RESEARCH ARTICLE

A standardised biologging approach to infer parturition: An application in large herbivores across the hider-follower continuum

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Abstract

1. The timing of birth has a predominant influence on both the reproductive success of the mother and the life-history trajectory of her offspring. Because early growth and survival are key drivers of population dynamics, there is an urgent need to understand how global change is affecting reproductive phenology and performance. However, identifying when and where birth occurs is often difficult in the wild due to the cryptic behaviour of females around parturition, although this information may also help managers to protect reproductive females and newborn against human disturbance. While several approaches to identify parturition based on movement metrics derived from GPS monitoring have previously been proposed, their performance has not been evaluated over a range of species with contrasted movement characteristics.

2. Here, we present a novel approach to detect parturition by combining data on animal movements, activity rate and habitat use. Using machine learning approaches, we evaluated the relative and combined performance of each category of metrics in predicting parturition for three large herbivores with contrasted life histories: a hider-type species, the roe deer *Capreolus capreolus* and two follower-type species, the Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. and the Alpine ibex *Capra ibex*.

3. We first showed that detection of parturition was much improved when birth-related modifications in the habitat use and activity rate of the mother were considered, rather than relying on movement metrics only. We then demonstrated that our approach was highly successful (76%–100% of events correctly identified) in detecting parturition in both follower and hider species. Furthermore, our

approach generated estimates for peak birth date and the proportion of parturient females that were comparable with those based on direct observations at the population scale. Finally, our approach outperformed the most commonly employed methods in the literature which generally failed to identify non-reproductive females for the three studied species, and provided birth timing estimates that only poorly match the true parturition date.

4. We suggest that by combining sources of information, we have developed a standardised methodological approach for inferring parturition in the wild, not only for large herbivores but also for any species where parturition induces marked behavioural changes in the mother.

KEYWORDS

accelerometry, activity, GPS, habitat use, machine learning, movements, random forests, reproduction

1 | INTRODUCTION

Identifying occurrence and timing of parturition is of crucial importance in animal ecology due to their pivotal role for determining female reproductive performance and, hence, the population dynamics of wildlife (Coulson et al., 2005; Gaillard et al., 1998, 2000). Birth timing is, indeed, a key determinant of offspring fate, through both short-term and long-lasting effects on early growth and survival (Albon et al., 1987; Côté & Festa-Bianchet, 2001; Gaillard et al., 2003; Van Noordwijk et al., 1995). This has motivated a strong research effort to evaluate how birth phenology may respond to rapid global warming and, in particular, earlier spring, either through phenotypic plasticity (Price et al., 1988; Charmantier et al., 2008; Devictor et al., 2008 in birds, Tao et al., 2018 in fishes, Plard et al., 2014; Kourkgy et al., 2016 in mammals) or rapid evolution (Bonnet et al., 2019). Furthermore, identifying and protecting areas where critical life-history events occur, such as birth and early maternal care, is a key to limit disturbance related to the encroachment of human activities into wildlife habitats (Beale & Monaghan, 2004; Liddle, 1997; Richardson & Miller, 1997). Determining whether, when and where an individual female gives birth is, therefore, of crucial importance for both ecologists and wildlife managers.

Parturition is especially difficult to detect when subsequent modifications in the behaviour of the mother are subtle, particularly in elusive species, and/or in species where the mother–young relationship is limited to brief bouts of parental care (Lent, 1974; Ralls et al., 1986). Focusing only on the presence/absence of offspring at heel to infer reproductive performance of an individual female can be misleading due to imperfect detection from direct observations and rapid neo-natal mortality (Bonenfant et al., 2005; Gimenez et al., 2008; Linnell et al., 1995). Repeated observations prior to and during the parturition period (sometimes using VHF telemetry to improve detection), blood tests (e.g. progesterone, pregnancy-specific protein B, pregnancy-associated glycoprotein), ultrasonography and

vaginal implant transmitters have all been implemented to overcome these challenges in detecting gestation and parturition (Garrott & Bartmann, 1984; Hildebrandt & Saragusty, 2015; Houston et al., 1986). However, these approaches incur additional costs related to intense field work, purchase of specific devices or laboratory analyses, and may raise ethical concerns due to their invasive or highly disturbing nature.

More recently, alternative approaches have been proposed to infer reproduction/parturition in wildlife from behavioural metrics derived from GPS monitoring and associated biologgers (e.g. Picardi et al., 2019 in birds, Cameron et al., 2018; Mahoney & Young, 2017; Wiesel et al., 2019 in mammals). For example, large herbivores are often classified along the hider-follower continuum in relation to the species' mother–young relationship and neonatal antipredatory strategy immediately following birth (Geist, 1981; Lent, 1974; Ralls et al., 1986). As these specific behaviours may result in typical movement characteristics linked to parturition, researchers have exclusively focused on movement metrics to infer parturition (e.g. DeMars et al., 2013; Nicholson et al., 2019). However, because many other factors not related to parturition may influence fine-scale movements, generalising these approaches across populations and species has proved difficult (see e.g. Bonar et al., 2018 and DeMars et al., 2013 for contrasting results in two caribou populations using the same approach). Yet, parturition generally provokes not only changes in movement characteristics of mothers but also in an array of other behaviours, such as habitat use, activity and social relationships (Bourgoin et al., 2008; Grignolio et al., 2007; Langbein, Scheibe, et al., 1998; Pérez-Barbería & Walker, 2018). Hence, our ability to infer parturition is likely to be improved by integrating time series of the numerous behavioural traits that may be modified during this period. Surprisingly, despite the availability of such data derived from biologging, combined with appropriate methodological approaches, very few studies have combined several behavioural metrics to infer parturition in wildlife (but see Mahoney & Young, 2017 in coyotes *Canis latrans*). For example,
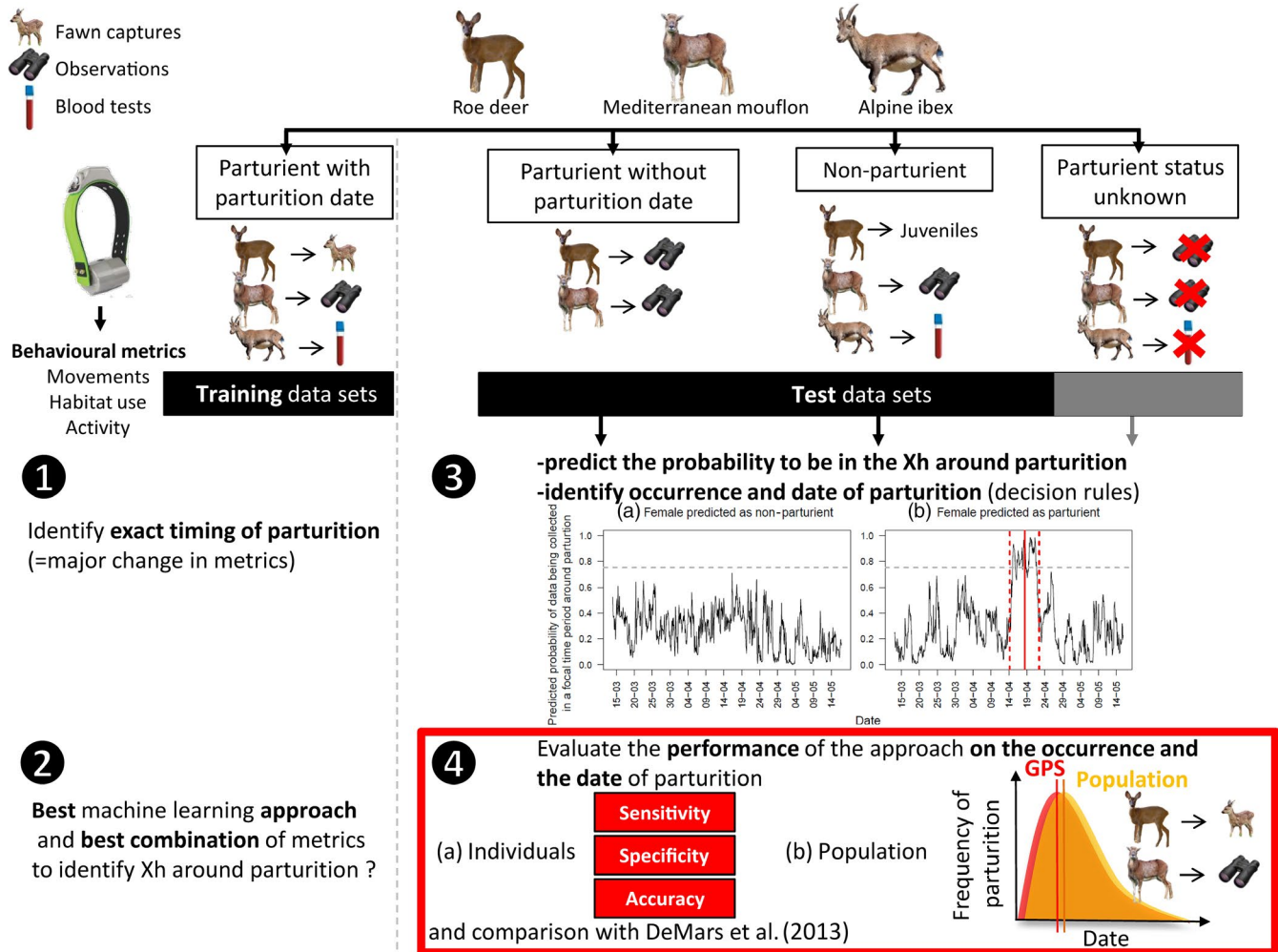
FIGURE 1 Datasets and methods used to implement and test machine learning approaches to infer parturition in three species of large herbivore (roe deer *Capreolus capreolus*, Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. and Alpine ibex *Capra ibex*)

change point detection analyses have been developed based on variation in mean, variance, regression slope, temporal autocorrelation and/or correlation between variables in time series (Cabrieto et al., 2017; Gurarie et al., 2009). Likewise, machine learning approaches have the ability to identify structure, extract knowledge and learn from complex, often nonlinear, training sets of multivariate time series, and can also be used to generate accurate models of predictions on new test datasets (Valletta et al., 2017). As such, they provide a prime candidate for detecting typical changes in multivariate behavioural metrics linked to parturition, which can then be used to identify parturition in datasets where reproductive status is unknown.

In this study, we developed an approach combining several behavioural metrics which are expected to change markedly in response to parturition. We evaluated the performance of this approach for inferring occurrence and date of parturition in species with contrasted mother–young relationships around parturition. To do so, we used biologging data recorded on females from three species of large herbivore across the hider-follower continuum, that is, roe deer *Capreolus capreolus*, classified as a hider-type species,

Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. and Alpine ibex *Capra ibex*, both classified as followers. We first analysed data collected on 70 roe deer, 29 Mediterranean mouflon and 11 Alpine ibex females with known date of parturition (Figure 1). We investigated the performance of several machine learning approaches to identify the critical parturition phase, in relation to the behavioural metrics included in the training datasets. We then tested the ability of the best machine learning approach to infer the occurrence of parturition in an independent dataset of females with known reproductive status (75 roe deer, 27 Mediterranean mouflon and 9 Alpine ibex). Finally, at the population scale, we compared the peak date of parturition estimated from biologging data with the peak determined by direct observations, and then evaluated the performance of our method relative to the most commonly used approach in the literature (DeMars et al., 2013).

2 | MATERIALS AND METHODS

The datasets and methods are summarised in Figure 1.

2.1 | Study area and species—GPS datasets

2.1.1 | Roe deer—Vallons et Coteaux de Gascogne study area (France)

We monitored roe deer in the Vallons et Coteaux de Gascogne study area (Zone Atelier PyGar; south-west of France; latitude: 43.283°N, longitude: 0.883°E, altitude: 350–450 m a.s.l.). Details on this rural and hilly study area and the monitoring of this population can be found in Morellet et al. (2011). As part of a capture–mark–recapture/resighting monitoring based on winter catches (mostly January and February), we equipped females (juveniles and adults) with visual marks and GPS collars (Lotek 3300S revision 2; Lotek Engineering Inc., Carp, Ontario, Canada; GPS PLUS-1C Store On Board, Vectronic Aerospace, Berlin, Germany for adults and GPS with GSM capability for remote data transmission Lotek Small WildCell GSM or Vectronic GPS PLUS Mini-1C for juveniles). We distinguished juveniles (<1 year old) from older deer by the presence of a tricuspid third pre-molar milk tooth (Ratcliffe & Mayle, 1992). Between 2005 and 2019 (mostly May–June), we also hand-caught fawns during their first days of life (median [min–max] = 3-day old [1–16]) for 70 females equipped with GPS collars. We inferred date of parturition based on repeated observations of the mother during the final phase of gestation and the fawn's estimated age at capture (following Jullien et al., 1992 and Linnell & Andersen, 1998). We used biologging data from these 70 females as the training dataset in machine learning approaches (see below and Figure 1). From repeated observations during autumn of a further 45 GPS-collared females with no prior information on parturition date, we identified 17 that had given birth during the previous spring and successfully weaned their fawn(s). The remaining 28 females were repeatedly observed without any fawns during autumn; hence, their reproductive status during spring was unknown. Finally, we also GPS-monitored 58 sexually immature juvenile females over the same period, during their second spring. Parturition is extremely unlikely in these females as roe deer almost always give birth for the first time at 2 (and occasionally 3) years of age (Gaillard et al., 1992; Hewison, 1996). We used data from these 17 adult and 58 juvenile females with known reproductive status to evaluate the performance of the best machine learning approach for identifying the occurrence of parturition (test dataset). We derived independent information at the population scale on the peak of parturition, from the aging of all captured newborn fawns during systematic searches of the entire study area (see section 2.2.4).

2.1.2 | Mediterranean mouflon—Caroux-Espinouse massif (France)

We monitored Mediterranean mouflon in the Caroux-Espinouse massif (southern France; latitude: 43.633°N, longitude: 2.967°E, altitude: 390–1124 m a.s.l.). Details on this low mountain area

and the monitoring of this population can be found in Marchand et al., (2014, 2015). As part of a long-term capture–mark–recapture/resighting monitoring based on spring catches (mostly April–June), we equipped adult females (≥2 years old) with visual marks and GPS collars (Lotek 3300S revision 2; Lotek Engineering Inc.). From repeated observations between the parturition period (March–May) and the end of year over the period 2010–2018, we recorded the presence/absence of a lamb at heel for 57 adult females equipped with GPS collars. Of these, we observed 29 females both just before and just after parturition, providing reliable information on parturition date (median [min–max] duration between last sighting before parturition and first sighting after parturition: 8.5 days [1.5–27.5]). We used data collected on these 29 females as the training dataset in machine learning approaches. Over the same period, we also observed 24 females that already had a lamb at heel (i.e. post-parturition only), but for which we had no information on the date of parturition. We used data collected on these 24 females to evaluate the performance of the best machine learning approach in identifying parturition (test dataset). Three GPS-monitored females were repeatedly observed without a lamb while one was not observed at all; hence, the reproductive status of these individuals was uncertain. We derived independent information at the population scale on the peak of parturition from intense visual monitoring when we systematically recorded sex and age composition of observed groups, as well as the presence/absence of a lamb at heel for females (see section 2.2.4; Bourgoin et al., 2018).

2.1.3 | Alpine ibex—Bargy massif (France)

We monitored Alpine ibex in the Bargy massif (northern French Alps; latitude: 46.000°N, longitude: 6.467°E, altitude: 1,500–2,438 m a.s.l.). Details on this mountain area and the monitoring of this population can be found in Marchand et al., (2017). As part of a capture–mark–recapture/resighting monitoring based on spring catches (mostly April–June), we equipped adult females (≥2 years old) with visual marks and GPS collars (GPS Plus, Vertex Plus and Vertex Lite; Vectronic Aerospace). Between 2013 and 2018, we also blood tested 20 captured females for pregnancy (Pregnancy Associated Glycoprotein; Humblot, 1992). We used biologging data from the 11 females that were blood tested as pregnant as the training dataset in machine learning approaches. We evaluated the performance of the best machine learning approach for identifying the occurrence of parturition using data from the nine females that were blood tested as non-pregnant and from the 19 other GPS-monitored females with unknown reproductive status.

2.1.4 | Metrics to index behavioural modifications linked to parturition from GPS data

We focused our analyses on GPS data collected during periods when nearly all births occurred in the studied species/populations, that is,

01 April–30 June in roe deer, 15 March–15 May in Mediterranean mouflon and 20 May–31 July in Alpine ibex (Garel et al., 2005; Plard et al., 2013; Villaret & Bon, 1995; hereafter called 'study periods').

Due to variable GPS scheduling, we resampled deer locations to obtain a common fix frequency, that is, one location every 6 hr. Regular fix frequencies were available in Mediterranean mouflon and Alpine ibex, that is, one location every 2 hr, alternating between even hours on one day and odd hours on the following day, and one location every hour, respectively. GPS collars also included two perpendicular captive-ball tilt switches (Lotek 3300; see Bourgoin et al., 2008 for details), or accelerometers (Vectronic, Lotek Small WildCell), recording side to side (SS) and forward-backward (FB) head motions or head acceleration, respectively, averaged per 5 min interval. To account for differences between both the two types of data, we scaled SS and FB data by their range for each individual/ collar and so obtained values between 0 and 1.

Changes in movement rates, daily/weekly home range size and overall activity rate around parturition and during the post-partum period (sensu Lent, 1974) have been described in most large herbivores. For example, social isolation in small home ranges with restricted movements and reduced activity is considered essential for proper formation of the mother–young bond and for protection against predators (Bourgoin et al., 2008; Grignolio et al., 2007; Linnell et al., 1998; Marchand et al., 2015; Van Moorter et al., 2009). Given that these behavioural changes may provide pertinent information on the occurrence of parturition in GPS-monitored females, we derived six behavioural metrics from GPS data and associated biologgers. We computed the distance between consecutive locations (dist), home range size (HR), activity levels recorded by side-to-side (SS) and forward-backward (FB) sensors, and an activity index (AI) combining data from SS and FB sensors in the same way as the Vectorial Dynamic Body Acceleration (VeDBA) metric in accelerometry analyses (AI = $\sqrt{SS^2 + FB^2}$; Qasem et al., 2012; see Benoit et al., 2020 for a similar approach). We expected all these behavioural metrics to decrease prior to parturition, reaching a short-term minimum during a few hours or days, corresponding to the post-partum period, and to increase thereafter. In contrast, we expected an increase in the residence time (RT) within a 100m circle during the parturition and post-partum periods (RT100; Barraquand & Benhamou, 2008). In addition, with reference to the hider-follower continuum (Geist, 1981; Lent, 1974), roe deer is classified as a typical hider-type species, whereas Mediterranean mouflon and Alpine ibex are generally classified as followers. To detect these specific behaviours following parturition, we derived species-specific metrics. First, although constrained to restrict their space use to a limited area around their offspring following parturition, habitat use by hider females is expected to be more independent from that of their offspring compared to followers, and mostly focused on the high-quality resources needed to offset the high energy expenditure due to lactation (Loudon, 1985). Thus, following parturition, we expected roe deer females to decrease their use of forested areas (forest), to increase their use of habitats providing high-quality resources, that is, cultivated fields and meadows outside forests (resources), and to decrease the distance to

habitat edge (dedge; Hewison et al., 2009; McLoughlin et al., 2007; Saïd & Servanty, 2005; Van Moorter et al., 2009). A hider neo-natal tactic requires the female to visit offspring bed sites frequently (6–8 times per day) to provide maternal care. Thus, for each roe deer female, we also computed the number of return visits to 100 m circular buffers centred on locations collected during the study period (visits; Bracis et al., 2018) and expected the use of frequently visited sites to increase after parturition. In contrast, to ensure offspring survival, females of follower species must trade-off access to high-quality resources with the use of secure habitats, generally steep rocky areas for mountain species such as Mediterranean mouflon and Alpine ibex (Grignolio et al., 2007; Marchand et al., 2015). For reproductive females in these species, we hence expected the proportion of locations in rocky areas (rock) and the slope they used (slope) to increase following parturition.

As these behavioural metrics could be highly sensitive to missing locations, GPS accuracy and the frequency of GPS locations, we computed them as the average over a 48-hr sliding window (see DeMars et al., 2013 for a similar approach). In addition, to account for inter-individual differences in habitat availability and collar sensitivity, during preliminary analyses, we performed analyses on both centred and non-centred data. To obtain centred data for each individual and each metric, we subtracted the average value computed over the study period from the raw data value. Given that scaled metrics were more informative for Mediterranean mouflon and Alpine ibex but not for roe deer, below we present the results obtained on either scaled or non-scaled metrics depending on the species.

2.2 | Statistical analysis

2.2.1 | Change point analysis to detect parturition date (step 1 in Figure 1)

We first employed a change point analysis to detect the major change in the behavioural metrics during the study period in 70 roe deer, 29 Mediterranean mouflon and 11 Alpine ibex females that were known to have reproduced (training datasets). Change point analysis is the process of detecting one or several distributional changes (i.e. variation in mean, variance, regression slope, temporal autocorrelation and/or correlation among variables; Cabrieto et al., 2017; Gurarie et al., 2009) that occur within univariate or multivariate time series (Matteson & James, 2014). We used a divisive hierarchical estimation algorithm for change point analysis (Matteson & James, 2014) focused on the ±5 days around the estimated parturition date (roe deer), on the period delimited by the last observation of the female alone and the first observation with a lamb at heel (Mediterranean mouflon), or around a pre-defined date at which major changes in metrics occurred based on visual inspection of individual data during preliminary analyses (Alpine ibex, for which no information on parturition date was available; see DeMars et al., 2013 for a similar approach). In this approach, change points are found through the use of the e-divisive method, combining a binary bisection approach and

permutation tests (Matteson & James, 2014). In the following analyses, we considered that parturition occurred at the point in time when an abrupt change was identified by the change point analysis.

2.2.2 | Performance of different machine learning approaches for identifying parturition (step 2 in Figure 1)

We compared the performance of eight commonly-used machine learning approaches (random forest, linear, quadratic and multiple discriminant analyses, support vector machine, multivariate adaptive regression splines, k-nearest neighbours and neural networks; Lee et al., 2005) for identifying parturition in the training datasets. Because of the differences in GPS schedules, we analysed a varying time window around parturition (from 24 hr [Mediterranean mouflon and Alpine ibex], or 48 hr [roe deer], to 240 hr [10 days] in all species, hereafter called 'parturition window'). Data collected during parturition windows comprised a small sample set (≈0.5%–10%) of data collected during the study period. These unbalanced datasets are likely to bias the classification capabilities of the prediction models towards the most common class. Hence, to improve classification abilities of the different approaches, we subsampled the training datasets so that the number of data collected outside the parturition window was the same as that within the parturition window. We also evaluated how the performance of these approaches varied

as a function of the type and combination of metrics included in the training datasets, that is, metrics of movement (dist, RT100, HR, visits), habitat use (rock, slope, forest, resources, dedge) and activity (SS, FB, AI). More specifically, for each species, we investigated the error rates of the different approaches for identifying either data collected in the focal parturition window, or those collected outside the parturition window, when trained with a variable combination of the behavioural metrics. We derived error rates from the confusion matrix provided by each classification approach. We were particularly interested in identifying the approach and the combination of behavioural variables that provided the lowest error rates using data collected during the parturition window. In addition, to better quantify the predictive power of the best machine learning approach trained with the most informative metrics, we generated 95% confidence intervals of the error rates derived from binomial tests (function *confusionMatrix*, package RFPERMUTE in R software).

2.2.3 | Predicting parturition in the test datasets (step 3 in Figure 1)

We used the machine learning approach that performed best on the training datasets (see above) and a number of decision rules to identify the occurrence and date of parturition in females in the test datasets (Figure 2). This approach generated a probability that a given data point of the time series was recorded during the
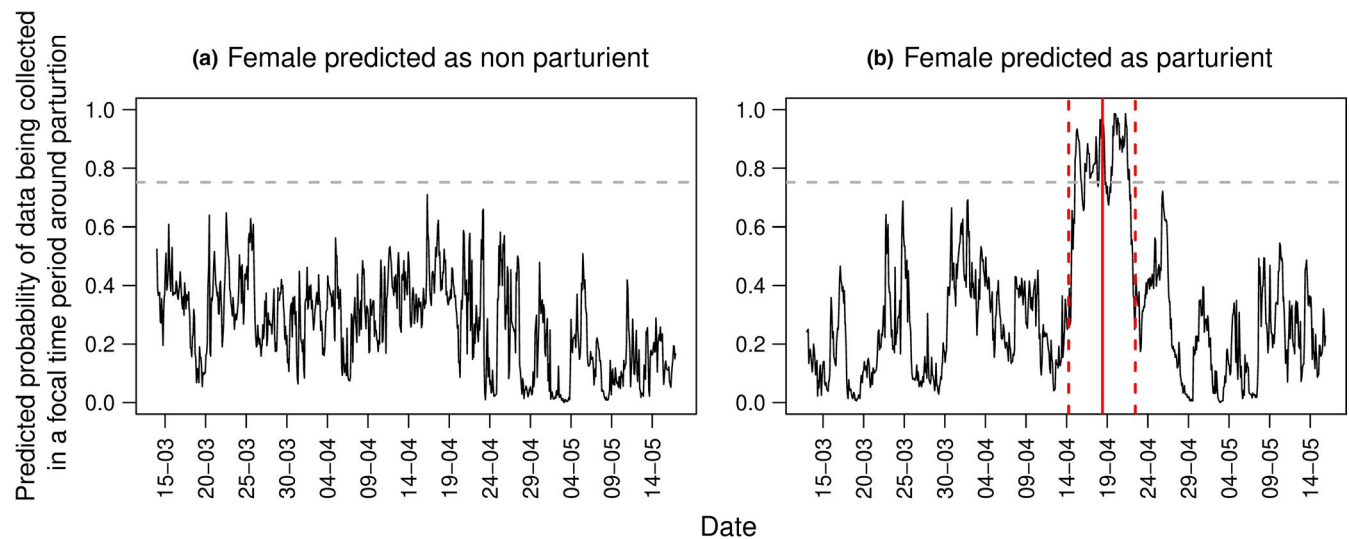

FIGURE 2 Description of the decision rules used to infer parturition in two Mediterranean mouflon females from the Caroux-Espinouse massif with unknown reproductive status. First, we determined a probability threshold above which we considered that probability values indicated parturition. This threshold was fixed as the 1% quantile of the predicted probabilities for data collected during the parturition window over all females in the training dataset (dashed horizontal grey line). Then, to account for the error rate of the approach (Figure 2), we considered the parturition window to comprise the period within the time series for which the proportion of time points predicted as parturition was at least 1 – the error rate (delineated by the two dashed vertical red lines on panel b). We considered females had given birth when we identified at least one parturition window within their time series, and we took the timing of parturition as the mean of the date–time over the identified period weighted by the corresponding probabilities of parturition (vertical solid red line on panel b). We repeated this process for different time windows (from 24 hr [Mediterranean mouflon and Alpine ibex], or 48 hr [roe deer], to 240 hr) and retained only the shortest identified parturition window as representing the true parturition. The temporal variation of the behavioural metrics recorded for this female identified as parturient are given in Supporting Information B. For a given female, if we were unable to identify any parturition over any of the time windows, we classified that individual as non-parturient (panel a)

FIGURE 3 Error rates for the random forest approach including all the behavioural metrics tested (movements, habitat use and activity) to identify time windows from 24–48 hr to 240 hr around parturition in (a) roe deer, (b) Mediterranean mouflon and (c) Alpine ibex. We derived error rates and 95% confidence intervals from the confusion matrix and binomial tests (function *confusionMatrix*, package RFPERMUTE in R software). A 0.15 error rate 24 hr around parturition means that 15% of the data collected during the 24 hr around parturition were wrongly predicted as occurring outside this parturition window by the random forest model
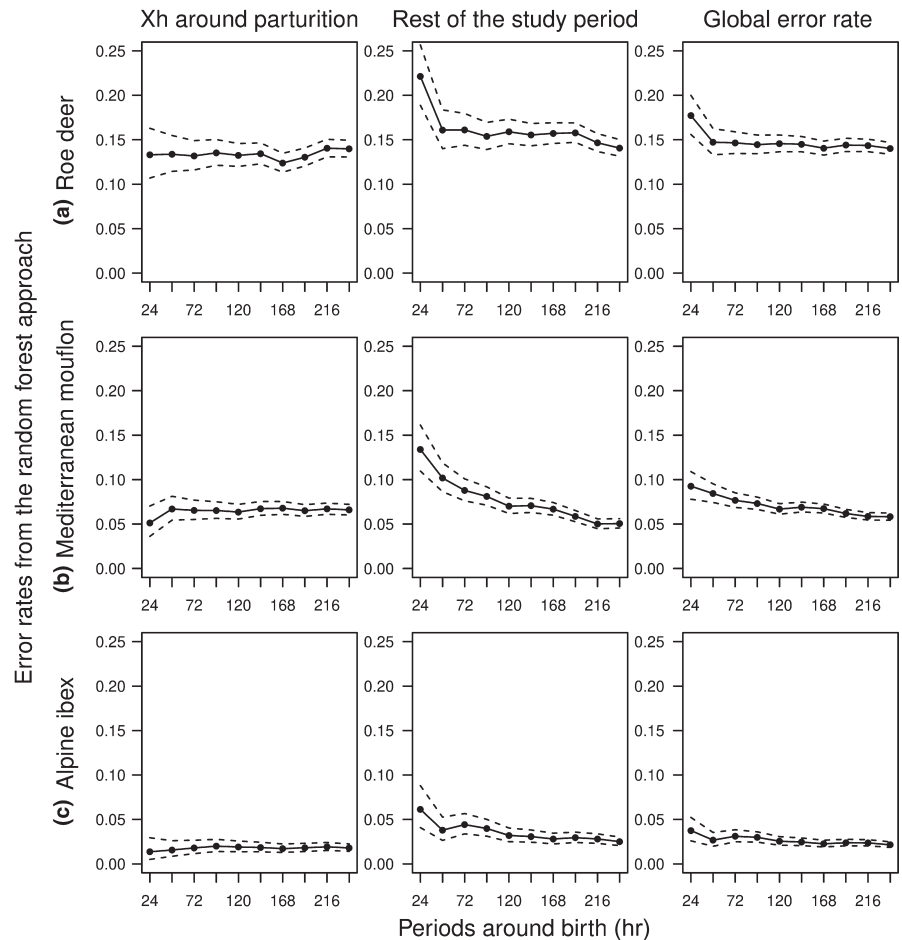
parturition window. Hence, we determined a probability threshold above which we considered probability values would indicate parturition. This threshold was fixed as the 1% quantile of the predicted probabilities for data collected during the parturition window over all females in the training dataset. Then, to account for the error rate of the approach (Figure 3), we considered the parturition window to comprise the period within the time series for which the proportion of time points predicted as parturition was at least 1 – the error rate. We considered females had given birth when we identified at least one parturition window within their time series, and we took the timing of parturition as the mean of the date–time over the identified period weighted by the corresponding probabilities of parturition (Figure 2). We repeated this process for different time windows (from 24 hr [Mediterranean mouflon and Alpine ibex], or 48 hr [roe deer], to 240 hr) and retained only the shortest identified parturition window as representing true parturition. For a given female, if we were unable to identify any parturition over any of the time windows, we classified that individual as non-parturient.

2.2.4 | Evaluating the performance of our approach (step 4 in Figure 1)

We quantified the sensitivity (proportion of reproductive females correctly identified), specificity (proportion of non-reproductive

females correctly identified) and accuracy (overall rate of true predictions) of this approach for the three species (step 4a in Figure 1). We also compared the median date of parturition determined from our biologging approach with the peak estimated using other approaches at the population scale (roe deer and Mediterranean mouflon only; step 4b in Figure 1). In roe deer, we derived this peak from the estimated age of captured newborn fawns during systematic searches of the entire study area. In Mediterranean mouflon, we estimated the birth peak based on intensive re-sighting monitoring during the birth period of all the females marked with visual tags with the specific aim of deriving the ratio of newborns to females using the approach from Caughley and Caughley (1974; see Kourkgy et al., 2016 for a similar approach). This approach could not be replicated in Alpine ibex as the hypothesis that most adult females reproduce each year was not supported in this population (Anses, 2015). For roe deer and Mediterranean mouflon, we focused on the comparison of the birth peaks provided by both approaches rather than comparing the full data distributions due to the low number of females identified as parturient in the test datasets.

Finally, we also compared our biologging approach with the most frequently employed approach in the literature to infer parturition in female ungulates (DeMars et al., 2013). This latter approach is based on expected sudden and marked changes in female movement patterns (i.e. movement rate, corresponding to the behavioural variable

'dist' in our approach; see Supporting Information D for details) linked to parturition.

We performed all statistical analyses using R 3.6.3 (R Core Team, 2020), adehabitatLT, adehabitatHR and recurse libraries for computing behavioural metrics (Bracis et al., 2018; Calenge, 2006), ecp for change point analyses (James & Matteson, 2014), and caret and rfPermute for machine learning analyses (Archer, 2020; Kuhn, 2019).

We provide an example dataset (i.e. biologging data from Mediterranean mouflon analysed in the manuscript) and a R script to enable the analyses to be replicated or applied to other species or behavioural metrics, available at https://github.com/pamarcha/infer_parturition.

3 | RESULTS

Of the eight machine learning approaches tested to identify parturition windows of varying length in the training datasets, random forests performed best in the three species (Supporting Information A). This approach was generally associated with the lowest error rates for data collected during the parturition windows (<15% in roe deer, <8% in Mediterranean mouflon and <3% in Alpine ibex), and the lowest overall error rates (<15% in roe deer except for 24 hr around parturition, <10% in Mediterranean mouflon and <5% in Alpine ibex; Figure 3). For most approaches, and in all three species, combining all the behavioural variables in the models generated lower error rates compared to models based on metrics of movement, habitat use or activity only (Supporting Information A).

Using random forests trained with the full set of behavioural metrics (movement, habitat use and activity) and the decision rules incorporating the species-specific error rates of this approach (see Section 2 and Figure 2), we were able to predict the occurrence of parturition in females in the test datasets with species-specific values of accuracy ranging from 79% (roe deer) to 88% (Mediterranean mouflon; Table 1). The proportion of parturient females correctly identified (sensitivity) ranged between 71% and 92%, while the proportion of non-parturient females correctly identified (specificity) ranged between 66% (Mediterranean mouflon) and 100% (Alpine ibex), respectively. The average (SD) retained time windows in pregnant females from test datasets for which we detected parturition were 89.1 hr (35.7) and 49.0 hr (3.4) in roe deer and Mediterranean mouflon, respectively. The average (SD) time periods identified as parturition periods were 121.7 hr (64.3) and 93.3 hr (50.3) in roe deer and Mediterranean mouflon, respectively. Such information was not available in Alpine ibex as no pregnant females were available in the test dataset.

The relative contribution of the various behavioural metrics to accurately identifying the parturition window varied markedly between time windows considered (for Mediterranean mouflon and Alpine ibex), species and metric type (Supporting Information C). Residence time in a 100m circle was generally the most informative metric in all three species, irrespective of the time window. For roe deer, average distance between consecutive locations was the second most informative metric. For short time windows (<72 hr), this metric was also the second most informative for Mediterranean mouflon, while in Alpine ibex, activity metrics (SS, FB, AI) were as informative as residence time. In contrast, with the exception of the number of visits in roe deer, the slope in Mediterranean mouflon and the proportion of rocky areas in Alpine ibex, the behavioural metrics expected to reflect changes in habitat use linked to parturition were less clearly informative.

From plots of the temporal variation in the various behavioural metrics over the ±30 days around identified parturitions, we were able to estimate the duration of these behavioural changes in parturient females (Figure 4). From this, movement rate (expressed as a marked increase in residence time in a 100 m circle, and a decrease in the distances between consecutive locations) and home range size clearly decreased at parturition in all three species. Similarly, activity metrics (side-to-side and forward-backward head movements, and the activity index combining both) were low during late gestation, decreased markedly at parturition (Mediterranean mouflon and Alpine ibex, only), before increasing rapidly a few days after parturition in all three species. Likewise, marked shifts in habitat use were evident in the mountain ungulates such that parturient Mediterranean mouflon and Alpine ibex females increased use of steep rocky slopes. In contrast, the expected modifications in habitat use of roe deer females linked to their need for high-quality resources (i.e. decrease in distance to habitat edge and in the use of forested areas, increase in the use of resource habitats in open areas) and frequent location revisits were less evident. Finally, from visual inspection, the length of the period just after parturition during which these behavioural metrics were markedly modified appeared to be longer in Mediterranean mouflon and Alpine ibex than in roe deer.

TABLE 1 Accuracy (overall rate of true predictions), sensitivity (proportion of parturient females correctly identified) and specificity (proportion of non-parturient females correctly identified) generated from random forests trained with metrics of movement, habitat use and activity in predicting parturition in roe deer, Mediterranean mouflon and Alpine ibex. The predicted proportions of parturient females for individuals with unknown status (parturient$_{unknown}$) are included for information. Sensitivity and hence accuracy could not be determined in Alpine ibex as data from all the females blood tested as pregnant were included in the training dataset

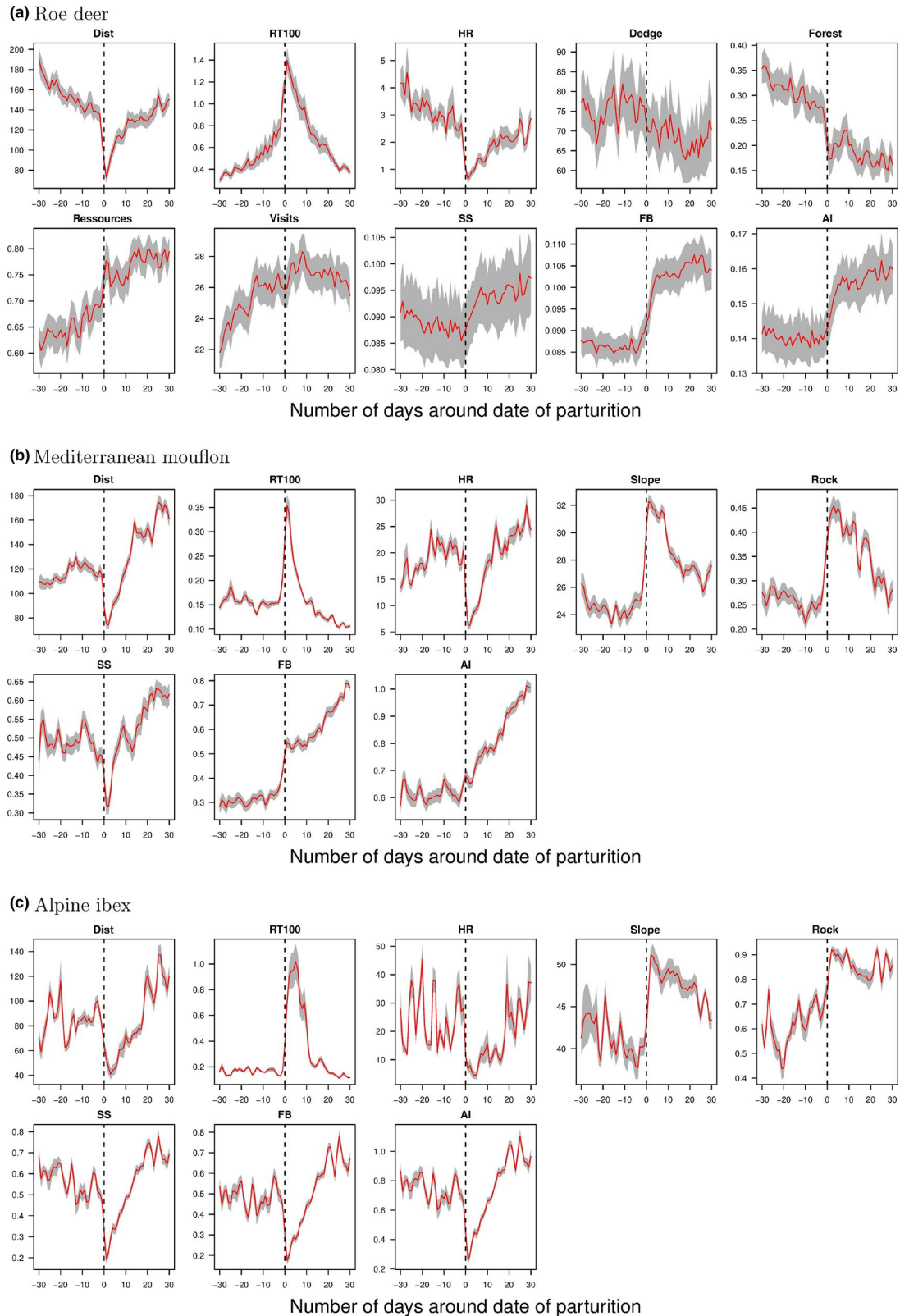| Species	Accuracy	Sensitivity	Specificity	parturient$_{unknown}$
Roe deer	76% (57/75)	71% (12/17)	79% (45/58)	61% (17/28)
Mediterranean mouflon	89% (24/27)	92% (22/24)	66% (2/3)	100% (1/1)
Alpine ibex	—	—	100% (9/9)	58% (11/19)

FIGURE 4 Temporal variation in the behavioural metrics used to infer parturition during the ±30 days around identified parturitions in (a) roe deer, (b) Mediterranean mouflon and (c) Alpine ibex. For each behavioural metric and each species, we first computed the mean daily values for each female identified as parturient. Then we reported the daily average values (red lines) and 95% confidence intervals (grey polygons) over all parturient females. The vertical dashed lines represent 0, that is, the identified date of parturition. dist = average distance (m) between consecutive locations, RT100 = residence time in a 100 m circle; HR = home range size (ha); slope = average slope (degrees); rock = proportion of locations in rocky areas; SS = average value from side-to-side sensor; FB = average value from forward-backward sensor; AI = activity index (see Section 2 for details)

In the three study species, our approach outperformed the most commonly employed method in the literature for identifying parturition in ungulates (DeMars et al., 2013; Supporting Information D). This was the case in particular for distinguishing parturient versus non parturient females. Furthermore, at the population scale, the predicted median birth date using our approach in roe deer (18 May) and Mediterranean mouflon (13 April) did not differ from that provided by other approaches (roe deer: median estimated birth of captured fawns from GPS-collared females: 18 May; Mediterranean mouflon: birth peak predicted using the Caughley and Caughley (1974) approach: 14 April), providing additional support for the power of our multi-metric approach for reliably identifying parturition date. Finally, among females of reproductive age, the proportions of parturient females that we identified (roe deer: 86% [99/115]; Mediterranean mouflon: 93% [53/57]; Alpine ibex: 56%; 22/39) were comparable with those previously determined at the population scale using other approaches (>90%, M. Hewison, unpublished data; 91%, Garel et al., 2005; 43%, Anses, 2015, respectively).

4 | DISCUSSION

Using machine learning approaches to analyse a suite of behavioural metrics derived from biologging, we were able to infer the occurrence of parturition with relatively high confidence (76%–100%) in three large herbivores with contrasting post-natal strategies of maternal care. Our approach also provided valuable information on birth timing at both individual and population scales in these species. Our approach provided better results in the two species classified as follower-type, that is, Mediterranean mouflon and Alpine ibex, than in roe deer, a hider-type species. Even so, across the three studied species, our approach, which combined metrics of movement with information on habitat use and activity outperformed the most frequently used approach in the literature based on movement metrics only (Supporting Information D). At the population scale, we obtained estimates for the birth peak and the proportion of reproductive females that were comparable with values derived from other observational approaches. Our results suggest that GPS devices and associated sensors can not only provide information on animal space use but may also help gain insights on demographic parameters of cryptic species which are of fundamental importance to evaluate the responses of wildlife populations to ongoing global change and increasing human encroachment into natural areas.

We built our approach based on the literature describing behavioural modifications in female large herbivores linked to parturition, which affects not only movements but also habitat use and activity levels (Bourgoin et al., 2008; Grignolio et al., 2007; Linnell et al., 1998; Marchand et al., 2015; Van Moorter et al., 2009). Although we were able to identify parturition with a relatively high degree of overall accuracy across the three studied species (Table 1), the performance of our method was somewhat superior for Mediterranean mouflon and Alpine ibex compared to roe deer,

possibly related to their relative position on the hider-follower continuum, and to the resulting magnitude of the associated behavioural modifications. Indeed, the continuous presence of offspring at heel in follower-type species such as Mediterranean mouflon and Alpine ibex may strongly constrain the movements, habitat selection and activity of mothers, potentially for a substantial time post-partum (i.e. the period during which females socially isolate in small home ranges, with limited activity; Lent, 1974; Figure 4). In contrast, although constrained to restrict their movements around their offspring, which they must frequently revisit, females of the hider-type such as roe deer may be more independent of their offspring as soon as the post-partum period is finished (Linnell et al., 1998). However, data quality may also be a contributing factor in the variable predictive power of our approach (DeMars et al., 2013). The frequency at which GPS locations were recorded was three to six times lower in roe deer (1 location per 6 hr) compared to Mediterranean mouflon (1 location per 2 hr) and Alpine ibex (1 location per hour). This could have a particularly strong influence on our ability to detect parturition given that the post-partum period, probably the most informative sequence for inferring parturition, is likely shorter in roe deer (a few hours; Espmark, 1969) than in Mediterranean mouflon (2–5 days; Pinelli, 1997; Langbein, Scheibe, et al., 1998; Langbein, Streich, et al., 1998) and Alpine ibex (see also Figure 4). This relatively coarse temporal grain in the roe deer data could also explain why we were unable to identify the expected frequent return visits to the offspring's bed sites that typically occur during early maternal care. Note that, for Mediterranean mouflon and Alpine ibex, we used sedentary adults of reproductive age in both the training and tests datasets, while we also included non-reproductive juvenile females in the roe deer test set (almost all adult females reproduce in this population). Because juvenile roe deer have a somewhat unstable pattern of space use, and may disperse at around one year of age, this likely influenced the behavioural metrics we analysed (Ducros et al., 2020). Dispersal may, for example, generate breakpoints in most metrics of movement (distances travelled, residence time, home range size) and activity levels, potentially mimicking the expected patterns for parturient females, and so influencing our ability to infer the absence of parturition in these individuals. Indeed, the misclassification of juvenile roe deer females as parturient was more than twice as high for juveniles that dispersed compared to non-dispersers (Ducros et al., 2020; 7/21 vs. 4/26, respectively).

The performance of our approach across the three species, both in terms of distinguishing parturient versus non-parturient females and providing valuable information on parturition date, was superior to that of DeMars et al., (2013), developed for caribou (Supporting Information D). However, compared to caribou, reproductive adult females of all our three study species are highly sedentary, have limited movement rates and use much smaller home ranges (Marchand, 2013; Marchand et al., 2017; Morellet et al., 2013; Figure D1 in Supporting Information D). All year round, the three species usually travelled very short distances

and, hence, usually reached the distance threshold below which the population-based method (PBM, see DeMars et al., 2013) predicted that a female was parturient. Similarly, the individual-based method (see DeMars et al., 2013) performed slightly better than the PBM in Mediterranean mouflon and Alpine ibex, but was again influenced by the many other factors that may result in breakpoints in movement rates. These difficulties in generalising the species-specific DeMars et al., (2013) approach to infer parturition in other large herbivore populations have already been identified (Bonar et al., 2018). In contrast, by combining metrics of movement with information on habitat use and activity levels and exploiting the power of machine learning approaches (Valletta et al., 2017), our approach performed better across species with contrasting life histories. We suggest that this may constitute a powerful methodological approach for inferring parturition of large herbivores across the entire hider-follower continuum, irrespective of baseline movement rates. In a similar way, if the choice of behavioural metrics is adjusted based on knowledge of the typical behaviours of females around parturition, we believe that our approach could be easily adapted to determine reproduction/parturition over a broad range of species (see e.g. Picardi et al., 2019 in birds, Wiesel et al., 2019 in carnivores, Fogarty et al., 2020 in domestic animals). More generally, this constitutes a promising starting point for developing methodologies to exploit multiple time series derived from a complex combination of sensors (e.g. accelerometry and magnetometry; Fogarty et al., 2020; Kays et al., 2015; Krieger et al., 2018) to infer significant events associated with changes in the behaviour of wildlife species, from daily routines to major life-history events (Bunnefeld et al., 2011; Davidson et al., 2020; Gurarie et al., 2009, 2016; Patin et al., 2020).

With the advent of GPS monitoring and associated biologgers over recent decades and the increasing duration of individual monitoring that is now possible due to technological improvements (e.g. battery performance, solar charging), our approach could constitute a novel avenue for wildlife research and management projects that need to identify major life events. For example, with reliable identification of parturition, it becomes possible to infer reproductive allocation, estimate age-specific female fecundity and monitor the phenological responses of wildlife to increasingly early springs (Davidson et al., 2020; Parmesan & Yohe, 2003). These parameters are of vital importance for the development of accurate population forecasts from models for age-structured populations (Gaillard et al., 1998, 2000) in the context of global change. Combined with complementary monitoring of reproductive success (e.g. with mark–resight monitoring, see methods) or with extensions of our approach to infer neonatal mortality (see DeMars et al., 2013; Obermoller et al., 2019; Picardi et al., 2019 for examples), this could also allow biologists to determine (lifetime) reproductive success, that is, essential information for monitoring and predicting changes in population dynamics (Coulson et al., 2005; Gaillard et al., 2000). Our approach could also provide information on habitat characteristics of parturition sites, that is, essential data in the context of increasing human encroachment into natural areas (Beale & Monaghan, 2004; Liddle, 1997; Richardson & Miller, 1997). We suggest that our unifying approach may, hence, constitute a valuable new tool for research in behavioural ecology, population dynamics and management of wildlife.

AUTHORS' CONTRIBUTIONS

P.M., M.G. and A.L. conceived the ideas and designed the methodology; P.M., M.G., N.M., Y.C., C.I., E.P., B.C. and A.J.M.H. collected the data; P.M., M.G., L.B. and N.M. analysed the data; P.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data available from the Zenodo Repository at https://doi.org/10.5281/zenodo.4537796 (Marchand et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.