Tools and Technology Article

Designating Seasonality Using Rate of Movement

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ABSTRACT Traditionally, seasons for animals have been designated based on single external variables such as climate or plant phenology, rather than an animal's response to the dynamic environments within which it lives. By interpreting a rate of movement function of cumulative movement through time we established a method that distinguishes transitions between behaviors limited by winter habitat conditions from those present during summer. Identification of these time periods provides temporal definition to subsequent home-range analyses and use–availability comparisons. We used location data from 32 Global Positioning System–collared female moose (*Alces alces*) to demonstrate the method. We used model selection (Akaike's Information Criterion) to differentiate between candidate rate of movement response curves. Of 32 moose, 29 clearly conformed to an annual movement pattern described by a logistic curve, with increased rates of movement in summer compared to winter. Conversely, 3 aberrant individuals did not alter their movement rate through the year and were best fit with a linear response curve. The seasonal rate of movement model we developed suggests an average summer period of 122 days (median = 119 days, range = 96–173 days) for moose in northwestern Ontario, Canada. The rate of movement model we applied to individuals indicated 1 May as the median date for the winter–summer transition (range = 2 Apr–24 May), and the median transition from summer to winter was 25 August (range = 1 Aug–23 Oct). Wide variation in timing and duration of summer and winter seasons among individuals demonstrates potential failure of the single external variable approach to capture the suite of factors potentially influencing animal behaviors. By plotting cumulative distance moved throughout the year, we elucidated individual variation in response to known and unknown variables that affect animal movement. Accounting for variability among individuals in designation of biologically significant temporal boundaries is critical to delineation of seasonally important habitats for conservation and sustainability of healthy wildlife populations. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1189–1196; 2009)

Much ecological and wildlife research is concerned with determination of habitat use by animals in relation to resource availability. In particular, there has been considerable interest in determination of space-use patterns through home-range analyses based on animal location data, and much has been written on biases and limitations of technology used to determine animal locations (i.e., radiotelemetry) and application of various home-range estimators (e.g., White and Garrott 1990, Millspaugh and Marzluff 2001). Less attention has been given to analysis of movement patterns and the lack of a temporal component in Burt's (1943) original definition of the home-range concept (White and Garrott 1990, Kernohan et al. 2001).

Turchin (1998) described movement as the interconnection that links spatial and temporal relations among animals, their populations, and environments. Movements are motivated, for example, by mating seasons, as an antipredator response, or to acquire resources. Resulting patterns of animal movement provide information on behavior and decision processes through time. However, movement and the reasons for moving are confounded for animals that experience distinct seasonality and are, therefore, required to adapt and consequently acclimate to a differential supply of resources and changing environmental conditions from year to year. These animals must capitalize on seasonally available resources that will, in part, sustain them through periods of resource scarcity. Studying animals on a seasonal time scale captures much of the variation inherent in animal response

to a dynamic environment but requires delineation of periods between which behaviors are expected to differ. Identification of these time periods provides temporal definition to subsequent home-range analyses and use–availability comparisons.

Proxies of when animals are affected by seasonal change are often used to designate seasonal boundaries. Typically these proxies consist of single variables, such as climate (e.g., snow depth, temp) or resource availability (e.g., plant phenology; Peek 1974, Peek et al. 1976, Stewart et al. 1977, Belovsky and Jordan 1981, Hundertmark 1998, Dussault et al. 2004). Using single explanatory variables, however correlated to an animal's environment, cannot fully represent the suite of factors influencing individual behavior through time. Forcing the use of such factors can perpetuate regional, as well as local inaccuracies, which fail to capture the natural variation of individuals and the ecosystem. To objectively understand specifics of what an animal perceives as summer, for example, it must be understood what is biologically important and which factors influence the animal during that time period, then designate when the season begins and ends.

Rather than proxies of seasonal change based on climate or resource availability, we suggest that seasonal boundaries can be designated more objectively for individuals by examination of temporal and spatial changes in animal movement patterns. For hibernating species, behavioral response of individuals to seasonal change is readily apparent from movement patterns; at some point, in response to diminished resources or weather change, the animal enters the

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hibernaculum and essentially stops moving until environmental conditions again become favorable. For migratory animals, seasonal boundaries may be determined from the onset of long-distance movements between ≥ 2 regularly used areas. In these studies, seasonal ranges must be well-defined and criteria must be established that allow segregation of long-distance movements from more localized movements (White and Garrott 1990, Dettki and Ericsson 2008).

Determination of seasonal boundaries for nonhibernating and nonmigratory species based on movement patterns is more difficult. These animals must adjust to a differential supply of in situ resources and changing environmental conditions over a smaller spatial scale than do migratory species. Thus, detection of behavioral changes based on movement patterns requires intensive monitoring of individuals and collection of accurate and precise location data, which has often been difficult because of the impracticality of direct observation and limitations of conventional very high frequency (VHF) radiotelemetry commonly used to estimate animal locations (White and Garrott 1990, Rodgers et al. 1996, Kernohan et al. 2001, Rodgers 2001). However, widely available tools, such as Global Positioning System (GPS) biotelemetry technology, which yields high resolution data, have made near-continuous tracking of large animals a reality (Rodgers et al. 1996, Kernohan et al. 2001, Rodgers 2001). When combined with various forms of habitat data (e.g., vegetation, elevation, climate) in a Geographic Information System, the result describes a highly detailed trail from which movement response to seasonal changes in resource requirements and availability can be inferred. Moreover, by plotting cumulative distance moved throughout the year, the annual movement pattern can be illustrated for individual animals assuming no a priori knowledge of an animal's behavior. The slope of the curve describing cumulative distance moved through time indicates the rate of movement, and the steeper the slope, the faster the animal is moving. Abrupt changes in the rate of movement through the year are primarily indicative of responses to seasonal resource availability (e.g., plant phenology) and environmental conditions (i.e., climate), whereas minor shifts may be related to fine-scale movements resulting from encounters with predators, mating, parturition, and rearing of young. Rate of movement thus provides a comprehensive measure of changes in animal behavior that can be used to designate seasonal boundaries. Rather than being contingent on one variable, such as plant phenology, examination of temporal and spatial changes in animal movement patterns takes into consideration expected and unanticipated factors that may influence an individual animal both locally and regionally from year to year.

We developed a general method that can be used to identify changes in animal behavior in response to seasonal resource availability and environmental conditions based on temporal shifts in movement rate. To demonstrate the applicability of our approach to a nonmigratory species, we used data from GPS-collared moose (*Alces alces*) in central North America to elucidate their movement patterns through the year. We derived mathematical models to describe movement patterns of individuals and a quantitative method for designating seasonal boundaries between summer and winter. Lastly, we assessed the extent of individual variation and the generality of using rate of movement to determine seasonal boundaries for moose and other animals inhabiting northern environments and having similar patterns of annual movement.

METHODS

Using Rate of Movement to Designate Seasonality

Characterization of the annual movement pattern of an individual animal is straightforward; cumulative distance moved is plotted against time. A standard curve-fitting technique (e.g., SPSS v.11.5, SPSS Inc., Chicago, IL; or R v. 2.72, R Foundation for Statistical Computing, Vienna, Austria) can then be used to obtain an equation describing the movement pattern of the individual through the year. Due to regional and individual variation in response to local conditions from year to year, or in the general case where there is no a priori expectation of a particular annual movement pattern, the data may be described by more than one functional form. Model selection using an information-theoretic approach such as Akaike's Information Criterion (AIC) may be used to identify the best model from among a set of plausible equations describing the annual movement pattern of the individual (Burnham and Anderson 2002). The actual form of the relationship is not critical as long as the movement pattern is nonlinear, in which case differential calculus can be used to derive inflection points from the equation of the best model; these inflection points indicate changes in the movement pattern of an animal in response to changes in seasonal resource availability and environmental conditions. If the pattern is linear, indicating no movement response to changing conditions, this general approach cannot be used to designate seasonal boundaries for an individual animal.

Unless the movement rate of an individual remains constant through time, producing a linear pattern, the exact functional form of the relationship between cumulative distance moved and time will depend on the point in time when distances begin to accumulate. Some of these functional forms may not be particularly convenient because estimation procedures or derivation of inflection points is difficult. A variety of starting points may be tried to produce a functional form that will allow straightforward parametric estimation of the relationship between cumulative distance moved and time, and subsequent derivation of inflection points. To begin the process, distances can be accumulated beginning 1 January and continuing to 31 December to correspond with the calendar year. The selected starting point, however arbitrary, must be used for all comparisons among alternative functional forms and for all individuals. In the end, the exact functional form of the relationship between cumulative distance moved and time is not as important as the inflection points derived from their mathematical relationship.

## Annual Movement Patterns of Adult Female Moose

To demonstrate our approach for a nonmigratory species that experiences seasonal changes in resource availability, we determined annual movement patterns for 32 adult female moose fitted with GPS collars (Model GPS_1000; Lotek Engineering Inc., Newmarket, ON, Canada) in northwestern Ontario, Canada, during 2000 (see Rodgers et al. 1995 and Rempel et al. 1997). We programmed collars to attempt a location estimate at least once every 4 hours between 1 January and 31 December. Our analysis used only differentially corrected GPS data with fixes based on 3-dimensional pseudo-ranges, having location accuracy of 3–7 m (Rempel and Rodgers 1997). The median number of relocations retained per animal was 1,561 (range = 664–2,075) for the year, which averages to one location per individual every 6.4 hours. Given the 4-hour duty cycle of the GPS collars and an average of 6.4 hours between locations, our determinations of movement patterns were not affected by differential error rates of GPS units due to habitat use or season (DeCesare et al. 2005).

We calculated cumulative distances moved (m) and associated times (sec) between successive relocations throughout the year (beginning 1 Jan 2000) for each animal using the Home Range Extension (Rodgers and Carr 1998) in ArcView 3.2a. We standardized both distance and time to range from zero to one to facilitate derivation of a generalized model describing the movement patterns and subsequent determination of seasonal boundaries. We divided each cumulative distance value by the total cumulative distance moved by the individual during the year and divided the elapsed time by the total time over which we recorded locations (i.e., 31,536,000 sec). We then plotted standardized cumulative distance (*SCD*) versus standardized cumulative time (*SCT*) for each animal.

Functional Form of the Annual Movement Pattern of Adult Female Moose

Unlike the general case, where there is no a priori expectation of a particular annual pattern, we hypothesized the functional form of the annual movement pattern of moose from previous studies of their seasonal movements. Distances moved by moose are greatest in summer and least in winter (Phillips et al. 1973, Best et al. 1978, Joyal and Scherrer 1978, Garner and Porter 1990, Miquelle et al. 1992). It follows that there will be a period of increasing movement at the beginning of summer and a period of decreasing movement with the onset of winter. Because we started the accumulation of distances moved on 1 January, we expected the annual movement pattern of adult female moose to have a logistic form that can be described by the sigmoidal function. To confirm our expectation, we plotted *SCD* versus *SCT* for all animals on one graph (Fig. 1).

Notwithstanding our expectation of a sigmoid pattern of annual movements, and to fully demonstrate the general approach, we used a nonlinear least-squares parameter-estimation procedure to fit both sigmoid and linear functions (nls() in R v. 2.72; R Foundation for Statistical Computing) to movement data of individual adult female
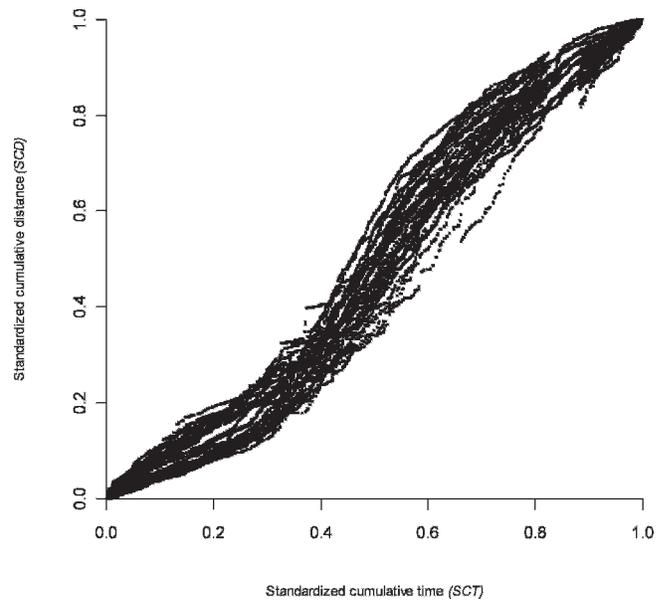
Figure 1. Standardized cumulative distances (*SCD*; $n = 44{,}473$) versus standardized cumulative time (*SCT*) for 32 Global Positioning System–collared adult female moose in northwestern Ontario, Canada, throughout 2000. Time on the abscissa approximates the calendar year, beginning in January. The graph shows the annual movement pattern of adult female moose has a logistic form that may be described by the sigmoidal function.

moose. We assessed model performance by AIC differences (ΔAIC_i) and weights (w_i; Burnham and Anderson 2002).

## Determination of Seasonal Boundaries

If the data approximate a sigmoid curve, as we expected for adult female moose, the equation describing the annual movement pattern takes the form

$$SCD = \frac{1}{\left[\dfrac{1}{u} + b_0 \left(b_1{}^{SCT} \right) \right]} \tag{1}$$

where u is the upper boundary value used to fit the logistic model, b_0 is a constant, and b_1 is the regression coefficient from the curve-fitting procedure. Subsequently, setting $u = 1$ (the max. value of the standardized distance axis), we determined an animal's instantaneous rate of movement at any point in time from the first-order derivative of the sigmoid curve (eq 1):

$$\frac{\partial SCD}{\partial SCT} = - \frac{b_0 b_1^{SCT} \ln(b_1)}{\left(1 + b_0 b_1^{SCT} \right)^2} \tag{2}$$

In the ideal case, where the cumulative distance moved through time was perfectly described by the sigmoid equation, and both cumulative distance moved and time were standardized, mean annual rate of movement for an animal would equal one. Thus, for an individual expected to increase movement at the beginning of summer and decrease movement with the onset of winter, we define summer for an individual by the portion of the logistic curve with a slope that exceeds mean annual rate of movement (i.e., >1) and, conversely, winter by the portion where the slope of the logistic curve is less than mean annual rate of movement (i.e., <1).
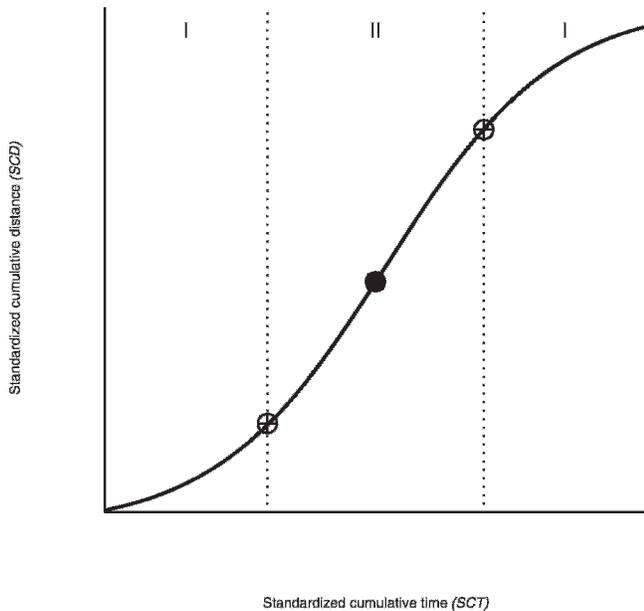
Figure 2. Hypothetical model of standardized cumulative distance (*SCD*) regressed against standardized cumulative time (*SCT*). The abscissa follows the calendar year. The model is divided into 3 sections: the first and third (I) are where movement rate is below the annual mean, whereas the second (II) is where movement rate exceeds the annual mean. Section II, bounded by the crosshaired circles, denotes when the rate of movement is greater than the annual mean (i.e., summer). The solid circle denotes when the instantaneous maximum rate of movement occurs.

If the annual movement pattern has a sigmoid form, seasonal boundaries between summer and winter occur at the 2 unique points (Fig. 2) where the slope of the sigmoid curve is equal to the mean annual rate of movement. We determined these 2 unique points by setting the first-order derivative (eq 2) equal to 1, then solved for *SCT*:

$$SCT = \frac{\ln\left(-\ln(b_1) - 2 \pm \sqrt{\ln(b_1)^2 + 4\ln(b_1)} - \ln 2b_0\right)}{\ln(b_1)} \quad (3)$$

Due to standardization of the time scale, we needed to multiply resulting values by the total time over which we recorded locations (i.e., 31,536,000 sec) to determine actual dates in the calendar year that demarcated the seasonal boundaries between summer and winter.

In addition to deriving seasonal boundaries for an individual, we used the equation of the sigmoid curve to determine the point at which the animal achieved its maximum rate of movement (Fig. 2), which occurred where the second-order derivative of the sigmoid curve (eq 1) equaled zero. At this inflection point, an animal's rate of movement stops increasing and begins to decelerate. Setting the second-order derivative of the sigmoid curve (eq 1) equal to zero, then solving for *SCT*, yielded

$$SCT = \frac{\ln\left(\frac{1}{b_0}\right)}{\ln(b_1)} \quad (4)$$

Again, due to standardization of the time scale, the result was a proportion that we needed to multiply by the total

time over which we recorded locations to determine the actual date in the calendar year when the rate of movement of the animal was at its maximum value.

As previously indicated, we premised our expectation of a sigmoid form to describe the annual movement pattern of adult female moose on the accumulation of distances beginning 1 January and continuing through the rest of the year. Other functional forms are possible depending on the arbitrary choice of the starting point, but these would have been more difficult to parameterize and derive inflection points. Nonetheless, for animal species where there is no expectation of a particular annual movement pattern and the movement pattern is nonlinear but does not have a sigmoid form, we could similarly use differential calculus, as outlined above, to derive inflection points from the equation of the best model.

RESULTS

For 29 of the 32 movement patterns we examined, the sigmoid function was unequivocally identified as the best of the candidate models (ΔAIC = 0.0 and w_i = 1.0 for each of these logistic models vs. ΔAIC > 350.0 and w_i = 0.0 for all others), indicating that for most adult female moose, the rate of movement is better described by a sigmoidal than a linear relationship with the calendar year; the rate of movement is less during winter compared to summer (e.g., Fig. 3a). Mean and median amount of variation in *SCD* explained by *SCT* in the logistic models for the 29 individual adult female moose were both 92% (Table 1), ranging from 85% to 97%. The remaining 3 movement patterns were best described by linear functions (e.g., Fig. 3b) with 98% to 99% of variation in *SCD* explained by *SCT*.

Subsequently, for those individual adult female moose whose annual movement patterns were best fit by a logistic model, we used the coefficients (b_0 and b_1) obtained from the curve-fitting procedure to determine seasonal boundaries by setting the first-order derivative of the fitted equation equal to one and solving for the 2 unique values of *SCT* (eq 3) where the instantaneous rate of movement was equal to the mean annual rate of movement. We also used the equation of the sigmoid curve to determine the point in the year at which the maximum rate of movement (eq 4) was achieved by each animal.

Mean and median dates for maximum rate of movement occurred on 4 July for those individual adult female moose whose annual movement patterns were best fit by a logistic model, but there was considerable variation, ranging from 17 June to 25 July (Table 1). There were also substantial differences among individuals in dates when movements exceeded the annual mean rate of movement, ranging from 2 April to 24 May ($\bar{x}$ = 30 Apr; median = 1 May), as well as when the rate of movement fell below the annual average, which varied from 1 August to 23 October ($\bar{x}$ = 31 Aug; median = 25 Aug). Consequently, the number of days where the rate of movement by individual adult female moose exceeded the annual mean (i.e., length of summer) ranged between 96 and 173 ($\bar{x}$ = 122; median = 119) days.
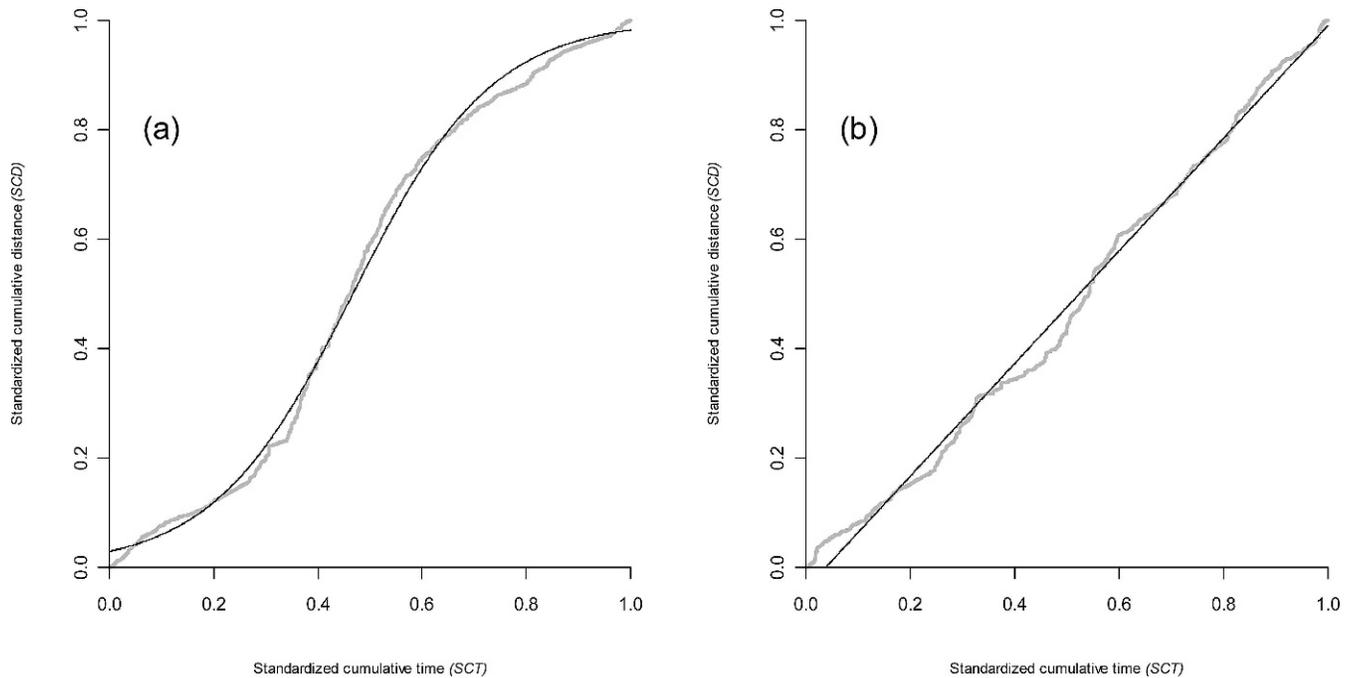
Figure 3. Examples of model-fitting results for adult female moose in northwestern Ontario, Canada, fitted with Global Positioning System telemetry collars. Compare the gray line, which is the standardized cumulative distance (*SCD*) moved through time (standardized cumulative time; *SCT*) from January to December 2000, with the curve-fit (smooth black line) of *SCD* against *SCT*. (a) An animal that represents 29 out of 32 test subjects whose movement is best approximated by a sigmoid curve, where movement rate increases in summer relative to winter. (b) This animal exhibits an atypical movement rate that we observed in the remaining 3 test subjects. The rate of movement does not appear to increase during summer, instead remaining constant throughout the year.

DISCUSSION

The annual pattern of adult female moose movements was best approximated by a sigmoidal relationship with the calendar year; moose generally had a greater rate of movement during summer relative to winter, where early summer was a period of accelerated movement and late summer a period of deceleration (e.g., Fig. 3a). These changes in movement rates by adult female moose generally coincide with seasonal changes in resource requirements and availability. The rate of movement increases with leaf flush and parturition in early May and reaches a peak at midsummer, when highly digestible and nutritious leafy forage is most accessible. During summer moose are hyperphagic (Schwartz 1992), exploiting a variety of forage species to increase digestibility and provide more nutrients in the diet (e.g., by using both terrestrial and aquatic vegetation [Belovsky 1978]). Moose increase their rate of intake to exploit available resources (Renecker and Hudson

1986), accommodate lactation, and store fats for winter (Timmermann and McNicol 1988) during summer when their metabolic rate is highest. Additionally, moose consume 2.6–3.5% of their body weight in dry matter per day in summer compared to 0.5–1.3% in winter (Schwartz et al. 1984). As forage quality declines through late summer, so too does the rate of movement; more time is spent ruminating and less time searching for food. Whereas adult female moose movements may continue to decline with the onset of the mating period in late August, adult males may actually increase their movements during the rut (Houston 1968, Phillips et al. 1973, Schwartz et al. 1984, Garner and Porter 1990), so there is reason to expect some sexual variation in the shape of the curve at that time of year. In either sex, the rate of movement generally declines as summer gives way to early winter, moose switch their diet from green forage to twigs and buds, metabolic rate decreases, and snow accumulates. The maximum rate of

Table 1. Dates of seasonal transitions and maximum movement rate of 29 adult female moose fitted with Global Positioning System telemetry collars in northwestern Ontario, Canada, in 2000, determined from logistic regression models of standardized cumulative distance moved versus standardized cumulative time throughout the calendar year.

Variable	Model fit (adjusted R^2)	Late winter to summer transition date[a]	Max. rate of movement date[b]	Summer to early winter transition date[c]
Median	0.92	1 May	4 Jul	5 Aug
$\bar{x}$	0.92	30 Apr	4 Jul	31 Aug
Range	0.85–0.97	2 Apr–24 May	17 Jun–25 Jul	1 Aug–23 Oct

[a] Late winter to summer transition date is the day when the animal's sustained rate of movement exceeded the annual mean rate of movement.

[b] Max. rate of movement date corresponds to the second-order derivative of the logistic model and demarcates the time when the animal reached its annual peak rate of movement, as well as the time when it began decelerating.

[c] Summer to early winter transition date is the day when the animal's sustained rate of movement receded below the annual mean rate of movement.

consumption reflects available diet, such that ingested usable biomass is markedly less in January than in July (Renecker and Hudson 1986). The consumption of less digestible winter browse increases ruminating time and limits nutrient acquisition (Hjeljord et al. 1982, Renecker and Hudson 1985, Saether and Andersen 1989). Combined, the result is decreased foraging time and fewer large movements in winter. Although increased energy costs of travel through snow in winter can increase basal metabolic rate, limited resources at that time of year can discourage animals from making large movements (Coady 1974). By late winter, typical movement rates of moose reach their lowest point in the year.

Application of our proposed approach to designating seasonality demonstrated a range of individual variation in response to seasonal resource availability and environmental conditions that would not be apparent from using single-variable proxies, such as climate (e.g., snow depth, temp) or resource availability (e.g., plant phenology), to specify seasonal boundaries for moose. Identification of this individual variation has important implications for subsequent analyses of home-range or habitat use–availability comparisons. Suppose, for example, the beginning and end of summer were based on mean dates of leaf inception and abscission of commonly used forage species and these dates had been determined to be 17 May and 4 October, respectively (Stewart et al. 1977). Selecting only locations between those 2 dates to calculate summer home ranges for individual moose in our example, or to carry out habitat use–availability comparisons between seasons, would exclude data from individuals who had already increased their rate of movement in response to seasonal resource availability and environmental conditions at the local level prior to 17 May or had not decreased their rate of movement until after 4 October (Table 1). Further, locations would be included from individuals whose rate of movement in response to local conditions increased sometime after 17 May as well as those from animals that decreased their movement prior to 4 October. Given that the length of summer based on movement rates varied between 96 days and 173 days among individual adult female moose, it is unlikely that these various differences would be balanced. Similar differences between individual summer seasons based on movement and start and end dates of the summer season based on plant phenology can be expected from year to year and place to place. Consequently, any subsequent calculation of summer and winter home ranges or habitat use–availability comparisons between seasons, years, or locations could be biased if based on a single variable such as plant phenology. Unfortunately, we did not record phenological information coincident with collection of moose location data, so we were unable to assess the magnitude of such bias, which would be a useful undertaking for future studies.

Our analyses also showed that annual movement patterns of almost 10% (3 of 32) of adult female moose were better fit by a linear model (e.g., Fig. 3b), which demonstrates a different behavioral response to seasonal resource availability and environmental conditions. These deviations from the typical sigmoid movement pattern we found for most adult female moose (e.g., Fig. 3a) may be related to optimal foraging behavior (Charnov 1976) and local resource availability (Renecker and Hudson 1986, Risenhoover 1986) or regional variations in environment or habitat quality. Further investigation of variables influencing these anomalous movement patterns is warranted. At a minimum, these results suggest that individuals who do not respond to seasonal resource availability and environmental conditions in the same way as most animals in a population need to be identified and considered separately in subsequent calculations of seasonal home ranges or use–availability comparisons.

The rate of movement model does not apply exclusively to moose, or large mammals for that matter. Rather, it can be applied to any animal expected to experience changed requirements and environments between or among seasons. Ultimately, using rates of movement as described by cumulative distance travelled over time to understand how and when animals respond to changing seasons can produce a variety of different movement patterns through a calendar year (Fig. 4). An animal that responds to seasonal environmental conditions by moving constantly to meet its changing needs shows a constant increase in movement throughout the year (Fig. 4a), as demonstrated by a small proportion of adult female moose in our example data set (e.g., Fig. 3b). Animals whose movement may be restricted by winter, such as moose, have a sigmoid movement pattern (Fig. 4b), as we have shown for most adult female moose (e.g., Fig. 3a). An animal whose summer movements may be restricted (Fig. 4c) might be indicative of a denning animal, such as the wolf (Canis lupus; Jedrzejewski et al. 2001). We could use spatial separation to designate seasonality in migratory species; however, a double sigmoid curve (Fig. 4d) might be the corresponding movement rate pattern exhibited by animals undertaking spring and autumn migrations, where we could identify travel to and from calving and wintering grounds by increased rates of movement. Movement rates which approximate exponential increase or decrease (Fig. 4d and Fig. 4e, respectively) might represent rapidly occurring or slower dispersal events, respectively; both curves are characterized by one vertex or change in rate of movement from a state of acceleration to deceleration, or vice versa. Movement patterns of central-place foragers, hibernating animals, et cetera would similarly produce characteristic patterns of annual movement that might also be used to identify individual variations in behavioral response to seasonally changing environmental conditions.

Our method is suitable for delineation of broad-scale changes in animal behavior induced by a differential supply of resources and changing environmental conditions through the year. However, movement rates of individuals may vary over shorter time intervals in response to changing local conditions (e.g., daily temp, snow depth, spatial distribution of resources, responses to predators), as evidenced by deviations of points from fitted annual parametric models (Fig. 3). To demarcate these intervals,
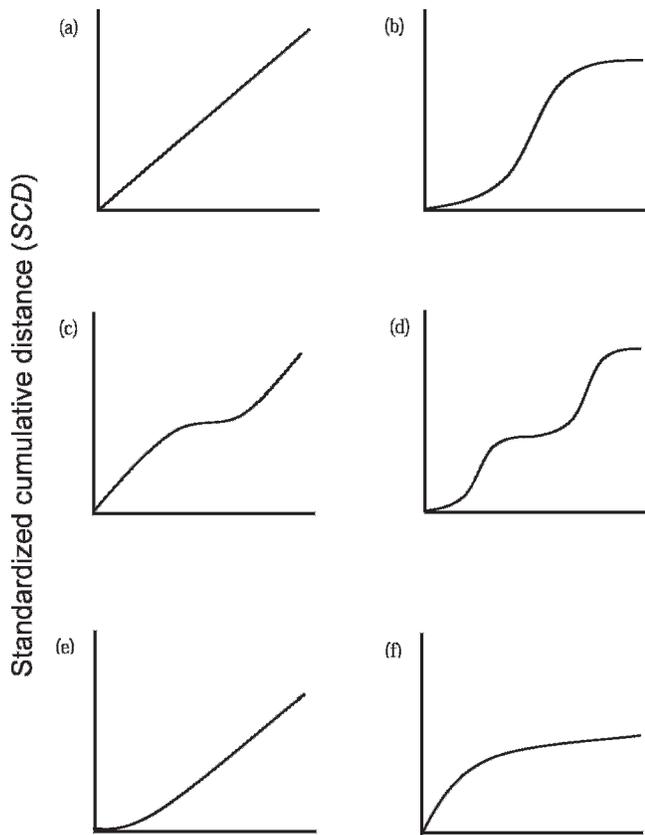
Figure 4. Six a priori models of distance against time, given the constraints of cumulative data, where the slope indicates the rate of movement. Model (a) is an example where the animal maintains a constant rate of movement throughout the year, irrespective of changing seasonal conditions. Assuming a time scale concurrent with the calendar year, the animal in model (b) increases its rate of movement in summer relative to winter. The opposite is represented by model (c) where the rate of movement is less during summer than winter. Model (d) represents the movement rate of an animal that travels between 2 areas within 1 year. Models (e) and (f) might represent slow or rapid initiation of ongoing dispersal events.

the temporal scale we used with our general approach can be adjusted to discern specific periods of important behavioral activity for individual animals. For example, North American moose give birth to their calves almost exclusively in May (Addison et al. 1993, Sigouin et al. 1997). Adult female moose restrict their movements at parturition then gradually increase movement as calves mature (Testa et al. 2000, Welch et al. 2000). Thus, we could use our approach to determine length of the neonatal period for individual adult female moose by examination of movements between the beginning of May and some later date in June or July. Similarly, we could determine length of the rutting period for individual adult moose from cumulative distances moved from late summer to early winter. Alternatively, we could use more complex nonparametric smoothing procedures such as smoothing splines (Wahba 1975, Green and Silverman 1993), locally weighted scatter-plot smoothing

(Cleveland and Devlin 1988), or locally weighted polynomial regression (Fan and Gijbels 1996) to model fine-scale changes in movement rates of individuals. Models resulting from these procedures may be evaluated and points at which movement rates change substantially could then be determined through exploratory data analysis (Chaudhuri and Marron 1999, Sonderegger et al. 2009).

The primary limitation of using movement rates to distinguish transitions between behaviors of individuals is availability of accurate and precise location data collected throughout the period of interest. The intensity of data collection through the period of interest will affect the range of plausible equations fitted to the distribution of cumulative distance moved versus time (e.g., coarse-scale relocation data may not capture tortuous small-scale movements where an animal has increased its rate of movement but over a smaller area). Using relocations spaced too far apart in time, or having large spatial errors, could mean the difference between fitting an oversimplified linear model as opposed to a more complex model. Frequency of data collection will also affect the precision with which the beginning and end points, as well as the length of a particular behavioral phase, can be specified within the overall period of interest. If animal locations were collected weekly, for example, it would not be appropriate to specify the beginning and end points or the duration of a behavioral phase on a daily time scale. Although these limitations can often be overcome with GPS biotelemetry technology, considerable effort may be needed to gather sufficient data using conventional VHF radiotelemetry or direct observation, precluding use of movement rates to better understand individual behavior through time.

MANAGEMENT IMPLICATIONS

It is important to construct biologically significant boundaries for seasons that can be used in subsequent home-range analyses and use–availability comparisons. The rate of movement approach has a number of advantages for understanding animal responses to seasonal resource availability and environmental conditions. Primarily it can be used to designate seasonality based on individual behavior rather than a single driving variable (e.g., phenology); it is a composite of known and unknown variables that affect animal movement. Thus, for a utilitarian dissection of an animal's yearly cycle of behavior, movement rates act as a comprehensive proxy for animal decisions. A designation of summer that encompasses all activities expressing several behaviors is more objective than summer contingent on a single independent variable.

ACKNOWLEDGMENTS

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