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Circadian periodicity in space use by ungulates of temperate regions: how much, when, and why?

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Abstract

1. When they visit and revisit specific areas, animals may reveal what they need from their home range and how they acquire information. The temporal dimension of such movement recursions, i.e., periodicity, is however rarely studied, yet potentially bears a species, population, or individual-specific signature.
2. A recent method allows estimating the contribution of periodic patterns to the variance in a movement path. We applied it to 709 individuals from 5 ungulate species, looking for species signatures in the form of seasonal variation in the intensity of circadian patterns.
3. Circadian patterns were commonplace in the movement tracks, but the amount of variance they explained was highly variable among individuals. It increased in intensity during spring and summer, when key resources were spatially segregated, and decreased during winter, when food availability was more uniformly low. Other periodicity-inducing mechanisms supported by our comparison of species- and sex-specific patterns involve young anti-predator behavior, territoriality, and behavioral thermoregulation.
4. Model-based continuous-time movement metrics represent a new avenue for researchers interested in finding individual-, population-, or species-specific signatures in heterogeneous movement databases featuring various study designs and sampling resolutions. However, we observed large amounts of individual variation, so comparative analyses should ideally use both GPS and animal-borne loggers to augment the discriminatory power; and be based on large samples. We briefly outline potential uses of the intensity of circadian patterns as a metric for the study of animal personality and community ecology.

Introduction

Animals rarely use space in a homogeneous manner, they stay longer in some locations than others, or return more frequently. This has motivated a wide array of studies into “movement recursion” (reviewed by Berger-Tal & Bar-David 2015). Movement recursions are a characteristic feature of home-range bounded animals, which by definition repeatedly use the same locations (Bastille-Rousseau et al., 2016; Riotte-Lambert et al., 2017). Movement recursions are furthermore significant to ecologists because the characteristics of revisited places offer insights into the animals’ motives and cognition (Nathan et al., 2008). For example, the recursion analysis of the movements of colonial birds would highlight their central-place foraging behavior during the breeding season and their ability to find and return to their colony each breeding season.

Another, less studied aspect of movement recursion is the temporal dimension (Bar-David et al., 2009; Li et al., 2011; Riotte-Lambert et al., 2013; Péron et al., 2016, 2017). Animals may or may not maintain a constant time period between recursions, i.e., a fixed movement schedule. For a home-range-bounded animal, the question of when to use a location is at least as important as the question of whether to use it or not. For example, many species shift to nocturnal schedules when persecuted by humans during the day (Kitchen et al., 2000; Di Bitetti et al., 2008; Tolon et al., 2009). This example highlights how the match between the periodicity in space use and the periodicity in abiotic factors such as daylight does not compulsorily indicate a direct causal relation but can instead be mediated by biotic interactions. It can be difficult to decipher the two pathways. For example, animals can move periodically to avoid heat, an abiotic factor (Long et al., 2014; Marchand et al., 2014) or to avoid predation, a biotic factor (Laundré et al., 2001; Marchand et al., 2014; Tolon et al., 2009). Both mechanisms would in many situations yield the same pattern of periodic preference for cover vs. open habitat. Periodic patterns of space use may furthermore also originate from the sequential exploitation of segregated resources, i.e., cases where animals follow the same optimal path between different resources patches every day. The most striking example of

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this mechanism is perhaps the diel vertical migration of many marine invertebrates (Lampert, 1989), which has a major influence on foraging patterns at upper trophic levels (Mukhin et al., 2009; Cruz et al., 2013; Péron et al., 2016). There are many other examples of species that alternate between feeding areas and breeding areas (e.g., Rothstein, Verner & Steven 1984; Péron *et al.* 2016). Lastly, periodic patterns of space use may also be self-generating. The most intuitive example is the cycle of sleep and wake periods (Panda et al., 2002; Merrow et al., 2005), which constrains space use in almost every species and can be represented as an intrinsic accumulating process. Other self-generating mechanisms involve resource depletion/recovery cycles (Bar-David et al., 2009; Ohashi & Thomson, 2009). “Trap-lining” by some hummingbirds and bumblebees is an example of such a process: individuals establish a circuit of nectar-producing flowers that they periodically revisit in sequence, allowing time for the replenishment of nectar stocks between two visits to a same flower (Ohashi & Thomson, 2009).

We thus have a large array of mechanisms known or suspected to yield periodic patterns of space use. Some mechanisms involve a direct response to periodicity in abiotic factors, in link with intrinsic needs (sleep, thermoregulation). Some entail a mediation by biotic interactions (predation, competition). A minority of proposed mechanisms involve no link with periodic abiotic factors (resource depletion/recovery cycles). We currently have little insights into how frequently these different mechanisms occur and how significant they are relative to other movement processes. To address that, we leveraged a recent method to extract the amount of variance explained by periodic patterns in a movement path. The method is relatively robust to variation in sampling design, allowing us to compare periodic patterns across species, habitats, and seasons.

Ungulates are particularly suited to perform a comparative analysis of periodic patterns of space use because they have been repeatedly documented to alternate between exposed feeding grounds with high predation risk, high thermoregulation costs, or both, and concealed roosting spots with low predation risk, low thermoregulation costs, or both (Brown et al., 1999; Lima & Bednekoff,

1999; Laundré et al., 2001; Di Bitetti et al., 2008; Tolon et al., 2009; Riotte-Lambert et al., 2013; Long et al., 2014; P. Marchand et al., 2014; Pascal Marchand et al., 2014; De Groot et al., 2016). We collated a large long-term database of movement data from five species of ungulates in France: roe deer (*Capreolus capreolus*, 298 individuals), red deer (*Cervus elaphus*, 92 individuals), Mediterranean mouflon (*Ovis gmelini musimon* x *Ovis* sp., 159 individuals), Alpine chamois (*Rupicapra rupicapra*, 112 individuals), and Alpine ibex (*Capra ibex*, 48 individuals). We looked for the archetypal way in which circadian patterns of space use varied throughout the year in each species and whether differences in life history or habitat are associated with specific periodic patterns of space use.

Since daylight influences both predation risk and thermoregulation costs, the most intense periodicity was expected to be the circadian one, i.e., a daily repetition of space use routines. However, well-documented differences in ungulate life history traits (Table 1) were expected to influence the season during which this periodicity would occur and how much variance it would explain. We formulated the following predictions pertaining to seasonal variation in circadian patterns (Table 2):

- (1) Circadian patterns should be dampened in winter, when the resources are uniformly of poor quality, compared to spring and summer, when the environment is more heterogeneous.
- (2) Neonatal anti-predator behavior (hiding or following; Lent 1974) was expected to influence the landscape of fear. We expected a peak in the intensity of circadian patterns of space use during the parturition period (May-June) for “hider” species (red deer and roe deer), but not for “follower” species (mouflon, chamois and ibex). The young of hider species remains motionless in a concealed spot, meaning the mother needs to periodically visit them to suckle, whereas the young of follower species start to follow their mother shortly after birth.
- (3) Among follower species, some species exhibit a more flexible pattern of association between mother and young than others. In chamois and ibex, females may temporarily leave their kids under the supervision of group mates, a behavior known as crèche or nursery formation

(Ruckstuhl & Ingold, 1998). If it occurred, this behavior would yield the same type of periodic patterns as the hiding behavior, except in June-July, not May-June, because crèches form when young are already quite large.

(4) Regarding the role of thermal constraints, we expected a contrast between mouflon and other species. Mouflon are known to thermoregulate behaviorally during the summer in our study population (Bourgoin et al., 2011; P. Marchand et al., 2014). The other species either have access to widespread shaded forage all year long (roe deer, red deer) or live in alpine environments (chamois, ibex). Chamois and ibex have elsewhere been documented to move upwards in summer which allows them to avoid both thermal stress and competition with livestock (Mason et al., 2014, 2017). Although this type of movement was not studied in our populations, we assumed nevertheless that chamois and ibex were less exposed to thermal stress than mouflon in their respective summer ranges. We therefore predicted that only mouflon would exhibit an increase in circadian patterns during the summer.

Some ungulates are also territorial. Territorial animals 'patrol' territory borders to deposit olfactory marks, advertise ownership vocally, or to physically chase intruders (Moorcroft et al., 2006; Giuggioli et al., 2011; Mahoney & Young, 2017). These behaviors are strongly suspected to yield periodic patterns (Péron et al., 2016, 2017). In our study, only roe deer males are territorial (Liberg et al., 1998).

(5) In roe deer, assuming that territories were small enough to patrol the entire border within a single day, or otherwise that territory defense was ritually performed every day, we expected that space use by male roe deer would be more circadian between March and October (territorial season) than during the rest of the year, that males would be more circadian than females, and that males from forest would be more circadian than males from cultivated land. The latter prediction stems from the fact that the social organization of roe deer changes with habitat in the study area. In forest, habitat is more homogeneous, home ranges are smaller, and population is denser than in

cultivated habitat (A. J. Mark Hewison et al., 2007). The species is also more gregarious in open than closed habitat.

Lastly, we will use our results to highlight the potential of the method to extract individual-, population-, and species-specific signatures from noisy movement data. Indeed, spectral analysis methodologies are relatively robust to variation in sampling design (cf. Method section), and the above list of mechanisms involves defining aspects of an animal's ecology, which looked promising for those needing to extract standardized metrics from heterogeneous animal tracking databases.

Material and methods

MEASURING THE INTENSITY OF CIRCADIAN PATTERNS OF SPACE USE IN ANIMAL TRACKING DATA

The method is a type of spectral analysis: we fit sinusoids to the movement data and look for the sinusoids that contribute the most to the variance in the movement data. Our analyses are based on the “periodic-mean model” from Péron *et al.* (2017) in which temporal autocorrelation is taken into account when fitting the sinusoids by way of a Kalman filter to compute the model likelihood (Fleming et al., 2017). In this model, the focal animal is attracted to a location that oscillates through time, while simultaneously being driven away from that location by random deviations and maintaining continuity in its speed and direction. This model generalizes the Ornstein-Uhlenbeck model (OU a.k.a. mean-reverting random walk; Dunn & Gipson 1977; Blackwell 1997) by replacing the constant mean term of the OU model by a periodic function (Péron et al., 2017) and by considering temporal autocorrelation in both the position and the velocity (Fleming et al., 2014). We fixed the period to one day (circadian period) after preliminary analyses and following the biology of the study species (cf. list of hypotheses in the introduction).

For each individual and month, we computed the intensity of circadian patterns of space use, denoted η_P (Eq. 1; Péron *et al.* 2017). η_P is analogous to the percentage of the variance in the movement path that was explained by the periodic pattern. It is reported in % points.

Eq. 1

$$\eta_P = \frac{D}{D + S} \text{ with } \begin{cases} D = \sum_{k=1}^K \|A_k\|^2 + \|B_k\|^2 \\ S = \text{tr}(\sigma_0) \end{cases}$$

K is the number of harmonics in the preferred model, A_k and B_k are the amplitudes of the cosine and sine waves, and σ_0 is the variance-covariance matrix of the non-periodic stochastic component of the movement.

We used the R-package *ctmm* (Calabrese, Fleming & Gurarie, 2016; Fleming & Calabrese, 2016) to fit the model to the tracking data and estimate η_P . We fit the model separately for each individual*month combination. We used the Akaike Information Criterion corrected for finite sample size (AICc) to decide whether any circadian signal was present, and how many harmonics of this periodicity were detectable (Péron *et al.* 2017). The AICc was also used to select other features of the model, as described by Calabrese, Fleming & Gurarie (2016).

NOTE ON PERIODS GREATER THAN ONE DAY

The framework allows exploration of periods other than one day, either by following the same process as above but with another period (e.g., one week, one lunar month, one year) which may superimpose on the circadian period or act in isolation, or by fitting a ‘circulation model’ of which the period would be estimated as a model parameter (Péron *et al.* 2017). Preliminary analyses indicated that periods longer than a day were rare in our study individuals.

FIELD METHODS AND STUDY SITES

Each dataset was collected as part of long-term research programs into the biology of each species; only a subset of the authors were involved in each program; the “we” in this section is colloquial.

We monitored adult roe deer of both sexes in Aurignac from 2003 onwards. The Aurignac study site is a 12,000-ha rural and hilly region in southwest France (N 43°17, E 0°53; 350-450 m.a.s.l.) with two large forest patches (672 and 463 ha) and numerous smaller ones. We distinguished two types of habitat depending on the extent of forest in a deer's home range: mostly forest or mostly open mosaic habitat. Roe deer are subject to hunting in Aurignac (drive hunts in fall-winter, stalking in summer). We captured roe deer in winter using a well-tested drive-netting method, with 30-100 beaters and up to 4 km of nets. We equipped deer with GPS collars (Lotek 3300 GPS, Lotek 3300GSM or VECTRONIC Aerospace GmbH GPS Plus). We only analyzed data from adults (>1 year old) in this study. Collars were programmed to obtain one GPS fix every 4 hours (2003-2004) or every 6 hours (subsequent years). In some individuals, we also programmed specific days during which we recorded one location every 10 min. A few collars were also programmed to record one GPS fix every hour. The monitoring period (including individuals that were fitted multiple times) lasted on average 372 days per individual (\pm standard error 338). Further details about the field methods can be found in Morellet *et al.* (2011).

We monitored adult Mediterranean mouflon of both sexes with GPS collars from 2010 onwards in the Caroux-Espinouse massif, a 17,000-ha hilly region in southern France (N 43°38, E 2°58; 390-1124 m.a.s.l.), where mouflon are distributed in and outside of a hunting-free reserve. Preliminary analyses indicated that hunting did not have a major influence on periodic patterns (Fig. 1). We distinguished mouflon whose home range is mostly in the reserve and those whose home range is mostly out of the reserve. We captured mouflon in spring and fitted them with GPS collars (Lotek 3300S revision 2). Collars were programmed to record locations on even hours on one day and odd hours on the other day (12 locations per day). The monitoring period lasted on average 411 days per individual (\pm standard error 297). Further details about the field methods for the mouflon study can be found in Marchand *et al.* (2014a).

We monitored adult female red deer in La Petite Pierre National Hunting and Wildlife Reserve. This is a 2,760-ha forest in northeastern France (N48°49, E7°20; 250-320 m.a.s.l.). Red deer are hunted in autumn. From 2002 onwards, we captured red deer using drive-netting or traps and fitted them with GPS collars Lotek 3300S, 3300L, 7000 and 4400M. Collars were programmed to obtain the location of the red deer with a schedule of 1 GPS fix every 4 or 6 hours. For one day each year, additional GPS fixes were recorded every 15 or 30 min. The monitoring period lasted on average 317 days per individual (\pm standard error 281). Further details about the field methods for the red deer study can be found in Richard *et al.* (2013).

We monitored adult female Alpine chamois with GPS-collars from 2003 onwards in the Bauges hunting reserve (N45°41, E6°08; 800-2217 m.a.s.l.), a 5200-ha mountainous area with a mosaic of forest and alpine meadows. Guided hunts are organized in autumn. We captured chamois in summer and fitted them with GPS collars (Lotek 3300S or Vectronics VERTEX Plus). Collars were programmed to records locations every 10 minutes, 20 minutes, or 4 hours, depending on the year and period of the year. The monitoring period lasted on average 406 days per individual (\pm standard error 212). For this study, we only analyzed the data from females (because too few males were fitted). Further details about the field methods for the chamois study can be found in Darmon *et al.* (2014).

We monitored adult Alpine ibex of both sexes with GPS-collars from 2013 onwards in the Bargy mountain range (N46°1', E6°29'; 1380-2230 m.a.s.l.), a mountain area with alpine vegetation. The Bargy ibex population was recently partially culled following an epidemic of brucellosis; culling operations were conducted in October 2013 and 2015 (respectively 233 and 70 ibexes were culled). Otherwise the species is strictly protected (not hunted). We captured most ibexes in spring and a few in autumn. We fitted them with VECTRONIC Aerospace GmbH GPS Plus collars. Collars were programmed to records locations every hour during one year (females) or two years (males). The

monitoring period lasted on average 406 days per individual (\pm standard error 212). Further details about the field methods for the Alpine ibex study can be found in Marchand *et al.* (2017).

DATA SELECTION

For each month, we selected the individuals that had a median sampling interval below 4 hours during the focal month, and that were monitored for at least 14 days of the focal month. This procedure yielded an ensemble of 2799 individual*month datasets for roe deer in Aurignac, 945 individual*month datasets for red deer in La Petite-Pierre, 1717 individual*month datasets for mouflon in the Caroux, 1184 individual*month datasets for chamois in the Bauges, and 343 individual*month datasets for ibex in the Bargy. For each individual*month dataset, we discarded location records more than four standard deviations from the centroid (roe deer) or more than 6 standard deviations (other species) (0-3% of records depending on individual; up to 8% in a few tracks when collars kept recording data after the end of the deployment). We visually checked that we did not remove biologically significant excursions and that all discarded locations were indeed spurious. We assumed that the telemetry noise was negligible once these outliers were removed.

POST-HOC REGRESSIONS

Separately for each species, we used cyclic penalized cubic regression splines (function `gam` from R-package `mgcv` with option “`cc`” in the smoother) to regress the intensity of circadian patterns of space use η_p against the month of the year, assuming a zero-inflated quasi-Poisson distribution. The zero-inflation accommodated the fact that η_p was estimated to zero if the circadian periodicity was not selected during the model selection procedure. We chose the minimum possible number of knots ($k = 4$) instead of optimizing k using the built-in generalized cross-validation routine, because the `gam.check` diagnosis revealed that the amount of missed features (k-index metric; Wood, 2017) did not improve with the number of knots, while the statistical power declined and over-fitting behavior (wiggliness) increased with the number of parameters.

As part of the test of our prediction about the role of territoriality, when both sexes were monitored (roe deer, mouflon, ibex) we considered the two-way interaction between month and sex. When two habitat types were identified (roe deer: forest/mosaic; mouflon: reserve/not reserve) we also considered the two-way interaction between month and habitat. To account for individual variation, we also considered the random effect of individual identity on the intercept and on the fixed effect of month (linear, quadratic and cubic), implemented through the analogy between a penalized spline with a ridge penalty and a Gaussian random effect (option “re”). Finally, to control for the fact that coarser sampling resolutions make it less likely that periodic patterns of space use are detected (Péron *et al.* 2017; Table S2 in Appendix S1), we included the fixed effect of the sampling interval (continuous variable), both on the intercept and in interaction with the fixed effect of month. Figures were drawn for a sampling resolution of one hour. Finally, we weighed all the regressions by the inverse of the sampling variance of the η_p estimates. The full details of the combinations of model features that we considered is given in Appendix S1. We used the Akaike Information Criterion to select the preferred combination (Table S1 in Appendix S1).

In addition to the sex- and habitat-effects in the regressions, we tested our predictions using the presence or absence of seasonal peaks in the intensity of circadian patterns of space use. These seasonal peaks were detected visually on plots of model predictions of the species- and month-specific expected intensity of circadian patterns of space use.

Results

Depending on species, between 25% and 50% of the variance in the intensity of circadian patterns of space use was accounted for by individual and temporal factors (Table S2 in Appendix S1).

SEASONAL PATTERNS

All species exhibited the least amount of periodicity in January-February (Fig. 2), as predicted. As a side note, lighter species (roe deer and mouflon; Table 1) exhibited the most winter periodicity,

however mouflon experienced much harsher winters than roe deer yet exhibited similar levels of winter periodicity.

YOUNG ANTI-PREDATOR BEHAVIOR

Red deer met our prediction that hider species should exhibit a peak in circadian patterns after parturition (Fig. 2b). Roe deer did not meet the prediction: the intensity of circadian patterns was not higher in spring than the rest of the year, nor were females more circadian than males in spring (Fig. 2a). Both mouflon (whose peak was later in the year and extended into summer; Fig. 2d) and ibex (which exhibited relatively constant periodicity outside of the winter; Fig. 2e) met our prediction that follower species should not exhibit a peak after parturition. Chamois exhibited a peak in June-July that could be explained by crèche formation (Fig. 2c). Therefore, the support for young anti-predator behavior as a driver of circadian patterns of space use was mixed. We did not find a clear-cut contrast between hider and follower species, because of the roe deer results and because crèche formation had to be invoked to explain the chamois patterns.

TERRITORIALITY

Roe deer males were more circadian than females between March and September, especially in the forest habitat (Fig. 2a; Table S2), as predicted. Conversely, in mouflon and ibex, which are not territorial, male patterns were parallel to female patterns (Fig. 2d, e).

BEHAVIORAL THERMOREGULATION

As predicted, only mouflon exhibited a peak in the intensity of circadian patterns in summer (June-August; Fig. 2d). The much weaker and wider peak in periodicity exhibited by ibex (Fig. 2e) could not entirely be ascribed to behavioral thermoregulation. In chamois the intensity dropped sharply in August (Fig. 2c), which is as warm as July, indicating that thermoregulation was not the cause of the peak in chamois. Similarly, in roe deer and red deer, the timing of the peak in the intensity of circadian patterns of space use contradicted the hypothesis that they were caused by rising temperature (Fig. 2a, b). In all species but especially mouflon, summer periodicity was more intense

in males than females, as predicted because males are larger thus have more thermoregulation constraints, and thus bringing additional support to the behavioral thermoregulation hypothesis. In summary, we found support for the behavioral thermoregulation hypothesis in the form of a summer increase in circadian patterns in mouflon, and the lack of such an increase in other species.

Discussion

In five species of ungulates living in contrasted environments, there was a species-specific signature in the way that the intensity of circadian patterns of space use, defined as the proportion of the variance in the movement path explained by circadian periodicity (i.e., fitted sine waves), varied throughout the year. This species-specific signature clearly came out amidst a large amount of individual variation, some explained by individual factors (sex and habitat), some remaining to be explained. We could relate the species-specific signatures to seasonal variation in resource distribution (Laundré et al., 2001), to young anti-predator behavior (Lent, 1974; Byers & Byers, 1983), to territoriality (Liberg et al., 1998), and to behavioral thermoregulation (Long et al., 2014; Marchand et al., 2014). So, our conclusions regarding the potential of the intensity of circadian patterns of space use as a generic movement metric are mixed. On the one hand, there was a species-specific signature that matched most of our biological expectations. But on the other hand, this signature appeared in the seasonal variation, not in the average value of the metric; and detecting it amidst a large amount of individual heterogeneity required larger-than-usual datasets in terms of numbers of individuals.

To go further into the study of periodic patterns of space use by ungulates, we envision insights from individual-level habitat heterogeneity quantifications. All of our predictions assumed a role for habitat heterogeneity, notably because it influenced the possibility and need to alternate between different habitats (Laundré et al., 2001; Martin et al., 2015). Quantifying heterogeneity at both the population and home range levels therefore appears as a natural next step to further support or inform the conclusions we drew from seasonal patterns. Other individual determinants of

periodic patterns, most notably reproductive status and weather anomalies, also offer avenues for further tests.

Several recent studies identified repeated sequences in animal tracking data using pattern recognition techniques, after annotating the tracks with habitat categories or with user-defined zones (De Groeve et al., 2016; Riotte-Lambert et al., 2017). We stress that our method is, fundamentally, complementary to these approaches. Movement sequences may be repeated without periodicity, and periodicity may be detected even if the stochastic component of the model conceals the repeated sequences. We envision that our method will be relevant to the analysis of large heterogeneous databases, while pattern recognition techniques will be relevant to focused analyses of individual home ranges.

Indeed, we believe that we pave the way for more integrated multi-traits comparative analyses of movement ecology. Effort to compare the movement ecology of species and populations are still limited by the restricted array of metrics available to characterize movement paths, and the sensitivity of most of these metrics to the sampling design (Fryxell et al., 2008; Abrahms et al., 2017; Tucker et al., 2018). To apply the available metrics, authors typically subsampled their datasets, but the effect of these data manipulations on inference is not compulsorily negligible: for example, estimated turn angles depend on the interaction between sampling design and the intrinsic sinuosity of the focal movement path (Fryxell et al., 2008). The η metric that we used in the present study is an example of a new type of model-based continuous-time movement metric, still general enough to be computed in most species and environments but specific enough to capture features that would evade a more superficial examination. An important aspect of the η metric that we employed is its relative robustness to variation in sampling design, allowing the comparison of datasets collected under varying conditions without leaving out most of the data collected. There are other such metrics, for example autocorrelation times and asymptotic variances (Fleming et al., 2014), which have to our knowledge never been employed for comparative purposes. Of course,

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movement metrics only represent coarse summaries of complex movement paths, in an attempt to assign each movement path to a movement type (Bastille-Rousseau et al., 2016; Abrahms et al., 2017). Combining several metrics should in the future make it possible to augment the number of movement types one can consider and the ability to discriminate among them (Bastille-Rousseau et al., 2016; Abrahms et al., 2017). But the biological inference will still come from confronting variation in movement metrics to variation in other quantities based on predictions from behavior ecology, i.e., from combining multiple approaches to movement ecology.

As a side note and to open a few perspectives, our study species actually occur in sympatry, at least for some of them, even if we studied them separately. Periodicity in space use is one way for species to coexist through partition of time (Kronfeld-Schor & Dayan, 2003; Darmon et al., 2014). The intrinsic drivers of periodic patterns of space use that we report might therefore promote coexistence between species and individuals that have different periodic patterns. Periodic patterns may also be modified as a direct response to competition. In addition, by analyzing multi-year datasets and correcting for individual factors such as sex and age, we could potentially investigate whether some individuals consistently use space in a more periodic manner than others and thus how the gradient of animal personalities, which is mostly documented from experiments in captivity, translates into space use patterns in the wild (Spiegel et al., 2017). For example, risk-taking personalities are expected to respond less strongly to predation risk and thus exhibit less periodic movements than shy personalities in the same landscape.

In conclusion, the species-specific signatures in the circannual variation in the intensity of circadian patterns of space use came out amidst a large amount of individual variation, but still allowed us to test the role of resource heterogeneity, young anti-predator behavior, territoriality, and thermoregulation as periodicity-inducing mechanisms. To go beyond patterns in seasonal variation, our hypotheses could be further tested within each population using between-year and between-individual variation, by adding covariates such as home range heterogeneity, reproductive

status, and thermal exposure. More generally, we provide one of the first instances of a comparative analysis based on a model-based continuous-time movement metric, opening a new avenue for comparative movement ecology.

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Data accessibility

The complete list of individual η estimates are available from the Dryad Digital Repository:
<https://doi.org/10.5061/dryad.cv45n3b> (Péron et al 2018).

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Accepted Article

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Tables

Table 1: Species traits, timing of important events in the annual cycle, and sampling design. For foraging specialization, we use “+” signs to indicate proximity to the “obligate browser” or “obligate grazer” ends of the gradient (i.e., nuancing the usual “intermediate feeder” terminology, based on collective knowledge from the long-term programs). For sociality, we use “+” signs to indicate proximity to the “always solitary” or “always in large groups” ends of the gradient. Female body mass was measured at capture, except in ibex (body mass data was sourced from another population: Belledonne).

Species	Female body mass (80% confidence interval; kg)	Young anti-predator behavior	Sociality	Foraging specialization	Parturition	Mating	Hunting	Median sampling interval (h)	Median sampling duration (day)
Roe deer	20-25	Hider ^(1,2)	Solitary+ ⁽³⁾	Browser++ ⁽⁴⁾	May-Jun	Jul-Aug	year-round (technique varies)	1	315
Red deer	80-110	Hider ⁽²⁾	Gregarious+ ⁽⁵⁾	Browser+ ⁽⁴⁾	May-Jun	Sep-Oct	Oct.-Jan.	0.25	267
Alpine chamois	25-34	Follower ⁽²⁾ (can form crèches)	Gregarious++ ⁽⁶⁾	Intermediate ⁽⁴⁾	Mid May-Jun	Mid Nov-Dec	Sep.-Feb.	0.33	383
Alpine ibex	37-51	Follower ⁽²⁾ (can form crèches)	Gregarious++ ⁽⁷⁾	Grazer+ ⁽⁸⁾	Jun	Dec	Culling only	1	253
Mediterranean mouflon	21-30	Follower ⁽²⁾	Gregarious++ ⁽⁹⁾	Grazer++ ⁽⁴⁾	end Mar-May	end Oct-Dec	Sep.-Feb.	2	359

(1) Linnell et al., 1998

(2) Fisher et al., 2002

(3) Hewison et al., 1998

(4) Redjadj et al., 2014

(5) Clutton-Brock et al., 1982

(6) Loison et al., 1999

(7) Toigo et al., 1995

(8) Hofmann, 1989

(9) Cransac et al., 1998

Table 2: Summary of the predictions about the circannual variation in the intensity of circadian patterns of space use. Predictions that were met in this study are highlighted in bold font. A hyphen indicates cases where the prediction could not be tested (lack of male data).

Species\Hypothesis	Seasonality	Young anti-predator behavior	Territoriality	Behavioral thermoregulation
Roe deer	Moderate drop in winter	Peak after parturition	More periodicity in males than females and forest than mosaic habitat, and drop between Oct and Feb	No increase in summer
Red deer	Sharp drop in winter	Peak after parturition	-	No increase in summer
Chamois	Sharp drop in winter	No peak after parturition, potentially a peak during the late rearing period	-	Moderate increase in summer
Ibex	Sharp drop in winter	No peak after parturition, potentially a peak during the late rearing period	No difference between males and females	Moderate increase in summer
Mouflon	Moderate drop in winter	No peak after parturition	No difference between males and females	Sharp increase in summer

Accepted Article

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Figures

Fig. 1: Visual representation of periodic patterns of space use with periodograms from a male mouflon monitored in a hunted area from July 2011 to July 2012. The black periodograms are from the location time series. The peaks (indicated by arrows) correspond to the circadian periodicity and a harmonic associated to it. The grey periodograms are from the timestamps only and serve to verify that the peaks in the black periodograms are not artefactual (Péron et al., 2016).

Fig. 2: Circannual variation in the intensity of circadian patterns of space use in five species of ungulates. Each symbol corresponds to one individual*month combination, with males in light grey and females in dark grey. The shaded areas represent the 95% confidence intervals of the preferred spline models (males in light grey and females in dark grey). For roe deer and mouflon, results are presented separately in two habitats (roe deer: forest mosaic or pure forest; mouflon: mostly inside or mostly outside the hunting-free reserve).



