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METHODS

Detecting grizzly bear use of ungulate carcasses using global positioning system telemetry and activity data

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Abstract Global positioning system (GPS) wildlife collars have revolutionized wildlife research. Studies of predation by free-ranging carnivores have particularly benefited from the application of location clustering algorithms to determine when and where predation events occur. These studies have changed our understanding of large carnivore behavior, but the gains have concentrated on obligate carnivores. Facultative carnivores, such as grizzly/brown bears (*Ursus arctos*), exhibit a variety of behaviors that can lead to the formation of GPS clusters. We combined clustering techniques with field site investigations of grizzly bear GPS locations ($n = 732$ site investigations; 2004–2011) to produce 174 GPS clusters where documented behavior was partitioned into five classes (large-biomass carcass, small-biomass carcass, old carcass, non-carcass activity, and resting). We used multinomial logistic regression to predict the probability of clusters belonging to each class. Two cross-validation methods—leaving out individual clusters, or leaving out individual bears—showed that correct prediction of bear visitation to large-biomass carcasses was 78–88 %, whereas the false-positive rate was 18–24 %. As a case study, we applied our predictive model to a GPS data set of 266 bear-years in the Greater Yellowstone Ecosystem (2002–2011) and examined trends in carcass visitation during fall hyperphagia (September–October). We identified 1997 spatial GPS clusters, of which 347 were predicted to be large-biomass carcasses. We used the clustered data to

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develop a carcass visitation index, which varied annually, but more than doubled during the study period. Our study demonstrates the effectiveness and utility of identifying GPS clusters associated with carcass visitation by a facultative carnivore.

Keywords *Ursus arctos* · GPS Cluster · Prediction · Multinomial model · Carcass visitation

Introduction

Technological advancements and cost reductions of global positioning system (GPS) telemetry devices have revolutionized data collection in field studies of large mammals (Cagnacci et al. 2010; Hebblewhite and Haydon 2010; Tomkiewicz et al. 2010). These advances have fostered analytical innovations as well as new challenges to data management and analysis (Cagnacci et al. 2010). One of the principal analytical challenges is matching the temporal scale of data collection to ecological phenomena to ensure inference from statistical approaches matches actual animal behaviors (Hebblewhite and Haydon 2010). Researchers have addressed this challenge by applying spatial clustering techniques that identify regions of positive spatial autocorrelation (Lu 2000). Spatial autocorrelation of GPS time-series gives information about when and where animals restrict their movements, providing an indicator of a change in space-use behavior. Once identified, spatial clusters can be ground truthed to facilitate linking them to a variety of habitats and behaviors. This approach has been applied across a number of behavioral phenomena and taxa including: parturition sites and neonate survival in caribou [*Rangifer tarandus* (DeMars et al. 2013)], movement pattern and foraging patch detection in elk [*Cervus elaphus* (Van Morter et al. 2010; Seidel and Boyce 2015)], and predation ecology in large carnivores (Knopff et al. 2009; Cavalcanti and Gese 2010; Rauset et al. 2012; Elbroch et al. 2013; Cristescu et al. 2015).

Several bear species, and grizzly/brown bears (*Ursus arctos*) in particular, can be effective predators and scavengers of ungulates (Murphy et al. 1998; Derocher et al. 2000; Zager and Beecham 2006; Swenson et al. 2007). Although GPS collars are frequently used in bear studies, clustering techniques have not been commonly applied, with a few exceptions (Rauset et al. 2012; Krofel et al. 2012; Cristescu et al. 2015). We speculate this may be due in part to complex space-use patterns associated with facultative carnivory. For example, grizzly bear foraging behaviors that generate GPS clusters are a function of the availability, distribution, and phenology of a large number of food types (Gunther et al. 2014). Feeding behavior can result in GPS clustering not related to carcasses, such as repeated visits to foraging patches (Valone 2006; Fortin et al. 2013; Cristescu et al. 2015). Furthermore, long handling times associated with large ungulate carcasses [e.g., up to 10 days for a carcass >136 kg (C. T. Robbins, Washington State University, unpublished data)] are often accompanied by extensive use of nearby daybeds (Rauset et al. 2012; Cristescu et al. 2015), which also complicates carcass cluster detection and interpretation. Finally, unlike in carnivores that are territorial, extensive home-range overlap (Schwartz et al. 2003) allows opportunity for multiple bears to access the same carcass. This social component of carcass use further complicates cluster interpretation because GPS patterns from bears may differ depending on their status within a dominance hierarchy. Subordinate bears may remain near a carcass but only use it when dominant animals are absent, often selecting daybeds some distance from carcass sites. Thus, discriminating among these varied and complex patterns may benefit from alternative clustering techniques that use attributes beyond search radius and duration of visitation, such as activity data (Rauset et al. 2012).

In this study we present an alternative approach for detecting GPS clusters associated with grizzly bear use of large-biomass carcasses of ungulates in the Greater Yellowstone Ecosystem (GYE). Grizzly bears typically leave ample evidence of carcass use, or consumption, such as inversion of the carcass hide and caching behavior; however, we cannot distinguish between predation and scavenging, nor can we accurately assess the amount of biomass consumed. Therefore, to better reflect the process we can detect, we hereafter refer to GPS locations associated with carcasses as "carcass visitation." We first demonstrate how information from field investigations of grizzly bear GPS locations can be combined with data from activity sensors and GPS location clustering methods to develop predictive models that discriminate among different behavioral phenomena associated with telemetry clusters. As a case study, we applied our method to develop an index of carcass visitation. Using that index, we investigated changes in fall carcass visitation by grizzly bears in the GYE during a 10-year period (2002–2011) in which grizzly bears experienced changes in the availability of several food resources (van Manen et al. 2016).

Changes in predator [i.e., wolf (*Canis lupus*)] and prey [elk, bison (*Bison bison*), and moose (*Alces alces*)] populations occurred during our study, alongside an ecosystem-level decline of whitebark pine (*Pinus albicaulis*), a variable but calorie-rich fall food item (Greater Yellowstone Whitebark Pine Monitoring Working Group 2014). The GYE is often considered unique grizzly bear habitat compared with other interior populations because of the relative paucity of fleshy fruits (i.e., berries) and large populations of ungulates (Hilderbrand et al. 1999; Ripple et al. 2014; Schwartz et al. 2014). Previous studies (Mattson 1997;

Schwartz et al. 2014) identified ungulate meat as an alternative food for grizzly bears during years exhibiting poor whitebark pine cone production. The importance of ungulates [mule deer (*Odocoileus hemionus*), elk, moose, and bison] for grizzly bears in the GYE is well documented, both as prey and for scavenging opportunities (Schleyer 1983; Gunther and Renkin 1989; Mattson et al. 1991; Green et al. 1997; Mattson 1997; Wyman 2002). Bison experienced large fluctuations in abundance due to disease management, but overall increased during the study period (Cross et al. 2010; White et al. 2011). Elk population dynamics varied throughout the GYE, decreasing in some herds, but increasing or remaining stable in others (Creel 2010; Cross et al. 2010; Foley et al. 2015). Changes in ungulate numbers are further complicated by the complex, multi-predator relationships that also includes gray wolves, which were reintroduced in 1995 and 1996, mountain lions (*Puma concolor*), American black bears (*Ursus americanus*), and coyotes (*Canis latrans*).

Whitebark pine seeds are a calorie-rich food source for many GYE grizzly bears in fall (Kendall 1983; Costello et al. 2014). Starting in the early 2000s, whitebark pine stands experienced increased mortality of mature trees, the cohort that produces the calorie-rich seeds used by grizzly bears, primarily because of mountain pine beetle infestations [*Dendroctonus ponderosae* (Macfarlane et al. 2010, 2013; Greater Whitebark Pine Monitoring Working Group 2014; Mahalovich 2014)]. Schwartz et al. (2014) indicated that grizzly bears exhibited diet shifts in response to the natural masting cycle of whitebark pine, substituting animal matter for seeds in poor seed years and obtaining fat levels in the alternate diet equal to those in years with abundant seed crops. Mattson (1997) also found evidence of a negative correlation between fall ungulate use and whitebark pine cone production. If grizzly bears are maintaining body condition and shifting diets to increase animal matter intake, as suggested by these findings, we hypothesized that the rate of fall carcass visitation would increase over the period of whitebark pine decline. A better understanding of the use of carcasses by grizzly bears is important not only to increase our understanding of grizzly bear ecology, but also for understanding ecological dynamics and ecosystem processes related to predation in the GYE.

Materials and methods

Ethics statement

Member agencies of the Interagency Grizzly Bear Study Team (IGBST) captured grizzly bears in the GYE for research and monitoring purposes and fitted selected individuals with GPS transmitters. Grizzly bear capture and handling procedures used for this study were reviewed and approved by the Animal Care and Use Committee (no. 201201) of the US Geological Survey; procedures conformed to the Animal Welfare Act and to US Government principles for the utilization and care of vertebrate animals used in testing, research, and training. Captures were conducted under US Fish and Wildlife Service Endangered Species Permit [section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40 (b)], with additional state research permits for Wyoming, Montana, and Idaho, and National Park Service research permits for Yellowstone and Grand Teton National Parks.

Study area

The study area extent covers more than 50,000 km^2 of occupied grizzly bear range in the GYE (Bjornlie et al. 2014a). The GYE is one of the largest intact temperate-zone ecosystems in the world and extends approximately 450 km north to south and 250 km west to east, and is primarily composed of elevations above 1500 m (Newman and Watson 2009). Yellowstone and Grand Teton National Parks and portions of five national forests make up the majority of the GYE. The central Yellowstone Plateau and the surrounding mountains are covered with forests of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (Pierce et al. 2007). The GYE contains the headwaters of 25 large rivers and drainages and is traversed by the Continental Divide. The training data set was composed of bear GPS data from animals captured near Yellowstone Lake in Yellowstone National Park and throughout Grand Teton National Park [see Schwartz et al. (2010) and Fortin (2011) for descriptions of study sites used for the training data of the predictive model]. The case study involved GPS data from throughout the GYE.

Bear capture and handling

Grizzly bears were captured using culvert traps or Aldrich leg-hold snares (Blanchard 1985). With the exception of dependent offspring, captured grizzly bears were fitted with Telonics GENIII or GENIV (Telonics, Mesa, AZ) GPS collars, with on-board data storage. For studies involving on-site validation of bear activity associated with GPS locations, Telonics spread-spectrum GPS collars were used to allow remote downloads of GPS locations and timely (<10 days) site visits of randomly selected sequences of GPS locations (Schwartz et al. 2009, 2010; Fortin 2011). Because some remotely downloaded GPS data did not include activity data and may have lower precision than data stored in the collar's internal memory, we

based all analyses on GPS data from the downloaded on-board memory after collar retrieval, regardless of collar type.

GPS data processing

Activity sensors within the GPS collars included mercury tip-switch sensors or accelerometers during the time frame of our data set (2002–2011). To account for the differences in how activity data were recorded, we transformed the accelerometer data to the scale of the tip-switch sensors. We attached two collars, one collar with each technology, to each other, exposed both to equivalent movements and developed a simple linear regression model from these data ($R^2 = 0.985$; $F_{1,16} = 1,068$; $P < 0.001$; IGBST, unpublished data) to conduct this data transformation. GPS acquisition interval (0.5–3.5 h) and GPS fix success (10th percentile = 63 %; median = 84 %; 90th percentile = 93 %) varied among individuals. We used a modified version of the fill-in approach of Frair et al. (2004) to address missing locations. We randomly allocated missing locations within a rectangle defined by the previous and subsequent successful GPS locations bounding missing locations. We considered this approach conservative because filled-in locations were only candidates for clustering if they were temporally buffered by successful fixes within the same spatial cluster. Although missing locations may represent an animal that temporarily left a cluster, failed to acquire a position, and returned to the cluster prior to the next successful fix, previous studies using grizzly bear GPS data indicate that behavioral factors (e.g., lying down on antenna while resting) are more likely reasons for unsuccessful fixes when bounded by successful locations in the same area (Moe et al. 2007; Schwartz et al. 2010). GPS collars continued to record activity sensor data even when a positional fix was not obtained. Thus, filled-in fixes, with valid activity data, were sometimes combined with successful fixes to form a GPS cluster, but clusters entirely comprising filled-in locations were not possible.

We first clustered GPS data spatially using the density-based spatial clustering of applications with noise (DBScan) algorithm (Ester 1996). This flexible clustering algorithm relies on the density-based notion of clusters, does not require defining the total number of clusters a priori, allows GPS locations to not belong to any cluster, and excels at finding clusters of arbitrary size and shape. We implemented the function in MATLAB [MATLAB 2012; an equivalent clustering function is available in the fpc() package (Hennig 2015) for Program R (R Development Core Team 2014)]. The DBScan algorithm requires only two parameters: the local search neighborhood (ε) and the minimum number of locations required to qualify as a cluster (γ). We used a fixed value of $\varepsilon = 20$ m based on

the search radius of field personnel for site investigations (Schwartz et al. 2010; Fortin 2011; Fortin et al. 2013) and GPS error associated with locational fixes. The DBScan algorithm's conceptual use of density reachability allows identification of clusters much larger than ε and exploratory analysis showed the 20-m search radius to be successful at finding clusters of various sizes and shapes. To account for the different acquisition intervals among collars, we allowed γ to vary as a function of the time between GPS locations ($\gamma = \frac{7}{\text{GPS acquisition interval in hours}}$). This resulted in a minimum cluster size of two locations for 3.5-h intervals [i.e., similar to the Knopff et al. (2009) rule of two locations] and 14 locations for 0.5-h intervals.

To identify grizzly bear behaviors associated with GPS clusters, we first reduced the full GPS training data set to only locations that were identified as contributing to a cluster. We then assigned each cluster a unique identification number, an identifier for bear-year (GPS data for an individual bear in a single year), a date/time identifier, and a suite of quantitative attributes (e.g., area, duration, number of times revisited; Table 1). Although the DBScan algorithm uses only spatial information (x and y coordinates) for cluster assignment, we explicitly incorporated temporal attributes of clusters as a secondary step.

Not all clusters are simply consecutive locations of GPS fixes whereby the animal arrives and leaves only once. For example, the consumable biomass of large ungulate carcasses greatly exceeds what grizzly bears can consume in a single foraging bout. Thus, resting and digestion follow bouts of foraging, which may occur at the carcass or at daybeds near the carcass in habitats that provide more cover. Similarly, bears move throughout their home range in search of a variety of vegetative foods, some of which may only be available during short periods (Mattson et al. 1991). This may result in multiple visits to the same habitat patch over time, before the food resource reaches a consumable stage [e.g., pondweed (*Potamogeton* spp.) rhizomes (Mattson 2005)]. Therefore, clusters are often series of repeated visits, or "blocks" of consecutive GPS locations, to the same location. These blocks of locations at a cluster are separated by locations not associated with that cluster, which themselves provide important information, such as how far away the bear was between revisits and activity levels. Using this two-stage approach of first clustering spatially and then analyzing temporal sequences, we quantified temporal covariates, such as life span of clusters (temporal range), 90th percentile of duration of consecutive locations at the cluster, 90th percentile duration between revisits, mean duration between revisits (mean re-visitation interval), and maximum distance traveled away from the cluster (Table 1). This provided a rich and diverse covariate suite to identify different behaviors associated with each cluster.

Table 1 Variables used in a multinomial model to predict five behavioral states (large-biomass carcass, small-biomass carcass, non-carcass activity, old carcass, resting) associated with global positioning system (GPS) location clusters of grizzly bears in the Greater Yellowstone Ecosystem, 2004–2011

	Variable	Variable abbreviation	Description
1	Time of year[a]	Time of year	Julian day of year of cluster formation
2	Temporal range (all locations)	Temporal range	The temporal range (hours) of all locations contained by the spatial cluster
3	90th percentile of cluster visitation duration	90th_pct visitation	For the life span (i.e., temporal range of locations) of a cluster, the consecutive blocks of locations at the cluster were identified and the duration of time (fractional hours) for each consecutive block was used to calculate the 90th percentile of the duration of visitation
4	90th percentile of cluster revisitation interval	90th_pct revisitation	For the life span (i.e., temporal range of locations) of a cluster, the consecutive blocks of locations not at the cluster were identified and the duration of time (fractional hours) for each block was used to calculate the 90th percentile of revisitation interval
5	Mean revisitation interval	Mean revisitation interval	For the life span (i.e., temporal range of locations) of a cluster, the consecutive blocks of locations not at the cluster were identified and the duration of time (fractional hours) for each block was used to calculate the mean revisitation interval
6	Mean activity value	Mean activity	Mean activity value while at the cluster between the start and end times of the cluster
7	Temporal core range (removing outliers)	Temporal core range	Core temporal range of the cluster excluding temporal outlier locations
8	Proportion of possible locations in cluster	Proportion possible	The proportion of total locations in the core range (see *temporal core range* for description), dropping end locations. If all locations in the core were at the cluster, this value equaled 1.0
9	Cluster area (m^2)	Cluster area	Cluster area calculated from a convex hull of locations identified as members of the cluster
10	Mean cluster time of day[b]	Time of day	Mean time of day of cluster locations, transforming time into a circular statistic
11	Number of core subclusters	Core subclusters	Count of the number of blocks of consecutive cluster locations identified as core [density-based spatial clustering of applications with noise (DBScan) algorithm identifies cluster locations as core or edge]
12	Maximum distance from cluster	Max. distance	For the life span (i.e., temporal range of locations) of a cluster, the maximum distance of locations not at the cluster from the nearest edge of the convex hull of cluster locations

[a] Time of year was modeled as a linear function rather than a circular statistic due to denning period and fall hyperphagia

[b] Circular mean using the Program R package circular (Agostinelli and Lund 2013)

We linked the attributed GPS clusters with data from two independent field studies involving site investigations of recent (<10 days) GPS locations ($n = 54$ bear-years). These studies quantified bear activity at individual GPS locations, without considering spatial clustering, during randomly selected 24-h time periods between mid-May and mid-October 2004–2011 (Schwartz et al. 2009; Fortin 2011; Fortin et al. 2013). This merging of GPS clusters and site visit information resulted in a model training data set of 174 GPS clusters where the foraging food source or bear behavior at each cluster was observed and classified into one of five classes (large-biomass carcass, small-biomass carcass, old carcass, non-carcass activity, resting), each representing a unique category of GPS cluster type for our analysis (Table 2; see Electronic Supplementary Material).

Statistical modeling

There are two general philosophies to statistical modeling: explanatory modeling emphasizes understanding of mechanisms underlying phenomena being studied, whereas predictive modeling focuses on generating accurate predictions (Breiman 2001; Shmueli 2010; Lele et al. 2013). We modeled the five behavioral classes assessed during site visits as a function of GPS cluster attributes from a purely predictive modeling framework. Predictive accuracy generally requires more model complexity

Table 2 Behavioral states of grizzly bears associated with GPS clusters used as the response variable in a multinomial predictive model

Grizzly bear behavioral state	Description
Large-biomass carcass visitation	Presence[a] of adult elk, bison, or moose, remains and qualitative assessment of recent carcass age[b]
Small-biomass carcass visitation	Presence[a] of adult deer, elk calf, bison calf, moose calf remains and qualitative assessment of recent carcass age[b]
Old carcass visitation	Presence[a] of adult elk, bison, or moose remains and qualitative assessment of old carcass age[b]. This category implicitly includes large-biomass carcasses because remains from the small-biomass carcasses would not be detectable over a period of several months to years
Resting	Presence[a] of day bed
Non-carcass activity	Presence[a] of behaviors other than resting and carcass visitation. These may include foraging (e.g., grazing or digging) and non-foraging (e.g., rub trees) activities

Behavioral states were assigned to clusters by spatially intersecting GPS clusters with data from field surveys conducted in Grand Teton National Park and Yellowstone National Park during 2004–2011 [see Schwartz et al. (2009) and Fortin (2011) for field methods]

GPS clusters with multiple behaviors from site visits (e.g., foraging and resting) were assigned to the "active" behavior. For example, foraging and resting would be assigned to the non-carcass activity; similarly, large-ungulate carcass visitation and resting would be assigned to the large-ungulate carcass visitation category

[a] Presence refers to at least one of the GPS locations assigned to a cluster having a described behavioral class based on information collected from Schwartz et al. (2010) and Fortin et al. (2013). For clusters with multiple classes (e.g., site visit showed daybed and carcass) we gave priority to carcass categories

[b] Age of carcasses observed at GPS locations was determined qualitatively (e.g., bone bleaching and regeneration of vegetation at disturbed areas and in nearby daybeds) by trained field personnel

than simple explanatory models; simple and interpretable functions often do not make the most accurate predictors (Breiman 2001). Because our goal was to identify the best set of covariates to maximize predictive accuracy, we used a large number of candidate covariates. Under a predictive modeling framework the role of individual regression coefficients and their individual contributions to model goodness of fit are not evaluated (Shmueli 2010). Furthermore, collinearity, a concern in explanatory regression models, does not affect a model's predictive accuracy (Makridakis et al. 1998; Shmueli 2010). Accordingly, our covariate suite was complex, containing multicollinearity and complex predictor combinations (e.g., three-way interactions) that would be problematic to interpret under an explanatory modeling framework. For model assessment, rather than interpreting model parameters and goodness of fit, we focused on how well predicted cluster classes matched field observations based on withheld data using cross-validation methods (Arlet and Celisse 2010).

For the longitudinal case study in the GYE, we demonstrated the utility of predictive modeling to generate new data (predicted large-biomass carcass visitations) that can subsequently be used to test ecological hypotheses. In that application, we switched to an explanatory modeling framework using an information-theoretic approach (Anderson 2008).

Predictive model

We predicted the five cluster classes (i.e., large-biomass carcass, small-biomass carcass, old carcass, non-carcass activity, and resting) associated with each cluster using multinomial logistic regression [multinom() function in the nnet() package (Venables and Ripley 2002) in Program R]. The multinomial logistic regression model estimates the probability of a GPS cluster being associated with each of the five cluster classes, where the total probability sums to 1 for each cluster. We developed a model (*Full*) based on a suite of 12 cluster covariates that we identified as relevant to the detection of bear carcass use based on exploratory analyses of GPS data (Table 1). The *Full* model contained two-way and three-way interactions, but did not include the individual covariates of the interaction terms as main effects. This approach is statistically valid because we did not use individual covariates for interpretation (Cleaves et al. 2010; Shmueli 2010). We evaluated the effect of including the main effects in the model, but it had lower predictive accuracy than the model without the main effects. To protect against over-fitting, we used stepwise model selection based on the in-sample Akaike information criteria [stepAIC() function in the MASS package for program R] to identify a reduced model. For the stepwise AIC procedures, we used forward and backward selection, specifying the *Full* model as the upper limit of model

complexity and an intercept-only model as the lower limit (Venables and Ripley 2002).

We extracted the predicted probabilities for each cluster type and assigned the cluster category with the greatest predicted probability for both the full and reduced models. We evaluated model performance using two cross-validation techniques (leave one cluster out and leave one bear-year out) and assessed model accuracy by comparing false-negative and false-positive error rates from the out-of-sample predicted cluster classes (Arlet and Celisse 2010). Because our specific interest was to maximize the predictive accuracy of detecting large-biomass carcasses, we focused our validation on this category. We averaged false-negative and false-positive error rates between the two cross-validation approaches to select a top model.

Explanatory modeling: a case study of carcass visitation by grizzly bears in the GYE (2002–2011)

We investigated trends in estimated large carcass visitation by grizzly bears in the GYE during 2002–2011, a period of substantial decline of high-calorie, though variable, fall food: seeds of whitebark pine. Using the top predictive model and a large data set of grizzly bear GPS locations, we explored trends in ungulate carcass (i.e., large-biomass carcass) visitation from 2002 to 2011, a period that encompassed the decline of whitebark pine in the GYE. We focused our analysis on the fall season (September and October) because it represents the hyperphagic period for bears (Schwartz et al. 2003) and is the time of greatest whitebark pine use during those years when seeds are available. Fall is also the period of ungulate ruts during which some bulls are injured or killed by others (Mattson 1997). Furthermore, big game hunts occurred on much of our study area outside Yellowstone National Park during this period, providing an additional carcass supply from wounding loss and gut piles left behind after field dressing animals (Ruth et al. 2003; Haroldson et al. 2004).

We applied our clustering algorithm to GPS locations obtained for bears monitored in the GYE during 2002–2011. Using the techniques described for the predictive model, we quantified cluster attributes and estimated the most likely bear behavior state associated with each cluster. Using this subset of data, we generated an index of monthly carcass visitation for each year, explicitly accounting for the intensity of bear GPS data for each month:

where i = month, j = year, and k = unique GPS-collared bear. Finally, we limited the analysis to clusters predicted to be large-biomass carcasses during September and October.

Using multiple linear regression and an information-theoretic framework, we tested the hypothesis of an increasing trend in the carcass visitation index over the period 2002–2011. The retrospective nature of the case study and lack of control for where collared bears reside in any given year may increase the potential for sampling bias in several ways. First, the number of GPS-collared bears occupying areas near hunt units with access to gut piles may change over time. Therefore, we developed a covariate (prop_hunt) that quantified the proportion of predicted carcasses ≤1 km from areas open to hunting during each fall month and examined its support. Second, not all bears have whitebark pine as a resource in their home range (Bjornlie et al. 2014b; Costello et al. 2014). Given our hypothesis related to diet shifts and alternative food sources, we evaluated the potential bias in model inference due to changes in whitebark pine availability during the study period. Unlike access to big game hunt units, the locations of carcass clusters themselves do not provide information on availability of whitebark pine. For example, animals experiencing high whitebark pine mortality may select for alternative resources during the fall period of our analysis, but still may have had access to whitebark pine in their annual home range. Accordingly, we examined changing availability of whitebark pine over the study period by measuring mapped whitebark pine (MacFarlane et al. 2010; Greater Yellowstone Coordinating Committee, Whitebark Pine Subcommittee 2011) in individual 95 % kernel density home ranges (Kie et al. 2010) and investigated distributions and trends over time. Finally, our training data did not cover the same extent as the case study data so we did not include habitat covariates in our predictive model to allow application to areas with different habitat composition. We thus reduced bias by basing our predictive model on movement metrics only.

Whereas temporal trend (i.e., covariate year) served as a proxy for the loss of whitebark pine over time, we also tested relationships with annual whitebark pine cone availability. Whitebark pine is characterized by synchronous and intermittent production of large seed crops (usually every 2–3 years), followed by a replenishment period before a subsequent mast event (Sala et al. 2012). Thus, we explored annual availability of whitebark pine cones as a predictor of

$$\text{Carcass visitation index}_{ij} = \frac{\sum_{k=1}^{n_{ij}} \left(\text{number of predicted carcasses for bear}_{ijk} \right)}{\sum_{k=1}^{n_{ij}} \left(\text{number of GPS days for bear}_{ijk} \right)},$$

Table 3 Cross-validation results for the top predictive model (*Full*) to predict five behavioral states of grizzly bears in the Greater Yellowstone Ecosystem based on 174 GPS clusters for which behaviors were documented during site observations, 2004–2011

	Observed[a]					Total	Proportion correct
	Resting	Non-carcass foraging	Large-biomass carcass	Small-biomass carcass	Old carcass		
Model: Full—cross-validation method 1							
Resting	74	5	0	9	4	92	0.80
Non-carcass foraging	2	17	3	2	5	29	0.59
Large-biomass carcass	0	4	25	3	1	33	0.76
Small-biomass carcass	3	1	3	6	1	14	0.43
Old carcass	0	5	1	0	0	6	0.00
Total	79	32	32	20	11	174	1.00
Proportion correct	0.94	0.53	0.78	0.30	0.00	1.00	
Model: Full—cross-validation method 2							
Resting	77	4	0	9	4	94	0.82
Non-carcass foraging	1	26	2	1	5	35	0.74
Large-biomass carcass	0	1	28	4	1	34	0.82
Small-biomass carcass	1	1	2	6	1	11	0.55
Old carcass	0	0	0	0	0	0	–
Total	79	32	32	20	11	174	1.00
Proportion correct	0.97	0.81	0.88	0.30	0.00	1.00	

Out-of-sample cross-validation was based on (1) individual GPS clusters and (2) individual bear-years

[a] Results of field observation and classification of GPS clusters into the five behavioral states

the index of carcass visitation using two covariates based on alternate measures of annual whitebark pine cone production: standardized annual cone count (wbp_count) and a binary variable (mast) indicating good versus poor whitebark pine cone production years (Haroldson et al. 2004). Our suite of models ($n = 10$) included simple univariate models for each of the four covariates (year, wbp_count, mast, prop_hunt) and models of increasing complexity with two or three variables. We fitted linear models using the lm() function in the stats package in Program R (R Core Development Team 2014), and assessed model support using AIC$_c$ [AICmodavg package (Mazerolle 2014)]. We used multi-model inference following methods outlined in Anderson (2008). We performed graphical diagnostics of residuals to assess the adequacy of model assumptions using the car() package in Program R (Fox and Weisberg 2011).

Results

Predictive model of GPS clusters

Our training data set contained 174 clusters of GPS locations associated with observations at field sites where bear behavior was documented. The stepwise AIC procedures removed four main effect variables. The retention

of most variables and all interaction terms during the variable reduction procedure indicated the need for a relatively complicated model to best capture the multinomial patterns of our training data. Classification accuracy for large-biomass carcasses was greatest for model *Full*, ranging from 78 % using cross-validation based on GPS clusters and 88 % for cross-validation based on bear-years (Table 3, respectively; see Table S.1 for parameter estimates). False-positive error rates (i.e., predicted large-biomass carcasses that were observed as a different behavioral state during GPS site visits) for this model were 24 and 18 % for the two cross-validation methods, respectively.

Explanatory modeling (case study)

Using 266 bear GPS-years for 2002–2011, we applied our top model (*Full*) clustering algorithm to our data set of GPS locations for September–October ($n = 69,302$), resulting in 1997 spatial clusters distributed across the GYE. Of these, 347 were predicted to be large-biomass carcasses. The monthly (September and October) carcass visitation index derived from these data ranged from 0.005 to 0.07. Of the ten models we developed to test our research and alternative hypotheses, model 5 was the top-ranked model [$R^2 = 0.50$; AIC$_c$ weight (AIC$_c$wt) = 0.34; Table 4] and contained the covariates year ($\beta = 3.25 \times 10^{-3}$, SE = 1.02×10^{-3}) and wbp_count ($\beta = -1.02 \times 10^{-3}$; SE = 5.65×10^{-4}). The top

Table 4 Model selection results based on Akaike's information criterion adjusted for small sample size (AIC_c) for linear models of monthly (September and October) carcass visitation index for grizzly bears in the Greater Yellowstone Ecosystem, 2002–2011

Model	Model number	K^a	AIC_c	ΔAIC_c^b	AIC_c wt	Log likelihood
$\hat{Y}_i = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{wbp\_count})$	5	4	−110.30	0.00	0.34	60.48
$\hat{Y}_i = \beta_0 + \beta_1(\text{year})$	1	3	−109.94	0.36	0.28	58.72
$\hat{Y}_i = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{mast})$	7	4	−108.65	1.65	0.15	59.66
$\hat{Y}_i = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{month})$	6	4	−107.83	2.47	0.10	59.25
$\hat{Y}_i = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{prop\_hunt})$	8	4	−107.19	3.11	0.07	58.93
$\hat{Y}_i = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{prop\_hunt}) + \beta_3(\text{mast})$	9	5	−105.53	4.77	0.03	59.91
$\hat{Y}_i = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{prop\_hunt}) + \beta_3(\text{month})$	10	5	−104.33	5.97	0.02	59.31
$\hat{Y}_i = \beta_0 + \beta_1(\text{wbp\_count})$	2	3	−104.09	6.21	0.02	55.80
$\hat{Y}_i = \beta_0 + \beta_1(\text{prop\_hunt})$	4	3	−100.13	10.17	0.00	53.82
$\hat{Y}_i = \beta_0 + \beta_1(\text{mast})$	3	3	−99.95	10.35	0.00	53.73

AIC_c wt AIC_c model weight

[a] Number of model parameters

[b] Difference in AIC_c compared with lowest AIC_c model

three models (models 5, 1, and 7; Table 4) comprised 77 % of the total AIC_c weight. All three models contained the covariate year. Model 1 ($R^2 = 0.40$; AIC_cwt = 0.28; Table 4) was the second-ranked model and contained year by itself ($\beta = 3.67 \times 10^{-3}$, SE $= 1.05 \times 10^{-3}$). The third-ranked model (model 7; $R^2 = 0.45$; AIC_cwt = 0.15) contained the covariates year ($\beta = 3.89 \times 10^{-3}$, SE $= 1.05 \times 10^{-3}$) and mast ($\beta = -4.98 \times 10^{-4}$, SE $= 3.86 \times 10^{-4}$). Whereas the wbp_count covariate increased the log likelihood, the model with only year (model 1) was <2 ΔAIC_c units from the top model, indicating a marginal amount of additional information was contained in the covariate wbp_count. Similarly, the covariate for whitebark pine mast in model 7 was an uninformative parameter [$\Delta AIC_{c(7,1)} = 1.29$ (Arnold 2010)] with a maximum log likelihood close to that of model 1. Univariate models with only whitebark pine covariates (models 2 and 3) were poorly supported relative to the year-only model [evidence ratio $(E)_{2,1} = 0.05$, $E_{3,1} = 0.007$; Table 4]. These results indicate that the covariate year had the largest effect on the carcass index response variable. The predicted mean response showed a 2.3-fold increase over the course of the study period for the univariate year model (model 1; Fig. 1). We observed no evidence of a temporal sampling bias due to changes in availability of whitebark pine habitat: the area of mapped whitebark pine in home ranges showed no trend over time (Fig. S.1). Similarly, our analyses showed no evidence for a spatial sampling bias relative to hunt units over time. The covariate describing proportion of clusters ≤1 km of hunt units (prop_hunt) was not supported in a univariate model (model 4; $\Delta AIC_c = 10.17$, AIC_cwt < 0.003) and was an uninformative parameter in other models (models 8, 9, and 10; Table 4).
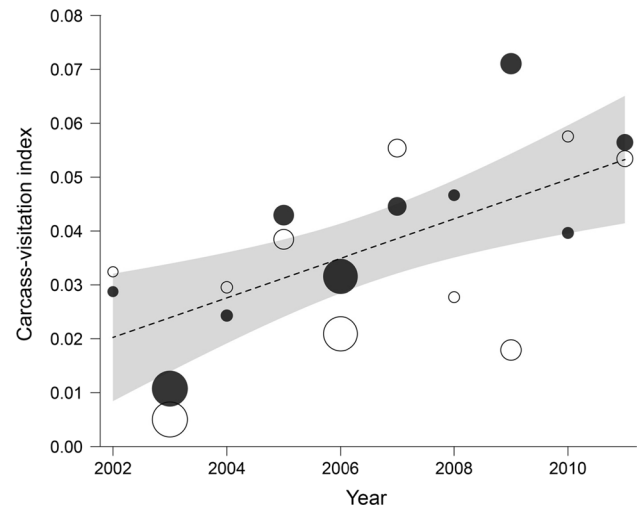

Fig. 1 Effect plot for model 1 (index ~ year) for the index of carcass visitation during September and October by grizzly bears based on predictions of behaviors associated with GPS clusters in the Greater Yellowstone Ecosystem, 2002–2011. *Area of circles* reflects the relative value of annual whitebark pine cone count. *White symbols* September, *black symbols* October, *dashed line* mean (i.e., predicted) regression response, *shaded region* 95 % confidence interval

Discussion

Advances in GPS technology for tracking wildlife have redefined our scientific approach toward, and understanding of, space use in free-ranging large mammals. Clustering of GPS telemetry locations is useful to identify restricted movements associated with long handling times of large prey species among carnivores. Until recently,

these applications have focused almost exclusively on obligate carnivores. Our study on grizzly bears, a facultative carnivore, supports conclusions from two other studies that habitat covariates are not necessary to identify grizzly bear presence at ungulate carcasses (Rauset et al. 2012; Cristescu et al. 2015). Our predictive model showed high classification accuracy for large-biomass carcasses, which was more similar to the accuracy reported by Rauset et al. (2012; ≈99 %) for small-biomass carcasses (moose calves) and Scandinavian brown bears than those reported by Cristescu et al. (2015; ≈48 %) for a grizzly bear study in Alberta, Canada. The differences in the reported accuracies between these previous studies may be partially explained by the different ecological contexts (moose calf predation by Scandinavian brown bears versus a complex, multiple predator–prey system in Alberta). Additionally, Cristescu et al. (2015) did not use activity sensor data, which helped distinguish location clusters associated with carcass visitation versus resting in our study and the Scandinavian study. Unlike the Rauset et al. (2012) study, we used activity sensor values as a continuous covariate, avoiding the loss of information associated with categorizing a continuous variable (Altman et al. 1994; MacCallum et al. 2002; Royston et al. 2006) and allowing us to directly measure behavior (e.g., foraging versus resting) at clusters. Using continuous activity data avoided potential bias from carcass visitations at times outside the normal, or a priori defined activity patterns.

Not all errors are ecologically equivalent when multiple categories for cluster types are considered. For example, the misclassification of small-biomass carcasses as large-biomass carcasses would have different ecological meaning than misclassification of resting clusters as large-biomass carcasses. Our model was robust regarding the latter of these errors, as none of these misclassifications occurred. For the former, we acknowledge that our original a priori classification of deer as small-biomass carcasses may have been inaccurate because they may generate GPS clustering patterns more similar to large-biomass carcasses. A post hoc evaluation not considering this misclassification supports this notion: overall classification accuracy increased from 78 to 88 % for cross-validation based on GPS clusters and from 88 to 94 % for cross-validation using bear-years. Similarly, false-positive errors decreased from 24 to 15 % and 18 to 6 %, respectively, for the two cross-validation methods (Table 3).

Knopff et al. (2009) suggested that GPS clustering techniques will work best for large carnivores that display high fidelity to kill locations and have long handling times. Although grizzly bears generally fit this description, visitation to carcasses can be a varied and complex phenomenon. For example, patterns of GPS clusters for bears with exclusive access to a carcass versus bears competing with conspecifics may be drastically different. Our data support field observations suggesting that subordinate bears may sometimes be restricted from prolonged access but remain nearby and repeatedly visit a carcass location for several hours to days (IGBST, unpublished data). Such behaviors result in revisits and looping patterns in the GPS data that are very different from those when a bear remains at a carcass (Fig. S.2). Similarly, the duration of GPS clusters may vary if the handling time is long and involves resting behavior, typical of carcasses with large biomass. Day beds may be either at the carcass location or nearby (10 to several 100 m) with bears repeatedly visiting the carcass to feed. Accordingly, GPS clusters at carcasses may represent feeding and resting behavior or just feeding behavior (Fig. 2). Finally, unlike obligate carnivores, grizzly bears will often usurp carcasses from conspecifics or other predators (e.g., wolves, cougars), which may be partially consumed. This variability in available biomass means not all carcasses require long handling times. Thus, the accuracy of clustering approaches developed for territorial obligate carnivores [e.g., variations on the Knopff et al. (2009) rule set] may not translate well to grizzly bears in multi-predator landscapes such as the GYE.

We suggest that the high predictive accuracy of our models is a function of using a two-step approach and a predictive modeling framework. We chose to first cluster only in the spatial dimension, using a flexible density-based algorithm (DBScan). We then explicitly incorporated time by identifying blocks of consecutive locations at, and away from, the cluster for the duration of each cluster and developed a suite of basic, yet behaviorally relevant, descriptive cluster attributes that served as predictor variables (Table 1). In contrast, other GPS clustering studies explicitly used temporal information in the clustering algorithm as a parameter (e.g., Webb et al. 2008; Knopff et al. 2009). We incorporated time external to the spatial clustering step to first capture the entire history of GPS locations for a cluster, rather than just locations within specific duration criteria. This allowed us to completely reconstruct visits to a location on the landscape for one or more GPS-collared individuals, providing information about revisits that can be useful to partition different behaviors associated with GPS clusters. For example, identifying blocks of consecutive times that a bear was at the cluster allowed us to generate useful covariates such as the number of times a bear visited the cluster, how long it stayed on average, and how far away it traveled between visits to the cluster. Whereas generation of these covariates requires complex computer coding routines, the covariates themselves are easily understood from an animal behavior perspective.

Our case study of changes in grizzly bear visitation to large-biomass carcasses demonstrates the utility of predictive modeling to generate new data that can subsequently be
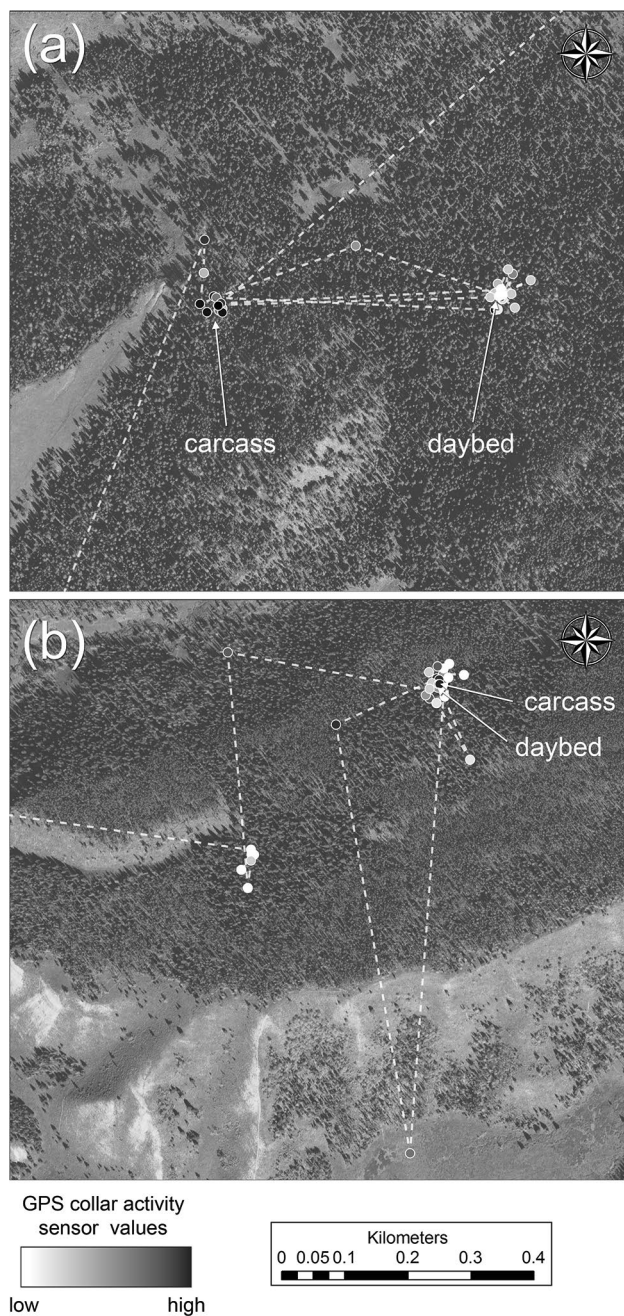
Fig. 2 Examples of grizzly bear global positioning system (GPS) telemetry locations, activity sensor data (*grey-scale* value), and cluster patterns associated with ungulate carcass visitation, Greater Yellowstone Ecosystem, 2005. **a** Bedding occurs away (450 m) from the carcass site; carcass locations are primarily high activity (*dark grey* and *black*) and day beds show low activity (*light grey* and *white*), with multiple visits to the day bed and carcass. **b** Bedding occurs at the carcass location with a mixture of activity levels represented in the cluster of GPS locations

used to explore ecological questions. Using our output of predicted clusters as a new response variable, we observed an increase in the carcass visitation index by grizzly bears during September and October over the time period of our

study. Although this time frame coincides with a period in which Costello et al. (2014) documented a decline in grizzly bear selection for whitebark pine habitat, changes to unmonitored resources may also have occurred during this time period and contributed to the decline. This unavailability of data across all potential causative factors, lack of experimental controls, and the retrospective nature of the analysis limit causal inferences for the increase in carcass visitation. Nevertheless, our findings provide additional evidence to support conclusions from previous research (Costello et al. 2014; Schwartz et al. 2014): at the population level, response of grizzly bears in the GYE to recent changes in resource availabilities may primarily be behavioral, shifting diets to alternate food sources to meet caloric and nutritional needs. Similar foraging responses (i.e., diet shifts) have been documented for other ursid populations under changing resource conditions, including polar bears [*Ursus maritimus* (Gormezano and Rockwell 2013)], black bears (Kasbohm et al. 1998), and grizzly bears (Mace and Jonkel 1986). The selection of ungulates as an alternate food is not surprising for GYE grizzly bears, a population known for its relatively high abundance of ungulate prey (Mattson 1997; Jacoby et al. 1999; Ripple et al. 2014).

Although GPS technology has provided valuable opportunities to improve the quantity of data collected on individual animals, it has also created challenges for understanding animal behavior. One of the greatest challenges is linking fine-scale GPS data with actual behavioral states associated with animal locations (Hebblewhite and Haydon 2010). Our analytical approach for grizzly bears is a key step toward this goal, linking GPS location data and animal behavior. The ability to identify locations of carcasses visited by grizzly bears may present new opportunities for researchers to better understand the drivers of grizzly bear movements, habitat use, and resource selection. Given that numerous behaviors can result in clustered animal locations, our modeling approach is broadly applicable to other species and a variety of ecological contexts. For example, revisitations to clusters may be useful for identifying parturition behavior in ungulates (e.g., Long et al. 2009,; DeMars et al. 2013), rendezvous sites and territorial boundary marking location in social carnivores (e.g., Shivik et al. 2011), and foraging dynamics in herbivores (e.g., Bar-David et al. 2009; van Morter et al. 2010).

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