Review

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

Mark S. Boyce1,*, Justin Pitt1, Joseph M. Northrup1, Andrea T. Morehouse1, Kyle H. Knopff1, Bogdan Cristescu1 and Gordon B. Stenhouse2

1 Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9
2 Foothills Research Institute, PO Box 6330, Hinton, Alberta, Canada T7V 1X6

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

* Author for correspondence (boyce@ualberta.ca).
the autocorrelation directly. A drawback from auto-
logistic regression is that it cannot be used directly
for prediction because one must know the distribution
or movement metrics of the target organism to calcu-
late 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 tele-
metry. 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 autocorrela-
tion 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
decreases because movement at some future time is less
and less likely to be the same as the current rate of move-
ment. 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; Wittmerter 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 move-
ment 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/hard-
wood 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 mana-
ged by the provincial government), but much of the
agricultural area to the east is privately owned and man-
aged. 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 investi-
gated 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 moun-
tains 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 pre-
dominantly 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
Televit Tellus (Televit 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
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).

Phil. Trans. R. Soc. B (2010)
(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.

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 2a). 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 2b).

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
can be attributed to the seasonal pattern that changes its cycle with the seasons. The rounded pattern in the ACF for all elk at 12 h autocorrelation 4 days removed (i.e. at the 96 h lag). We observed very little decay in the 24 h periodicity in step lengths, but there do not exist corresponding longer 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.

<table>
<thead>
<tr>
<th>lag (h)</th>
<th>0</th>
<th>20</th>
<th>40</th>
<th>60</th>
<th>80</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACF</td>
<td>0.4</td>
<td>0.2</td>
<td>0.1</td>
<td>0.0</td>
<td>-0.1</td>
<td>-0.2</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th>lag (h)</th>
<th>0</th>
<th>20</th>
<th>40</th>
<th>60</th>
<th>80</th>
<th>90</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACF</td>
<td>0.4</td>
<td>0.2</td>
<td>0.1</td>
<td>0.0</td>
<td>-0.1</td>
<td>-0.2</td>
</tr>
</tbody>
</table>

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.

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 5b).

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

ACF's 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.
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.

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.

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.

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

for period length $\tau$, 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 straightforward. 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.

We thank the Natural Sciences and Engineering Research Council of Canada (NSERC), Shell Global, Alberta Sustainable Resource Development, Safari Club International, Alberta Parks, Alberta Conservation Association, Spray Lakes Saw Mill, Devon, Alberta Beef Producers, Alberta Sports, Recreation, Parks and Wildlife Foundation, Alberta Professional Outfitters Society, World Wildlife Fund Endangered Species Recovery Fund, Environment Canada, Parks Canada and Alberta Ingenuity for support. We thank Jerome Cranston and Karen Graham for logistical and GIS support for the grizzly bear portions of the study. Most ideas presented in this paper were stimulated by discussions at the GPS-Telemeter Data: Challenges and Opportunities for Behavioural Ecology Studies workshop organized by the Edmund Mach Foundation (FEM) in September 2008 and held in Viote del Monte Bondone, Trento, Italy. Funding of the workshop by the Autonomous Province of Trento is gratefully acknowledged.

REFERENCES


