

Multiple movement modes by large herbivores at multiple spatiotemporal scales

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Edited by Ran Nathan, The Hebrew University of Jerusalem, Jerusalem, Israel, and accepted by the Editorial Board July 14, 2008 (received for review February 22, 2008)

Recent theory suggests that animals should switch facultatively among canonical movement modes as a complex function of internal state, landscape characteristics, motion capacity, and navigational capacity. We tested the generality of this paradigm for free-ranging elk (*Cervus elaphus*) over 5 orders of magnitude in time (minutes to years) and space (meters to 100 km). At the coarsest spatiotemporal scale, elk shifted from a dispersive to a home-ranging phase over the course of 1–3 years after introduction into a novel environment. At intermediate spatiotemporal scales, elk continued to alternate between movement modes. During the dispersive phase, elk alternated between encamped and exploratory modes, possibly linked to changes in motivational goals from foraging to social bonding. During the home-ranging phase, elk movements were characterized by a complex interplay between attraction to preferred habitat types and memory of previous movements across the home-range. At the finest temporal and spatial scale, elk used area-restricted search while browsing, interspersed with less sinuous paths when not browsing. Encountering a patch of high-quality food plants triggered the switch from one mode to the next, creating biphasic movement dynamics that were reinforced by local resource heterogeneity. These patterns suggest that multiphasic structure is fundamental to the movement patterns of elk at all temporal and spatial scales tested.

elk | foraging | group formation | motivation

The movement ecology framework proposes that animals switch facultatively among canonical movement modes as a complex function of internal state, landscape characteristics, motion capacity, and navigational capacity (1). This is a critical assumption underlying much contemporary theoretical work in movement ecology, as evidenced by a growing number of models based on multiphasic random walks (2–9). Provided that animals exhibit a set of different behaviors (e.g., searching and foraging) that are statistically distinguishable, changes in behavioral state should be inferable in principle from systematic variation in the distribution of movement parameters (3, 10–18).

In this article, we test the multiphasic hypothesis using movement patterns by elk (*Cervus elaphus manitobensis*) reintroduced into southern Ontario, Canada. Unlike previous studies, we have tested this hypothesis at a variety of spatiotemporal scales, ranging in temporal resolution from years to within-daily movements and spatial resolution from hundreds of kilometers to meters. This allows us to evaluate the generality of the assertion that multiple movement modes are central to understanding animal movement (1). We explore the underlying causes of multiphasic movement patterns by linking switches between movement modes with plausible ecological, social, and demographic correlates.

Several data sources were used for this comparison. All translocated animals in the population were equipped with VHF radio-transmitters. Biweekly radio-telemetry from vehicles, aug-

mented occasionally by fixed-wing aircraft, was used to evaluate movement patterns over several years, which have coarse spatial resolution (roughly 1-km sample error). GPS satellite telemetry was used to evaluate daily movements within a year, but with high spatial resolution (≈ 10 - to 100-m sample error). Fine-scale winter movements were studied by using fresh elk tracks left in the snow (< 1 -m sample error). For each of these data sources, we used individual animals as our sample unit for subsequent statistical evaluation of movement parameters.

Results

Coarse-Scale Movement. After release, the female elk dispersed a distance of 10–110 km (Fig. 1A). Most females (30 of 48 individuals, with 2,843 locations) dispersed 10–30 km, 13 of 48 females dispersed 30–60 km (based on 1,076 locations), and 4 individuals dispersed 90–110 km (based on 188 locations). There was no significant difference in dispersal distance between the two releases ($P > 0.05$). Overall, the shape of the net-squared displacement over time deviated strongly from the linear pattern expected for a Gaussian dispersal process, indicating that the elk switched from unrestricted to a locally bounded space use (i.e., home-range behavior) 1–3 years after release (Fig. 1B–D). Short-distance dispersers (10–30 km) continued to slowly drift until stabilizing 3 years after release (Fig. 1B), whereas medium-distance dispersers showed a stationary space-use pattern 1 year after release (Fig. 1C). Although data for the long-distance dispersers were sparse, there is some evidence that long-distance dispersers also started to switch to a more stable space-use pattern (Fig. 1D).

Intermediate-Scale Movement. Movements of individual animals during the first year after herd introduction alternated between periods of rapid directional movement (termed the exploratory mode) and more sedentary behavior (termed encamped mode). Individuals often spent several days in an area < 1 hectare in size, before suddenly relocating several kilometers away (Fig. 2). In encamped mode, elk moved 0.23–0.66 km/day (means for the four individuals), whereas in the exploratory mode, they typically moved an order of magnitude more quickly (5.23–7.00 km/day; Fig. 3). When encamped, move reversals were more common, whereas more linear movement trajectories were favored during the exploratory mode (Fig. 3). Although there was substantial variation among individuals, such saltatory jumps were common, suggesting alternation among movement modes. Invariably, models with mixtures of movement modes were favored relative

Author contributions: J.M.F., D.T.H., J.M.M., and R.C.R. designed research; M.H., L.B., and T.M. performed research; M.H., L.B., B.D.D., D.T.H., and J.M.M. analyzed data; and J.M.F., M.H., L.B., and B.D.D. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. R.N. is a guest editor invited by the Editorial Board.

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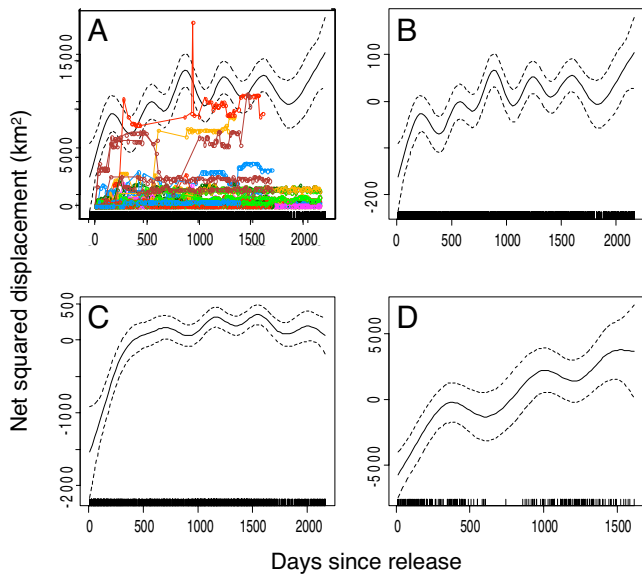


Fig. 1. Net squared displacement from the release site of 48 female elk introduced into the Bancroft region. (A) Observed squared displacement (km^2) in relation to time ("Days since release"). (B and C) Smoothed relationship between net squared displacement (km^2 , scaled around the average) and time since introduction as obtained from nonparametric generalized additive mixed models (GAMM) for short-distance dispersers (B, corresponding to 10–30 km net displacement), intermediate-distance dispersers (C, 30–60 km), and long-distance dispersers (D, 90–110 km; note the change in scale on the x axis). The model term is presented as a continuous line, dashed lines represent 95% confidence intervals, and tick marks show the locations of the observations. Overall, the shift from a highly dispersive phase during the first year to a home-ranging phase thereafter can be observed.

to simpler models based on a single distribution for turn frequency and another for move length (17). No single mixed model was best for all individuals tested, although models with

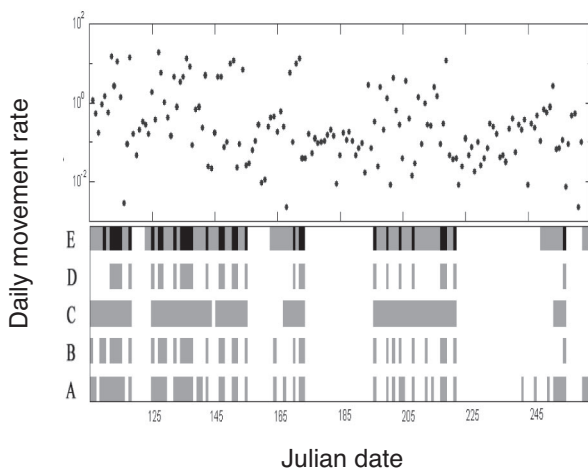


Fig. 2. Variation in movement rate (km/day) for a single female elk individual over time during the first year following introduction to the Bancroft region. Best-fit estimates of behavioral modes are displayed in the movement rate panel, for a range of alternative multiphasic models (A, two-phase; B, two-phase with ecological covariates; C, two-phase with probabilistic transition switch; D, two-phase with probabilistic transition switch constrained to positive values; E, three-phase with probabilistic transition switch). Exploratory movements predicted by each model are shaded, whereas the encamped mode is open. [Reprinted with permission from ref. 17 (Copyright 2004, Ecological Society of America).]

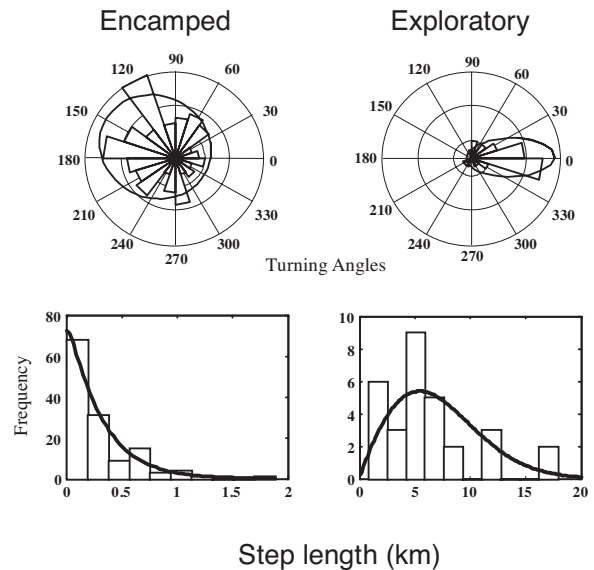


Fig. 3. Variation in frequency distributions of turn angles and step lengths for an individual female elk during the first year after introduction to the Bancroft region, comparing encamped versus exploratory movement modes (16). Best-fit Weibull and wrapped Cauchy distributions (solid curves) are shown relative to the observed data (histograms). [Reprinted with permission from ref. 17 (Copyright 2004, Ecological Society of America).]

a Markovian switching function for transitions among movement modes were favored most consistently.

We extended this general approach to consider the influence of social structure on movement patterns and demography (19). For gregarious animals like elk, maintaining close proximity to other members of the herd could conceivably supersede any probabilistic tendency to move on. We estimated the transition probabilities most consistent with patterns of group displacement, and directly estimated the causal factors associated with group fragmentation and fusion. The results of this social analysis suggest that individuals were strongly attracted to nearby groups and, once formed, rarely left large groups (19). Interestingly, the rate of movement by individuals depended strongly on the amount of time they spent in groups, with highly gregarious individuals being much more sedentary than more solitary individuals (19). Far-roaming, solitary individuals had a higher risk of mortality than did more sedentary, gregarious individuals (19). Hence, sociality triggered changes in movement modes that had important demographic consequences.

After the herds became consolidated, 2–3 years after introduction, individuals developed predictable home-ranges (20). Not all areas in the home-range were equally used; rather, the tendency was for concentrated use of a small area for a period, punctuated by rapid transfer to another part of the home-range, leaving large tracts poorly exploited (20). There are at least two obvious hypotheses that could explain such behavior: animals are attracted to particular habitats that provide food or shelter, or animals tend to revisit places they have already been, perhaps because they know they can safely find vital resources at these locations. A simpler hypothesis, however, is that long moves are simply rare, whereas most daily moves are shorter. We tested among these alternative hypotheses by comparing the likelihood of artificial neural net models based on resource maps, distance, and memory of previous visits. Results of this analysis suggest that all three factors shape probabilistic movement patterns (20). The shape of the multidimensional movement kernel clearly shows that home-range use derives from a tendency to use familiar places with preferred resources (such as open areas with

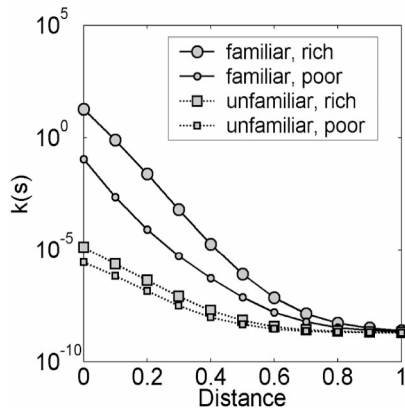


Fig. 4. The best-fit dispersal kernel for a home-ranging elk in the Bancroft region in relation to resource richness and degree of previous experience.

abundant forbs and grasses for feeding), particularly when those areas are nearby (Fig. 4).

Fine-Scale Movement During Winter. At a fine spatiotemporal scale, elk trajectories were highly variable in form, ranging from large loops to zigzag patterns to spirals. Turn angle distributions differed significantly (bootstrap test, $P < 0.05$) between foraging and nonforaging modes, identified directly from field observations, in 20 of the 21 trajectories tested. Turn angle distributions during foraging were more variable and less concentrated around a bearing of zero, suggesting that foraging behavior was associated with sinuous movement. In contrast, turn angle distributions while not foraging had a concentrated range, suggesting that the animals moved in a more direct manner (Fig. 5).

Move length distributions differed significantly (bootstrap test, $P < 0.05$) between foraging and nonforaging modes for all 21 trajectories. Nonforaging distributions had longer tails as a result of a greater range in move lengths, whereas the foraging frequency distributions had a higher proportion of short step lengths, resulting in blunter tails (Fig. 5). The mean move length (3.2 ± 4.3 m) while foraging was significantly shorter than the mean move length (4.6 ± 2.19 m) used when individuals were not foraging (one-tailed t test, $t = 9.62$, $df = 1,846$, $P < 0.001$). Group-forming elk made significantly longer moves than isolated elk both while foraging (two-tailed t test, $t = 6.68$, $df = 1100$, $P < 0.001$) and not foraging (two-tailed t test, $t = 3.27$, $df = 533$, $P = 0.001$).

There was obvious evidence that transitions between movement modes at a fine scale were strongly influenced by food availability. Long, directed moves tended to occur in patches with low resource abundance, whereas shorter, more sinuous moves were associated with patches of high resource abundance. Interestingly, elk did not simply respond to dense food patches by foraging exhaustively at a single station, but rather foraging individuals moved continually among different patches. This meant that intervals of foraging were repeatedly punctuated by intervals of search. Nonetheless, encounters with local resource hotspots triggered consistent changes in movement patterns, with a tendency for more concentrated search in the vicinity of abundant resources, largely due to modifications in turn angle distribution with subtle, but nonetheless significant, reduction in move length. Space considerations in this review preclude a detailed evaluation of alternative foraging models, which we defer to a separate publication. Our general conclusion from such modeling, however, is that spatially selective foraging enhances the rate of daily dry matter intake and digestible energy gain by elk (Fig. 6). By linking spatially selective feeding with

biphasic movements, elk improve the rate of resource acquisition and reduce the time expenditure to acquire those resources.

The fine-scale observations also yield anecdotal evidence of the importance of motion capacity. Accidentally disturbed animals bounded across the snow, with massive increase in stride length. Because we did not use trajectories in which such avoidance behavior occurred, however, we cannot evaluate the impact of altered gait on move length and turn angle distributions.

Discussion

A key tenet of much current research in movement ecology is that changes in the animal's internal state and/or changes in the local landscape trigger facultative changes in movement mechanics. Our research on translocated elk demonstrates several clear examples of behavioral transitions in movement patterns, at each spatiotemporal scale studied.

At the coarsest scale, elk demonstrated a clear shift from dispersive to home-ranging behavior over several years. After introduction into a novel environment, elk rapidly dispersed away from the point of origin. During this dispersive phase, the pattern of expansion was consistent with that predicted by simple Gaussian models of diffusion (21, 22). By the second year, however, introduced animals dramatically slowed the rate of expansion, coincident with the establishment of stable home-ranges. While dispersal for introduced populations is commonly modeled as a diffusion process, stationary space-use patterns due to home-range behavior require different assumptions about movement mechanics (7, 21, 23). The key result, however, is that even the coarsest level of spatial analysis over extended time clearly suggests a biphasic pattern of movement. These changes are a likely consequence of changes in the internal motivational state of individuals, signaling a transition over time from an emphasis on exploratory movement to regular use of a familiar landscape.

At intermediate spatiotemporal scales, there were a number of intriguing complexities shaping elk movement. Animals dispersing from the point of introduction showed clear alternation between periods of encamped behavior, punctuated by bursts of rapid, straight moves (17). This direct movement was of sufficient magnitude to place several individuals >100 km from the introduction site within a matter of weeks.

A key factor influencing dispersive spread, however, was proximity to other elk. Individuals whose movement trajectories by chance brought them near to other elk tended to aggregate into herds, whereas those that were unlucky enough to miss these coalescent groups tended to drift far away (19). Demography was similarly affected, leading to rapid emergence of two classes of individuals: gregarious, slow-moving individuals with high survival rates versus solitary, fast-moving individuals with low odds of survival. Clearly, both population growth and spatial dynamics are influenced by the mixture of individuals in each class, dependent in turn on chance events experienced during simultaneous random walks by the participants.

Resources of importance to animals are typically distributed heterogeneously in space. Theory predicts that animals should take advantage of this spatial distribution of resources in their environment, by spending most of their time in areas of high resource abundance and reducing their time in areas with low resource abundance. This can be achieved by either foraging selectively in patches of high resource abundance (24, 25) or altering movement patterns to stay preferentially in areas of high resource abundance, a behavior known as area-restricted search (26, 27). Within patches of abundant resources, animals should benefit by reducing velocity and increasing the sinuosity of their search path. In patches of low resource abundance, in contrast, foraging animals should benefit by moving more quickly and in a straighter fashion.

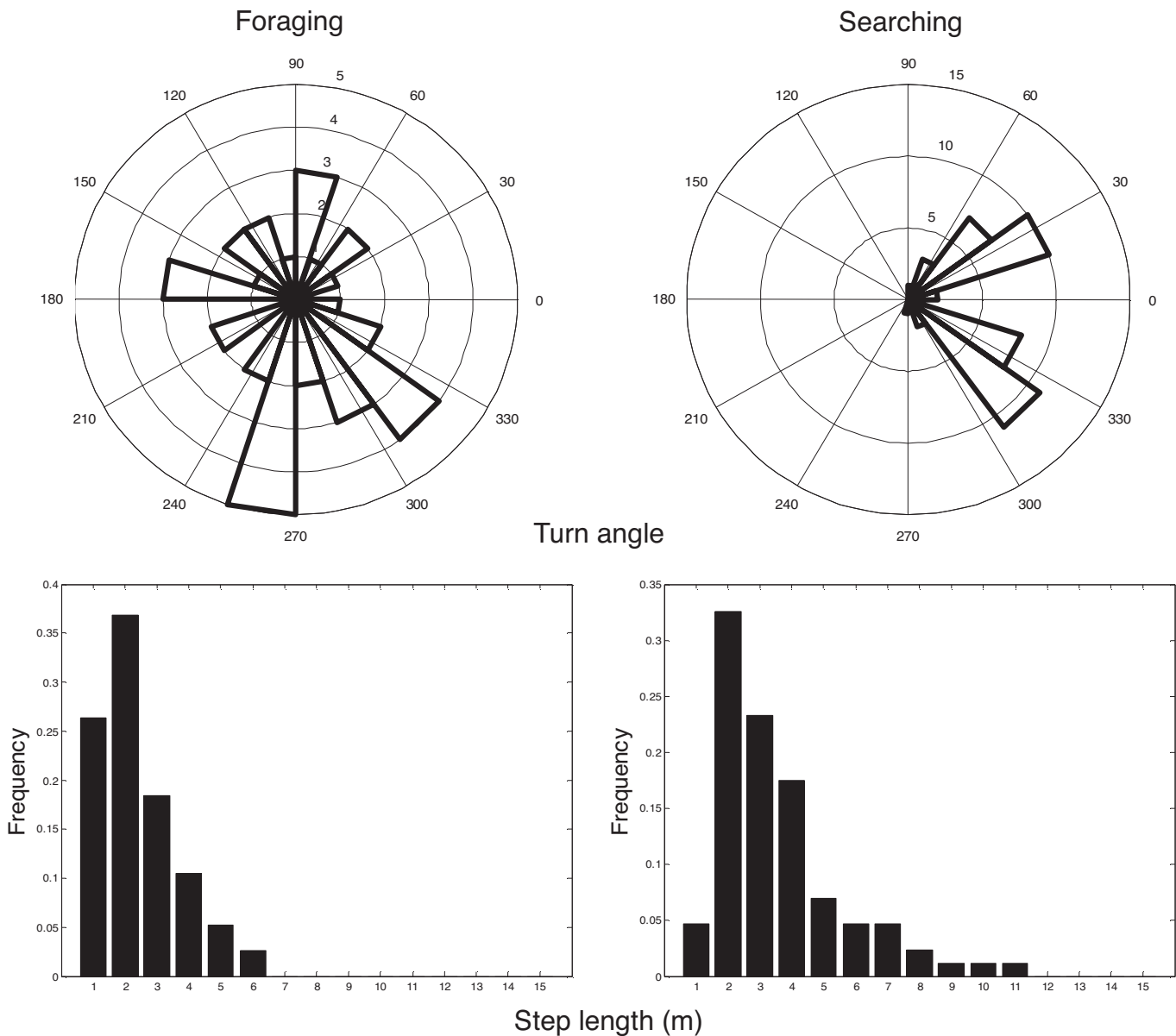


Fig. 5. Example of variation in frequency distributions of turn angles and step lengths for an individual Bancroft elk during winter in foraging versus searching mode.

Our work shows evidence of facultative behavioral response to local resources at a fine spatiotemporal scale, shaping the distribution of movement parameters. Elk turned more frequently and took shorter moves while foraging than when they were moving between patches of high resource abundance. Alternation between foraging and nonforaging modes was clearly a consequence of spatial resource heterogeneity experienced over the course of the daily movement trajectory. A growing number of field studies have demonstrated that large herbivores alter their search behavior in relation to the distribution of resources in their environment (28–31). Like most herbivores, elk did not completely deplete food resources within any single feeding station, but rather moved continually. As a result of local restricted movements, female elk in the Bancroft area maintained a strong association with stands of trembling aspen (32), a primary food source for elk during winter.

Animals tended to use sites that had been visited before, often many days prior (20). In winter, at least two elk groups tended

to frequently revisit sites where local residents provided hay. Given that memory plays a demonstrable role in determining movement probabilities, elk apparently have navigational abilities allowing them to find previously used locations, suggesting that elk may have a cognitive map that allows them to order their movements among favored habitats.

In sum, multiphasic movement patterns were evident at every spatiotemporal scale examined, suggesting that a fully synthetic approach, linking internal state, landscape characteristics, and navigational capability, is necessary for a complete understanding of elk movement (1). This suggests that such a synthetic quantitative model, based on alternation among canonical movement modes, has great predictive potential (33). Achieving such a synthesis is no simple matter, however, for several reasons.

There are enormous statistical challenges associated with identifying mixtures of movement behaviors from a continuous stream of time series data. New methodical approaches, like Markov chain Monte Carlo methods, can help solve these issues

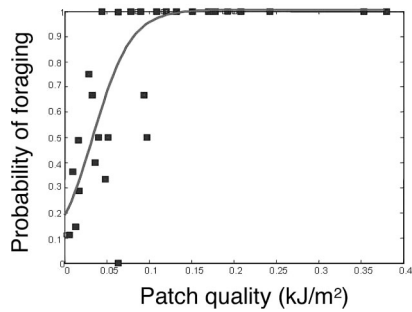


Fig. 6. The probability of foraging by elk in relation to patch quality (measured as digestible energy density kJ/m^2), based on logistic regression for merged data for 11 solitary elk.

(17), but these are often time-consuming and challenging to implement. Theoretical expectations for functional relationships between internal state, prior experience, and landscape characteristics are poorly developed. In the absence of parametric models, flexible regressive approaches such as artificial neural nets are a useful alternative (20), albeit at the cost of mechanistic understanding.

The most serious challenge, however, is accurate measurement of local variables, like food abundance or the distribution of other population members, at a meaningful landscape scale. Habitat may be a suitable proxy for critical resources in some cases, but this has been rarely tested. The reliability of this assumption will no doubt profoundly influence the predictive ability of resource-based movement models. Only at fine scales can we feel truly confident about our ability to link transitions in movement mode with underlying ecological variables (33). At this fine scale, however, other processes such as social interactions are less apparent. Although reliable identification of causal factors will be challenging in the extreme, the analytical tools now available suggest that the effort would be amply repaid.

Materials and Methods

Study Area. The study was carried out near the town of Bancroft, located in east-central Ontario. The terrain is flat to rolling, with vegetated areas punctuated by areas of exposed bedrock. Small rivers and lakes are common throughout the region. The larger landscape is a heterogeneous mix of abandoned farmland, cleared plots occupied by housing, and dominant, extensive tracts of secondary growth forest. Moist low-lying areas tend to be dominated by coniferous species, such as *Picea glauca* or *Abies balsamea*, whereas higher, drier areas are dominated by deciduous species, such as *Acer saccharum*, *Betula papyrifera*, or *Populus tremuloides*.

Movement Data. One hundred twenty elk originating from Elk Island National Park, Alberta, were transferred to the Bancroft region in 2000 and 2001 as part of a province-wide reintroduction program (34). Almost all of these individuals were VHF radio-collared and tracked and located approximately once every 2 weeks, for up to 6 years. Most locations are based on triangulation of telemetry fixes on the ground, sometimes confirmed by visual sightings, with occasional aerial coverage. During the course of the study, 11 elk cows were fitted with LOTEK GPS radio-telemetry collars, 4 individuals in 2001 and 7 individuals in 2003, which automatically stored GPS locations on fixed sampling schedules (typically one fix every 4 h, with hourly fixes on one day every 2 weeks).

Elk movement behavior at a fine spatiotemporal scale was studied by snow-tracking in the winters of 2003 and 2004. Tracking only occurred within 12 h after fresh snowfall to ensure that measurements reflected recent movement. We initially located study animals on foot using radio-telemetry and thereafter used direct physical mensuration of elk tracks to estimate movement parameters. Sections of elk tracks that deviated $<10^\circ$ were operationally defined as line segments. Deviations of $>10^\circ$ were used to define turning points. We then recorded the bearing between sequential turning points, measured the segment length, and counted the number of strides per movement segment. The longest, clearly decipherable section of a movement trajectory was investigated, starting from a bed site and ending at another

bed site or when the tracks became obscured by tracks of other individuals. We recorded information on 21 movement paths of female elk: 11 paths were of solitary animals and 10 of individual animals moving in groups. Within the herds, sex was determined by footprint size and stride length using observations from the known solitary animals as the standard female track size.

Data Analysis. Coarse scale. We used biweekly location data to investigate the form of the relationship between the net squared displacement and time since release, the main statistics used to characterize movement patterns over long time scales. Diffusive processes lead to a linear or power function relationship between the average net squared displacement and time, whereas a switch to an asymptotic curve is indicative of locally restricted space use patterns, such as home-ranges (7, 21–23).

For the analysis of net squared displacement, we selected females followed for at least a year with at least 15 biweekly VHF telemetry locations. Of the initial sample of 120 radio-collared elk, 48 females, aged 0–12 years at release and followed for up to 6 years (4 years on average), met these criteria. On average, 72 locations were available per individual (range 15–128) for a total of 4,197 locations.

Data analysis was performed in the R software environment, version 2.6.1 (35). We used generalized additive mixed models with thin plate regression splines estimated using a generalized cross-validation procedure [mgcv, version 1.3–29 (36)], to explore the shape of net squared displacement over time (days since release) without imposing *a priori* any parametric function. This procedure allowed us to include the identity of individuals as a random effect. Serial autocorrelation between biweekly locations was accounted for by using autoregressive models of order three for the within-group errors, based on AIC scores, and we allowed the variance to change over time and between the two release years (36, 37). We also included the release year as a two-level factor in the fixed-effects specification to test for differences in displacement distances.

Intermediate scale. For analysis of movement at intermediate spatiotemporal scales, we subsampled one location per day from the GPS data, using the first GPS location recorded each day. Movement during the dispersive phase was described by using a biphasic correlated random walk. Parameters for each movement model, including the switching rates between modes, were estimated by using Markov chain Monte Carlo methods. Supplementary statistical material for model selection is provided in ref. 17. Using also the VHF data, for specified dates, we computed an inter-elk location distance matrix on which we performed cluster analysis. We assumed that individuals <2 km apart belonged to the same group. For each location datum, we asked how many other collars had been tracked within 2 km of this location within 4 days of either side of the focal date. Location data around which no other collars were to be found were termed solitary, otherwise grouped. Changes in group status were also recorded, allowing estimation of the rate at which individuals left groups or the rate that new groups were formed. We assumed that individuals in the same group followed the same biphasic correlated random walk that had been parameterized for solitary individuals but with different switching rates between behavioral states (for full details, see ref. 19).

After elk dispersion had slowed over time, we selected five new elk with GPS collars that had settled into home-ranges. Landscape structure was represented in Cartesian grids with 10×10 elements superimposed over each individual's annual home-range (termed the resource map). We used the Ontario Landcover Database to assign landscape values, using the following procedure. Separate binary maps were constructed by using the presence or absence of each of 28 landcover types within each cell. The 28 separate layers were combined by using principal components analysis to provide a single habitat value at each spatial location, as described in detail in ref. 20.

At each daily time step, we constructed 10×10 element matrices depicting the distance from the animal to each cell in the landscape (termed the distance map) and the distance to the closest approach during a previous time interval (termed the memory map). Because animal positions were constantly in flux, the distance and memory maps needed to be updated with each daily time step, whereas the resource map was static. The three maps were linked in multifactorial fashion to predict the likelihood of movement during the next time step, and these stepwise probabilities were multiplied together to yield the likelihood surfaces for movement, based on the influence of resources, memory, and distance from the current position. Because we had no *a priori* model with which these variables could be linked, we used an artificial neural net to parameterize nonlinear likelihood models to minimize residual spatial positioning error (for full details, see ref. 20).

Fine scale. Fine-scale movements during the winter were studied by closely examining elk footprints in the snow in relation to the local abundance of vegetation in the immediate vicinity. Typically, movement paths led directly to browsed stems. Any woody stem within 1 m of the movement path with fresh,

green bites removed from it was defined as being browsed. A given segment was defined as a foraging segment when at least one browsing event occurred. Typically, there was either a great deal of browsing or none at all during segments, so the distinction between foraging versus nonforaging segments was straightforward. There was little evidence of deer or moose in the fine-scale study areas used by elk. Previous cervid foraging studies have documented that black-tailed deer base local foraging decisions on resources within 5 m of the forager's trajectory (38), which we arbitrarily assumed for elk. All woody stems within 5 m of an individual's movement path (a 10-m corridor in total) were recorded. All available woody stems above the snow were counted, as well as species identity, stem diameter, and orthogonal distance from the movement path. Stem biomass was estimated from stem diameter by using published allometric regression equations (39–41) and then multiplied by stem density to estimate local woody biomass.

Bootstrapping was used for statistical comparison of the distributions of turn angles and move lengths of segments in which elk foraged versus segments without foraging. For both parameters (angle and move length), we used nonforaging segments as the expectation against which foraging seg-

ments were compared. Turn angle data were grouped into 10° bins, whereas move length data were grouped into 1-m bins. Bootstrap sampling was done with replacement, using a χ^2 statistic to score the deviation between bootstrapped and observed distributions. The bootstrapped χ^2 distribution was then examined to determine the proportion of values that were as extreme as the observed χ^2 statistic, giving an estimate of the probability of overlap under the null statistical hypothesis.

ACKNOWLEDGMENTS. We gratefully acknowledge field assistance by a large number of individuals over the years, as well as very useful editorial suggestions by Ran Nathan and an anonymous reviewer. We warmly thank the Institute for Advanced Studies at the Hebrew University of Jerusalem for the opportunity to develop some of these ideas through the Movement Ecology Working Group. This work was made possible with the financial support of the Ontario Graduate Scholarship Program, the Ontario Ministry of Natural Resources, the Rocky Mountain Elk Foundation, the Natural Sciences and Engineering Research Council of Canada Collaborative Research Opportunities Program, and U.S. National Science Foundation Integrated Research Challenges in Environmental Biology Program Grant 6078130.

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