

Periodic continuous-time movement models uncover behavioral changes of wild canids along anthropization gradients

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Abstract. Most species exhibit periodic behaviors in response to cycles in resources and risks in the environment (circadian, lunar, seasonal, and so on). The ability to respond to anthropogenic perturbations by modifying periodic behaviors remains little studied, as does the question of whether and how periodic behaviors translate into periodic patterns in animal space use, on which we focus. Extending existing continuous-time stochastic movement models, we propose two new parametric approaches to detect and quantify periodic patterns of space use in animal tracking data, via periodicity in the expected position or circulation in the stochastic component of the path. We use them to study the movements of maned wolves (*Chrysocyon brachyurus*) and coyotes (*Canis latrans*) along anthropization gradients. These case studies illustrate how periodic patterns can be of natural origin (cycles in the environment) or anthropogenic origin (periodicity in human activity or restrictions on available habitat), suggesting a role for periodic patterns of space use in species persistence in anthropized areas. The method builds upon and extends existing functionalities in the R-package *ctmm*, in which the necessary tools are made available.

Key words: carnivore; circadian cycle; conservation behavior; disturbance; habituation; movement ecology; periodicity; plasticity; spectral analysis.

INTRODUCTION

Natural environments are cyclic (circadian, lunar, seasonal, and so on). As a consequence, animal physiology and behaviors are also periodic (Panda et al. 2002, van Oort et al. 2005). Beyond this well-known pattern, many questions are still pending, however, in particular the extent to which periodic behaviors are hard wired through an internal clock mechanism (Suter and Rawson 1968, Coppack and Pulido 2004, Merrow et al. 2005, Ehlinger and Tankersley 2006), or whether periodic behaviors can be plastically modified depending on the light environment (van Oort et al. 2005) or on other environmental and individual factors (Wittemyer et al. 2008). Another pending question involves the way periodicity in activity levels, i.e., periodicity in movement speed, acceleration, feeding rate, or other metric of activity, translates into periodic patterns of space use, i.e., the way certain areas of animal home ranges may be regularly reused to respond to cycles in resource and risk. The above-cited studies exclusively focus on activity, but

at least one study has shown that periodicity in activity levels does not necessarily translate into periodicity in space use (Péron et al. 2016). In any case, periodic patterns of space use remain strongly understudied compared to periodicity in activity levels (Bar-David et al. 2009, Li et al. 2010, Riotte-Lambert et al. 2013). Yet, in the context of the Anthropocene, the ability for animals to use space in a periodic manner may become increasingly important to cohabitate with humans, who are themselves highly periodic in their use of space and activity levels. Building upon the existing *ctmm* framework (Calabrese et al. 2016), we develop a new set of methods to detect and quantify periodic patterns of space use in animal tracking data. These new methods focus on space use instead of activity, and are parametric instead of nonparametric (see *Method* section).

We use the new methods to analyze periodic patterns of space use in two application cases where there is a strong spatial gradient of anthropization, i.e., human footprint. We expect that animals respond to anthropization by modifying their periodic patterns of space use. Landscape anthropization (Vitousek 1997) implies both that habitats are modified and that people are present in the landscape. Human presence presents a direct or perceived

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predation risk for most species (Frid and Dill 2002). In response to that risk, animals are expected to avoid areas of their range when people are active in those areas, and use them only when people are absent (Tolon et al. 2009, Martin et al. 2010, Muhly et al. 2011). Similarly, human activities may make resources cyclic (e.g., through agriculture) and induce periodic use of space through that pathway (Berthold et al. 1992).

Perhaps less intuitively, periodic patterns of space use can also be induced by aspects of an animal's ecology other than cycles in resources and risks. First, most animals must optimize their use of space along several gradients that may be hard to reconcile, such as breeding and foraging habitat quality (Weimerskirch 2007) or predation risk and foraging efficiency (Wittemyer et al. 2008, Riotte-Lambert et al. 2013). Under these conditions, the individuals may oscillate between the most profitable ends of each gradient, yielding a periodic pattern with a period scaling to the mean expected travel time (Weimerskirch 2007, Martin et al. 2015). For example, Galapagos Albatrosses (*Phoebastria irrorata*) alternate between brooding on land and foraging far at sea with a constant period during the breeding season (Péron et al. 2016).

Second, individuals may negatively influence their habitat: they may deplete resources (Kotler et al. 1994, Bar-David et al. 2009, Ohashi and Thomson 2009), influence prey behavior (Brown et al. 1999, Fortin et al. 2005, Arias-Del Razo et al. 2011), attract predators, or enhance parasite abundance (Van Vuren 1996, Boulinier et al. 2001). In these scenarios, individuals are expected to leave any given patch as soon as it becomes less profitable than the average, and return only when resources and risk have recovered to profitable levels (Fretwell and Lucas 1969). This mechanism generates a periodic pattern of space use related to the expected duration of one depletion/recovery cycle.

Third, periodic patterns of space use may have a social origin. Territorial conflicts bear a cost in time, stress, and risk of injury, and most species have developed conflict avoidance behaviors that are in part based on space use tactics (Eason and Hannon 1994, Laidre et al. 2013, Elbroch et al. 2014). By following a predictable pattern of presence/absence along territory borders, and relying on olfactory or auditory cues to enforce borders and advertise patrolling times (Giuggioli et al. 2011), individuals are implementing a dissuasion policy based on the assumption that neighbors also do not want to meet (Rabinowitz and Nottingham 1986). Under these conditions, the need to regularly renew territorial marks can induce periodic patterns of space use, especially if the territory is large relative to the movement capabilities of the individual.

These three types of periodicity-inducing mechanisms share the common feature that they are grounded in the way resources and risks are distributed in space and time, but that the resources and risks do not need to be themselves periodic. Since anthropization alters the

distribution of resources and risks, these mechanisms constitute a pathway for anthropization to modify existing periodic patterns of space use or create new ones, in addition to the more obvious pathway through periodicity in resources and risks.

For our case studies, we ranked situations along gradients of anthropization. At the "wilderness" extreme, we expected natural periodicities, the period of which could be predicted from the species' ecology (cf. previous paragraphs). At the anthropized extreme, we expected anthropogenic periodicities, either linked to periodicity in human activities or to anthropogenic restrictions on habitat. In between these two extremes, we expected that human activities would be less predictable and that habitat alterations would not be as constraining. Thus, we expected that intermediate and moderate anthropogenic perturbation regimes would force the animals to abandon their natural periodic patterns, but without enforcing an artificial periodic pattern yet (Fig. 1). In short, we predicted a switch from a natural to an artificial periodic pattern of space use along gradients of increasing anthropization, with an aperiodic regime in between. Note that a similar prediction could be made regarding periodicity in activity levels, but our study focuses on periodic patterns of space use.

We analyzed GPS tracking data from two species of wild canids, a family known for the expression of periodic patterns of space use (although few if any quantitative assessments exist in the literature): maned wolf (*Chrysocyon brachyurus*) and coyote (*Canis latrans*). Our study individuals collectively sampled the full gradient of anthropization, from the interior of a national park to urban areas, with the maned wolves mostly documenting the first half of the gradient, the coyotes documenting the second half, and the two species overlapping in the middle of the gradient. All the methods and tools in this study are available in the R package *ctmm* (Calabrese et al. 2016, Fleming and Calabrese 2016), along with a semi-automated routine reproducing the analytical protocol of our case studies.

METHODS

Periodic patterns of space use: definitions

The study of periodic patterns of space use draws on concepts from movement ecology and spectral analysis (Table 1). There is a fundamental distinction between repeat visits and periodic visits to a given location. An animal may repeatedly visit specific locations of its home range without being periodic, if there is no characteristic time period separating two visits to the focal locations. We hereafter further assume that periodic patterns are not restricted to a specific place or period of time, i.e., occur throughout the study period and the animals' home range when they occur, although that specific assumption could easily be relaxed.

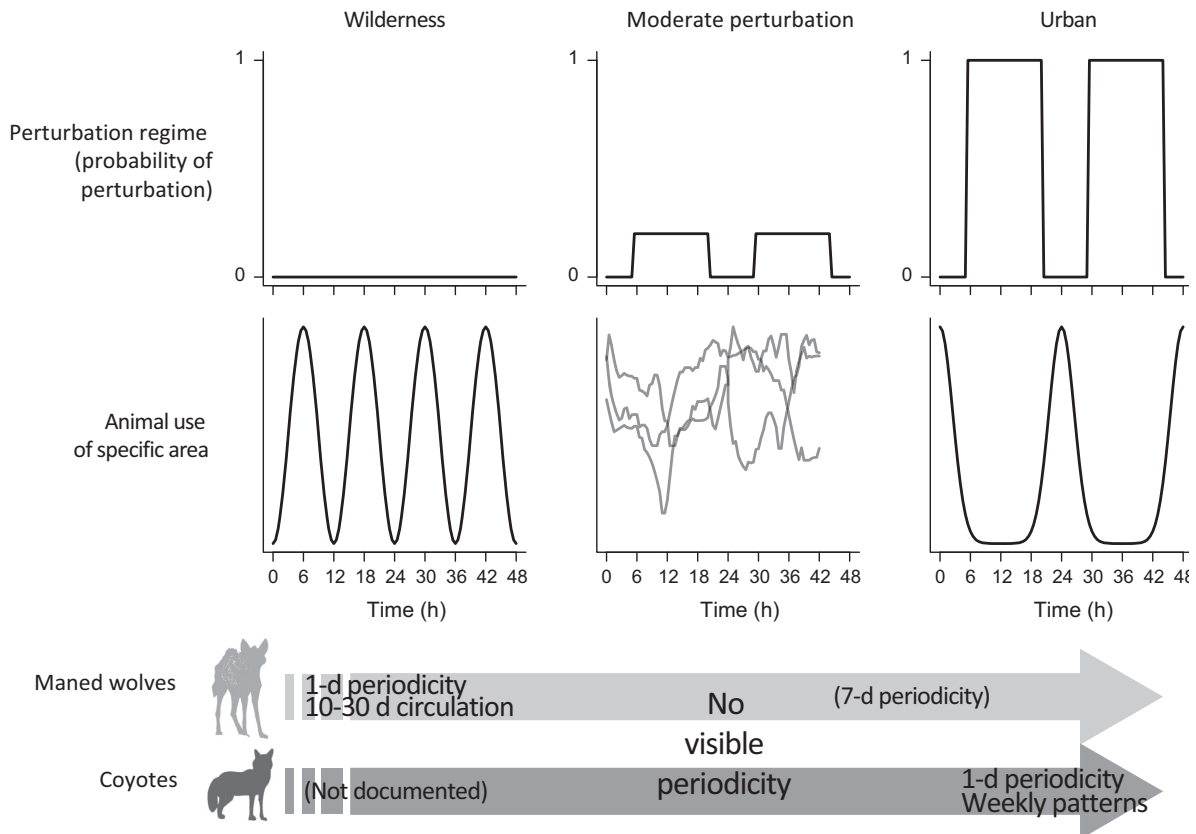


FIG. 1. Schematic representation of the hypothesized relationship between anthropization and periodic patterns of space use, focusing on circadian periodicities. In “wilderness,” there is no human presence and the animals exhibit “natural” periodic behavior. In “moderate perturbation,” there is a probability < 1 that humans will occur in the home range. Animals avoid disturbed areas when humans are present and compensate by increasing their use of these areas during unperturbed time. Each gray curve is one realization of that process. In “urban,” humans are always present during daytime and the animals track the period in human presence. The lower panel (arrows) is a summary of the main findings in this study.

A short primer on continuous-time stochastic movement models

Continuous-time stochastic movement models (Blackwell 1997, Johnson et al. 2008), upon which our approach is built, describe the movement path of an animal continuously through time. They are based on the assumption that the position of the animal, its velocity, or both, are autocorrelated through time. They are in that way opposed to discrete-time movement models, in which the path is constructed in a step-by-step fashion, the duration of each step being dictated by the sampling schedule of the data set (Gurarie and Ovaskainen 2011, McClintock et al. 2012, Benhamou 2014).

In their simplest form, continuous-time stochastic movement models can be described as the sum of a “movement process mean” $\mu(t)$ and a “movement process noise” $\varepsilon(t)$. The movement process mean represents the expected path of the animal, and the movement process noise represents random deviations from that expected path. The location of the animal at time t , $X(t)$, can then be represented as the sum of these two components (Eq. 1).

$$X(t) = \mu(t) + \varepsilon(t) \quad (1)$$

$X(t)$, $\mu(t)$, and $\varepsilon(t)$ are all vectors of size N , where N is the number of spatial dimensions ($N = 2$ hereafter).

Standard movement models (Table 1) assume a simple form for the movement process mean $\mu(t)$: either constant or with a constant derivative. These standard movement models focus on the stochastic component $\varepsilon(t)$ (Table 1). Two types of such models describe range-resident processes relevant to analyze periodic patterns of space use: the Ornstein-Uhlenbeck position process (OU-p) and the Ornstein-Uhlenbeck-F movement process (OUF). The OUF has temporal autocorrelation in both the position and the velocity, whereas the OU-p has autocorrelation in the position only. Animals following these movement processes tend to revert to their point of origin, at a rate driven by the position autocorrelation time τ_P , while they are simultaneously driven away from it, at a rate driven by the volatility parameter σ . τ_P is typically interpreted as the home range crossing time. For the OUF, the velocity autocorrelation time τ_V further describes how the

TABLE 1. Glossary of movement ecology and spectral analysis terms and their biological meaning in the context of periodic patterns of space use.

Term	Notation or acronym	Biological meaning
Movement ecology		
Movement process mean	$\boldsymbol{\mu}(t)$	The expected path of an animal through time t , i.e., the non-random component of its movement process.
Movement process noise	$\boldsymbol{\varepsilon}(t)$	The random deviations from the expected path, i.e., the stochastic component of its movement process.
Observation noise		The telemetry error. This component is not part of the movement process, represents a nuisance term, and should not be confused with process noise.
Brownian motion		An endlessly diffusing movement process described by a single parameter, the instantaneous diffusion, which controls step lengths.
Ornstein-Uhlenbeck position process	OU-p or OU	Also known as the Ornstein-Uhlenbeck movement process. A home range-bounded movement process described by two parameters: the instantaneous diffusion (volatility) and the position autocorrelation time. An Ornstein-Uhlenbeck process reverts to the origin through the autocorrelation structure, and deviates from it through the random structure.
Ornstein-Uhlenbeck velocity process	OU-v or IOU	Also known as the Integrated Ornstein-Uhlenbeck process. An endlessly diffusing movement process described by two parameters: the velocity autocorrelation time and the instantaneous diffusion of velocities. This is a movement process of which the velocity follows an Ornstein-Uhlenbeck process. The velocity autocorrelation time insures the continuity of velocity through time and controls the conservation of the direction and speed of the movement.
Ornstein-Uhlenbeck-F movement process	OUF	A home range-bounded movement process described by three parameters: the instantaneous diffusion (volatility), the position autocorrelation time, and the velocity autocorrelation time. This model mixes features from the OU-p and OU-v models. It generalizes these two models.
Volatility	$\boldsymbol{\sigma}$	Instantaneous diffusion. Quantifies the rate at which the animal departs from its expected path (its process mean).
Position autocorrelation time	τ_p	Quantifies the rate at which the animal reverts back to its expected path after a random deviation.
Velocity autocorrelation time	τ_v	Quantifies the level of conservatism in the direction and speed of the movement process.
Spectral analysis terms		
Periodicity		A pattern that reappears in a signal on a regular basis, and that can be decomposed into a sum of sinusoids (Fourier transform).
Period	T	Duration of the repeated sequence of a periodic pattern. For clarity, we use notation T for periodicity in the movement process mean, and \bar{T} for circulation.
Periodogram		The basis for nonparametric tests of periodic patterns. Quantifies the amplitude associated to a given frequency and therefore the fit of a sinusoid of given period to the data.
Circulation		A bi-dimensional random process whose displacement is biased toward a direction that rotates through time.
Fundamental frequency	$f = 2\pi/T$	The strongest frequency in a signal of period T .
Harmonic frequencies	$f_k = 2k\pi/T$	Components of a signal of period T that modulate its shape. $k > 1$.
Amplitudes	\mathbf{A}_k and \mathbf{B}_k	The intensities of the different frequencies that compose a periodic signal.
Nyquist frequency	f_N	The largest frequency that can be detected, depending on the temporal sampling resolution of the data.

movement velocity (speed and direction) persists through time, whereas for the OU-p, the instant velocity is not defined. The OU-p has a rather long history of use in movement ecology (Dunn and Gipson 1977, Blackwell 1997, Codling et al. 2008). The OUF is more recent, and some of its properties were studied by Fleming et al. (2014, *unpublished manuscript*). The OUF was in particular shown to generalize the OU-p, since OUF reduces to OU-p when τ_v tends toward zero.

Our objective is to extend the cTMM framework, which currently allows fitting OUF and OU-p models to animal tracking data (Calabrese et al. 2016), to

explicitly incorporate periodic patterns of space use in the movement models. We propose two non-exclusive ways to do this: periodic mean processes and circulation processes.

Periodic mean processes

In the models that we hereafter term “periodic mean processes”, periodic patterns of space use are incorporated into Eq. 1 via the movement process mean $\boldsymbol{\mu}(t)$. The expected path of the animal is periodic, with $\boldsymbol{\mu}(t)$ modelled as a sum of sinusoids

$$\boldsymbol{\mu}(t) = \boldsymbol{\mu}_0 + \sum_{k=1}^K \mathbf{A}_k(T) \cos\left(\frac{2k\pi t}{T}\right) + \mathbf{B}_k(T) \sin\left(\frac{2k\pi t}{T}\right) \quad (2)$$

where $\boldsymbol{\mu}_0$ is the range centroid, frequency $f_1 = 2\pi/T$ is called the fundamental frequency, and frequencies $f_k = 2k\pi/T (k = 2 \dots K)$ are called harmonic frequencies. The series $\{\mathbf{A}_k(T); k = 1 \dots K\}$ and $\{\mathbf{B}_k(T); k = 1 \dots K\}$ are called the amplitudes (Table 1). Each amplitude is a vector of size N . The values of the amplitudes regulate the waveform, i.e., the shape of the repeated section of path. In practice, the number of detectable harmonics, K , depends on the signal-to-noise ratio and on the sampling schedule: the harmonic frequencies need to be below the Nyquist frequency $f_N = 1/2\Delta t$ where Δt is the (median) sampling interval of the location time series (Smith 1999). If relevant, multiple periodicities (T_1, T_2, \dots, T_M) can be considered, each with their associated harmonic series, to study, for example, the animals' response to both circadian and lunar cycles.

If the stochastic component $\boldsymbol{\varepsilon}(t)$ is OU-p or OUF, Eq. 2 models the reversion toward a mean position that oscillates through time (Fig. 2, center panel). The model therefore reproduces a range-resident behavior with within-range periodic patterns of space use. Other specifications

of $\boldsymbol{\varepsilon}(t)$ than OU-p or OUF could also be considered where relevant, but since the resulting model would not be bounded to a home range, this option is hereafter ignored.

The intensity of the periodicity in the mean relative to the movement process noise is computed as

$$\eta_p(T) = \frac{D(T)}{D(T) + S} \quad \text{with} \quad \begin{cases} D(T) = \sum_{k=1}^K \|\mathbf{A}_k(T)\|^2 + \|\mathbf{B}_k(T)\|^2 \\ S = \text{tr}(\boldsymbol{\sigma}_o) \end{cases} \quad (3)$$

where \mathbf{A}_k and \mathbf{B}_k are the periodic amplitudes as defined in Eq. 1, $\boldsymbol{\sigma}_o$ is the stationary variance, equal to $\boldsymbol{\sigma}^2\tau_p$ for an OU-p process of volatility $\boldsymbol{\sigma}$ and position autocorrelation time τ_p , or $\boldsymbol{\sigma}^2 \frac{(\tau_V\tau_p)^2}{4(\tau_p - \tau_V)}$ for an OUF process of volatility $\boldsymbol{\sigma}$, position autocorrelation time τ_p and velocity autocorrelation time τ_V . $\|\cdot\|$ denotes the Euclidian norm of a vector and $\text{tr}(\cdot)$ the trace of a matrix.

$\eta_p(T)$ quantifies the part of the temporal variance in the position of the animal that is due to periodicity in the movement process mean. The formula in Eq. 3 can easily be extended to the case of multi-periodic signals to estimate the total contribution of multiple periodicities, by

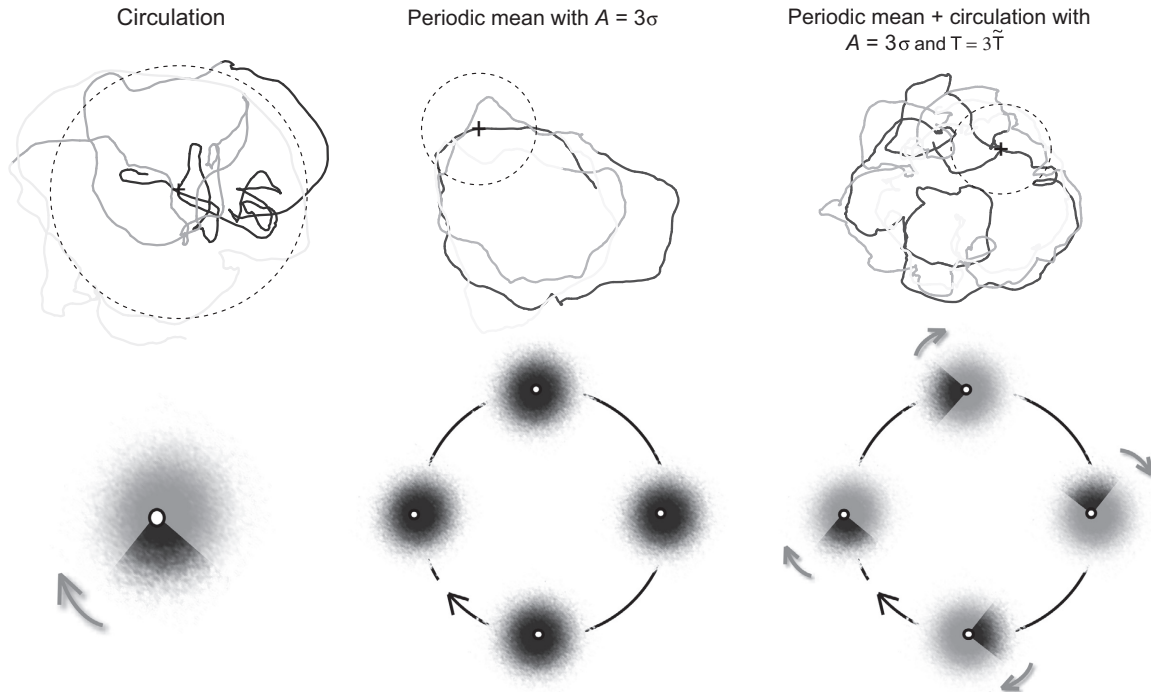


FIG. 2. Illustration of the model principles. Left: circulation process. Middle: periodic mean process. Right: periodic mean circulation process. Upper row: the process is run for three periods (gray color scale code for the period number), showing the stochasticity. Dashed circles quantify the scale of stochastic variation relative to the oscillations in the mean. Lower row: schematic representation, in which the temporal autocorrelation in the aperiodic process noise is omitted. The large black circular arrows represent the oscillations in the process mean. The shorter gray arrows represent the circulation of the stochastic component around the process mean. In this example, the magnitude of the oscillations in the mean (A) are larger than the magnitude of stochastic variation (σ), but the reverse can be true (and was true in some maned wolves for example).

summing $D(T)$ over T values, which is what is implemented by default in `ctmm`. The proof of concept and analytical derivation of Eq. 3 from the position autocorrelation function is detailed in Appendix S1. A similar index, but based on the decomposition of the variance in the velocity instead of the variance in the location, is proposed in Appendix S1. The velocity-based index includes a term associated with circulation (see *Circulation processes*), whereas the position-based index η_p does not (Eq. 3).

In movement ecology applications, periodic mean processes explicitly decompose an animal's path into what can be interpreted as a deterministic component on the one hand, possibly representing the intention of the animal or its most profitable option under average conditions, and a stochastic component on the other hand, possibly representing the response of the animal to unexpected events.

Circulation processes

In the models that we hereafter term “circulation processes” (Alt 1990, Blackwell 1997, Gurarie et al. 2011), periodic patterns of space use are incorporated into Eq. 1 via the stochastic component of the path, $\epsilon(t)$

$$\epsilon(t) = \mathbf{R} \left(\frac{2\pi t}{\tilde{T}} \right) \cdot \tilde{\epsilon}(t) \quad (4)$$

where $\tilde{\epsilon}(t)$ is an OU-p or OUF process, \tilde{T} is the period of the circulation, and \mathbf{R} denotes the rotation operator (described in full in Appendix S1). This model enforces the circulation of the stochastic component of the path around the movement process mean (Fig. 2, left panel; see also Blackwell 1997: Fig. 9). The random deviations of the animal from its expected path are always biased toward a direction that is rotating through time, with period \tilde{T} . The term “circulation” is an analogy with the circulation of a charged particle in a magnetic field. Circulation and periodic mean processes are not mutually exclusive: animal paths may derive from a periodic mean circulation process (Fig. 2, right panel). Compared to Blackwell's (1997) model, our framework therefore offers three new features: (1) the ability to fit circulation models in which the underlying stochastic process, $\tilde{\epsilon}(t)$, is OUF rather than OU-p (this produces more clear-cut periodic patterns because of velocity persistence), (2) the possibility that $\tilde{\epsilon}(t)$ is anisotropic, and (3) the possibility to combine circulation in the stochastic component and periodicity in the movement process mean in the same model. Circulation processes have also been described in the past as biased correlated random walks with a non-zero average turning angle (Codling et al. 2008). Our framework generalizes this approach by separating movement rates from the period of the circulation.

Importantly, circulation processes are not always visible in periodograms. Periodograms are the usual, non-parametric method to detect periodic patterns, including

periodic patterns of space use (Péron et al. 2016). We recommend them at the data exploration stage. Periodograms are estimators of the spectral density function, which itself is designed to exhibit peaks for values of the period corresponding to periodic patterns in the signal (Appendix S1). However, the spectral density function of circulation processes exhibits a peak with a width that depends on the home range crossing time τ_p (Appendix S1). When the circulation period exceeds approximately four times the home range crossing time, then the peak associated with the circulation becomes too wide to detect in the spectral density function (Appendix S1). The threshold is even more restrictive in the periodogram (Appendix S1), because the latter is a biased estimate of the spectral density function (Smith 1999). This made circulation almost impossible to see on periodograms in our case studies (Appendix S3: section S1). The parametric methods we developed account for this and will therefore often represent the only way to detect circulation processes.

Model fitting with maximum likelihood

Within the `ctmm` framework (Calabrese et al. 2016, Fleming and Calabrese 2016), the likelihoods of the continuous-time stochastic movement models are computed using the Kalman filter, based on the Langevin equations presented in Appendix S1 and studied in full detail by Fleming et al. (*unpublished manuscript*). We extend the `ctmm` framework to incorporate periodic patterns of space use. This does not require much modification of the `ctmm` algorithms, since the Kalman filter readily accommodates time variation in the movement process mean. The derivative of $\mu(t)$ must, however, be subtracted from the derivative of $\epsilon(t)$, before the latter is entered into the classical Langevin equation (Appendix S1). To fit circulation processes, we first normalize the stochastic component by applying the inverse rotation operator $\mathbf{R}(-2\pi t/\tilde{T})$ to Eq. 1, and then proceed as usual. Throughout, observation error is treated within the Kalman filter algorithm, assuming a Gaussian distribution of errors, with a standard deviation that may vary through time as a function of recorded covariates such as dilution of precision factors (Fleming et al. under review). In `ctmm`, negative \tilde{T} values represent counter-clockwise circulation, while positive \tilde{T} values represent clockwise circulation. The sign of the initial \tilde{T} value fed to the likelihood optimization routine may have undesirable consequences on the convergence success; in `ctmm`, the optimization is automatically conducted twice, once with a positive and once with a negative initial value for \tilde{T} .

Analytical protocol with model selection procedure

In this paragraph, we adopt a user's manual format to present the analytical protocol that we applied in our case studies and that we have semi-automated in `ctmm` in the function `ctmm.select`.

- 1) At the exploration stage, periodograms are used to identify likely periodicities in the position time series (Péron et al. 2016). Based on this examination and on biological hypotheses, the user proposes a model prototype with the periodicities of interest. Although theoretically the values of the periods could be estimated directly, we prefer to ask the user to provide a few likely values and then confront these values with the data through model selection. Only the amplitudes of the periodic mean process (Eq. 1) are estimated from the data. By contrast, the period \bar{T} of circulation processes is estimated directly from the data, jointly with the other parameters of the movement model. This is because (1) circulation processes are not as easy to detect using exploratory nonparametric analyses and (2) circulation may often originate from less intuitive periodic behaviors, therefore many users will not have any preconceived idea about likely periods for circulation processes.
- 2) Apart from the period values, other model features include the autocorrelation structure of ϵ (OU-p or OUF), whether ϵ is anisotropic or not, whether ϵ is circulating or not, and how many harmonics are detectable in the process mean for each candidate periodicity. The number of possible combinations of these model features results in an excessively large set of candidate models. An initial filter is therefore applied to discard very unlikely features based on the confidence intervals in the fitted full model, which includes all possible features. This step can be made more or less selective using the “level” option in the function `ctmm.select`; it is very conservative by default.
- 3) Among the remaining model features, the preferred combination is selected using the Akaike information criterion corrected for small finite sample size (AIC_c). The model selection procedure starts with the most complicated autocorrelation model and least complicated mean model (zero harmonics). We proceed from this initial model in a stepwise fashion, first decreasing autocorrelation complexity and then increasing mean complexity. The intent is to avoid fitting trends to autocorrelation, i.e., allocating variation to the process mean that is actually caused by autocorrelated noise, while still selecting from a moderate pool of candidate models. We then increment the number of harmonics (K) as long as the AIC_c decreases.

Simulation study

We conducted a simulation study to illustrate the influence of signal-to-noise ratio and of sampling design (time interval between records, study duration) on the ability to uncover periodic patterns caused by periodic mean processes, circulation processes. We also used simulations to empirically demonstrate model identifiability, i.e., the ability to distinguish periodicity in the mean and

circulation. We used the AIC_c in a model selection procedure to conclude in each of the simulations whether any periodicity had been detected. The details of the data simulation method and the full results are presented in Appendix S2.

Briefly, we found that, for typical signal-to-noise ratios, the detection of periodic patterns required a study duration more than five times as long as the period and with more than four location records per period. To separate a periodic mean process from a circulation process of same period, when both occur simultaneously in an animal path, the study duration had to exceed 15 times the period with >12 location records per period. The ability to separate these two patterns was high when the study design was adequate, which empirically confirmed parameter identifiability.

We also used the simulations to highlight the risk of flawed results when the sampling schedule (the rate at which missing data occur) is itself periodic. For example, with a period of 24 h, a sampling interval of 1 h, and a signal to noise index of 4 (cf. Appendix S2), the periodicity was always detected if the sampling schedule was even, but never detected if the sampling schedule was periodic with 12 h of monitoring followed by 12 h without records. In our application cases, the sampling schedule was even so this issue was avoided. In general, we recommend even sampling to maximize the possibility of detecting periodic patterns in the data.

Maned wolf case study

The maned wolf (*Chrysocyon brachyurus*), the largest South American canid, is exceptional among similarly sized canids for its solitary foraging behavior and omnivorous diet (Carbone et al. 1999, Macdonald et al. 2004). Previously, Péron et al. (2016) detected a periodic pattern with a 1-d period using periodograms. Given the natural history of the species (Motta Junior et al. 2002, Emmons et al. 2012, Consorte-McCrea and Santos 2014), it is hypothesized that this periodic pattern of space use has both social (Macdonald et al. 2004) and energetic origins (Carbone et al. 1999). On the social front, maned wolves likely aim at reducing interspecific conflict by scent marking and patrolling territory borders at set, predictable times (Gese and Ruff 1997, Giuglioli et al. 2011, Elbroch et al. 2014). On the energetic front, the campo grassland that these animals inhabit is likely less productive than farmland (Knapp and Smith 2001, Fay et al. 2015, see *Discussion*). This supposedly forces maned wolves to perform extensive movements between food patches, such as fruiting vegetation or places where rodents are easier to catch (Motta Junior et al. 2002, Emmons et al. 2012, Consorte-McCrea and Santos 2014).

The habitat gradient went from the relatively pristine interior of the Serra da Canastra National Park, Brazil, to surrounding farmland, thereby representing mostly the first half of the anthropization gradient (Fig. 1). Maned

wolves were captured using live traps baited with cooked chicken and sardines, sedated with direct injection of tiletamine-zolazepan, and equipped with VHF/GPS-Collars (Lotek Wireless GPS 3300S and Iridium Track 1D, and Sirtrack Limited Pinnacle Lite G5C 275D, Lotek Wireless Inc., Newmarket, ON, Canada). The devices were programmed to record one location every 1–4 h (depending on the individual). A total of 13 individuals were monitored: 7 in or near the national park and 6 in agricultural land. We delimited the wolves' home ranges using the 95% utilization distribution of autocorrelated kernel density estimates (Fleming et al. 2015). We used the proportion of natural campo grassland to represent the anthropization of the home ranges (more grassland means less anthropized). Other habitat types made up to 20% of the home ranges but were not analyzed. Based on preliminary examination of the data and on precision estimates provided by the manufacturers, we considered observation error to be small and symmetrical around the true position, and therefore negligible. The ctm algorithms can handle Gaussian error when such error is non-negligible.

Coyote case study

The coyote (*Canis latrans*) is a medium-sized canid endemic to North America, where it is remarkably versatile in terms of habitat use and food sources (Gehrt 2007, Mitchell et al. 2015). Although periodic behaviors in coyotes have never been formally quantified, some known coyote behaviors are likely to produce periodic patterns of space use, such as scent-marking territory

borders, and using preferred foraging paths (Gese and Ruff 1997, Atwood et al. 2004). Furthermore, pronounced periodic patterns can sometimes be detected visually in the raw tracking data of coyotes (Fig. 3).

We studied coyotes in Rhode Island, USA. We used data from 11 individuals. The habitat gradient that these individuals sampled went from a mosaic of cropland and forest to urban areas, representing the second half of the anthropization gradient (Fig. 1). For nine individuals, we fitted Habit Research (Victoria, British Columbia, Canada) GPS/VHF collars, mounted with Telonics BCP-2 (Mesa, Arizona, USA) or Sirtrack (Havelock North, New Zealand) programmable release mechanisms enabling detachment of the collars 12 months after capture (but they sometimes were dropped or stopped working earlier, resulting in shorter tracking periods). The collars were programmed to record GPS locations every hour. The two other individuals were fitted with collar prototypes (ATT TeleNav, Sunnyvale, California, USA or Mr Lee Technologies, Anderson, South Carolina, USA). These collars reported data at regular 15-min intervals by SMS, over tracking periods of 14.5 and 7.5 d, respectively. Home ranges were calculated as described in *Maned wolf case study*. Home range composition was determined using the Rhode Island Land Cover and Land Use GIS (RIGIS 2014). We used the proportion of developed land, corresponding to all the residential, commercial, institutional and industrial land use classes, to represent the home range anthropization. Additional details about the Rhode Island coyote study are presented in Mitchell et al. (2015).

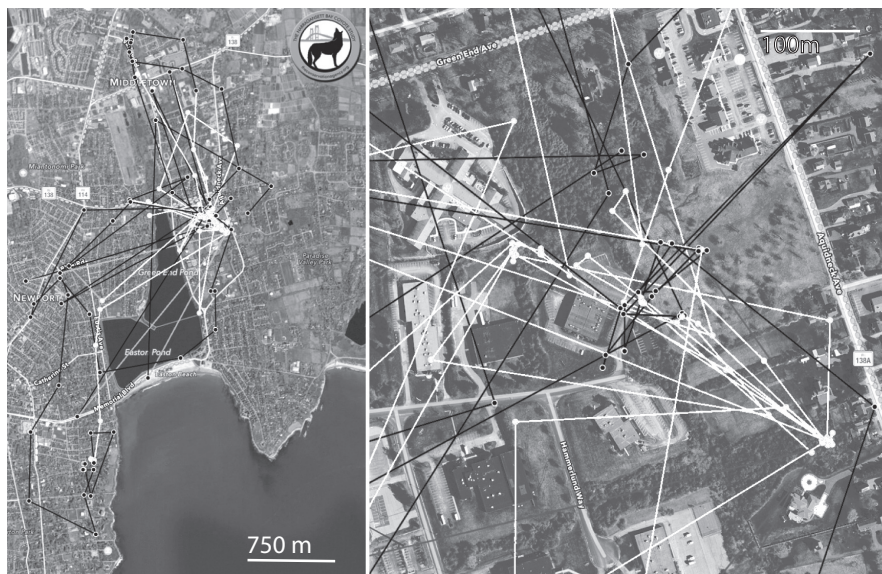


FIG. 3. Tracking data from 22–29 June 2016 for an adult male coyote with dependent pups. Black lines represent nocturnal movement. White lines represent diurnal movement. The right panel is a zoom on the pup feeding area where diurnal records are concentrated in bush patches used for concealment. The left panel shows several occurrences of nightly patrols along territory borders, which are often large streets. Generated using CoyoteTracks for iOS devices (v1, 2015 from High Point Studios).

Between-individual regression

To test our prediction that periodic patterns of space use should be linked to anthropization, we regressed across individuals the intensity $\eta_p(T)$ and period T of periodic patterns of space use against the habitat composition of the individual home range, separately for each species. We used ANOVA to evaluate statistical significance and pathway analysis (Rosseel 2012) to determine the most likely causal pathway linking anthropization to periodic patterns. Because of spatial autocorrelation, however, these regressions might be prone to elevated type I error. We used mixed regressive spatial autoregressive model (MRSAR; Ord 1975) to take spatial autocorrelation into account in the regressions. MRSARs estimate the fixed effect of spatially explicit explanatory covariates while accounting for spatial autocorrelation in the dependent variable using a weight matrix. They provide a measure of spatial autocorrelation (λ parameter) and of the remaining spatial variance. MRSAR typically yield much lower levels of association between predictors and dependent variables than conventional regression, because part of the correlation is attributed to spatial autocorrelation. Consequently, ANOVA results may be too optimistic because they ignore spatial autocorrelation; MRSAR results may be too pessimistic because they sometimes falsely attribute a trend in the data to spatial autocorrelation. The weight matrix contained, in the (i,j) th cell, the inverse of the Euclidian distance between the centroids of the home ranges of individuals i and j (rescaled to range between 0 and 1). Proportion variables were logit-transformed and normalized to a mean of zero and standard deviation of one before analysis. Due to the small sample size of our application cases (13 wolves and

11 coyotes), we did not carry over the sampling error of the dependent variables (estimated from the GPS tracks) in the MRSARs. It would certainly have decreased the statistical significance of the relationships.

RESULTS

Maned wolves

Periodogram analysis uncovered strong evidence of daily periodicity in several individuals, as well as weaker evidence for periods of 1 week to 1 month (Appendix S3: Fig. S1; see also Péron et al. 2016). Using our new method, daily periodicity in the movement process mean was selected in all seven maned wolves living in or near the national park, but in only three out of six wolves living in farmland. The intensity of the daily periodicity in the movement process mean was positively correlated to the intersection of the home range with the national park (ANOVA $F_{1,11} = 8.6$, $P = 0.01$; Fig. 4), which was partly explained by the effect of the percentage of campo grassland in the home ranges (MRSAR, slope 0.25 ± 0.21 [mean \pm SE], autocorrelation λ 0.32 ± 0.08 ; Fig. 4). There appeared to exist a threshold of $\sim 40\%$ grassland in the home range below which periodicity in the mean was suppressed.

Circulation was detected in six of the seven maned wolves living in or near the park, and in none of the six wolves in farmland. Circulation periods ranged from 10 d to 1 month. The circulation frequency increased with the percentage of campo grassland in the home range (ANOVA $F_{1,11} = 28.3$, $P = 0.0002$; MRSAR, slope 0.41 ± 0.18 , autocorrelation λ 0.26 ± 0.08 ; Fig. 5), meaning that individuals with more grassland in their

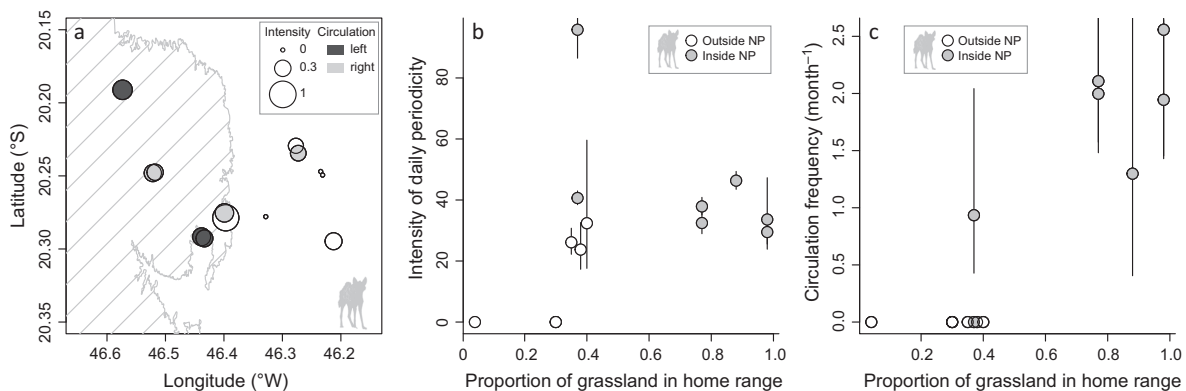


FIG. 4. Periodic patterns of space use in 13 maned wolves in and near the Serra da Canastra National Park, Brazil. (a) Intensity of the daily periodicity in the process mean, i.e., $\eta_p(1 \text{ day})$ from Eq. 3. Each circle represents the centroid of one maned wolf territory. Circle color indicates whether circulation was detected and in which direction the circulation occurred (dark gray for counter-clockwise, light gray for clockwise); circle size scales to the intensity of daily periodicity in the process mean. The national park is delineated by the gray hashed area (source: IUCN and UNEP-WCMC; www.protectedplanet.net). (b) Relationship between the intensity of daily periodicity in the process mean and the proportion of campo grassland in the home ranges of the maned wolves. The 95% confidence intervals are represented by black bars; their orientation indicates the statistical covariance. The color of symbol fillings indicates whether the home range intersects the national park (gray) or not (white). (c) Relationship between the circulation frequency (inverse of the circulation period) and the proportion of campo grassland in the wolves' home ranges. NP, national park.

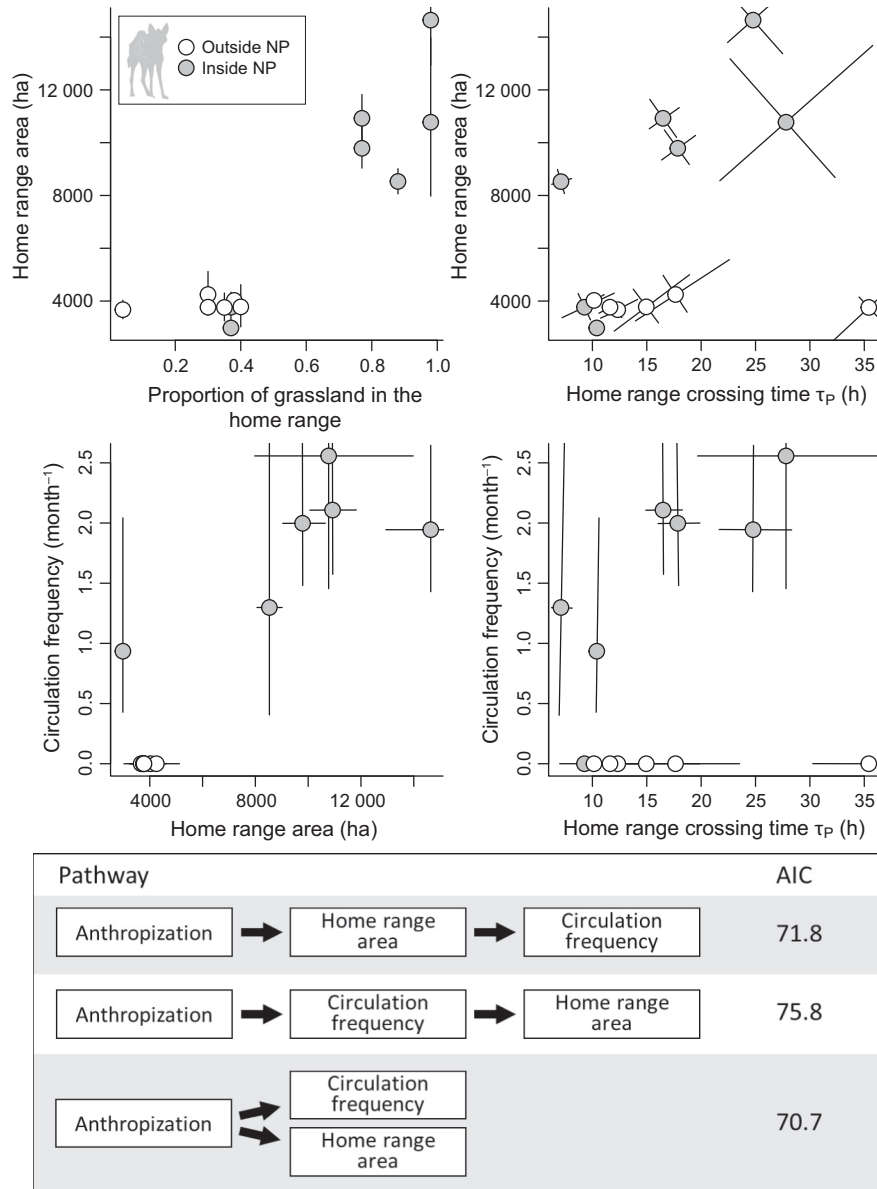


FIG. 5. Relationship between home range area, home range composition (proportion of grassland in home range or anthropization rate), home range crossing time, and circulation period in maned wolves. Home range area corresponds to the 95% utilization area. When no circulation was detected, the circulation period is plotted as zero (rather than infinity). Vertical and horizontal bars represent the 95% confidence intervals; their orientation indicates the statistical covariance. The lower panel represents the results of the pathway analysis. AIC, Akaike information criterion.

home range circulated faster around their home range than those with more farmland in their home range. The hypothesis that circulation frequency increased because home range size increased received almost as much support from the data as the hypothesis of two independent relationships with the proportion of grassland in the home range (pathway analysis, AIC difference < 2; Fig. 5).

The occurrence of lunar periodicity in the movement process mean was rejected in all 13 wolves. The weekly periodicity was selected in one individual. This wolf's

territory was, by far, the most anthropized of our study sample (78% farmland vs. 45% for the second most anthropized territory). In addition, even if not statistically significant, the weekly periodicity in the movement process mean was markedly more intense outside of the national park than inside of it (Fig. S3 in Appendix S3).

To summarize the maned wolves results, along a gradient going from relatively pristine campo grassland to mostly farmland, maned wolves exhibited increasingly weaker periodicity at the daily scale, increasingly slower

circulation (with circulation periods of several weeks), and increasingly stronger periodicity at the weekly scale.

Coyotes

Periodogram analysis uncovered strong evidence of daily periodicity in several individuals, as well as weaker evidence for periods from ~ 7 to 30 d (Appendix S3: Fig. S2). Using our new method, daily periodicity in the movement process mean was selected in 8 out of 11 coyotes. The intensity of the daily periodicity in the process mean increased with the proportion of records occurring in developed land (ANOVA $F_{1,9} = 6.2$, $P = 0.03$; MRSAR, slope 0.95 ± 0.48 , autocorrelation $\lambda 1.95 \pm 0.23$; Fig. 6). A similar but weaker correlation was found when using the proportion of developed land in the home ranges rather than the proportion of records in developed land. The weakening of the correlation was due to some of the study individuals behaving like active urban avoiders within their home range, i.e., the home range envelope failed to account for fine-scale avoidance of developed land (Mitchell et al. 2015). There was some support (pathway analysis, AIC difference = 2) for a role of home range crossing time τ_p as a mediator in the relationship between anthropization and the intensity of periodicity, i.e., periodicity became more intense because home range crossing time decreased (Fig. 7).

Weekly periodicity in the movement process mean was selected for two individuals, one of which also had daily periodicity. Monthly periodicity was selected for one individual. Circulation was selected in three individuals, with estimated circulation periods of ~ 6 , 7, and 14 d, respectively. There was some support for a positive correlation between the proportion of developed land in the home range and the expression of a period >1 d (ANOVA

$F_{1,9} = 3.2$, $P = 0.10$; MRSAR, slope 1.06 ± 0.55 , autocorrelation $\lambda 0.49 \pm 0.55$; Fig. 6), but no support for a correlation between the proportion of actual records in developed land and the expression of a period >1 d.

To summarize the coyote results, along a gradient going from farmland/forest mosaics to urbanized land, coyotes exhibited increasingly stronger periodic patterns of space use, with periods ranging from 1 d (eight individuals), to about 1 week (four individuals), to 1 month (one individual).

DISCUSSION

We addressed some of the methodological bottlenecks that previously prevented the study of periodic patterns of space use using animal tracking data. Our method is based on an extension of the Ornstein-Uhlenbeck class of continuous-time stochastic movement models. The method is therefore parametric, whereas preexisting frameworks are nonparametric (Wittemyer et al. 2008, Heurich et al. 2014, Péron et al. 2016). Some periodic patterns, namely those originating from circulation processes, can only be detected using parametric methods (Appendix S1). Our method distinguishes two types of movement processes that both create periodic patterns of space use: periodic mean processes and circulation processes. The ecological implications of this distinction are still far from clear, i.e., there is no clear-cut prediction regarding when an animal should follow one or the other process. However, when analyzing animal tracking data, fitting circulation processes only or periodic mean processes only can lead to flawed inference, hence our recommendation to combine both types of processes in the initial model, and simplify the initial model using model selection.

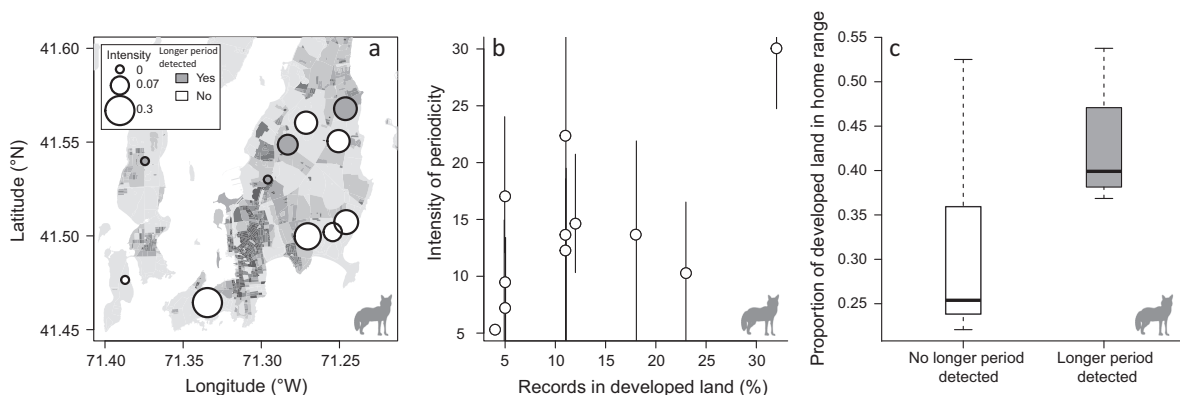


FIG. 6. Periodic patterns of space use in 11 coyotes from Rhode Island, USA. (a) Intensity of the daily periodicity in the process mean, summed over daily, weekly, and monthly periodicities, i.e., $\sum_T \eta_p(T)$ with η_p from Eq. 3, and $T = 1$ day, 1 week, or 1 month. Each circle represents the centroid of one coyote territory. Circle size scales to the intensity of periodicity in the process mean. Circle color indicates whether a period >1 d was detected (gray) or not (white). The background map is the human population density data from the 2014 census. (b) Relationship between the intensity of the periodicity in the process mean and the percentage of records in developed land. The 95% confidence intervals are represented by black bars whose orientation indicates the statistical covariance. (c) Relationship between whether a period >1 d was detected (gray) or not (white) and the proportion of developed land in the coyote's home ranges.

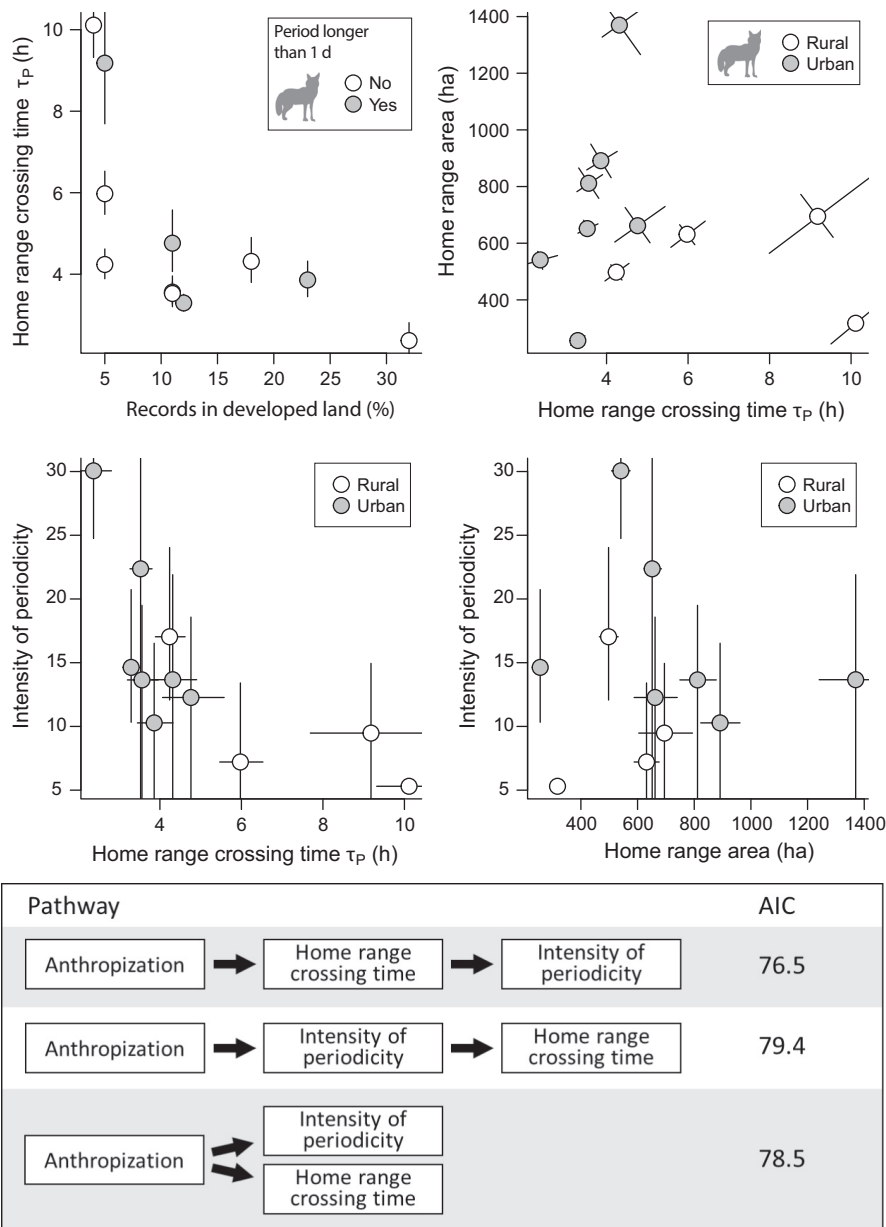


FIG. 7. Relationship between home range area, home range composition (percentage of records in developed land or anthropization rate), home range crossing time, and the expression of periods >1 d in coyotes. Home range area corresponds to the 95% utilization area. In the upper left panel, gray symbols indicate that a period >1 d was detected. In other panels, gray symbols indicate that >10% of records occurred in developed land. Vertical and horizontal bars represent the 95% confidence intervals. The lower panel represents the results of the pathway analysis.

Maned wolves

The individual variation in the expression of periodic patterns of space use matched our prediction that “natural” periodic patterns of space use should disappear under moderate regimes of anthropogenic perturbations. Regarding the proximal causes of the circulation patterns in maned wolves, we propose two hypotheses. The first hypothesis involves the renewal of scent marks that

delimit territory borders (Gese and Ruff 1997, Giuggioli et al. 2011, Elbroch et al. 2014). Using a simplistic model based on the minimization of the average age of the scent marks (Appendix S3: section S3), we could reproduce in simulations the observation that maned wolves with large home ranges circulate faster (shorter period) than maned wolves with small home ranges (Fig. 5). We note that maned wolves maintained much larger home ranges in grassland than in farmland

(Fig. 5). The second hypothesis to explain circulation in maned wolves involves resource depletion. Maned wolves are assumed to sequentially exploit subsets of their home range: they leave them when resources are depleted and return after the resources have recovered (see Bar-David et al. [2009] and Owen-Smith and Martin [2015] about ungulate species, for which this type of behavior is better characterized, and Ohashi and Thomson [2009] about traplining behavior in nectar-feeding hummingbird and bee species). In the case of maned wolves, grassland is probably less productive than field margins in terms of primary production and rodent population density (Medan et al. 2011, Fay et al. 2015), which we confirm in this study with our result that home ranges are larger in grassland than in farmland. Therefore, depletion/recovery cycles are expected to be shorter in grassland than in farmland, which may explain the observation that the amount of grassland in the home range correlated to the circulation frequency (Fig. 4).

Last, the maned wolf that had settled in the most anthropized home range (78% farmland) exhibited a weekly periodicity. Although no definitive conclusion can be reached based on one individual, we note that all the other wolves outside of the national park also tended to exhibit the same weekly periodicity (AIC difference >2 but <5 ; Appendix S3: Fig. S3). This suggests the interpretation that the farmland wolves resumed their normal ranging behavior on the weekends, when human rate of use of the agricultural landscape was reduced compared to weekdays. The weekly periodic pattern of space use might be tracking a periodic pattern in human activities.

Coyotes

The individual variation in the expression of periodic patterns of space use matched our prediction that intense regimes of anthropogenic perturbations in urban areas force the animals to adopt artificial periodic patterns of space use. Regarding the proximal causes underlying the periodic patterns of space use in urban coyotes, we propose two hypotheses. (1) These patterns may be carbon copies of periodic patterns of human presence. For example, 24-h periods might result from people routinely placing compost, unprotected garbage, or feeding pets outside each day. Periods of 1 week, which were detected in four coyotes, might be related to work-week schedules. (2) Increased urbanization of the coyotes' home ranges probably correlated with increased fragmentation of appropriate habitat within the home ranges (Atwood et al. 2004, Gehrt et al. 2011, Mitchell et al. 2015). This fragmentation hypothesis is also supported by the fact that urban coyotes in this study tended to have larger home ranges and to travel faster across them than rural coyotes (Fig. 7), as expected if living in an urbanized home range composed of a larger proportion of low-use areas than rural home ranges. Habitat fragmentation might induce the daily periodic patterns we report by forcing the repeated use of the same corridors (Atwood

et al. 2004). It might also induce circulation by forcing the repeated use of the same safe roosting spots, with circulation frequency perhaps representing the rate at which these regularly used spots are rendered conspicuous by repeated visits, or become infested with parasites.

Implications for conservation biology in anthropized landscapes

Coyotes are often cited as an example of an adaptable species (Levy 2012), in which both the demography (Knowlton et al. 1999) and the ranging behavior (Kitchen et al. 2000, our study) respond quickly to new conditions of resources and risks, allowing the species to thrive in various habitats including very anthropized ones. In our study, maned wolves, a declining species considered much less adaptable than coyotes, were also able to locally modify their ranging behavior, which likely helped them persist in farmland. Importantly, these changes in coyote and maned wolf behavior are not compulsorily plastic. In passerine birds, Mueller et al. (2013) report significant population genetic structure across a gradient of urbanization, including at a locus known to control circadian rhythm and therefore periodic behavior; Helm and Visser (2010) further report that circadian patterns of activity are heritable. We also note that the Eastern coyote subspecies (to which our study individuals belong) historically provided what is possibly the best example of a major range expansion concomitant with, and most likely driven by, a change in genotype (Kays et al. 2010). From a conservation perspective, this raises the issue of what is conserved when a species is forced into increasingly anthropized habitats. From a human-wildlife conflict perspective, this highlights the complex and possibly irreversible nature of the behavioral changes that accompany life in anthropized environments.

In conclusion, our new method is expected to facilitate the study of periodic patterns of space use, which may arise in many different ecological and conservation-relevant contexts, and which have, to date, received little research attention. We demonstrated how our new method can be used to investigate ways in which individuals and populations respond to anthropization by modifying their periodic patterns of space use, which may prove critical for animal species to persist in an anthropized world.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eem.1260/full>

DATA AVAILABILITY

The data have been uploaded to the MoveBank (<https://www.movebank.org/>) “Tracking Data Map” tool under ID numbers 248232724 (coyotes), and 250063614 (maned wolves).