—
Rangifer tarandus	132	210	—	m	—
Rupicapra rupicapra	32	170	—	m	—
Saiga tatarica	32	140	1	p	Bekenov et al. (1998)
Procapra gutturosa	22	158	1.5	p	Habibi et al. (1993)

Duration of the hiding phase period of newborns in large herbivores retrieved from the literature. BM stands for body mass in kilograms, GL for gestation length in days, and D for the duration of the hiding phase of newborns in weeks. Note that we could find an estimate of the hiding phase duration for 52% (13/25) of the species we studied in this paper.