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Original Article

Predicting multiple behaviors from GPS radiocollar cluster data

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Advancements in GPS radiotelemetry allow collection of vast data for a variety of species including those for which direct observations are typically not feasible. Predicting behavior from telemetry data is possible, but telemetry fix rate can influence inferences, and animal behavior itself can affect fix success. We use multinomial regression to predict behavior from GPS radiocollar data field validated with behavioral state information. Our study organism was a facultative carnivore, the grizzly bear (*Ursus arctos*) (n = 10) from a threatened population in Alberta, Canada, monitored during 2008–2010. Models using GPS cluster parameters alone successfully predicted ungulate consumption, whereas bear bedding was sufficiently identified by models that included site-level information. Predicting more complex behaviors required models incorporating both cluster parameters and habitat characteristics. No model reliably predicted vegetation feeding, probably because this activity is shorter than the time required for cluster formation. Models built using infrequent fix rates underestimated all behaviors, with bear presence at ungulate carcass sites least sensitive to fix rate variability. Behavior influenced fix success, with highest fix acquisition occurring when bears fed on vegetation. Placing predictions into a conservation context, we show that grizzly bears modify their behavior as they move through a landscape with complex human-activity patterns on reclaimed open-pit mines, foothill, and mountain regions. The modeling approach we tested needs further applications across species and ecosystems including behavioral monitoring, quantifying activity budgeting, and identifying areas/habitats important for specific behaviors that may warrant conservation.

Key words: **bedding, behavioral state, fix rate, fix success, grizzly bear, habitat, mining, multinomial model, telemetry.**

INTRODUCTION

Patterns of animal distribution in space and time are a product of the underlying process of animal movement (Turchin 1998; Mueller and Fagan 2008; Nathan et al. 2008). Identifying behavioral states along an animal's movement path is straightforward when visual observation of a focal animal is possible (Gillingham and Klein 1992; Bates and Byrne 2009; Hayward et al. 2009). Directly observing an individual to record its behavior is a common and effective method for investigating animal behavior and the least prone to errors of assigning true behavioral state (Loettker et al. 2009; Shamoun-Baranes et al. 2012).

In contrast, observing the behavior of rare, cryptic, and wide-ranging animals that inhabit difficult study environments presents major challenges to researchers. Such species can be difficult to locate often resulting in small sample sizes (Caro 2007) and potentially data insufficient for statistical inference. For study animals that pose threats to researcher safety, such as large terrestrial mammals, investigating behavior via direct observation adds another level of difficulty.

Considerable recent advances in GPS radiocollar technologies allow tracking of animals for long sampling periods, providing large data sets of georeferenced locations at time intervals programmed by the researcher (Cagnacci et al. 2010). On direct or remote data retrieval from the radiocollar, the GPS locations can be used to investigate habitat selection (Hebblewhite and Haydon 2010), spatiotemporal movements (Nathan et al. 2008), or habitat influences on animal movement (Schick et al. 2008). By setting the GPS acquisition schedule at regular time intervals, radiocollars can collect data that fit the focal sampling with instantaneous recording methodology used in animal behavior studies (Martin and Bateson 2007). Despite this opportunity, few studies have successfully estimated mammalian behavioral states from GPS radiocollar data. To predict movement, some studies have decomposed an individual's movement trajectory into a broad set of movement bouts based on rates of movement (Johnson et al. 2002). Others have inferred behavioral states based on time required for an animal to first move out of a circle centered on a location along the path (Frair et al. 2005) or total time spent in the vicinity of a location (Barraquand and Benhamou 2008). Patterns of animal space and behavior can also be investigated using autocorrelation analysis (Wittemyer et al. 2008; Boyce et al. 2010) or generalized additive models for

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either net squared displacement (Fryxell et al. 2008) or step length (Ciuti et al. 2012). Biotic and abiotic influences along the movement path have also been studied (Fortin et al. 2005), sometimes by incorporating a hidden behavioral state in the analytical procedure (Forester et al. 2007). The latter approach represents an application of state-space modeling, a framework increasingly used for modeling cryptic behavior of marine mammals from satellite-linked datalogger data (Jonsen et al. 2005; Breed et al. 2009). Bayesian state-space models have been shown to be capable of high classification accuracy for behavioral states from animal movement paths (Beyer et al. 2013).

All the above studies focused on large herbivores or marine mammals, likely reflecting greater availability of detailed movement data for these species compared with terrestrial carnivores, which are often difficult to capture because of rarity, cryptic nature, and/or potential danger to researchers (however, see carnivore studies by Dickson et al. 2005; Roever et al. 2010; Byrne and Chamberlain 2012). In carnivore studies in which authors attempt to derive behavior from GPS relocation data, the main goal has often been to identify GPS location clusters indicative of predation events (Merrill et al. 2010). Clusters form when an animal spends a certain amount of time within a site of a given radius, where time and radius are specified by the researcher and should be tailored to the behavior of the study species and field conditions. For example, a large kill might necessitate a longer time to consume and can result in multiple smaller clusters for the same carcass (Tambling et al. 2012). Less frequent relocation frequencies (hereafter, fix rates) might minimize the problem of multiple clusters for the same kill, but could result in decreased detection of small carcasses, which likely require shorter consumption time (Bacon et al. 2011). Regardless of fix rate, if the predator is guarding the prey and the carcass is not moved, the cluster will likely have a small radius. Once clusters have been identified, most authors use logistic regression with a binomial response variable to model kill presence/absence at location clusters based on cluster and/or habitat characteristics (e.g., Webb et al. 2008; Knopff et al. 2009; Tambling et al. 2010; Pitman et al. 2012). Another example of the way in which field-based knowledge informs pure telemetry data is to separate movement behavior from clustered denning, bedding, and carcass-processing relocations by wolves (Gurarie et al. 2011).

Early attempts to identify location clusters included assigning circles of given radii around carnivore GPS locations (Sand et al. 2005) and using software originally conceived to identify epidemiological clusters (Webb et al. 2008). The publication of a cluster identification algorithm to detect cougar (*Puma concolor*) kill clusters (Knopff et al. 2009), which is easily modifiable to address individual study aims and biology of other species, represented a breakthrough for animal ecology researchers interested in identifying carnivore kills from GPS radiocollar data. However, variability in proportion of relocations successfully acquired by the GPS radiocollar (hereafter, fix success) can lead to misinterpretation of biological data (Frair et al. 2010; Mattisson et al. 2010). In an attempt to account for poor fix success, some researchers have positioned GPS radiocollars at stationary locations in different habitats (Graves and Waller 2006; Heard et al. 2008), applying the resulting corrections to radiocollar data from monitored animals. Nonetheless, certain animal behaviors could affect fix success (Mattisson et al. 2010), and no study has assessed fix success based on GPS fixes from mobile animals in conjunction with knowledge of animal behavior from field settings (Frair et al. 2010). For indisputable knowledge, such investigations should be performed by directly observing the GPS-radiocollared animal and recording its behavior. In practice, field visitation of GPS radiocollar locations after the animal's departure will generally be more logistically feasible although subjected to uncertainty over "post hoc" recording of behavior. Realistic assessments of fix success from GPS collared animals will be based on the assumption that the desired behaviors can actually be viewed or identified post hoc, which will not be possible for some behaviors.

We extend the binary logistic regression framework typically applied in carnivore studies to include a multinomial response that reflects the ecology of facultative and obligate diets as well as bedding behavior. This enables identification of multiple behavioral states and is readily applicable to carnivores when the goal is to identify behavioral states not restricted to kill consumption. Building on the Knopff et al. (2009) cluster algorithm, we present an application of the multinomial method to the study of a facultative carnivore (grizzly bear, *Ursus arctos*) from a threatened population at the southeastern edge of this species' range in Canada. Our main objective is to predict 4 grizzly bear behavioral states: vegetation feeding, bedding, vegetation feeding with bedding, and carcass feeding with or without bedding. In addition, we vary the fix rate to estimate its effect on detecting different behavioral states and test whether behavior affects fix success in specific habitat types. We discuss the findings on bear behavior in relation to human activity and habitat characteristics and highlight conservation implications.

MATERIALS AND METHODS

Study area and study animals

We carried out the study in a 3200-km^2 area located in west-central Alberta, Canada (approximate central coordinates 53°05′N, 117°25′W), which is included in the broader area described by Munro et al. (2006) (Figure 1; details in Supplementary Appendix S1). Sampled grizzly bears persist at one of the lowest densities recorded for the Alberta threatened grizzly bear population, with 4.79 bears/1000 km^2 based on DNA sampling (Boulanger et al. 2005). In 2008–2010, with assistance from the Foothills Research Institute Grizzly Bear Program (Hinton, Alberta), we captured and deployed remotely downloadable GPS radiocollars (Telus UHF; Followit, Lindesberg, Sweden) on 12 adult grizzly bears. Captures occurred in accordance with the Program's capture, handling, and sampling protocol. The protocol and progress reports were annually reviewed and approved by the University of Alberta Animal Care and Use Committee for Biosciences (558804). We attempted to sample the bear population randomly in the foothills (elevation <1700 m), mountains (≥1700 m), and on reclaimed mines, using helicopter darting and ground capture (culvert traps and limited leghold snaring) (Cattet et al. 2008).

Two large male bears dropped their collars within a month from capture and were excluded from analyses. We monitored the remaining 10 bears ($n_{\text{males}} = 4$; $n_{\text{females}} = 6$) for a total of 67.1 bear-months (6.7 ± 4.1 months per bear). One female had cubs in 2009 but was single in 2010. Another female was only monitored in 2010 when she had cubs. The other 4 females did not have cubs during the monitoring period. Radiocollars were set to acquire a location hourly during March 15–December 1, when bears were primarily outside their winter dens. This fix rate was a compromise between sufficiently detailed data for tracking behaviors and radiocollar battery life. To acquire data for field visitation of sites used by bears each month, we approached every bear on foot or via fixed-wing aircraft or helicopter and triggered its radiocollar to send GPS data remotely via very high frequency transmission.

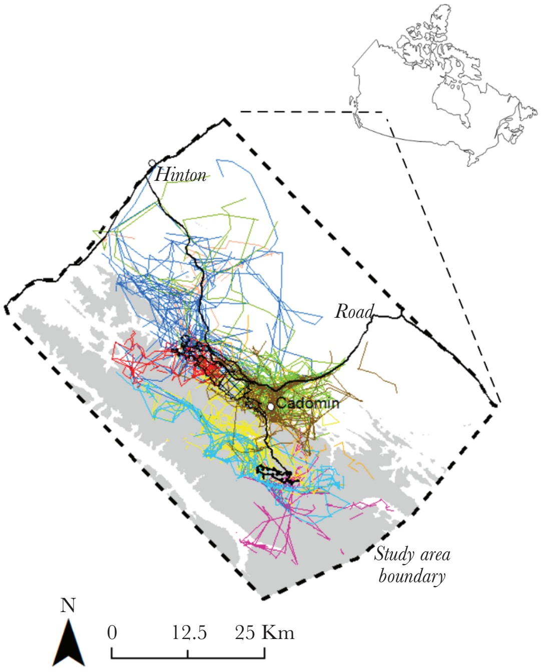

Figure 1
Study area for grizzly bear behavior in west-central Alberta, Canada, including major roads (black lines), towns (empty dots), and mine disturbance areas: reclaimed mines (crosshatch) and active mine (black dots). Shading within study area boundary (dashed line) represents mountains (≥1700 m; gray) with the rest being foothills (<1700 m; white). Movement trajectories of GPS-radiocollared grizzly bears are color coded for each individual, with monitoring duration varying between animals. Segments not connected to main paths depict instances when the GPS collar did not acquire a relocation fix.

GPS cluster visitation

We sampled telemetry clusters for field recording of bear behavior by running the Python algorithm originally designed for cougar kill site identification (Knopff et al. 2009), which we modified to include 50-m seed cluster radius because we considered that it was not feasible to search radii >50 m (i.e., >7850 m^2). The algorithm identified pairs of GPS fixes from a bear's movement trajectory that were within 50 m and occurred within 6 days of each other and computed a centroid for these points. It then iteratively searched for additional fixes within the same spatial–temporal constraints, using the original centroid as reference and recalculating the centroid based on each additional point. Because of logistical limitations, for each bear during each month, we attempted to visit the largest 4 clusters and randomly picked other clusters, provided they had ≥3 telemetry relocations within a temporal window of 6 days.

At the cluster centroid, 2-person crews systematically searched for evidence of bear behavior on a 50-m radius using protocols adapted from Munro et al. (2006) who studied the same bear population. A 20 × 20 m square plot (oriented north to south) was centered on the most time-consuming bear activity, where ungulate carcass feeding (not differentiating between predation and scavenging) was designated as the lengthiest activity, followed by bedding and vegetation feeding. All bear behavior sign and habitat characteristics within the plot were recorded (details in Supplementary Appendix S2).

Grizzly bear behavior predictions

We modeled bear behavior assigned during GPS cluster field visitation using STATA v.11.2 (StataCorp, College Station, TX). Behavior was coded as 1) vegetation feeding (root digging, grazing, or berry feeding), 2) bedding, 3) vegetation feeding with bedding, and 4) carcass feeding with or without bedding. Although we initially attempted to create separate models for each bear social group (males, females, and females with cubs), we ran into convergence problems because of insufficient sample sizes and all analyses reported herein are for data pooled across social groups.

We applied the framework detailed in Zuur et al. (2009) to decide whether to use a fixed-effects modeling approach or more complex mixed models incorporating fixed effects and a random intercept for bear unique identity (Bear_id). We used a likelihood ratio (LR) test to compare the global fixed-effects and global mixed-effects models (incorporating all a priori relevant predictor variables). Fixed- and mixed-effects models were implemented using generalized linear latent and mixed models (STATA's gllamm) with multinomial logistic regression (mlogit) link. The mixed-effects model did not show any performance improvement over the fixed-effects model (LR: $\chi^2 = 0.00$, degrees of freedom [df] = 1, $P = 1.00$); therefore, we used multinomial regression with fixed effects for all analyses.

We formulated a priori hypotheses on model variables that might influence model fit and grouped them into 3 sets: behavior (based on location cluster features), habitat (only habitat features), and behavior and habitat (based on both cluster and habitat characteristics). Behavioral variables intrinsic to the cluster were as follows: number of locations in cluster divided by the proportion of successful fixes during cluster persistence to account for varying fix success ($\text{Points}_{\text{cl}}$; hypothesized to be biologically indicative of behaviors with long durations such as ungulate consumption or bedding), a categorical variable for whether cluster spanned 24-h (1) or more (0) (24h_{cl}; distinguishing all behaviors from consumption of subadult and adult ungulates), cluster fidelity defined as a ratio of number of locations at cluster divided by number of locations away (>50 m) from the cluster during the cluster duration ($\text{Fidelity}_{\text{cl}}$; revisitation likely indicative of an attractant such as a large carcass), the average distance from each cluster location to the centroid of the cluster ($\text{Avg\_dist}_{\text{cl}}$; greater distance expected to be indicative of movements within the cluster area, such as vegetation feeding), and cluster radius defined as the maximum distance from the centroid to the outermost point in the cluster ($\text{Radius}_{\text{cl}}$; smallest radius expected for fully stationary behavior such as bedding). Habitat variables in candidate models were as follows: land cover class (Hab_class)—including barren and herbaceous (1), shrub (2), conifer forest (3), and mixed forest (4)—and abiotic habitat covariates (Hab_abiot), including slope in percentage (Slope) and site severity index (Nielsen and Haney 1998) (SSI):

$$\text{SSI} = \sin(\text{Aspect} + 225) \times \frac{\%\,\text{Slope}}{45}$$

For each model set (behavior, habitat, and behavior and habitat), we also tested the potential influences on bear behavior caused by season (Season), time of day (Time_day), and location (Land_class) on the landscape. Seasonal classification cutoffs followed Nielsen et al. (2004) and included spring (den emergence to June 14) (1), summer (June 15–August 7) (2), and autumn (August 8 to den entrance) (3). Time of day was computed based on the first location within the cluster and classified as diurnal (sunrise to sunset) (1), crepuscular (morning twilight to sunrise and sunset to evening twilight) (2), or nocturnal (evening twilight to morning twilight) (3). The time of day variable was used to account for potential onset of a specific animal behavior in a certain time period during a given 24-h cycle. For example, bears might be more likely to rest after sunset or forage on vegetation during daylight hours. Sunrise, sunset, and civil twilight tables (http://www.cmpsolv.com/los/sunset.html, accessed 17 October 2011) corresponded to study area location. Finally, we accounted for cluster location based on a combination of elevation and land use, distinguishing between reclaimed open-pit mines regardless of elevation (1), foothills (<1700 m) (2), and mountains (≥1700 m) (3). Bear diet composition and resting-site selection differ among these 3 locations (Cristescu et al. 2013), which also have varying human activity (see Study area and study animals).

We tested for correlations between predictor variables and excluded highly correlated variable combinations ($|r| > 0.6$) from all candidate models. Cluster radius was correlated with cluster average distance; therefore, we tested 2 sets of candidate models, one for each of these 2 variables. The best models based on log likelihood were the ones incorporating cluster average distance; therefore, the respective model set was withheld and the cluster radius variable was dropped. All models were fitted by specifying the robust standard error to estimate asymptotically correct variances. For each model in each set, we calculated Akaike's Information Criterion for small sample sizes (AIC_c). We ranked models within sets based on the difference in AIC_c between a given model and the model with the lowest AIC_c (ΔAIC_c) as well as model weights. We checked for potential collinearity between predictor variables for all top models using variance inflation factors (VIF) and calculated percent deviance explained for each top model.

We assessed model fit with Wald chi-square tests and plotted Pregibon leverage values against predicted probabilities of specific behaviors to detect potential observations that disproportionately influenced fit. The multinomial output with 4 categories for the response variable included 4 probabilities, one for each behavior. We used the probability output from the top multinomial regression model to assign type of behavior at a cluster, with assigned behavior being the one corresponding to the largest probability. We assessed the predictive capacity of the top models for each of the 3 sets (behavior, habitat, and behavior and habitat) by using 4-fold cross-validation, based on Huberty (1994), at a 75/25 model training-to-testing ratio.

Influence of fix rate on behavioral inferences

GPS radiocollars required users to preprogram relocation frequency (fix rate). To assess how fix rate influences outcome of the cluster algorithm, and hence behavioral inferences, we reran the algorithm maintaining spatial (50 m) and temporal (6 days) constraints but varying fix rate as follows: 1 (baseline), 2, 4, 6, 8, and 12 h. Using behavioral data based on model predictions, we calculated proportion of different behaviors detected by the cluster algorithm at different fix rates. We assumed the algorithm correctly identified behavior if the cluster centroid was located within 50 m of the actual behavior location. We inspected the confidence limits around the proportion of behaviors identified by the algorithm for each fix rate to assess the rate necessary to identify specific behaviors.

Influence of behavior on fix success

GPS radiocollar fix success was high (mean ± standard deviation [SD], 93 ± 11% for clusters visited in the field). We took advantage of behavior data collected during field visitation to test the hypothesis that behavior of the radiocollared animal influences fix success. We used generalized linear models (STATA's glm) where the response variable (% fix success) was rescaled to proportion fix success (values in the [0,1] range) to allow application of models in the binomial family with logit link. Proportion successful fixes for relocation clusters were calculated as:

$$\text{Fix success}_{\text{cl}} = \frac{\text{Fixes}_{\text{cl}} + \text{Away}_{\text{cl}}}{\text{Theoretical}_{\text{cl}}}$$

where Fixes_{cl} are fixes successfully acquired at the cluster; Away_{cl} are fixes acquired between the first and last fix in the cluster, but not at the cluster; and $\text{Theoretical}_{\text{cl}}$ represents the total number of fixes between the first and last fix in the cluster, as expected given 100% fix success. To obtain conservative estimates by making analyses relevant to the scale at which we had recorded bear behavior and habitat class in the field, we restricted the data to clusters with radii <15 m and with 0 fixes away from the cluster as per the cluster algorithm output. We estimated univariate models with behavior as independent variable, separately for each habitat, for a total of 4 models. The behavioral variable was categorical and had the same classes as described under "Grizzly bear behavior predictions." Robust standard errors were used to account for potential misspecification of the distribution family. For each model, we computed VIF, calculated percent deviance, and assessed fit by inspecting deviance residuals for potential outliers or influential observations. Finally, we correlated predicted values to observed values of the dependent variable, considering high correlations indicative of good predictive power (Zheng and Agresti 2000).

Grizzly bear behavior in a multiple-use landscape

We used predictions from the most accurate of the 3 top models across sets (behavior at cluster, habitat at cluster, and behavior and habitat at cluster) to calculate frequency of occurrence of the specific behaviors (vegetation feeding, bedding, vegetation feeding with bedding, and carcass feeding) by land designation. Predictive accuracy among top models was assessed based on the results of 4-fold cross-validation. For each behavioral state, we calculated differences between observed and expected frequencies of occurrence between land designations using chi-square analyses, for a total of 4 tests. We set expected frequencies to be equal among land designations and applied a correction factor to each observed frequency value to account for unbalanced sampling design between land designations (details in Supplementary Appendix S3).

RESULTS

During the 3-year study, we visited 550 grizzly bear GPS location clusters. Cluster site visits occurred on average 40.6 (±15.5) days following the first fix in the cluster due to logistical constraints of the study area. Additionally, we aimed to minimize safety concerns arising from our initial experiences of surprising bears on foot at large ungulate kill clusters even 3 weeks after cluster initiation.

We found evidence of bear behavior on average 10.6 ± 18.3 m away from the geometric center of the cluster. Rarely detected or unknown bear behaviors as described below occurred at 49 clusters (8.9%), which were excluded from analyses to minimize concerns over predictive ability. Nine excluded clusters had unknown bear activity, and 34 clusters had rodent digging, ant consumption, or tree rubbing. We also eliminated 4 clusters with complex behavior including bedding, carcass, and vegetation feeding and 2 clusters on active mine sites. The final data set of 501 field validated clusters (mean ± SD, 50.1 ± 34.0 clusters/bear) included 4 behavioral states: vegetation feeding (n = 53), bedding (n = 232), vegetation feeding with bedding (n = 83), and carcass feeding with/without bedding (n = 133). Most clusters visited were in the foothills (n_{clusters} = 247, 49.3%) and mountains (n_{clusters} = 179, 35.7%), with 75 clusters (15%) visited on reclaimed mines.

Grizzly bear behavior predictions

Of the total of 43 models considered (behavior at cluster, n_{models} = 13; habitat at cluster, n_{models} = 11; and behavior and habitat at cluster, n_{models} = 19), only the top model for each a priori defined set of hypotheses received support, with all other models receiving no support ($\Delta\text{AIC}_c > 10$) (Supplementary Tables S1–S3). The top 3 models were global models that included 7 predictor variables (behavior set and habitat set) and 11 predictor variables (behavior and habitat set). Each of these top models had an AIC_c weight of 1 within its respective set, explaining up to 35.7% of deviance (Table 1). Although the top model from the behavior and habitat set explained the highest deviance, it was not the best at predicting the field observed behavioral composition across all 4 behavioral states considered (Table 2).

At the level of individual bears, proportion of correctly classified behavioral states varied to a certain extent between animals. The largest as well as smallest variation occurred for individuals with small associated sample sizes (Supplementary Figures S1–S3). We summarize below strong patterns of behavioral state occurrence as predicted by the top 3 models and report all patterns in Tables 3–5. According to model predictions, clusters corresponded primarily to feeding on vegetation and bedding, or bedding alone, with fewer clusters representing vegetation feeding or ungulate consumption, respectively.

Vegetation feeding

Vegetation feeding was poorly predicted by all models, with the habitat model being slightly better than the other models (0.18 ± 0.20). Vegetation feeding clusters averaged 5 ± 2.8 locations, and this behavior was less likely to occur compared with bedding if clusters included a large number of locations (Tables 3 and 5). Vegetation feeding clusters had highest cluster average distances of all behaviors (14.9 ± 6.8 m). Vegetation feeding was less likely in conifer forest compared with bedding (Table 4). Based on all 3 top models, clusters occurring in the autumn were less likely to include vegetation feeding behavior than those in spring. According to the 2 models that included behavior, clusters occurring in summer were

Table 1

Model structure and deviance for multinomial models predicting grizzly bear behavior at GPS radiocollar location clusters in west-central Alberta, Canada (2008–2010)

Model set	Variables	K_i	−2LL	AIC_c	Δ_i	w_i	% dev. explained
Behavior at cluster							
Top	$\text{Points}_{\text{cl}}$ + 24h_{cl} + $\text{Fidelity}_{\text{cl}}$ + $\text{Avg\_dist}_{\text{cl}}$ + Season + Time_day	8	899.7	916.0	0.0	1.00	27.8
Null	+ Land_class	1	1246.5	1248.5	332.5	0.00	0.0
Habitat at cluster							
Top	Hab_class + Slope + Slope^2 + SSI + Season + Time_day +	8	1029.5	1045.8	0.0	1.00	17.4
Null	Land_class	1	1246.5	1248.5	202.8	0.00	0.0
Behavior and habitat at cluster							
Top	$\text{Points}_{\text{cl}}$ + 24h_{cl} + $\text{Fidelity}_{\text{cl}}$ + $\text{Avg\_dist}_{\text{cl}}$ + Hab_class + Slope +	12	801.5	826.1	0.00	1.00	35.7
Null	Slope^2 + SSI + Season + Time_day + Land_class	1	1246.5	1248.5	422.4	0.00	0.0

Top models for each candidate set are reported, as these were the only models that received support (w_i = 1.00 and $\Delta\text{AIC}_c < 10$). The null model also is reported for comparison. Model complexity (number of parameters) is given by K_i, deviance is given by −2LL (where LL is Log Likelihood), and % dev. explained is the percentage deviance explained. Model sets included a priori variable combinations with/without season, time of day, and land class.

Table 2

Proportion of the true composition of grizzly bear behavioral states predicted by top multinomial models for behavior at cluster, habitat at cluster, and behavior and habitat at cluster

		4-Fold cross-validation					
Model set	Behavioral state	Partition 1	Partition 2	Partition 3	Partition 4	Mean	SD
Behavior at cluster	Veg w/o Bed	0.00	0.00	0.05	0.00	0.01	0.03
	Bed	0.39	0.00	0.75	0.48	0.40	0.31
	Veg w Bed	0.61	0.90	0.50	0.50	0.63	0.19
	Carcass w or w/o Bed	0.48	0.48	0.48	0.47	0.48	0.01
Habitat at cluster	Veg w/o Bed	0.38	0.00	0.32	0.00	0.18	0.20
	Bed	0.97	0.56	0.92	0.54	0.75	0.23
	Veg w Bed	0.00	0.70	0.23	0.61	0.38	0.33
	Carcass w or w/o Bed	0.04	0.00	0.00	0.00	0.01	0.02
Behavior and habitat at cluster	Veg w/o Bed	0.08	0.00	0.26	0.00	0.09	0.12
	Bed	0.37	0.00	0.53	0.37	0.32	0.22
	Veg w Bed	0.65	0.95	0.82	0.78	0.80	0.12
	Carcass w or w/o Bed	0.37	0.31	0.32	0.22	0.31	0.06

Data were acquired in 2008–2010 in west-central Alberta and randomly partitioned (n = 4) without replacement. A value of 1.00 for 4-fold cross-validation represents correct prediction. Veg, vegetation feeding site (root digging, grazing, berry foraging); Bed, bedding/resting site; Carcass, mammal carcass; w, with; w/o, without.

Table 3

Estimated coefficients (β_i), robust standard errors (SE), and 95% confidence intervals (CIs) for the top multinomial model based on behavior at cluster, as assessed by Δ_i and w_i

	Vegetation feeding				Vegetation feeding with bedding				Ungulate carcass w/without bedding			
			95% CI				95% CI				95% CI	
Variable	β_i	Robust SE	Lower	Upper	β_i	Robust SE	Lower	Upper	β_i	Robust SE	Lower	Upper
Cluster												
$\text{Points}_{\text{cl}}$	**−0.543**	**0.105**	**−0.750**	**−0.337**	**0.092**	**0.045**	**0.003**	**0.181**	**0.157**	**0.049**	**0.061**	**0.254**
24h_{cl}	−1.185	0.639	−2.437	0.067	0.320	0.522	−0.703	1.343	−0.594	0.483	−1.541	0.353
$\text{Fidelity}_{\text{cl}}$	0.003	0.008	−0.013	0.020	−0.002	0.003	−0.008	0.004	**−0.007**	**0.003**	**−0.013**	**−0.000**
$\text{Avg\_dist}_{\text{cl}}$	**0.123**	**0.033**	**0.058**	**0.188**	−0.031	0.026	−0.082	0.020	**−0.073**	**0.027**	**−0.127**	**−0.020**
Season												
Summer	**−0.939**	**0.443**	**−1.807**	**−0.071**	0.142	0.374	−0.590	0.874	−0.494	0.360	−1.200	0.212
Autumn	**−1.708**	**0.552**	**−2.790**	**−0.626**	0.091	0.368	−0.631	0.813	**−1.042**	**0.380**	**−1.787**	**−0.297**
Time_day												
Crepuscular	0.194	0.528	−0.840	1.228	**0.824**	**0.368**	**0.103**	**1.545**	**−1.266**	**0.495**	**−2.236**	**−0.296**
Nocturnal	−0.805	0.463	−1.712	0.101	0.176	0.322	−0.456	0.807	**−1.014**	**0.382**	**−1.763**	**−0.265**
Land_class												
Foothills	−0.661	0.548	−1.736	0.414	**−1.072**	**0.389**	**−1.834**	**−0.310**	−0.157	0.447	−1.032	0.719
Mountains	0.480	0.490	−0.480	1.439	−0.120	0.370	−0.845	0.605	−0.759	0.522	−1.782	0.264

Estimates for which the CI did not overlap 0 are given in bold. Bedding behavior was withheld as a reference category in the dependent variable. For the independent variables, spring (Season), diurnal (Time_day), and reclaimed mine (Land_class) were withheld as reference categories.

Table 4

Estimated coefficients (β_i), robust SEs, and 95% CIs for the top multinomial model based on habitat at cluster, as assessed by Δ_i and w_i

	Vegetation feeding				Vegetation feeding with bedding				Ungulate carcass w/without bedding			
			95% CI				95% CI				95% CI	
Variable	β_i	Robust SE	Lower	Upper	β_i	Robust SE	Lower	Upper	β_i	Robust SE	Lower	Upper
Hab_class												
Shrub	0.711	0.781	−0.819	2.241	−0.451	0.579	−1.585	0.684	0.121	0.768	−1.384	1.627
Conifer forest	**−2.295**	**0.649**	**−3.567**	**−1.023**	**−1.706**	**0.453**	**−2.593**	**−0.818**	−0.260	0.587	−1.411	0.890
Mixed forest	−0.909	0.885	−2.643	0.825	−0.259	0.628	−1.491	0.973	0.080	0.699	−1.290	1.449
Hab_abiot												
Slope	−0.021	0.031	−0.081	0.040	0.024	0.020	−0.015	0.062	**−0.040**	**0.018**	**−0.076**	**−0.004**
Slope^2	0.000	0.000	−0.001	0.001	−0.000	0.000	−0.001	0.000	0.000	0.000	−0.001	0.001
SSI	−0.387	0.263	−0.903	0.128	0.079	0.225	−0.362	0.521	0.113	0.304	−0.483	0.709
Season												
Summer	0.095	0.417	−0.723	0.913	0.149	0.375	−0.586	0.884	**−0.664**	**0.315**	**−1.282**	**−0.047**
Autumn	**−1.508**	**0.562**	**−2.610**	**−0.406**	0.205	0.383	−0.547	0.956	**−0.958**	**0.348**	**−1.640**	**−0.277**
Time_day												
Crepuscular	−0.080	0.559	−1.175	1.015	0.662	0.375	−0.074	1.397	**−1.269**	**0.447**	**−2.145**	**−0.392**
Nocturnal	−0.846	0.443	−1.716	0.023	−0.042	0.318	−0.665	0.581	**−1.192**	**0.294**	**−1.769**	**−0.615**
Land_class												
Foothills	−0.192	0.712	−1.587	1.204	−0.141	0.462	−1.046	0.763	0.208	0.486	−0.745	1.161
Mountains	**1.419**	**0.647**	**0.150**	**2.687**	0.630	0.439	−0.230	1.490	−0.338	0.503	−1.323	0.648

Estimates for which the CI did not overlap 0 are given in bold. Bedding behavior was withheld as a reference category in the dependent variable. For the independent variables, barren/herbaceous class (Hab_class), spring (Season), diurnal (Time_day), and reclaimed mine (Land_class) were withheld as reference categories.

less likely to represent vegetation feeding than spring clusters. Based on the habitat, and behavior and habitat models, vegetation feeding clusters were more likely in the mountains, likely reflecting availability of bear foods (vegetative foods more available than animal foods in the mountains).

Bedding

The habitat model was the best at predicting bedding alone (0.75 ± 0.23). Bedding clusters averaged 7 ± 4.5 locations, and cluster average distance was 12.2 ± 6.1 m.

Vegetation feeding with bedding

Based on 0.80 mean predicted proportion of true composition and low variability between partitioned data sets (SD = 0.12), the behavior and habitat model was the best for predicting vegetation feeding with bedding. Vegetation feeding with bedding was more likely to occur when clusters had many locations (Tables 3 and 5) and clusters with this behavioral state had 9 ± 7.9 locations. Vegetation feeding with bedding clusters were less likely in conifer forest compared with bedding (Table 4). Based on the behavior model, clusters representing vegetation feeding with bedding were predicted to occur

Table 5

Estimated coefficients (β_i), robust SEs, and 95% CIs for the top multinomial model based on behavior and habitat at cluster, as assessed by Δ_i and w_i

	Vegetation feeding				Vegetation feeding with bedding				Ungulate carcass w/without bedding			
			95% CI				95% CI				95% CI	
Variable	β_i	Robust SE	Lower	Upper	β_i	Robust SE	Lower	Upper	β_i	Robust SE	Lower	Upper
Cluster												
Points$_{cl}$	**−0.613**	**0.133**	**−0.873**	**−0.353**	**0.103**	**0.046**	**0.012**	**0.194**	**0.153**	**0.049**	**0.057**	**0.250**
24h$_{cl}$	−0.634	0.776	−2.154	0.887	0.555	0.563	−0.548	1.658	−0.586	0.484	−1.535	0.363
Fidelity$_{cl}$	0.001	0.009	−0.016	0.019	−0.002	0.003	−0.008	0.004	**−0.006**	**0.003**	**−0.013**	**−0.000**
Avg_dist$_{cl}$	**0.156**	**0.039**	**0.080**	**0.232**	−0.013	0.027	−0.067	0.040	−0.053	0.028	−0.108	0.003
Hab_class												
Shrub	0.538	1.015	−1.450	2.527	−0.440	0.591	−1.598	0.717	−0.462	1.189	−2.793	1.868
Conifer forest	**−3.168**	**0.875**	**−4.883**	**−1.452**	**−1.744**	**0.469**	**−2.664**	**−0.824**	−0.458	0.639	−1.710	0.794
Mixed forest	−1.402	0.960	−3.282	0.479	−0.269	0.653	−1.548	1.011	−0.051	0.846	−1.709	1.607
Hab_abiot												
Slope	−0.018	0.033	−0.082	0.047	0.023	0.019	−0.016	0.061	−0.029	0.025	−0.078	0.019
Slope^2	0.000	0.000	−0.001	0.001	−0.000	0.000	−0.001	0.003	−0.000	0.000	−0.001	0.001
SSI	−0.313	0.319	−0.939	0.312	0.060	0.221	−0.374	0.494	0.281	0.397	−0.497	1.059
Season												
Summer	**−1.076**	**0.529**	**−2.113**	**−0.038**	0.346	0.384	−0.406	1.098	−0.535	0.365	−1.250	0.181
Autumn	**−2.761**	**0.676**	**−4.086**	**−1.436**	0.256	0.384	−0.497	1.010	**−1.201**	**0.400**	**−1.985**	**−0.416**
Time_day												
Crepuscular	0.037	0.674	−1.284	1.359	0.715	0.380	−0.029	1.459	**−1.434**	**0.541**	**−2.494**	**−0.375**
Nocturnal	−0.927	0.483	−1.873	0.019	0.110	0.348	−0.572	0.791	**−1.050**	**0.364**	**−1.762**	**−0.337**
Land_class												
Foothills	0.721	0.887	−1.017	2.459	−0.309	0.484	−1.257	0.638	−0.295	0.561	−1.395	0.805
Mountains	**2.170**	**0.845**	**0.513**	**3.827**	0.560	0.434	−0.291	1.410	−0.389	0.587	−1.540	0.762

Estimates for which the CI did not overlap 0 are given in bold. Bedding behavior was withheld as a reference category in the dependent variable. For the independent variables, barren/herbaceous class (Hab_class), spring (Season), diurnal (Time_day), and reclaimed mine (Land_class) were withheld as reference categories.

more when the cluster started during crepuscular periods. Lastly, the behavior model predicted that vegetation feeding with bedding clusters were less likely in the foothills.

Carcass feeding with/without bedding

The behavior model was best at predicting ungulate consumption (0.48 ± 0.01). Carcass feeding was more likely to occur when clusters had many locations (Tables 3 and 5), with ungulate consumption clusters having 26 ± 26.9 locations. Bears were more likely to show fidelity to bedding sites (5.5 ± 3.7) compared with carcass sites (8.7 ± 13.8) (Tables 3 and 5). Cluster average distance also was lower than the corresponding vegetation feeding measure when bears fed on a carcass (13 ± 5.7 m) (Tables 3 and 5). The habitat at cluster model predicted that ungulate consumption clusters were more likely as slope decreased. Based on all 3 top models, clusters occurring in the autumn were less likely to include ungulate consumption behavior than those in spring. In addition, the habitat model predicted carcass feeding clusters to occur less frequently in summer than in spring. All models predicted ungulate consumption clusters to occur less when clusters were initiated during crepuscular and nocturnal periods compared with daytime.

Influence of fix rate on behavioral inferences

Hourly step length for the bears monitored in our study was 1030 ± 259 m. Decreasing fix rate from 1 to 2 h resulted in a mean drop in detection of at least 30% across vegetation feeding, bedding, and vegetation feeding with bedding, respectively (Figure 2). Further dropping the fix rate to 4 h resulted in less than 40% of clusters still detected for these 3 behaviors. When the fix rate was dropped to 6 h, a maximum of 25% of clusters were still detected. Further dropping to 8 h resulted in up to 15% of cluster detection, with 12-h fix rate only preserving approximately 10% of clusters.

Carcass feeding with/without bedding

Ungulate feeding behavior was least sensitive to fix rate decrease, with 80% of ungulate consumption clusters still detected at fix rates of 2 and 4 h. Further decreases in fix rate resulted in detection below 70%, but even a 12-h fix rate still resulted in detection of almost 50% of ungulate feeding clusters. These relatively high mean retention rates for carcass clusters are even more substantial if only the top ungulate consumption predictive model (behavior at cluster) is considered.

Influence of behavior on fix success

Vegetation feeding

Of all behavioral states, cluster fix success was highest at vegetation feeding sites, averaging 98.1 ± 5.2%.

Bedding

Fix success at bedding sites was 93.2 ± 10.8%. When we controlled for habitat type, closed habitats (shrub, conifer, and mixed forest) had lower fix success when bears bedded compared with when they fed on vegetation only (Table 6).

Vegetation feeding with bedding

Fix success was 92.6 ± 11.3% at vegetation feeding with bedding sites. Closed habitats had lower fix success when bears fed on vegetation and bedded compared with when they fed on vegetation only (Table 6). In open habitats (barren land and grassland), fix success was also lower for vegetation feeding and bedding behavior when compared with vegetation feeding alone. However, the latter result should be interpreted with caution because it resulted from a small sample size.

Carcass feeding with/without bedding

Fix success was 92.3 ± 10.7% at ungulate consumption sites. We did not have carcass consumption samples for shrub and mixed forest,

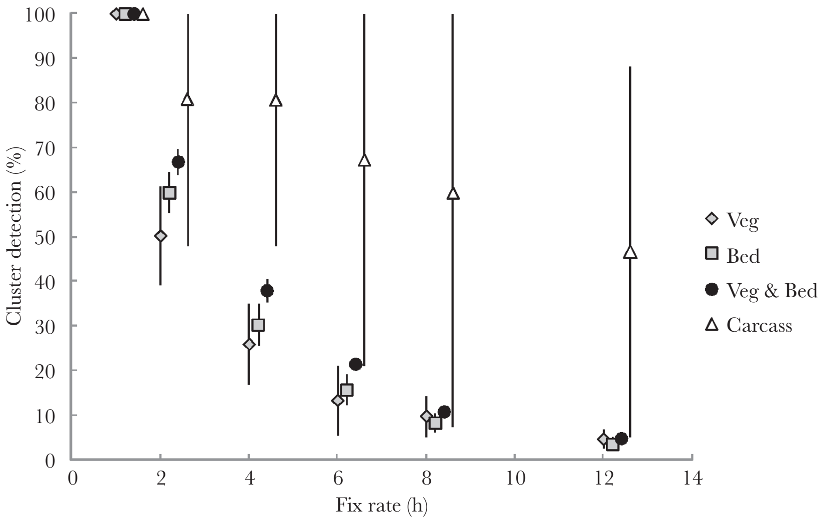

Figure 2
Detectability of grizzly bear behavioral states from location clusters in west-central Alberta, based on manipulating GPS radiocollar fix rates. Error bars are standard deviations calculated based on top models for each set of candidate models (behavior, habitat, and behavior and habitat). Veg, vegetation feeding; Bed, bedding; Carcass, ungulate carcass consumption.

Table 6
Estimated coefficients (β_i), robust SEs, and 95% CIs for generalized linear models illustrating GPS radiocollar fix success as a function of grizzly bear behavioral state

	Bedding				Vegetation feeding with bedding				Ungulate carcass w/without bedding			
			95% CI				95% CI				95% CI	
Variable	β_i	Robust SE	Lower	Upper	β_i	Robust SE	Lower	Upper	β_i	Robust SE	Lower	Upper
Habitat												
Model 1: Barren/herbaceous	−1.940[a]	0.815	−1.597	1.597	**−17.043**	**0.966**	**−18.937**	**−15.149**	−1.940[a]	1.262	−2.474	2.474
Model 2: Shrub	**−17.752**	**0.642**	**−19.010**	**−16.494**	**−16.483**	**0.896**	**−18.239**	**−14.727**				
Model 3: Conifer forest	**−14.699**	**0.648**	**−15.969**	**−13.430**	**−15.511**	**0.736**	**−16.954**	**−14.068**	**−14.225**	**1.064**	**−16.311**	**−12.140**
Model 4: Mixed forest	**−16.883**	**1.198**	**−19.231**	**−14.536**	**−16.296**	**1.140**	**−18.530**	**−14.061**				

Separate models were run for each of 4 broad habitat categories, using data collected during field visitation as input. Results of all 4 models are presented in the same table. Estimates for which the CIs did not overlap 0 are given in bold. Vegetation feeding was withheld as a reference category in the dependent variable.
[a] Coefficient reported at 10^9 times its original value.

but for conifer forest, fix success was lower for ungulate consumption behavior compared with vegetation feeding (Table 6).

Grizzly bear behavior in a multiple-use landscape

Although the 4 behavioral states we considered occurred on all land designations (foothills, mountains, and reclaimed mines), these behaviors occurred at different frequencies among land designations (Figure 3). Although we report data only from the best predictive model for each specific behavior, we observed the same patterns of frequency differences for the other 2 top models. Only data from the best predictive model for a specific behavior are reported, but the observed patterns of frequency differences maintained for the other 2 top models.

Vegetation feeding

Based on behavioral state predictions, vegetation feeding differed between land designations (χ^2 = 156.9, df = 2, P < 0.0001), occurring more in the mountains than in the foothills or reclaimed mines, although these results need to be interpreted with caution because of the low accuracy of prediction for vegetation feeding.

Bedding

Frequency of bedding differed between land designations (χ^2 = 474.9, df = 2, P < 0.0001), with most bedding alone predicted for the foothills.

Vegetation feeding with bedding

Occurrence of vegetation feeding with bedding also differed between land designations (χ^2 = 245.6, df = 2, P < 0.0001), being more frequent in the mountains and on reclaimed mines compared with foothills.

Carcass feeding with/without bedding

Ungulate consumption differed by land designation (χ^2 = 79.0, df = 2, P < 0.0001), with most frequent consumption occurring in the foothills.

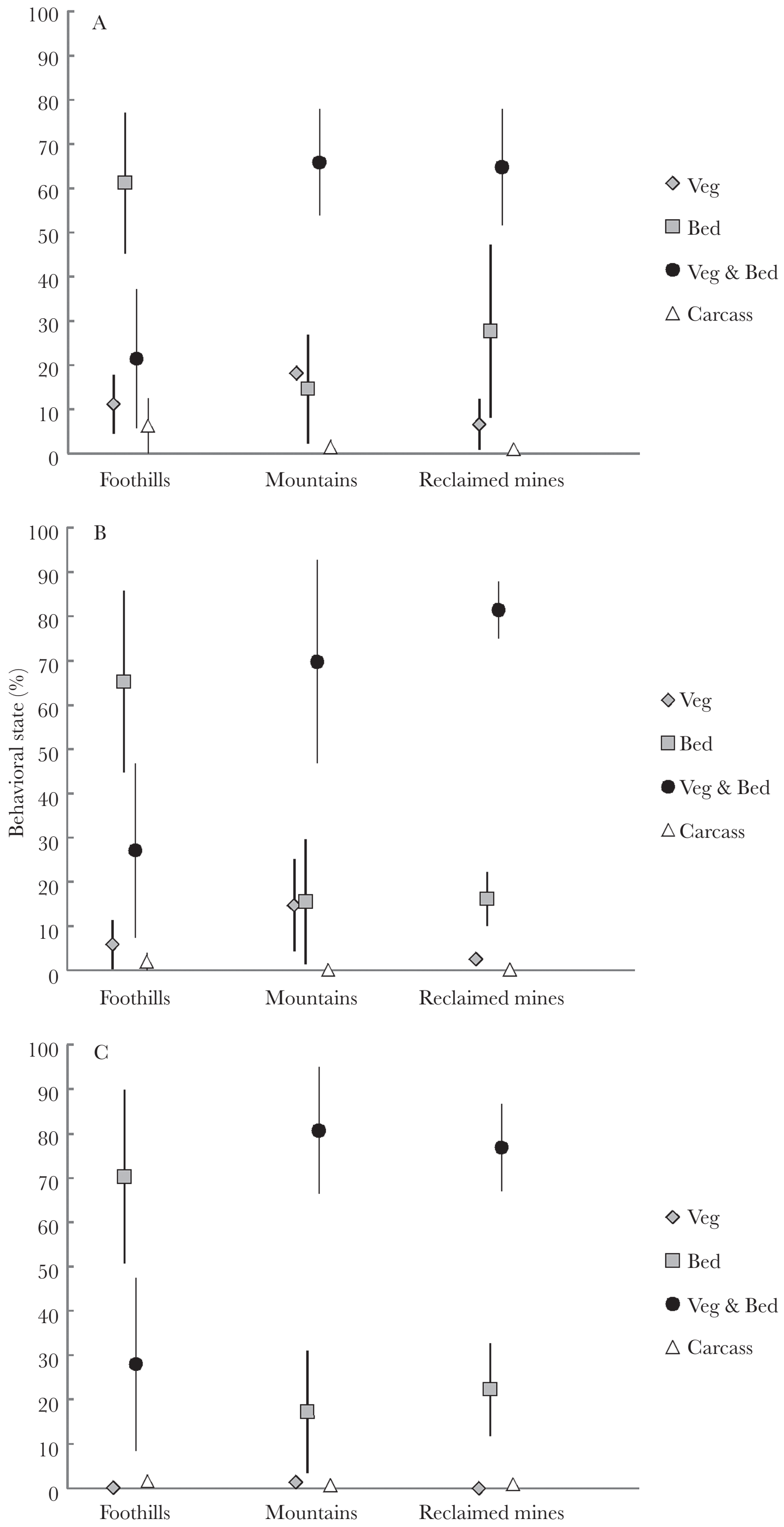

Figure 3

Proportion of grizzly bear behaviors by land designation, based on predictions from multinomial logit models with behavioral state as categorical dependent variable. Proportions are presented by season, including spring (A), summer (B), and autumn (C). Error bars are standard deviations calculated based on top models for each set of candidate models (behavior, habitat, and behavior and habitat). Veg, vegetation feeding; Bed, bedding; Carcass, ungulate carcass consumption.

DISCUSSION

GPS technologies allow unprecedented resolution in monitoring animal use of the landscape, but understanding the link between GPS locations and animal behavior requires a concerted effort of researchers interested in extracting biological information from technological tools. Many advances in the interpretation of behavior from GPS radiocollar data have come from studies on carnivores, but these have typically focused on distinguishing carnivore predatory events from no-kill locations. However, because human activity and associated mortality risk are substantial limiting factors for carnivore populations (Creel and Creel 1998; Andren et al. 2006; Goodrich et al. 2008), behavioral studies and conservation decisions would benefit from obtaining additional information from GPS radiocollar data, such as understanding carnivore behavior in relation to human land use. This information could, for example, assist in minimizing human-carnivore encounters or help mitigate the effects of land use change on carnivore populations.

Using the behavior-conservation unified framework called for in the recent literature (Blumstein and Fernandez-Juricic 2004; Caro 2007), we found that habitat variables were not important at predicting ungulate consumption by grizzly bears in a complex landscape, with cluster characteristics alone providing good carcass site prediction. Once a kill had been made or a carcass located that had been killed by another predator, bears spent more time at the carcass compared with sites with other behaviors. Because ungulate consumption can be readily identified from cluster patterns without the need for habitat information, model parameters estimated from the top behavior at cluster model can be used to direct field visitation for studies of grizzly bear ungulate prey composition. Based on the low variability in predictive accuracy (SD 1%), the 48% accuracy of ungulate consumption predictions can also be used to correct kill rate estimates (by multiplication of predicted carcass consumption by 2). The resulting estimate will have lowest error for times of the year when bears are predominantly predatory, such as ungulate calving season. The higher incidence of kill clusters in the foothills compared with mountainous areas or reclaimed mines is corroborated by dietary analysis that identified higher ungulate consumption by bears in the foothills (Cristescu B, Stenhouse GB, Boyce MS, unpublished data). This is likely due to higher moose and elk (*Cervus elaphus*) availability in the foothills (Cristescu B, Stenhouse GB, Boyce MS, unpublished data) and lower ungulate predation risk in open areas (Hebblewhite et al. 2005) such as sparsely vegetated mountains and reclaimed mines.

Predicting bear bedding alone was best achieved by incorporating habitat variables only, which strengthens previous findings that microsite level habitat variables influence resting-site selection in brown bears (Ordiz et al. 2011). Ability to identify bedding sites is particularly important for carnivores inhabiting areas with extensive human activity, where preservation of fine scale habitat features favoring bedding is required for target species conservation (Te Wong et al. 2004; Purcell et al. 2009). Alternatively, GPS locations associated with bedding as predicted from the multinomial behavioral state model could be extracted from the data set, facilitating analyses exclusively for foraging habitat selection. Such an approach should be treated with caution because of the likely connection between foraging and bedding behaviors.

Predicting vegetation feeding with bedding required a complex combination of variables that included behavior and habitat characteristics. Ability to predict where such complex sites occur is important because their conservation can have the double benefit of protecting bedding and foraging habitat. Interestingly, bears foraged and bedded at the same site less in the foothills than in the mountains or on reclaimed mines, possibly reflecting differences in food habits between land designations. Because bears in the foothills have more meat in their diet, plant foods may not influence their activity patterns as much as ungulate distribution. Alternatively, in the foothills, bears may be displaced by greater human activity, therefore not spending much time at a site unless they obtain a substantial energetic benefit, such as by consuming an ungulate carcass.

We were unable to predict vegetation feeding when it did not occur in conjunction with bedding. Our definition of location clusters required bears to spend ≥3 h in an area with a radius of up to 50 m for the seed cluster (sensu Knopff et al. 2009). Based on opportunistic direct observations of bears digging for roots and grazing on herbaceous plants (n = 10), vegetation feeding does not occur within the above spatial and temporal cluster constraints. The GPS radiocollar fix rate would need to be set at lower intervals than hourly as defined in this study, but one caveat of a more frequent fix rate is that animal movements occurring at such fine temporal scales could be confounded by GPS error, resulting in inference problems at least for elk (Jerde and Visscher 2005). Rapid movement rates of carnivores are better suited for more frequent fix rate schedules (McKenzie et al. 2012), and such schedules should be tailored to the research organism under study, preferably after a pilot study with radiocollars set at high fix rate. Our simulations involving varying fix rates showed rates of ≥4 h result in <50% of clusters being detected for all behavioral states, with the exception of kill clusters that are more robust to fix rate decrease (Figure 2). Even at a fix rate of 2 h, only up to 75% of clusters were detected, with vegetation feeding and bedding clusters being most affected by fix rate decrease. We recommend a fix rate of 1 h or more frequent for inferring behavioral states of grizzly bears. If the focus of a study is researching grizzly bear predation on large ungulates, then a 4-h fix rate appears sufficient to preserve a substantial portion of the clusters (80%). Researchers should acknowledge that using such an infrequent fix rate may underrepresent the importance of young and/or small ungulates/other mammals, as well as scavenging by grizzly bears.

Animal behavior predictions based on GPS radiocollar data can be affected if behavior influences fix success (Frair et al. 2010). The finding that fix success was highest for vegetation feeding across most habitat categories suggests that behaviorally induced bias in fix success could affect predictions of animal behavior. Because we assigned behavioral states and performed habitat categorization based on field visitation, our inferences eliminate spurious effects present in previous studies that attempt to disentangle effects of animal behavior and land cover on fix success based on behavioral assumptions and low accuracy GIS habitat data (e.g., 60–90% accuracy for Landsat land cover data; Wickham et al. 2004; Mayaux et al. 2006).

Despite their ability to incorporate a dependent variable with >2 categories, multinomial models have rarely been applied to data collected during direct field observations of behavior (Borkowski et al. 2006; Witter et al. 2012), to infer behavior from animal sign data, or for terrestrial carnivores. We demonstrated that such models can be useful to infer behavioral states based on GPS radiocollar technology and behavioral sign, for example, prey carcasses, hair, bones, excavated ground, sheared plant stems, or bedding depressions. This approach enables predictions of behavioral states for the entire duration of animal GPS radiocollar monitoring, provided fix rate, fix success, and field protocols for sampling behavior are adequate. Movements determining home range use differ between mammal species based on body size and diet (Swihart et al. 1988), with home range being dependent on species-specific body size, group living, or solitary habits (Gittleman and Harvey 1982). This variation in movements will likely affect the potential of the cluster parameters outputted by our models to predict behavioral states beyond our study species. However, our approach can be readily used to parameterize models for other study systems using situation-specific covariates. In addition, the straightforward ability to modify the original Python algorithm (Knopff et al. 2009) maximizes the flexibility of the framework outlined herein for predicting behavioral states from GPS data. Field protocols for cluster visitation should strive to reach a balance between visiting clusters soon after the animal was there, thereby minimizing site disturbance by nonmonitored animals, and care not to interfere with animal behavior. In addition, if the study species is potentially dangerous, visiting the site too early can put field personnel at risk, such as surprising large carnivores feeding or resting at ungulate carcasses.

Although the number of field visited GPS location clusters was large, sample size of individual bears monitored was relatively low ($n = 10$) due to low bear densities in the study area (Boulanger et al. 2005) and logistical constraints. This limitation is likely not a major issue with regard to technique development, which is the focus of the article. It might, however, influence the generality of findings related to grizzly bear behavioral patterns in the multiple-use landscape of our study area; therefore, the respective results should be interpreted with caution. We were unable to radiocollar all grizzly bears and other large carnivores present in the area including black bears (*Ursus americanus*), wolves (*Canis lupus*), and cougars (*P. concolor*). Some ungulate consumption events might have been missed if a nonradiocollared carnivore moved the carcass before field crews visited the cluster site. We minimized this problem by performing thorough site investigations looking for evidence of hair, drag marks, carnivore scat, and its relative age. An additional potentially confounding issue was that larger bodied grizzly bears have higher per minute meat intake than smaller bears (Wilmers and Stahler 2002), and we expected that characteristics of individual bears may influence behavioral inferences based on GPS cluster duration. However, models using a random intercept for unique bear identity did not outperform multinomial models, suggesting that our modeling approach was adequate. When compared with body size differences between individuals in coastal bear populations, body sizes of animals monitored in our study were relatively similar, which might reflect in relatively similar intake rates. Further, variation in bedding behavior and bed site selection is negligible for brown bears (Ordiz et al. 2011), which would also contribute to the good performance of fixed-effects modeling applied to our data set.

Whether facultative or obligate, carnivores display complex behavioral states, and their structural role in ecosystems (Sergio et al. 2008) justifies augmented research efforts into carnivore behavioral ecology. Knowledge of where carnivores perform certain behaviors would enable a level of detail far beyond the traditional approach of understanding habitat selection based on GPS locations with unknown behavior. For example, areas where bears consume ungulates are important because they facilitate body mass gain and associated increase in reproductive success (Hilderbrand et al. 1999). In the case of grizzly bears on mined landscapes, which change habitats from forested to artificial open areas, ungulates are consumed in tree patches left undisturbed during mining (Cristescu et al. 2014). By discriminating multiple behavioral states from telemetry data, our modeling framework enables identification of areas in need of protection and is transferable to other species and populations that may experience loss of behaviors (sensu Caro and Sherman 2012) as a result of human-caused environmental change.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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