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STATE–SPACE MODELS LINK ELK MOVEMENT PATTERNS TO LANDSCAPE CHARACTERISTICS IN YELLOWSTONE NATIONAL PARK

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Abstract. Explaining and predicting animal movement in heterogeneous landscapes remains challenging. This is in part because movement paths often include a series of short, localized displacements separated by longer-distance forays. This multiphasic movement behavior reflects the complex response of an animal to present environmental conditions and to its internal behavioral state. This state is an autocorrelated process influenced by preceding behaviors and habitats visited. Movement patterns depending on the behavioral state of an animal represent the broad-scale response of that animal to the environment. Quantifying how animals respond both to local conditions and to their internal state reveals how animals respond to spatial heterogeneity at different spatial scales. We used a state–space statistical approach to model the internal behavioral state and the proximate movement response of elk (*Cervus elaphus*) to available forage biomass, landscape composition, topography, and wolf (*Canis lupus*) density during summer in Yellowstone National Park, USA. We analyzed movement paths of 16 female elk fitted with global positioning system (GPS) radio collars that recorded locations at 5-h intervals. Habitat variables were quantified within 175 m radii (one-half of the median 5-h displacement) centered on the beginning location of each interval. Stepwise model selection identified models that best explained the movement distances of each animal. The behavioral state changed very slowly for most animals (median autocorrelation $r = 0.93$), and all animals responded strongly to time of day (with more movement in the crepuscular hours). However, the spatial variables included in the best-fitting models varied substantially among individual elk. These results suggest that strong patterns of habitat selection observed in other studies may result from frequent visits to preferred areas rather than a reduction of movement in those areas.

Key words: animal movement; Cervus elaphus; *elk; heterogeneous landscapes; Kalman filter; landscape ecology; multiphasic movement path analyses; state–space; ungulate; wapiti; Yellowstone National Park, USA.*

Introduction

Understanding how animals interact with heterogeneous landscapes remains a central goal of ecological research (Wiens et al. 1993, Turchin 1998, Ellner et al. 2001). The characteristics of an animal's movement reflect its relationship with numerous biotic and abiotic factors that influence energy intake and expenditure, predation risk, and social interactions. These relationships have implications for the spatial structure of populations and metapopulation dynamics (Pulliam and Danielson 1991, Stapp and vanHorne 1997, Hanski 1998, Revilla et al. 2004, Armsworth and Roughgarden 2005), spread of exotic species (Dean 1998), disease ecology (Gudelj and White 2004), and trophic cascades (Ripple et al. 2001, Ripple and Beschta 2004, Fortin et al. 2005*a*). However, extracting biologically meaningful information from animal paths is difficult because movement is a multi-scale, stochastic process (Lima and Zollner 1996, Turchin 1996, Morales and Ellner 2002).

A substantial body of theory has been developed to describe animal movement patterns. The most general models are correlated random walks (CRW) in which the straight-line distances moved between time periods (step lengths) are either fixed or independently drawn from the same distribution; "random" turning angles are assumed to be autocorrelated and, in the case of biased random walks, weighted toward one location or direction (Turchin 1998). Correlated random walk models often fail to predict empirical patterns over long time periods, but represent reasonable null models for short series of movements. Other methods explicitly model certain characteristics of a path, such as the

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distribution of step lengths (e.g., Lévy flights; Viswanathan et al. 1996, 2002) or the fractal dimension (Nams 2005), but these methods usually relate path characteristics to the landscape surrounding the entire path, rather than relating changes in path characteristics to the local environment (but see Nams and Bourgeois 2004, Fortin et al. 2005*b*).

Of major interest to ecologists is how movement trajectories change in response to various stimuli, because these changes provide insight to the behavioral mechanisms mediating movement. For example, in spatially heterogeneous landscapes, animals may exhibit "preytaxis" and congregate around concentrations of food resources simply by conditioning their movement rate or turning frequency on patch quality or prey capture rates (Kareiva and Odell 1987, Bovet and Benhamou 1988, Walsh 1996). Similarly, responses of animals to the boundaries of suitable habitat patches may influence the distribution both of animals within patches and of animals among patches (Sisk et al. 1997, Morales 2002). However, even in the absence of animal behavioral responses to resources and habitat, apparently nonrandom distribution patterns such as density-independent aggregation may arise (Olson et al. 2000), and this argues for caution when inferring patterns of animal movement based on static patterns of animal distributions.

The interaction between behavior and landscape pattern may produce unexpected distributions of animals and is therefore of current concern to ecologists and wildlife managers studying animals that have the potential to affect ecosystems across broad spatial scales. In North America, for example, native ungulates can exert a strong influence on community structure (Waller and Alverson 1997, Opperman and Merenlender 2000, Ripple et al. 2001, Rooney et al. 2002, Beschta 2005) and ecosystem processes (Pastor et al. 1993, 1998, Frank and Groffman 1998, Ritchie et al. 1998). Therefore, understanding how ungulates respond to and create landscape pattern is key for effective landscape-level management (Adler et al. 2001, Manning et al. 2004).

Two broad questions that ecologists have asked about ungulate habitat use are how and at what spatial scales ungulates respond to their environment. These questions have been explored theoretically (e.g., Turner et al. 1994*b*, Adler et al. 2001) and empirically, especially in the context of resource use (e.g., Kie et al. 2002, Boyce et al. 2003, Anderson et al. 2005*a*, *b*). One disadvantage of these empirical analyses is that information associated with movement behavior is not considered (but see Preisler et al. 2004, Fortin et al. 2005*a*). However, global positioning system (GPS) technology has become more accessible and has thus made quantitative analyses of detailed movement a tractable option (Johnson et al. 2002, Morales et al. 2004, Fortin et al. 2005*a*, Frair et al. 2005).

One pattern observed in movement paths is an apparent "switching" between behaviors that produce fine- or broad-scale movement (e.g., foraging within or relocating between habitat patches). Because animals may respond to different factors while exhibiting each of these behaviors, analysis of such multiphasic paths is difficult. One way to consider these different behaviors is to identify the states statistically and to separately analyze those groups of path segments (Turchin 1998). Yet, very often interest lies in understanding the entire movement path. Characteristics of the path, such as fractal dimension or first passage time, can be considered in relation to characteristics of the home range (Frair et al. 2005, Nams 2005). Or, the switching between states can be explicitly modeled (Morales et al. 2004, Jonsen et al. 2005).

As an alternative to the switching models, we propose a conceptual framework that considers the length of each step as a function of two stochastic behavioral processes. One describes an animal's response to the landscape immediately surrounding it at a given time and the other describes the behavioral state of the animal at that time; the latter we describe by a temporally autocorrelated process that governs the animal's propensity to move. To model this system we chose a state–space approach, which has been used to track satellite and missile paths, community stability, and, recently, animal movement (Harvey 1989, Ives et al. 2003, Jonsen et al. 2003, 2005, Royer et al. 2005). This class of models can use time series of observed data to infer unobservable states by simultaneously modeling time-independent and time-dependent stochastic processes. One advantage of this framework is that it can include responses to the environment at both fine and broad scales while modeling the latent behavioral state in a continuous fashion.

Our goals in this paper are threefold. First we generate movement paths based on simple simulation models and demonstrate that linear state–space models can efficiently estimate the behavioral coefficients underlying animal movement paths. Second, we move into an empirical system and examine elk (*Cervus elaphus* L.) movement paths in Yellowstone National Park (USA) to uncover what landscape covariates affect short- and long-term movement rates. Finally, we determine if elk respond in a consistent fashion to landscape covariates and if variation in the strength of autocorrelation can be explained by variation in animal (e.g., age) and home range characteristics (e.g., mean patch size of grassland). Specifically, we were interested in how individual elk alter their movement in response to time of day, wolf (*Canis lupus* L.) density, landscape composition, forage availability, and topography, all factors found to be important in habitat selection by elk in previous research (Boyce et al. 2003, Forester 2005, Fortin et al. 2005*a*, Mao et al. 2005). We expected to see a strong crepuscular activity pattern, with more movement around dawn and dusk (Green and Bear

1990, Ager et al. 2003). Because of vigilance behavior and foraging requirements, we expected that the animals would move less in areas of high wolf density or plentiful forage (Zollner and Lima 2005, Moorcroft et al. 2006). Likewise, we expected the elk to move less in areas dominated by regenerating coniferous forest due to the combination of moderate forage abundance and plentiful cover in which to escape from predators (Bergman et al. 2006). Finally, the elk were expected to have high movement rates at high elevations and steeper slopes, because most ideal elk habitat is in lower elevation valley bottoms.

METHODS

State–space model formulation

We propose an approach to the state–space model that involves two components to describe how far an animal moves in a fixed period of time: (1) an immediate response to the local environment, and (2) an unmeasurable, or "hidden," behavioral state of movement propensity that is autocorrelated and also affected by previously experienced environmental conditions. The behavioral state represents a reduction of many internal states that might interact to affect movement, such as a quality assessment of recently visited areas (Dukas and Real 1993), gut fullness or satiation (Kareiva and Odell 1987, Wallin and Ekbom 1994, Jeschke and Tollrian 2005), or predation risk (Mitchell and Lima 2002, Zollner and Lima 2005). This formulation allows the behavior to be represented by a continuum, rather than a step function.

Although additional complexity can be added to this class of models by using the extended Kalman filter or Bayesian filters (Jonsen et al. 2003, 2005, Morales et al. 2004, Royer et al. 2005), many dynamics of interest can be approximated in the simple, linear case (Ives et al. 2003). We are interested primarily in how animals adjust their movement rates within seasonal home ranges in response to covariates, so we focus only on the step length within a given period of time. This step length represents an integration of all step lengths and turning angles realized at finer temporal scales. Coarser scale analyses can be accommodated by using subsets of the data.

The path of each individual elk is described by the linear distance between sequential, discrete locations collected at 5-h intervals and considered as a time series where $t = 1, 2, \ldots, T$. We assume that these time series can be approximated by a first-order, autocorrelated process (AR(1)) that is independent from turning angle (this assumption is tested in the empirical data). We further assume that observation error is small relative to the stochasticity in the data (this is justified by an estimated location error of <10 m, described in the *Empirical analyses* section). The observed data are described by a measurement equation:

$$y_t = x_t + \mathbf{b}\mathbf{A}_t + \varepsilon_t$$

where y_t is the realized step length (natural log-transformed) at time t; x_t is the autocorrelated behavioral state; $\mathbf{b}$ is a $1 \times p$ vector of coefficients that describe the linear relationship of y to the $p \times n$ matrix of covariates, $\mathbf{A}$; and ε represents a Gaussian error term with mean 0 and variance σ^2. The behavioral state is modeled as an AR(1) process that is also influenced by covariates and is described by the following process (or transition) equation:

$$x_t = rx_{t-1} + \mathbf{c}\mathbf{U}_{t-1} + \delta_t$$

where r represents the autocorrelation coefficient; $\mathbf{c}$ represents the process equation coefficients for the matrix of covariates ($\mathbf{U}$) associated with the autocorrelated process; and δ represents the Gaussian process error term that has mean 0 and variance ρ^2.

These two equations can be combined and expanded out for τ time steps:

$$y_t = \sum_{i=1}^{\tau} r^i \mathbf{c}\mathbf{U}_{t-1} + \sum_{i=0}^{\tau-1} r^i \delta_{t-1} + r^{\tau} x_{t-\tau} + \mathbf{b}\mathbf{A}_t + \varepsilon_t.$$

The first term on the right-hand side of this equation contains the environments experienced by the animal for the preceding τ time steps, with r serving as a "discount rate." When r is close to zero, the role of past environments in dictating the current movement of the animal diminishes rapidly with time; in effect, the animal has little memory of past behavioral states. In contrast, when r is large, the behavioral state changes slowly and past experiences are integrated into current movement patterns. The unexplained variability, δ_t, is similarly discounted by r. In general, the lower the variance in δ_t, the greater the importance of covariates in the process equation in explaining the movement pattern of the animal.

This model structure is powerful because it allows an interpretation of the approximate spatial scale at which an animal is responding to a particular covariate. Covariates in the process equation represent broad-scale effects contributing to the behavioral state, whereas those in the measurement equation represent fine-scale effects influencing immediate responses. The associated strength of autocorrelation for that animal determines how broad the scale of response is for all parameters in the process equation. Because covariates can simultaneously occur in both equations, multi-scale dynamics in the movement process can be detected.

We computed likelihood functions recursively using a Kalman filter (Harvey 1989, Künsch 2001), and parameters were estimated by minimizing the negative log-likelihood for a given model. Confidence intervals were developed via bootstrapping, using the fitted model to simulate 1000 response vectors (bootstrap data sets) based on the original covariate matrix. New maximum-likelihood estimates for the parameters were then calculated for each of the bootstrap data sets and 95% confidence intervals for model parameters were obtained

TABLE 1. The original parameters of the six models used to simulate movement paths.

Model	Original parameters			Mean site quality			Maximum displacement			Null : best
	r	b	c	Multi	Broad	Fine	Multi	Broad	Fine	ΔAIC
1	0.95	−2	0	0.29*	0.48*	0.45	81.55*	59.06*	133.069*	72
2	0.95	0	−0.2	0.21	0.42	0.23	65.88	56.76*	69.94	23
3	0.2	−2	0	0.28*	0.37	0.52*	34.90	29.35	41.40	122
4	0.2	0	−0.2	0.021	0.071	0.021	38.41	38.23	38.61	12
5	0	−2	0	0.28*	0.37	0.51*	34.91	29.15	40.011	122
6	0	0	−0.2	0.017	0.057	0.020	38.45	38.26	38.51	7

Notes: All models had the same process error, measurement error, and intercept (0.3, 0.7, and 0, respectively). Measurement and process coefficients for response to the landscape quality are represented by b and c, respectively. Mean site quality and maximum displacement represent the mean of these statistics calculated from 1000 simulated paths (350 time steps each) generated for each parameter set in each of the three landscapes (multi-, broad-, and fine-scale). Numbers followed by an asterisk (*) represent the highest values for that landscape (significant at $\alpha = 0.05$). The ΔAIC from the null model to the lowest AIC model is also reported.

from the simulated values. For the following analyses, only main effects are considered; however, interaction terms can be included in the model structure. All model selection used AIC-based stepwise selection. Covariates, when present in a model, were allowed to appear in the process equation, measurement equation, or both. Linearity and homoscedasticity assumptions were checked by visual inspection of residual plots. All state–space analyses were carried out in MATLAB (MathWorks 2004).

Simulation analyses

To confirm that the state–space model was capable of detecting patterns of animal movement, we simulated animal paths on artificial landscapes. We used a mixture of sine waves to generate three landscapes that represented resource variation at fine ($\sin(x) \cdot \sin(y)$), broad ($\sin(x/10) \cdot \sin(y/10)$), and multiple ($(\sin(x/10) \cdot \sin(y/10) + \sin(x) \cdot \sin(y))/2$) spatial scales. Elk movement paths were simulated on these landscapes according to each of six state–space movement models based on a wide range of parameter values (Table 1). Each model was used to generate 1000 paths of 350 log-normally distributed step lengths with random, uniform turning angles in each of the three landscapes. The starting location was fixed for all simulations and the initial random number seed was identical for each case within an iteration. The mean and standard deviation of experienced habitat quality as well as the maximum and final net displacement were calculated to demonstrate the scale-specific "payoff" of each model strategy.

To demonstrate the ability of the state–space model to detect movement parameters, we randomly selected one simulated path in the multi-scale landscape from each of the six parameter sets, and we then fit four state–space models to these data to determine the maximum-likelihood estimates of all parameter values. These models represent: null (no covariate), covariate in process equation, covariate in measurement equation, and covariate in both process and measurement equations. The model with the lowest AIC value was chosen for each set of simulated data, and 95% confidence intervals were calculated for the model parameters.

Empirical analyses

Study area.—The study was conducted during 2001–2004 in Yellowstone National Park (YNP). The park was established in 1872 and encompasses $\sim$ 9000 km^2 in the northwest corner of Wyoming and adjacent parts of Montana and Idaho (USA). Elevations in the park range from 1500 m to >3000 m (Houston 1982). The elk we studied were from the Northern Range herd, a population of ~12 000 animals, during the three years of this study, that migrates seasonally between a low-elevation winter range in the northern portion of YNP and a high-elevation summer range (Craighead et al. 1972, Houston 1982). The summer range of the northern herd extends onto the subalpine plateaus that cover much of Yellowstone and also into the higher elevations of the Lamar River drainage (Houston 1982). Vegetation on the subalpine plateaus is dominated by lodgepole pine (*Pinus contorta* Loudon var. *latifolia* Engelm.) forests of varying age, including extensive areas that burned in 1988 (Despain 1990, Turner et al. 1994*a*). Subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), whitebark pine (*Pinus albicaulis* Engelm.), and sagebrush (*Artemisia* spp.) grasslands are less common cover types, but are locally abundant (Despain 1990). At lower elevations, sagebrush grasslands are more common and are interspersed with coniferous forest, primarily lodgepole pine and Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco), aspen groves (*Populus tremuloides* Michx.), and riparian willow communities (*Salix* spp.).

Movement path analyses.—Sixteen cow elk were captured by helicopter net-gunning in the Northern Range of YNP during the winters of 2001, 2002, and 2003 (Cook et al. 2004*b*). Each animal was fitted with a Telonics GPS radio collar that collected locations at 5-h intervals. To estimate location error, we left three collars in fixed locations and found that the average mean and standard deviation of location errors were 6.15 m and 5.24 m, respectively (sample frequency = 5 h, 5 h, 2 h; $n =$ 125, 112, 814 samples; pooled SD = 6.46 m). Pregnancy and condition data for each animal were analyzed by Cook et al. (2004*b*). The elk were located by air every 12–14 d using Very High Frequency (VHF) beacons on the collars and approximate group size and presence of calves were recorded. The collars were recovered up to a year later after falling off in concordance with their program or following animal mortality. For this study, only the summer locations (15 June to 15 September) were used (Fig. 1).

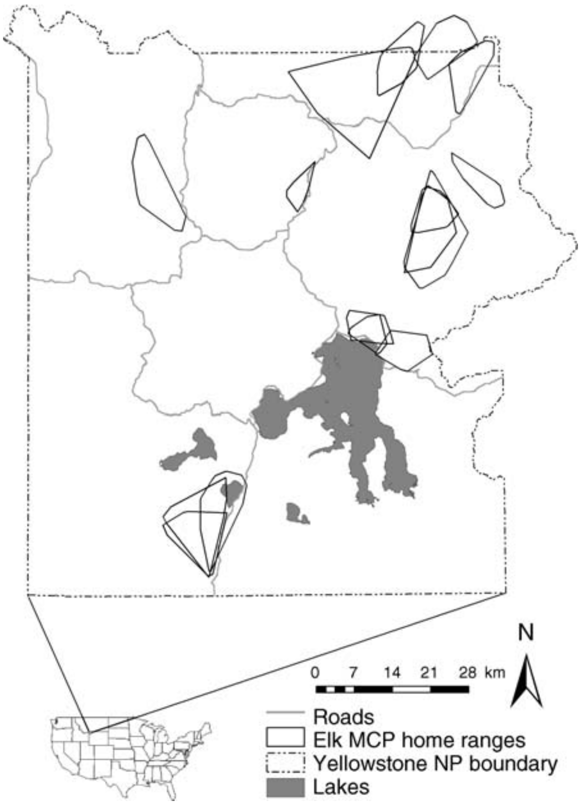

FIG. 1. The boundary of Yellowstone National Park Wyoming, USA, showing the summer minimum convex polygon (MCP) home ranges for each of the 16 elk studied.

To test our assumption that step lengths were independent from turning angle, the relationship between step length and turning angle was calculated using linear-angular versions of both correlation and regression techniques (Fisher 1993, Zar 1996). Several elk home ranges overlapped, but of those that overlapped during the same year, only three elk pairs had locations within 350 m. Because the number of close locations was relatively small (20%, 9%, and 0.07% of the temporally paired locations), these animals were assumed to be independent for the purposes of this analysis.

We examined histograms of movement distances to identify within-day movement patterns, and found that a wave function with a 12-h period would approximate the observed data. Thus we included time of day (t) as two covariates in the measurement equation:

$$\mathrm{SIN}_t = \sin(2\pi t/12)$$

and

$$\mathrm{COS}_t = \cos(2\pi t/12).$$

We then simulated 95% confidence intervals for all parameters. Because we expected a strong time-of-day effect on movement, we used "null-with-time" models as an additional null case for model comparisons to detect if there were also strong responses to landscape covariates.

In addition to the two temporal covariates, spatial covariates obtained from several sources were added to the analysis. Elevation was derived from a U.S. Geological Service (USGS) 10 × 10 m digital elevation model (DEM), from which slope and aspect were also calculated. The grain size of these three layers was coarsened to match the 28-m resolution of other data layers. Road and water feature polygons were supplied by the National Park Service (Yellowstone Center for Resources).

Landscape cover type was based on a classified Landsat image from August 2003. The image was classified using the iterative decision tree approach (Franklin et al. 2001) and was validated using >200 ground truth points, near infrared aerial photography (Kashian et al. 2004, Turner et al. 2004), and high-resolution aerial videography. The overall classification accuracy was greater than 80%. This classification yielded 12 vegetation classes that described canopy density for mature coniferous forest and moisture gradients for the open vegetation classes in addition to isolating an aspen/shrub complex and regenerating coniferous forest. For purposes of landscape analysis, we grouped these 12 cover types into six functional classes based on forage availability: (1) barren (rock, geothermal features, developed areas), (2) mature coniferous forest, (3) regenerating coniferous forest (sparse and dense regeneration), (4) low-forage grassland (dry grassland), (5) high-forage grassland (mesic, wet and alpine grasslands), and (6) high-forage shrubland (aspen/shrub complex and wet shrubland).

To estimate herbaceous forage biomass, we established 83 60-m transects at random locations within 3 km of a road and stratified by cover type. Of these transects, 34 were in the five original forest cover classes (3–10 transects per class) and 49 in the three open classes (3–24 transects per class). We sampled each transect four times from mid-June to late August in 2003 (two transects were not sampled during the last session due to fire closures). During each visit, we recorded the resting height of a calibrated 0.25-m^2 plastic disc on six plots along each transect. At each plot, we also used a double-sided wire frame to identify 40 point intercepts at which the functional group (nonvegetated, forb, grass, sedge, rush, woody vegetation) was identified to provide an estimate of percent cover. The biomass calibration was based on 214 plots that were clipped to ground level, separated by functional group, dried to constant mass at

40°C for 48 h, and then weighed ($R^2_{\text{adj}} = 0.83$, $P < 0.0001$, $N = 214$; see Vartha and Matches [1977] for a description of methods). Biomass peaked in mid-July, and there was no significant difference in biomass between the last two visits, based on a likelihood ratio test of repeated-measures linear mixed-effects models with and without visit ($P = 0.65$). Thus, the last two data points were pooled to estimate the mean peak forage biomass at each transect. There was no significant difference among the peak forage biomass estimates of coniferous forest cover types, nor was there an effect of topography, so the mean was used. In open areas and in the aspen–shrub complex, we found that the best model included only the normalized difference vegetative index (NDVI) and the compound topographic index (CTI, Gessler et al. 1995), which respectively represent the greenness of the vegetation and the relative wetness of the soil ($R^2_{\text{adj}} = 0.54$, $P < 0.001$, $N = 52$). For a more detailed description of these methods, see Forester (2005).

The relative density of wolves was calculated for each summer (June to October) using VHF location data collected by scientists from the Yellowstone Center for Resources (Smith et al. 2002, 2003, 2004). Abode software (Laver 2005) was used to calculate the least squares cross validation (LSCV), fixed smoothing factor (H) for the biweight kernel home ranges of each pack with at least 25 locations. This nonparametric method for estimating home-range utilization is described in detail by Seaman and Powell (1996) and Worton (1989). The mean H (5 km) was then used to calculate biweight kernel densities for each summer with all nonredundant locations, weighted by pack size. The resulting map represents a relative estimate of wolf density on the landscape.

Relative wolf density and distances to roads and forest/open edges were calculated at the beginning location of each move. Mean forage biomass and proportions of aspen/shrub complex, mature forest, and regenerating forest were calculated within a 175 m radius buffer around each point. This radius is one-half of the median 5-h step length and was chosen to represent local conditions while minimizing overlap among temporally adjacent locations. All covariates were examined prior to analysis, and all showed low pairwise correlations ($|\text{Pearson's } r| < 0.5$). Proportion data were square-root transformed and all other covariates were (natural log + 1)-transformed to improve the linearity of the relationship to step length.

A global model containing all covariates hypothesized to affect movement was fit to each animal's path. Variables were included in both the measurement and process equations, with the exception of time and distance covariates, which are implicitly correlated between steps and were thus included only in the measurement equation. The best model for each animal was identified using AIC-based stepwise selection and, for all cases, 95% confidence intervals were bootstrapped for each parameter estimate using the same method described in the *State–space model formulation* section. Finally, to determine the generality of each of the best models, 15 additional models were estimated for each animal using only the variables included in each of the other animals' best models. The increase in AIC from the best-model AIC (i.e., the lowest AIC) to other models is reported as ΔAIC. When considering these differences, we use the basic rules of thumb described by Burnham and Anderson (2002:70) where a difference of ΔAIC = 2 units is small, 4–7 is moderate, and >10 is extreme.

The area-weighted mean patch size, contagion (a measure of aggregation), and proportion of landscape were calculated for each functional class of cover type within the 100% minimum convex polygon (MCP) home range of each elk using FRAGSTATS (McGarigal et al. 2002). In post hoc analyses, differences in landscape metrics and other home range and animal characteristics (MCP area, mean wolf density, mean forage abundance, mean group size, and winter body fat percentage; see Tables 2 and 3) were compared among groups of animals (split by whether the 95% CI of r included zero), using permutation t tests in R (R Development Core Team 2005).

RESULTS

Simulation analyses

The simulated elk from both high-autocorrelation models, on average, used a larger area in all three landscapes (Table 1, Fig. 2). This difference in movement was associated with the highest mean site quality visited in the broad-scale landscape. However, the lower autocorrelation cases performed better in the fine-scale landscape, and there was no difference of mean site quality in the multi-scale landscape (Table 1). When the data from a randomly chosen set of simulations from the multi-scale landscape were fit using the state–space model, the "correct" model form was chosen by AIC for all six cases. The full model (i.e., the model with the landscape covariate in both the process and measurement equation) was consistently chosen second.

The state–space model was able to detect high autocorrelation well, with tight confidence intervals around the estimates (Fig. 3). For one of the low-autocorrelation cases, the confidence interval for r included zero, but both cases showed narrower confidence intervals than seen for the zero-autocorrelation models. When autocorrelation was low, the error estimates were less precise than in the high-autocorrelation cases. This was caused by the model attempting to fit the very flat likelihood space associated with data showing weak to no autocorrelation. In these cases, the absolute value of r could be large when nearly all of the variance was pushed to the measurement error, and small when process error was larger. In low-autocorrelation cases, the process and measurement errors enter the model in structurally the same way and consequently are impossible to separate; therefore, the total error

TABLE 2. Summary data on the condition of each elk during the winter of capture.

Elk individual	No. locations†	Year	Age (yr)	Mean group size	Pregnant‡	Body fat (%)
1	366	2002	6	28.4	1	15.03
2	270	2002	7	14.4	0	5.87
3	390	2002	3	4.9	1	13.64
4	350	2002	1	25.5	0	8.82
5	265	2002	11	2.0	1	5.87
6	310	2002	11	43.0	1	13.23
7	380	2001	14	23.4	1	4.97
8	380	2001	7	44.1	1	7.89
9	354	2001	8	7.8	1	3.99
10	339	2001	5	22.6	1	11.98
11	363	2001	11	12.6	1	10.6
12	344	2001	10	13.5	1	8.43
13	368	2001	7	8.6	0	6.21
14	378	2001	8	48.2	1	16.55
15	294	2001	11	10.8	1	12.66
16	342	2003	12	20.7	0	9.716

† The number of times that an animal was located.

‡ Status is designated as: 1, pregnant; 0, not pregnant.

estimate is of more interest. In all cases, the confidence interval around total error ($\rho + \sigma$) was within the range expected from the values used in the simulations. This leads to a caution and a useful diagnostic. For the case in which the true value of r is close to zero, the estimate of r may nonetheless be large due to the uncertainty of the estimate and a low estimate of the variance of the process error. However, a bootstrap simulation of the data will reveal large confidence limits for r and, hence, correctly identify a lack of significant difference from zero.

The landscape coefficients were estimated with tight confidence intervals. The very weak signal from the process-only model was estimated to be stronger than the actual value; however, the true value was included in the confidence intervals. The stronger signal associated with the measurement-only model was slightly underestimated, but was likewise included in the confidence intervals. The intercept was better fit as autocorrelation decreased and the mean became more predictable. Overall, this analysis indicates that the state–space model can extract movement parameters from a limited number of data points accurately.

Empirical analyses

The 5-h step lengths for all 16 elk followed an approximate negative exponential distribution (Appendix A: Fig. A1) and were thus natural log-transformed for all analyses. The set of turning angles for each animal deviated significantly from a uniform distribution (Kuiper's one-sample test of uniformity, $P < 0.01$), with the average circular mean by animal very close to zero ($\bar{\theta} = -1.2°$, $\mathrm{var}(\theta) = 0.54°$; Appendix A: Fig. A2). The linear-angular correlation between ln(step length)

TABLE 3. Home range statistics, calculated within the summer minimum convex polygon (MCP) for each animal.

Elk indiv.	MCP area (km^2)	CV elev.	Mean wolf density	Mean forage ($\mathrm{g/m}^2$)	Prop. forest	Prop. regen.	Prop. open	Prop. mesic-wet	AWMPS mesic-wet	Clumpy index mesic-wet
1	140	0.074	40	45.69	0.24	0.45	0.26	0.21	93.3	0.72
2	20	0.056	22	34.76	0.40	0.34	0.21	0.11	21.7	0.72
3	110	0.050	0	32.93	0.16	0.60	0.19	0.03	7.8	0.59
4	40	0.020	141	54.60	0.44	0.13	0.31	0.25	608.8	0.82
5	60	0.083	0	30.32	0.55	0.13	0.24	0.07	76.5	0.70
6	31	0.016	121	49.27	0.41	0.12	0.26	0.22	214.8	0.80
7	88	0.049	339	48.24	0.23	0.44	0.29	0.24	108.7	0.73
8	74	0.101	2	38.70	0.29	0.38	0.28	0.16	75.9	0.72
9	83	0.055	0	32.76	0.20	0.56	0.20	0.02	7.8	0.60
10	88	0.062	68	38.46	0.26	0.45	0.24	0.14	119.7	0.74
11	251	0.121	241	53.42	0.19	0.24	0.53	0.21	344.4	0.72
12	48	0.072	460	46.59	0.22	0.45	0.29	0.25	137.7	0.77
13	93	0.038	0	28.19	0.17	0.61	0.07	0.04	8.0	0.58
14	65	0.108	38	64.81	0.17	0.30	0.48	0.35	721.3	0.70
15	52	0.060	2	33.00	0.59	0.22	0.13	0.08	54.9	0.73
16	37	0.063	7	31.10	0.41	0.34	0.21	0.07	13.2	0.65

Notes: The area of the home range polygon (MCP), the coefficient of variation for elevation (CV elev.), the mean value of relative wolf density (unitless), the mean predicted forage biomass, and the proportions (Prop.) of mature forest, regenerating forest, open areas, and mesic-wet meadows. The configuration of the mesic-wet meadows is described by both the area-weighted mean patch size (AWMPS) and the clumpy index (McGarigal et al. 2002).

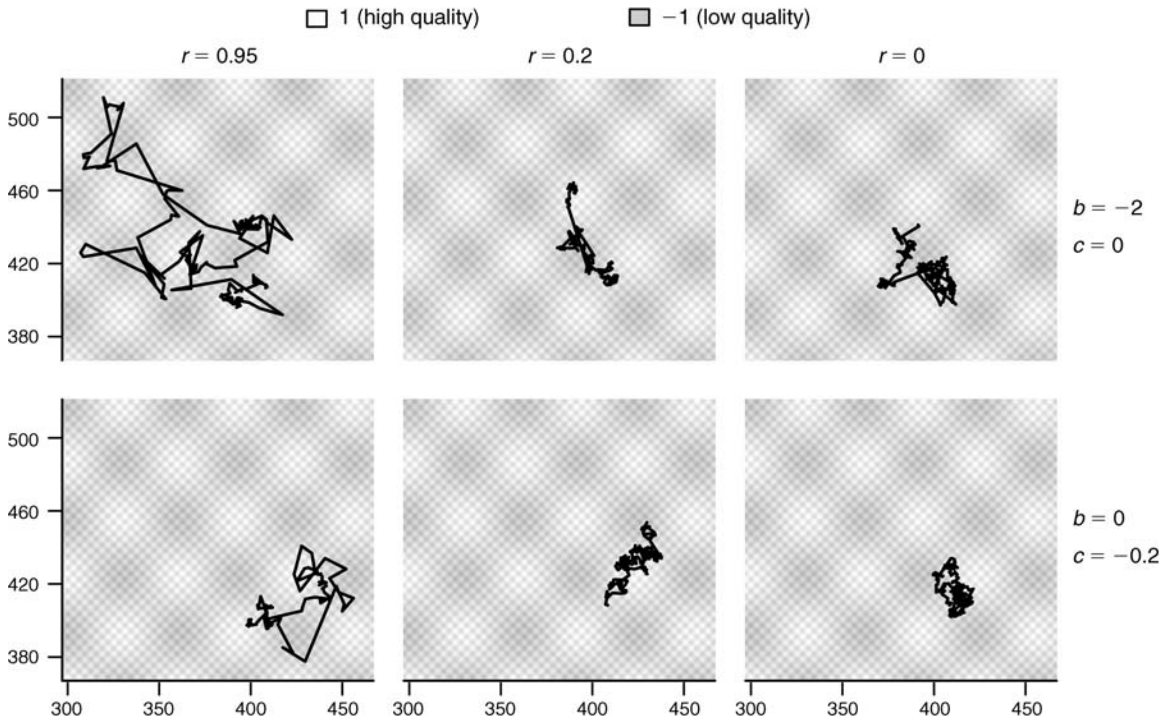

FIG. 2. Simulated elk paths (each consisting of 350 five-hour movements) based on three values of *r* (representing the strength of temporal autocorrelation in movement distance) and two sets of coefficients that determine how the landscape "quality" (ranging from −1 to 1) affects movement. The coefficients for the landscape variable in the measurement and process equations are represented by *b* and *c*, respectively. Turning angles were randomly generated from a circular uniform distribution. The spatial scale is defined in terms of arbitrarily sized pixels; each pixel can be thought of as having 100-m sides.

and turning angle was weakly significant for two elk (circular correlation coefficient = 0.16, 0.22; $P < 0.05$ by permutation correlation test, $N = 337$, 225 step-length–turning angle pairs for each individual). However, when ln(step length) was regressed against the cosine of turning angle (to indicate whether longer steps were associated with more forward movement), no relationship was found for any of the animals ($P > 0.05$, $R^2_{\mathrm{adj}} < 0.001$, $N = 202$–369).

In the time-only analysis, 12 of the animals had *r* values that were significantly greater than zero (based on simulated 95% CI; Fig. 4). Estimates for the two error terms varied by animal, except those with very tight confidence intervals around *r* ($N = 5$). However, the total error estimates were much more stable and indicate that the distribution of error between the two terms is less reliable when *r* cannot be precisely estimated. Very good estimates of both time variables show a clear and consistent crepuscular activity pattern, with longer moves beginning at 05:30 hours and 17:30 hours (Appendix B: Fig. B1). This model fit the data better than the null, intercept-only model for all animals (ΔAIC = 21–124; Table 4).

The best models, based on stepwise selection, fit the data moderately to extremely well compared to the corresponding time-only models (15 time-only models have $\Delta\mathrm{AIC} > 4$; Table 4). The magnitudes of the autocorrelation values were again mostly consistent with the time-only model; however, the confidence intervals of some of these estimates increased with the addition of covariates because the spatial autocorrelation in those variables accounted for some of the temporal autocorrelation between steps. The best model for 13 animals included elevation and/or slope in the process or measurement equations. Although the response to elevation was slightly mixed, the behavioral state (step distance) of six animals increased with greater elevation. Shorter movements were associated with steeper slopes in seven animals (Table 5). Nine of the 12 elk with established wolf packs present in their home ranges showed a response to wolf density in their best model. Of these, seven animals reduced movement in areas of high wolf density and two increased movement, although one animal in each group had a confidence interval that included zero. Six elk decreased their movement in areas of high forage availability, and another set of six decreased their movement in landscapes dominated by mature coniferous forest. The behavioral state of three animals increased with greater proportions of regenerating forest; however, another three animals responded by decreasing their immediate movement. Several animals increased their movement with distance to roads or forested edge. The

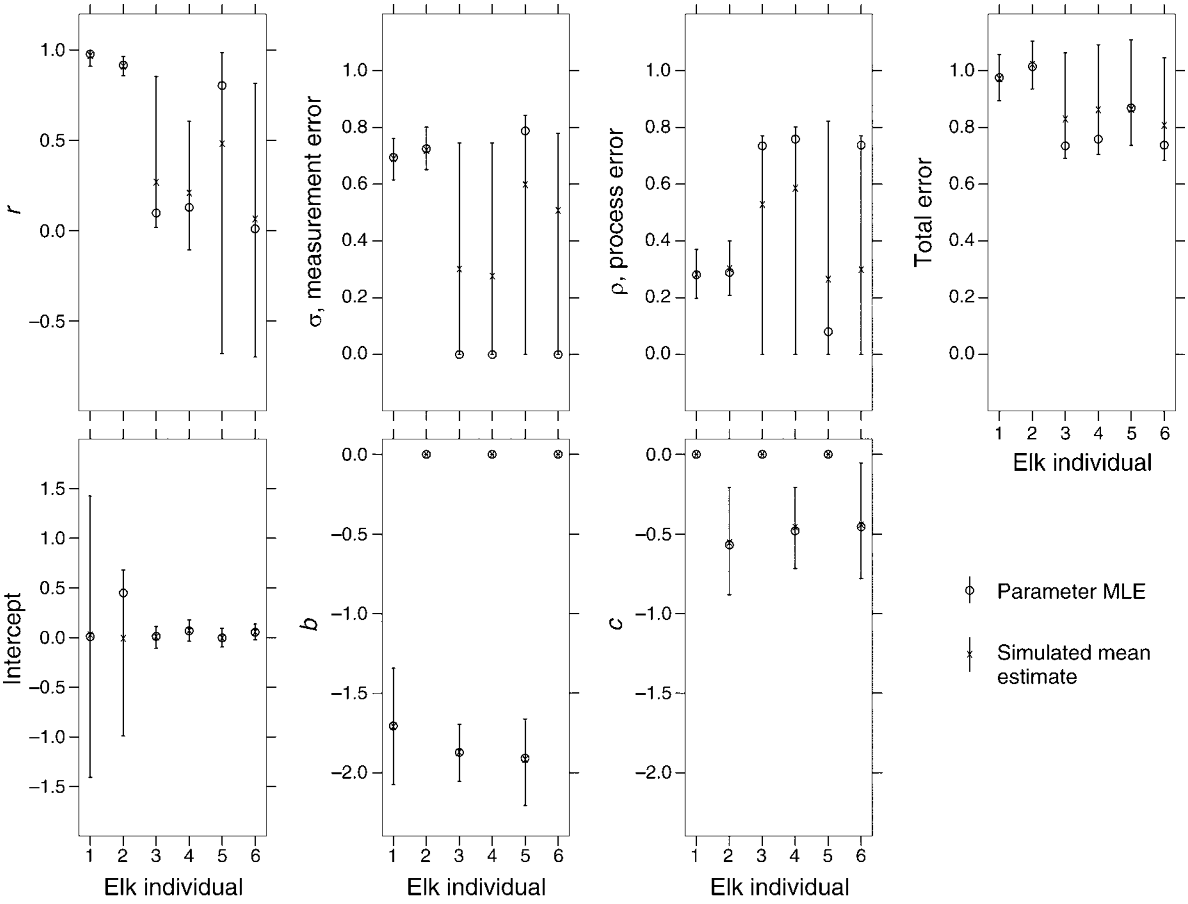

FIG. 3. Parameter estimates based on one 350-step path for each set of simulation parameters (represented by simulated elk 1–6; see Table 1); the parameter r is as defined in Fig. 2. The standard deviations for measurement and process error are represented by σ and ρ, respectively. Open circles show the parameter MLE (maximum-likelihood estimate); X symbols indicate the simulated mean estimate. The 95% confidence intervals shown (error bars) were simulated from the fitted values.

response to the proportion of the landscape in the aspen/shrub complex was mixed.

In general, the covariates that best fit one animal's movement poorly explained the movement patterns of most of the other 15 animals. On average, for any given model, only two of the 15 elk had ΔAIC values less than 7 (Table 6). When we attempted to relate differences in estimated r to home range characteristics, we found that the areas of the MCP home ranges for animals with strong autocorrelation in behavioral state were larger than those with weak autocorrelation (106 km^2 vs. 54 km^2; permutation t test of ln(area), $P = 0.04$, $N = 16$ individual elk). The other home range and elk-specific factors did not show a strong relationship to r ($P > 0.05$).

DISCUSSION

We demonstrated that the linear state–space model is an effective tool for describing animal movement paths and used it to gain insight into how elk respond to complex landscapes. Separating the response coefficients into process and measurement equations affords an intuitive, ecological interpretation of the final model. Overall, this method provides an accessible framework in which to approach the challenges of multi-scale analysis of animal movements, and can easily be implemented in MATLAB or other software such as Octave or R. Our results highlight the importance of considering individual variation, especially when animals are exposed to home ranges with very different compositions and arrangements of covariates.

In our simulation analyses, the simulated animals had no spatially explicit knowledge of the landscape. Turning angles were random, and move distances were affected only by the current landscape and the behavioral state (which, when $r > 0$, included information about previously visited landscapes). However, in both the simulation and empirical analyses, the landscape area used was directly related to the autocorrelation coefficient (Fig. 2, Tables 1–3) and no other home range metrics were found to explain this relationship in the empirical data. The result from the simulated data suggests that intraspecific variation in home range size may be related not only to local, exogenous landscape

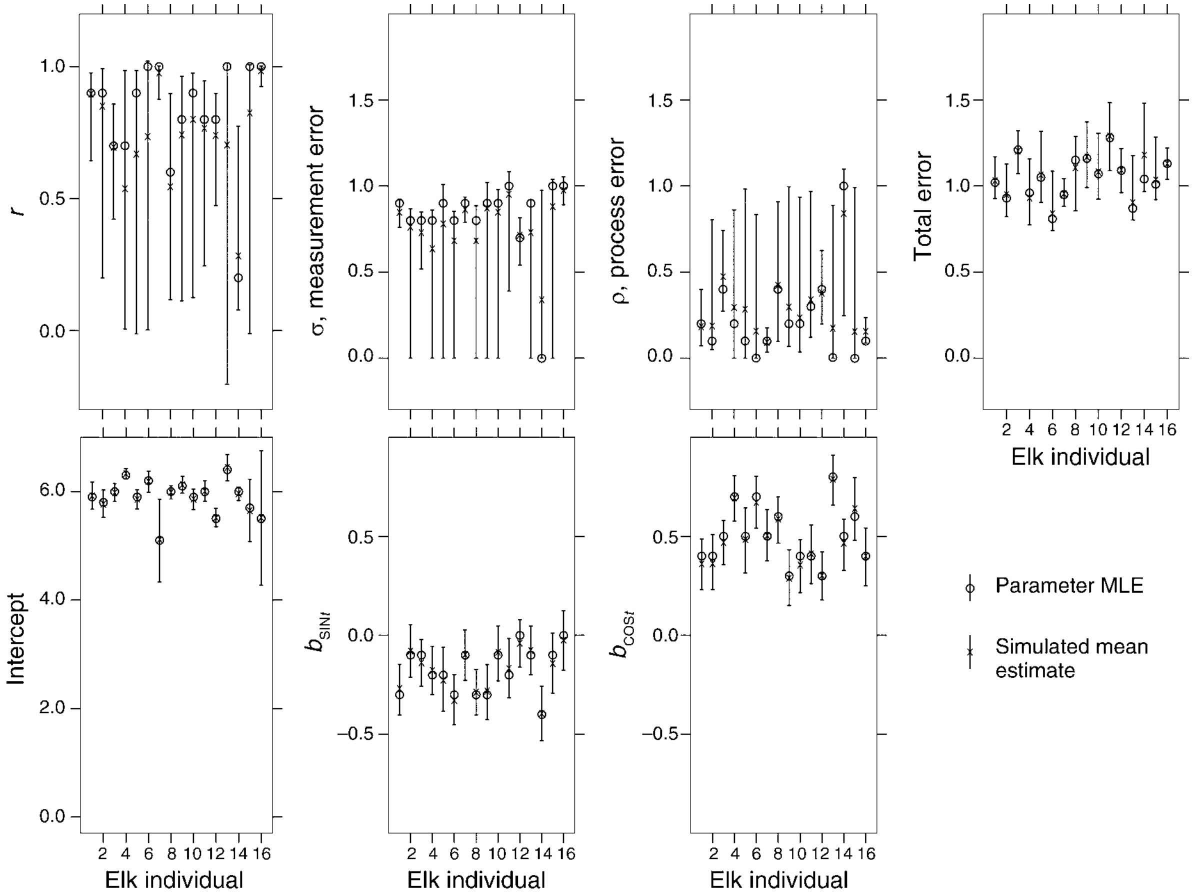

FIG. 4. The parameter estimates (open circles, parameter MLE [maximum-likelihood estimate]; X symbols represent simulated mean estimates) for the time-only model with simulated 95% confidence intervals (error bars). The coefficients for the sine and cosine of time ($b_{\mathrm{SIN}t}$, $b_{\mathrm{COS}t}$) correspond to Universal Time and represent activity peaks at approximately 05:30 and 17:30 hours, local time. Other parameters are as defined in Fig. 3.

TABLE 4. Best-model estimates of *r*, process error, measurement error, and intercept for each elk (individuals 1–16).

Elk	ΔAIC, by model type						
	Null	Time-only	Full	*r*	Process error	Measurement error	Intercept
1	60	19	20	0.99*	9.3×10^{-5}	0.89	5.4*
2	33	11	22	0.84	0.14	0.79	5.4*
3	68	13	21	0.73*	0.32	0.82	6.6*
4	119	9	20	−0.81	0.16	0.77	5.3*
5	40	4	16	0.05	0.94	6.8×10^{-7}	−5.8
6	109	13	17	−0.63	0.23	0.74	6.2*
7	80	24	7	0.92*	0.08	0.85	3.9*
8	95	7	24	0.65*	0.27	0.82	6.7*
9	32	5	18	0.90	0.13	0.96	4.8*
10	46	24	10	0.90	0.10	0.89	51.75*
11	44	15	17	0.79*	0.26	0.98	9.52*
12	45	24	25	1.00	3.7×10^{-6}	0.84	−5.52*
13	143	19	7	1.01*	6.6×10^{-8}	0.84	6.1*
14	76	15	22	0.95	7.5×10^{-4}	1.00	22.1
15	64	10	28	0.99*	4.9×10^{-8}	0.97	5.6*
16	24	1	32	1.00*	0.16	0.96	6.3*

Notes: The ΔAIC values compare the full, null with time, and null models to the corresponding best model. The *r* and intercept values with an asterisk (*) have 95% CIs that do not overlap zero. A "significant" *r* associated with a low process error indicates that the autocorrelation is well described by the covariates in the process equation.

TABLE 5. Summary of the best-model fits showing the distribution of coefficient signs, across 16 individual elk, for each variable in the process (broad-scale) and measurement (fine-scale) equations (the number of fits with 95% confidence intervals that do not overlap zero are in parentheses).

								Distance			
Sign	Elevation	Slope	Wolf density	Mean forage	Prop. forest	Prop. regen.	Prop. aspen	To edge	To road	SIN_t	COS_t
Process equation											
+	6 (3)	0	1 (0)	1 (1)	0	3 (2)	0				
0	7	12	11	11	11	13	15				
−	3 (0)	4 (2)	4 (3)	4 (1)	5 (3)	0	1 (0)				
Measurement equation											
+	1 (0)	0	2 (1)	1 (0)	2 (0)	0	2 (1)	4 (2)	2 (2)	0	16 (16)
0	13	12	10	12	13	13	12	11	13	0	0
−	2 (1)	4 (2)	4 (3)	3 (1)	1 (0)	3 (3)	2 (0)	1 (1)	1 (1)	16 (8)	0
Total no. elk											
	11	7	9	8	8	6	5	5	3	16	16

Notes: The total number of elk represents the number of individual models that include a variable in at least one equation. Entries show the number of elk for which correlations are positive, negative, or nonexistent; in parentheses are the number of elk showing significant correlations. SIN_t and COS_t refer to the sine and cosine transformations of $(2\pi t/12)$, where t represents the time of day in decimal hours. Collectively, these variables describe within-day cyclic activity patterns. Distance and time variables are omitted from the process equation because they are implicitly correlated between steps. For more detailed information, including coefficient estimates and 95% confidence intervals, see Appendix C.

factors (e.g., Kie et al. 2002, Anderson et al. 2005*a*), but also to the endogenous tendency of animals to move in an autocorrelated fashion. All simulation cases produced movement paths that, on average, stayed in areas that were above the mean quality level of the landscape. This indicates that strong autocorrelation in behavior may not inherently confer a benefit in terms of site quality visited, but it allows an animal to visit more patches distributed across a larger area.

The long-term implications of the composition and use of home range resources by elk are difficult to quantify. Elk do make foraging decisions based on available energy content (Wilmshurst et al. 1995), and relatively small reductions in the quality of summer and autumn diet will decrease the probability of harsh winter survival of cows and calves in addition to decreasing conception rates (Cook et al. 2004*a*). Because even small energetic demands from travel are predicted to influence foraging decisions (WallisDeVries 1996, Moen et al. 1998), the composition and use of the summer home range is a critical factor affecting both individual survival and population-level dynamics. However, one of our most surprising results was that, despite strong evidence of summer habitat selection by elk in YNP (Boyce et al. 2003, Forester 2005), there was not a consistent movement response by elk to the important habitats and other covariates (Table 5). The fact that habitat selection occurs without animals reducing their five-hour movement rates in preferred areas suggests that animals may respond individually to immediate

TABLE 6. Each row represents the increase in AIC from the best-model fit for that elk when those data are fit to a model selected for another individual; the final row is the number of data sets for which a given animal's model produced ΔAIC values < 7.

	Proposed model for individual elk																
Elk	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	ΔAIC < 7
1	0	17.5	22.6	15.0	16.5	26.7	13.0	23.3	18.7	22.5	25.4	26.9	19.3	18.5	20.1	14.3	0
2	10.6	0	13.2	10.5	10.9	18.1	14.7	19.0	7.2	12.7	8.5	13.6	10.4	13.7	10.4	9.5	0
3	18.5	6.7	0	16.9	6.3	15.3	6.3	15.6	17.2	14.1	11.6	20.0	11.8	18.6	17.5	17.2	3
4	8.8	15.5	13.9	0	12.4	14.2	10.5	7.5	10.8	14.1	14.6	12.2	14.7	17.2	2.9	9.4	1
5	2.2	9.8	7.1	6.1	0	6.5	5.2	7.1	7.5	6.4	9.5	8.2	9.6	6.5	3.8	6.1	8
6	16.2	32.6	7.7	14.5	28.1	0	21.4	14.0	12.6	20.3	19.3	14.8	9.6	23.6	10.6	14.7	0
7	6.6	13.7	20.2	27.0	20.8	20.3	0	26.0	23.6	23.1	23.6	14.0	18.9	23.6	18.8	24.1	1
8	12.1	13.9	10.4	11.4	9.4	7.4	7.9	0	8.2	9.6	13.6	11.6	13.2	9.7	9.5	8.1	0
9	5.6	5.3	5.9	9.5	5.9	6.4	7.0	4.3	0	5.7	6.2	7.8	2.4	3.1	2.4	5.9	12
10	25.6	16.8	21.5	27.5	12.5	16.5	25.1	30.0	26.0	0	19.5	12.3	25.1	8.7	27.3	25.7	0
11	17.8	11.8	6.8	16.0	18.8	13.2	19.3	19.1	16.1	16.5	0	21.2	4.2	18.2	17.8	14.2	2
12	22.5	20.5	28.1	26.3	27.9	25.9	30.0	27.3	23.5	12.8	21.2	0	26.7	23.3	25.2	25.9	0
13	10.6	36.1	10.4	11.5	35.1	41.9	39.6	16.7	19.4	30.3	18.4	17.4	0	37.2	21.9	12.7	0
14	14.5	16.9	20.5	17.2	21.8	24.4	20.0	16.7	18.1	17.8	13.7	20.4	19.2	0	18.0	15.2	0
15	13.2	12.3	15.8	12.2	8.8	19.1	7.2	10.4	12.6	11.1	9.5	8.0	16.4	28.7	0	13.2	0
16	13.8	5.4	4.7	4.3	7.5	14.2	11.4	5.5	4.7	5.0	11.9	8.8	7.1	15.5	4.0	0	7
ΔAIC < 7	3	3	3	2	2	2	2	2	1	3	1	0	2	2	4	2	

landscapes, but frequently move between preferred areas within their home range.

In Yellowstone, most of the preferred grassland habitat is concentrated in a few large patches, with many small patches distributed throughout a matrix of coniferous forest with relatively little forage biomass. Elk face the decision of frequently traveling among patches or foraging extensively in a relatively small area and accepting increased predation risk from wolves and other predators. In heterogeneous landscapes, this trade-off can represent a "shell game" (sensu Mitchell and Lima 2002) between predators and prey, with the efficacy of the predator strongly affecting the optimal movement strategy of the prey.

Dispersing animals should slow down in high-risk areas or in low-risk areas with plentiful food in order to maintain vigilance and maximize energy reserves (Zollner and Lima 2005). Ten of our animals demonstrated this behavior, although they were not dispersing, by slowing down (i.e., shorter step lengths) in areas of high wolf density and/or high forage biomass. Still, the strongest influence on movement for all animals was time of day, with long moves during the crepuscular hours and much shorter moves during the ruminating/-resting times (12:00, 23:00 hours). In a study of elk movement in the Starkey Experimental Forest and Range, Oregon, Kie et al. (2005) also found that hourly movement distance was strongly affected by time of day, although they found only weak relationships between movement and landscape characteristics. This strong effect of daily movement patterns, independent of spatial covariates, illustrates the importance of using a null-with-time model as the baseline for comparisons with models that are more parameter rich.

Ungulates have been shown to respond to landscapes in a hierarchical fashion (Senft et al. 1987, Rettie and Messier 2000, Johnson et al. 2002, Boyce et al. 2003, Anderson et al. 2005*b*). In this study we were not examining the extreme scales of response (large-scale home range location or micro-scale bite selection), but rather the broad-to-fine scales of movement within home ranges. We found that while some patterns in response to landscape covariates appeared, the spatial scale at which individual animals responded to those covariates differed.

Rettie and Messier (2000) suggested that caribou make broad-scale habitat selection decisions based on factors such as predation risk that have a high probability of affecting individual survival, and then fine-scale decisions on more long-term problems such as optimizing energy balance. If elk were responding in this fashion, those with home ranges established in areas of highest wolf density would be expected to respond to that density in the process equation (i.e., a broad-scale response). The 16 elk that we studied established home ranges across a wide gradient of wolf density; however, there was no clear distinction of model structure between elk in areas of low vs. high wolf density. This lack of a consistent response to wolf density may simply be a result of transient or fine-scale behavioral responses to recent wolf presence (Creel et al. 2005, Creel and Winnie 2005) instead of consistent responses to broad-scale wolf density. Likewise, the inter-animal variation in responses to other covariates may be partially due to the five-hour time step missing important, fine-scale behaviors that do not scale up effectively. These hypotheses may be tested as higher resolution GPS and GIS data become available.

We have demonstrated that using the process equation of a linear state–space model to describe the behavioral state of an animal is a useful technique for decomposing animal movement paths into immediate and broad-scale responses. Our simulation models estimated expected parameters with high precision and accuracy, and the time-only models were consistent across animals (Appendix A: Fig. A2, Table 5). When other covariates were added to the elk model, we discovered inconsistent responses to landscape features. This variation was not explained by characteristics of individual home ranges, so the large amount of unexplained dissimilarity in model fits indicates that elk have highly individual responses to the landscape. The observed individuality is probably composed of inter-animal behavioral differences as well as undetected variation in the distribution and relative quality of resources (Bélisle 2005). The best models for half of our animals included strong autocorrelation terms for the behavioral state, which suggests that some elk may respond more strongly to internal rather than external drivers. The modeling of the behavioral state helped to explain some of the complex individual behavior of elk, as it has in other organisms (Morales and Ellner 2002). These insights may be particularly relevant to the application of other, more mechanistic and spatially explicit methods such as two-dimensional movement models and mechanistic home range models (Turner et al. 1993, Moorcroft et al. 1999, 2006, Lewis and Moorcroft 2001, Zollner and Lima 2005). Furthermore, this study suggests that the strong patterns of habitat selection described in other studies are not created by a reduction of movement in those habitats, but by frequent visits to preferred areas.

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APPENDIX A

Two figures displaying the empirical distributions, pooled from all elk, of five-hour step lengths and turning angles (*Ecological Archives* M077-009-A1).

APPENDIX B

A figure showing the fitted effect of time on the five-hour step length of individual elk (*Ecological Archives* M077-009-A2).

APPENDIX C

Tables showing the model coefficients, with simulated 95% confidence intervals, for individual elk (*Ecological Archives* M077-009-A3).