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INFERRING PARTURITION DATE IN ROE DEER (*CAPREOLUS CAPREOLUS*): APPLICATIONS AND OPPORTUNITIES FOR STUDYING REPRODUCTIVE PHENOLOGY IN THE FACE OF GLOBAL CHANGE

Master's THESIS by Maxime Balandier


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INTRODUCTION

Over the past decades, a large body of research has demonstrated the ecological impacts of global change (e.g. Vitousek, 1992; Parmesan, 2006). Indeed, anthropogenic activities and cascading consequences through ongoing climate change have been applying a significant pressure on biodiversity (Bellard et al., 2012). Shifts in species abundance and distribution have been documented in plants and animals across different regions but may not be sufficient for organisms to cope with such rapid environmental changes (Parmesan, 2006). Global temperatures have risen by more than 0.8°C since 1880 (Bhattacharya et al., 2020) and have led to an advance in plant phenology, especially in spring. Phenology corresponds to the « timing of recurring seasonal biological events » (Forrest & Miller-Rushing, 2010) and is hence directly related to climate. In plants, the timing of budburst and leaf colouring have shifted over the years (Piao et al., 2019), especially at high latitudes (Jeong et al., 2011). This may have consequences for herbivores and the food chains depending on them. Flexibility in the timing of these life-history events is likely crucial for adjusting to changing environmental conditions, especially because synchronizing resource availability with energy requirements may have long-term benefits for individuals. Indeed, the mismatch hypothesis considers that individuals that are unable to synchronize the timing of their reproduction with the peak availability of resources should not be able to maximize their reproductive success (Dunn et al., 2011). As food is the only source of energy for animals, species with seasonal life cycles are thought to generally produce and raise offspring according to the peak of food availability, to meet the energetic demands associated with the final phase of gestation, early offspring growth and lactation in mammals (Allen et al., 2017; Long et al., 2016). Synchrony in phenology between herbivores and plants may potentially increase fitness of consumers (Van Asch & Visser, 2006). In mammals, giving birth earlier during the growing season may increase offspring body mass (Solberg et al., 2007), survival and have long-term effects on the life-history trajectory of individuals (Plard et al., 2014), as juveniles may benefit from the high quality and quantity of forage resources during a long period prior to the onset of winter. Body mass is a reliable indicator of individual quality and is generally associated with higher reproductive success in herbivores (Festa-Bianchet et al., 1998). Thus, the reproductive phenology of herbivores should be selected to match the peak of forage availability so as to maximize individual fitness. In this sense, variation in forage availability should act as a selective pressure on animals living in seasonal environments (Wong & Forrest, 2021). Identifying and understanding the consequences of climate change on the reproductive phenology of animals is therefore crucial to predict population dynamics and implement management plans.

Some taxa have reportedly tracked directional environmental change related to climate change and so shifted their reproductive phenology, either through phenotypic plasticity (e.g. Charmantier et al., 2008 in great tit (*Parus major*); Froy et al., 2019 in red deer (*Cervus elaphus*) or/and through microevolution (e.g. Davidson et al., 2020 in caribou (*Rangifer tarandus*); Lyons et al., 2015 in yellow perch (*Perca flavescens*)). Phenological shifts can have important demographic consequences (Iler et al., 2021). However, some species have failed to respond to directional environmental changes related to climate change or have manifested an insufficient response (Devictor et al., 2008), hence creating a trophic mismatch. Some studies have reported contrasting patterns with others obtained on the same species (e.g. Visser et al., 1998 on great tit; Post & Forchhammer, 2008 on caribou), suggesting that the response to climate change can differ among populations of the same species, depending on their geographical location. If natural selection or phenotypic plasticity are insufficient to ensure synchrony in phenology between resources and consumers, climate change may have detrimental consequences on their population dynamics.

For some species, the phenological response to climate change remains ambiguous. For instance, female roe deer (*Capreolus capreolus*) were revealed to have a highly repeatable parturition date at the individual level (Plard et al., 2016), suggesting low phenotypic plasticity. Moreover, a lack of response in parturition timing to earlier springs was also identified in a French lowland woodland population (Plard et al., 2014). This generated a mismatch between the peak in availability of high-quality foraging resources and parturition, potentially affecting juvenile survival and population growth (Gaillard et al., 2013). A more recent study did find a small trend toward an advance in roe deer parturition timing, but only at higher altitudes and not of sufficient amplitude to avoid a mismatch with the advance in plant phenology (Rehnus et al., 2020). This response may be due to constraints related to gestation length. Indeed, roe deer is the only ungulate species with an embryonic diapause. Photoperiod, which does not vary in time, seems to be the proximal cue triggering the implantation of the embryo after diapause (Fenelon & Renfree, 2018). However, parturition dates seem to be later with increasing latitude and altitude, and to be more synchronized with altitude, probably in relation with plant phenology (Peláez et al., 2020). Subsequently, the latest published study on parturition date in roe deer found evidence for an advance of between 1.6 and 3.3 days per decade in parturition date across a large region in Germany, especially for high elevations and coinciding with plant phenology (Hagen et al., 2021). The response of this large herbivore to climate change is thus not well understood yet.

Estimating parturition date can be quite challenging. Data on reproductive phenology of large mammals are best collected by direct and repeated observations of individually marked reproductive females, potentially followed by capture of neonates. For example, roe deer is a hider-type species (Lent, 1974) so that during the first 6-8 weeks of their life, fawns do not follow their mothers. Instead, they hide, isolated from them, without moving and with a reduced metabolic activity. Mothers only come to the bedding site a few times a day to feed their fawns. This specific behaviour around parturition is quite subtle and often difficult to observe. To reliably assess birth date, researchers involved in such field studies also have to find neonates rapidly after parturition as they are highly vulnerable to predation from red fox (*Vulpes vulpes*) (Panzacchi et al., 2009). Estimating birth date can also be difficult depending on the age of the fawns at capture. However, in agricultural landscapes, neonates also suffer from mowing (Jarnemo, 2002) so that wildlife managers may conduct capture operations in relation to mowing activity that year (Hagen et al., 2021). However, meadows are directly impacted by climate change, with increasingly early growth and harvest over time due to CO_2 emissions and increasing temperatures (Hopkins & Prado, 2007). Hence, studies that generate data on birth date during fawn rescue operations linked to mowing activity may therefore be misleading and result in a biased estimated distribution of parturition date in the population.

To avoid these sampling problems, different approaches have been developed to estimate parturition date in animals. Blood tests to estimate quantities of pregnancy-specific proteins (Houston et al., 1986) or vaginal implant transmitters (Garrott & Bartmann, 1984) have sometimes been used but are considered as quite invasive for many species. More recently, GPS monitoring and biologging approaches have been developed to infer parturition in mammals (e.g. Wiesel et al., 2019) and birds (e.g. Picardi et al., 2019). As females display specific behaviours around parturition, extracting information from movement data should help us to identify the timing of such events. Modelling approaches have already been developed to infer parturition in ungulate species, such as in caribou (De Mars et al., 2013), but have proven difficulty to generalize to other species, probably because movement dynamics differ (Bonar et al., 2018). To improve our ability to infer parturition, multi-metric approaches have been used to infer parturition, accounting for changes in habitat use or home range size. Based on algorithms and models, they consist of a « suite of methodologies that learn patterns in the data amenable for prediction » (Valletta & Madden, 2017). Marchand et al. (2021) recently developed a method based on machine learning to infer parturition timing in three ungulate species: Mediterranean mouflon (*Ovis gmelini musimon x Ovis sp*.), Alpine ibex (*Capra ibex*) and roe deer. This method, accounting for movement characteristics, resource use, home range and activity data, was highly successful, with accuracy ranging from 76% to 100%. However, it worked less well on roe deer. Furthermore, multi-metric approaches are useful tools to study behaviour around parturition but are usually complex and may be difficult to extrapolate to big databases across different populations, mostly because researchers from different study areas do not always collect data of the same quality or do not have access to the equivalent data, such as candidate environmental drivers. There is thus a need to develop methods which can be applied and generalised to different study areas and species.

In this study, we built on previous work from Marchand et al. (2021) to infer parturition date in roe deer based on time-specific individual profiles in residence time of GPS-collared females, a simple approach that we expected to be user-friendly and hence highly generalizable. We developed our method on GPS data from 61 reproductive females with known parturition date and 41 non-reproductive females from a wild population of roe deer living in a heterogeneous agricultural landscape in Aurignac, south-west France. As habitat is known to have an effect on movement characteristics (Coulon et al., 2008), we attempted to refine the method to incorporate habitat-specific movement characteristics. We then used our method i/ to predict birth date for 46 females with unknown parturition dates in the same study area, and ii/ to validate our approach using 21 females with known reproductive status and parturition date from a population in Bavaria, Germany. Finally, we applied our approach to a large collaborative dataset (n = 388 females from 11 populations; EURODEER, www.eurodeer.org) to investigate the environmental drivers of parturition in roe deer at the continental scale.

Roe deer is an income breeder, accumulating very few fat reserves, and hence directly depends on current available resources to offset the increase in energy requirements during gestation and lactation (Jönsson, 1997). In the past century, roe deer populations have colonized agricultural landscapes (Andersen et al., 1998) where forage of high-quality is available. For this reason, females are usually heavier and obtain higher quality diets in open habitats (Hewison et al., 2009). Furthermore, females with higher body mass were found to give birth earlier than low-quality females in woodland habitat (Plard et al., 2014). Hence, from the above, we expected parturition date to be habitat-dependent so that births occurred earlier in mothers living in mainly open habitats (1). We also expected parturition date to vary across a latitudinal and altitudinal gradient in Europe, in particular, to occur later with increasing latitude and altitude (2) to coincide with plant phenology, as previously suggested by Peláez et al. (2020). However, as the effect of climate change is known to be more marked at higher latitude, we expected any difference between vegetation onset and parturition date to decrease with increasing latitude to mitigate the impact of a shorter growing season (3) (Neumann et al., 2020).

MATERIAL AND METHODS

Improvement of a method to infer parturition date in roe deer

Study area and data collection

Roe deer females were monitored in the Aurignac study area, located in the south-west of France (Zone Atelier PyGar, latitude: 43.13°N, longitude: 0.52°E, max. altitude: 380 m a.s.l.). This site covers 7500 ha of a fragmented agricultural landscape, including a central forest, woodland patches and hedgerows (about 23% of the total area), meadows (32%) and crops (36%) (Morellet et al., 2011). Roe deer individuals were captured as part of long-term capture-mark-recapture/resighting monitoring taking place each year between December and March since 2003. There are currently six capture sites in the study area, each characterised by a predominant landscape structure (Figure 1). One capture site is located in a forest, others in open agricultural fields or a mixed landscape with small woodland patches and agricultural fields (Hewison et al., 2009).

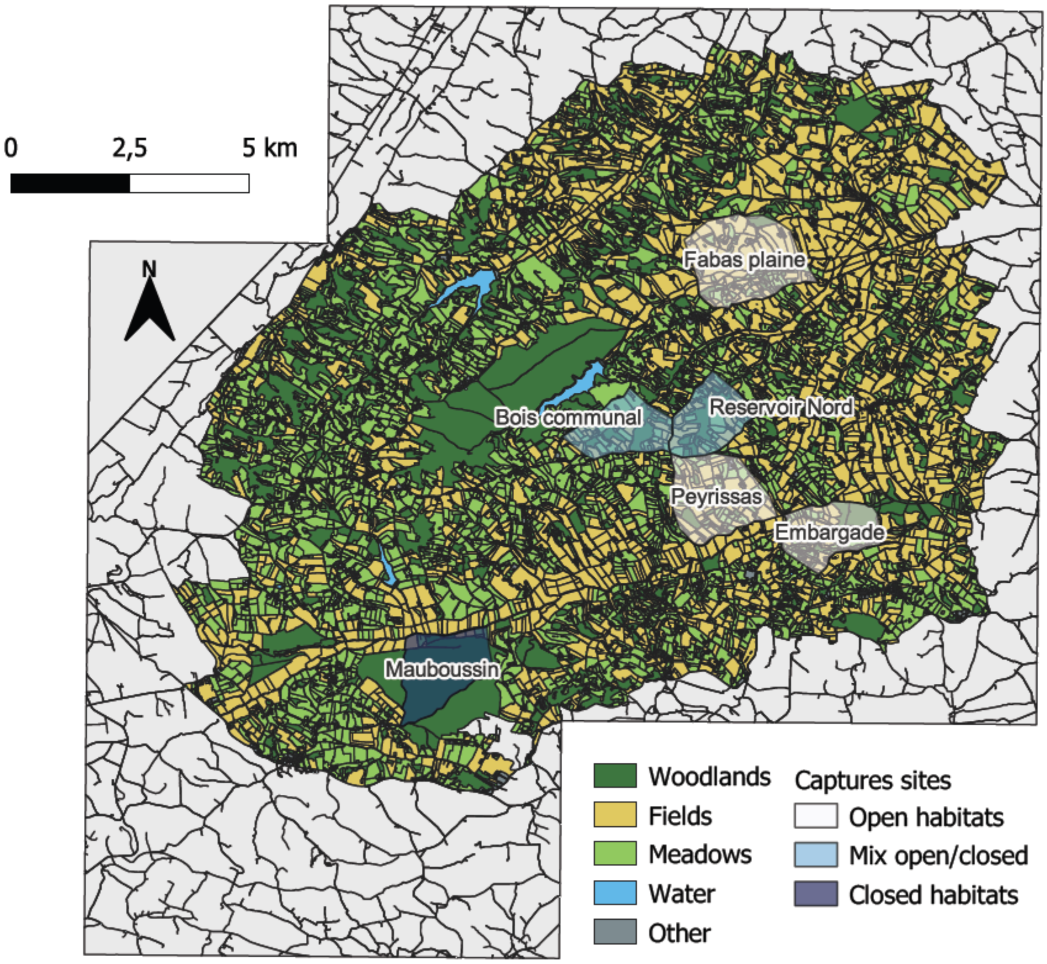

Figure 1. Map of the Aurignac study area (7500 ha) with associated main habitat types and location of the different capture sites. The category « other » includes anthropogenic structures and areas with unknown field occupations.

These capture sessions were done with the use of nets. Animals were tranquillized and transferred to wooden boxes to reduce stress and risk of injuries. Individuals were then weighted and their age estimated. Juveniles (< 1 year old) are distinguished from yearlings (between 1 and 2 years old) and adults (> 2 years old) by the identification of milk teeth (Ratcliffe & Mayle, 1992) and progressive tooth wear (Van Laere et al., 1989). Before releasing individuals, we ear-tagged and equipped them with GPS collars (Lotek 3300S revision 2 or GPS PLUS-1C Store on Board, Vectronic Aerospace for adults; Lotek Small WildCell GSM or Vectronic GPS PLUS Mini-1C for juveniles). GPS locations were recorded at a frequency of one per hour.

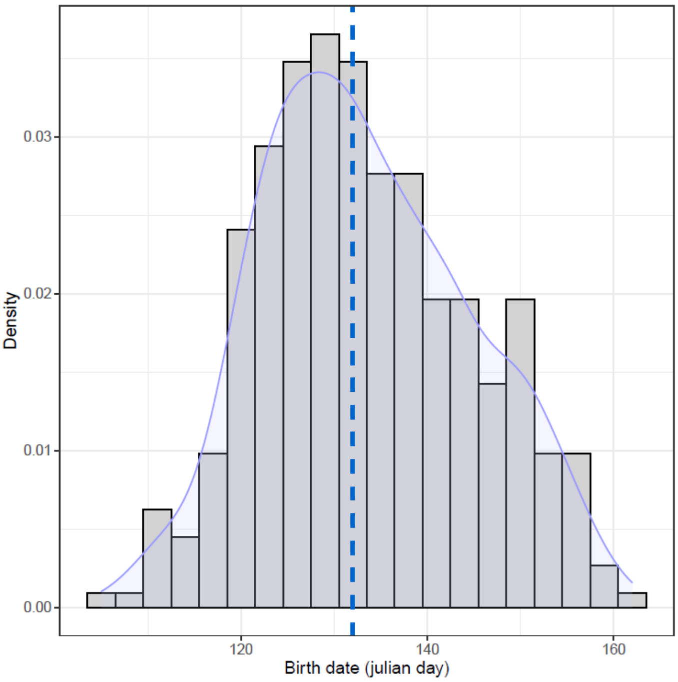

Figure 2. Distribution of birth dates (Julian date, 1 January = 1 julian day) in the Aurignac population, estimated via fawn captures or sightings of pregnant females (n = 364, range: 20 April-11 June). The density function is represented in clear blue, the dashed vertical line corresponds to the median birth date in the population (12 May, 132 julian day).

Each year since 2004, between the end of April and the beginning of June, fawns were hand-caught, ear-tagged, sexed, weighed and aged. As roe deer is a hider species, females are more independent from their fawns (Lent, 1974). Neonates remain hidden in bed-sites with significant vegetation cover as a strategy to limit the risk of predation (Linnell et al., 2004). Therefore, locating fawns mainly relies on prior observations of females and their specific behaviour following parturition. For instance, roe deer females are expected to increase their use of habitats providing high-quality resources like cultivated fields and meadows, in order to meet the energetic requirements related to lactation (Marchand et al., 2021). Some females may also manifest aggressive behaviours (Monestier et al., 2015).

Individual parturition dates were estimated by subtracting the fawn’s age to capture date. Age at capture was estimated after repeated observations of pregnant mothers or based on the fawn’s behaviour and weight (Jullien et al., 1992). In our dataset, median fawn age at capture was 3 days (range: 1-16 days). The median parturition date in Aurignac is 12 May (Plard et al., 2016) (Figure 2). Mortality sensors in the collars provided information about the fate of fawns. When signals were detected, fawns were recovered and the cause of their deaths was determined when possible. We used this data on mortality to understand the behaviour of some females after the death of their fawn. The identity of mothers was determined by observations of direct interactions between the female and the fawn, e.g. during lactation or by proximity between the female and the fawn. In our study, we only considered parturition dates from marked mothers, equipped with GPS collars.

Please note that all animal handling and other procedures described were carried out in accordance with the national law concerning animal research ethics and animal welfare.

Residence time in a restricted area as a predictor of birth

To estimate parturition dates in roe deer, our starting point was the multi-metric approach developed by Marchand et al. (2021). This approach did not perform as well in roe deer as in Mediterranean mouflon and Alpine ibex, possibly because the latter two species are followers. Indeed, unlike roe deer, the presence of offspring at heel in follower-type species may constrain the movement and behaviour of females after parturition (Lent, 1974). Even though roe deer females are considered to be more independent after parturition, parturient females are expected to spend more time around locations where they gave birth so that they can regularly revisit and feed their fawns during the day. In this sense, Marchand et al. (2021) estimated the residence time of females within a circle of 100-meter radius (RT_{100}) as a predictor of parturition events. This behavioural metric was the most informative among other metrics of movement, habitat use and activity used in this approach.

Therefore, we used residence times of females around restricted areas to develop a simpler method to infer parturition in roe deer. Calculations can be generalized to other databases, no matter the frequency at which GPS locations are recorded. However, estimations are necessarily more accurate with fine-scale GPS data. The frequency at which GPS locations were recorded for roe deer in Marchand et al. (2021) was only of 1 location per 6 hours, which may not be precise enough to detect parturition events. Therefore, to obtain a more informative metric of roe deer movement around parturition, we used GPS data collected every hour on 61 reproductive females with known parturition dates (estimated via direct observation of pregnant females and/or capture of fawns) and 41 juveniles that we considered as a negative control. Indeed, juveniles are sexually immature and hence do not reproduce. Moreover, all adult females generally reproduce in wild roe deer populations (Gaillard et al., 1992), and no data on non-reproductive females was available in our study site. We analyzed GPS data between 15 April and 15 June, which corresponds to the approximate duration of the fawning season in this population (Plard et al., 2016), from females monitored between 2009 and 2020. Data available for each female was highly variable during this period. On average, 7 weeks of data (1167 GPS locations) was collected per individual between 15 April and 15 June (min = 585 (4 weeks), max = 1485 (9 weeks)). Prior to analyses, we removed females with a known parturition date outside the individual monitoring period. We also removed dispersers from the juvenile dataset according to Ducros et al. (2019). Indeed, non-reproductive juveniles may disperse during the study period (at around one year of age) and hence be misclassified as reproductive females. They may generate movement patterns similar to reproductive females around parturition and thus alter the performance of our approach. In Marchand et al. (2021), dispersers were more than twice likely to be classified as parturient than non-dispersers. Finally, we removed outlier GPS positions according to Bjørneraas et al. (2010). We used $\Delta = 2000$ m (distance from the median position within a sliding window of 21 fixes) and $\mu = 1500$ m (distance from the mean of remaining GPS locations within a sliding window of 21 fixes) as predefined threshold distances. Points located farther from the surrounding points than these distances were therefore considered as outliers.

Therefore, using the selected dataset described above, for each individual mother, we computed residence time (in hours) within a circle of 100-meter radius centred around each GPS location (RT_{100}) using the function ‘residenceTime’ from the package ‘adehabitatLT’ (Calenge, 2006) in the R software (R Core Team, 2021). This approach estimates the time spent inside this circle, from the first time the individual enters the circle to the first time it leaves (Barraquand & Benhamou, 2008). The area of the circle was 3.14 ha, which represents, on average, about 4 to 6% of a roe deer’s home range in our study site (between 55.4 to 76.5 ha on average; Morellet et al., 2013). We did not apply any tolerance on the maximum time the individual could spend outside of the circle before reentering and hence did not include recursions in the calculation of residence time. Prior to these computations, we also tested for residence times within circles of different radiuses (range: 20-500 meters) but RT_{100} was the most informative. We expected values of RT_{100} would be at their maximum to coincide with parturition events of individual females. To obtain smoothed profiles of RT_{100} over the study period for each individual, we took the average of the RT_{100} values for each GPS location (max. 48) within a sliding window of 48 hours (24 hours before and 24 hours after a given point). An example of R script to compute residence times is provided in Appendix 1.

Identifying parturition events using residence time

To detect peaks in the dataset that corresponded to parturition events, we sought to identify sequences with a certain proportion of data above a RT_{100} threshold for a given minimum duration. In order to identify the best approach to infer parturition in our training dataset, we varied three parameters (Figure 3): a RT_{100} threshold, a minimum duration above this threshold (D_{min}) and a tolerance on the proportion of data below this threshold (which equals to 1 – proportion of data above a threshold). We used the ‘rollapply’ function from the package ‘zoo’ (Zeiles & Grothendieck, 2005) to identify a proportion of data above a RT_{100} threshold within a sliding window of duration D_{min} = D/prog, in which prog is the resolution of our GPS data (1 hour in our dataset) and D a duration (h). Then, we identified sequences above a threshold with a proportion of data greater than 1 – tolerance (in %) using the function ‘rle’ in the R software. If one RT_{100} peak was identified in the data, we considered it to be associated with parturition. If more than one peak was identified, we considered the peak closest to the median parturition date in the population to be associated with parturition for that individual. However, as the median parturition date may not be known in every roe deer population, we also tested to associate parturition events in individuals with the peak that have the maximum amplitude above the RT_{100} threshold. We compared the results of both approaches. Once the peak that was most likely to be associated with parturition was identified, we estimated the timing of parturition in three different ways: by computing the median of the values above the RT_{100} threshold for that peak ($Part_{med}$), the mean of the values weighted by the duration of the peak ($Part_{wm}$), or by considering that parturition occurred at the moment the data first exceeded the RT_{100} threshold ($Part_{cross}$; Figure 3). A R script is provided in Appendix 2. Finally, we selected the best combination of variables (threshold, D_{min}, tolerance), which gave the minimum error rate (i.e. maximized the number of females well-predicted as parturient for reproductive females and as non-parturient for juveniles), and a minimum difference between the observed parturition date and parturition dates estimated using the RT_{100} metric (ΔPart). Finally, we used this approach to infer parturition in 26 reproductive females with unknown parturition date and 20 females with unknown reproductive status from the same population.

Influence of habitat on residence time of females

From initial investigations, we suspected that habitat structure might influence our estimates of residence time for reproductive females. We hypothesised that females living mainly in closed habitats would have a lower average RT_{100} than females living in open habitats due to a difference in

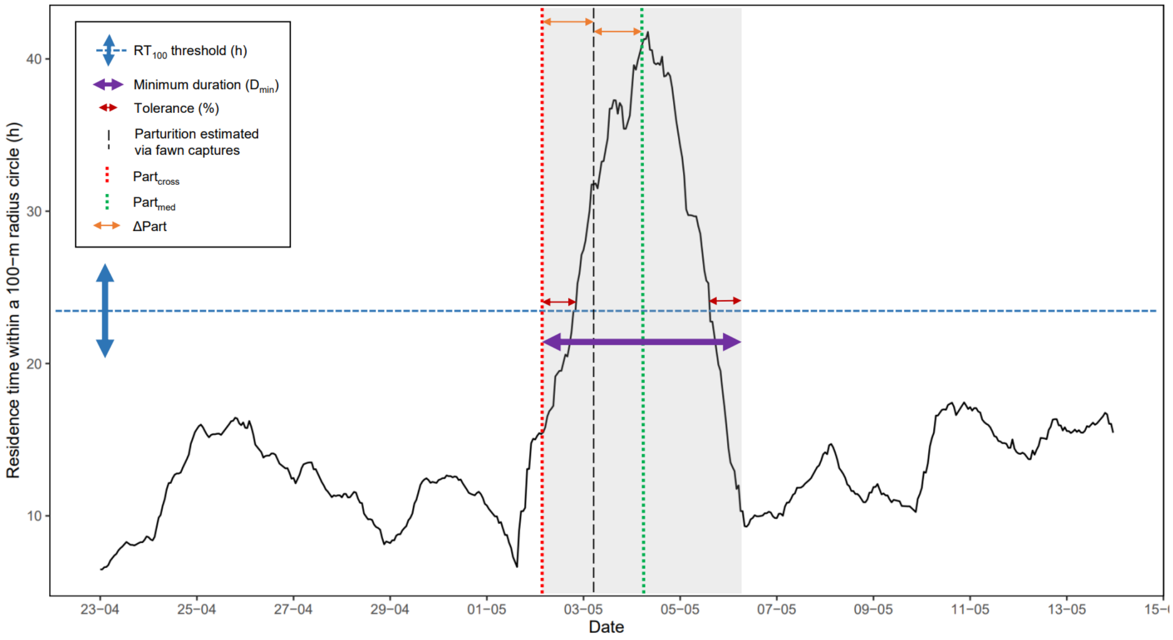

Figure 3. Illustration of RT_{100} variations in a female from Aurignac, south-west France, over time. The different varying parameters used to infer parturition and the estimations of the timing of parturition are represented in colors. The grey area corresponds to an identified sequence with a certain proportion of data above the RT_{100} threshold.

resource distribution (Hewison et al., 2009). Indeed, resources of high quality are concentrated in open habitats while they are more heterogeneously distributed in closed habitats. As roe deer is a high selective feeder (Duncan et al., 1998), individuals living mainly in closed habitats may have to visit broader areas to obtain the resources they need. To control for this effect, we ran our RT_{100}-based approach separately on 3 groups of females depending on the landscape structure of their capture site (Figure 1). With this approach, we expected parturitions to be detected with a lower RT_{100} threshold for individuals living mainly in closed habitats. We hence separated females into: (i) females captured in Mauboussin (mainly closed habitat; 19 reproductive females with known parturition date and 10 juveniles), (ii) females captured in Peyrissas, Fabas plaine and Embargade (open habitat; 62 reproductive females with known parturition date and 36 juveniles) and (iii) females captured in Bois Communal and Réservoir Nord (mix between both habitats; 21 reproductive females with known parturition date and 15 juveniles) (Figure 1). To control for the effect of habitat on residence time of females, we also tested to centre and scale our data. As it did not improve our approach, we decided not to present the results in this report.

Inferring parturition using residence time in another population

To validate our approach, we used the best combination of parameters obtained on the Aurignac population to infer parturition for females in a population from west-Bavaria, Germany, which obtained equivalent data during 2021 provided by the Bavarian Institute of Forestry (Baur, S. & Wibke, P.). This population is located in a fragmented agricultural landscape similar to Aurignac, France. GPS data was collected at 15-min intervals between 15 April and 15 June on 19 reproductive females with known parturition date (Figure 4) and 2 adult females classified as non-parturient as no change in their body shape was observed around winter and birth season (6798 GPS locations on average, min = 6184, max = 7151). Parturition dates were estimated by subtracting estimated fawn age from the date of fawn capture. From this data, the median parturition date in the population was estimated as 12 May. However, median parturition date is increasingly late with increasing latitude (Peláez et al., 2020). Given that the Bavarian population is about 6° further north than Aurignac, this estimate is likely biased, probably due to small sample size. Therefore, when multiple peaks were detected in the RT_{100} profile of a given female from this population, we assumed that the peak with the maximum amplitude above a RT_{100} threshold was indicative of parturition.

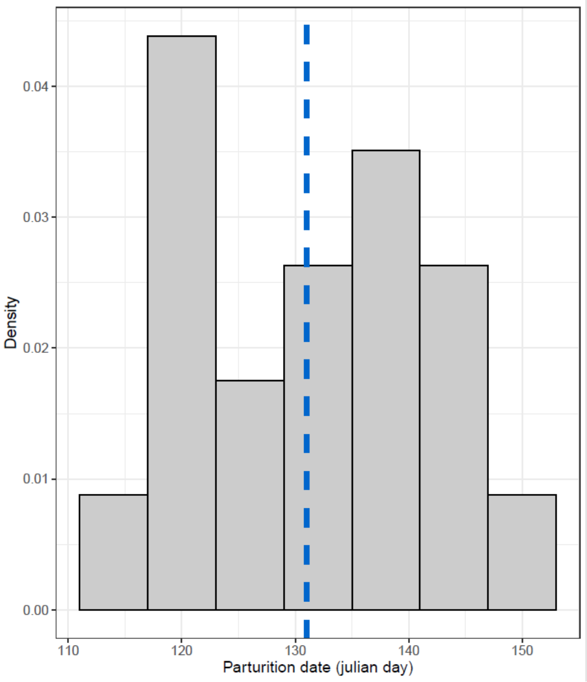

Figure 4. Distribution of birth dates (Julian date, 1 January = 1 julian day) in the population from Bavaria, Germany, estimated via fawn captures (n = 19). The dashed vertical line corresponds to the median parturition date in the sample (12 May, 132 julian day).

Identifying the environmental drivers of parturition timing

Assessing the habitat composition of maternal home ranges

In order to analyse the relationship between parturition date and habitat composition of mothers in the Aurignac population, we determined the home range of females during their individual study period between 15 April and 15 June. A home range is the « area traversed by the individual in its normal activities: of food, gathering, mating, and caring for young » (Burt, 1943). In Aurignac, different types of habitats are contrasted in terms of structure and food availability, and may therefore have an influence on the occurrence of parturition date. During the study period, closed habitats are characterized by a low plant diversity and biomass (Hewison et al., 2009). In open habitats, resources are usually of greater quality, especially in natural meadows, which are characterized by a high diversity of nutritious resources such as low fibre dicotyledonous plants which roe deer tend to eat more and digest better.

We used GPS data from 61 reproductive females from our dataset with a known parturition date and 33 females for which we estimated parturition date with our RT_{100}-based approach based on the median parturition date in the population. Additionally, we also used data from 16 females followed for 4 to 6 weeks during the study period but with a known parturition date that occurred only a few days after the recording of their GPS data ended. We considered their home range to be consistent and the same as around parturition. In total, data on 110 females was used. Home ranges were estimated with 95% minimum convex polygons (MCP) by using the function ‘mcp’ from the package ‘adehabitatHR’ (Calenge et al., 2006) in the R software. The MCP estimates the smallest polygon around GPS relocations with all interior angles less than 180 degrees.

The landscape of the study area was digitized into polygons from aerial photographs. Field work during summer since 2004 allowed us to assign annually a habitat type to each of these polygons. Therefore, in order to estimate the proportion of habitat types in individual home ranges, we used a Geographic Information System (QGIS 2022). We intersected the minimum convex polygons of females with the map of the study area and collected the areas of each type of habitat inside the polygons from the attribute table of the intersected layer. We then grouped each type of habitat into main categories: woodlands and hedgerows were grouped into a ‘closed habitat’ category, natural and artificial meadows, as well as crops were grouped into ‘open habitat’, human infrastructures and unknown land uses were grouped into ‘others’. Closed habitats represented on average 29.10 ± 4.13 % (range: 4.23-99.50%) of the individual home range among females, open habitats on average 68.45 ± 3.99 (range: 0-93.5%).

Variation in roe deer parturition date across Europe

To analyse variation in roe deer parturition date across Europe, we used the collaborative EURODEER database (www.eurodeer.org). We selected GPS data from females over a period of 60 days between 20 April and 20 June, based on the known distribution of parturition dates from different areas in Europe (Plard et al., 2013). Only study areas with at least 15 females monitored with GPS collars were kept for the analysis. We considered all the GPS resolutions (from 15 min to 5 hours). Thus, we obtained data from 388 females (yearlings and adults) along a latitudinal and altitudinal gradient from 11 different study sites. We used our RT_{100}-based method to infer parturition in females from the selected areas. For that, we used the combination of variables that performed the best in the roe deer population from Aurignac, France, and used the approach based on the selection of peaks with the maximum amplitude above the RT_{100} threshold to estimate parturition. Finally, we added data from Aurignac to our dataset. In total, we obtained parturition events from 12 study sites (Figure 5).

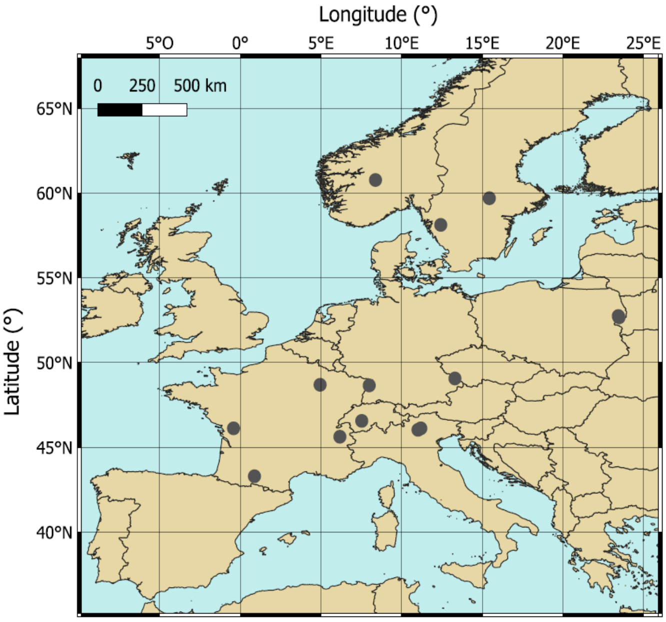

Figure 5. Map of Europe with the locations of the 12 study sites (grey dots). The lowest latitude corresponds to Aurignac, France (43.13°N), the highest to NINA west, Norway (60.77°N).

Populations from the different selected study areas occupy various landscapes, from intensively farmed agricultural areas fragmented by small woodland patches (e.g. Aurignac and Baden, Germany) to forests (e.g. Bavarian National Park; Cailleret et al., 2014) or pastoral landscapes. Some study areas are also characterized by a mountainous landscape with high elevations, e.g. Monte Bondone, north-east Italy (description in De Groeve et al., 2016) and Bernese Oberland in Switzerland. Latitudes were obtained based on the coordinates of the centroid of each study area or sub-area. Indeed, certain study sites can be divided in sub-sites with different environmental characteristics. Median altitudes were also collected for each individual based on its GPS locations (range: 48-1702 meters a.s.l.). Prior to analyses, we removed individuals with no data on the median altitude of their GPS locations. We aimed to extract the average start of the growing season of vegetation for each study area, derived from the MODIS Normalized Difference Vegetation Index (NDVI) across Europe (https://modis.gsfc.nasa.gov) but were unable to access the data. Therefore, we used latitude and altitude as a proxy of plant phenology in our study. Indeed, the onset of vegetation directly depends on climate, which varies along a latitudinal and altitudinal gradient. These gradients have similar patterns as climatic conditions are harsher and result in a marked seasonality at their extremity (Hopkins, 1938). In this sense, latitude and altitude are reliable predictors of plant phenology at large scales. Hopkins' bioclimatic law relates spatial patterns of phenological timing with latitude and altitude and predicts a delay in key phenological events for plants of 4 days for each increase of 1° in latitude and 120 m in altitude (Hopkins, 1938). However, to meet energetic requirements during lactation and maximize juvenile survival, roe deer should synchronize parturition with the peak in forage availability. Accordingly to Hopkins' law, and based on previous work from Peláez et al. (2020), we thus expected roe deer parturition timing to occur later with increasing latitude and altitude, related to spatial variation in plant phenology.

Statistical analyses

In order to test our hypotheses, we used linear mixed models (LME) from the package 'lme4' (Bates et al., 2015). To control for pseudoreplication, we assigned the identity of mothers and year as random effects in all models. Indeed, 11 females were monitored in more than one year in Aurignac, and 89 in our dataset from the EURODEER collaborative database. To control for the effect of age (yearling or adult) on parturition date, we assigned age class as a fixed effect in all models.

In model (1), associated with hypothesis (1), we included mass and the interaction between mass and age as fixed effects. Indeed, we expected parturition date to occur later in yearlings due to a trade-off between the allocation of resources in reproduction and somatic growth (Plard et al., 2014). We also expected the effect of maternal mass to differ according to the maternal age class. Moreover, we included the proportion of closed habitats in the maternal home range in this model and its interaction with age class to account for variations in parturition timing among age classes in relation to habitat composition. Additionally, we assigned the method used to estimate parturition date (fawn capture or RT_{100}-based approach) as a fixed effect and its interaction with the proportion of closed habitats in the individual home range. This would allow us to detect any difference in estimations between both methods. Finally, as the length of individual monitoring was variable between females, we gave more weight to females with more GPS data in model (1).

In model (2), all covariates were included as fixed effects (Table 1). In addition, we included the study area as a random effect to control for a cohort effect. Please note that we could not include data on the start of the growing season in this model and test our hypothesis (3) as we did not manage to have access to phenological data for our study.

All models were ordered using the second-order Akaike information criterion (AIC_c) and Akaike weights (Burnham & Anderson, 2002). Models with $\Delta AIC_c < 2$ offer a similar level of support to explain variation in the response variable. According to the parsimony principle, we then selected from these models the one with the fewest parameters. We verified the distribution and homoscedasticity of residuals from the best models. Finally, we plotted the predictions of the best models with their associated 95% confidence intervals and used the function 'rsq.lmm' from the package 'rsq' to estimate the marginal coefficient of determination R^2, which corresponds to the proportion of variance explained by the fixed factors only (Zhang, 2020). All analyses were performed with R Studio (RStudio Team, 2020). A script is provided in Appendix 3.

Table 1. Linear mixed models (LME) used to test our two hypotheses.

Hypothesis	Fixed effects	Data
(1)	Parturition date ~ habitat[a] + age + method + mass + age*habitat + method*habitat + mass*age	Aurignac (n = 110)
(2)	Parturition date ~ latitude + altitude + age	EURODEER and Aurignac (12 study areas, n = 393)

[a] Proportion of closed habitats in the maternal home range

RESULTS

Using residence time to infer parturition in roe deer

When specifying that the peak associated with parturition was the one closest to the median in the Aurignac population (12 May), our RT_{100}-based approach performed the best with a threshold of 20h, a minimum duration of 24h (D_{min}) and a tolerance between 6 to 8% in the proportion of data above the threshold (Table 2). This combination of parameters helped to minimize the error rate of the approach and the median difference with the observed parturition date from fawn capture which was 82 hours ($\Delta Part_{cross}$). We identified parturition in 51/61 reproductive females (84%) and correctly predicted 25/41 non-reproductive juveniles (61%) as non-parturient. The estimated parturition date was the closest to the parturition date estimated from fawn capture when we specified the timing of parturition as the moment the data exceeded the threshold value, i.e. at the beginning of the detected RT_{100} peak. We detected parturition from this combination of parameters in 20/26 (77%) reproductive females with unknown parturition date and 13/20 (65%) females with unknown reproductive status (33 parturition events detected in total). Examples of RT_{100} profiles are provided in Appendix 4.

By running the method separately for females living in the three different types of landscape, we increased accuracy by 2% (overall rate of true predictions), sensitivity by 1% (rate of reproductive females well predicted as parturient) and specificity by 7% (rate of non-reproductive females well predicted as non-parturient). However, this approach identified parturition in 17/26 (65%) reproductive females with unknown parturition date and 14/20 (70%) females with unknown reproductive status (31 additional parturition events in total). It also helped us to decrease the difference between estimated parturition date and observed parturition date by 9 hours only. the median difference to parturition date estimated by direct observations was important in females captured in closed habitats (between 229h and 250h).

Table 2. Performance of the general RT_{100}-based approach to infer parturition. Values of T_{RT100} (threshold), D_{min} and tolerance represent the combination of parameters that minimized the overall error rate and the time difference with the observed parturition date (from fawn capture), ΔPart.

T_{RT100}	D_{min}	Tolerance	Accuracy	Sensitivity	Specificity	$\Delta Part_{cross}$	$\Delta Part_{wm}$	$\Delta Part_{med}$
20h	24h	6-8%	75% 76/102	84% 51/61	61% 25/41	82h	93.1h	93.5h

Table 3. Performance of the RT_{100}-based approach per landscape structure (open/mix/closed habitat).

T_{RT100}	D_{min}	Tolerance	Accuracy	Sensitivity	Specificity	$\Delta Part_{cross}$	$\Delta Part_{wm}$	$\Delta Part_{med}$
Open habitat								
20h	36h	10%	78% 49/62	86% 31/36	69% 18/26	65h	105.4h	103.5h
Mix habitat								
18h	36h	20%	81% 17/21	80% 12/15	83% 5/6	75h	47.2h	45.5h
Closed habitat								
17h	12h	18-20%	74% 14/19	90% 9/10	56% 5/9	229h	250h	250h

When specifying that the peak associated with parturition was the one with the maximum amplitude, we obtained similar results as in the previous approach. However, the median difference to the observed parturition date was higher. Indeed, it was estimated on average 20.8 hours later across the three methods to estimate the timing of parturition ($Part_{cross}$, $Part_{med}$, $Part_{wm}$), compared to the approach that assigned a parturition event to the peak that was closest to the median in the population. This approach also detected parturition on 33 additional females (20 with an unknown parturition date and 13 with an unknown reproductive status). Moreover, the approach by capture site identified parturition in 31 additional females. Full results for this approach based on the amplitude of RT_{100} peaks are available in Appendix 5.

Method validation on a Bavarian roe deer population

This population was characterized by an average RT_{100} of about 6 hours over the individual study period (n = 21), which was about 2 times less than roe deers from Aurignac, France (14 hours, n = 102). Only 5 reproductive females were detected as parturient in this roe deer population from Bavaria, Germany. Moreover, the median difference to the observed parturition date was 3 days in the best case. Both non-reproductive females were well predicted as non-parturient (Table 4).

Table 4. Performance of the RT_{100}-based approach applied to a population of roe deer from Germany. T_{RT100}, D_{min} and Tolerance were determined according to the results in the roe deer population from Aurignac.

T_{RT100}	D_{min}	Tolerance	Sensitivity	Specificity	$\Delta Part_{cross}$	$\Delta Part_{wm}$	$\Delta Part_{med}$
20h	24h	6-8%	26% 5/19	100% 2/2	3 days	5 days	5 days

Effect of habitat composition on the timing of parturition

The model that best described the variation in the timing of parturition in roe deer females in Aurignac, France (n = 110) included, as fixed effects, the proportion of closed habitat in the maternal home range, the age class of the female (yearling vs. adult), the method used to estimate parturition date (observed vs. inferred) and the interaction between the age of the female and the proportion of closed habitat in her home range ($AIC_c = 816.81$, $\Delta AIC_c = 0$, $AIC_cWt = 0.26$, Table 5).

Table 5. Summary of the models describing the effect of habitat composition on the timing of parturition in female roe deer in Aurignac, France (n = 110). Model selection was based on the second-order Akaike information criterion (AIC_c, Burnham and Anderson, 2002). AIC_cWt corresponds to the weight of the model. Only models with $\Delta AIC_c < 5$ and the null model are shown in the table. The model that best described the variation in parturition date is in bold. K is the number of parameters estimated for each model. 'habitat' corresponds to the proportion of closed habitats in the maternal home range.

Model	K	AIC_c	ΔAIC_c	AIC_cWt
habitat + age + method + age * habitat	**8**	**816.81**	**0**	**0.26**
habitat + age + method + mass + age * habitat	9	817.34	0.53	0.19
habitat + age + method + age * habitat + method * habitats	9	818.74	1.93	0.10
habitat + age + method + mass + age * habitat + method * habitat	10	819.09	2.28	0.08
habitat + age + method + mass	8	819.41	2.60	0.07
habitat + age + method + mass + age * habitat + age * mass	10	819.47	2.67	0.07
habitat + age + method	7	820.45	3.63	0.04
habitat + age + method + mass + age * mass	9	820.56	3.74	0.04
habitat + age + method + mass + method * habitat	9	820.69	3.88	0.04
habitat + age + method + mass + age * habitat + age * mass + method * habitat	11	821.35	4.54	0.03
Null model	4	849.68	32.87	10^{-8}

Parturition was about 5.52 days earlier when inferred using the RT_{100} method rather than direct observations. Parturition was also earlier when the proportion of closed habitat in the maternal home range was higher, but this was only true for adults and not yearlings. Indeed, adults living in closed habitats (100% of closed habitats in the home range) gave birth on average 18 days before adults living purely in open habitats (Table 6 and Figure 6). Habitat composition did not seem to significantly influence birth timing in yearlings. However, yearlings gave birth about 3.47 days later than females in open habitats. This lag in parturition date between yearlings and adults increased by 0.21 days every additional 1% of closed habitat in the home range. The fixed effects of the model explained 34% of the total variance (${}_{\text{marginal}}R^2 = 0.34$). A R script of the statistical approach with outputs and additional summary statistics is provided in Appendix 3.

Table 6. Estimates and associated 95% confidence intervals as predicted by the best-supported model (n = 110 parturition dates).

Predictors	Estimates	95% CI
(Intercept)	132.31	[127.90, 136.72]
Age (yearling)	3.47	[-2.32, 9.27]
% closed habitats in the home range	-0.18	[-0.28, -0.09]
Method (direct observations)	5.52	[2.16, 8.88]
Age (yearling * % closed habitats)	0.21	[0.04, 0.38]

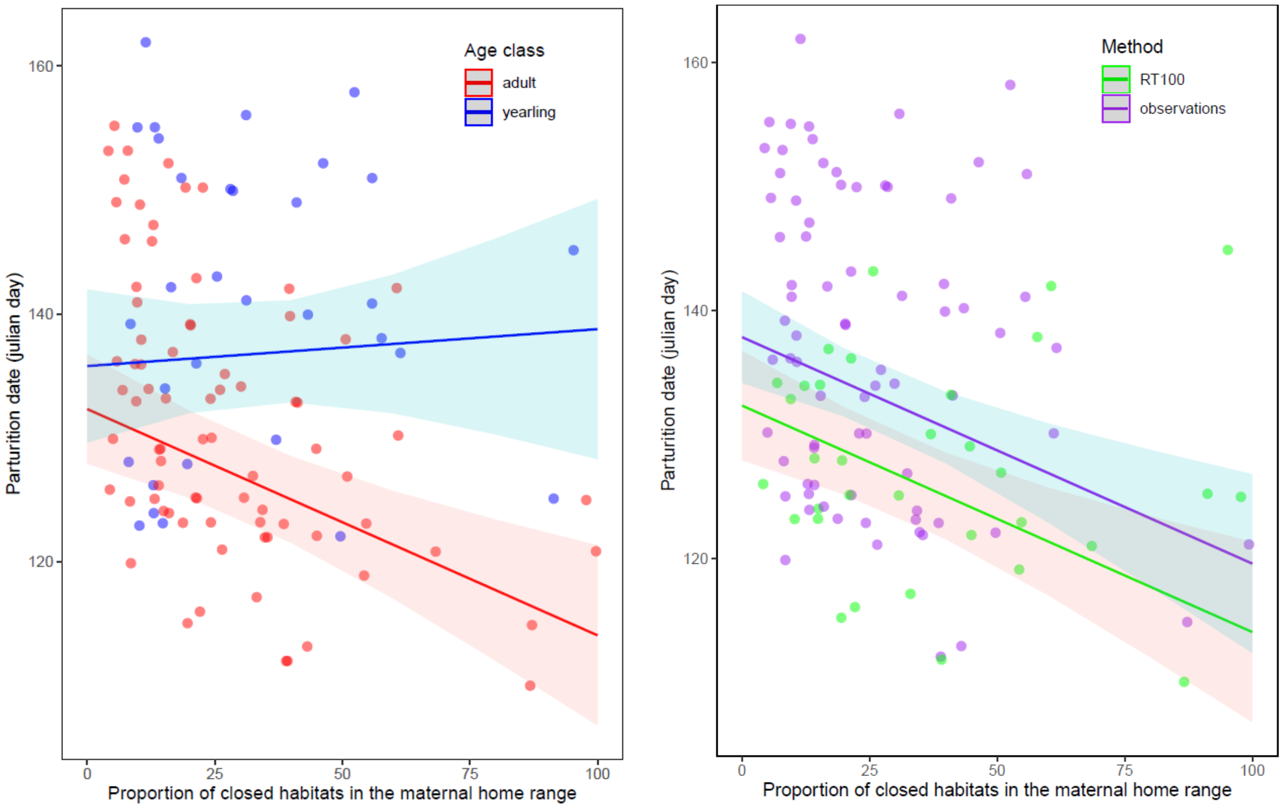

Figure 6. Relationship between parturition date and the proportion of closed habitats in the maternal home range as predicted by the best model (n = 110, $_{\text{marginal}}R^2 = 0.35$), depending on the age class of the females (left) or the method used to estimate parturition date (direct observations or RT_{100}-based method, on the right). Shadows around the best-fit lines represent 95% confidence intervals.

Variation in parturition date along a latitudinal and altitudinal gradient

We detected parturition events in 314/388 (81%) females from the 11 study areas selected and only kept 79/110 parturition dates from Aurignac as no information on the altitude of GPS locations was available for 21 females. Therefore, we obtained data on 393 parturition events across Europe from 12 study areas in total. The model that best described the variation in the timing of parturition in roe deer females included latitude, altitude and age as fixed effects ($AIC_c = 2970.54$, $\Delta AIC_c = 0$, $AIC_cWt = 0.75$, Table 7).

Table 7. Summary of the models describing the variation in parturition timing along a latitudinal and altitudinal gradient (n = 393). Model selection was based on the second-order Akaike information criterion (AIC_c, Burnham and Anderson, 2002). AIC_cWt corresponds to the weight of the model. Only models with $\Delta AIC_c < 10$ and the null model are shown in the table. The model that best described the variation in parturition date is in bold. K is the number of parameters estimated.

Model	**K**	**AIC_c**	**ΔAIC_c**	**AIC_cWt**
latitude + altitude + age	**8**	**2970.54**	**0**	**0.75**
latitude + altitude	7	2972.73	2.18	0.25
Null model	5	2992.274	21.73	10^{-5}

Yearlings consistently gave birth about 2.93 days later than adults. Additionally, parturition date in both age classes increased with latitude and altitude (Table 8 and Figure 7). Indeed, females from the lowest latitude (43.13°N) gave birth on average 19.8 days earlier than females from the highest latitude (60.77°N). In the same way, females from the lowest altitudes gave birth on average 21.5 days earlier than females living in the highest altitudes (range: 48-1702 meters). The effect of 1°N increase in latitude was similar to 87 m increase in altitude. The fixed effects of the model explained 26% of the total variance ($_{\text{marginal}}R^2 = 0.26$).

Table 8. Estimates and associated 95% confidence intervals as predicted by the best-supported model (n = 393 parturition dates).

Predictors	Estimates	95% CI
(Intercept)	81.07	[59.9, 102.23]
Age (yearling)	2.93	[0.16, 5.69]
Latitude	1.12	[0.72, 1.52]
Altitude	0.01	[0.01, 0.02]

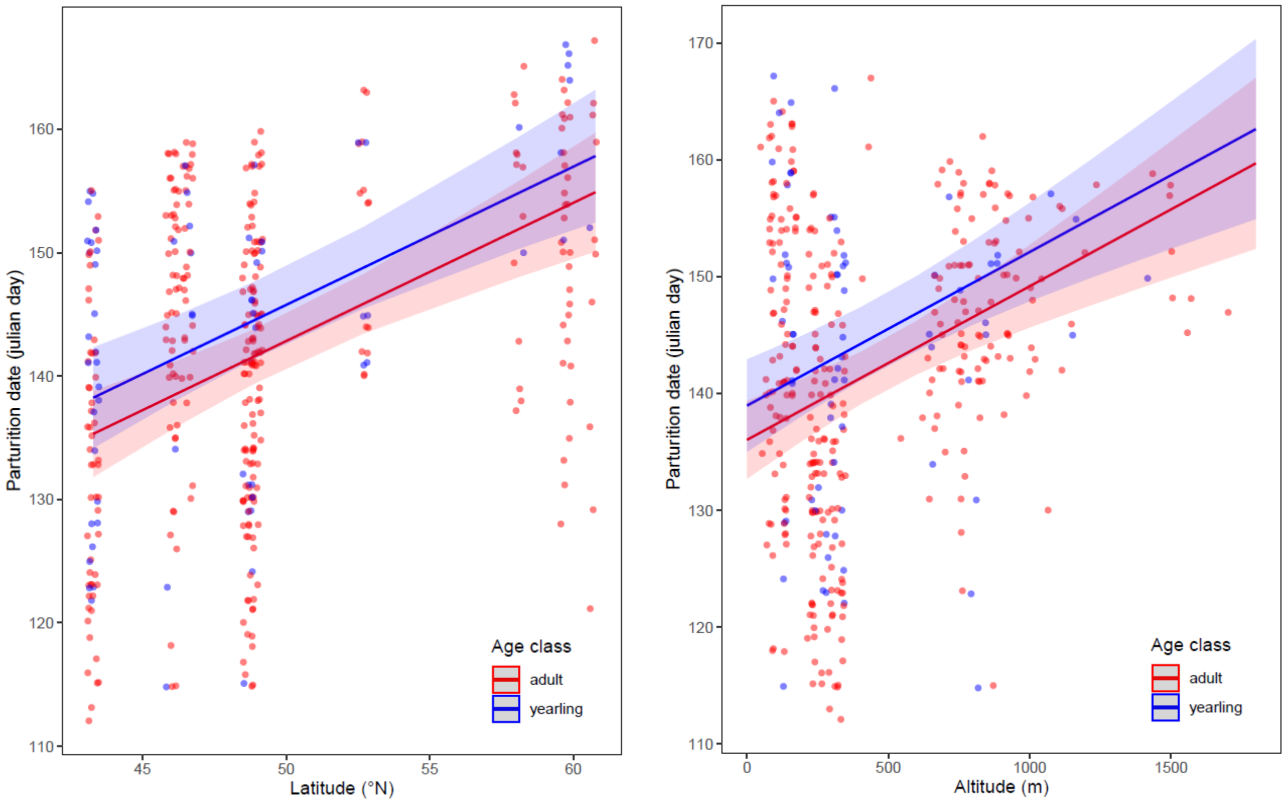

Figure 7. Relationship between parturition date, latitude and altitude, as predicted by the best model (n = 393, $_{\text{marginal}}R^2 = 0.26$), depending on the age class of the females. Shadows around the best-fit lines represent 95% confidence intervals.

DISCUSSION

Using a simple approach based on the residence time (RT_{100}) of females around GPS relocations in a French population of roe deer (Aurignac), we were able to infer parturition occurrence and timing with reasonable confidence. We indeed obtained a sensitivity of 84% and a mean time interval of 82 hours between birth timing detected by our approach and the one estimated from direct observations of fawns in hands. Although this approach provided more contrasted results in detecting the absence of parturition in non-reproductive females (specificity: 61%) and in another roe deer population (Bavaria, Germany), it allowed us to reveal that adult females from the Aurignac population gave birth earlier with increasing proportion of closed habitats in their home range (contrary to our hypothesis). We also found evidence for variation in the timing of parturition along a large latitudinal and altitudinal gradient, probably coinciding with variation in plant phenology. This approach hence constitutes a step forward in the inference of such important events in the life-cycle of animals and may hence provide a simple tool to investigate further reproductive ecology and phenology in a context of climate change and increasing human encroachment into natural areas.

The accuracy of our approach was in the range of accuracies from previous approaches developed to infer parturition in different ungulate species (76-100%) (Dzialak et al., 2011; DeMars et al., 2013; Marchand et al., 2021; Mohr et al., 2020; Hooven et al., 2022). However, only Marchand et al. (2021) worked on parturition timing in roe deer, while other studies mainly focused on migratory or bigger ungulate species, with higher movement rates than roe deer (Tucker et al., 2018). Studying parturition timing in species with long step lengths may be easier as breaking points in movement metrics may be more easily detectable and thus explain why these approaches worked better in larger/ highly mobile species. Moreover, multi-metric approaches based on machine learning predictions are quite complex and not generalizable to every population as data on environmental parameters or activity may not be available in all study areas. We chose to use the metric that was the most informative in the prediction of roe deer parturitions in Marchand et al. (2021) to simplify the existent approaches to infer parturition and hence have proven that simple approaches can perform as well as more complex approaches. Indeed, our accuracy was less important by only 1% and our sensitivity higher by 4% compared to Marchand et al. (2021). However, this also proves that GPS data with higher resolution (1 fix/hour in Aurignac) may not help us improve the detection of parturitions.

When multiple peaks of residence time were detected in individuals, the approach considering the peak associated with parturition as the closest to the median in the population was the most performant. Indeed, it predicted parturition dates with a median difference to the observed parturition (estimated via fawn captures) of 82 hours. The approach selecting the peak with the maximum amplitude in individual profiles detected parturition timing with a median difference to the observed parturition date of 103 hours, which allowed us to use this approach to infer parturition in populations with an unknown median parturition date. It is more convenient to use this latter approach to infer parturition for big datasets. However, as there is already an uncertainty on the estimation of parturitions from direct observations on which we based the training of our method, inferences may be more or less accurate. Important errors in estimations from our approach were mostly due to the presence of other important peaks in residence time in some female profiles (see Appendix 4 for examples). We failed to improve further our detection of parturition in these females. Multiple hypotheses could explain why females have peaks in residence time days before or after parturition.

For instance, a few females may reduce their movement around located productive areas or because of extreme weather conditions, although rare during the fawning season (Thurfjell et al., 2013 in wild boar). Another hypothesis would be that the mortality of fawns could affect the behaviour of females. Indeed, some females were observed to stay around fawns after their death, especially when fawns suffered from cachexia. However, data on the mortality of fawns was not available for all females in Aurignac to investigate further this issue. The hunting season starting in June may also explain why females would stay in specific areas and constrain their movement (Picardi et al., 2018). Other mechanisms affecting the residence time of females around areas remain unknown, but individual behaviour probably plays an important role and should thus be considered when studying parturition. As roe deer females are from the hider type, they are more independent from their fawns but come to the bedding site a few times a day to feed them. Therefore, for females with multiple peaks in residence time, an eventual approach to detect the one associated with parturition would be to localize areas associated with high residence times and estimate the frequency of recursions in each of these areas (Riotte-Lambert et al., 2013). However, doing this at the scale of individuals may be time-consuming and only fine-scale GPS data would allow to detect these recursions with precision.

Our approach provided more contrasted results when investigating the absence of parturition in non-reproductive females (specificity). Indeed, only 61% of non-reproductive juveniles were well predicted as non-parturient in the general approach. Even though dispersers were removed from our dataset, juveniles can have a particular movement pattern that mimicks the behaviour of females around parturition and influence our ability to predict them as non-parturient. For instance, juvenile explorers may stay longer around located areas (Ducros et al., 2020) and may hence not be the best control for our approach. However, we did not have a lot of data on non-reproductive females in the population from Aurignac, especially because adult females are almost all pregnant every year. Conception rate in a population of roe deer can reach 98% (Gaillard et al., 1992). In comparison, other studies working on approaches to infer parturition in ungulates used portable ultrasound to detect pregnancy in captured adult females (e.g. Mohr et al., 2020; Hooven et al., 2022 in elk). Although these tools may be useful to detect non-reproductive females, they are also very expensive.

By separating our RT_{100}-based approach into different categories of capture sites depending on their landscape structure, we slightly increased the accuracy of our method (1%), mainly due to an increase in specificity (7%). However, we did not improve our estimation of parturition dates in females with unknown reproductive status or parturition date and hence did not consider the effect of habitat to be significant enough to be accounted in our approach. In addition, we did not manage to find a statistical relationship between the average RT_{100} over individual study periods and the proportion of closed habitats in the home range of females, and thus decided not to present these results. Average RT_{100} of females was highly influenced by its increase around parturition and did not help us identify variations between habitats.

Despite the results we obtained in the Aurignac population, we did not manage to extrapolate our RT_{100}-based approach to a population from Bavaria, Germany. In most cases, females did not spend a higher time around a specific location, and oscillations in residence times were quite regular, without at least one peak being more detectable than the others. A few females also had an estimated parturition date from fawn capture at moments where no peaks in residence time were detected at all. Additionally, the residence time of females around restricted areas from this population was on average more than twice lower (around 6 hours) than in Aurignac (14 hours). Females from this study area have relatively small home ranges and high roe deer densities that may increase competition for resources in females (Kjellander et al., 2004). This may constrain females to move more in these small areas in order to find high-quality forage. This could be especially true for females living in closed habitats where resources are even more dispersed (Hewison et al., 2009). The performance of our approach to infer parturition may therefore depend not only on individual behaviours but also on the general behavioural pattern of a given population, which may depend on other factors (such as density) and be highly variable across study areas. However, it is important to note that despite the low sensitivity of our approach in this population (26%), the median time interval between inferred birth timing and the one estimated from fawn capture was 3 days. This result is therefore very similar to what we obtained in Aurignac. This suggests that even though individual behaviour or other external constraints may alter our ability to detect parturition in some females, our estimation of parturition timing was accurate for predicted parturient females. We are aware of the importance of validation when developing such approaches and we felt that this approach could be used to address other hypotheses related to variations in parturition date. However, in the future, in the same way that we did with Aurignac on investigating the influence of habitat composition on movement, further research should be done to understand why parturition events cannot be detected in some females, and particularly to estimate what may alter our ability to detect parturition.

We identified an effect of habitat composition on the timing of parturition in females from Aurignac. However, this effect was contrary to our hypothesis that females exploiting more open habitats give birth earlier than females living in open habitats. Indeed, adult females gave birth 1.8 days earlier every 10% increase in closed habitat in the home range. It is known that females giving birth earlier in the growing season can benefit from resources of high-quality for a longer time and hence provide a nutritious milk for their offspring which can have short and long-term effects on neonates (Plard et al., 2014). This difference in parturition timing between habitats could be related to a stronger selective pressure towards earlier parturition in closed habitats than in more open habitats. Indeed, open habitats provide forage of high quality for a longer period during the year as the phenology of crops or meadows can differ between fields depending on the plant species. Additionally, multiple growing seasons per year can be observed in open habitats, especially with intercropping. Therefore, the duration of the growing season in closed habitats should be more constraining and lead to local adaptations in parturition timing. To confirm this differential selective pressure between habitats, it would be interesting to study correlations between parturition dates from individuals of the same generation and their fitness. However, long-term data on the same individuals are difficult to obtain. Potential fitness could however be estimated via data on reproductive success. Moreover, open habitats may mitigate the effects of climate change on this species for which some populations do not seem to be able to match parturition date with the vegetation onset (Plard et al., 2016) and impact more individuals exploiting closed habitats. It would be interesting to compare the degree of coincidence between parturition and the vegetation onset between habitats to confirm this hypothesis. Another explanation for earlier parturitions in closed habitats would be that it results from a trade-off between resource acquisition and predation risk (Bongi et al., 2008). Indeed, open habitats are also characterized by a high predation risk from red fox (*Vulpes vulpes*) (Jarnemo, 2004). In such habitats, fawns born earlier or later than the peak in parturitions may not benefit from a dilution effect (Jarnemo et al., 2014) and may be highly vulnerable to predation risk. It is especially true at the beginning of the fawning season when the vegetation height in open habitats is not optimal for fawns to hide. Therefore, females giving birth earlier may exploit closed habitats as a strategy to mitigate predation risk, even though forage may be of lower quality than in open habitats. Surprisingly, we did not detect this effect of habitat composition on parturition date in yearlings. This may be explained by the limited sample of parturition dates that we had from this age class compared to adults (29%), especially for parturition events in closed habitats. Indeed, yearlings may be less captured because they disperse more. Another possible explanation would be that there is a trade-off between energy allocation for reproduction and growth in yearlings, as parturition date in yearlings corresponds to their first pregnancy (Gaillard et al., 1992). Moreover, we identified that our approach to infer parturition in roe deer estimated new parturition dates earlier than fawn captures. This may be explained by the difficulty to hand-catch fawns in closed habitats. Females giving birth early may be missed during the capture season which starts at the end of April each year. Therefore, our approach may be very useful to estimate early parturition dates and especially in closed habitats.

Moreover, we found that parturition timing occurred later with increasing latitude and altitude. Females at the highest latitude gave birth on average about 19.8 days later than females from the lowest latitude (range: 43.13°N-60.77°N), where the onset of vegetation should occur earlier (Rötzer & Chmielewski, 2001). These results are consistent with previous work from Peláez et al. (2020), in which a difference of 18 days in parturition timing between the lowest and the highest latitude was found (range: 40°N-64°N). Moreover, in our study, the effect of 1°N increase in latitude was similar to a 87 m increase in altitude. Therefore, we have proven that the timing of parturition in roe deer is adjusted along a latitudinal and altitudinal gradient, probably to match the peak in abundance and quality of forage resources. Indeed, plant phenology was already reported to be a driver of parturition in other large herbivores (e.g. Stoner et al., 2016 in mule deer). Neumann et al. (2020) have also proven that the reproductive phenology of moose occurred later with increasing latitude, in relation with plant phenology. However, further investigation with data on plant phenology is needed to verify the correlation between phenology of roe deer and the vegetation onset, as well as to verify the degree of coincidence between both. We aimed to answer this issue in hypothesis (3) but did not have access to phenological data across Europe. This would have allowed us to test for variations in the difference between the start of the growing season and the birth phenology of roe deer along a latitudinal and altitudinal gradient. In our study, we identified parturition timing to occur on average 1.12 days later with an increase of 1°N in latitude. Hopkin's bioclimatic law predicted plant phenology to be delayed by 4 days per degree of increase in latitude (Hopkins, 1938). With current climate change, recent studies have predicted plant phenology to be delayed by 1.8 to 3.1 days per degree of increase in latitude (Burgess et al., 2018; Geng et al., 2022). These delays in plant phenology are more important than what is observed in roe deer phenology (more important slope). Therefore, we can imagine the peak in roe deer parturition dates to be closer to the onset of vegetation at higher latitudes, probably as a strategy to mitigate the effect of short growing seasons (Neumann et al., 2020). More importantly, different papers reported the inability of roe deer reproductive phenology to match the peak in foraging resources at the level of populations with increasing climate change (Plard et al., 2016; Rehnus et al., 2020). Even though roe deer parturition seems to be adjusted with plant phenology along a latitudinal and altitudinal gradient, we suggest that the response of roe deer phenology to climate change may strongly depend on the intensity of this change and local environmental conditions.

To conclude, studying the reproductive phenology of animals is important to predict population dynamics (Gaillard et al., 2000). The timing of births determines juvenile survival and can have long-term effects on the life-history trajectory of individuals (Plard et al., 2014). Therefore, there is an urgent need to understand the consequences of global change on reproductive phenology in order to implement management plans to protect females and neonates from the disturbance of human activities. In this sense, we developed a simple approach to infer parturition in roe deer based on the residence time of females around restricted areas. Contrasting results obtained in different populations suggest that our approach may be improved by further research and especially relies on the identification of factors affecting the movement of females around parturition. However, we managed to identify variation in parturition timing along environmental gradients at the level of a population and at a larger scale, suggesting a possible ability of roe deer to adjust its phenology at large scales. Therefore, we suggest that this approach may be useful to address issues at the level of populations or species, and may be generalized to other species with observed behavioural changes around parturition events.

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APPENDICES

Appendix 1. R script to compute the residence time of females within a circle of 100-meter radius from a data frame. We used the function ‘residenceTime’ from the package ‘adehabitatLT’ (Calenge et al., 2006).

```
setwd("~/path/to/working/directory")

# load data
load("data.RData")

# our dataframe contains a column with:
## - the identity of the individual ("id" hereafter)
## - dates associated with each pair of coordinates (format POSIXct)
## - coordinate x
## - coordinate y
## - the known parturition date of the individual (not mandatory) (“part_date”)
## - the name of the study area (not mandatory) (“study_area”)

library(adehabitatLT)
traj <- data

# convertion into an objet of class ltraj containing the trajectory of the animal
# the function as.ltraj stores the coordinates (x, y) and creates different
variables:
## - dx = increase of the move in the x direction
## - dy = increase of the move in the y direction
## - dist = length of each move
## - dt = time interval between successive relocations
## - R2n = squared net displacement between the current relocation and the first
relocation of the trajectory
traj <- as.ltraj(xy = traj[, c("x","y")], id = traj$id, date =
as.POSIXct(traj$date), infolocs = data.frame(part_date = traj$part_date,
study_area = traj$study_area))

# convertion of the ltraj object into a dataframe
traj <- ld(traj)

# recalculate R2n based on the distance between the current relocation and the
barycentre of the trajectory of the locations (Marchand et al., 2021) (not from
the first relocation of the trajectory)
traj <- as.ltraj.nsd.barycentre(traj[,c("x","y")], date = as.POSIXct(traj$date),
id = traj$id, infolocs = data.frame(female = traj$female, part_date =
traj$part_date, study_area = traj$study_area))
data <- ld(traj)
data <- data[!is.na(data$x), ]
pts <- data
coordinates(pts) <- c("x", "y")
```

```r
# RESIDENCE TIME OF FEMALES AROUND GPS LOCATIONS

slwin <- 48 # sliding window of 48 hours
for(indiv in unique(data$id)){
  sub <- data[data$id %in% indiv,]
  sub <- droplevels(sub)

  # the function sliwinltr used below imposes to create an ltraj object and to compute R2n from the first relocation of the trajectory
  # we want R2n from the barycentre of the points
  # we will reaffect the new value of R2n after recreation of ltraj object
  latraj <- dl(sub)
  goodR2n <- sub$R2n
  sub <- droplevels(sub)
  trj <- dl(sub)
  trj[[1]]$R2n <- goodR2n

  # calculate residence time within a circle of 100-meter radius in seconds (RT100)
  # maxt = 1: the individual is not allowed to spend more than 1 sec outside the circle (no tolerance)
  trj <- residenceTime(trj, radius = 100, maxt = 1, addinfo = T, units = "sec")

  # mean of RT100 values over a sliding window of 48 hours (24 points before and 24 points after the GPS location; step = 24 values)
  # the final results are in sec but we divided by 3600 to obtain the mean in hours
  sub$rt100sw <- as.numeric(sliwinltr(trj, function(x){mean(x$RT.100, na.rm = T)}, step = slwin/2, type = "time", units = "hour", plotit = F)[[1]]$y)/3600

  # store the results in a dataframe for each individual
  subfin <- sub[,c("id", "date", "rt100sw", "part_date", "study_area")]
  subfin$date <- round(subfin$date, "hour") # round the date
  subfin$date <- as.character(subfin$date)
  res <- subfin
  res$date <- strptime(res$date, format = "%Y-%m-%d %H:%M:%S")
  print(paste(which(unique(data$id) %in% indiv), length(unique(data$id)), sep="/")) # counter
  save(res, file=paste("your/path/data_female_", indiv, ".RData", sep=""))
}

# bind all the files to obtain one dataframe with all the values of RT100 for each female
fichiers <- list.files("your/path/", pattern =".RData", full.names=T)
dataok <- do.call(rbind, lapply(fichiers, function (x){
  load(x)
  return(res)
}
))
```

Appendix 2. R script to identify parturition events in individual profiles of residence time (RT_{100}). We sought to identify sequences with a certain proportion of data above a RT_{100} threshold for a given minimum duration. We varied three parameters: a RT_{100} threshold, a minimum duration above this threshold (D_{min}) and a tolerance on the proportion of data below this threshold (which equals to 1 – proportion of data above a threshold).

```
setwd("~/path/to/working/directory")

# load data
load("data_rt100.RData")
# this dataframe contains at least:
## - a column with the identity of the individual ("cap_bague" hereafter)
## - a column with dates (POSIXct format)
## - a column with values of RT100 ("rt100sw" hereafter)
## - a column with known parturition (if known)
## - a column with the reproductive status of females (if known)

# specify parameters to test
tvalues <- seq(10, 50, 2) # test different thresholds
durations <- seq(12, 48, 12) # test durations (duration with data > threshold)
tolerances <- seq(0, 20, 2) # test tolerance (proportion of data < threshold)

# specify the median parturition date in the population if known
medianref <- strptime("2021-05-12", "%F")$yday

# the function birth_date() takes into arguments:
## - the identity of the individual (id)
## - 3 parameters: a threshold, a duration, a tolerance
## - the resolution of the GPS data (prog = 1 means 1 fix/hour)
## it returns a list
# the library 'zoo' is required

res <- list()
for(id  in  unique(data_rt100$cap_bague)){birth_date  <-  function(id,  threshold,
duration, tolerance, prog = 1){

  # subset your dataframe for each individual
  sub <- data_rt100[data_rt100$cap_bague %in% id, ]

  # store dates and RT100 values separately
  sub <- sub[order(sub$date), ]
  tsdates <- sub$date
  tsrt100 <- sub$rt100sw

  # store all values of RT100 greater than the threshold
  yesno <- tsrt100 >= threshold

  # the function 'rollapply' computes the proportion of data > threshold within a
sliding window of amplitude duration/prog:
  # it counts the number of values above the threshold in the sequence
```

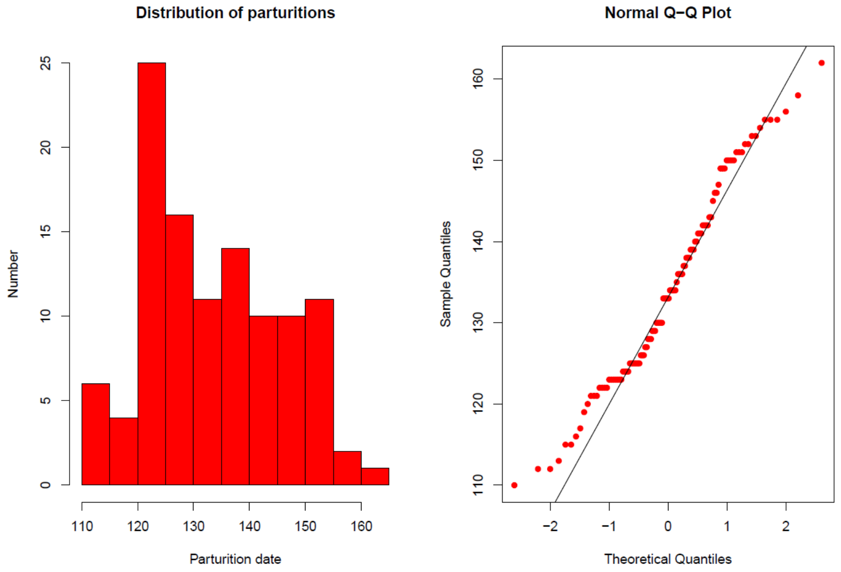
```
  tmp <- as.vector(zoo::rollapply(zoo::zoo(tsrt100), duration/prog,
function(x){mean(sum(as.numeric(x > threshold), na.rm = T), na.rm = T)}, fill =
NA, align = "left")) / as.vector(zoo::rollapply(zoo::zoo(tsrt100), duration/prog,
function(x){length(x[!is.na(x)])}, fill = NA, align = "left"))

  # the function 'rle' allows to identify sequences above a threshold with a
proportion > 1 - tolerance (%) of data:
  # it assigns "0" if the proportion of data is lower than 1 - tolerance or "1"
if it is not the case
  sequences <- rle(as.vector(as.numeric(tmp > (1-(tolerance/100)))))

  if(length(which(sequences$values == 1)) > 0){
    # a cumulative sum of "1" values is computed if such values are identified
(cumsum)
    toto <- data.frame(end = cumsum(sequences$lengths)[sequences$values %in%
"1"], duration = sequences$lengths[sequences$values %in% "1"])

    # for each sequence identified with a proportion 1- tolerance of data above
the threshold identified,
    # we noted the start and the end of the sequence, the duration
    # and stored other information about the individual to create a new dataframe
    toto$start <- format(sub$date[toto$end - toto$duration + 1], "%F %T")
    toto$end <- format(sub$date[toto$end], "%F %T")
    toto$duration <- as.vector(difftime(strptime(toto$end, "%F %T"),
strptime(toto$start, "%F %T"), unit="hours"))
    toto$id <- id
    toto$threshduration <- duration
    toto$threshrt100 <- threshold
    toto$tolerance <- tolerance

    # we only keep the sequences if their duration is greater than the minimum
duration fixed
    toto <- toto[toto$duration > duration,]
    toto <- toto[,c("id","threshduration", "threshrt100", "tolerance", "start",
"end", "duration")]

    # if one peak is detected: we associated it with a parturition event and
estimated parturition
    if(nrow(toto) > 0){
      for(line in 1:nrow(toto)){
        toto$rt100[line] <- mean(sub[sub$date >= toto$start[line] & sub$date <=
toto$fin[line],"rt100sw"], na.rm=T)
        toto$prop[line] <- sum(yesno[sub$date >= toto$start[line] & sub$date <=
toto$end[line]] / length(yesno[sub$date >= toto$start[line] & sub$date <=
toto$end[line]]))
        # 3 methods to infer parturition (see report):
        toto$mb_cross[line] <- format(min(sub$date[sub$date >= toto$start[line] &
sub$date <= toto$end[line]]), "%F %T")
        toto$mb_med[line] <- format(median(sub$date[sub$date >= toto$start[line]
& sub$date <= toto$end[line]]), "%F %T")
        toto$mb_wm[line] <- format(weighted.mean(sub$date[sub$date >=
toto$start[line] & sub$date <= toto$end[line]], w = sub[sub$date >=
toto$start[line] & sub$date <= toto$end[line], "rt100sw"], na.rm = T), "%F %T")
```

```
      }
      toto$mbseuilrt100 <- 1

    # if multiple peaks are detected, we keep the one that is the closest to the
median parturition date
      if(nrow(toto) > 1){
        toto <- toto[which.min(abs(strptime(toto$mb_wm, "%F %T")$yday -
medianref)),]
        # or: toto <- toto[which.max(toto$duree),] (when the median parturition
date is not known)
      }
      return(toto)
    }
    # if a RT100 peak is not detected with the fixed parameters, we assign NAs in
columns of the final dataframe for the individual
    else{
      return(data.frame(id = id, dmin = duration, trt100 = threshold, tolerance =
tolerance, start = NA, end = NA, duration = NA, rt100 = NA, prop = NA, mb_cross
= NA, mb_med = NA, mb_wm = NA, part_detected = 0))
    }
  }
  else{
    return(data.frame(id = id, dmin = duration, trt100 = threshold, tolerance =
tolerance, start = NA, end = NA, duration = NA, rt100 = NA, prop = NA, mb_cross
= NA, mb_med = NA, mb_wm = NA, part_detected = 0))
  }
}
for(threshold in tvalues){
  for(duration in durations){
    for(tolerance in tolerances){
      res[[paste(id, threshold, duration, tolerance, sep = "_")]] <- birth_date(id
= id, threshold = threshold, duration = duration, tolerance = tolerance, prog =
1)
      print(paste(id, threshold, duration, tolerance, sep = "_"))
    }
  }
}
save(res,file="your/path/res.RData")
}

# convert the list of results in a dataframe
res <- do.call(rbind, res)
```

Appendix 3. R script for the statistical analyses of hypotheses (1) and (2) accompanied by outputs to illustrate our approach and our results.

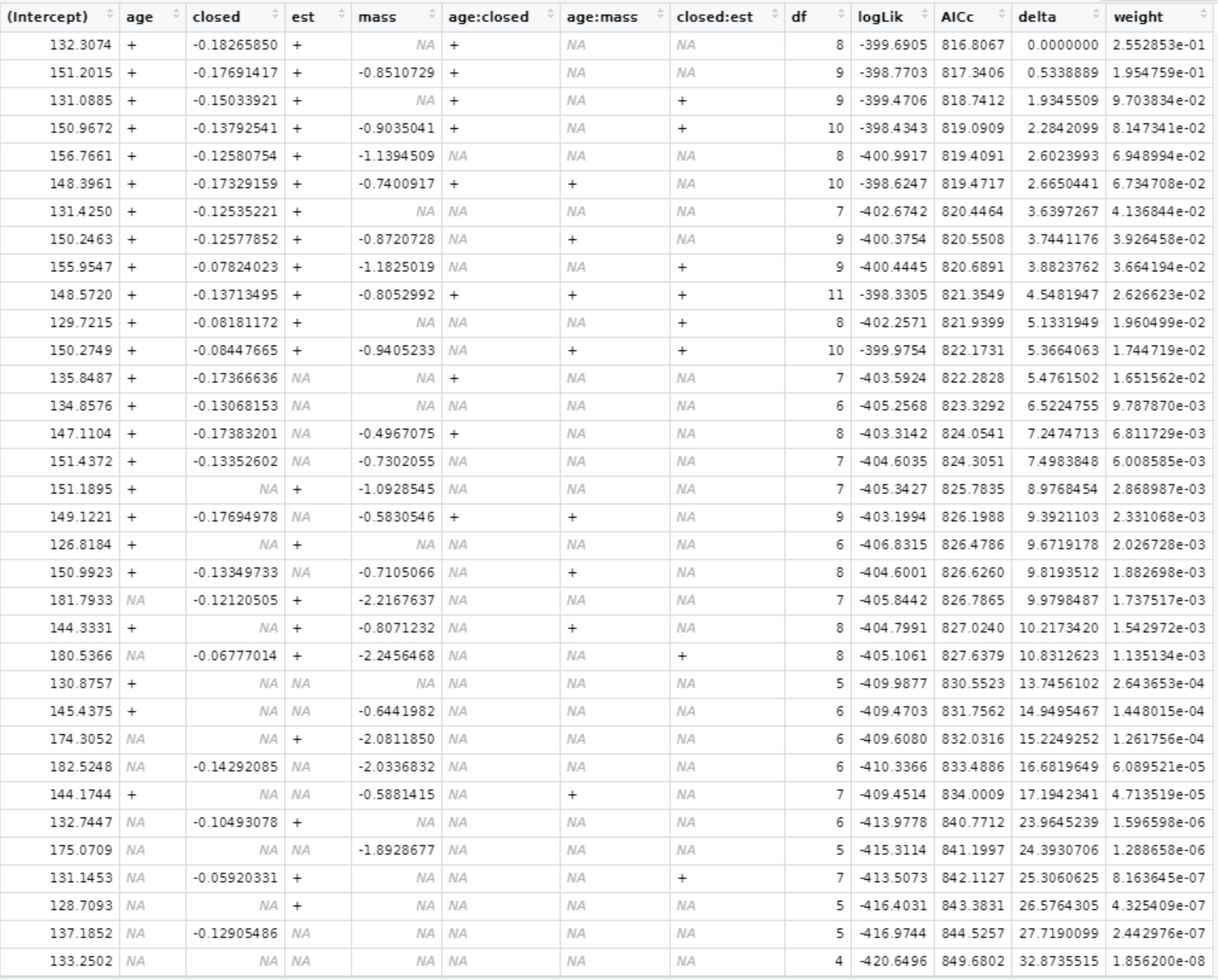
Hypothesis (1): we expected parturition date to be habitat-dependent so that births occurred earlier in mothers living in mainly open habitats.

```
# model to be built: linear mixed model (LMM)
# - dependent variable: parturition date (‘mb_deb’ hereafter)
# - fixed effects: proportion of closed habitat in the home range = closed
#    (numeric), method (factor, ‘est’ hereafter), mass (numeric), age class
#    (factor), interaction between mass and age class, interaction between method
#    and closed, interaction between age class and closed
# - random effects: identity (‘id’), year

# DATA EXPLORATION

# dataframe with the dependent and explanatory variables was named ‘mb’

# outlier detection
par(mfrow=c(1,1))
dotchart(mb$mb_deb, pch = 16, col = 'red')
# no outlier detected

# distribution of parturitions (we may have to transform our data)
par(mfrow=c(1,2))
hist(mb$mb_deb, breaks = 8, col = 'red', main = "Distribution of parturitions",
xlab = 'Parturition date', ylab = 'Number')
qqnorm(mb$mb_deb, col = 'red', pch = 16)
qqline(mb$mb_deb)
```



```
# MODEL SELECTION

library(lme4) # for linear mixed models
```

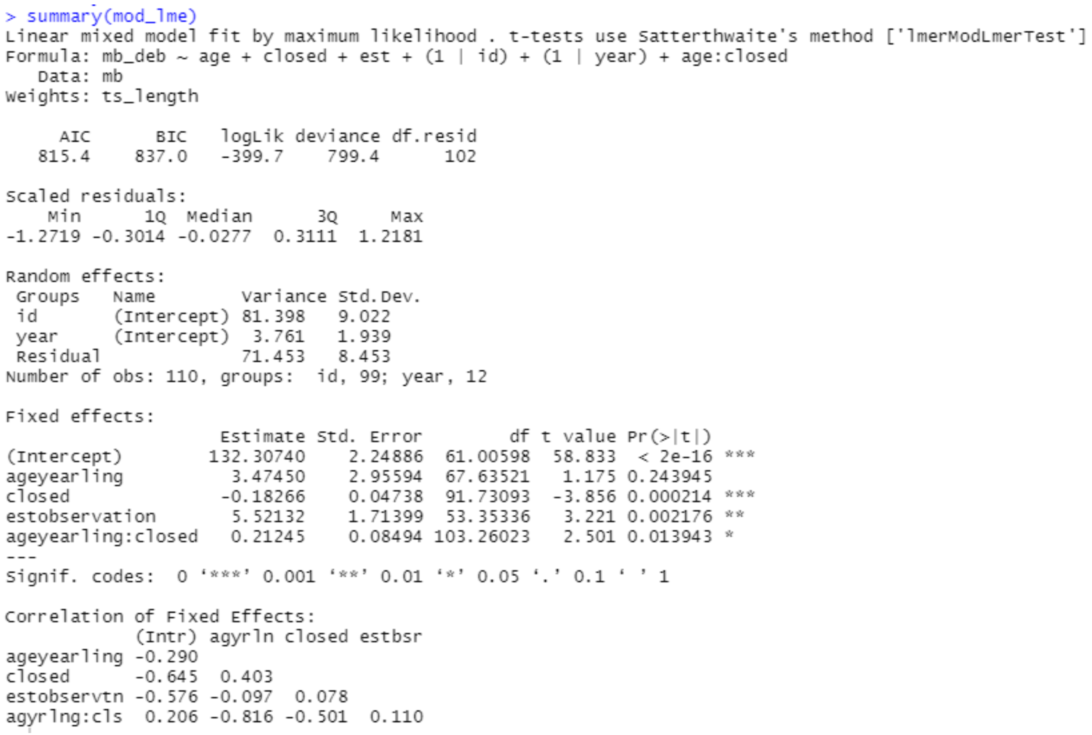
```
# full model (model fit by maximum likelihood)
# ts_length: duration of individual monitoring period (we aimed to give more
# weight to females with a long monitoring period)
# est: method used to estimate parturition (fawn captures or RT100)

mod <- lmer(mb_deb ~ closed + mass + age + est + age:closed + age:mass +
est:closed + (1|id) + (1|year), data = mb, weights = ts_length, REML = F)

library(MuMIn)
# generate a model selection table of models with combinations of fixed effect
# terms in the global model, with optional model inclusion rules
tab_mod = dredge(mod)

# dataframe obtained with the function 'dredge':
```



(Intercept)	age	closed	est	mass	age:closed	age:mass	closed:est	df	logLik	AICc	delta	weight
132.3074	+	-0.18265850	+	NA	+	NA	NA	8	-399.6905	816.8067	0.0000000	2.552853e-01
151.2015	+	-0.17691417	+	-0.8510729	+	NA	NA	9	-398.7703	817.3406	0.5338889	1.954759e-01
131.0885	+	-0.15033921	+	NA	+	NA	+	9	-399.4706	818.7412	1.9345509	9.703834e-02
150.9672	+	-0.13792541	+	-0.9035041	+	NA	+	10	-398.4343	819.0909	2.2842099	8.147341e-02
156.7661	+	-0.12580754	+	-1.1394509	NA	NA	NA	8	-400.9917	819.4091	2.6023993	6.948994e-02
148.3961	+	-0.17329159	+	-0.7400917	+	+	NA	10	-398.6247	819.4717	2.6650441	6.734708e-02
131.4250	+	-0.12535221	+	NA	NA	NA	NA	7	-402.6742	820.4464	3.6397267	4.136844e-02
150.2463	+	-0.12577852	+	-0.8720728	NA	+	NA	9	-400.3754	820.5508	3.7441176	3.926458e-02
155.9547	+	-0.07824023	+	-1.1825019	NA	NA	+	9	-400.4445	820.6891	3.8823762	3.664194e-02
148.5720	+	-0.13713495	+	-0.8052992	+	+	+	11	-398.3305	821.3549	4.5481947	2.626623e-02
129.7215	+	-0.08181172	+	NA	NA	NA	+	8	-402.2571	821.9399	5.1331949	1.960499e-02
150.2749	+	-0.08447665	+	-0.9405233	NA	+	+	10	-399.9754	822.1731	5.3664063	1.744719e-02
135.8487	+	-0.17366636	NA	NA	+	NA	NA	7	-403.5924	822.2828	5.4761502	1.651562e-02
134.8576	+	-0.13068153	NA	NA	NA	NA	NA	6	-405.2568	823.3292	6.5224755	9.787870e-03
147.1104	+	-0.17383201	NA	-0.4967075	+	NA	NA	8	-403.3142	824.0541	7.2474713	6.811729e-03
151.4372	+	-0.13352602	NA	-0.7302055	NA	NA	NA	7	-404.6035	824.3051	7.4983848	6.008585e-03
151.1895	+	NA	+	-1.0928545	NA	NA	NA	7	-405.3427	825.7835	8.9768454	2.868987e-03
149.1221	+	-0.17694978	NA	-0.5830546	+	+	NA	9	-403.1994	826.1988	9.3921103	2.331068e-03
126.8184	+	NA	+	NA	NA	NA	NA	6	-406.8315	826.4786	9.6719178	2.026728e-03
150.9923	+	-0.13349733	NA	-0.7105066	NA	+	NA	8	-404.6001	826.6260	9.8193512	1.882698e-03
181.7933	NA	-0.12120505	+	-2.2167637	NA	NA	NA	7	-405.8442	826.7865	9.9798487	1.737517e-03
144.3331	+	NA	+	-0.8071232	NA	+	NA	8	-404.7991	827.0240	10.2173420	1.542972e-03
180.5366	NA	-0.06777014	+	-2.2456468	NA	NA	+	8	-405.1061	827.6379	10.8312623	1.135134e-03
130.8757	+	NA	NA	NA	NA	NA	NA	5	-409.9877	830.5523	13.7456102	2.643653e-04
145.4375	+	NA	NA	-0.6441982	NA	NA	NA	6	-409.4703	831.7562	14.9495467	1.448015e-04
174.3052	NA	NA	+	-2.0811850	NA	NA	NA	6	-409.6080	832.0316	15.2249252	1.261756e-04
182.5248	NA	-0.14292085	NA	-2.0336832	NA	NA	NA	6	-410.3366	833.4886	16.6819649	6.089521e-05
144.1744	+	NA	NA	-0.5881415	NA	+	NA	7	-409.4514	834.0009	17.1942341	4.713519e-05
132.7447	NA	-0.10493078	+	NA	NA	NA	NA	6	-413.9778	840.7712	23.9645239	1.596598e-06
175.0709	NA	NA	NA	-1.8928677	NA	NA	NA	5	-415.3114	841.1997	24.3930706	1.288658e-06
131.1453	NA	-0.05920331	+	NA	NA	NA	+	7	-413.5073	842.1127	25.3060625	8.163645e-07
128.7093	NA	NA	+	NA	NA	NA	NA	5	-416.4031	843.3831	26.5764305	4.325409e-07
137.1852	NA	-0.12905486	NA	NA	NA	NA	NA	5	-416.9744	844.5257	27.7190099	2.442976e-07
133.2502	NA	NA	NA	NA	NA	NA	NA	4	-420.6496	849.6802	32.8735515	1.856200e-08

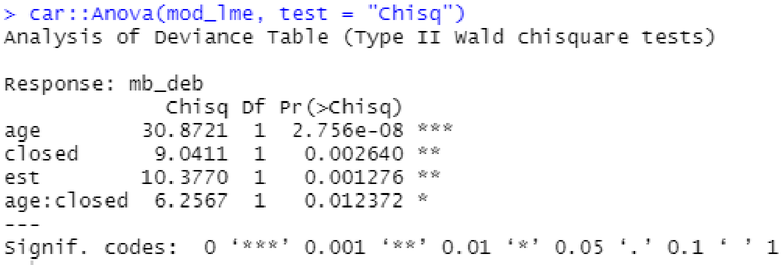
```
# selection of the model with deltaAICc < 2 and with a minimum number of
# parameters (parsimony) (this is the first one in the table)
mod_lme = (get.models(tab_mod, 1)[[1]])
```

```
# SUMMARY STATISTICS

library(lmerTest)
summary(mod_lme)
# check the significance of the fixed effects (but model selection based on AICc
# and not on the p-values)
```



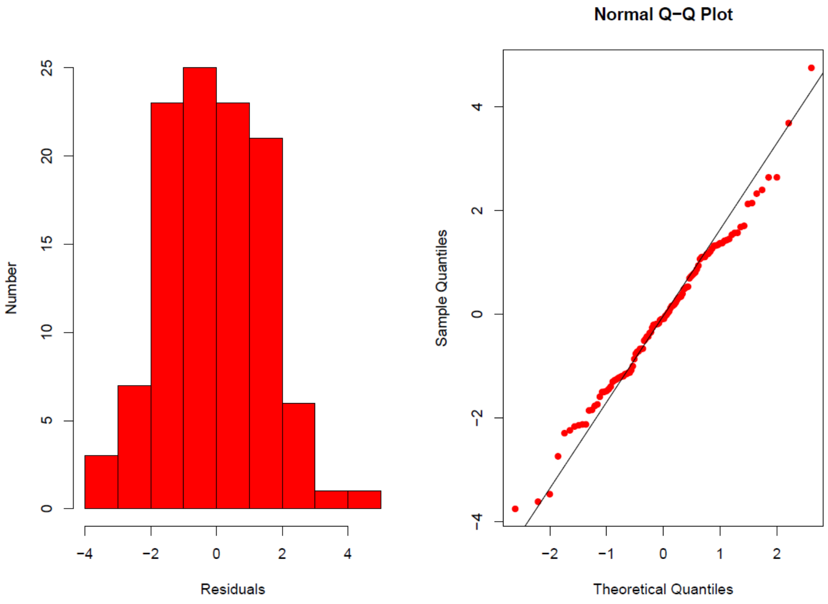
```
> summary(mod_lme)
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: mb_deb ~ age + closed + est + (1 | id) + (1 | year) + age:closed
   Data: mb
Weights: ts_length

     AIC      BIC   logLik deviance df.resid
   815.4    837.0   -399.7    799.4      102

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.2719 -0.3014 -0.0277  0.3111  1.2181

Random effects:
 Groups   Name        Variance Std.Dev.
 id       (Intercept) 81.398   9.022
 year     (Intercept)  3.761   1.939
 Residual             71.453   8.453
Number of obs: 110, groups:  id, 99; year, 12

Fixed effects:
                    Estimate Std. Error        df t value Pr(>|t|)
(Intercept)        132.30740    2.24886  61.00598  58.833  < 2e-16 ***
ageyearling          3.47450    2.95594  67.63521   1.175 0.243945
closed              -0.18266    0.04738  91.73093  -3.856 0.000214 ***
estobservation       5.52132    1.71399  53.35336   3.221 0.002176 **
ageyearling:closed   0.21245    0.08494 103.26023   2.501 0.013943 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) agyrln closed estbsr
ageyearling -0.290
closed      -0.645  0.403
estobservtn -0.576 -0.097  0.078
agyrlng:cls  0.206 -0.816 -0.501  0.110
```

```
car::Anova(mod_lme, test = "Chisq") # additional statistics
```

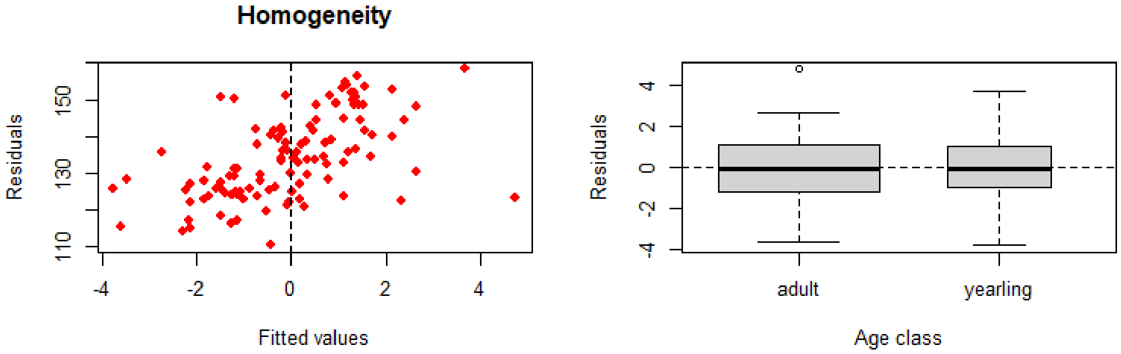


```
> car::Anova(mod_lme, test = "Chisq")
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: mb_deb
             Chisq Df Pr(>Chisq)
age        30.8721  1  2.756e-08 ***
closed      9.0411  1   0.002640 **
est        10.3770  1   0.001276 **
age:closed  6.2567  1   0.012372 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

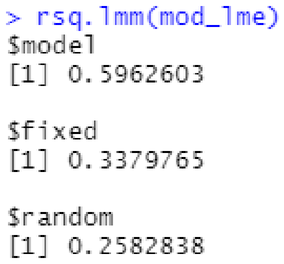
```
# MODEL VALIDATION

# normality of residuals
par(mfrow=c(1,2))
hist (residuals(mod_lme), breaks = 10, col='red', xlab='Residuals',
ylab='Number', main = "")
qqnorm(residuals(mod_lme), col='red', pch=16)
qqline(residuals(mod_lme))
# residuals are normally distributed
```



```
# homogeneity of the variance
par(mfrow=c(2,2))
plot(residuals(mod_lme),fitted(mod_lme), col='red', pch=16, xlab = "Fitted
values",ylab = "Residuals", main = "Homogeneity")
abline(h = 0, v = 0, lty = 2)
boxplot(residuals(mod_lme)~ mb$age, varwidth = TRUE,ylab = "Residuals", xlab =
"Age class",main = "")
abline(h = 0, v = 0, lty = 2)
# variance of residuals is homogeneous
```



```
# rsquared associated with the selected model
library(rsq)
rsq.lmm(mod_lme)
# '$model' corresponds to the variance explained
# by the random and fixed effects
# '$fixed' only fixed effects
# '$random' only random effects
```



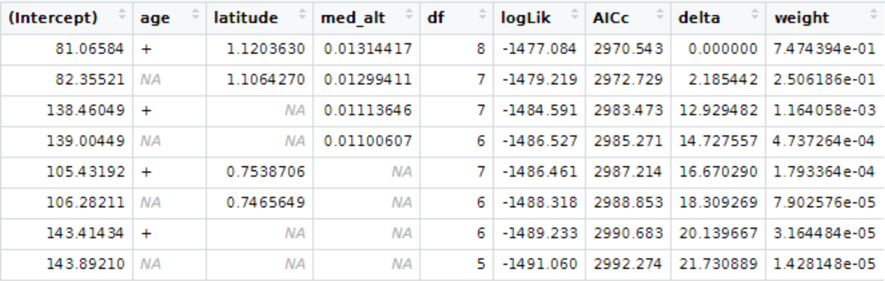
```
> rsq.lmm(mod_lme)
$model
[1] 0.5962603

$fixed
[1] 0.3379765

$random
[1] 0.2582838
```

```
# plot the models (outputs are in the report)
library(sjPlot)
library(ggplot2)

a <- plot_model(mod_lme, type = "pred", terms = c("closed", "age"), colors =
c("red", "blue"), title = "", show.data = T, show.p = T, axis.title =
c("Proportion of closed habitats in the maternal home range", "Parturition date
(julian day)"), legend.title = "Age class")
a + theme(legend.position = c(0.8,0.9), panel.border =
element_rect(fill=NA,color="black", size=0.5, linetype="solid"),
panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
panel.background = element_blank()) + scale_color_manual(values = c("red",
"blue"))

b <- plot_model(mod_lme, type = "pred", terms = c("closed", "est"), colors =
c("red", "blue"), title = "", show.data = T, show.p = T, axis.title =
c("Proportion of closed habitats in the maternal home range", "Parturition date
(julian day)"), legend.title = "Method")
b + theme(legend.position = c(0.8,0.9), panel.border =
element_rect(fill=NA,color="black", size=0.5, linetype="solid"),
panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
panel.background = element_blank()) + scale_color_manual(name="Method",
breaks=c("method", "observation"), labels=c("RT100", "observations"), values =
c("green", "purple"))
```

Hypothesis (2): we expected parturition date to vary across a latitudinal and altitudinal gradient in Europe, in particular, to occur later with increasing latitude and altitude.

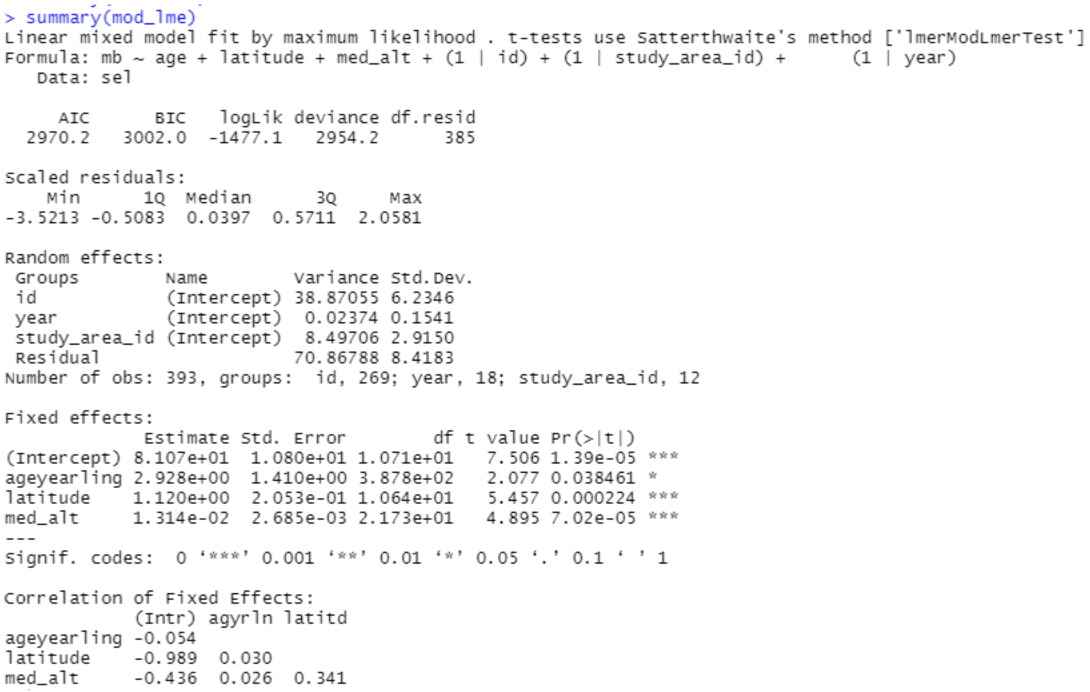
The statistical analysis for this model is the same as for model (1). Therefore, we only present hereafter the outputs of the model selection (summary statistics).

```
# model to be built: linear mixed model (LMM)
# - dependent variable: parturition date ('mb' hereafter)
# - fixed effects: latitude (numeric), median altitude (numeric), age
#   class(factor)
# - random effects: identity ('id'), year, study area ('study_area_id')

# MODEL SELECTION

mod <- lmer(mb ~ latitude + med_alt + age + (1|id) + (1|study_area_id) +
(1|year), data = eurodeer, REML = F)

# Output of the 'dredge' function (to obtain all the models)
```

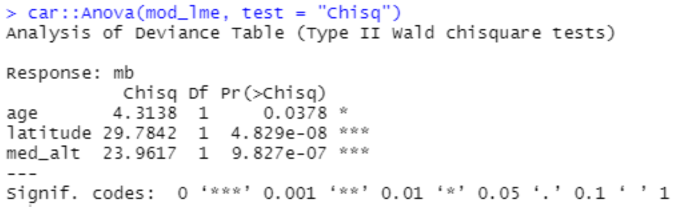


(Intercept)	age	latitude	med_alt	df	logLik	AICc	delta	weight
81.06584	+	1.1203630	0.01314417	8	-1477.084	2970.543	0.000000	7.474394e-01
82.35521	NA	1.1064270	0.01299411	7	-1479.219	2972.729	2.185442	2.506186e-01
138.46049	+	NA	0.01113646	7	-1484.591	2983.473	12.929482	1.164058e-03
139.00449	NA	NA	0.01100607	6	-1486.527	2985.271	14.727557	4.737264e-04
105.43192	+	0.7538706	NA	7	-1486.461	2987.214	16.670290	1.793364e-04
106.28211	NA	0.7465649	NA	6	-1488.318	2988.853	18.309269	7.902576e-05
143.41434	+	NA	NA	6	-1489.233	2990.683	20.139667	3.164484e-05
143.89210	NA	NA	NA	5	-1491.060	2992.274	21.730889	1.428148e-05

SUMMARY STATISTICS (outputs only)

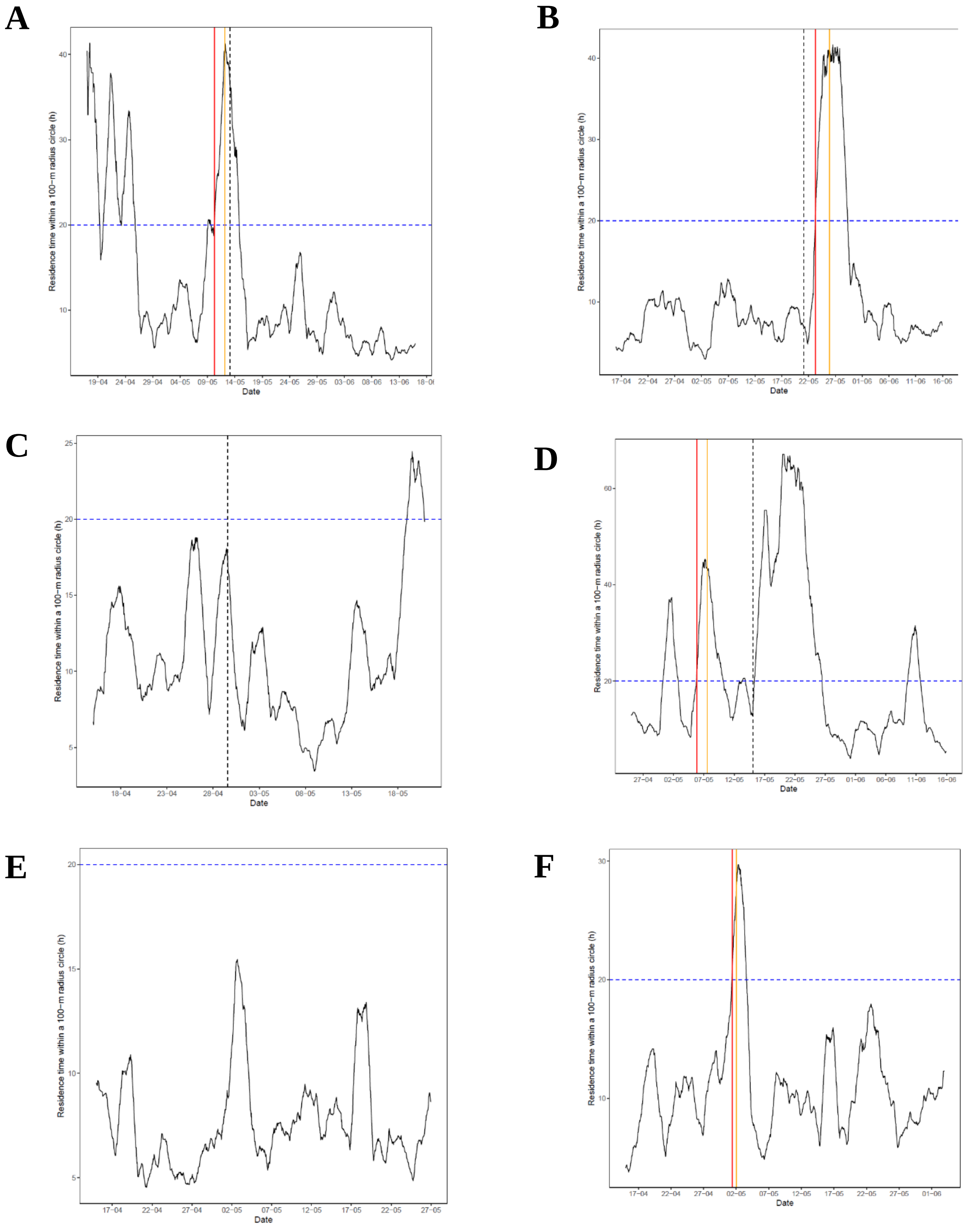


```
> summary(mod_lme)
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: mb ~ age + latitude + med_alt + (1 | id) + (1 | study_area_id) +      (1 | year)
   Data: sel

     AIC      BIC   logLik deviance df.resid 
  2970.2   3002.0  -1477.1   2954.2      385 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-3.5213 -0.5083  0.0397  0.5711  2.0581 

Random effects:
 Groups        Name        Variance Std.Dev.
 id            (Intercept) 38.87055 6.2346  
 year          (Intercept)  0.02374 0.1541  
 study_area_id (Intercept)  8.49706 2.9150  
 Residual                  70.86788 8.4183  
Number of obs: 393, groups:  id, 269; year, 18; study_area_id, 12

Fixed effects:
             Estimate Std. Error        df t value Pr(>|t|)    
(Intercept) 8.107e+01  1.080e+01 1.071e+01   7.506 1.39e-05 ***
ageyearling 2.928e+00  1.410e+00 3.878e+02   2.077 0.038461 *  
latitude    1.120e+00  2.053e-01 1.064e+01   5.457 0.000224 ***
med_alt     1.314e-02  2.685e-03 2.173e+01   4.895 7.02e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) agyrln latitd
ageyearling -0.054              
latitude    -0.989  0.030       
med_alt     -0.436  0.026  0.341
```



```
> car::Anova(mod_lme, test = "Chisq")
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: mb
           Chisq Df Pr(>Chisq)    
age       4.3138  1     0.0378 *  
latitude 29.7842  1  4.829e-08 ***
med_alt  23.9617  1  9.827e-07 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Appendix 4. Examples of RT$_{100}$ profiles for different females. When multiple peaks were detected, the closest to the median parturition in the population was associate with parturition. A and B: females for which the approach well predicted a parturition event. C: reproductive female predicted as non-parturient, D: reproductive female with an important error in the identification of the peak associated with parturition. E: juvenile well predicted as non-parturient. F: juvenile predicted as parturient. Horizontal blue dashed line represents a RT$_{100}$ threshold. Vertical red line corresponds to Part$_{\text{cross}}$. Vertical orange line corresponds to Part$_{\text{med}}$. Vertical black dashed line corresponds to the estimated parturition date by fawn capture.



Appendix 5. Performance of the approach to infer parturition in female roe deer based on the maximum amplitude of the peak in residence time: general approach (table 1) and approach by capture site (table 2).

Table 1. Performance of the general RT_{100}-based approach to infer parturition. Values of T_{RT100} (threshold), D_{min} and tolerance represent the combination of parameters that minimized the overall error rate and the time difference with the observed parturition date (from fawn capture), ΔPart.

T_{RT100}	D_{min}	Tolerance	Accuracy	Sensitivity	Specificity	$\Delta Part_{cross}$	$\Delta Part_{wm}$	$\Delta Part_{med}$
20h	24h	6-8%	75%	84%	61%	103h	118.6h	109.5h
			76/102	51/61	25/41			

Table 2. Performance of the RT_{100}-based approach per landscape structure (open/mix/closed habitat).

T_{RT100}	D_{min}	Tolerance	Accuracy	Sensitivity	Specificity	$\Delta Part_{cross}$	$\Delta Part_{wm}$	$\Delta Part_{med}$
Open habitat								
20h	36h	10%	78%	86%	69%	83h	118.6h	115.5h
			49/62	31/36	18/26			
Mix habitat								
18h	36h	20%	81%	80%	83%	90h	63.7h	56.8h
			17/21	12/15	5/6			
Closed habitat								
17h	24h	18-20%	74%	90%	56%	226h	244.3h	244h
			14/19	9/10	5/9			

INFERER LA DATE DE MISE BAS CHEZ LE CHEVREUIL (*CAPREOLUS CAPREOLUS*): APPLICATIONS ET OPPORTUNITES POUR L'ETUDE DE LA PHENOLOGIE DE LA REPRODUCTION FACE AUX CHANGEMENTS GLOBAUX

L'occurrence de la mise bas est déterminante pour la survie juvénile et peut avoir des effets à court et long termes sur la trajectoire d'histoire de vie des individus. Elle influe notamment sur la survie et la croissance précoce, des facteurs qui déterminent la dynamique des populations. Ainsi, la date de mise bas chez les herbivores devrait être synchronisée avec le début de la saison de végétation pour pallier aux besoins énergétiques importants liés à la parturition et maximiser la valeur sélective des consommateurs. Il y a donc un besoin croissant de comprendre comment les changements globaux affectent la phénologie de la reproduction des animaux. Pour répondre à ces questions, il est important de déterminer où et quand les femelles mettent bas. Cependant, détecter une mise-bas peut parfois s'avérer difficile en raison du comportement cryptique des femelles et des nouveau-nés. Ces dernières années, plusieurs méthodes ont été développées dans le but d'inférer la date de mise-bas chez les animaux, souvent basées sur des approches complexes qui pourraient ne pas être généralisables à différents sites d'étude. Dans cette étude, nous avons simplifié une approche existante pour inférer la date de mise-bas chez le chevreuil (*Capreolus capreolus*). En étudiant le temps de résidence des femelles au sein de zones restreintes, nous avons pu inférer la date de mise-bas avec une certitude raisonnable, notamment dans une population de chevreuils du sud-est de la France. Même si les résultats de notre approche ont été plus contrastés dans la détection de l'absence de mise-bas chez des juvéniles et dans une autre population d'Allemagne de l'est, elle nous a permis de montrer que les femelles adultes mettent bas plus tôt dans les habitats majoritairement fermés, contrairement à des femelles qui vivent dans des habitats plus ouverts et donc plus riches en ressources de haute qualité. Ceci est probablement le fruit d'une force de sélection pour une mise-bas précoce plus importante dans les milieux fermés, en lien avec la distribution des ressources dans le temps et dans l'espace. De plus, à large échelle, nous avons montré que la date de mise-bas du chevreuil variait avec la latitude et l'altitude. Les chevrettes mettent en moyenne bas plus tard aux hautes latitudes qu'aux basses latitudes, probablement coïncidant avec les variations de la phénologie de la végétation à cette échelle. Cela suggère un possible ajustement de la phénologie de la reproduction du chevreuil le long de gradients environnementaux. Nous suggérons que notre méthode pourrait être améliorée en identifiant d'autres facteurs qui pourraient influencer le mouvement des femelles autour de la mise-bas. Enfin, l'approche que nous avons adoptée pour comprendre les variations de la phénologie de la reproduction du chevreuil peut sans doute être généralisée à des espèces qui auraient des changements brusques de comportement autour de la parturition. Cette démarche a été réalisée dans le but d'apporter des réponses quant aux conséquences du changement climatique et de la fragmentation des habitats sur la phénologie d'un grand herbivore largement distribué en Europe et constitue une avancée dans l'inférence de ces événements clés de la trajectoire d'histoire de vie des herbivores, et plus largement des animaux, face aux changements globaux.

MOTS-CLES - *phénologie de la reproduction, chevreuil, changement global, mouvement, herbivores, parturition, GPS*

INFERRING PARTURITION DATE IN ROE DEER (*CAPREOLUS CAPREOLUS*): APPLICATIONS AND OPPORTUNITIES FOR STUDYING REPRODUCTIVE PHENOLOGY IN THE FACE OF GLOBAL CHANGE

The timing of parturition is crucial for juvenile survival and may have short and long-term effects on the life-history trajectory of individuals. Survival and early growth are important factors influencing population dynamics. Therefore, births in herbivores should be synchronized with the vegetation onset to meet the energetic requirements related to parturition and maximize the fitness of consumers. There is hence an increasing need to understand how global change is affecting the reproductive phenology of animals. To address such issues, it is of importance to know when and where females give birth. However, detecting parturition may be difficult, due to the cryptic behaviour of females around parturition or neonates. Over the past few years, several methods have been developed to infer parturition in animals, often based on complex approaches which may not be generalizable to different study areas. In this study, we simplified an existent approach to infer parturition in a hider species, roe deer (*Capreolus capreolus*). Using the residence time of females within restricted areas, we were able to infer parturition occurrence and timing in reproductive females with reasonable confidence. Although this approach provided more contrasted results in detecting the absence of parturition in non-reproductive females and in another roe deer population, it allowed us to reveal that adult females gave birth earlier with increasing proportion of closed habitats in their home range, probably due to a stronger selection towards earlier parturition in closed habitats where resources of high quality are available mostly at the beginning of the growing season. At a larger scale, we also found evidence for variation in the timing of parturition along a latitudinal and altitudinal gradient, probably coinciding with variations of plant phenology along these gradients, which supports results of previous studies. This shows a possible adjustment of roe deer parturition timing along environmental gradients. We suggest that our approach to infer parturition may be improved with further investigation on the factors influencing movement of females around parturition. With this study, we aimed to understand the responses of roe deer reproductive phenology to climate change at the level of populations and species. We think that our approach may be generalized to other species with similar marked changes in movement around parturition events. Our work hence constitutes a step forward in the inference of key events in the life-cycle of large herbivores and the understanding of further animal reproductive phenology and ecology in a context of climate change and increasing human encroachment into natural areas.

KEY WORDS - *reproductive phenology, global change, roe deer, movement, herbivores, parturition, GPS*