Ecological Modelling 273 (2014) 242–250

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

The Brownian bridge synoptic model of habitat selection and space use for animals using GPS telemetry data

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ARTICLE INFO

Article history:
Received 17 June 2013
Received in revised form 4 November 2013
Accepted 8 November 2013
Available online 8 December 2013

Keywords:
Brownian bridge
GPS telemetry
Habitat selection
Oreamnos americanus
Synoptic model

ABSTRACT

The growing application of GPS telemetry in wildlife studies created need for analytical methods to meet both practical and theoretical concerns when conducting analyses of habitat or resource selection. We devised a new analysis approach of individual-based movement models for estimation of resource selection based on probability of use. We merged the Brownian bridge model of space use with the synoptic model of habitat selection to describe and estimate patterns of habitat selection from GPS telemetry data. In doing so, our approach implicitly defines availability based on movement data when conducting analysis of GPS telemetry data. To do so, we employed a step-by-step approach, based on sequential triplets of observations of the animals' movements. Availability was portrayed as a circular normal distribution at every middle GPS location, based on the existing Brownian bridge model of space use. This middle observation within the sequential triplet also reflected habitat selection, estimated by maximum likelihoods, based on the deviation from otherwise random movement between the first and third observations. This approach allowed each triplet across time to be treated as independent, identically distributed observations when estimating habitat selection. To demonstrate the utility of the model, we analyzed GPS location data collected from free-ranging mountain goats (*Oreamnos americanus*) in the Cascade Mountains of the western United States to evaluate patterns of habitat selection while foraging during late spring and early summer. Slope of the terrain was the primary factor influencing resource selection by mountain goats in our study, with females selecting steeper areas closer to escape terrain than males. Finally, we derived a resource selection function applicable over a broad geographic extent to evaluate sites for potential release of mountain goats to augment the population in Washington, which has declined over the last 50 years.

1. Introduction

Use of telemetry to evaluate ecological relationships is a common approach in science and modeling. The growing application of GPS telemetry, in particular, has resulted in increased volumes of data that offer a means to rapidly advance understanding and predicting the habitats of wildlife. Refinements in GPS and associated technologies allow for nearly continuous collection of animal locations, but although use of GPS telemetry is increasingly common, techniques for data analysis and inference have lagged behind technological advances. To capitalize on the information collected and contained in growing databases accrued via GPS technology, new approaches for analysis and inference are needed (Beyer et al., 2010). A growing body of theory regarding animal movements and new applications for analysis of GPS telemetry data, have been forwarded and are becoming more accessible to researchers and practitioners alike (Bullard, 1999; Marzluff et al., 2004; Horne et al., 2007; Dalziel et al., 2008; Horne et al., 2008; Hengl et al., 2008; Johnson et al., 2008; Kneib et al., 2011). To enhance our understanding of factors shaping resource selection to expand upon current modeling approaches, we developed an individual-based movement model for estimating resource selection based on probabilities of space use at a fine spatiotemporal-scale, the Brownian bridge synoptic model (BBSM).

From a statistical perspective, recent advances in GPS telemetry have resulted in increasingly correlated data. Accounting for the lack of independence among locations or psuedoreplication

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http://dx.doi.org/10.1016/j.ecolmodel.2013.11.008

(Hurlbert, 1984; Millspaugh et al., 1998; Magnusson, 1999) has pushed the limits of resource selection analysis (Swihart and Slade, 1985; Manly et al., 2002). We agree with Johnson et al. (2008) and Fieberg et al. (2010) that a solution to this challenge lies in incorporating the serial correlation into the resource selection analysis based on spatial and temporal data. To meet this need, we merged the Brownian bridge movement model (BBMM; Horne et al., 2007) with the synoptic model of space use (Horne et al., 2008) in program (R Development Core Team, 2012). This approach directly incorporated serial dependency into an evaluation of habitat selection and space use under the general framework of analysis of telemetry data proposed by Johnson et al. (2008). Additionally, this approach explicitly accounted for and provided an ecological rationale for defining resource availability, which is a primary challenge for analyses of resource selection (Manly et al., 2002; Keating and Cherry, 2004; Johnson et al., 2006).

Here we detail the methodological development of the BBSM and present an example using GPS telemetry data from mountain goats (*Oreamnos americanus*) in the Cascades mountain range of Washington State, USA. We used the BBSM to model resource selection based simultaneously on habitat and space use at approximately a third (within home range) to fourth (feeding site) order of selection (Johnson, 1980). Specifically, this example was designed to evaluate the importance of the distribution and abundance of forage resources, as derived from LandSat 5 TM data (Wells et al., 2012), to mountain goats during late spring through early summer. The results were used to evaluate potential release sites for mountain goat populations that have suffered substantial population declines.

2. The Brownian bridge synoptic movement model

The conceptual framework that describes the BBSM is fairly straightforward. As the model is under the general framework of Johnson et al. (2008), we adopted the same notation to illustrate the mechanics of our approach to estimate resource selection based on probability of space use. Johnson et al.'s (2008; Eq. (1)) general framework describes resource selection as a distribution $f_u(\boldsymbol{x})$, at a given point in space $\boldsymbol{s}$ and time $\boldsymbol{t}$, for an overall time period of interest H_t, as

$$f_u(\boldsymbol{x}) = K^{-1} w(\boldsymbol{x}) f_a(\boldsymbol{x}) \tag{1}$$

in which $\boldsymbol{x}(\boldsymbol{s})$ is a vector of covariates describing a resource ($\boldsymbol{x}$) or a "suite of resources". The values of ($\boldsymbol{x}$) may take the form of either continuous or categorical variables, typically as measures of topography or vegetation. The distribution of used resources $f_u(\boldsymbol{x})$ is based on the availability of the resource $f_a(\boldsymbol{x})$ as modified by a weighting function $w(\boldsymbol{x})$, where

$$w(\boldsymbol{x}) = \exp(\beta_0 + \beta_1 x_1 + \cdots + \beta_p x_p) \tag{2}$$

is typically a resource selection function (RSF; Manly et al., 2002) in which β indicates strength of selection for or against a particular resource. With the addition of habitat parameters or covariates, the BBSM estimates the resource selection function $w(\boldsymbol{x})$ at $\boldsymbol{s}_t$ over all H_t. The time period of interest, H_t, can be characterized by differing behavioral states as illustrated by Johnson et al. (2008) or simply as a range of dates or movements (dispersal, seasonal, resting, foraging, or migrating). The normalizing constant K is simply the integral of $w(\boldsymbol{x})f_a(\boldsymbol{x})$, or the total area of availability, which standardizes the resultant distribution to an area of 1. Furthermore, the spatial ($\boldsymbol{s}$) and temporal ($\boldsymbol{t}$) components, or timeframe, of the model can be constrained by the history of observations $H_{t-1} = \{s_1, \ldots, s_{t-1}\}$ to derive Eq. (2) of Johnson et al. (2008). The distributions are now reformulated from $f_u(\boldsymbol{x})$ to $g_u(\boldsymbol{x})$ and $f_a(\boldsymbol{x})$ to $g_a(\boldsymbol{x})$ where $g_u(\boldsymbol{x})$ and $g_a(\boldsymbol{x})$ are conditioned upon the "history of used locations during the study" (Johnson et al., 2008). Correspondingly, this adjusts

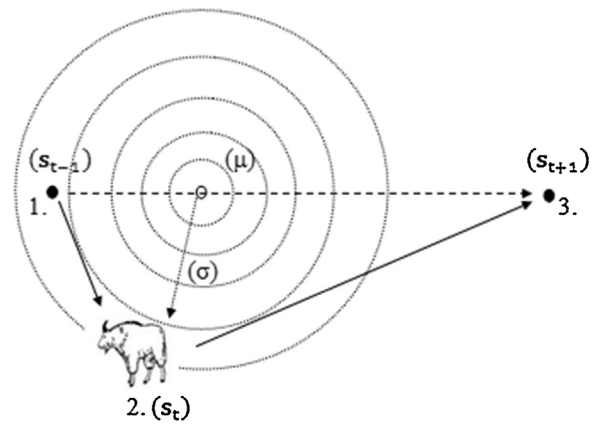

Fig. 1. Conceptual diagram of a single triplet of animal locations ($h_{t\pm1}$) indicating the relative position of the center (μ) of the circular normal probability distribution function used to assign probabilities to the distribution of available habitat and for calculation of the normalizing constant in the Brownian bridge synoptic model.

the use distribution to $g_u(\boldsymbol{s}_t|H_{t-1})$ and the availability function to $g_a(\boldsymbol{s}_t|H_{t-1})$, which, again, are probability densities are conditioned on the history of preceding observations. This modifies Eq. (1) to

$$g_u(\boldsymbol{s}_t|H_{t-1}) = K_t^{-1} w(\boldsymbol{s}_t|H_{t-1}) ga(\boldsymbol{s}_t|H_{t-1}), \tag{3}$$

indicating that the distribution of use is based on the history of all observations at point $\boldsymbol{s}_t$. As per the suggestion of Johnson et al. (2008), we temporally and spatially realize availability, $g_a(\boldsymbol{s}_t|H_{t-1})$, by shifting the frame of analysis to a history of observations defined by triplets of observations $H_{t\pm1} = \{\boldsymbol{s}_{t-1}, \boldsymbol{s}_t, \boldsymbol{s}_{t+1}\}$. This adjusts the distribution of use to $g_u = (\boldsymbol{s}_t|H_{t\pm1})$ with the corresponding availability as $g_a = (\boldsymbol{s}_t|H_{t\pm1})$. In other words, for the triplet $H_{t\pm1}$ the point at $\boldsymbol{s}_t$ is dependent on both the previous location and the following location based on the BBMM (Horne et al., 2007), thereby temporally and spatially realizing g_a and g_u. This decreases the spatial scale of the model and modifies Eq. (3) to

$$g_u(\boldsymbol{s}_t|H_{t\pm1}) = K_t^{-1} w(\boldsymbol{s}_t|H_{t\pm1}) ga(\boldsymbol{s}_1|H_{t\pm1}) \tag{4}$$

To characterize the initial, or null, distribution of use, which is the probability of space use in the absence of habitat resources, we estimated the spatial variance (σ^2) under the BBMM over all triplets as $\boldsymbol{s}_t$. The Brownian bridge characterizes the spatial variance for the null model of the BBSM. Thus, the null model for the BBSM is a circular normal distribution

$$f(\boldsymbol{s}_t; \mu, \sigma^2) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(s_t-\mu)^2}{2\sigma^2}} \tag{5}$$

centered at (μ) between point $\boldsymbol{s}_{t-1}$ and point $\boldsymbol{s}_{t+1}$ proportionally shifted in time to where point $\boldsymbol{s}_t$ would have occurred if the animal had taken a conditional random walk from the points $\boldsymbol{s}_{t-1}$ to the point $\boldsymbol{s}_{t+1}$ (Fig. 1). The probability of use becomes the distribution of availability, $g_a(\boldsymbol{s}_t|H_{t\pm1})$, and is estimated and defined at the point $\boldsymbol{s}_t$ for each triplet of observations. The required independence for maximum likelihood estimation is achieved under the assumption that point $\mathbf{s}_t$ is conditionally independent of other triplets from the underlying distribution of probabilities that define the availability distribution.

To solve the BBSM and derive estimates for β, or strength of selection, we estimate the log-likelihood as

$$L(\theta; H_t) = g_u(\boldsymbol{s}_t) \prod_{t=0}^{T} gu(\boldsymbol{s}_t|H_{t\pm1}), \tag{6}$$

similarly to Eq. (4) in Johnson et al. (2008) and Eq. (3) in Horne et al. (2008) where θ represents parameter vectors for both $w(\boldsymbol{x})$

and $f_a(\boldsymbol{x})$. Like the synoptic model (Horne et al., 2008), the BBSM also allows habitat covariates, $\boldsymbol{x}$, to vary temporally. This allows availability to change over time, for example snow depth, relaxing a basic assumption of Manly et al. (2002) when estimating a resource selection function. The normalizing constant, K, is based on the same circular normal distribution used to define availability at $\boldsymbol{s}_t$. The normalizing constant includes the 99th percentile of the volume of the distribution centered on the point (μ) along the straight line connecting $\boldsymbol{s}_{t-1}$ and $\boldsymbol{s}_{t+1}$, again proportionally shifted by the observed time intervals before and after $\boldsymbol{s}_t$. We assume independent and identically distributed sampling of point $\boldsymbol{s}_t$ for all triplets H_{t+1} when estimating the likelihood. This approach estimates and habitat selection based on probabilistic estimates of space use and availability under the general framework proposed by Johnson et al. (2008) and Horne et al. (2008).Example: habitat selection by mountain goats

To demonstrate the application of the BBSM modeling technique, we evaluated GPS telemetry data and activity sensor data from mountain goats ($n = 41$) in the Cascade mountain range of Washington, USA (Fig. 2). We collected data during 2003 through 2008 using Vectronic-Aerospace GPS telemetry collars (GPS plus collar v6, Vectronic-Aerospace GmbH, Berlin, Germany). Collars were programmed to record a location every 3 h for at least 2 years (Rice and Hall, 2007), a suitable scale for identification of habitat selection in relation to foraging (Owen-Smith et al., 2010). We used the BBSM to estimate the strength of selection for particular forage resources and projected the estimates of habitat selection across the landscape for management decisions. To assess the location accuracy of the collars, a necessary component of the BBSM, we benchmarked collars across a range of conditions in the study area (Wells et al., 2010) and determined the 95% circular error probable (Lewis et al., 2007).

Mountain goat populations in Washington State have experienced a long term population decline over the last 40–50 years, resulting in heavy restriction of legal harvest in the mid-1990s (Rice and Gay, 2010). Since the restriction, notable increases in abundance of mountain goats have occurred in some regions of the Washington Cascades, typically in areas with the largest remnant populations (Rice, 2006). However, other populations have not increased, even where historical evidence suggests greater numbers of mountain goats existed. Consequently, there is interest in conducting population augmentation via translocation to assist in recovery and re-establishment of local populations in the Washington Cascades.

Typically, mountain goats, as well as other mountain ungulates and the Caprinae as a whole, forage on a wide range of plant species (Hamel and Côté, 2007). To understand the influence of vegetation communities on patterns of habitat selection by mountain goats in historically occupied ranges, we tested and evaluated multiple hypotheses regarding selection of forage resources during spring green up. We constrained our analysis to time periods when mountain goats were active during June and July, because late spring and early summer are critical time periods for the growth and survival of mountain goats (Robbins, 1993). We also wanted to assess whether previously determined release sites for translocation and population augmentation (Fig. 3) contained suitable foraging habitat for mountain goats during this nutritionally critical time period based on the results of the modeling.

To identify time periods or behaviors of interest for analysis, we filtered the telemetry locations by activity data collected via onboard accelerometer sensors. The accelerometers recorded count data on a 5-min interval based on movement of the GPS collar in two highly correlated axes (X and Y). During the study, we observed mountain goats wearing GPS collars and continuously recorded two distinct behavior bouts (browsing versus resting with head down) to relate activity data to animal behaviors. We compiled the activity data such that if the cumulative proportion of browsing observations in the 5-min interval was greater than 0.80 (4 min), then we classified the interval as browsing. Likewise, if we compiled more than 4 min of observation of resting with head down over the 5-min interval, we classified the interval as inactive. We used discriminant function analysis ($F = 305.9$, $df = 1, 395$, $p = 0.00001$) to differentiate the classification of behaviors based on the average value (browsing = 38.0; resting = 4.9) of the activity data (count of accelerations/5 min) collected in the X-dimension. The overall classification accuracy of the behavioral observations was 82%, based on a threshold value of 16.7. These results allowed us to classify all telemetry locations as either resting or foraging and to extrapolate the behavioral observations to the entire record of GPS data for which we had corresponding activity data. For our analysis, we retained only GPS telemetry locations classified as foraging, thereby excluding resting from the analysis.

Table 1
Suite of candidate models and associated variables developed to test patterns of resource selection by mountain goats foraging during spring green up in the Cascade mountains of Washington, USA.

Model	Variables
Null	SDBB
Global	SDBB, D2ET, SLP, ELEVM, FOR, SRB,TAL
Normal	SDBB, D2ET, SLP, ELEVM
Basic	SDBB, D2ET, SLP
D2et	SDBB, D2ET
Vegetation	SDBB, FOR, SRB, TAL
Rock Goat	SDBB, D2ET, SLP, TAL
Forage	SDBB, D2ET, SLP, SRB
Normal Rock	SDBB, D2ET, ELEVM, SLP, TAL
Talus	SDBB, D2ET, TAL

Note: Variable definitions: standard deviation of the Brownian Bridge model alone (SDBB), distance to escape terrain (D2ET), slope (SLP) elevation in meters (ELEVM), and the percent cover of forest (FOR), shrub (SRB), and rock or talus (TAL) within the 95% circular error probable of the GPS telemetry units.

We used the BBSM and took an information theoretic approach (Burnham and Anderson, 2002) to evaluate a simple suite of a priori models (Table 1) or hypotheses to quantify selection of forage resources (Table 1). We derived variables for inclusion in the modeling framework based on a 10 m digital elevation model (DEM) and a series of LandSat 5 TM images. As mountain goats are almost always associated with steep terrain, we derived topographic predictor variables from the DEM including distance to escape terrain (defined as slopes > 35°), slope and elevation. The forage variables were based on a supervised classification of spectral reflectance values obtained from LandSat 5 TM during July 2005 and included percent cover of talus, shrub-meadow and forested communities (Wells et al., 2012).

The BBSM estimated strength of selection (β) for a particular resource ($\boldsymbol{x}$) for each individual. This allowed us to determine the relative selection of topographic and forage resources and to quantify the magnitude of selection for these resources. Our interest however, was to determine the suitability of habitat in release sites for a population of mountain goats. Therefore, we averaged the unstandardized parameter estimates of the BBSM for top models across all individuals (Marzluff et al., 2004; May et al., 2008) to estimate a population-level estimate of habitat selection. With the average estimates, we were able to project the relative habitat value across the entire study area based on the form of the RSF $w(\boldsymbol{x})$. Averaged parameter estimates were used for both visualization of the habitat model and for comparisons across individuals and by sex. To evaluate the predictive success of the model, we withheld 25% of the 41 study animals from model development and used k-fold cross validation ($k = 5$) to evaluate the correlation between frequency of observations and the RSF value (Boyce et al., 2002). For the correlation, we used area adjusted frequencies

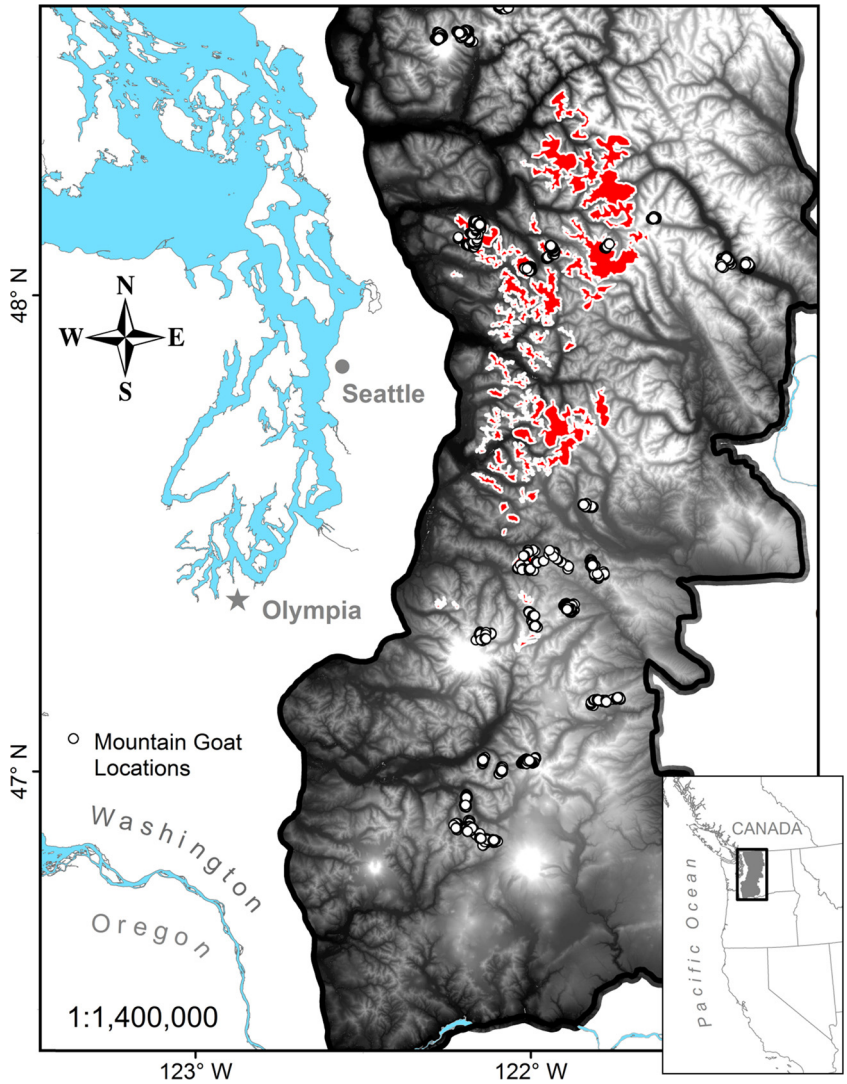

Fig. 2. Study area, outlined in black, depicting a digital elevation model of the Cascade mountain range in Washington State, USA. Candidate sites for translocation are shown in red and GPS location data used for example analysis are shown as white dots.

of the withheld locations compared to binned values of the resource selection model. Area adjusted frequencies is simply the total number of withheld locations in each bin divided by the area of the resource selection model contained by the binned values, essentially a density of withheld locations. We included all of the parameter estimates to generate an average, population-level habitat model to evaluate potential translocation sites for conservation and management plans.

Candidate restoration sites were determined by the Washington Department of Fish and Wildlife (WDFW) based on historical records and previous habitat mapping work (Wells et al., 2010). Potential release sites were intentionally focused in the western Cascades due to the prominence population declines in that region, and our task was to evaluate foraging habitat within the predetermined potential release sites. We projected the RSF across the landscape in a GIS based on the form of the weighting function $w(\boldsymbol{x})$ generating a population-level model of mountain goat habitat and cross-tabulated zonal statistics of each potential release site with the population-level RSF. We estimated the average relative value of foraging habitat and estimated the overall density (sum of relative habitat values/area) of habitat within each release site and ranked the top ten sites. This allowed us to make recommendations to WDFW based on the amount of foraging habitat and overall density of foraging habitat within potential release sites (Fig. 3).

2.1. Results of mountain goat example

The results suggested that out of the ten a priori models, the most parsimonious models were composed of topographic predictor variables. In more than half of the analyses of habitat selection by mountain goats during June and July, distance to escape terrain was the only habitat variable included in the top model for an individual animal (ΔAIC = 0; Table 2). Inclusion of the vegetation variables rarely improved model estimation. Overall, the averaged, or population-level, RSF had a negative parameter estimate for distance to escape terrain and a positive parameter estimate with steeper terrain, indicating that mountain goats selected for areas closer to escape terrain with steeper slopes (Table 3), however, the confidence intervals bounded zero indicating weak significance statistically. The standard errors of the population-level estimates of average selection for elevation, forest and shrub cover all bounded zero, indicating little evidence of selection. Overall, mountain goats showed selection for talus or rock, although again the association was not strongly significant due to variability

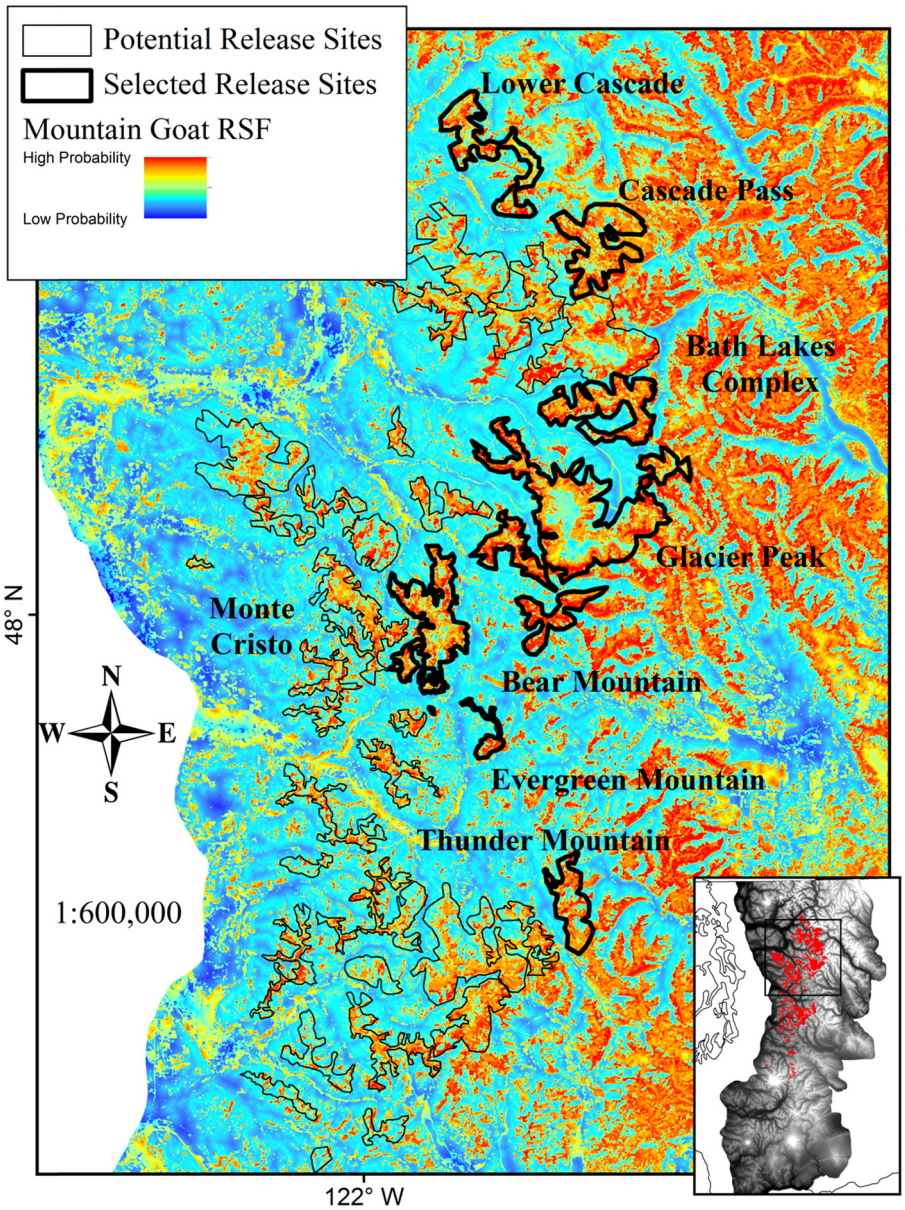

Fig. 3. Potential habitat for mountain goats based on extrapolation of the results of the Brownian bridge synoptic model, in which warm colors indicate higher probabilities of selection interpreted as higher quality foraging habitat; the candidate sites for translocation and population augmentation are outlined in black (higher priority release sites in bold). *Note that candidate restoration sites were devised separately based on historical records specifically focused in the western Cascades, due to the prominence of population declines there.*

among individual estimates. Interestingly, when we separated the individuals by sex male mountain goats selected areas further from escape terrain while females showed selection for areas closer to escape terrain, although sample size of males was relatively small. Female mountain goats also exhibited selection for steeper slopes, which is consistent with other mountain ungulates and life-history theory.

Our evaluation of the models based on *k*-fold cross validation showed substantial correlation ($r_s = 0.65$) supporting the predictive ability of the population-level RSF model. Therefore, we projected the RSF across the landscape (Fig. 3) based on averaging of all individuals in Table 3. From the projected RSF, we ranked all potential release sites. The top ten release sites were the same and in virtually the same order, for rankings based on the greatest density of habitat and the highest mean value of habitat. The sites from highest to lowest were as follows: Coral Pass/Norse Peak, Cascade Pass, Bath Lakes Complex, Glacier Peak, Mutton Mountain, Bear Mountain, Thunder Mountain, Lower Cascade, Monte Cristo and Evergreen Mountain. Eight of these sites are located in north-central Washington shown in Fig. 3, while two sites (not shown in Fig. 3) are further south near Mount Rainier.

3. Discussion

We developed and implemented a novel approach for analysis of GPS telemetry locations and landscape GIS data to estimate patterns of resource selection by free-ranging wildlife. This approach combines modeling of movement by individuals with modeling of habitat selection. We merged two existing approaches, the BBMM and the synoptic model, into the BBSM; in doing so, we addressed two major concerns related to current approaches for analysis of GPS telemetry data, defining availability of resources and the lack of independence among observations. The BBSM is an individual based model movement model that provided an understanding of

Table 2
Results of model selection (models containing a cumulative weight of 0.95) based on a priori candidate models for estimation of habitat selection by mountain goats in the Washington Cascades during periods of foraging in June and July; repeats in Goat ID indicate more than one year of observations during June and July (n = number of locations per animal, ΔAIC of 0 indicates 1 top model selected.

Goat ID	Model	K	ΔAIC	w_i
Year 1				
001SCF (n = 126)	D2et	2	0	1.00
003SCF (n = 125)	Basic	3	0	1.00
004DDF (n = 169)	Normal	4	0	1.00
005DDM (n = 32)	D2et	2	0	0.78
	Talus	3	3.63	0.13
	Forage	4	5.35	0.05
013MBF (n = 111)	D2et	2	0	1.00
014MBF (n = 174)	D2et	2	0	1.00
015MBF (n = 174)	Global	7	0	1.00
018MPF (n = 147)	D2et	2	0	0.97
019MBF (n = 199)	Forage	4	0	1.00
020WHM (n = 232)	D2et	2	0	1.00
021WHF (n = 181)	D2et	2	0	0.99
022TFF (n = 140)	D2et	2	0	0.74
	Basic	3	2.34	0.23
024KRF (n = 140)	Basic	3	0	1.00
025BRM (n = 152)	Talus	3	0	1.00
026RLF (n = 130)	Global	7	0	1.00
027FCF (n = 147)	Normal	4	0	1.00
031DDM (n = 230)	D2et	2	0	0.53
	Talus	3	2	0.20
	Basic	3	2.78	0.13
	Rock Goat	4	3.86	0.08
034GPF (n = 75)	Normal	4	0	0.48
	D2et	2	1.24	0.26
	Basic	3	2.28	0.15
	Talus	3	3.99	0.07
036LCF (n = 115)	D2et	2	0	0.88
	Basic	3	4.07	0.12
040CPF (n = 147)	D2et	2	0	0.63
	Normal	4	1.87	0.25
	Basic	3	3.56	0.11
041BUF (n = 184)	Global	7	0	1.00
042BRF (n = 149)	D2et	2	0	1.00
045MRF (n = 78)	D2et	2	0	0.43
	Basic	3	1.19	0.23
	Normal	4	1.81	0.17
	Talus	3	2.4	0.13
046NPF (n = 138)	Normal	4	0	1.00
048LCF (n = 145)	Normal	4	0	1.00
049GRM (n = 165)	D2et	2	0	0.97
050GRM (n = 172)	D2et	2	0	0.70
	Basic	3	1.74	0.29
Year 2				
004DDF (n = 220)	D2et	2	0	1.00
005DDM (n = 99)	Basic	3	0	1.00
020WHM (n = 215)	Global	7	0	1.00
021WHF (n = 115)	D2et	2	0	0.69
	Basic	3	2.12	0.24
024KRF (n = 151)	Global	7	0	1.00
028SHF (n = 21)	D2et	2	0	0.67
	Basic	3	2.71	0.17
	Normal	4	4.29	0.08
036LCF (n = 138)	D2et	2	0	0.33
	Normal	4	0.64	0.24
	Basic	3	1.85	0.13
	Talus	3	2.07	0.12
	Rock Goat	4	2.46	0.10
	Global	7	3.89	0.05
040CPF (n = 93)	Basic	3	0	1.00
041BUF (n = 172)	D2et	2	0	0.57
	Talus	3	2.19	0.19
	Basic	3	2.67	0.15
	Forage	4	4.72	0.05
042BRF (n = 123)	Normal	4	0	1.00
046NPF (n = 151)	Global	7	0	1.00
048LCF (n = 156)	Global	7	0	1.00
Year 3				
004DDF (n = 70)	D2et	2	0	1.00
005DDM (n = 24)	D2et	2	0	0.58
	Talus	3	2.16	0.20
	Basic	3	3.57	0.10
	Forage	4	5.09	0.05
	Normal	4	4.8	0.05

individual patterns of selection. While this individual approach is a powerful tool for understanding an individual's behavior and spatial ecology, ultimately we were concerned with conservation of the population and the management decisions that will follow from these modeling efforts.

We used GPS data collected from mountain goats in the Washington Cascades to improve upon past efforts to delineate and evaluate mountain goat habitat in the region for conservation and management planning. The BBSM modeling allowed for simple extrapolation of the patterns of resource selection to the entire mountain range facilitating for prioritization of potential release sites. Our results indicated that slope of the terrain was the primary factor influencing habitat selection by mountain goats. Overall, there was less support for the effect of distance to escape terrain on habitat selection by mountain goats however we detected different patterns of selection between the sexes. Female mountain goats selected steeper areas closer to escape terrain than males, a pattern documented in other mountain ungulates and likely related to increased vulnerability of maternal females and young to predation. While not unexpected, these results are an improvement over previous efforts to understand patterns of resource selection by mountain goats in the Cascades (Wells et al., 2010). Application of our population-level model to potential release sites for mountain goats supported prioritization of potential sites based on habitat value for further assessment and potential population management activities. This example demonstrates the utility of the BBSM approach for both analyses of individual behavior and population-level patterns of resource selection.

Analysis of wildlife telemetry data has been challenged by serial correlation, theoretical concerns over specifying the availability of resources to an animal, and practical concerns regarding the scale of analysis. The BBSM provides researchers and managers with a powerful approach to analyze GPS data from wildlife telemetry collars collected at fine spatial and temporal scales. The BBSM is an individual-based movement model that directly addresses these three issues by: (1) incorporating the lack of independence among locations by taking a step-wise approach during estimation of likelihoods; (2) explicitly identifying what is available to an animal as it moves across the landscape and assigning probabilities to those available resources; and (3) analyzing habitat selection at a fine-scale comparable to a third or fourth order analysis (Johnson, 1980). The BBSM falls under the general framework proposed by Johnson et al. (2008) and offers a means to derive estimates of habitat selection for development of habitat models and RSFs using GPS data.

Serial dependency in GPS telemetry has been problematic for analysis routines based on the implicit assumption that the data are fundamentally independent. Often, and quite understandably, this assumption is violated during analysis of GPS data and creation of RSFs. Nonetheless, the issue is germane to analysis of such data seeking to gain insight to the factors influencing habitat selection. The step-wise approach of the BBSM utilizes the serial nature of telemetry data rather than trying to make an exception for the lack of independence by approaches such as identification of a threshold of independence (Swihart and Slade, 1985), or modeling of the covariance (Wells et al., 2010). At each step along the movement path, the BBSM defines a unique underlying distribution of

Table 3
Standardized parameter estimates for top models of habitat selection by mountain goats ($n = 41$) in the Washington Cascades, USA, during periods of activity in June and July. *Note*: Individual estimates of standard error will be available with further coding of Hessian matrix into the code base.

Goat ID	D2ET	SLP	ELEVM	FOR	SRB	TAL
001SCF ($n = 126$)	0.0422					
003SCF ($n = 125$)	−0.1483	0.1184				
004DDF ($n = 169$)	−0.0917	0.0726	−0.0851			
005DDM ($n = 32$)	0.0729					
013MBF ($n = 111$)	−0.0929					
014MBF ($n = 174$)	2.5135					
015MBF ($n = 174$)	−0.0538	0.1979	−0.2614	0.2580	−0.1809	−0.0275
018MPF ($n = 147$)	0.0906					
019MBF ($n = 199$)	−10.490	4.0552			3.4548	
020WHM ($n = 232$)	1.1374					
021WHF ($n = 181$)	0.0025					
022TFF ($n = 140$)	−0.0013					
024KRF ($n = 140$)	−0.0010	0.001				
025BRM ($n = 152$)	0.3159					1.9733
026RLF ($n = 130$)	0.1020	0.0209	−0.1485	−0.1411	0.0201	0.1089
027FCF ($n = 147$)	−0.6073	1.1668	0.0689			
031DDM ($n = 230$)	0.0072					
034GPF ($n = 75$)	−0.0121	0.0259	0.0062			
036LCF ($n = 115$)	0.5126					
040CPF ($n = 147$)	0.0001					
041BUF ($n = 184$)	−0.0330	0.1985	−0.2052	0.0414	−0.1788	0.2488
042BRF ($n = 149$)	1.2962					
045MRF ($n = 78$)	−0.0052					
046NPF ($n = 138$)	−3.4739	0.1453	8.5514			
048LCF ($n = 145$)	−0.0246	−0.0103	0.0199			
049GRM ($n = 165$)	−0.0147					
050GRM ($n = 172$)	−0.0008					
004DDF ($n = 220$)	1.0324					
005DDM ($n = 99$)	−0.0383	0.1959				
020WHM ($n = 215$)	0.0042	0.0044	−0.0053	−0.0122	−0.0084	0.0141
021WHF ($n = 115$)	0.0032					
024KRF ($n = 151$)	−0.0197	0.0263	−0.0209	0.0381	−0.0389	0.0052
028SHF ($n = 21$)	0.0607					
036LCF ($n = 138$)	−0.0012					
040CPF ($n = 93$)	−0.7532	1.2312				
041BUF ($n = 172$)	0.0012					
042BRF ($n = 123$)	−0.1794	0.1612	−0.1164			
046NPF ($n = 151$)	0.0361	−0.0101	−0.0414	−0.0119	0.0085	0.1136
048LCF ($n = 156$)	0.1082					
004DDF ($n = 70$)	0.0432	0.3065	−0.019	−0.378	0.136	−0.028
005DDM ($n = 24$)	0.0292					
Total						
Average ($n = 41$)	−0.2105	0.1929	0.1889	−0.0050	0.0784	0.0587
Standard deviation	1.8171	0.6722	1.3400	0.0761	0.5424	0.3099
Standard error	0.2838	0.1050	0.2093	0.0119	0.0847	0.0484
Upper CI	0.3571	0.4028	0.6074	0.0188	0.2478	0.1555
Lower CI	−0.7781	−0.0171	−0.2297	−0.0288	−0.0911	−0.0380
Female ($n = 32$)						
Average	−0.2730	0.2410	0.2420	−0.0064	0.1004	0.0136
Standard deviation	2.3995	0.7679	1.5178	0.0864	0.6143	0.0516
Standard error	0.4242	0.1357	0.2683	0.0153	0.1086	0.0091
Upper CI	0.4571	0.5082	0.7786	0.0241	0.3176	0.0318
Lower CI	−1.0031	−0.0262	−0.2946	−0.0370	−0.1168	−0.0046
Male ($n = 9$)						
Average	0.2353	0.0218				0.2193
Standard deviation	0.4611					
Standard error	0.1537					
Upper CI	0.4205	0.0218				0.2193
Lower CI	−0.0843	0.0218				0.2193

Note: Variable definitions provided in Table 1. Average, standard deviation and standard error included an estimate of zero for blank spaces in the table to provide a population level estimate of resource selection. Goat IDs ending in F identify females and those ending in M identify males.

availabilities and treats the observed location as one observation drawn from the underlying distribution. At the next step, a new distribution is created and again the middle observation is drawn from the underlying distribution. This allows each observation to be freely drawn while still conditioned on the history of observations leading to that point.

With the BBSM, the concept of availability is implicitly defined and leads directly to an estimated probability of use that can be applied to estimation of habitat selection for extrapolation across the landscape. The probability is based on the observed mobility of the individual (i.e., the variance from the Brownian bridge) and calculated for each GPS location used in estimation of the BBSM. This design reduces the subjectivity of use-availability approaches to habitat selection in which some area is defined as available, and randomly selected points often are assigned within that area. Such an approach reduces the error in diffusion models in which random

points are paired with used points based on an assignment of a random aspect and distance, when, in fact, the observed GPS telemetry data might actually indicate a persistent and long-term move in one direction. With the BBSM, the probabilities of availabilities are higher in the direction of the persistent movement since the availabilities are drawn around the middle point of the triplet rather than the first. Availability is based on observed movements of the individual and calculated probabilistically, analogous to a conditional random walk (Turchin, 1998; Horne et al., 2007).

By design, the BBSM is a fine-scale approach for analysis of telemetry data. The BBSM uses a step-by-step approach along the movement path of the individual. The estimation of likelihoods and parameters is optimized over each step along the way rather than over all locations at once, which substantially increases the computational burden, but narrows the extent of the analysis to an area based on the immediate vicinity of the individual. This approach necessitates the inclusion of a temporal variable to keep track of movement paths and to proportionally shift the center point of the bivariate normal distributions. While the BBSM is an analysis approach based on individual movement data at fine scale, the results can nevertheless be used to estimate population-level habitat parameters.

While the BBSM has several advantages, the conceptual portion of the BBSM implies that an overall time period of interest already has been determined. If there is no rationale for selecting the time period of interest (i.e., diurnal, seasonal, etc.), then the modeling framework might not produce meaningful results, due to the volume of data and the differing estimates of initial variance among overlapping behaviors (e.g., resting versus foraging). Johnson et al. (2008) suggested using indicator functions to model different behaviors or time periods and provided the conceptual framework to do so. We utilized additional data collected by store-on-board activity sensors to limit our analysis to time periods when we estimated that mountain goats were actively foraging. The BBSM could likewise be used for analysis of habitat selection over other time periods of interest for other species, such as long distance migration, diurnal patterns of habitat selection, or those of a highly mobile territorial animal if the boundary of the territory can be identified and included as a covariate as done in the example illustrated by Horne et al. (2008). The choice of analysis depends largely on the species of interest, the research hypotheses, intended scale of analysis, accessible GIS data, and the ecology of the species and system of study.

3.1. Future directions

The growing use of GPS technology in wildlife telemetry is creating a demand for new approaches for analyses of complex spatiotemporal data sets. The BBSM is one analytical tool designed to help meet this demand and in doing so maximize and exploit the wealth of data accrued during costly and crucial studies of GPS collared wildlife. Application of the BBSM and other modeling approaches, such as the RSFs presented by Manly et al. (2002), synoptic model of Horne et al. (2008), and the resource utilization functions of Marzluff et al. (2004), to GPS animal location data will help researchers and managers gain deeper insight into the ecology of species under study by revealing patterns of habitat selection. Future use of the BBSM, and other modeling techniques, can help managers and researchers understand both individual and population-level patterns of resource selection by animals fitted with GPS telemetry collars where sufficient digital data exist to map and characterize the underlying landscape. The growth of this field of modeling however will necessitate careful consideration of scale, choice of modeling technique and understanding the differences among techniques in their design, implementation and the results. With the growing use of GPS data to track and monitor wildlife, these considerations, as well as refinement of existing analysis techniques and development of new approaches to understand resource selection will continue to grow to meet the demand for rigorous statistical and scientific treatment of these data.

Acknowledgments

Funding was provided by the Seattle City Light Department Wildlife Research Program, the Washington Department of Fish and Wildlife (WDFW), the WDFW Aquatic Lands Enhancement Account (ALEA), the Sauk-Suiattle Indian Tribe, the United States Forest Service, the United States National Park Service, the University of Idaho, Western Washington University, the Mountaineers Foundation and the DeVlieg Foundation. The authors thank Chris Danilson, Phyllis Reed and Don Gay for continuing support.

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