



Original Article

Application of Activity Sensors for Estimating Behavioral Patterns

CALEB P. ROBERTS,¹ *Department of Natural Resources Management, Texas Tech University, Goddard Building, Box 42125, Lubbock, TX 79409, USA*

JAMES W. CAIN, III,² *U.S. Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, Department of Fish, Wildlife and Conservation Ecology, New Mexico State University, P.O. Box 30003, MSC 4901, Las Cruces, NM 88003, USA*

ROBERT D. COX, *Department of Natural Resources Management, Texas Tech University, Goddard Building, Box 42125, Lubbock, TX 79409, USA*

ABSTRACT The increasing use of Global Positioning System (GPS) collars in habitat selection studies provides large numbers of precise location data points with reduced field effort. However, inclusion of activity sensors in many GPS collars also grants the potential to remotely estimate behavioral state. Thus, only using GPS collars to collect location data belies their full capabilities. Coupling behavioral state with location data would allow researchers and managers to refine habitat selection models by using diel behavioral state changes to partition fine-scale temporal shifts in habitat selection. We tested the capability of relatively unsophisticated GPS-collar activity sensors to estimate behavior throughout diel periods using free-ranging female elk (*Cervus canadensis*) in the Jemez Mountains of north-central New Mexico, USA, 2013–2014. Collars recorded cumulative number of movements (hits) per 15-min recording period immediately preceding GPS fixes at 0000, 0600, 1200, and 1800 hr. We measured diel behavioral patterns of focal elk, categorizing active (i.e., foraging, traveling, vigilant, grooming) and inactive (i.e., resting) states. Active behaviors (foraging, traveling) produced more average hits (0.87 ± 0.69 hits/min, 4.0 ± 2.2 hits/min, respectively; 95% CI) and inactive (resting) behavior fewer hits (-1.1 ± 0.61 95% CI). We differentiated active and inactive behavioral states with a bootstrapped threshold of 5.9 ± 3.9 hits/15-min recording period. Mean cumulative activity-sensor hits corresponded with observed diel behavioral patterns: hits increased during crepuscular (0600, 1800 hr) observations when elk were most active (0000–0600 hr: $d = 0.19$; 1200–1800 hr: $d = 0.64$) and decreased during midday and night (0000 hr, 1200 hr) when elk were least active (1800–0000 hr: $d = -0.39$; 0600–1200 hr: $d = -0.43$). Even using relatively unsophisticated GPS-collar activity sensors, managers can remotely estimate behavioral states, approximate diel behavioral patterns, and potentially complement location data in developing habitat selection models. © 2016 The Wildlife Society.

KEY WORDS activity budget, behavior, *Cervus canadensis*, diel, elk, New Mexico, scale, telemetry, ungulate.

Habitat selection studies often use animal locations obtained from telemetry collars to estimate relative importance of various habitat characteristics (Johnson 1980, Rumble et al. 2001, Beyer et al. 2010). The majority of studies apply a use-versus-availability framework to estimate the value of a particular habitat attribute for animals by comparing characteristics of used and available locations, at a specified spatiotemporal scale (Johnson 1980, Millspaugh and Marzluff 2001, Johnson et al. 2006, Mayor et al. 2009, Beyer et al. 2010). Although this is a reasonable method for

making large-scale inferences on species' habitat needs, problems may arise if habitats are disproportionately important compared with their frequency of use (Spencer et al. 1990, Rettie and McLoughlin 1999, Wilson et al. 2012, Harju et al. 2013, Poessel et al. 2014). For example, habitat conditions required for specific behaviors such as mating, parturition, and foraging might not always be detectable if the spatial or temporal scales considered in the study are not correctly identified (Wiens 1989, Beyer and Haufler 1994, Mayor et al. 2009, Onorato et al. 2011, Wilson et al. 2012). Arbitrarily delineating spatial and temporal scales also exacerbates the danger of failing to detect necessary habitat components in relation to specific animal behavioral states (Rettie and McLoughlin 1999, Beyer et al. 2010, Wilson et al. 2012, Harju et al. 2013, Poessel et al. 2014).

The use of Global Positioning System (GPS) collars has become standard for habitat selection studies, with most

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¹Present address: *University of Nebraska-Lincoln, 1825 N 38th Street, Keim Hall, Lincoln, NE 68503, USA*

²E-mail: jwcain@nmsu.edu

studies using them to obtain location data (Millspaugh and Marzluff 2001). The location-obtaining capabilities of GPS collars are well-known and allow researchers to record accurate locations at fixed intervals, throughout a day, and in remote locations (Rumble et al. 2001, Kochanny et al. 2009, Frair et al. 2010). These features give researchers the opportunity to widen or narrow spatial and temporal scales assessed to nearly any specification (Moe et al. 2007, Biggs et al. 2010, Woodside 2010, De Knecht et al. 2011, Onorato et al. 2011). Although these applications provide immense benefit by aiding understanding of habitat requirements and movements by animals (Millspaugh et al. 1998, Johnson et al. 2002b, Joly 2005, Stewart et al. 2010), simply using GPS collars for location data belies their full potential as data gathering tools (Janis et al. 1999, Moe et al. 2007, Schwartz et al. 2010, Soltis et al. 2012, Wang et al. 2015).

Many GPS collars also come equipped with activity sensors that have the potential to detect and record neck and upper body movements (Ungar et al. 2005). Even for non-GPS location-measuring collars, activity sensors have been available and used for some time (Green and Bear 1990, Merrill 1991). These sensors provide the opportunity to remotely estimate animal behavior (Umstätter et al. 2008, Löttker et al. 2009, Ungar et al. 2010, Soltis et al. 2012). The most sophisticated sensors can differentiate between, and separately record, vertical and horizontal motion and tilt angle, whereas less complex models simply record any sufficiently forceful motion (Coulombe et al. 2006, Umstätter et al. 2008, Ungar et al. 2010, Wang et al. 2015). Less advanced activity sensors that separately recorded vertical and horizontal motion were still able to distinguish foraging and resting bouts in deer (*Odocoileus virginianus*; Coulombe et al. 2006), active versus inactive periods in bears (*Ursus thibetanus japonicus*; Yamazaki et al. 2008), and cattle behaviors (e.g., resting, grazing, traveling; Ungar et al. 2005, Augustine and Derner 2013). Thus, less sophisticated sensors could provide general behavioral data or gather exploratory data before researchers embark on a study with more advanced sensors (Coulombe et al. 2006, Yamazaki et al. 2008).

Although automated recording of animal behavior is useful for remotely estimating activity budgets, given that habitat characteristics sought out by animals often vary with behavior (i.e., foraging area characteristics vs. resting areas), perhaps the greatest potential benefit of GPS-collar activity-sensor data, and any other location-measuring collar, is combining location and behavior data to relate habitat selection to behavioral states. Coupling time-stamped location and behavioral data could allow researchers to empirically delineate behaviorally driven diel shifts in habitat selection without the need for direct observation of animals (Spencer et al. 1990, Arthur and Schwartz 1999, Moe et al. 2007, Wilson et al. 2012, Roberts 2015). Even using less sophisticated activity-sensor data alongside location data could grant researchers and land managers a more detailed understanding of species' habitat use and a greater ability to prioritize habitat management actions

in a time- and cost-effective manner (Hansen et al. 1992, Rumble et al. 2001, Yamazaki et al. 2008, Wilson et al. 2012).

Because elk (*Cervus canadensis*) is often a species of conservation interest and subject of numerous studies on habitat selection (Skovlin et al. 2002, Hebblewhite et al. 2008, Beck et al. 2013), behavior, and habitat use (Collins et al. 1978, Green and Bear 1990, Becker et al. 2012), it is a species with well-studied characteristics on which to test GPS-collar activity sensors. Some studies have reported on use of sophisticated GPS-collar activity sensors to delineate active and inactive behavioral states in captive elk (Naylor and Kie 2004, Gaylord 2013) and European red deer (*C. elaphus*; Adrados et al. 2003, 2008; Löttker et al. 2009). However, these studies do not assess the capability of GPS-collar activity sensors to associate elk behavioral data with location data, and 3 of 4 of these studies were conducted with captive animals, some of which were habituated to humans and not at risk of predation (Adrados et al. 2003, 2008; Löttker et al. 2009; Gaylord 2013; Roberts 2015). Human disturbance and predation risk can alter elk behavior, increasing frequency of vigilant behavior, running, and rapid erratic movements (Childress and Lung 2003, Creel et al. 2005). These types of behaviors have the potential to confound behavioral predictions from data derived from activity sensors in GPS collars (Yamazaki et al. 2008, Löttker et al. 2009).

Remotely estimating animal behavior with GPS-collar activity sensors could grant researchers and land managers greater insight into species' habitat use and requirements by 1) obtaining behavioral data throughout diel periods without time-consuming observations and 2) relating behavioral states to location data. Using free-ranging elk as an example, our objectives were to 1) use activity sensor data to remotely estimate behavioral states of free-ranging elk and 2) compare behavioral patterns throughout diel periods to activity sensor data.

STUDY AREA

We conducted this study in the Valles Caldera National Preserve (VCNP; 36,017 ha) in the Jemez Mountains of north-central New Mexico, USA, from January to August 2014. The VCNP consisted of grasslands, ponderosa pine (*Pinus ponderosa*) forests, mixed conifer forests of Douglas fir (*Pseudotsuga menziesii*), spruce (e.g., *Picea engelmannii*, *P. pungens*), firs (*Abies concolor*, *A. lasiocarpa*), and aspen stands (*Populus tremuloides*; Allen and Station 2001, Roberts 2015). Elevation ranged from 1,500 to >3,000 m. Climate was considered semiarid continental, and annual precipitation and snowfall averaged 58 cm (SD = 25 cm) and 305 cm (SD = 97 cm), respectively (National Oceanic and Atmospheric Administration 2014, Western Regional Climate Center 2015). The area had recently experienced notable wildfire activity: the Las Conchas (2011, approx. 63,536 ha) and Thompson Ridge (2013, approx. 9,712 ha) were the most recent wildfires on the VCNP at the time of the study, having burned nearly two-thirds of the preserve. On the VCNP, the Thompson Ridge fire was of

mixed severity—stand-replacing in some areas and low-severity in other areas. The Las Conchas fire was almost exclusively a stand-replacing, high-intensity fire. These fires created a mosaic of early successional shrub–forb communities between matchstick snags and patches of largely intact forests. Common predators and ungulates on the VCNP were mountain lion (*Puma concolor*), black bear (*Ursus americanus*), coyote (*Canis latrans*), and mule deer (*Odocoileus hemionus*). Limited grazing by domestic cattle (*Bos taurus*), hunting, hiking, and fishing also occurred on the VCNP.

METHODS

GPS Collars

We captured and collared adult female elk by net-gunning and darting from helicopter, or by darting from a vehicle. We deployed 6 Iridium GPS collars (Model G2110E; Advanced Telemetry Systems, Isanti, MN, USA) in January 2014, and we deployed 4 more Iridium GPS collars in March 2014. Because this study took place within a larger habitat selection study that required maximum battery life for GPS collars, we set collars to record locations every 6 hr, at 0000, 0600, 1200, and 1800 hr. Activity sensor data were recorded by collars for 15 min prior to each GPS fix. All capture and handling procedures followed acceptable methods and were approved by the New Mexico State University Institutional Animal Care and Use Committee (IACUC protocol #2011-038; Sikes et al. 2011).

Collar activity sensors were designed to detect movement in the animal and record each detected movement as a “hit.” Hits could represent any sufficiently forceful movement by the animal, from neck and head movements such as foraging or grooming to entire body movements such as walking or running. Thus, our activity sensors were relatively unsophisticated when compared with those that record movements independently along horizontal and vertical axes. For each 15-min interval in which activity sensors were recording data, collars recorded the cumulative number of hits without time-stamping them beyond the GPS fix with which they were associated. Activity sensor data were transmitted via the Iridium satellite system every 3 days along with the GPS location data.

Behavioral Data Collection

To estimate behavioral states, we used focal sampling to collect behavioral data (Altmann 1974) on GPS-collared elk during the 15-min activity-sensor recording interval prior to programmed GPS location fixes. During a focal survey, we recorded date, time, and behavioral state every minute on the minute. We considered 7 behavioral categories: foraging (browsing, grazing, drinking, standing, or moving with head below shoulder level), vigilance (standing immobile with head above or at shoulder level), resting (lying on the ground with head in any position), traveling (walking or running with head at or higher than the shoulder), aggression (social interactions involving biting, kicking, or charging), nursing (standing immobile with calf suckling), and grooming (scratching or licking; Childress and Lung 2003). When

possible, we conducted surveys from open roads, using a vehicle as a blind. Otherwise, we followed the focal animal at a great enough distance so as not to disturb it and observed it with a spotting scope or binoculars. If the focal animal was visibly disturbed so that it stopped whatever behavior it was engaged in or moved away in response, we discontinued observation of that animal immediately. As a result of the high visibility in grassland and burned portions of the VCNP, almost all collared focal animals were observed in these areas. When possible, we also used radiotelemetry to track and observe elk in spruce–fir, ponderosa pine, and burned forests. If multiple GPS-collared elk were in the same herd or area, we identified individuals by strength and direction of radio signals. Because collar very-high-frequency transmitters did not transmit between 1800 and 0600 hr, we conducted all 15-min observations except one before the 1200-hr and 1800-hr fix times. We used the Animal Behaviour Pro application installed on an Apple iPad mini 2 to record behavior (Apple, Cupertino, CA, USA; Newton-Fisher 2014, Roberts 2015).

When we had continuous, unimpeded visuals on the focal animal during activity sensor recordings, we also simultaneously performed continuous focal sampling, in which we recorded every change in the focal animal’s behavior (in practice, behavior was recorded accurately down to changes in seconds; Altmann 1974, Childress and Lung 2003). We added this continuous sampling to obtain finer scale behavioral data to relate to activity sensor data. Hereafter, we refer to the focal sampling method described in Roberts (2015) as the minute method and the continuous method described here as the continuous method.

To compare diel behavioral patterns to activity sensor data, we also used focal sampling (see above) to collect behavioral data across 24-hr diel periods on adult female elk within the same population as the collared elk. We sampled each diel hour a minimum of 3 times over a minimum of 14 days every month (Roberts 2015). We selected animals with GPS activity-sensor collars for observation when possible, but if we could not locate collared animals, we opportunistically selected adult female elk. All nocturnal behavioral observations were made from a vehicle and with light-amplifying night vision goggles (Morovision Night Vision, Inc., Laguna Hills, CA, USA).

Analysis

Comparing activity sensor hits to observed behavior.—The GPS-collar activity sensors in our study did not distinguish motion direction or time-stamp movements beyond the GPS location fix; therefore, we sought only to use activity sensor data to differentiate active from inactive behavioral states. We validated the separation of active from inactive behavioral states with multiple regression; that is, if active and inactive behavior coefficients had opposite signs (e.g., active behaviors increased the no. of hits, whereas inactive behaviors decreased the no. of hits), we could validly differentiate them. We used the amount of time elk were exhibiting specified behaviors (i.e., foraging, resting) as potential predictor variables, with the number of activity

sensor hits as the response variable in the multiple regression models. Although grouping all behaviors into active or inactive categories would meet our objectives, we also chose to estimate separate coefficients for each behavior to estimate their relative contributions to the number of activity sensor hits per recording interval. We chose predictor variables using stepwise forward and backward selection based on Akaike Information Criterion corrected for small sample size (AIC_C ; Anderson 2008, R Core Development Team 2014). Foraging and resting almost never occurred in the same observation and were the 2 most common behaviors; therefore, there was a negative correlation between them ($r = -0.89$), which prevented their inclusion in the same model. Thus, we tested 2 models, one with only active behaviors (i.e., foraging, traveling, grooming, aggression) and one with only inactive behaviors (i.e., resting, nursing). We also tested for nonlinear effects in models by adding quadratic and higher order terms. We tested regressions for heteroscedasticity of variance with the Breusch–Pagan test from the “lmtest” package in R (Zeileis and Hothorn 2002). Some previous studies considered standing or vigilance as inactive behaviors (Ungar et al. 2005, Umstätter et al. 2008), but in elk, vigilance is often interspersed with traveling and foraging (Childress and Lung 2003, Löttker et al. 2009, St Clair and Forrest 2009). To determine whether vigilance should be counted as an active or inactive behavior, we added it as a potential variable in both the active and inactive regression models. We applied stepwise model selection to the minute and continuous methods separately. We included standard error estimates for all regression coefficient estimates.

We also compared observed diel behavioral patterns to the mean number of activity sensor hits from all collared individuals. To summarize diel behavioral patterns, we calculated the percent time per hour each observed individual spent engaged in each behavioral category (Roberts 2015). We estimated the mean number of activity sensor hits for all collared elk for each 15-min pre-GPS fix interval with 95% confidence, excluding records used to validate the regressions and threshold values. We qualitatively compared activity sensor hits and behavioral patterns by creating side-by-side plots for activity sensor hits and diel behavior data. We also estimated temporally sequential effect sizes (Cohen’s d) for differences between mean activity sensor hits across diel activity-sensor recording intervals (Cohen 1988).

Threshold values.—We delineated active and inactive behavioral states during 15-min recording intervals by creating an activity sensor hit “threshold” as described by Coulombe et al. (2006) and Yamazaki et al. (2008). We considered values greater than the threshold as active and values less than or equal to the threshold as inactive (Coulombe et al. 2006, Yamazaki et al. 2008). To generate a threshold value of activity sensor hits, we selected observations completely consisting of either active or inactive behaviors, omitting mixed observations, and designed an algorithm to select the optimal threshold value. Because the success rate of a given threshold value was not the same for

active and inactive predictions, we applied the algorithm separately to active and inactive observations.

The flow of the algorithm was as follows: 1) determine the observed range of activity sensor hits per observation period; 2) predict whether each activity sensor recording was active or inactive using all values within the observed range; 3) compare active versus inactive predictions from each threshold value to the observed active versus inactive periods; 4) calculate a percent success rate of the predictions (we considered hit values where active and inactive prediction success rates differed minimally as the optimal threshold value); 5) bootstrap the sample 999 times; and 6) derive mean, standard error, and 95% confidence interval for threshold and percent success rate values from bootstrapped replicates (Coulombe et al. 2006, Yamazaki et al. 2008, R Core Development Team 2014). To determine whether vigilance was best considered active or inactive behavior, we compared bootstrapped threshold and success rate values for both categorizations. We performed all plotting and data analyses in R (Wickham 2009, R Core Development Team 2014).

RESULTS

We obtained 70 observations for the minute method and 26 for the continuous method. The number of activity sensor hits per observation ranged from 0 to 71, with an average of 18.5 (± 5.02 , 95% CI). Foraging and resting behaviors dominated observations, but elk also commonly engaged in traveling and vigilance. In minute method observations, elk never exhibited vigilance and resting in the same observation and were never vigilant or traveling for the entire length of an observation. Grooming, nursing, and aggression occurred so infrequently they could not serve as predictors for the minute method, although they were testable in the continuous method.

Multiple regression models successfully differentiated active versus inactive behaviors based on the number of activity sensor hits. Stepwise model selection found foraging and traveling behaviors to be the best predictors in the active model and only resting behavior for the inactive model. Foraging and traveling were positively associated with activity sensor hits ($\beta_{\text{foraging}} = 0.87 \pm 0.35$; $\beta_{\text{traveling}} = 4.0 \pm 1.13$; intercept = 7.75 ± 3.37 SE), and resting was negatively associated with activity sensor hits ($\beta_{\text{resting}} = -1.08 \pm 0.32$; intercept = 24.19 ± 3.05 SE). Within the active model, time spent traveling was a stronger predictor of hits than foraging. Stepwise selection did not choose vigilance for either active or inactive models. Both models were significant (active: $F_{2,67} = 9.73$, $P < 0.001$; inactive: $F_{1,68} = 11.72$, $P = 0.002$), although their R^2 values were relatively low ($R^2 = 0.20, 0.14$, respectively).

The continuous method produced model structures identical to the minute method. Both models were also significant (active: $F_{2,26} = 9.92$, $P = 0.001$, $R^2 = 0.39$; inactive: $F_{1,27} = 12.63$, $P = 0.001$, $R^2 = 0.29$); however, the continuous method increased R^2 values in the active models from 0.20 to 0.39 and in the inactive models 0.14 to 0.29 over the minute method models. The coefficients in both

models also showed the same pattern as in the minute method. Traveling still proved a stronger predictor than foraging ($\beta_{\text{foraging}} = 0.069 \pm 0.01$; $\beta_{\text{traveling}} = 0.032 \pm 0.02$; intercept = 0.68 ± 5.43 SE), and resting was negatively associated with sensor hits ($\beta_{\text{resting}} = -0.031 \pm 0.01$; intercept = 29.19 ± 4.57 SE).

Mean number of activity sensor hits differed by hour (95% CI), peaking at 0600 hr (16.36 ± 0.66 hr) and 1800 hr (20.48 ± 1.14 hr) and dropping at 0000 hr (12.66 ± 0.61 hr) and 1200 hr (8.65 ± 0.51 hr; Fig. 1). Effect sizes also demonstrated this pattern: mean activity sensor hits increased slightly between 0000 and 0600 hr (Cohen's $d = 0.19$), decreased between 0600 and 1200 hr ($d = -0.43$), increased again between 1200 and 1800 hr ($d = 0.64$), and decreased between 1800 and 0000 hr ($d = -0.39$). Over a diel period, elk engaged in active behaviors most during crepuscular periods and inactive behaviors most at midday (Fig. 1). During the night, elk switched between active and inactive behaviors (Fig. 1).

Because we never observed vigilance and resting in the same observation, we effectively either counted vigilance as an active behavior or completely removed it from the threshold analyses. Counting vigilance as an active behavior, 67 out of the total 70-min method observations consisted of either completely active or inactive behaviors. Of those 67 observations, 40 were completely active and 27 were completely inactive. Removing observations with vigilance, 18 were completely active and 27 were completely inactive. Neither the bootstrapped threshold nor the success rates changed whether vigilance was counted as active (threshold = 5.95 ± 3.68 ; success rate = $69\% \pm 13\%$) or inactive (threshold = 6.89 ± 4.27 ; success rate = $71\% \pm 15\%$), although counting vigilance as active reduced standard errors and confidence interval widths. Only 2 observations in the continuous method contained completely active or

inactive behaviors, so it could not be used to determine an activity-sensor-hit threshold value.

DISCUSSION

Our qualitative comparison of activity sensor hits across diel periods indicates that these activity sensors can be used for remotely estimating diel behavioral states and associating behavioral states with location data. Mean number of activity sensor hits over diel periods coincided with observed diel behavioral patterns of free-ranging elk. These observed patterns are also consistent with results of previous behavioral studies on elk, which tend to be most active during crepuscular periods, less active during midday, and oscillate between active and inactive behaviors at night (Green and Bear 1990, Toweill and Thomas 2002). We did not always perform diel behavioral observations on collared elk; therefore, we could not directly assess the relationship between activity sensor hits and diel behavioral patterns outside periods of our observations. Despite this, we found active behaviors (foraging and traveling) to be positively related to GPS-collar activity-sensor hits and inactive behavior (resting) to be negatively related to activity sensor hits, even with a relatively low sample size.

Our study also demonstrated the potential to estimate diel behavioral patterns with relatively coarse activity sensor data. Although studies with similar objectives and methods obtained greater success rates ($\geq 90\%$), those studies used captive animals and much more sophisticated motion-sensor-equipped GPS collars capable of recording much finer scale movement data (Ungar et al. 2005, 2010; Umstätter et al. 2008; Löttker et al. 2009; Gottardi et al. 2010; Gaylord 2013). However, the less sophisticated motion sensors used in our study still produced relatively accurate estimates of active and inactive behavioral states and reflected the diel behavioral patterns commonly observed in elk. Thus, less sophisticated sensors would be sufficient for describing general behavioral state, associating behavioral patterns with location data, or providing preliminary behavioral data before launching a more in-depth behavioral or habitat selection study (Moe et al. 2007, Schwartz et al. 2010).

For managers and researchers wishing to remotely estimate the behavioral states of free-ranging animals, logistical and budgetary constraints are often essential considerations. Given the time and cost of capturing animals and replacing collars because of battery depletion, the short fix and frequent activity-sensor recording interval commonly used in studies of captive animals may not be applicable to studies of free-ranging wildlife (Johnson et al. 2002a, Latham et al. 2015; but see Brown et al. 2012). Studies of captive animals obtained more frequent fixes, larger sample sizes, did not have to balance fix frequency with battery longevity, and could replace collars at will with relative ease (Ungar et al. 2005, 2010; Coulombe et al. 2006; Löttker et al. 2009; Gaylord 2013). More frequent fixes and larger sample sizes in controlled, captive settings would tend to improve model and threshold fits—an undoubtedly desirable goal (Frair et al. 2004). Our results suggest that use of less sophisticated collars that record somewhat infrequently may still allow for

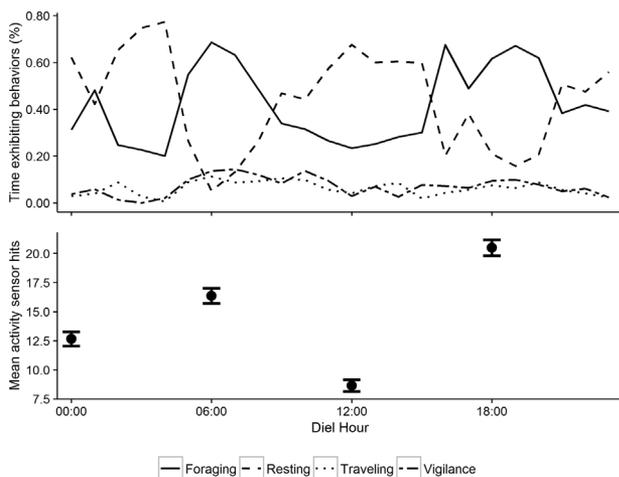


Figure 1. Mean percent of each diel hour female elk exhibited foraging, resting, traveling, or vigilance behavior (top panel), and mean number of cumulative activity sensor hits per 15-min period recorded every 6 diel hours by GPS-collar activity sensors on female elk (bottom panel) in the Jemez Mountains, New Mexico, USA, during 2014. Error bars indicate 95% confidence limits.

remote estimation of behavioral state. Our study coincided with a long-term habitat selection study on free-ranging elk; therefore, we set relatively wide temporal intervals between activity sensor recordings (6 hr) to optimize battery longevity. This provided only isolated samples of behavior within a wide range of variability over diel periods, but it still corresponded with observed diel behavioral patterns. For future studies seeking to gather more continuous behavioral data via activity sensors, we suggest that synchronizing activity sensor recordings with location fixes and spacing recordings out so that each diel hour is evenly sampled (e.g., 5-hr fix intervals) could allow researchers to estimate diel behavior and empirically establish temporal delineations for modeling of diel habitat selection or activity budgets while avoiding temporal and spatial autocorrelation issues and optimizing battery longevity (Orians and Wittenberger 1991, Millsaugh and Marzluff 2001, Latham et al. 2015).

Inaccuracies and lower precision in threshold predictions in this study may have stemmed from several sources. Foraging dominated most active observations; although elk often moved while foraging, they tended to keep their heads and necks down and relatively still. This could contribute to the reduced magnitude of effect of foraging on activity sensor hits compared with traveling. Also, the inactive regression model only explained a small amount of variation in activity sensor hits likely because even while resting, any head or neck movement could produce an activity sensor hit. In most inactive observations, resting elk kept their heads up, surveying their surroundings, ruminating, or grooming. Because we defined any behavior while lying on the ground as resting, we could not distinguish movements while resting from more completely inactive behaviors. Idiosyncratic behavioral differences between individual elk and the tightness of the collars on their necks also could have influenced how motion registered on collar sensors (Löttker et al. 2009).

The accuracy of threshold predictions could be increased by accounting for how collars are fitted on individuals, individual elk behaviors, and minimum amount of force necessary to result in a hit (Yamazaki et al. 2008, Löttker et al. 2009, Gaylord 2013). Physiological differences in elk could also explain more variation in activity sensor hits (Löttker et al. 2009). Perhaps most importantly, recording head and neck movements alongside categorical behaviors could account for variation in activity sensor hits between active and inactive states (Coulombe et al. 2006, Löttker et al. 2009, Gaylord 2013).

Behavioral prediction success rates did not differ when defining vigilance as an active or inactive behavior, but defining vigilance as active did narrow confidence intervals because more samples were included in the analysis. Although vigilance was not related to activity sensor hits in regression models, it always occurred amid active behaviors (foraging, traveling, and grooming) during our observations. Other behavioral studies on free-ranging elk have found vigilance to be associated with active behaviors (Childress and Lung 2003, Wolff and Van Horn 2003). Also, transitions between foraging or traveling and vigilance

could have triggered activity sensors as elk raised and lowered their heads. Thus, it seems reasonable to categorize vigilance as an active behavior for the purpose of GPS activity-sensor behavioral predictions.

Most habitat selection studies using GPS technology collect incredible amounts of location data, but they often do not explore its full potential. Using GPS-collared elk as an example, our study demonstrates the potential and benefits of associating animal behavioral data with location data and outlines a time- and cost-effective method to remotely estimate behavior. It also shows that accurate predictions of general behavioral state can be made even with relatively unsophisticated activity sensors.

MANAGEMENT IMPLICATIONS

Using less sophisticated GPS-collar activity sensors with coarser recording intervals could provide general behavioral data while also optimizing GPS-collar battery longevity. Monitoring animal behavior remotely could also reduce time and resources needed to obtain behavioral data, minimize stress from human disturbance, and decrease the bias human presence may impose on behavioral observations. Other specific ways in which researchers and land managers could benefit from remote estimation of animal behavior include 1) the ability to associate animal behavioral states with location data, which could aid in understanding the importance organisms allocate to those habitats and further inform management decisions regarding those habitats; 2) the ability to address questions regarding behavioral responses to various stimuli such as predator presence, human-induced (e.g., recreation, logging), or natural disturbances (e.g., wildfires); and 3) obtaining behavioral data from all diel hours, which could establish empirical temporal delineations for diel habitat selection analyses or simply provide behavioral data on species that are difficult to observe at night.

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