Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden Markov models

Alastair Franke [a,*], Terry Caelli [b], Robert J. Hudson [a]

[a] *Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, Alta., Canada T6G 2H1*
[b] *Department of Computing Science, University of Alberta, 221 Athabasca Hall, Edmonton, Alta., Canada T6G 2E8*

Abstract

We explore how doubly stochastic, multiple-observation hidden Markov models (HMMs) may infer meaningful descriptions of woodland caribou (*Rangifer tarandus*) movement and behavior. Parameterized models allowed us to predict behavioral states (bedding, feeding and relocating), relative bout length and transitions, as well as most likely behavioral state sequences. Identification of state transitions and bout lengths appear specific to individuals and may identify dissimilar strategies of resource selection, behavior-specific habitats that are more important than is simply suggested by time spent there (pattern) and transitions between the same or different states that may be evidence for decision-making (process). Using only estimated model parameters, multiple-observation HMMs permitted us to successfully simulate movement and behavior representative of individual caribou through space and time.
© 2003 Elsevier B.V. All rights reserved.

1. Introduction

Quantification of wildlife resource selection is critically important in impact assessment and management planning but continues to be notoriously difficult (Garshelis, 2000). In addition, recent ecological theory has made it progressively more apparent that the relationship between animal movement and factors such as environmental heterogeneity can have sweeping effects on the distribution and abundance of organisms (Dunning et al., 1995; Turchin, 1998). New models that detail the spatial-temporal behaviors of individuals therefore need to be explored. To facilitate our understanding of these dynamic, spatially explicit processes, solutions to the conceptual and methodological problems associated with studying movement and resource selection behavior of individuals need to be explored—the topic of this paper.

Investigations of animal movement in natural environments generally fall within one of three general frameworks: (1) phenomenological studies which describe patterns of habitat use, but without addressing the underlying mechanisms (Wiens et al., 1997); (2) theoretical analyses that usually simplify assumptions about movements and their underlying mechanisms (Skellam, 1973; Stinner et al., 1983; Turchin, 1989) and; (3) individual-based movement models (IBMMs) tailored to context and organism-specific conditions that yield little generalized information (Turner et al., 1993, 1994).

* Corresponding author. Tel.: +1-780-492-4413;
fax: +1-780-492-4323.
E-mail address: kfranke@ualberta.ca (A. Franke).

Animal movement models date back to early 1900. Brownlee (1911) used random walk models to describe movement, Dobzhansky and Wright (1943) modeled the dispersal of fruit flies and Skellam (1951) modeled range expansion of small mammals. Okubo (1980) treated movement of groups of animals as a diffusion process which, when combined with terms that describe ecological processes such as density dependence, population drift or attraction become progressively more biologically meaningful. However, diffusion models were criticized (Skellam, 1973; Stinner et al., 1983; Turchin, 1989) because they assume organisms proceed at infinite velocity along infinitely random paths. Levins (1974) modeled dispersal of individuals of two competing species between two patches in order to illustrate the importance of a spatial component in modeling ecological interactions. Jones (1977) applied a simple random walk in two-dimensional space to describe patterns of population distribution for cabbage butterflies (*Pieris rapae* L.). Random walks may be augmented by varying the length of, and/or imposing directional bias on successive moves. In this case move length and angle are randomly selected from distributions, with each consecutive angle correlated with the preceding one (Skellam, 1973; Kareiva and Shigesada, 1983; Othmer et al., 1988). Many modeling strategies aggregate individuals and their interactions with the environment, but following several important publications (Huston et al., 1988; DeAngelis and Gross, 1992; Judson, 1994), IBMMs were widely adopted by ecologists. This approach acknowledges two fundamental biological principles; first, individuals are behaviorally and physiologically distinct and, second, interactions among individuals are inherently localized, i.e. organisms are influenced mostly by nearby organisms. Although IBMMs are capable of modeling variation among individuals and the interaction between them, most are quite complex, often requiring arbitrary estimates for some model parameters. More recently, Johnson et al. (2002) used a non-linear curve-fitting model of movement rates to identify natural breaks with regard to scales of movement by individual woodland caribou. The authors of this study point out that the application of non-linear models can aid in the development of mechanism-based approaches to the study of resource selection and animal behavior.

In this study, we explore multiple-observation HMMs as an individual-based predictive modeling technique and assess the degree to which inferred state (bedding, feeding and relocating) and observation (distance traveled and turn-angle) components of HMMs can encapsulate use of space, movement and behavior in woodland caribou that reside year-round in central Alberta, Canada. To describe this "space–time–action" system (the tendency of animals to engage in certain activities, in certain places at certain times), we encoded the contribution of distance traveled and turning angles in the form of multiple-observation hidden Markov models.

HMMs are both interesting and unique compared to other solutions because they infer optimal hidden states from observation sequences; time series solutions, for example, can only predict observations from observations. These are quite different problems as the latter simply asks about temporal correlations in the data whereas the former poses the question of optimal inference of a causal model (Markov chain) from the data. So, again, assuming the states are known, the advantage of HMMs over other modeling techniques is that HMMs are able to provide the optimal state sequence from observed data.

The most common HMM structure is a doubly stochastic, first order (unit time lag) model for representing time-varying systems (such as animals moving across a landscape). Assuming a finite number of observations, hidden states and time periods, discrete HMMs can be defined by three basic components: (1) a vector containing the prior probability of each hidden state; (2) the state transition probabilities (A matrix: the first-order Markov assumption) and, (3) the probability of the observations given a state (B_l matrices). More formally, a discrete[1] HMM, λ is defined by

$$\lambda = \{\pi, A, B\}$$

where

$$\pi = p(S_i), \qquad A = p\frac{S_j(t+1)}{S_i(t)}, \qquad B_l = p\left(\frac{O_k^l}{S_i}\right)$$

---

[1] Continuous HMMs are not conceptually different from the discrete case except for replacing individual probabilities by probability density functions.

for states (S_j, $j = 1$, M), independent observation variables, l, with observations (O_k^l, $k = 1$, $N_l)_k$. Given suitable estimates of these quantities, solutions (Rabiner, 1989) are well known for: (1) generating (predicting) observation and state sequences from the model by Monte Carlo sampling methods; (2) determining the most likely behavioral "state" sequence given the model and an observation sequence (the Viterbi algorithm); (3) updating the model estimate given new observations (the Baum Welch algorithm). We do not present details of the Viterbi or Baum Welch solutions here (see Rabiner, 1989), however, these techniques have been widely employed in speech recognition (Levinson et al., 1983; Rabiner, 1989), automated cartographic applications (Caelli et al., 2001a), genetics (Henderson et al., 1997) and human movement production (Caelli et al., 2001b). In accord with the HMM formulation, transitions between the same or different behavioral states can be predicted from the state transition matrix (the model Markov matrix, A) and the state-dependent observation matrices (model B matrices). The latter defines the context sensitive nature of the behavioral states and can be quantified using Bayes rule. The π vector refers to the (aggregated or steady state) likelihood that an individual is bedding, feeding or relocating.

2. Method

The issues related to developing a HMM for caribou movement involve determining a set of interpretable states, the behaviors to which they correspond, and which observations to make. We examined the possibility of three "hidden" states that corresponded to bedding, feeding and relocating. In most large herbivores, including caribou and reindeer, these activities typically account for over 90% of time spent over all activities. Furthermore, we assume that "distance-between-location" (DBL) and "turn-angle" (TA) are suitable observations for encapsulating movement behavior and use of space.

The Boreal Caribou Committee and Alberta Pacific Forest Industry provided the dataset (15-min fixes during a 10-day period in August 1998). Point locations from 12 caribou were collected by satellite tracking using collars outfitted with Lotek Global Position-

ing System 1000 (GPS) location technology (Lotek Engineering Systems, Newmarket, Ontario 1998) and differentially corrected using N3Win (Lotek Engineering Systems, Newmarket, Ontario 1998), which reduced location error to less than 10 m (Rempel and Rodgers, 1997). Collar number, date, time, latitude, longitude, activity, and ambient temperature were converted to *Arc Info*™ point coverage format.

Distance-between-locations and turning angles were calculated from UTM coordinates and resulting observation sequences were used to train models for all individuals. Where locations were not acquired, DBL was standardized by dividing total distance traveled by the number of elapsed 15-min intervals. DBL data were subsequently clustered, resulting in four discrete observations; distances of less than 20 m between locations were considered equal to zero (i.e. the caribou was stationary: observation value $O = 1$), those greater than 20 m and less than 100 m were considered "short" distance moves ($O = 2$), those greater than 100 m and less than 250 m were considered "medium" ($O = 3$), distances equal to or greater than 250 m were considered "long" ($O = 4$) distance moves. Turning angles were clustered in the following manner: 316° through 45°, 46° through 135°, 136° through 225°, 226° through 315° were assigned "ahead" ($O = 2$), "right" ($O = 3$), "back" ($O = 5$) and "left" ($O = 4$), respectively. In the case where an animal remained stationary (according to the distance between location calculation) between fixes, the assigned observation was "stationary" ($O = 1$).

Our initial interest was to determine the degree of association between observation sequences predicted by HMMs and the data for each individual. Commonly used measures that indicate the degree of correspondence include percent correct (PC) and the average absolute difference (AAD). Accordingly, HMMs for each individual were estimated using the Baum Welch procedure (Rabiner, 1989). We used PC and AAD scores for both observations and compared HMM performance within and between all individuals as well as with more traditional time series analysis from data collected from four individuals (caribou 502, 506, 508 and 509). In addition, we trained, estimated and evaluated these models using the full dataset (FDS) and split-half datasets (training on the first half sequence and testing on the remaining unseen sequence, SDS) on each of the four caribou (502, 506, 508 and 509).
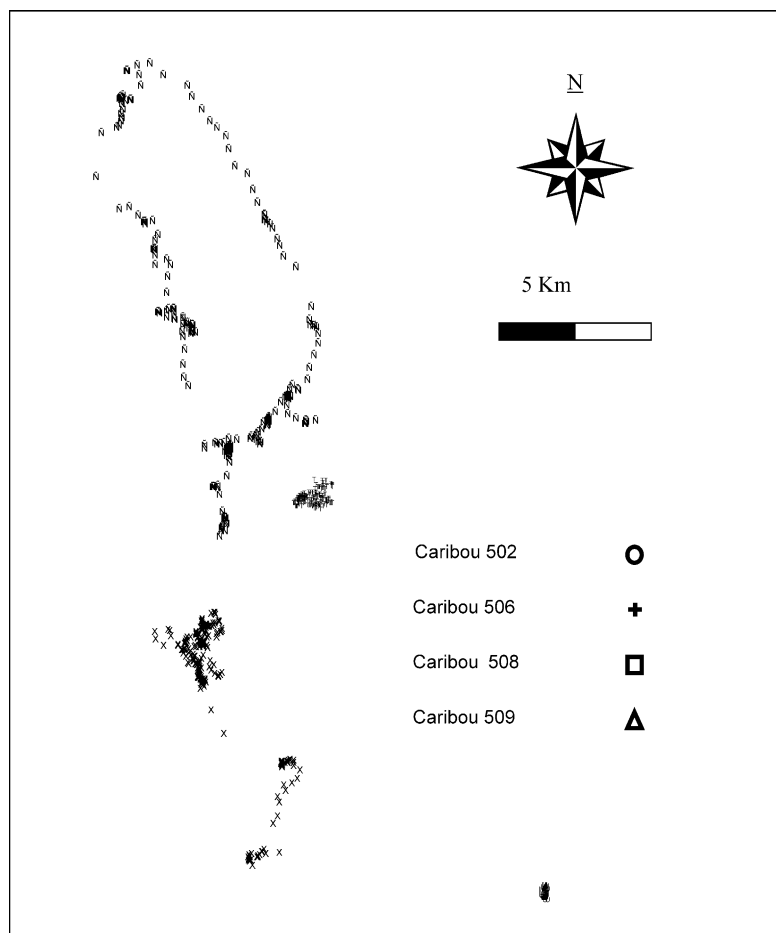
Fig. 1. GPS telemetry point locations for caribou 502, 506, 508 and 509 between 3 August 1998 and 12 August 1998.

These animals were selected based upon different spatial distributions of satellite telemetry point locations (Fig. 1). Caribou 508 presented a formation of "very clustered" point locations, whilst those for caribou 509 were considered "somewhat clustered." Point locations for caribou 502 were "widely" distributed and those of caribou 506 were "ambiguous" (both diffuse and clustered). Apart from apparent differences in use of space, the four individuals were residents of the same region, their locations were recorded over the same 10 days at the same interval and total number of fixes was similar (range 618–630); all four were cows of similar age, but, whether these individuals had a calf is unknown.

We examined estimated model parameters for differences in relative bout length, transition and state-dependent observation probabilities. Finally, by combining DBL and TA in the form of multiple-observation HMMs, we have predicted typical space–time–action systems for the caribou subset purely from estimated model parameters using Monte Carlo sampling methods.

3. Results

Correspondence between models trained and estimated using the FDS and SDS are summarized in Table 1. Sample variances for the dependent measures in both groups were equal and two-sample t-test for equality between means showed no difference in either PC or AAD between the FDS and SDS,

Table 1
Percent correct and absolute average differences for models trained and estimated for all caribou using full and split-half data sets

Model	PC non-partitioned	PC partitioned	AAD non-partitioned	AAD partitioned
502	0.73	0.73	0.40	0.39
504	0.81	0.81	0.29	0.29
505	0.72	0.74	0.41	0.38
506	0.75	0.79	0.38	0.31
508	0.95	0.96	0.08	0.05
509	0.75	0.73	0.37	0.39
510	0.75	0.74	0.37	0.38
511	0.79	0.78	0.31	0.32
512	0.76	0.72	0.36	0.42
513	0.94	0.93	0.13	0.14
515	0.74	0.79	0.39	0.29
522	0.74	0.71	0.37	0.43

demonstrating the initial robustness of model parameter estimation using either the full data set or the split-half procedure—involving testing on data not used in training.

Percent correct values for all individuals ranged from 0.72 to 0.95 (mean = 0.76 ± 0.08), those for caribou 502, 506, 508 and 509 were 0.73, 0.75, 0.95 and 0.75, respectively. Such scores indicate that the underlying models could, on average (Monte Carlo sampling) predict the correct observation at the correct time-step between 73 and 95% of the time. Absolute average distances for all individuals ranged from 0.08 to 0.41 (mean = 0.32 ± 0.12) for DBL and TA, respectively. Mean AAD within the caribou subset was (0.31 ± 0.15). These results indicate that among the four individuals in the caribou subset, an incorrect prediction was on average only 0.31 units (on a 4-point scale) incorrect. These results are encouraging as they

Table 2
Auto-regressive time-series models for caribou 502, 596, 508 and 509

Time-series model
$502 = 0.502 \times (t_{-1}) + 0.065 \times (t_{-2})$
$506 = 0.733 \times (t_{-1}) + 0.013 \times (t_{-2}) + (-0.028) \times (t_{-3})$ $+ (-0.026) \times (t_{-4}) + 0.108 \times (t_{-5})$
$508 = 0.604 \times (t_{-1}) + (-0.261) \times (t_{-2}) + 0.196 \times (t_{-3})$ $+ (-0.074) \times (t_{-4}) + (-0.000) \times (t_{-5}) + 0.063 \times (t_{-6}) + (-0.017) \times (t_{-7}) + (-0.006) \times (t_{-8})$ $+ (-0.037) \times (t_{-9}) + 0.117 \times (t_{-10})$
$509 = 0.464 \times (t_{-1}) + 0.115 \times (t_{-2}) + (-0.089) \times (t_{-3})$ $+ 0.086 \times (t_{-4}) + 0.009 \times (t_{-5}) + (-0.085) \times (t_{-6})$ $+ 0.170 \times (t_{-7}) + (-0.075) \times (t_{-8})$

indicate excellent prediction in so far as incorrect predictions were less than one discrete unit from observed values for DBL and TA.

Time-series equations and coefficients estimated for caribou 502, 506, 508 and 509 are reported in Table 2. Although the number of proceeding time-steps required for prediction in each auto-regression model varied by individual (2nd to 10th order), without exception, the greatest predictive power was contained in the first term of each model (Table 2). This provides clear evidence for a first-order Markov process as used in the HMM formulation. Other biological systems have also been well represented by first order processes (Tanner et al., 1996; Yemshanov and Perera, 2002).

A comparison of model-data correspondence between HMMs and time series analysis is shown in Fig. 2. Here it can be seen that the HMMs consistently outperformed the time series (auto-regressive) model on both measures.
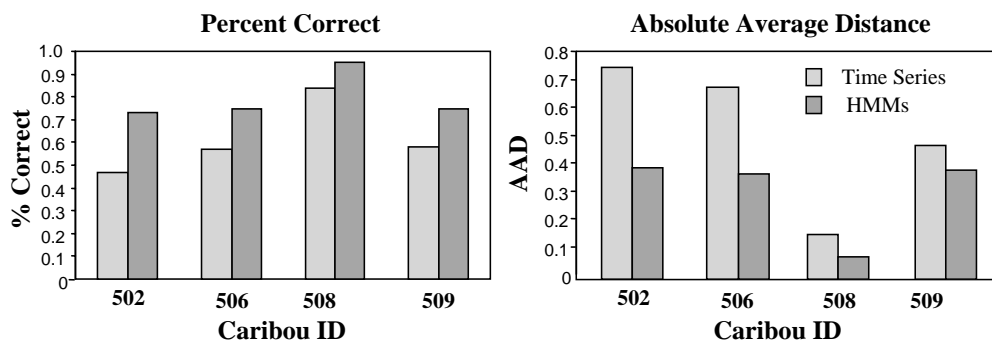

Fig. 2. Model-data correspondence comparing time series and HMM analysis.

Table 3
Multiple-observation HMM for caribou 502

	State $1_{(t+1)}$ (B)	State $2_{(t+1)}$ (F)	State $3_{(t+1)}$ (R)		
A: State transitions					
State $1_{(t)}$ (B)	0.89	0.11	0.00		
State $2_{(t)}$ (F)	0.00	0.00	1.00		
State $3_{(t)}$ (R)	0.21	0.00	0.79		
	Stationary	Short	Medium	Long	
B1: Distance between locations					
State $1_{(t)}$ (B)	0.94	0.05	0.01	0.00	
State $2_{(t)}$ (F)	0.00	0.70	0.26	0.05	
State $3_{(t)}$ (R)	0.00	0.34	0.33	0.33	
	Stationary	Ahead	Right	Left	Backward
B2: Turn angle					
State $1_{(t)}$ (B)	1.00	0.00	0.00	0.00	0.00
State $2_{(t)}$ (F)	0.00	1.00	0.00	0.00	0.00
State $3_{(t)}$ (R)	0.00	0.39	0.26	0.19	0.16

Estimated multiple-observation HMM parameters for caribou 502, 506, 508 and 509 are shown in Tables 3–6, respectively. The Markov structure (*A* matrices) permits interpretation of behavioral transitions (the likelihood that an individual will remain in or change states) and relative bout lengths. For example, in the case of caribou 502 (Table 3), the probability is 0.21 that this individual will bed in the next time step given relocating in the current time step. Similarly, given bedded (the current state),

the likelihood is 0.11 that the next state will be foraging.

Cells aligned along the principal diagonal of the transition matrix are indicative of relative, behavior-specific bout lengths. Generally, models indicated that the caribou showed a propensity to forage for short periods, but would bed and relocate over long periods. In addition, the animals were most likely to bed after a relocating bout and forage after a bedding bout. Such relocating behavior is supported

Table 4
Multiple-observation HMM for caribou 506

	State $1_{(t+1)}$ (B)	State $2_{(t+1)}$ (F)	State $3_{(t+1)}$ (R)		
A: State transitions					
State $1_{(t)}$ (B)	0.87	0.037	0.09		
State $2_{(t)}$ (F)	0.90	0.04	0.06		
State $3_{(t)}$ (R)	0.14	0.02	0.84		
	Stationary	Short	Medium	Long	
B1: Distance between locations					
State $1_{(t)}$ (B)	0.97	0.03	0.01	0.00	
State $2_{(t)}$ (F)	0.52	0.46	0.02	0.00	
State $3_{(t)}$ (R)	0.00	0.42	0.20	0.38	
	Stationary	Ahead	Right	Left	Backward
B2: Turn angle					
State $1_{(t)}$ (B)	1.00	0.00	0.00	0.00	0.00
State $2_{(t)}$ (F)	0.91	0.01	0.02	0.00	0.06
State $3_{(t)}$ (R)	0.00	0.60	0.15	0.18	0.08

Table 5
Multiple-observation HMM for caribou 508

	State $1_{(t+1)}$ (B)	State $2_{(t+1)}$ (F)	State $3_{(t+1)}$ (R)		
A: State transitions					
State $1_{(t)}$ (B)	0.68	0.29	0.02		
State $2_{(t)}$ (F)	0.69	0.28	0.03		
State $3_{(t)}$ (R)	0.21	0.10	0.69		
	Stationary	Short	Medium	Long	
B1: Distance between locations					
State $1_{(t)}$ (B)	0.99	0.01	0.00	0.00	
State $2_{(t)}$ (F)	0.91	0.09	0.00	0.00	
State $3_{(t)}$ (R)	0.00	0.85	0.11	0.04	
	Stationary	Ahead	Right	Left	Backward
B2: Turn angle					
State $1_{(t)}$ (B)	1.00	0.00	0.00	0.00	0.00
State $2_{(t)}$ (F)	1.00	0.00	0.00	0.00	0.00
State $3_{(t)}$ (R)	0.00	0.50	0.11	0.17	0.22

by evidence indicating average distance moved per time step among all 12 animals showed a typical diel cycle, with long periods of relatively stationary behavior during the hottest part of the day and relocating behavior during relatively cooler parts of the day (Fig. 3).

Examination of the *B* matrices showed that all caribou had a strong tendency to move "ahead" and a much weaker tendency to move "backward." Caribou 506 (Table 4) in particular had a strong tendency to move ahead in comparison to other individu-

als, a condition that would be required to produce the widely distributed point locations evident in the data.

Differences between individuals were also apparent from the HMMs. For example observing long relocating bouts was more likely in the case of caribou 502 (Table 3) and 506 (Table 4) compared to caribou 508 (Table 5) and 509 (Table 6). This is interesting when considered in the light of how point locations of each individual are distributed spatially (Fig. 1); individuals with long relocating bouts associated with

Table 6
Multiple-observation HMM for caribou 509

|	State 1 (B)	State 2 (F)	State 3 (R)		
A: State transitions					
State $1_{(t)}$ (B)	0.87	0.03	0.10		
State $2_{(t)}$ (F)	0.33	0.02	0.65		
State $3_{(t)}$ (R)	0.21	0.02	0.77		
	Stationary	Short	Medium	Long	
B1: Distance between locations					
State $1_{(t)}$ (B)	0.95	0.04	0.01	0.00	
State $2_{(t)}$ (F)	0.81	0.19	0.00	0.00	
State $3_{(t)}$ (R)	0.00	0.54	0.30	0.16	
	Stationary	Ahead	Right	Left	Backward
B2: Turn angle					
State $1_{(t)}$ (B)	1.00	0.00	0.00	0.00	0.00
State $2_{(t)}$ (F)	0.91	0.09	0.00	0.00	0.00
State $3_{(t)}$ (R)	0.00	0.47	0.21	0.20	0.12
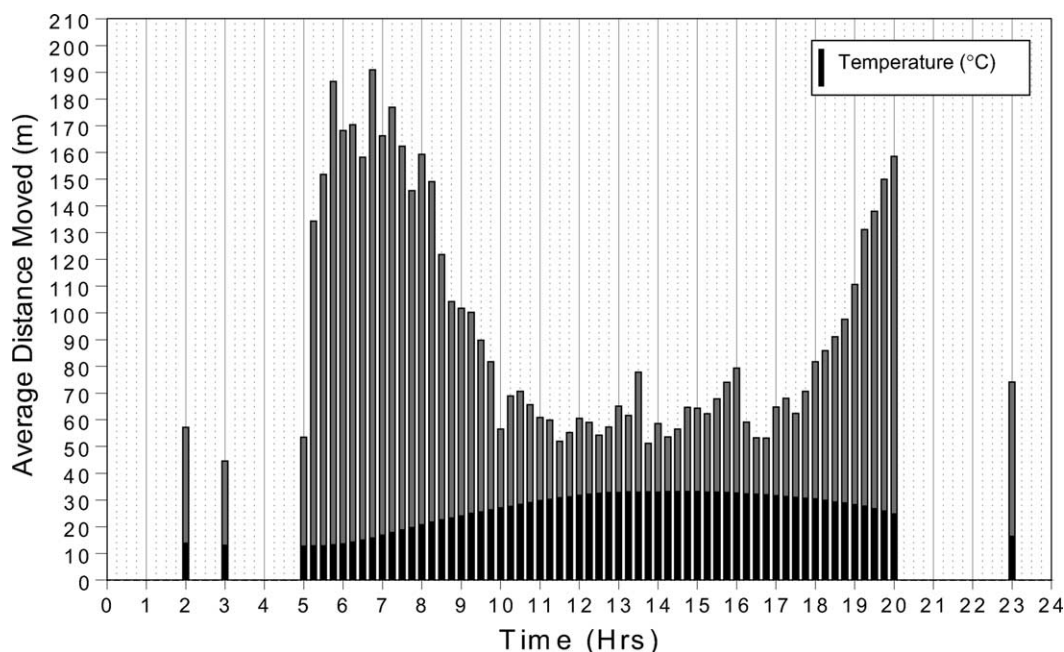
Fig. 3. Average distance traveled between 15-min GPS telemetry point locations for 12 woodland caribou 3–12 August 1998 expressed as a single 24-h period.

relatively shorter distances should present comparatively more clustered point locations than those with long relocating bout lengths associated with longer distances.

Bout lengths, transition and state-dependent observation probabilities permitted rich interpretation of individual caribou behavior. For example, given "relocating" in the current time step, the model predicted caribou 508 (Table 5) would most likely continue relocating ($P = 0.69$) in the next time step and would do so for relatively long periods. Although movements were most likely directionally ahead ($P(\text{ahead}/R) = 0.50$), this animal was more likely than the others to move backward ($P(\text{backward}/R) = 0.22$). In addition, relocating distances were most likely to be short ($P(\text{short}/R) = 0.85$) and quite unlikely to be long ($P(\text{short}/R) = 0.04$). In the event that caribou 508 stopped relocating, it did so in favor of a long bedding bout ($P(B|R) = 0.21$ and $P(B|B) = 0.68$). Finally, in the situation that caribou 508 suspended a bedding bout, it did so in preference for a relatively short foraging bout ($P(F|B) = 0.29$ and $P(F|F) = 0.28$). In summary, our model indi-

cates that this animal was bedded for long periods, relocated short distances ahead, quite likely reversed direction and foraged for short periods.

In contrast to the well-localized point location pattern exhibited by caribou 508, caribou 506 (Table 4) presented a widely distributed point location pattern. Both animals (508 and 506), however, share some common behaviors: for example, given relocating, our models indicate that both caribou would most likely continue relocating for a relatively long periods. Movements were also most likely ahead. In the event that caribou 506 stopped relocating, the model indicates that, like caribou 508, it would do so in favor of a long bedding bout ($P(B|R) = 0.14$ and $P(B|B) = 0.87$). Unlike caribou 508, however, caribou 506 was least likely to move backward ($P(\text{backward}/R) = 0.08$), and, in addition, relocating distances were likely to be long ($P(\text{long}/R) = 0.38$) and unlikely to be short ($P(\text{short}/R) = 0.04$). Generally, our model indicates that caribou 506 bedded and relocated for long periods, relocation distances were long and directionally ahead, backward movements were unlikely and foraging bouts were short.

Important distinctions between these two animals remain; caribou 508 apparently embarked upon short-distance relocating bouts and with some tendency to reverse direction (resulting in clustered point locations; a condition evident from Fig. 1) and caribou 506 undertook long-distance relocating bouts with almost no tendency to reverse direction (resulting in more widely distributed point locations (Fig. 1)).

Fig. 4 summarizes model simulations of the space–time–action system for caribou 502, 506, 508 and 509. For example, our simulations clearly demonstrate the aggregated nature of point locations displayed by caribou 508 as well as the wandering quality of those displayed by caribou 506. It is apparent that the HMMs are capable of simulating the apparently different land-use strategies of each animal, which lends support to our interpretation of model parameters.
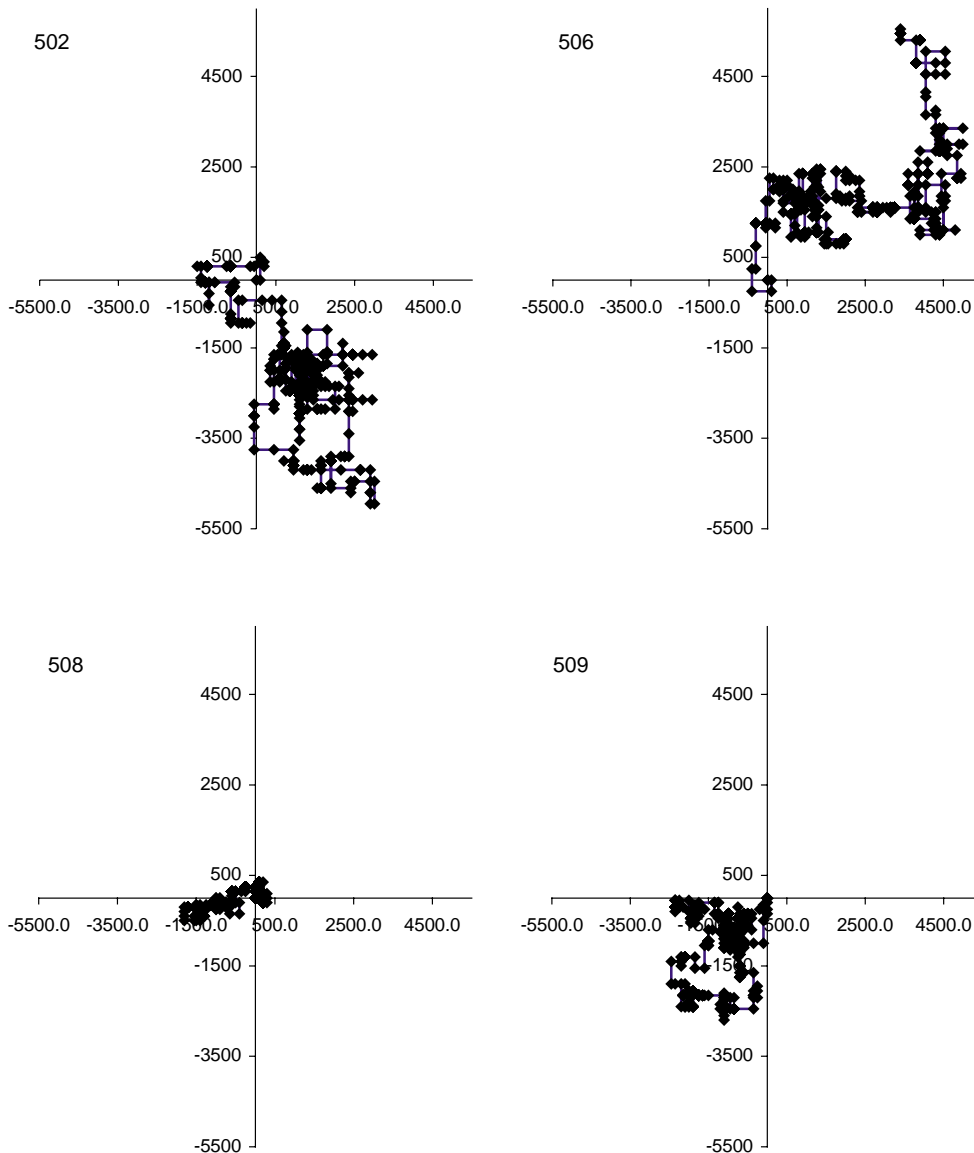

Fig. 4. HMM simulations predicting use of space (m) for caribou 502, 506, 508 and 509.

4. Discussion

We have successfully applied discrete state, multiple-observation HMMs as a predictive modeling technique for animal behavior, assessed the degree to which state and observation components can encapsulate use of space, and illustrated the propensity of animals to engage in certain behaviors (activity budget) in certain places (habitat and diet selection) at certain times; a space–time–action system describing resource selection. Although we selected only three states and proposed that they corresponded to bedding, foraging and relocating, obviously they do not describe all possible caribou behavior and were merely inferred from the data. In addition, the underlying cause of these apparently different resource-use strategies remains unknown but might be related to factors such as landscape grain, degree of disturbance or some feature operating as an anchor.

For example, a calf (Rettie and Messier, 2001) or well-localized (fine grain) resources may anchor an individual to a particular location for a period of time. On the other hand, widely distributed resources (course grain) would result in relocation bouts of longer duration and distance in order for that individual to meet its resource requirements. Furthermore, collared animals repeatedly disturbed by humans, predators or insects should show a propensity to exhibit widely distributed point location patterns. All of these factors are important to biologists studying ways to reverse the decline in caribou numbers throughout the boreal zone of Western Canada.

Resource selection is widely applied in wildlife management to maintain habitat or evaluate impacts of human activity, but despite its widespread use, conventional phenomenological analyses reveal disappointing predictability. The difficulty seems related to scale and to problems inherent in averaging behaviors of individual animals.

Resource selection is scale dependent in both spatial (resolution and extent) and temporal dimensions, but analysis between scales (landscapes, stands and sites) is seldom performed (Senft et al., 1987). This approach improves predictability of behavior but by avoiding integration across ecological scales, fails to address population-level processes or predict impacts of human activity on wildlife. In addition, individual animals likely have distinctive resource selection strategies, which are lost when results are pooled for a population.

In our study, for example, caribou 506 bedded for long periods, relocated over long distances, seldom reversed direction, likely foraged for short periods within sub-patches of about 18 ha (fine spatial) from a total of approximately 14,500 ha (MCP) and moved between them approximately on a daily basis (fine temporal scale) over the entire 10 days (coarse temporal) of data collection. On the other hand, caribou 508 remained bedded for long periods, relocated short distances ahead, quite likely reversed direction and foraged for short periods within a 19-ha patch (spatial) for the entire 10 days (fine temporal scale); if data were collected for a longer period of time, it is possible that caribou 508 may have moved to another 19 ha patch (spatial) for another 10 days (coarse temporal).

Habitat selection studies routinely use an analysis that involves "use" (time spent in a location, number of GPS fixes or distance moved in a habitat type) as a function of "availability" to infer differential use of specific habitat by individuals. The assumption is that selection of, or preference for, superior habitat relates to the fitness of an individual and hence to population growth or stability. Indices of preference, however, are frequently established by pooling the data from many individuals, which potentially obscures individual selection of resources that are truly related to fitness and also accounts for resources used by individuals that have no bearing on fitness. In addition, the spatial extent and arrangement of resources (i.e. landscape context) varies by individual home ranges to the point that transitions between behavioral states (bout lengths) will likely also vary by individual. This would also be the case if landscapes were suddenly altered; an individual obliged to accommodate to relatively rapid changes in the spatial extent and arrangement of resources (e.g. fire or logging) should exhibit concurrent behavioral changes in bout length and transitions between behaviors. Individuals would be compelled to quickly gain knowledge of the "recent renovations" or its decisions (and indecisions) may, in fact, make it more vulnerable to predation or energetic deficit.

For example, caribou residing in un-logged uplands may be at reduced predation risk from wolves simply because diminished accessibility concomitantly diminishes the probability of wolf-caribou encounters. Abrupt changes to the landscape (e.g. fire, logging

or seismic lines) leading to improved accessibility by wolves (and other predators) would likely increase the odds of wolves encountering resident caribou. It logically follows that the probability of survival due to available resources (cover in the case of the caribou and travel routes in the case of the wolves) should shift away from the caribou toward the wolves in more accessible landscapes.

In other words, we allow that different individuals use different locations, in different amounts and at different times, in different amounts. If, as it appears, resource selection is individually based, then grouping similar bouts of activities that occur at similar spatial and temporal scales may allow researchers to appropriately aggregate resource selection data between individuals and decrease the ambiguity common to resource selection studies. For example, combining a vegetation-coverage at scales meaningful to individuals may identify behavior-specific resources that are more important than is suggested by time spent (number of locations) there.

In fact, the 15-min interval at which the data were collected may be too coarse to appropriately study turning angle in foraging bouts. The Markov chains often indicate that the probability of foraging in the next time step given foraging in the current time step to be very low or even zero. The interpretation here is that foraging bout lengths are seldom longer than 15 min and almost certainly never longer than 30 min. It follows then that the occurrence of three consecutive time-steps (the minimum required to calculate a turning angle) during a foraging bout are very rare. The implication of this is that foraging behavior/resource selection may be occurring at very localized spatial scales that are currently not measured either temporally (high frequency GPS point locations) or spatially (high resolution remote sensed data). In addition, the 15-min interval may be too course only during summer months when individuals are disturbed by biting insects not present in winter; such differences could easily be examined by studying bout length and state transitions between seasons.

5. Conclusion

Here, we promote a new direction in the study of animal movement and use of space that explic-

itly recognizes the individual as the central unit of measure. Using distance and turning angle between locations to reflect behavioral states, we have shown that hidden Markov models can be used to describe and predict the complexities of animal movement and decision-making behavior. Model parameters allowed us to estimate inferred behavioral states (bedding, feeding and relocating), their relative bout length and transitions, as well as the most likely behavioral state sequence which, in this case were inferred from patterns in the data. By combining distance-traveled with turn-angle information, we have described a space–time–action system for woodland caribou. Although we have decomposed individual caribou movement data into simple observations of distance traveled and turning angle, the determinants of these simple observations remain unspecified; individual site selection and the decision to move between or remain within a site is likely related to factors such habitat quality and quantity, landscape grain, degree of disturbance or some feature operating as an anchor. These determinants are critical to the maintenance of habitat and the evaluation of environmental impacts due to resource extraction activity. Finally, multiple-observation HMMs could easily be applied to interactions of individuals of the same or different species. For example, multiple-observation HMMs describing the behavior and decision-making strategies of wolves, moose and caribou may provide additional insight into the much-discussed spatial separation hypothesis (Bergerud and Page, 1987).

References

Bergerud, A.T., Page, R.E., 1987. Displacement and dispersion of parturient caribou at calving as anti-predator tactics. Can. J. Zool. 65, 1597–1606.

Brownlee, J., 1911. The mathematical theory of random migration and epidemic distribution. Proc. R. Soc. Edinburgh Sec. A 31, 262–289.

Caelli, T., McCabe, A., Briscoe, G., 2001a. Shape tracking and production using hidden Markov models. Int. J. Pattern Recognit. Artif. Intell. 15, 197–221.

Caelli, T., McCabe, A., Binsted, G. (2001b). On learning the shape of complex actions. In: Arcelli, C., Cordella, L., Sanniti di Baja, G. (Eds.), International Workshop on Visual Form: IWVF, Visual Form, Lecture Notes in Computer Science, LNCS 2059, Springer, pp. 24–39.

DeAngelis, D.L., Gross, L.J. (Eds.), 1992. Individual Based Models and Approaches in Ecology. Chapman and Hall, New York.

Dobzhansky, T., Wright, S., 1943. Genetics of natural populations. Rate of diffusion of a mutant gene through a population of *Drosophila pseudoobscura*. Genetics 32, 303–324.

Dunning, J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L., Lamberson, R.H., Stevens, E.E., 1995. Spatially explicit population models: current forms and future uses. Ecol. Appl. 5, 3–11.

Garshelis, D.L., 2000. Delusions in habitat evaluation: measuring use, selection, and importance. In: Boitani, L., Fuller, T.K. (Eds.), Research Techniques in Animal Ecology; Controversies and Consequences. Columbia University Press, New York, pp. 111–164.

Henderson, J., Salzberg, S., Fasman, K.H., 1997. Finding genes in DNA with a hidden Markov model. J. Comput. Biol. 4, 127–141.

Huston, M., DeAngelis, D.L., Post, W.M., 1988. New computer models unify ecological theory. BioScience 38, 682–691.

Johnson, C.J., Parker, K.L., Heard, D.C., Gillingham, M.P., 2002. Movement parameters of ungulates and scale-specific responses to the environment. J. Anim. Ecol. 71, 225–235.

Jones, R.E., 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol. 45, 195–212.

Judson, O.P., 1994. The rise of the individual based model in ecology. TREE 9, 9–14.

Kareiva, P.M., Shigesada, N., 1983. Analyzing insect movement as a correlated random walk. Oecologia 56, 234–238.

Levins, S.A., 1974. Dispersion and population interactions. Am. Nat. 108, 207–228.

Levinson, S.E., Rabiner, L.R., Sondhi, M.M., 1983. An introduction to the application of the theory of probabilistic functions of a Markov process to automatic speech recognition. Bell Syst. Tech. J. 62, 1035–1074.

Lotek Engineering Inc., 1998. Lotek GPS 1000 Animal Location System Users Manual Version 2.40. Newmarket, Ontario.

Okubo, A., 1980. Diffusion and Ecological Problems: Mathematical Models. Springer-Verlag, Heidelberg, Berlin, New York.

Othmer, H.G., Dunbar, S.R., Alt, W., 1988. Models of dispersal in biological systems. J. Math. Biol. 26, 263–298.

Rabiner, L.R., 1989. A tutorial on hidden Markov models and selected applications in speech recognition. Proc. IEEE 77 (2), 257–286.

Rempel, R.S., Rodgers, A.R., 1997. Effects of differential correction on accuracy of a GPS animal location system. J. Wildl. Manage. 61, 525–530.

Rettie, W.J., Messier, F., 2001. Range use and movement rates of woodland caribou in Saskatchewan. Can. J. Zool. 79, 1933–1940.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhous, L.R., Sala, O.E., Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies. BioScience 37, 789–799.

Skellam, J.G., 1951. Random Dispersalo in theoretical populations. Biometrika 38, 196–218.

Skellam, J.G., 1973. The formulation and interpretation of mathematical models of diffusionary processes in population biology. In: Bartlette, M.S., Horns, R.W. (Eds.), The Mathematical Theory of the Dynamics of Biological Populations. Academic Press, London, pp. 63–85.

Stinner, R.E., Barfield, C.S., Stimac, J.L., Dose, L., 1983. Dispersal and movement of insect pests. Ann. Rev. Entomol. 28, 319–335.

Tanner, J.E., Hughes, T.P., Connell, J.H., 1996. The role of history in community dynamics: a modeling approach. Ecology 77, 108–117.

Turchin, P., 1989. Beyond simple diffusion: models of not so simple movement in animals and cells. Comm. Theor. Biol. 1, 65–83.

Turchin, P., 1998. Quantitative Analysis of Movement. Sinauer Associates, Sunderland, MA.

Turner, M.G., Wu, Y., Romme, W.H., Wallace, L., 1993. A landscape simulation model of winter foraging by large ungulates. Ecol. Model. 69, 163–184.

Turner, M.G., Wu, Y., Romme, W.H., Brenkert, A., 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. Ecol. Appl. 4, 472–496.

Wiens, J.A., Schooley, R.L., Weeks Jr., R.D., 1997. Patchy landcapes and animal movements: do beetles percolate? Oikos 78, 257–264.

Yemshanov, D., Perera, A.H., 2002. A spatially explicit stochastic model to simulate boreal forest cover transitions: general structure and properties. Ecol. Model. 150, 189–209.