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Review

Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data

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Autocorrelation has been viewed as a problem in telemetry studies because sequential observations are not independent in time or space, therefore violating assumptions for statistical inference. Yet nearly all ecological and behavioural data are autocorrelated in both space and time. We argue that there is much to learn about the structure of ecological and behavioural data from patterns of autocorrelation. Such patterns include periodicity in movement and patchiness in spatial data, which can be characterized by an autocorrelogram, semivariogram or spectrum. We illustrate the utility of temporal autocorrelation functions (ACFs) for analysing step-length data from GPS telemetry of wolves (*Canis lupus*), cougars (*Puma concolor*), grizzly bears (*Ursus arctos*) and elk (*Cervus elaphus*) in western Alberta. ACFs often differ by season, reflecting differences in foraging behaviour. In wilderness landscapes, step-length ACFs for predators decay slowly to apparently random patterns, but sometimes display strong daily rhythms in areas of human disturbance. In contrast, step lengths of elk are consistently periodic, reflecting crepuscular activity.

Keywords: Alberta; autocorrelation; GPS radiotelemetry; movement; periodicity; step length

1. INTRODUCTION

Recent advances in radiotelemetry, such as GPS-based technologies, facilitate the collection of vast quantities of data in space and time (Tomkiewicz *et al.* 2010; Urbano *et al.* 2010). Clearly, such sequential observations on an individual are not independent and therefore the statistical inferences associated with such data require special consideration (Otis & White 1999). A common perception is that autocorrelation is a 'problem' that must be fixed by subsampling (Swihart & Slade 1985) or variance inflation (Nielsen *et al.* 2002). Certainly, this is true if one feels compelled to use traditional parametric statistical methods (see Cherry 1999). More efficiently, the autocorrelation can be modelled explicitly as part of the likelihood, but even this might not be desirable (e.g. eliminating autocorrelation has been shown to erode home-range models; De Solla *et al.* 1999). Furthermore, because animal behaviour is almost always temporally autocorrelated, we expect that autocorrelated observations will reveal more relevant behavioural information than independent observations would (Lair 1987; Gurarie *et al.* 2009). Indeed, we believe that autocorrelation structure is an interesting property of the data and should be understood in its own right (Cagnacci *et al.* 2010).

Spatial data collected by radiotelemetry are autocorrelated because of the structure of underlying topography, geology, soils, hydrology and vegetation. Spatial autocorrelation can be a consideration in habitat modelling because the scale of sampling can determine whether one is actually capturing the extent of variation in a predictor covariate (Fieberg *et al.* 2010; Boyce *et al.* 2003). One approach to account for this autocorrelation is to estimate spatial models that include landscape features as predictor covariates and then to examine residuals for spatial autocorrelation (Radeloff *et al.* 2000; Boyce 2006). In our experience, modelling the underlying landscape covariates often accounts for the primary autocorrelation signal in the data. In other words, much spatial autocorrelation in animal-use data can be attributed to the fact that landscapes are highly autocorrelated.

Yet residual autocorrelation might exist owing to dispersal (Bahn *et al.* 2008), social behaviour, predator distribution or an unmeasured ecological driver. Autologistic regression can be used to model the dependency of observations on the presence of the organism in adjacent pixels (Augustin *et al.* 1996). This involves including the presence (1) or absence (0) in a buffer of adjacent pixels, thereby modelling

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One contribution of 15 to a Theme Issue 'Challenges and opportunities of using GPS-based location data in animal ecology'.

the autocorrelation directly. A drawback from autologistic regression is that it cannot be used directly for prediction because one must know the distribution or movement metrics of the target organism to calculate the response to the presence of a conspecific. Therefore, the method is most useful as a diagnostic tool rather than as a predictive tool. Bayesian methods such as the Gibbs sampler have been proposed as a possible approach to this problem (Augustin *et al.* 1998). Models that directly incorporate the structure of spatial autocorrelation have been used to predict patterns of species composition (Büchi *et al.* 2009) and genetic isolation by distance (Yang 2004).

Temporal autocorrelation is common in attributes associated with sequential observations from GPS telemetry. For example, one can record step length as the distance between two sequential observations (Turchin 1998) and examine the lagged correlation in step length. Autocorrelation functions (ACFs) of other sequential data could be studied as well (e.g. turning angles, physiological data, depth observations for marine mammals, etc).

Autocorrelation analysis has been used in ecological studies, with perhaps the earliest application to detect periodicity in population size (e.g. the 10-year cycle in furbearer harvests; Moran 1954). Plotting autocorrelation in step lengths as a function of time lag yields patterns that would begin high because step length in the next step is likely to be similar to the length of the current step (i.e. if the animal is moving it is likely to continue to move). But with time this correlation declines because movement at some future time is less and less likely to be the same as the current rate of movement. If the time series contains a repeated pattern of activity, say daily or monthly, we expect the ACF to become negative at about half the length of the activity period and then to go positive with a peak in correlation coincident with the actual period length. And we might see regular oscillations in ACF through several lags depending on the regularity in the periodicity and the frequency of relocations. ACFs can be used for statistical inference to discern patterns of movement from stochastic movements.

Few studies of ecology or behaviour have used ACFs to detect patterns in radiotelemetry data. Exceptions include two studies of African elephant (*Loxodonta africana*) movements (Cushman *et al.* 2005; Wittemyer *et al.* 2008), where patterns in ACFs stimulated further investigation that revealed environmental factors influencing movement. Here, we illustrate how ACFs of step length, a simple movement metric, can yield insights into ecology and behaviour of four species of large mammals: grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), cougars (*Puma concolor*) and elk (*Cervus elaphus*). We predict that studies building on patterns revealed by ACFs will allow more robust and novel interpretations of behaviour from GPS-based location data.

2. MATERIAL AND METHODS

All studies were conducted on the east slopes of the Rocky Mountains in western Alberta, from Waterton Lakes National Park north to the Foothills Model Forest near the town of Hinton, east of Jasper National Park. This is a diverse landscape, from agriculturally developed grasslands in the east to mixed conifer/hardwood forests in the foothills and abrupt mountains at the continental divide in the west. Most of the foothills and mountains are Crown land (i.e. owned and managed by the provincial government), but much of the agricultural area to the east is privately owned and managed. Human population density and agricultural and recreational use are highest in the southern portions of our study area. All four species occupy the entire area.

(a) *Grizzly bears*

In the Yellowhead area near Hinton, Alberta, we investigated the autocorrelation structure in the movements of nine female grizzly bears with radiocollars programmed to acquire GPS locations at 4 h ± 10 min intervals during 1999–2003. To compare movement rates for bears living in the mountains with those found in the more heavily developed foothills, only bears with greater than 90 per cent of their home ranges in either mountains or foothills and for which we had greater than 150 movement steps per season (spring: den emergence to 15 July; autumn: 15 July to den entrance) were included in the analysis. Home ranges of six bears were located in protected areas in the mountains, whereas home ranges of three bears were in developed areas in the foothills. Human activities in the foothills are diverse and include open-pit mining, logging, oil and gas development, and recreation. In addition, we examined ACFs for seven grizzly bears inhabiting a predominantly agricultural landscape in southwest Alberta, west of Pincher Creek. These bears had radiocollars set to acquire hourly relocations for various periods in 2008–2009. Because we were collecting locations more frequently in this area, we required greater than 500 steps per bear before estimating ACFs. We used Televilt Tellus (Televilt Ltd., Lindesberg, Sweden) and ATS (Advanced Telemetry Systems, Isanti, MN, USA) radiocollars for grizzly bear monitoring.

(b) *Wolves*

Wolf step lengths were collected from three female wolves radiocollared in southwest Alberta, west of Pincher Creek. We obtained GPS locations each hour using Lotek (Lotek Ltd., Newmarket, Ontario, Canada) uploadable radiocollars. We obtained 4422 steps from the Crowsnest Pass pack, 4863 steps from the Castle-Carbondale pack and 903 steps from a wolf in the Bob Creek pack during June 2008 to March 2009.

(c) *Cougars*

Movement data from 41 cougars were obtained with 3 h fix frequency from the East Slopes study area west of Rocky Mountain House, Alberta during 2005–2008 using Lotek uploadable radiocollars. We defined all moves within 200 m of kill sites to be 'handling' moves ($n = 13\,302$) and moves further than 200 m to be searching moves ($n = 19\,533$). Kill sites ($n = 1254$) were identified by visiting clusters of GPS relocations, where cougars spent more than 6 h at the same place (Knopff *et al.* 2009).

(d) *Elk*

Our largest dataset was for elk in southwest Alberta, with an average of 3538 steps (s.e. = 215) from each of 52 elk (34 females, 18 males), obtained in 2007–2008 mostly in the Castle-Carbondale area, west of Pincher Creek. Telemetry relocations were obtained every 2 h using Lotek uploadable radiocollars. We deployed radiocollars on elk in seven unique herds in the Beauvais, Castle-Carbondale, Crowsnest Pass, Livingston, Porcupine Hills, Waterton and Whaleback areas. Many of the elk in these areas migrate seasonally (except for elk residing in Waterton National Park) into the mountains during April and May, returning to winter ranges at lower elevations during November and December. We used the seven herd designations to generate herd-level home ranges using kernel methods. These home ranges were then used to calculate road density within each herd and we subsequently examined the relationship between mean absolute ACFs for each herd and road density using linear regression.

We generated movement and home-range metrics using ArcMap 9.2 (Environmental Systems Research Institute Inc., Redlands, CA) with the Hawth's Tools (*Geospatial Modelling Environment*: www.spatialecology.com) extension. Movements over missed fixes were eliminated from analysis. Estimation of ACFs was performed using the 'corrgram' command in STATA 10 (StataCorp LP, College Station, TX) software. For each species, we examined ACFs to 100 h, an arbitrary limit chosen for consistency only. The number of lagged correlations plotted in ACF functions varied depending on the number of hours between GPS fixes, with as many as 100 lags plotted when relocations were obtained each hour (e.g. grizzly bears and wolves in southwest Alberta).

3. RESULTS

Bears in protected areas in the mountains east of Jasper National Park had step-length ACFs that rapidly decayed, fluctuating around zero, with some exhibiting positive autocorrelation in movements at six lags (24 h), but not further back in time. There were substantial individual differences in the autocorrelation coefficients among and within individuals (the latter by season). Only one female in the mountains had autocorrelated step lengths (maximum $r = 0.2$), and only during spring. Her autocorrelated spring movements might have been attributable to the fact that she had cubs. During autumn, the same bear had a weak ($r = 0.1$) autocorrelation peak at six lags, but no evidence of autocorrelation further back in time.

Of three bears using heavily roaded areas in the foothills, two exhibited autocorrelation in their movements. One of these bears had no autocorrelated movements in spring, but had autocorrelated movements up to 12 lags during autumn. The other bear had weak autocorrelation in step length up to six lags (24 h) during spring, and strong autumn autocorrelation declining gradually from a maximum of $r = 0.3$ at six lags to 0.05 at 24 lags (figure 1). The third bear using roaded areas had no autocorrelated pattern in movements during spring or autumn.

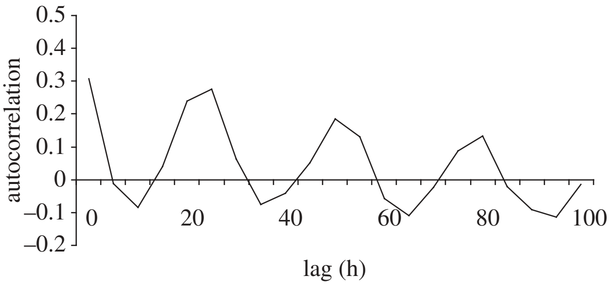

Figure 1. Autocorrelation function of step length for a female grizzly bear (G027) with 4-h interval between GPS telemetry fixes. Observations were from a heavily roaded area in the vicinity of the Cheviot Mine near Hinton, Alberta during late summer and autumn, 15 July to denning.

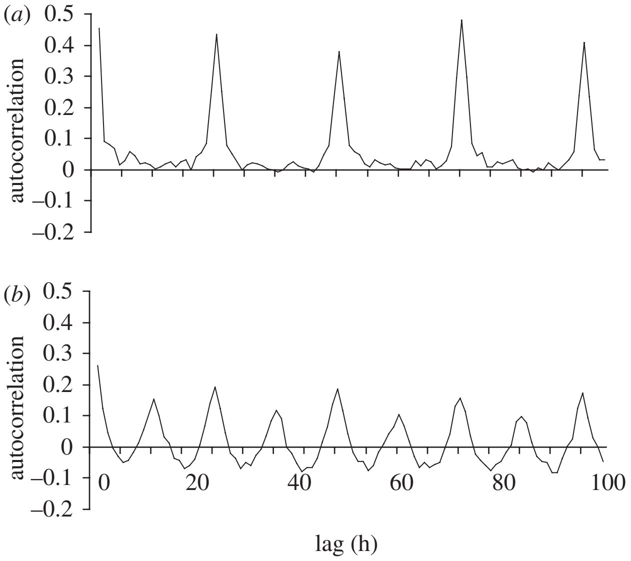

Figure 2. (*a*) ACF of step length for a female grizzly bear with cubs (G077) from den emergence until 15 July 2008 and 2009 with essentially all positive correlations. The bear occupied agricultural lands in southwest Alberta on the east front of the Rocky Mountains. The daily rhythm is driven by regular nocturnal movements averaging 800 m h^{-1} at 23.00 h and 24.00 h. Autocorrelations are essentially zero at other lags indicating no periodicity in movements beyond the midnight movements for this bear. (*b*) Step-length ACF for the same bear (G077) during autumn, 15 July to denning, showing a distinctive crepuscular pattern with two peaks in activity per day, with longest steps occurring at 07.00 h and 19.00 h.

A female grizzly bear with cubs occupied a heavily roaded area of private land, where the primary land use was cattle grazing. Not surprisingly, this bear avoided high human use by adopting nocturnal behaviour with longest step lengths during spring and early summer occurring in the middle of the night. This is reflected by a strong positive autocorrelation every 24 h (figure 2*a*). During late-summer and autumn, we observed crepuscular behaviour by the same bear with peak in activity at 07.00 h and 19.00 h and a clear peak in autocorrelation every 12 h (figure 2*b*).

Both wolves (figure 3) and cougars (figure 4) had relatively weak autocorrelation in step lengths with a 24 h rhythm. By separating steps near known kill

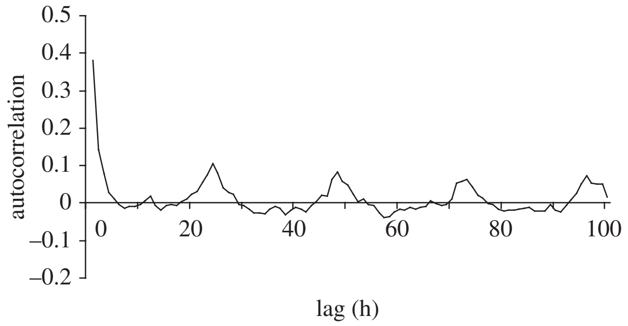

Figure 3. Wolf step-length ACF across three packs in southwest Alberta in an area of high livestock conflict. Although there is a weak peak in the ACF of step length with a 24 h rhythm, the correlation is not strong.

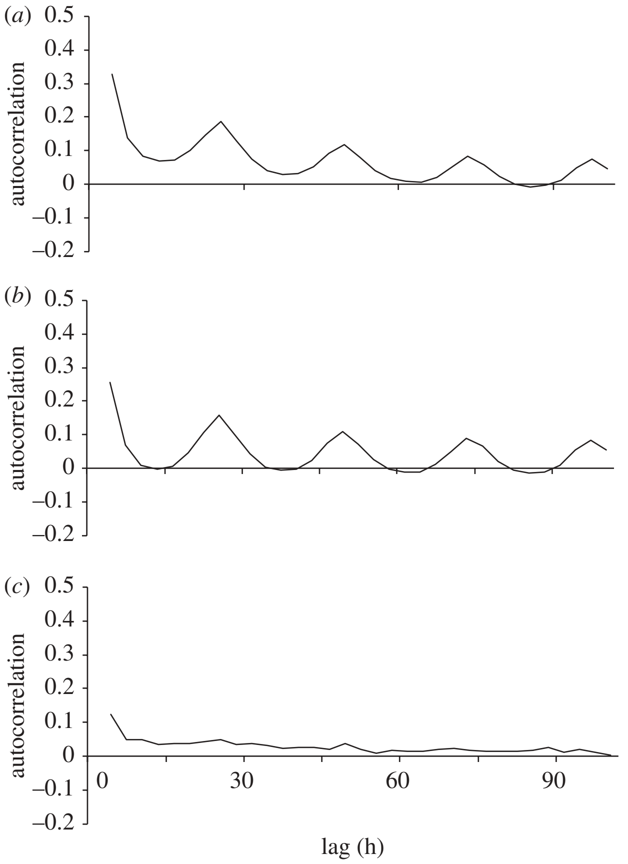

Figure 4. (*a*) Cougar step-length ACFs from an area near Nordegg, Alberta. (*b*,*c*) The same data decomposed into (*b*) searching steps and (*c*) prey handling steps near kill sites.

sites, we were able to decompose the variation attributable to prey handling versus searching for cougars. Although there is a 24 h repeated pattern in the autocorrelation for cougars, the ACF remains positive for 3.5 days (figure 4*a*). Part of this appears to be attributable to the positive autocorrelation in steps taken within 400 m of a kill site (figure 4*b*,*c*).

The regularity of the ACF pattern in elk is striking, with a spiked value at 24 h and a slightly lower peak at 12 h (figure 5). In contrast to many of the carnivores, we observed very little decay in the 24 h periodicity in autocorrelation 4 days removed (i.e. at the 96 h lag). The rounded pattern in the ACF for all elk at 12 h can be attributed to the seasonal pattern that changes depending on the timing of sunrise and sunset. Spring and autumn values are closest to 12 h and the autocorrelation patterns remain similar among all seasons (figure 5*b*).

The amplitude of autocorrelation in elk step lengths appears to be dampened by human disturbance. In figure 6, we plot the inverse relation between the mean absolute value of ACF and road density for seven elk herds in southwest Alberta ($r = 0.851$, $p = 0.015$).

4. DISCUSSION

ACFs reveal patterns in the ecology and behaviour of these large mammals. Autocorrelation patterns are potentially arbitrary because sequential observations are sampled across time periods. Pairing ACFs with models of habitat use and movement, movement over time and knowledge of species provides a more complete view of the behavioural patterns exhibited by animals. For example, the normal crepuscular rhythm of elk step lengths is influenced by human activity, as reflected by the inverse correlation between the mean autocorrelation and road density; the absolute value of the autocorrelation is strongest in areas with lowest road density, whereas areas with higher road density result in disruptions to the intrinsic behavioural rhythm of activity by the elk. Conversely, grizzly bears in wilderness areas do not entrain on a diel cycle, and temporal variation in their step lengths was essentially random. The only exception was a female bear with cubs inhabiting an area of high road density and high human use. This bear may have restricted her movements to make use of food resources during times of human inactivity or when male bears were absent so as to avoid sexually selected infanticide during the spring reproductive season (Dahle & Swenson 2003). However, in areas near roads, most grizzly bears move in a daily pattern reflecting periodicity in human use of the roads. Bears in areas with substantial human disturbance are more likely to become nocturnal, bedding or being less active during times when humans are using roads. In both elk and grizzly bears, human activity disrupts adaptive daily patterns of activity, which we speculate might influence food consumption and energy budgets.

The pattern in grizzly bear step-length ACFs contrasts with the periodic ACFs for furbearer population cycles (Moran 1954; Foley 1980). Instead of the expected negative autocorrelation at half cycle (Moran 1954), the ACF remains positive or near zero but with high positive autocorrelation values at regular intervals. For bear G077, the pattern during spring and early summer was consistently long step lengths in the middle of each night, but no apparent pattern in movements during other times of the day. The strong positive correlation at a consistent lag of about 24 h (figure 2) reflects a daily rhythm of long step lengths, but there do not exist corresponding periods when step lengths are particularly short. During all the other times, the correlation converges on zero meaning that except for the regular midnight forays, the bear had little rhythm to foraging or movement patterns.

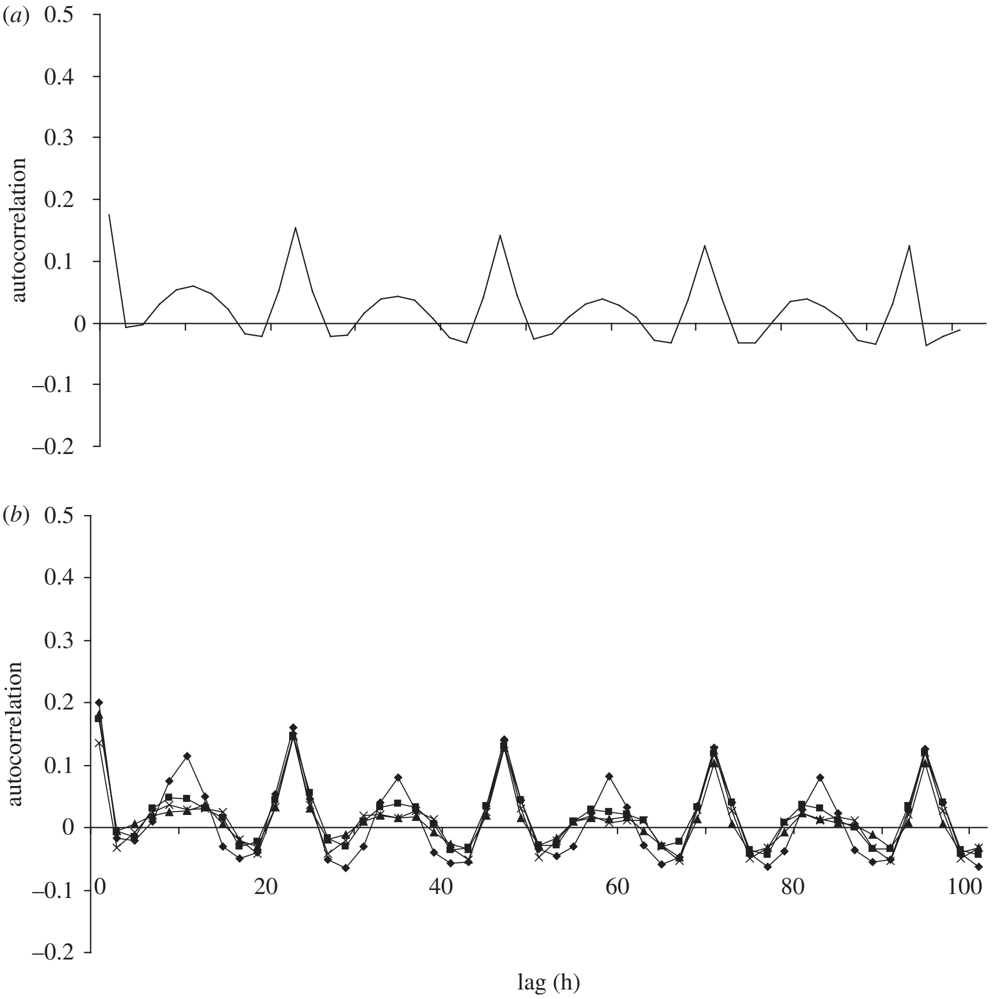

Figure 5. (*a*) Elk ACF over all seasons during 2007–2008 in the Pincher Creek area of southwest Alberta. (*b*) Step-length ACF by season for 52 elk in southwestern Alberta (filled diamonds, filled squares, filled triangles and crosses symbolize spring, summer, autumn and winter, respectively).

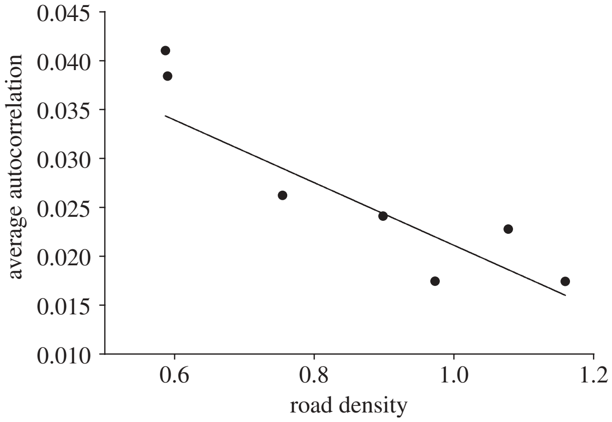

Figure 6. Average absolute value of autocorrelation in elk step lengths as a function of road density near Pincher Creek, Alberta.

Although dampening daily periodicity is evident in several species, the pattern in elk is a persistent one that does not dampen with time, reflecting crepuscular movements well known for cervids. Such a consistent pattern will influence the interpretation of any step-length data for elk, and accounting for the crepuscular movements must be included in movement models for any species with such a dominant daily rhythm. Comparisons of movement sampled at different times of the day could not be interpreted without an appreciation for the daily movement pattern.

Wolf step-length ACF decayed to low values with weak 24 h signals. The wolf telemetry monitoring was in an area of conflict between wolves and livestock ranching, with many cattle being killed by wolves, especially during the grazing season, June through mid-October. The weak daily rhythm might relate to daytime activity patterns by ranchers and other people using the area. Additionally, as a result of livestock depredation, several wolves have been removed from the area, perhaps shifting pack dynamics and contributing to the weak daily rhythm.

As we observed for wolves, a weak daily rhythm was observed in step lengths of cougars. Decomposing the movements into search time and handling time helped in explaining some of the slow deterioration in ACF. Because handling movements were always short (by definition less than 400 m), analysing search moves separately eliminated positive autocorrelation at the half cycle when cougars were hunting. The ACF for handling time was persistently weak, declining to approximately zero after about 4 days, indicating that cougars exhibited no consistent diel movement patterns when handling prey. Low and deteriorating amplitude of autocorrelation values for step lengths of predators such as cougars or wolves may reflect temporal uncertainty in hunting behaviour, thereby allowing the predator to manage prey vigilance temporally as well as spatially (Lima 2002; Mitchell 2009).

There might be reason to remove variation attributable to regular patterns in the time series when searching for other signals in the data. When there is regular periodicity (e.g. a 12 h crepuscular or 24 h daily cycle) these probably relate to the rotation of the Earth and therefore might have an underlying sinusoidal pattern. Indeed, such periodic patterns of behaviour can persist for a very long time (Cushman *et al.* 2005), and can be intrinsic attributes of the behaviour of a species. This can be modelled for a sinusoidally oscillating response variable, $y(t)$, using harmonic regression to fit a generalized linear model with both sine and cosine terms, e.g.

$$y(t) = \beta_0 + \beta_1 \cos\left(\frac{2\pi t}{\tau}\right) + \beta_2 \sin\left(\frac{2\pi t}{\tau}\right) + \varepsilon,$$

for period length τ, and then examining the residuals from this harmonic. Alternatively, one might partition data into various periods of the day for separate analyses, or we might incorporate sinusoidal variation in $y(t)$ explicitly into the model and then examine interaction terms with other covariates. Crepuscular activity may persist indefinitely dominating the ACF, but by measuring step length at the same time each day additional structure (e.g. seasonality) becomes apparent in the ACFs. Cross-correlation of step-length data with environmental data (e.g. rainfall) has been used to unravel some of the underlying causes of autocorrelation structure in radiotelemetry data (Cushman *et al.* 2005; Wittemyer *et al.* 2008).

ACFs and related time-series methods such as spectral analysis only point to patterns in the data. Sometimes behavioural states of the study organism make the interpretation of patterns simple and straight-forward. More often, however, identifying patterns in data generates hypotheses that require additional study, as illustrated by the analysis of movements for the four species that we present here. A challenge remains to account for individual variation in models of animal movement that use temporally autocorrelated data. Individual rather than population-level models can be built to recognize differences among individuals associated with age, sex, genetics, phenotype or experience (Holyoak *et al.* 2008).

As Legendre (1993) emphasized for spatial autocorrelation, we believe that temporal autocorrelation is an interesting and fundamental attribute of time-varying behavioural data. Therefore, characterizing ACFs should form an integral step in the analysis of GPS telemetry data.

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