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BIOLOGGING

Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore

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Abstract

1. Dispersal is a key mechanism enabling species to adjust their geographic range to rapid global change. However, dispersal is costly and environmental modifications are likely to modify the cost–benefit balance of individual dispersal decisions, for example, by decreasing functional connectivity.
2. Dispersal costs occur during departure, transience and settlement, and are levied in terms of energy, risk, time and lost opportunity, potentially influencing individual fitness. However, to the best of our knowledge, no study has yet quantified the energetic costs of dispersal across the dispersal period by comparing dispersing and philopatric individuals in the wild.
3. Here, we employed animal-borne biologgers on a relatively large sample (N = 105) of juvenile roe deer to estimate energy expenditure indexed using the vector of dynamic body acceleration and mobility (distance travelled) in an intensively monitored population in the south-west of France. We predicted that energy expenditure would be higher in dispersers compared to philopatric individuals. We expected costs to be (a) particularly high during transience, (b) especially high in the more fragmented areas of the landscape and (c) concentrated during the night to avoid disturbance caused by human activity.
4. There were no differences in energy expenditure between dispersers and philopatric individuals during the pre-dispersal phase. However, dispersers expended around 22% more energy and travelled around 63% further per day than philopatric individuals during transience. Differences in energy expenditure were much less pronounced during the settlement phase. The costs of transience were almost uniquely confined to the dawn period, when dispersers spent 23% more energy and travelled 112% further than philopatric individuals. Finally, the energetic costs of transience per unit time and the total distance travelled to locate a suitable settlement range were higher in areas of high road density.
5. Our results provide strong support for the hypothesis that natal dispersal is energetically costly and indicate that transience is the most costly part of the process, particularly in fragmented landscapes. Further work is required to link dispersal

costs with fitness components so as to understand the likely outcome of further environmental modifications on the evolution of dispersal behaviour.

KEYWORDS
biologging, circadian rhythm, energy expenditure, movement, philopatric, roe deer, transience

1 | INTRODUCTION

Climate change and human-driven modification of land use are having rapid and widespread impacts on the geographic range and spatial dynamics of wildlife populations (Crooks et al., 2017; Warren, Price, Graham, Forstenhaeusler, & VanDerWal, 2018). Landscape fragmentation and human infrastructure are generating ecological and/or artificial barriers across much of the globe, limiting the spatial extent of animal movements (Tucker et al., 2018). This is especially the case for long-distance movements (Tucker et al., 2018), with dispersal (e.g. Schtickzelle, Mennechez, & Baguette, 2006) and migration (e.g. Sawyer et al., 2013) likely to be particularly affected. For example, forest fragmentation reduces dispersal rates among local populations of several amphibian species (Rothermel & Semlitsch, 2002). Dispersal is a key life-history trait governing the spatial dynamics of populations (Clobert, Danchin, Dhondt, & Nichols, 2001) and has been identified as a primary mechanism enabling species to adjust their geographic range in response to rapid environmental change (Kokko & López-Sepulcre, 2006). Hence, the impact of global change on dispersal behaviour may have far-reaching consequences for population persistence (e.g. Reinhardt, Köhler, Maas, & Detzel, 2005).

At the individual level, behavioural decisions are regulated by the cost–benefit balance of dispersal (Bowler & Benton, 2005) which may differ across the three successive phases of dispersal: departure, transience and settlement (Bonte et al., 2012). For example, transience is assumed to be costly due to the time and energy expended related to increased locomotor activity (Boldt & Ingold, 2005) and exposure to risk (Johnson, Fryxell, Thompson, & Baker, 2009). However, the lost opportunity costs of exploratory movements prior to departure (Kingma, Komdeur, Hammers, & Richardson, 2016) and unfamiliarity with a novel environment or loss of social rank during settlement (Bonte et al., 2012) may also be substantial. As a result, dispersal decisions are often highly plastic and condition-dependent (sensu Ims & Hjermann, 2001). For example, dispersing individuals are often in better condition (Debeffe et al., 2012) and/or less parasitized (Debeffe et al., 2014). In the context of rapid global change, there is a strong assumption that the cost–benefit balance underlying dispersal decisions will be modified as a result of human-driven modifications to the landscape (Bonte et al., 2012; Fahrig, 2007). In particular, increasing landscape fragmentation may reduce functional connectivity for many species (Taylor, Fahrig, Henein, & Merriam, 1993), which is predicted to increase dispersal costs (Ronce, Perret, & Olivieri, 2000), with direct impacts on the evolution of dispersal behaviour (Travis & Dytham, 1999).

The currencies of dispersal costs are levied in terms of energy expenditure, risk, time and lost opportunity (Bonte et al., 2012) and are, thus, predicted to influence individual fitness. For example, the risk of mortality increases with dispersal distance in American martens *Martes americana*, particularly in human-modified forest, possibly because of higher energetic costs of dispersal in fragmented landscapes (Johnson et al., 2009). Indeed, the costs of dispersal have either been evaluated in the currency of decreased individual performance (Massemin, Maho, & Handrich, 1998; Récapet et al., 2016), rather than in energy per se, or inferred based on the supposition that dispersal transience necessarily implies increased locomotion costs (Bonte et al., 2012). Our study provides, to our knowledge, the first empirical quantification of dispersal costs across the entire dispersal process based on a direct comparison of dispersers and philopatric individuals in any wild mammal. Landscape structure likely has a pivotal role in determining the movement of individuals (Martin et al., 2018) and, in particular, their natal dispersal decisions, providing a mechanistic link to understand the impact of landscape modifications on spatial population functioning.

The technological revolution of animal-borne biologgers has recently opened new horizons for studies of energetic expenditure (Wilmers et al., 2015). Indeed, by measuring movements and dynamic acceleration of the body at a very fine temporal scale (Gleiss, Wilson, & Shepard, 2011), it is possible to generate indices of energy expenditure linked to body movement (Grémillet et al., 2018) and absolute values of energy expenditure linked to an animal's behaviour (Williams et al., 2014). The cost of increased locomotor activity is a strong selective force governing the evolution of migration (Hein, Hou, & Gillooly, 2012), and this is likely also the case for dispersal.

Here, we use a relatively large sample of individually intensively monitored juvenile roe deer *Capreolus capreolus* to evaluate the energetic costs of natal dispersal in a wild population inhabiting a highly fragmented and human-dominated landscape in southern France. We combined intensive monitoring of movement behaviour using GPS technology to quantify mobility with acceleration/activity data and evaluated energetic costs across the dispersal process. First, we predicted that energy expenditure would be higher in dispersing individuals compared to philopatric individuals, but particularly during transience due to increased locomotor activity. Costs may be incurred prior to departure linked to exploration events (Debeffe et al., 2013), while settlement may be costly due to unfamiliarity with the local environment (Bonte et al., 2012). Second, we predicted that energy expenditure would be higher for individuals that dispersed across more fragmented areas of the landscape due to the lower availability of refuge habitat. We also predicted that dispersers

would pay the additional energetic costs of transience mainly during the night in order to avoid disturbance in this human-dominated landscape (Gaynor, Hojnowski, Carter, & Brashares, 2018). Third, because sexual dimorphism is low in this species (Hewison et al., 2009) and because the dispersal behaviour of male and female juveniles is very similar (Debeffe et al., 2012), we expected that energy expenditure during dispersal transience would not differ between the sexes. However, because males disperse in response to intra-sexual competition for territories (Wahlström, 1994), while female dispersal appears to be voluntary (Linnell, Wahlström, & Gaillard, 1998), we predicted that the energetic costs of settlement would be greater for male dispersers.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was carried out at Aurignac in the south-west of France (43°13′N, 0°52′E) in a 19,000 ha rural region. It is a hilly area containing two large forests (672 and 463 ha), numerous small woodland patches (2.4 ± 11.5 ha, 18.8% of the site), meadows (37.2%), crops (cereals, oilseed and fodder crops, 31.6%) and hedgerows (3.6%) (based on aerial photographs of the study site from the IGN's BD Ortho, http://professionnels.ign.fr, see Morellet et al., 2011, for more details). Human presence is high, distributed throughout the study site in small villages, farms and isolated houses. Roe deer density was estimated using a capture–mark–resighting approach to average around 10 individuals/100 ha in the mixed open landscape (Hewison et al., 2007). Roe deer hunting occurs regularly from the second Sunday of September to the end of January (until 2008) or February (since 2009), mostly using dogs for drive hunting. During summer, that is from 1 June to the 2nd Sunday of September, male roe deer can also be hunted by stalking.

2.2 | Capture

From 2002 to 2017, during winter (from 16 November to 27 March), roe deer were caught using nets, tranquilized (with an intramuscular injection of acepromazine) and transferred to a wooden retention box (to reduce stress and risk of injuries). Each individual was marked with ear tags, weighed and sexed (see Bonnot et al., 2017, for more details). Natal dispersal of roe deer is highly temporally synchronized within a short time window, occurring almost exclusively during the spring at around 1 year of age, when the mother–juvenile bond breaks down prior to the mother giving birth to her next litter (between late April and mid-June at this latitude, Linnell et al., 1998). Juveniles (<1 year old) were distinguished from older roe deer by the presence of a tricuspid third pre-molar milk tooth (Ratcliffe & Mayle, 1992). Finally, to monitor potential natal dispersal behaviour during the following spring, we equipped juveniles with a GPS collar (Lotek 3300 GPS or Vectronic GPS PLUS-1C Store On Board) or a GPS with GSM capability for remote data transmission (Lotek Small WildCell GSM or Vectronic GPS PLUS Mini-1C). During the study period, we caught 219 juveniles, of which 191 were equipped with a GPS collar. All capture and marking procedures were done in accordance with local and European animal welfare laws (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection).

2.3 | Biologging data

GPS collars were scheduled to obtain a location every 6 hr over the entire year and, for individuals captured since 2009 (N = 114), every hour from March to May in order to maximize the probability of detecting the dispersal event. We performed differential correction to improve fix accuracy (Adrados, Girard, Gendner, & Janeau, 2002), as only 50% of uncorrected fixes were located within 14 m of their true position in our study area (Cargnelutti et al., 2007). Following Bjørneraas Van Moorter Rolandsen and Herfindal (2010), we eliminated potentially erroneous data points (0.01% of the total locations) when consecutive locations indicated a step speed that was biologically unfeasible. In order to describe the three successive stages of dispersal (departure, transience and settlement), only juveniles monitored from their first capture in winter to at least the end of June were retained for subsequent analysis (N = 137).

Most GPS collars hosted an activity sensor which recorded activity as the difference in acceleration between two consecutive measurements along the x (forward/ backward)- and the y (sideways)-axes (www.lotek.com and www.vectronic-aerospace.com). These measurements were taken four times per second, but recorded as mean values per 5-min interval transformed into a standardized measure for each axis ranging between 0 and 255. For Lotek 3300 GPS only, activity data were also measured over each 5-min interval, but as a count of vertical X (sideways) and horizontal Y (forward/backward) movements. Of the total sample, 12 individuals were equipped with a Vectronic collar which, in addition, hosted an acceleration sensor scheduled to obtain data with a sampling frequency of 8 (2017) or 32 (2016) measures per second (8 or 32 Hertz, respectively). This sensor measured acceleration in the three perpendicular axes, with values ranging between −125 (=−8 g) and 125 (=8 g) for each axis (1 g = 9.81 m/s^2). The x-axis measures the anteroposterior movements (surge or forward/backward), the y-axis the dorso-ventral movements (heave or up/down) and the z-axis the transversal movements (sway or sideways).

Biologging data were retrieved at the end of the GPS programme, usually after an almost full year of monitoring. We removed the first eight days of biologging data because of the potential alteration of spatial behaviour due to capture (Morellet et al., 2009).

2.4 | Defining philopatry versus natal dispersal

For each individual, we segmented the time series of GPS locations (longitude and latitude) using Lavielle's (1999) method developed for

a one-dimensional variable and recently adapted by Patin, Etienne, Lebarbier, Chamaillet-Jammes, and Benhamou (2019) to handle bi-dimensional data. This approach detects change points in a time series which we used to identify spatio-temporal units corresponding to distinct ranges and, thus, to distinguish individual-based movement tactics (package 'segclust2d' in R software). We assumed that the individual was 'philopatric' when we detected one home range only, that is the individual remained on their natal range until the end of monitoring (i.e. at least until the end of June). We assumed that the individual was 'disperser' when segmentation identified two (or more) spatially separate home ranges, assumed to represent the natal and settlement ranges, and there was no return movement to the initial (natal) range, regardless of the distance travelled during the transience phase (Appendix S1). We assumed that the individual was a 'pseudo-disperser' (Debeffe et al., 2012) when we detected two separate ranges which the animal occupied for a period of at least 6 days, which we considered as the maximum duration of an exploration event (Debeffe et al., 2013), followed by a return movement to the initial (natal) range. Although pseudo-dispersers (N = 4) probably reproduced for the first time within their natal home range, for subsequent analyses they were pooled with the dispersers as they left their natal area during the dispersal period for a substantial duration and were therefore assumed to have suffered similar dispersal costs. Then, because we wished to focus on the energetic costs of dispersal, we discarded individuals moving in a way that was not clearly attributable to a classic philopatric or dispersal tactic (e.g. the multi-range tactic, Couriot et al., 2018) so that we subsequently retained 119 individuals (68 philopatric individuals and 51 dispersers). Of these 119 individuals monitored during the dispersal period, 105 had activity data, comprising 46 dispersers (27 females and 19 males) and 59 philopatric individuals (34 females and 25 males); 12 had acceleration data, comprising 6 dispersers (1 females and 5 males) and 6 philopatric individuals (4 females and 2 males); and 71 had an interfix interval of one GPS location per hour, comprising 27 dispersers (16 females and 11 males) and 44 philopatric individuals (27 females and 17 males, Appendix S2).

2.5 | Defining the phases of natal dispersal

In order to evaluate the energetic costs across the three phases of dispersal, we defined a pre-dispersal, a post-dispersal and a transience phase for all individuals. To do so, the dates of departure and settlement for each disperser were determined from the segmentation approach described above, using the last location in the natal range and the first in the settlement range as cut-off points. These two dates were taken to delimitate the transience phase of a disperser at the individual level and ranged between 2 April and 10 June (median duration = 6.4 days [min: 0.125, max: 39.7]). We used the median dates of departure and settlement across all dispersers to define an equivalent seasonal phase for all philopatric individuals (from 24 April to 7 May, i.e. 14 days). To facilitate comparisons, we used an equivalent duration of 14 days for the other phases for both dispersers and philopatric individuals. We defined a common pre-dispersal phase of 14 days from 16 to 29 March which was at least 10 days after the last winter capture, but prior to the observed departure date for the first disperser. Similarly, we defined a common post-dispersal phase of 14 days running from 11 to 24 June which was later than the observed settlement date of the latest disperser, but prior to the summer rut so as to avoid potential behavioural alteration due to sexual interactions.

2.6 | Statistical analyses

2.6.1 | Indexing energy expenditure with VeDBA

We used the vector of dynamic body acceleration (VeDBA) as a proxy of individual energy expenditure (Grémillet et al., 2018; Qasem et al., 2012). Given that only 12 individuals were monitored using an acceleration sensor compared to 105 individuals using an activity sensor (Appendix S2), we first examined whether the information recorded by the activity sensors provided a reliable estimate of energy expenditure. We expected the activity sensors and the acceleration sensors to provide comparable information as both types of sensor were positioned on the animal's neck and, therefore, measured the same body movements. To do so, we compared daily VeDBA estimates calculated using activity sensor data (see Equation 1) with those using acceleration sensor data (see Equation 2).

$$\mathrm{VeDBA}_{\mathrm{activity}} = \sqrt{X^2 + Y^2}. \quad (1)$$

The VeDBA based on activity sensor data was calculated using the raw data values recorded by X and Y sensors, providing a value of VeDBA per 5-min interval.

$$\mathrm{VeDBA}_{\mathrm{acceleration}} = \sqrt{\mathrm{DBA}X^2 + \mathrm{DBA}Y^2 + \mathrm{DBA}Z^2}. \quad (2)$$

The VeDBA based on acceleration sensor data was calculated using the dynamic body acceleration of each axis, obtained by subtracting the static acceleration values from gross acceleration values (corresponding to a mobile average calculated over a sliding window of 1 s, see Collins et al., 2015). From acceleration data, we obtained 8 to 32 values of VeDBA per second.

To enable comparison of these two metrics, we then generated average $\mathrm{VeDBA}_{\mathrm{acceleration}}$ estimates based on acceleration sensor data per 5-min interval.

To compare the two VeDBA estimates from acceleration and activity sensors, we generated daily mean estimates for both $\mathrm{VeDBA}_{\mathrm{acceleration}}$ and $\mathrm{VeDBA}_{\mathrm{activity}}$ over a sub-set of 15-day monitoring for the sub-set of 12 individuals for which we had both types of data. We used linear mixed-effects models (lmer; package 'lme4', Bates, Maechler, Bolker, & Walker, 2015) to investigate the correlation between these two metrics, including individual identity as a random intercept in order to control for repeated measures per individual.

2.6.2 | Estimating daily energy expenditure

In order to investigate differences in energy expenditure between disperser and philopatric individuals across the three phases of

dispersal, because $VeDBA_{activity}$ provided an extremely satisfactory approximation of $VeDBA_{acceleration}$ (see Results), we analysed variation in daily $VeDBA_{activity}$ estimates (square root transformed) in relation to the dispersal phase (three modalities: pre-dispersal, transience and post-dispersal), dispersal status (two modalities: disperser or philopatric) and sex (two modalities: male or female) using lmer (package 'LME4', Bates et al., 2015). As we expected that the difference in energy expenditure between dispersers and philopatric individuals would be particularly pronounced during the transience phase, and in order to control for possible sex differences in energy metabolism, the most complex model included the three-way interaction between dispersal phase, dispersal status and sex. We included individual identity and year as random effects on the intercept to control for repeated measures per individual and to account for possible cohort effects (i.e. the fact that individuals born in the same year experience the same environmental conditions: Gaillard, Loison, Toïgo, Delorme, & Van Laere, 2003). For $VeDBA_{activity}$ analyses, we only retained days for which at least 50% of $VeDBA_{activity}$ records (144 values per day) were available (i.e. 97% of the full dataset). When there were missing data in the remaining records for a given individual on a given day, we divided the total $VeDBA_{activity}$ estimate by the number of records taken on that day and then multiplied the result by the theoretical number of $VeDBA_{activity}$ values per day (i.e. 288). Finally, as standardizing values of VeDBA to control for seasonal fluctuations in absolute activity did not alter the results, we present the analysis based on untransformed data for simplicity.

2.6.3 | Estimating daily mobility

In order to estimate the proportion of energy expenditure during dispersal due to movements per se, we calculated an estimate of daily mobility, namely the sum of distances travelled between all locations on a given day (with the function 'as.ltraj' [package 'ADEHABITATLT', Calenge, Dray, & Royer, 2009]). As the GPS collars were scheduled to obtain a location every hour from March to May only, we were not able to generate estimates of daily mobility across the three dispersal phases previously described. Therefore, we investigated temporal variation in daily mobility during a period centred on the process of transience for each individual by considering a window of a maximum of 45 days before and after the median date of transience. We used an individual-based date of transience for dispersers (the median date of their individual transience trajectory), while for philopatric individuals we used the population-level median date of all transience events. We used generalized additive mixed models (GAMMs) to investigate variation in log-transformed daily mobility, including individual identity and year as random effects on the intercept (with the GAMM4 function in the 'GAMM4' library, Wood & Scheipl, 2017). We used thin plate regression splines to smooth the effect of time before and after the median date of transience (Julian date). For model selection, we compared a constant model, a model containing only the spline of the Julian date, a model including a sex-specific temporal effect (i.e. a separate spline of Julian date for each sex), a model including a status-specific temporal effect (i.e. a separate spline of Julian date for dispersers and philopatric individuals) and a model including both a sex-specific and a status-specific temporal effect. For these analyses, we retained only those days when at least 80% of programmed GPS locations (i.e. 20 locations per day) were available (i.e. 97% of the full dataset). When there were missing data in the remaining records, we divided the total distance moved on a given day by the number of records on that day and then multiplied the result by the theoretical number of records per day (i.e. 24).

2.6.4 | Investigating the circadian rhythm

To assess how any differences in energy expenditure and/or mobility between dispersers and philopatric individuals might be expressed in terms of their circadian rhythm across the three phases of dispersal (only across pre-dispersal and transience phases for mobility), we analysed variation in hourly averages of VeDBA from activity sensors (square root transformed) and distance travelled (log + 1 transformed) using GAMMs. We included individual identity and year as random effects on the intercept and used cyclic cubic splines to smooth the effect of time of day (hour). For model selection, we compared nine models: a constant model, a model containing only the spline of time of the day, a model including a sex-specific temporal effect (i.e. a separate spline of time of the day for each sex), a model including a status-specific temporal effect (i.e. a separate spline of time of the day for dispersers and philopatric individuals), a model including a phase-specific temporal effect (i.e. a spline of time of the day for each dispersal phase) and four models including the different possible combinations of sex-specific and/or status-specific and/or phase-specific temporal effects.

2.6.5 | Investigating the influence of landscape fragmentation on the energetic costs of dispersal transience

In order to investigate the influence of landscape fragmentation on the energetic costs of dispersal during the transience phase, we analysed variation in daily $VeDBA_{activity}$ estimates and total dispersal distance, defined as the straight line between the first and last location of transience, in relation to landscape structure. Based on previous work on the same study site (Martin et al., 2018), we expected the energetic costs of dispersal to be influenced by proximity to refuge habitat (woodlands) and disturbance linked to anthropogenic infrastructures (roads and buildings). A high level of human-related disturbance in the landscape likely causes animals to move more during transience to locate stop-over refuges and to travel further before locating a suitable settlement range. Hence, for each disperser, we calculated the proportion of woodland, buildings and roads (based on aerial photographs from the BD Topo, professionnels.ign.fr) in a buffer of 1 km (the diameter of a typical juvenile home range on our study site) centred on the straight line between the first and last location of their transience. Then, we analysed variation in daily $VeDBA_{activity}$ estimates (log transformed) in relation to the proportion of woodland, buildings and roads (considered as additive effects)

using a linear mixed model, including the three sex × landscape interactions, with individual identity and year as random effects on the intercept. Similarly, we analysed variation in total dispersal distance (log transformed) in relation to the proportion of woodland, buildings and roads (considered as additive effects), including the three sex × landscape interactions, using a simple linear model.

All analyses were performed in R version 3.4.3 (R Core Team, 2017). The models were fitted using maximum likelihood, and we used Akaike's information criterion (AIC; Burnham & Anderson, 2002) and Akaike weights to select the model with the most support. When ΔAIC < 2 between competing models, following rules of parsimony, we retained and interpreted the model with the fewest parameters.

3 | RESULTS

Among dispersing individuals, we observed an average dispersal duration of 9.6 days, ranging between 0.1 and 39.7 days and an average dispersal distance of 11.86 km, ranging between 0.53 and 46.82 km.

3.1 | $VeDBA_{activity}$ as an index of energy expenditure

There was a strong linear relationship between daily VeDBA estimates generated from acceleration sensors and those generated from activity sensors (conditional R^2 = 96.6%, marginal R^2 = 91.1%, Figure 1). We therefore considered that VeDBA obtained from activity sensors was a reliable index of energy expenditure across the 105 individuals monitored for activity over the study period.

3.2 | Daily energy expenditure of dispersing versus philopatric individuals

The retained model describing variation in daily $VeDBA_{activity}$ included the three-way interaction between phase, sex and dispersal status, with individual identity and year as random effects on the intercept (AIC weight = 0.842, Table S3.1 in Appendix S3). Based on this model, dispersers had a daily $VeDBA_{activity}$ which was 21.7% higher, on average, than philopatric individuals during the transience phase (mean daily $VeDBA_{activity}$ ± *SE*: 41.9 ± 3.4 for dispersers vs. 34.4 ± 2.9 for philopatric individuals) and 10.4% higher, on average, during the post-dispersal phase (mean daily $VeDBA_{activity}$ ± *SE*: 34.8 ± 3.1 for dispersers vs. 31.6 ± 2.8 for philopatric individuals, Figure 2). This difference in daily $VeDBA_{activity}$ between dispersers and philopatric individuals was globally more pronounced among females (28.5% and 19% for the transience and post-dispersal phases, respectively) than among males (15.7% and 3.4% for the transience and post-dispersal phases, respectively). In contrast, there was no difference in daily $VeDBA_{activity}$ between dispersers and philopatric individuals during the pre-dispersal phase. Finally, in philopatric individuals, males had a daily $VeDBA_{activity}$ that was 14.9% higher, on average, than females across all phases, whereas for dispersers,

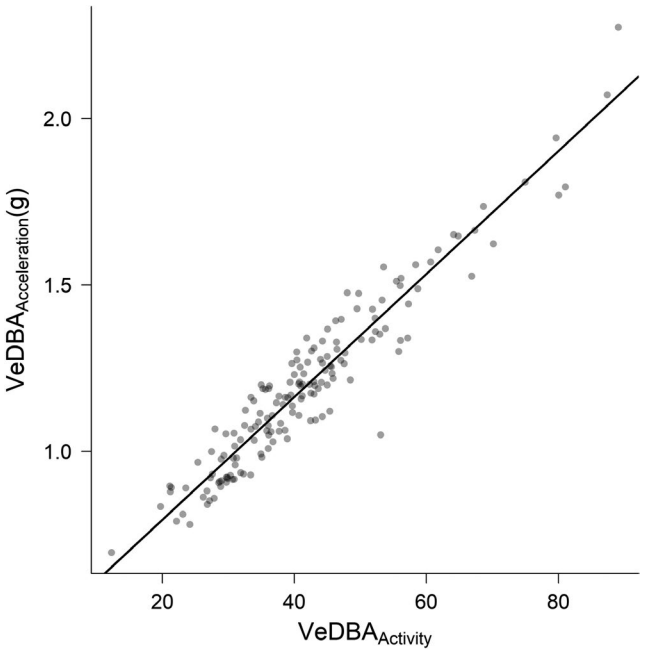

FIGURE 1 Relationship between average daily VeDBA generated from acceleration sensors and those generated from activity sensors. Points are observed values, and the line represents the best-fit linear model (with the identity of the individual included as a random factor). Abbreviation: VeDBA, vector of dynamic body acceleration

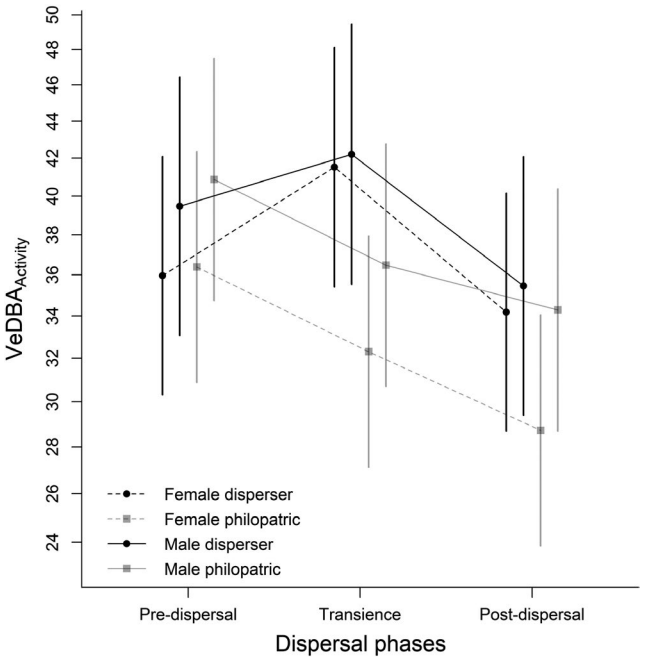

FIGURE 2 Variation in daily $VeDBA_{activity}$ for disperser and philopatric males and females across the three phases of dispersal. Points (and bars) represent predictions (and associated 95% confidence intervals) of the retained model including the three-way interaction between dispersal phase, sex and dispersal status, with individual identity and year as random effects on the intercept. Abbreviation: VeDBA, vector of dynamic body acceleration

the difference between the sexes was less pronounced and varied among phases. Indeed, males had a daily $VeDBA_{activity}$ that was 9.8% higher, on average, than females during the pre-dispersal phase and 3.7% higher, on average, during the post-dispersal phase, but there was no detectable difference between the sexes during the transience phase of dispersal. When we performed the equivalent analysis using variation in daily $VeDBA_{acceleration}$ as our proxy of energy expenditure, we obtained very similar results, indicating that energy expenditure was higher for dispersers than for philopatric individuals essentially during the transience phase (Appendix S4).

3.3 | Daily mobility of dispersing versus philopatric individuals

The retained model describing variation in daily mobility included the Julian date (relative to median date of transience) and dispersal status, with individual identity and year as random effects on the intercept (AIC weight = 1, Table S3.2 in Appendix S3). According to this model, daily mobility varied markedly in relation to dispersal status, particularly around the median date of transience, such that dispersers were much more mobile than philopatric individuals during transience (Figure 3). For example, at the median date of transience, dispersers had a daily mobility that was 63% (i.e. 0.94 km) greater than philopatric individuals (mean daily mobility ± *SE*: 2.44 ± 0.13 km for dispersers vs. 1.50 ± 0.07 km for philopatric individuals).

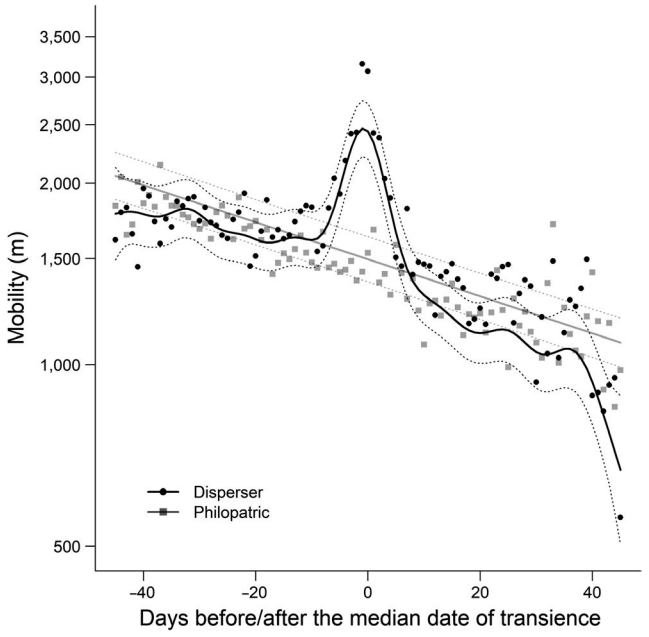

FIGURE 3 Variation in daily mobility of dispersers and philopatric individuals during the days preceding and following the median date of transience. Lines (and dotted lines) represent predictions (and their associated 95% confidence interval) of the retained model which included a smoothed effect of time before/after the median date of transience which differed between dispersal status, with individual identity and year as random effects on the intercept. Points represent observed values averaged per day and dispersal status

3.4 | The circadian rhythm of dispersal and of its energetic costs

The retained models describing time-related variation in hourly $VeDBA_{activity}$ and hourly mobility over the circadian cycle included a separate smoothed effect (i.e. a separate cyclic cubic spline) for time of the day for each phase and each dispersal status, with individual identity and year as random effects on the intercept (AIC weight = 1 for both models of hourly $VeDBA_{activity}$ and hourly mobility, Tables S3.3 and S3.4 in Appendix S3). Overall, according to these models, both hourly $VeDBA_{activity}$ and hourly mobility fluctuated over the circadian cycle and across all three phases of dispersal for both dispersers and philopatric individuals. In particular, for both dispersers and philopatric individuals, hourly $VeDBA_{activity}$ was much greater at dawn and dusk across all phases (Figure 4). However, at dawn during the transience phase, dispersers had an hourly $VeDBA_{activity}$ that was 22.7% higher, on average, than philopatric individuals (at 5 a.m., mean hourly $VeDBA_{activity}$ ± *SE*: 70.8 ± 3.3 for dispersers vs. 57.7 ± 2.8 for philopatric individuals, Figure 4c). In a similar way, during the pre-dispersal phase, hourly mobility was similarly greater at dawn and dusk for both dispersers and philopatric individuals, whereas dispersers were markedly more mobile than philopatric individuals during the transience phase, especially at dawn (at 5 a.m., dispersers had a hourly mobility that was 111.7% (i.e. 0.10 km) higher than philopatric individuals, mean hourly mobility ± *SE*: 0.19 ± 0.02 km for dispersers vs. 0.09 ± 0.01 km for philopatric individuals, Figure 4d).

3.5 | The influence of landscape fragmentation on the energetic costs of dispersal transience

The retained model describing variation in daily $VeDBA_{activity}$ only included the proportion of roads, with individual identity and year as random effects on the intercept (AIC weight = 0.126, Table S3.5 in Appendix S3 and Figure 5a). Similarly, the retained model describing variation in total dispersal distance also only included the proportion of roads (AICc weight = 0.097, Table S3.6 in Appendix S3 and Figure 5b). Overall, according to these models, dispersers had a higher daily $VeDBA_{activity}$ during the transience phase and covered a greater total dispersal distance when the proportion of roads in the landscape was higher (29.1 ± 5.1 and 1.03 ± 0.52 km for the smallest value of proportion of roads vs. 51.7 ± 7.3 and 25.02 ± 9.70 km for the highest value, for daily $VeDBA_{activity}$ and total dispersal distance, respectively). We used a simulation approach on randomly shifted and rotated dispersal trajectories to demonstrate that this correlation was unlikely ($p < .001$) to be due to sub-structure in the landscape (i.e. longer dispersal distances located by chance in areas with more roads, see Appendix S5).

4 | DISCUSSION

Natal dispersal entails costs which accumulate across the three phases of dispersal and likely play a crucial role in determining

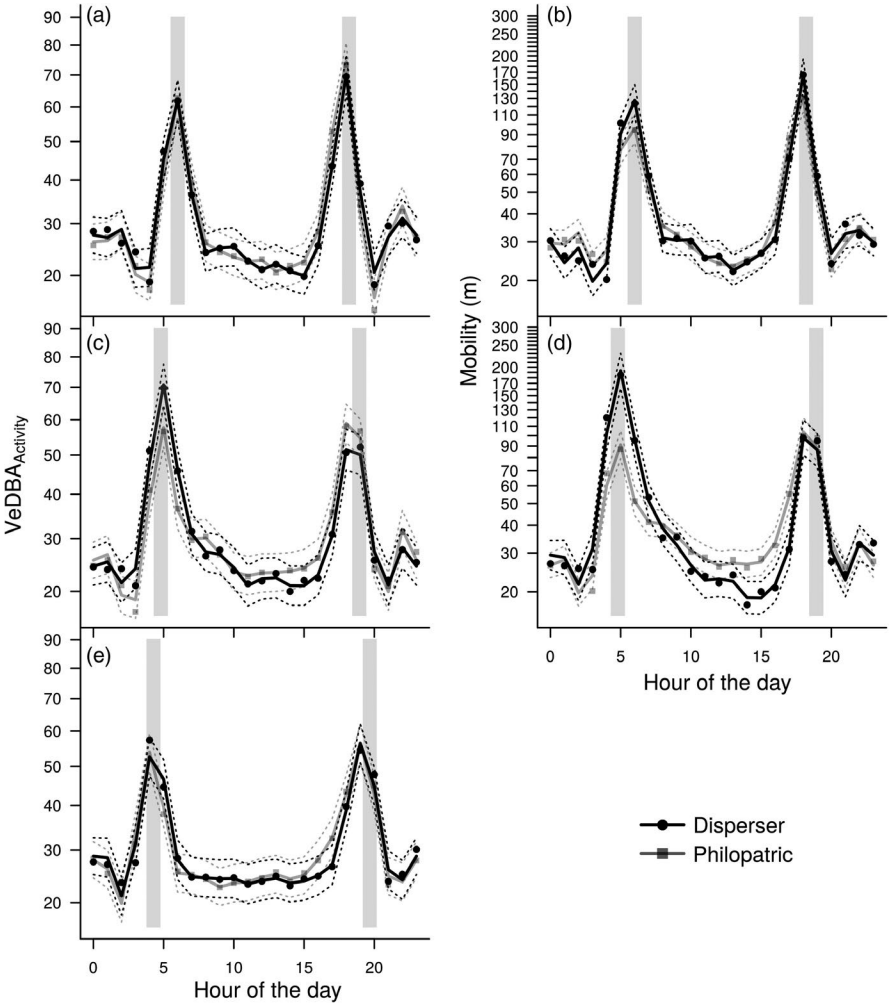

FIGURE 4 Circadian variation in hourly VeDBA$_{activity}$ (a,c,e) and hourly mobility (b,d) of dispersers and philopatric individuals during pre-dispersal (a,b), transience (c,d) and post-dispersal (e). Lines (and dotted lines) represent predictions (and their associated 95% confidence intervals) of the retained models which both included a smoothed effect of time of the day (hour) which differed between dispersal status and dispersal phases, with individual identity and year as random effects on the intercept. Points represent observed values averaged per hour and dispersal status. Grey bars indicate twilight. Abbreviation: VeDBA, vector of dynamic body acceleration

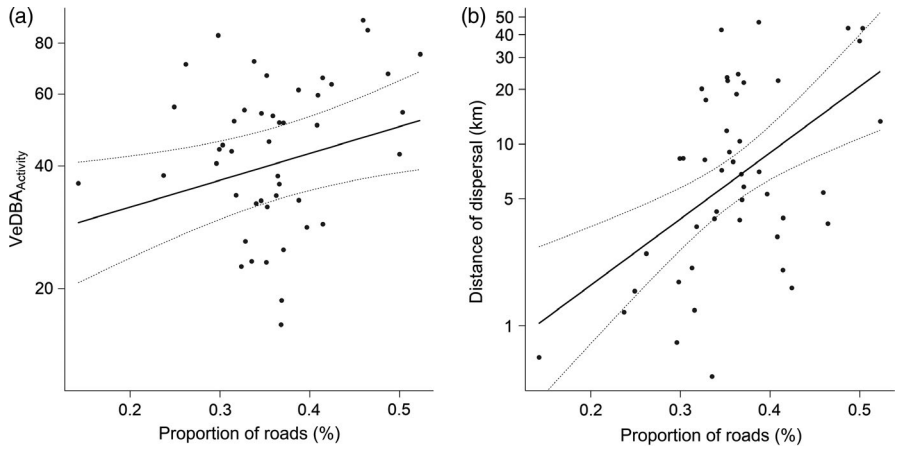

FIGURE 5 Variation in daily VeDBA$_{activity}$ during the transience phase (a) and total dispersal distance (b) in relation to the proportion of roads in the landscape. Lines (and dotted lines) represent predictions (and their associated 95% confidence intervals) of the retained models which included the proportion of roads, with individual identity and year as random effects on the intercept for the model describing variation in daily VeDBA$_{activity}$. Points represent observed values averaged per individual (a) and observed value per each individual (b). Abbreviation: VeDBA, vector of dynamic body acceleration

subsequent individual performance (Bonte et al., 2012). Because dispersal is a key process enabling wildlife to adjust to rapid human-driven alterations of the environment (Kokko & López-Sepulcre, 2006), quantifying dispersal costs is paramount for addressing the evolutionary ecology of this behaviour. Here, we showed that dispersing roe deer incur higher levels of energy expenditure due to

higher levels of activity and mobility, essentially during the transience phase, which were particularly elevated in fragmented areas of the landscape. Estimated dispersal costs were of a similar magnitude in males and females, but were especially pronounced at dawn during transience, indicating that roe deer mostly disperse at this time of the day.

Estimating energy expenditure in the wild has proved a methodological challenge that is currently being solved by the rapid development of animal-borne biologgers which reliably measure movements and dynamic acceleration of the body at a fine temporal scale (Gleiss et al., 2011). Using this approach in combination with simultaneous intensive GPS monitoring, we were able to derive two complementary measures of energy expenditure linked to activity and mobility which provided consistent evidence of substantial dispersal costs in this system. The VeDBA provides an informative proxy of field metabolic rate (Grémillet et al., 2018; Miwa et al., 2015). We first showed that this proxy provided equivalent information whether derived from true acceleration data or from data generated by activity sensors (Figure 1), allowing us to infer energy expenditure for a relatively large sample of juveniles across the three phases of dispersal. The VeDBA integrates energetic costs across behaviours, including locomotion, but also other behaviours such as feeding or grooming (Graf, Wilson, Qasem, Hackländer, & Rosell, 2015). It does not, however, incorporate the energetic costs of any process that does not involve motion, such as those linked to maintaining the immune system or thermoregulation (Grémillet et al., 2018). Thus, it is difficult to predict how a given increase in the VeDBA-based estimate of daily energy expenditure will translate into daily metabolic rate and, consequently, the expected effect on individual condition over the short term. However, because $VeDBA_{accelerometry}$ has been shown to be informative in a large number of taxa and for different types of locomotion (Miwa et al., 2015; Qasem et al., 2012), it appears likely that $VeDBA_{activity}$ has similar qualities and limitations and may, therefore, reliably index energy expenditure within and across taxa which use the same modes of locomotion.

While dispersal costs have previously been inferred from observations of a post-dispersal decrease in fitness-related traits such as survival, body condition or reproductive success (e.g. Wiens, Noon, & Reynolds, 2006), our study is the first, to our knowledge, to provide a direct comparison of energy expenditure between dispersers and philopatric individuals across the entire dispersal process. In particular, in support of our first prediction, we showed that dispersing roe deer were ca. 22% more active (Figure 2) and covered ca. 63% greater distance per day during the peak of transience (Figure 3) compared to philopatric individuals. By definition, transience involves movement away from the natal range (Clobert et al., 2001) and is therefore likely to involve increased mobility, although this is not necessarily so (Hovestadt, Binzenhöfer, Nowicki, & Settele, 2011). However, the transience phase is also associated with additional costs in terms of moving through unfamiliar and potentially risky environments which likely increase stress and daily energy requirements (Bonte et al., 2012). Dispersal costs during the pre-dispersal phase have been inferred in many insects which must develop appropriate wing morphology prior to departure, impacting condition and subsequent fecundity (e.g. Crnokrak & Roff, 2000), while loss of social rank during settlement is frequently reported in birds (e.g. Jeugd, 2001). However, transience is likely the most costly part of the process in many organisms. Indeed, we found little or no differences in activity or mobility between dispersing and philopatric roe deer during the pre-dispersal and post-dispersal phases, although there was some evidence that higher levels of energy expenditure among dispersers persisted into the post-dispersal phase in females (Figures 2 and 3). This latter result does not support our prediction of higher settlement costs in males due to intra-sexual competition for territories (Wahlström, 1994). We speculatively suggest that this could be linked to aggressive female–female interactions with resident female adults that are caring for their newborn young at this time of year (Maublanc et al., 2012). To better understand the cognitive processes that trigger departure and settlement, it would be informative to investigate the fine-scale temporal dynamics of energy expenditure during the period immediately preceding and following transience at the individual scale.

Metabolic rate is tightly linked to body size at both inter- and intra-specific levels (Brown, Gillooly, Allen, Savage, & West, 2004). In our study, irrespective of whether they dispersed or not, males generally had slightly higher levels of overall activity (Figure 2), but they were not more mobile. This result was to be expected given that the roe deer is a weakly polygynous ungulate (Vanpé et al., 2008) with a low level of sexual dimorphism (Hewison et al., 2011). However, in support of our third prediction, there was no sex difference in levels of energy expenditure among dispersers during transience, suggesting that the high costs incurred during this phase can swamp any underlying differences between the sexes due to metabolic or behavioural factors (Stache, Heller, Hothorn, & Heurich, 2013). Additionally, notwithstanding the peak in estimated energy expenditure for dispersers during transience, we observed a marked general decrease in both activity and mobility across the monitoring periods (Figures 2 and 3). We interpret this gradual decline as a response to seasonal variation in resource availability (cf. Krop-Benesch, Berger, Hofer, & Heurich, 2013), which increases from March to June in this landscape and has been shown to strongly determine home range size in roe deer (Morellet et al., 2013).

Because dispersing individuals encounter unfamiliar and potentially hostile matrix habitat, they should adjust their behavioural rhythms during transience to minimize costs (Bonte et al., 2012). In this highly anthropized landscape, where natural predators are absent (except for fox *Vulpes vulpes* predation on fawns during the first month of life), we predicted that roe deer would concentrate their movement and activity during the night so as to avoid human-related sources of risk (cars, dogs) and disturbance (other activities). Instead, we found clear evidence that, compared to philopatric animals, dispersers had higher levels of both activity and mobility almost exclusively during dawn (Figure 4). Large herbivores show a pronounced circadian rhythm across species (Ensing et al., 2014) and contexts (e.g. predator presence: Bonnot et al., 2016; photic conditions: Arnold et al., 2018), with activity peaks at dawn and dusk modulated by both

internal physiological state (Daan, Honma, & Honma, 2013) and external environmental conditions (e.g. Pohl, 1998). Our results indicate that almost all additional energy expenditure attributable to the costs of transience is concentrated within a few hours of the day, around sunrise. Hence, it seems that the circadian clock (sensu Dibner, Schibler, & Albrecht, 2010) influences how the costs of dispersal are accounted for in this system. Further work is required to understand why dispersal seems to be synchronized at dawn, but we suggest that this could be a risk management tactic to avoid human disturbance, which is higher during the day, combined with increased feeding requirements to offset the costs of transience. Indeed, dispersing roe deer appear to be considerably less active during daytime (see Figure 4), probably because they avoid moving in unfamiliar habitat during the riskiest part of the day. They may, therefore, be constrained to feed more intensively during the night prior to continuing their dispersal transience the following dawn during daylight. In any case, given that road kills are likely a common form of cost for dispersing animals in human-dominated landscapes (e.g. Massemin et al., 1998), these results are likely to have important implications for predicting and mitigating road traffic accidents involving roe deer which peak during the spring season due to juvenile dispersal (Lagos, Picos, & Valero, 2012). Importantly, our results indicate that the energetic costs of dispersal transience are influenced by landscape fragmentation. Indeed, both daily energy expenditure during transience and the total dispersal distance were higher for individuals that dispersed through a local landscape with a high road density (see Figure 5). This last relationship could arise either because animals disperse greater distances in areas with more roads or because those animals that disperse greater distances encounter a greater density of roads. According to our simulations (see Appendix S5), we found strong support for the hypothesis that this relationship is driven by animal behaviour. These results suggest that a high level of anthropization imposes a high daily energetic burden on dispersers during transience, as they must locate stop-over refuges which are sparsely distributed in the landscape to rest during daytime, and ultimately forces them to travel further to locate a suitable settlement range. As a result, dispersal appears to be more costly in human-dominated landscapes. Future work comparing dispersal movements among species along a gradient of anthropization within the framework of the Eurougulates initiative (www.eurougulates.org) will advance our understanding of how global change is likely to impact the spatial distribution of large herbivores at the continental scale by modifying dispersal costs in human-dominated landscapes.

While our study provides support for the general hypothesis that natal dispersal is energetically costly (Bonte et al., 2012), further analyses are required to investigate the fitness consequences of these costs. Establishing a detailed ethogram of dispersing animals using increasingly sophisticated analyses of acceleration data will be an important next step for understanding the behavioural basis of increased energy expenditure during dispersal and, hence, the exact nature of the associated costs (Williams et al., 2014). Dispersal has evolved because the benefits in terms of reduced inbreeding and competition for resources and/or mates often exceed the potential costs (Clobert et al., 2001). However, in the current context of global change, landscape fragmentation likely substantially increases the costs of dispersal (Fahrig, 2007), altering predicted evolutionary outcomes for dispersal behaviour (Travis & Dytham, 1999) and, therefore, metapopulation dynamics.

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AUTHORS' CONTRIBUTIONS

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

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.mm324rv (Benoit et al., 2019).

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REFERENCES

Adrados, C., Girard, I., Gendner, J. P., & Janeau, G. (2002). Global positioning system (GPS) location accuracy improvement due to selective availability removal. *Comptes Rendus Biologies*, *325*, 165–170. https://doi.org/10.1016/S1631-0691(02)01414-2

Arnold, W., Ruf, T., Loe, L. E., Irvine, R. J., Ropstad, E., Veiberg, V., & Albon, S. D. (2018). Circadian rhythmicity persists through the Polar night and midnight sun in Svalbard reindeer. *Scientific Reports*, *8*, 14466. https://doi.org/10.1038/s41598-018-32778-4

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Benoit, L., Hewison, A. J. M., Coulon, A., Debeffe, L., Grémillet, D., Ducros, D., … Morellet, N. (2019). Data from: Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore. Dryad Digital Repository. https://doi.org/10.5061/dryad.mm324rv

Bjørneraas, K., Van Moorter, B., Rolandsen, C. M., & Herfindal, I. (2010). Screening global positioning system location data for errors using animal movement characteristics. *The Journal of Wildlife Management*, *74*, 1361–1366. https://doi.org/10.1111/j.1937-2817.2010.tb01258.x

Boldt, A., & Ingold, P. (2005). Effects of air traffic, snow cover and weather on altitudinal short-term and medium-term movements of female Alpine chamois *Rupicapra rupicapra* in winter. *Wildlife Biology*, *11*, 351–363. https://doi.org/10.2981/0909-6396(2005)11[351:EOATSC]2.0.CO;2

Bonnot, N. C., Hewison, A. J. M., Morellet, N., Gaillard, J.-M., Debeffe, L., Couriot, O., … Vanpé, C. (2017). Stick or twist: Roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Animal Behaviour*, *124*, 35–46. https://doi.org/10.1016/j.anbehav.2016.11.031

Bonnot, N. C., Morellet, N., Hewison, A. J. M., Martin, J. L., Benhamou, S., & Chamaillé-Jammes, S. (2016). Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) adjust habitat selection and activity rhythm to the absence of predators. *Canadian Journal of Zoology*, *94*, 385–394. https://doi.org/10.1139/cjz-2015-0227

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., … Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, *87*, 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biological Reviews*, *80*, 205–225. https://doi.org/10.1017/S1464793104006645

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/10.1890/03-9000

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer.

Calenge, C., Dray, S., & Royer, M. (2009). The concept of animals' trajectories from a data analysis perspective. *Ecological Informatics*, *4*, 34–41. https://doi.org/10.1016/j.ecoinf.2008.10.002

Cargnelutti, B., Coulon, A., Hewison, A. J. M., Goulard, M., Angibault, J. M., & Morellet, N. (2007). Testing GPS performance for wildlife monitoring using mobile collars with known reference points. *Journal of Wildlife Management*, *71*, 1380–1387. https://doi.org/10.2193/2006-257

Clobert, J., Danchin, E., Dhondt, A. A., & Nichols, J. (2001). *Dispersal*. Oxford, UK: Oxford University Press.

Collins, P. M., Green, J. A., Warwick-Evans, V., Dodd, S., Shaw, P. J., Arnould, J. P., & Halsey, L. G. (2015). Interpreting behaviors from accelerometry: A method combining simplicity and objectivity. *Ecology and Evolution*, *5*, 4642–4654. https://doi.org/10.1002/ece3.1660

Couriot, O., Hewison, A. J. M., Saïd, S., Cagnacci, F., Chamaillé-Jammes, S., Linnell, J. D. C., … Morellet, N. (2018). Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore. *Oecologia*, *187*(1), 47–60. https://doi.org/10.1007/s00442-018-4131-5

Crnokrak, P., & Roff, D. A. (2000). The trade-off to macroptery in the cricket *Gryllus firmus*: A path analysis in males. *Journal of Evolutionary Biology*, *13*, 396–408. https://doi.org/10.1046/j.1420-9101.2000.00188.x

Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R., Di Marco, M., Rondinini, C., & Boitani, L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 7635–7640. https://doi.org/10.1073/pnas.1705769114

Daan, S., Honma, S., & Honma, K. I. (2013). Body temperature predicts the direction of internal desynchronization in humans isolated from time cues. *Journal of Biological Rhythms*, *28*, 403–411. https://doi.org/10.1177/0748730413514357

Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Bon, R., Gaillard, J.-M., & Hewison, A. J. M. (2012). Condition-dependent natal dispersal in a large herbivore: Heavier animals show a greater propensity to disperse and travel further. *Journal of Animal Ecology*, *81*, 1327–1327. https://doi.org/10.1111/j.1365-2656.2012.02014.x

Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Coulon, A., Gaillard, J. M., … Hewison, A. (2013). Exploration as a key component of natal dispersal: Dispersers explore more than philopatric individuals in roe deer. *Animal Behaviour*, *86*, 143–151. https://doi.org/10.1016/j.anbehav.2013.05.005

Debeffe, L., Morellet, N., Verheyden-Tixier, H., Hoste, H., Gaillard, J.-M., Cargnelutti, B., … Hewison, A. J. M. (2014). Parasite abundance contributes to condition-dependent dispersal in a wild population of large herbivore. *Oikos*, *123*, 1121–1125. https://doi.org/10.1111/oik.01396

Dibner, C., Schibler, U., & Albrecht, U. (2010). The mammalian circadian timing system: Organization and coordination of central and peripheral clocks. *Annual Review of Physiology*, *72*, 517–549. https://doi.org/10.1146/annurev-physiol-021909-135821

Ensing, E. P., Ciuti, S., de Wijs, F. A., Lentferink, D. H., ten Hoedt, A., Boyce, M. S., & Hut, R. A. (2014). GPS based daily activity patterns in European red deer and North American elk (*Cervus elaphus*): Indication for a weak circadian clock in ungulates. *PLoS ONE*, *9*, e106997. https://doi.org/10.1371/journal.pone.0106997

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, *21*, 1003–1015. https://doi.org/10.1111/j.1365-2435.2007.01326.x

Gaillard, J. M., Loison, A., Toïgo, C., Delorme, D., & Van Laere, G. (2003). Cohort effects and deer population dynamics. *Ecoscience*, *10*, 412–420. https://doi.org/10.1080/11956860.2003.11682789

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*, 1232–1235. https://doi.org/10.1126/science.aar7121

Gleiss, A. C., Wilson, R. P., & Shepard, E. L. (2011). Making overall dynamic body acceleration work: On the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution*, *2*(1), 23–33. https://doi.org/10.1111/j.2041-210X.2010.00057.x

Graf, P. M., Wilson, R. P., Qasem, L., Hackländer, K., & Rosell, F. (2015). The use of acceleration to code for animal behaviours; a case study in free-ranging Eurasian beavers Castor fiber. *PLoS ONE*, *10*, e0136751. https://doi.org/10.1371/journal.pone.0136751

Grémillet, D., Lescroël, A., Ballard, G., Dugger, K. M., Massaro, M., Porzig, E. L., & Ainley, D. G. (2018). Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. *Functional Ecology*, *32*, 1203–1213. https://doi.org/10.1111/1365-2435.13074

Hein, A. M., Hou, C., & Gillooly, J. F. (2012). Energetic and biomechanical constraints on animal migration distance. *Ecology Letters*, *15*, 104–110. https://doi.org/10.1111/j.1461-0248.2011.01714.x

Hewison, A. J. M., Angibault, J. M., Cargnelutti, B., Coulon, A., Rames, J. L., Serrano, E., … Morellet, N. (2007). Using radio-tracking and direct observation to estimate roe deer *Capreolus capreolus* density in a fragmented landscape: A pilot study. *Wildlife Biology*, *13*, 313–320. https://doi.org/10.2981/0909-6396(2007)13[313:URADOT]2.0.CO;2

Hewison, A. J. M., Gaillard, J. M., Delorme, D., Van Laere, G., Amblard, T., & Klein, F. (2011). Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass–size allometry in roe deer. *Oikos*, *120*(8), 1217–1226. https://doi.org/10.1111/j.1600-0706.2011.19316.x

Hewison, A. J. M., Morellet, N., Verheyden, H., Daufresne, T., Angibault, J.-M., Cargnelutti, B., … Cebe, N. (2009). Landscape fragmentation

influences winter body mass of roe deer. *Ecography*, *32*, 1062–1070. https://doi.org/10.1111/j.1600-0587.2009.05888.x

Hovestadt, T., Binzenhöfer, B., Nowicki, P., & Settele, J. (2011). Do all inter-patch movements represent dispersal? A mixed kernel study of butterfly mobility in fragmented landscapes. *Journal of Animal Ecology*, *80*, 1070–1077. https://doi.org/10.1111/j.1365-2656.2011.01848.x

Ims, R. A., & Hjermann, D. O. (2001). Condition-dependent dispersal. In J. Clobert, E. Danchin, A. A. Dhondt, & J. D. Nichols (Eds.), *Dispersal* (pp. 203–216). Oxford, UK: Oxford University Press.

Jeugd, H. P. V. D. (2001). Large barnacle goose males can overcome the social costs of natal dispersal. *Behavioral Ecology*, *12*, 275–282. https://doi.org/10.1093/beheco/12.3.275

Johnson, C. A., Fryxell, J. M., Thompson, I. D., & Baker, J. A. (2009). Mortality risk increases with natal dispersal distance in American martens. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3361–3367. https://doi.org/10.1098/rspb.2008.1958

Kingma, S. A., Komdeur, J., Hammers, M., & Richardson, D. S. (2016). The cost of prospecting for dispersal opportunities in a social bird. *Biology Letters*, *12*, 20160316. https://doi.org/10.1098/rsbl.2016.0316

Kokko, H., & López-Sepulcre, A. (2006). From individual dispersal to species ranges: Perspectives for a changing world. *Science*, *313*, 789–791. https://doi.org/10.1126/science.1128566

Krop-Benesch, A., Berger, A., Hofer, H., & Heurich, M. (2013). Long-term measurement of roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in GPS-collars. *Italian Journal of Zoology*, *80*, 69–81. https://doi.org/10.1080/11250003.2012.725777

Lagos, L., Picos, J., & Valero, E. (2012). Temporal pattern of wild ungulate-related traffic accidents in northwest Spain. *European Journal of Wildlife Research*, *58*, 661–668. https://doi.org/10.1007/s10344-012-0614-6

Lavielle, M. (1999). Detection of multiple changes in a sequence of dependent variables. *Stochastic Processes and their Applications*, *83*, 79–102. https://doi.org/10.1016/S0304-4149(99)00023-X

Linnell, J. D. C., Wahlström, K., & Gaillard, J. M. (1998). From birth to independence. In R. Andersen, P. Duncan, & J. D. C. Linnell (Eds.), *The European roe deer: The biology of success* (pp. 257–283). Oslo, Norway: Scandinavian University Press.

Martin, J., Vourc'h, G., Bonnot, N., Cargnelutti, B., Chaval, Y., Lourtet, B., … Morellet, N. (2018). Temporal shifts in landscape connectivity for an ecosystem engineer, the roe deer, across a multiple-use landscape. *Landscape Ecology*, *33*, 937–954. https://doi.org/10.1007/s10980-018-0641-0

Massemin, S., Maho, Y. L., & Handrich, Y. (1998). Seasonal pattern in age, sex and body condition of Barn Owls *Tyto alba* killed on motorways. *Ibis*, *140*(1), 70–75. https://doi.org/10.1111/j.1474-919X.1998.tb04543.x

Maublanc, M.-L., Bideau, E., Willemet, R., Bardonnet, C., Gonzalez, G., Desneux, L., … Gerard, J.-F. (2012). Ranging behaviour of roe deer in an experimental high-density population: Are females territorial? *Comptes Rendus Biologies*, *335*, 735–743. https://doi.org/10.1016/j.crvi.2012.11.003

Miwa, M., Oishi, K., Nakagawa, Y., Maeno, H., Anzai, H., Kumagai, H., …Hirooka, H. (2015). Application of overall dynamic body acceleration as a proxy for estimating the energy expenditure of grazing farm animals: relationship with heart rate. *PLoS ONE*, *10*, e0128042. https://doi.org/10.1371/journal.pone.0128042

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., …Mysterud, A. (2013). Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, *82*, 1326–1339. https://doi.org/10.1111/1365-2656.12105

Morellet, N., Van Moorter, B., Cargnelutti, B., Angibault, J.-M., Lourtet, B., Merlet, J., … Hewison, A. J. M. (2011). Landscape composition influences roe deer habitat selection at both home range and landscape scales. *Landscape Ecology*, *26*, 999–1010. https://doi.org/10.1007/s10980-011-9624-0

Morellet, N., Verheyden, H., Angibault, J. M., Cargnelutti, B., Lourtet, B., & Hewison, A. J. M. (2009). The effect of capture on ranging behaviour and activity of the European roe deer *Capreolus capreolus*. *Wildlife Biology*, *15*, 278–287. https://doi.org/10.2981/08-084

Patin, R., Etienne, M. P., Lebarbier, E., Chamaillé-Jammes, S., & Benhamou, S. (2019). Identifying stationary phases in multivariate time-series for highlighting behavioural modes and home range settlements. *Journal of Animal Ecology*, in press.

Pohl, H. H. (1998). Temperature cycles as zeitgeber for the circadian clock of two burrowing rodents, the normothermic antelope ground squirrel and the heterothermic Syrian hamster. *Biological Rhythm Research*, *29*, 311–325. https://doi.org/10.1076/brhm.29.3.311.1436

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., … Wilson, R. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE*, *7*, e31187. https://doi.org/10.1371/journal.pone.0031187

R Core Team. (2017) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/.

Ratcliffe, P. R., & Mayle, B. A. (1992). *Roe deer biology and management*. London, UK: HMSO.

Récapet, C., Zahariev, A., Blanc, S., Arrivé, M., Criscuolo, F., Bize, P., & Doligez, B. (2016). Differences in the oxidative balance of dispersing and non-dispersing individuals: An experimental approach in a passerine bird. *BMC Evolutionary Biology*, *16*, 125. https://doi.org/10.1186/s12862-016-0697-x

Reinhardt, K., Köhler, G., Maas, S., & Detzel, P. (2005). Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: The Orthoptera of Germany. *Ecography*, *28*, 593–602. https://doi.org/10.1111/j.2005.0906-7590.04285.x

Ronce, O., Perret, F., & Olivieri, I. (2000). Landscape dynamics and evolution of colonizer syndromes: Interactions between reproductive effort and dispersal in a metapopulation. *Evolutionary Ecology*, *14*, 233–260. https://doi.org/10.1023/A:1011068005057

Rothermel, B. B., & Semlitsch, R. D. (2002). An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conservation Biology*, *16*, 1324–1332. https://doi.org/10.1046/j.1523-1739.2002.01085.x

Sawyer, H., Kauffman, M. J., Middleton, A. D., Morrison, T. A., Nielson, R. M., & Wyckoff, T. B. (2013). A framework for understanding semi-permeable barrier effects on migratory ungulates. *Journal of Applied Ecology*, *50*(1), 68–78. https://doi.org/10.1111/1365-2664.12013

Schtickzelle, N., Mennechez, G., & Baguette, M. (2006). Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology*, *87*, 1057–1065. https://doi.org/10.1890/0012-9658(2006)87[1057:DDWHFI]2.0.CO;2

Stache, A., Heller, E., Hothorn, T., & Heurich, M. (2013). Activity patterns of European roe deer (*Capreolus capreolus*) are strongly influenced by individual behaviour. *Folia Zoologica*, *62*(1), 67–75. https://doi.org/10.25225/fozo.v62.i1.a10.2013

Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, *68*, 571–573. https://doi.org/10.2307/3544927

Travis, J. M., & Dytham, C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*, 723–728. https://doi.org/10.1098/rspb.1999.0696

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., … Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*, 466–469. https://doi.org/10.1126/science.aam9712

Vanpé, C., Kjellander, P., Galan, M., Cosson, J. F., Aulagnier, S., Liberg, O., & Hewison, A. J. M. (2008). Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. *Behavioral Ecology*, *19*, 309–316. https://doi.org/10.1093/beheco/arm132

Wahlström, L. K. (1994). The significance of male-male aggression for yearling dispersal in roe deer (*Capreolus capreolus*). *Behavioral Ecology and Sociobiology*, *35*, 409–412. https://doi.org/10.1007/BF00165843

Warren, R., Price, J., Graham, E., Forstenhaeusler, N., & VanDerWal, J. (2018). The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. *Science*, *360*, 791–795. https://doi.org/10.1126/science.aar3646

Wiens, J. D., Noon, B. R., & Reynolds, R. T. (2006). Post-fledging survival of northern goshawks: The importance of prey abundance, weather, and dispersal. *Ecological Applications*, *16*, 406–418. https://doi.org/10.1890/04-1915

Williams, T. M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., … Wilmers, C. C. (2014). Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science*, *346*, 81–85. https://doi.org/10.1126/science.1254885

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, *96*, 1741–1753. https://doi.org/10.1890/14-1401.1

Wood, S., & Scheipl, F. (2017). *gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4'. R package version 0.2-5*. Retrieved from https://CRAN.R-project.org/package=gamm4

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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