Contrasting daily and seasonal activity and movement of sympatric elk and cattle.

Patrick E. Clark^{1*}, Douglas E. Johnson², David C. Ganskopp³, Martin Varva⁴, John G. Cook⁵,
Rachel C. Cook⁵, Frederick B. Pierson¹, and Stuart P. Hardegree¹.

Abstract

Elk (*Cervus elaphus* L.) and cattle (*Bos taurus* L.) co-occur on rangelands throughout western North America. Literature regarding range relations between elk and cattle, however, is contradictory describing interspecific competition in some cases and complementary or facilitative relations in others. A better understanding of how sympatric elk and cattle behave at fine spatiotemporal scales is needed to properly allocate resources for these species. We used intensively-sampled GPS tracking data (1-sec intervals) to classify elk and cattle behavior and investigate their activity and movement strategies in the Blue Mountains of northeastern Oregon, USA, during summer and fall 2007. An ensemble classification approach was used to identify stationary, foraging, and walking behavior classes within the GPS datasets of mature beef and captive elk cows grazing in forested pastures during two randomized experiments, one in summer and the other fall. During summer, elk traveled further per day, had larger walking budgets, exhibited more and longer walking bouts, and had higher walking velocities than beef cows. Cattle tended to emphasize intensive foraging over extensive movement and thus displayed larger foraging budgets and longer foraging bouts than elk. Site by species interactions, however, were detected for some foraging responses. During fall, when forage quality was limiting, elk exhibited a more foraging-centric mobility strategy while cattle emphasized an energy conservation strategy. These differing movement and energetic strategies tended to support the concept that elk and cattle occupy differing behavioral niches. Extensive foraging by elk and intensive foraging by cattle during summer correspond well with behaviors expected for elk searching out forbs in graminoid-dominated habitats and cattle foraging intensively on graminoids. Behaviors exhibited in the fall were consistent with elk continuing to

1 exercise more selectivity among the available forage than cattle. These differing strategies,
2 consequently, would moderate the potential for direct interspecific competition during summer
3 and fall.

4

5 **Keywords:** Behavior, *Bos taurus*, *Cervus elaphus*, GPS tracking, Range relations.

1 **Introduction**

2
3 Elk (*Cervus elaphus* L.) and cattle (*Bos taurus* L.) co-occur on range and forest lands throughout
4 much of western North America. In the continental U.S. alone, sympatric elk and cattle may
5 interact on more than 1.1 million km². As a native ungulate, elk function as an important
6 ecosystem component and as a huntable/viewable species elk represent a high-value income
7 source for rural economies (Bolon, 1994). Revenues from rangeland cattle production are also of
8 critical importance to many rural economies. Annually, many millions of kg of beef are
9 produced on rangelands shared with elk (NASS, 2016). Consequently, proper management of
10 sympatric elk and cattle is of substantial ecological and economic importance.

11 Elk and cattle exhibit some broad similarities in dietary and habitat preferences (Beck
12 and Peek, 2005; Hansen and Reid, 1975; Mackie, 1970; Sheehy and Vavra, 1996; Steven, 1966).
13 Consequently, there has been a long-standing concern that these species compete with each for
14 space and resources (Julander and Jeffery, 1964; Morris, 1956; Nelson, 1982; Olson, 1943;
15 Skovlin, 1968; Smith, 1930; Stewart et al., 2002; Yeo et al., 1993). Yet, despite these
16 similarities and overlaps, sympatric elk and cattle are not necessarily competitors. There is, in
17 fact, suggestive evidence of neutral or even complementary or facilitative relations between
18 these species (Anderson and Scherzinger, 1975; Grover and Thompson, 1986; Hobbs et al.,
19 1996). The question of whether elk and cattle are competing for resources, partitioning
20 resources, or sharing resources is complex and may have multiple answers depending on the
21 scale and seasonal timing of interest.

22 Regrettably, most if not all studies of resource partitioning between elk and cattle have
23 been conducted at relatively coarse scales (e.g., habitat type or broader). Even as the increasing

1 use of GPS tracking technologies improves the spatial resolution of available data, the temporal
2 coarseness of the typical tracking dataset (e.g. hours or 10s of minutes) largely precludes their
3 use for investigating elk-cattle relations at the patch and finer scales. For example, studies at the
4 Starkey Experimental Forest and Range (SEFR) within the Blue Mountains of northeastern
5 Oregon have reported evidence of resource partitioning and competitive exclusion between elk
6 and cattle (Coe et al., 2001; Stewart et al., 2002). Data in these studies were acquired with
7 LORAN-C automated telemetry at intervals of about 1-1.5 hr and thus allowed resource-
8 selection analyses at the landscape scale. Evidence of resource partitioning at landscape scales,
9 however, does necessary translate to range relations occurring at the patch scale.

10 Comparative studies suggest dietary overlaps between elk and cattle are often temporally
11 offset (e.g., winter elk diets $\approx$ summer cattle diets) and occur more often in specific habitat types
12 than in others (Beck and Peek, 2005; Stevens, 1966). Research at the SEFR suggests elk and
13 cattle may occupy differing dietary niches during summer (Stewart et al., 2003). Elk summer
14 diets tend to be dominated by forbs while cattle diets are graminoid-dominated (Scasta et al.,
15 2016; Torstenson et al., 2006). Consequently, from a dietary perspective, elk and cattle could
16 occupy the same vegetation patch but exploit that patch quite differently. It is also quite likely
17 these differing dietary preferences would promote differing behavior patterns between sympatric
18 elk and cattle. In habitats where the understory is dominated by graminoids, as is common
19 throughout the Blue Mountains, cattle foraging on graminoids would likely be less motivated
20 towards mobility than elk searching out forbs within a background of graminoids. In such cases,
21 elk would probably travel further per day and express more transitions between foraging and
22 walking bouts than cattle. Selective foraging and a focus on mobility by elk would, however,
23 come with an increased energy cost. Foraging theory suggests these increased expenditure costs

1 must be offset by nutritional gains (Charnov, 1976; Parker et al., 1996; Wickstrom et al., 1984)
2 and that elk seeking out a forb-rich diet might pursue an energetic strategy quite different from
3 that of cattle at the patch-scale (Bergman et al., 2001). Our understanding of these fine-scale
4 relations between elk and cattle, however, is still quite narrow. This limitation stems largely
5 from past difficulties in continuously observing cryptic ungulates like elk throughout both day
6 and night (e.g., Crane et al., 2016). While developments in GPS tracking technologies certainly
7 have the potential to address this observation problem, to date no comparative GPS tracking
8 studies of sympatric elk and cattle have been conducted at scales fine enough to resolve patch-
9 scale behaviors. Consequently, management of sympatric elk and cattle has depended on science
10 conducted at relatively coarse scales and thus the influence and complexity of fine-scale
11 interspecific relations remain poorly understood and largely unaccounted for.

12 The goal of the current study was to address this knowledge gap using intensively-
13 sampled GPS tracking (1-sec intervals) data acquired from elk and cattle at the SEFR during
14 summer and fall 2007. The specific objectives were to: i) contrast behavioral responses (e.g.,
15 daily distance traveled, activity budgets, and movement path characteristics) of sympatric elk and
16 cattle at fine spatiotemporal scales on forested rangeland and, ii) interpret fine-scale behavioral
17 similarities and/or differences within contexts of niche partitioning, competitive or
18 complementary range relations, and comprehensive resource-allocation management.

Materials and Methods

Study Area

This study was conducted at the SEFR, a USDA Forest Service research area (45.24367° N Lat, 118.51333° W Lon) in the Blue Mountains of northeastern Oregon about 48 km southwest of La Grande (see Rowland et al., 1997 for additional background). Two sites, Barn-Upper and Cuhna, located near the Handling Facilities of SEFR were subdivided by electric fencing into a two adjacent pastures per site. Barn-Upper contained the Barn and Upper pastures while Cuhna contained the Cuhna East and Cuhna West pastures.

The Barn pasture (8.1 ha) was located at a mean elevation of 1,256 m and gently sloped (3.1-6.5°) towards the northeast. Mean elevation of the Upper pasture (13.7 ha) was 1,268 m with a northeasterly aspect and slopes of 0.63-6.1°. Based on the Hall (1973) plant community-type classification system, vegetation on both the Barn and Upper pastures was dominated by a mixed conifer community (Ponderosa pine [*Pinus ponderosa* Lawson & C. Lawson], Douglas-fir [*Pseudotsuga menziesii* {Mirb.} Franco], and grand fir [*Abies grandis* {Douglas ex D. Don} Lindl.]) with a pinegrass (*Calamagrostis rubescens* Buckley) understory (Hall CW-G1-12). Mean graminoid cover for this community generally ranges from 20-80% while forb cover ranges from 0-20%. The Upper pasture also contained about 1.9 ha of a dry meadow community (Hall MD) composed of primarily of Sandberg bluegrass (*Poa secunda* J. Presl) and rough bentgrass (*Agrostis scabra* Willd.). Forbs are generally uncommon or rare in this community type but western yarrow (*Achillea millefolium* L.), tapertip onion (*Allium acuminatum* Hook.) and few other forb species did occur as trace-1% cover within the grasslands at this site.

Herbaceous standing crop in forested communities ranged 1,108-2,237 kg DM ha⁻¹ when sampled on 29 June 2007 (Summer). Standing crop in the dry meadow community at Upper was 1,573 kg DM ha⁻¹ on that date. Fall standing crop (sampled on 22 September 2007) ranged 641-821 kg DM ha⁻¹ in forested communities and 428 kg DM ha⁻¹ in the dry meadow. Soils underlying the forested community at both Barn and Upper were coarse-loamy, isotic, frigid vitrandic haploxerepts and soils associated with the dry meadow community were classified as loamy-skeletal, mixed, superactive, frigid lithic haploxerolls.

The Cuhna West (16.6 ha) and Cuhna East (17.1 ha) pastures occurred on a northeasterly aspect at mean elevations of 1,207 m and 1,185 m and slopes of 2.3-7.6° and 0.71-7.9°, respectively. Within the Cuhna West pasture, an area of 4.3 ha, representing the lowest elevations, was dominated by a Ponderosa pine-Douglas fir-snowberry (*Symphoricarpos albus* [L.] S.F. Blake)-oceanspray (*Holodiscus discolor* [Pursh] Maxim.) community (Hall CD-S6-11; Hall, 1973). Graminoid cover generally ranges from 10-40%, forb cover from 0-5%, and shrub cover 20-70% in this community type. A dry meadow community of rough bentgrass, Kentucky bluegrass (*Poa pratensis* L.), intermediate wheatgrass (*Thinopyrum intermedium* [Host] Barkworth. & D.R. Dewey), and rushes (*Juncus* sp.) with trace amounts of forbs (e.g. western yarrow) occurred on the remainder of the pasture. Vegetation in the lowest elevations of Cuhna East was also classified to the Ponderosa pine-Douglas fir-snowberry-oceanspray community (6.4 ha). An additional 1.6 ha of these low-lying areas occurred as a Ponderosa pine-Douglas fir-elk sedge (*Carex geyerii* Boott) community (Hall CD-G1-11). Graminoids typically occur with 30-60% cover, forbs 0-5%, and shrubs 0-30 cover in this community type. The remainder of the pasture was dominated by the dry meadow community type described above. Summer standing crop ranged 2,901-4,039 kg DM ha⁻¹ in forested communities and 2,513-3,084 kg DM ha⁻¹ in the

dry meadow community. Standing crop in fall ranged from 1,252-1,546 kg DM ha⁻¹ in forested communities and 1,003-1,059 kg DM ha⁻¹ in the dry meadow. Soils under the forested communities were coarse-loamy, isotic, frigid vitrandic haploxerepts and were loamy-skeletal, mixed, superactive, frigid lithic haploxerolls under the dry meadow community.

Experimental Design

This study included two experiments, one conducted during summer coinciding with peak production of native forages in the study pastures and the other occurred during early fall after these forages had fully senesced and cured. The availability of palatable, high quality forage was not limiting during the summer experiment. Although the quantity of forage was not limiting during the fall experiment, the nutritional quality and palatability were almost certainly limiting (Clark et al., 1998, 2000; Westenskow-Wall et al., 1994). Two trials were conducted sequentially during each experiment. A crossed or within-subjects experimental design (Jones and Kenward, 2003), commonly used in medical trials, was employed here to detect and isolate any pasture effects on animal behavior. As such, animal subjects randomly assigned to one pasture during first trial (i.e., trial A) of an experiment were assigned to the remaining pasture within the site for the second trial (i.e., trial B).

Cattle used in this study were mature beef cows of Hereford, Black Angus, and crossbred breeding provided by the Eastern Oregon Agricultural Research Center at Union, Oregon. These cattle were selected from a herd which grazed the SEFR each summer and thus were familiar with the terrain and vegetation on the study area. The summer experiment was stocked with lactating cows with calves at the heel. This cow-calf pair composition is typical of herds grazing

publicly-owned forested rangelands in the Pacific Northwest and Northern Rocky Mountain regions during summer. In fall, however, calves are typically removed from the range for weaning while the cows, now dry, remain on the range. Consequently, to simulate this typical context, we stocked our fall experiment with dry cows whose calves had recently been weaned. Elk were mature, dry cows which had been raised since birth as research animals and were thus accustomed to and tolerant of human proximity. These elk were part of a research herd maintained at SEFR in a forested pasture near the study sites and, consequently, were familiar with the site conditions and accustomed to wearing research instrumentation. While the use of dry elk cows in our experiments may initially seem somewhat discordant, some points of context are necessary here to justify our stocking decisions. First, lactating captive elk cows are difficult to obtain and, in our case, were simply not available. Captive, dry elk cows were, however, quite readily available at the SEFR. Second, about 60-75% of cow elk within wild herds of the Pacific Northwest and Northern Rocky Mountains are dry and without calves during summer and fall (IDFG, 2014; MFWP, 2004; ODFW, 2003). As such, use of dry elk cows in our experiments is, in fact, representative of a substantial component of wild elk herds. The reader is cautioned, however, to recognize that dry elk cows are contrasted with lactating beef cows in the summer experiment thus, for strict interpretations, species and lactating status are confounded. The reader should also note that, although these were captive elk, we assumed their behavior, activity budgets, and movement characteristics would be similar to those of free-roaming wild elk under typical wildland settings within the Blue Mountains.

The first of the two summer trials began on 21 June 2007. Ten beef cows and ten elk cows were fitted with custom GPS collars (Clark et al., 2006) programmed to acquire positional fixes, fix-quality parameters, and instantaneous velocities at 1-sec intervals. According to a

1 randomized assignment within the crossed experimental design, 5 of the collared beef cows were
2 released into the Barn pasture and the remaining 5 cows were released into the Cuhna West
3 pasture. Five of the collared elk cows were released into the Upper pasture and 5 elk into the
4 Cuhna East pasture. Since none of the study pastures contained natural water or mineral sources,
5 cattle and elk were supplied with a water trough and a mineral block at one central location
6 within each pasture. Cattle and elk were allowed to graze the study pastures for 7 days with the
7 first day considered as a pre-trial acclimatization period. Beginning on the second day (22 June
8 2007), direct observations of animal behavior were recorded using the focal-animal methodology
9 described by Altmann (1974) and previously applied under study conditions similar to ours by
10 Ganskopp (2001) and Ganskopp and Bohnert (2009). Within each study pasture, a focal animal
11 was selected from the 5 animals present and this animal was visually observed continuously from
12 a distance of 25-50 m for up to 8 hr during the daylight hours. Behaviors exhibited by this
13 animal which lasted longer than a 30-sec minimum duration were classified and recorded into an
14 ethogram as one of 5 non-mobile classes; bedding, standing, grooming, drinking, and mineral
15 consumption or one of 2 mobile classes; foraging and walking. The timing of each transition
16 between exhibited behaviors was recorded to the nearest 30-sec interval. If the focal animal
17 moved out of visual range of the observer, the session was either suspended until the observer
18 reacquired visual tracking of the focal animal or terminated and a new focal animal was selected.
19 Observation sessions of less than 30 min total (i.e., excluding suspended time segments) were
20 discarded as inadequate in length. Only one or two observers were allowed within a study
21 pasture at any one time in order to reduce any potential behavior disruption in the study animals.
22 During the course of 5 days of observation (22-26 June 2015), attempts were made to observe
23 each of the twenty study animals for at least the 30-min minimum duration. On 27 June 2007,

the first trial ended and the animals were gathered and removed from the pastures, GPS collars were recovered, data downloaded, and the collars were refitted for the next trial.

The pre-trial period for the second summer trial (B) began on 27 June 2007, after the study animals had been re-collared and released into their assigned pastures. According to the crossed design, animals formally in the Barn pasture were released into the Upper pasture and vice versa. A similar reversal was applied for animals in the Cuhna study site. The GPS tracking and visual observations of behavior were conducted as in the first trial (A). The summer experiment ended on 4 July 2007. The fall experiment was conducted in a similar fashion to that of the summer experiment. Animals entered the first fall trial (A) on 19 September 2007 and on 25 September during the second fall trial (B).

Most of the GPS collars provided viable tracking data sets throughout the study. All cattle collars functioned well during both, summer trial A (n=10) and trial B (n=10). However, one of the ten elk collars failed during summer trial A (n=9) and 2 elk collars failed during summer trial B (n=8). During fall, only one collar failed, which was a cattle collar deployed during trial A (n=9). Despite these equipment failures, data sets were produced for both the summer and fall experiments which were well replicated at the species, pasture, and trial levels.

Classification of GPS Data

Concurrently-collected subsets of visual observations and GPS data were used to develop a training set for classifying all GPS data from both experiments into behavioral classes. Visual data from 3 beef cows and 4 elk having the longest, uninterrupted observation periods were used for this training set. Visual data not included in the training set were reserved for use later in

1 assessing classification model predictions. A review of the behavioral classification literature for
2 cattle indicated accurate classification of the non-mobile behaviors into separate classes would
3 likely be extremely difficult with GPS-based predictors alone, i.e., without the benefit of data
4 from accelerometers or other activity sensors (e.g., Augustine and Derner, 2013; Dutta et al.,
5 2015; Gonzalez et al., 2015; Ungar et al., 2005; Wang et al., 2015). Our early analysis attempts
6 confirmed this assumption. Consequently, the 7 behavior classes recorded in the visual
7 observation data were reduced to 3 classes by combining all the non-mobile classes into a single
8 class, stationary, and retaining the two mobile cases, foraging and walking.

9 The GPS data from the training set were used to derive 39 predictor variables pertaining
10 to net displacement, cumulative distance traveled, velocity, or tortuosity of movement. These
11 variables were developed by aggregating the 1-sec GPS data as 30-sec or 30-row moving sums,
12 averages, and differences. Leading, lagging, and centered windows were applied. In addition,
13 15-sec leading and lagging windows and their average were also applied. Shorter and longer
14 moving windows (e.g., 10- and 60-sec) were considered but given the 30-sec resolution of the
15 visual observation data, we choose to use the 30-sec window size to derive our predictors.

16 Classification was conducted using bootstrapped averaging of decision trees, an ensemble
17 classification modeling approach implemented in the Bootstrap Forest routine of the software
18 package, JMP Pro®. An ensemble is a supervised machine-learning approach that applies
19 multiple models to obtain enhanced predictive performance over that of the individual
20 constituent models. The mathematical foundations for bootstrap aggregating of trees was
21 developed by Breiman (2001), whose trademarked implementation, RandomForests™, has
22 become quite well known as its utility has spread across many scientific disciplines. In general,
23 this approach is based on the development of many decision trees from random samples (with

replacement) of observations drawn from a training set of response and predictor variables. In Bootstrap Forest, the predicted values from these many constituent trees are averaged to provide predicted values for the ensemble. Recent studies have applied the bootstrap-aggregation approach to classifying animal behavior from accelerometer sensor data (Dutta et al., 2015; Wang et al., 2015). However, to our knowledge, this approach to behavioral classification has not previously been used with predictors derived solely from GPS-derived data.

Within Bootstrap Forest, we used the visual classification data as the response (Y) and the 39 predictors as the factors (X). The original training dataset were split in to 3 random subsets where 60% were used for model development and 20% each were reserved as validation and testing subsets. Three classification models were developed; one using the full training set of elk and cattle data combined and separate models for elk only and for cattle only. A maximum of 500 decision trees were fitted for each model with a maximum of 10 sampled predictors per split. The multi-species model involved 45 decision trees with 9 sampled predictors per split and yield an overall misclassification rate of 10.2% for the validation subset. The elk model consisted of 81 trees and 9 predictors per split and misclassified 8.9% of the validation data overall. Overall, the cattle model misclassified 10.1% of the validation set and consisted of 108 trees with 9 predictors per split. The variables Vel30, Chord30, VelAvg15, and ChordAvg15 were the 4 top contributing predictors in all 3 models. Vel30 represents velocity (kmh) based on net displacement during a 30-sec centered moving window. Chord30 represents net displacement (m) for a 30-row moving window and thus does not compensate for missing positions in the GPS time series. VelAvg15 is the average of velocities (kmh) for 15-sec leading and lagging windows. Similarly, ChordAvg15 is the average net displacement (m) for 15-row leading and lagging windows. In the elk model, Arc30, which represents the cumulative distance

traveled during a 30-row centered window, was the fifth top contributor. AVel30, velocity based on cumulative distance traveled during a 30-sec centered moving window was the fifth top contributor in the cattle model. The remaining factors in each model made only relatively minor contributions to the classifications.

We used the Model Comparison routine in JMP Pro® to conduct an Area Under Curve (AUC) comparison of the 3 classification models to determine if the species-specific models outperformed the multi-species model. Chi Square tests indicated the cattle model performed better than the multi-species model for classifying foraging ($P < 0.0001$) and stationary ($P < 0.0001$) behavior from cattle GPS data but the two models performed similarly for walking ($P = 0.1553$). The elk model performed better than the multi-species model for all 3 behavioral classes ($P < 0.0001$). Consequently, rather than using the multi-species model, we choose to apply the species-specific models to classify the elk and cattle behaviors from the full GPS data set. The predictive performance of these two models on the full set was assessed using the reserved visual observation data from 4 beef cows and 4 elk. Tables 1 and 2 present the resultant classification accuracy, specificity, sensitivity, F_1 score, and false discovery rate (FDR) for each behavioral class of the elk and cattle models, respectively. Classification accuracy was calculated as: $(\text{true positive} + \text{true negative}) / (\text{true positive} + \text{false positive} + \text{true negative} + \text{false negative})$. Specificity was: $\text{true negative} / (\text{true negative} + \text{false positive})$. Sensitivity was calculated as: $\text{true positive} / (\text{true positive} + \text{false negative})$. The F_1 score is the harmonic mean of precision and recall calculated as: $2 * \text{true positive} / (2 * \text{true positive} + \text{false positive} + \text{false negative})$. The false discovery rate was: $\text{false positive} / (\text{true positive} + \text{false positive})$. Generally, the classifier performed quite well yielding an overall accuracy of 94.4% for the elk model and 93.1% for the cattle model. These findings confirm intensively-sampled GPS data alone are

adequate for accurately classifying elk and cattle behavior into basic classes like stationary, foraging, and walking behaviors.

Calculation of Response Variables

Once behavioral classification was completed, the 7 response variables of interest for this study were derived. Daily travel distance (km day^{-1}) was calculated for each animal-day as the cumulative sum of displacement distances for 1-sec GPS positional data classified as either foraging or walking. Individual bouts (30-sec minimum duration) of each of the 3 behavior classes were identified and tallied for each animal-day. Duration (sec) of each bout was also recorded by behavior class for each animal-day. Activity budgets for each animal-day were determined by summing the bout durations by class and calculating the proportion of the animal-day represented by each behavior class. Movement path lengths were determined for each foraging or walking bout based on cumulative distance moved during the bout. Foraging and walking path tortuosities were calculated as the ratio between the cumulative distance moved and the net displacement distance between the start and ending position of the bout (i.e., the arc/chord ratio). Foraging and walking velocities were determined from the cumulative distance moved and the duration of the bout.

Due to the equipment failures noted above, the number of animals and animal-days with viable GPS tracking data varied among pastures and study sites during each experiment.

However, after excluding the first and last days as pretrial and post-trial acclimation and/or animal handling periods, respectively, most collared animals had 5 complete or nearly complete 24-hr days of GPS tracking data per trial. Animal-days with less than 90% of expected GPS

locations (< 77,760 locations) were excluded from further analysis to avoid bias. For the remaining data, response values for each animal-day were corrected, based on actual GPS success rate, to values expected for a full, 24-hr day with 100% GPS success rate.

Statistical Analysis

Results from summer and fall experiments were analyzed and interpreted separately. Mixed models with repeated measures were developed for each response using the Mixed procedure in SAS/STAT® v.9.2 (SAS, 2008). Species (cattle vs. elk) and site (Barn-Upper vs. Cuhna) were included as fixed effects; trial, site by trial, pasture within site, and trial by pasture within site were random effects; and day of trial was the repeated measures term. Subjects were each GPS-collared animal within trial by site by species combinations. Selection of the covariance structure used in the final models was based on AICc scores. Model denominator degrees of freedom were computed using the Kenward-Roger method (Kenward and Roger, 2009). The studentized maximum modulus (SMM) adjustment was used for pair-wise comparisons of least-squared means. Differences were declared significant at the 0.05 alpha level. Data for daily travel distance (summer experiment only), walking activity budget, walking bout counts, walking bout durations, walking path lengths (summer only), stationary bout durations, foraging bout durations (summer only), and foraging velocities were log transformed to meet normality assumptions. Least-squared means and 95% confidence intervals for these responses were back-transformed for presentation.

Results

Summer experiment

Dry elk cows traveled further per day than lactating beef cows during the summer experiment (Table 3). This finding was robust, with no site ($P = 0.1106$; 1.32 df) or site by species interactions ($P = 0.1383$; 27.3 df) detected.

Counts of stationary bouts per day and the mean duration of those stationary bouts were both similar for elk and cattle during summer. Consequently, stationary budgets (i.e., proportion of time spent stationary per day) for elk and cattle were also similar (Table 3).

Elk engaged in more foraging bouts per day than cattle during summer. This species effect, however, was limited to the Barn-Upper site ($P < 0.0001$, 27.6 df; Fig. 1). Cattle foraging bouts were longer in duration than elk but this difference was also limited to the Barn-Upper site only ($P < 0.0001$, 29.5 df; Fig. 2). Overall, however, cattle had larger foraging budgets than elk. Elk and cattle exhibited similar mean foraging path lengths and mean foraging path tortuosities. However, elk foraged at faster velocities than cattle during summer (Table 3).

Elk engaged in more and longer walking bouts per day than cattle during summer. Consequently, elk also had larger walking budgets than cattle. Elk had longer mean walking path lengths and walked faster than cattle during summer (Table 3).

1 *Fall experiment*

2
3 Dry elk traveled further than dry cattle per day during the fall experiment (Table 4). This species
4 difference in travel distance, however, was primarily limited to the Cuhna site ($P = 0.0053$, 30.6
5 df; Fig. 3).

6 Elk engaged in more stationary bouts per day than cattle during fall. Cattle, however,
7 exhibited longer mean stationary bout durations than elk. Cattle also had larger stationary
8 budgets than elk during fall (Table 4).

9 Elk displayed more and longer foraging bouts per day than cattle during fall.
10 Consequently, elk foraging budgets were larger than those of cattle. Elk also had longer foraging
11 paths than cattle. Foraging path tortuosities were similar between elk and cattle. Elk, however,
12 foraged faster than cattle during fall (Table 4).

13 Elk and cattle engaged in similar numbers of walking bouts per day during fall. Cattle
14 walking bouts, however, were longer in mean duration than elk. Yet, this difference in bout
15 duration was not large enough to produce a statistical difference between the walking budgets of
16 elk and cattle. While walking path lengths were similar between elk and cattle during the fall
17 experiment, elk walked at faster velocities than cattle (Table 4).

Discussion

Mobility strategies and motivations

During summer, the dry elk cows in our study tended to emphasize a strategy of greater and more extensive mobility compared to that of cattle. Elk traveled further per day, had larger walking budgets, exhibited more and longer walking bouts, and had higher walking velocities than lactating beef cows. Elk also exhibited more foraging bouts and higher foraging velocity than cattle during summer. Cattle tended to emphasize intensive foraging rather than extensive movement during summer. Cattle had larger foraging budgets and longer foraging bouts than elk.

It could be argued this emphasis on mobility by elk and foraging by cattle may be, at least partially, a result of differing lactation status between our elk and cattle subject animals. All else held equal, lactating animals experience higher nutritional demand than dry animals (Cook, 2002; Neville and McCullough, 1969). Our lactating cattle, consequently, may have had a stronger motivation than dry elk to balance heightened nutritional demands by reducing mobility-related expenditures. However, since our summer experiment was conducted at least two months after peak lactation, when lactation costs for these cattle were greatly diminished, it seems unlikely that differing lactation status was an important driver behind the elk-cattle mobility differences we observed.

These differing strategies may, instead, be a reflection of dietary preference differences which have been reported between cattle and elk during summer at the SEFR (Stewart et al., 2003), in the Northern Rockies (Stevens, 1966; Torstenson et al., 2006), and the Great Basin

(Beck and Peek, 2005). Elk exhibit a much stronger preference for forbs during summer than cattle. Elk summer diets at the SEFR may contain 25-47% forbs while cattle consume only 1-11% forbs (Stewart et al., 2003). Palatable forbs occur more sparsely and are less uniformly distributed than graminoid forages in the Blue Mountains of northeastern Oregon (Hall, 1973; Johnson and Clausnitzer, 1992). A strong dietary focus on forbs would, consequently, tend to promote more extensive movement and foraging patterns as elk sought out scattered forbs amongst the background of more ubiquitous graminoids. Forbs common in elk diets generally have higher protein content than graminoids (Alldredge et al., 2002; Baker and Hobbs, 1982; Clark, 2003; Skovlin, 1967). Accordingly, the nutritional gain for elk consuming a summer diet with substantial forb content would likely offset the increased mobility costs required to obtain this forage type in graminoid-dominated habitats (Geist, 1982). Cattle, whose summer diets typically contain a very high percentage of graminoids (Scasta et al., 2016), >90% in some cases (Stewart et al., 2003), could likely forage less extensively in SEFR habitats and still meet their nutritional needs by engaging in longer foraging bouts with fewer transitions between foraging and walking bouts.

During fall, dry elk exhibited a more foraging-centric mobility strategy. Elk had larger foraging budgets, more and longer foraging bouts, longer foraging paths, and faster foraging velocities than the dry beef cows. Elk also traveled further per day and had higher walking velocities than cattle during fall. Conversely, cattle emphasized an energy-conservation strategy having both, larger stationary budgets and longer stationary bout durations than elk during fall. When cattle did choose to walk, however, they had longer walking bouts than elk.

These differing mobility strategies in fall were likely driven by differences in digestive physiology which promoted greater foraging selectivity in elk than cattle. Although elk have

disproportionately large rumino-reticular volumes relative to their body size, elk are still classified as intermediate feeders with faster rates of passage than cattle which are bulk feeders (Hanley, 1982). Consequently, to meet their nutritional needs, elk must select for more digestible foods than cattle. As the availability of palatable forbs decreases from summer to fall, elk shift their diets increasingly toward graminoids (Mackie, 1970; Stevens, 1966). Diet composition of elk and cattle, therefore, would generally become increasingly similar. However, elk would be expected to selectively graze for graminoid species or individual plants of higher digestibility than those consumed by cattle. Selective grazing by elk would lead to more and longer foraging bouts and faster foraging velocities which is consistent with what we observed during the fall experiment. Cattle, on the other hand, could afford to feed less selectively and spend more time per day ruminating their coarser diet which is also consistent with our activity and movement observations.

Site by species interactions

Results from the summer experiment included site by species interactions for the foraging bout count and foraging bout duration responses. Both these interactions indicated the detected species differences were primarily limited to the Barn-Upper site. The Barn-Upper site had greater areal proportion of forested vs. open habitats, smaller pastures, lower herbaceous standing crop, and was in closer proximity to human developments (e.g., buildings and a lightly trafficked road) than the Cuhna site. Since both the cattle and captive elk were well accustomed to the pasture settings and human presence through pretrial exposure and/or past experience, we doubt whether these two factors played substantial roles in producing these interactions.

Differences in available forage standing crops and/or proportions of forested vs. open habitat between sites may have influenced one ungulate species more than the other but, given available data, it is difficult to speculate as to the mechanisms behind the site by species interactions during the summer experiment.

Daily travel distance was the only response during fall experiment which exhibited a site by species interaction and, interestingly, this involved the Cuhna rather than Barn-Upper site. The Cuhna site had a much larger proportion of open grassland habitat than Barn-Upper. The fall standing crop within this grassland habitat at Cuhna was more than twice as large as that in Barn-Upper. In addition, the forest overstory at Cuhna was more open than at Barn-Upper thus light and soil moisture impacts on forb palatability in fall were likely greater at Cuhna than Barn-Upper. Combined, these habitat factors appear to have motivated elk to make more extensive use grassland habitats at Cuhna than cattle under fall forage quality conditions. This differing use pattern likely contributed to the larger species difference in daily travel distance at Cuhna than Barn-Upper.

Implications

This study confirms intensively-sampled GPS data alone are adequate for accurately classifying elk and cattle behavior into stationary, foraging, and walking classes. Activity sensor data, as described by other studies of fine-scale animal behavior (Dutta et al., 2015; Gonzalez et al., 2015; Wang et al., 2015), were not necessary for classifying behavior into these 3 basic classes. Our work reveals and endorses the usefulness of intensive GPS tracking for investigating animal behavior at the patch scale.

Findings here support the results of previous studies (Beck and Peek, 2005; Stevens, 1966; Torstenson et al., 2006) conducted at coarser scales which indicated differing behavioral strategies likely moderate the potential for direct competition between elk and cattle during summer and fall. The differing mobility strategies we observed between elk and cattle are consistent with those expected if these species were occupying different behavioral niches in Blue Mountain habitats. Extensive foraging by elk and intensive foraging by cattle during summer correspond well with mobility patterns expected from elk searching out forbs in graminoid-dominated habitats and from cattle intensively foraging on the graminoids. Activity budgets and mobility patterns exhibited in the fall experiment were consistent with elk continuing to exercise more selectivity among the available forage than cattle. By exercising these differing mobility strategies, it is reasonable to infer sympatric elk and cattle can occupy the same habitats and even exploit similar food sources but still moderate their potential for direct competition during summer and fall. These findings at the patch-scale contribute to a more comprehensive understanding of elk-cattle range relations in the Blue Mountains and other similar habitats. They perhaps also reopen some long standing questions. While other studies in the SEFR (Coe et al., 2001; Skovlin, 1968; Stewart et al., 2002) and elsewhere (Yeo et al., 1993) have reported evidence of elk being displaced by the presence of cattle during summer, our work lends support to the argument that these observations may be less about cattle and elk competing head-to-head spatiotemporally for the same resource and more about other factors like social intolerance of elk for cattle (Lyon et al., 1985; Nelson and Burnell, 1975).

Acknowledgements

We thank Michael Johnson of the Harvard-Smithsonian Center for Astrophysics for development of custom software. We also thank Tim Delcurto and the staff from the Eastern Oregon Agricultural Research Center, Union Station for providing and transporting the beef cattle used in this study. We are grateful to the National Council on Air and Stream Improvement (NCASI) for providing the captive elk. Our thanks also go to Brian Dick and Ryan Kennedy of the USFS Forestry and Range Sciences Laboratory for their expertise in animal handling and for the use of the pastures and facilities at the Starkey Experimental Forest and Range. Funding was provided by the USDA Agricultural Research Service and Oregon Agricultural Experiment Station.

References

- Allredge, M.W., Peek, J.M., Wall, W.A., 2002. Nutritional quality of forages used by elk in northern Idaho. *J. Range Manage.* 55, 253-259.
- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227-267.
- Anderson, E.W., Scherzinger, R.J., 1975. Improving quality of winter forage for elk by cattle grazing. *J. Range Manage.* 28, 20-125.
- Augustine, D., Derner, J., 2013. Assessing herbivore foraging behavior with GPS collars in a semiarid grassland. *Sensors* 13, 3711-3723.
- Baker, D.L., Hobbs, N.T., 1982. Composition and quality of elk summer diets in Colorado. *J. Wildl. Manage.* 46, 694-703.
- Beck, J.L., Peek, J.M., 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. *Rangel. Ecol. Manage.* 58, 135-147.
- Bergman, C.M., Fryxell, J.M., Gates, C.C., Fortin, D., 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *J. Anim. Ecol.* 70, 289-300.

- Bolon, N.A., 1994. Estimates of the values of elk in the Blue Mountains of Oregon and Washington: evidence from the existing literature. General Technical Report PNW-GTR-316. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA, 38 pp.
- Breiman, L., 2001. Random forests. *Machine Learning* 45, 5-32.
- Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. *Theoret. Pop. Biol.* 9, 129-136.
- Clark, P.E., 2003. Date and plant community effects on elk sedge forage quality. *J. Range Manage.* 56, 21-26.
- Clark, P.E., Johnson, D.E., Kniep, M.A., Jermann, P., Huttash, B., Wood, A., Johnson, M., McGillivan, C., Titus, K., 2006. An advanced, low-cost, GPS-based animal tracking system. *Rangel. Ecol. Manage.* 59, 334-340.
- Clark, P.E., Krueger, W.C., Bryant, L.D., Thomas, D.R., 1998. Spring defoliation effects on bluebunch wheatgrass: I. winter forage quality. *J. Range Manage.* 51, 519-525.
- Clark, P.E., Krueger, W.C., Bryant, L.D., Thomas, D.R., 2000. Livestock grazing effects on forage quality of elk winter range. *J. Range Manage.* 53, 97-105.

- 1 Coe, P.K., Johnson, B.K., Kern, J.W., Findholt, S.L., Kie, J.G., Wisdom, M.J., 2001. Responses
2 of elk and mule deer to cattle in summer. *J. Range Manage.* 54, A51-A76.
3
- 4 Cook, J.G., 2002. Nutrition and food. In: Toweill D.E., Thomas, J.W. (Eds.), *North American*
5 *Elk: Ecology and Management*. Smithsonian Institution Press, Washington D.C., USA,
6 pp. 259-349.
7
- 8 Crane, K.K., Mosley, J.C., Mosley, T.K., Frost, R.A., Smith, M.A., Fuller, W.L., Tess, M.W.,
9 2016. Elk foraging site selection on foothill and mountain rangeland in spring. *Rangel.*
10 *Ecol. & Manage.* 69, 319-325.
11
- 12 Dutta, R., Smith, D., Rawnsley, R., Bishop-Hurley, G., Hills, J., Timms, G., Henry, D., 2015.
13 *Dynamic cattle behavioural classification using supervised ensemble classifiers. Comp.*
14 *Electron. Agric.* 111, 18-28.
15
- 16 Geist, V., 1982. Adaptive behavioral strategies. In: Thomas, J.W., Toweill, D.E. (Eds.), *Elk of*
17 *North America Ecology and Management*. Stackpole Books, Harrisburg, PA, USA, pp.
18 219-277.
19
- 20 Ganskopp, D., 2001. Manipulating cattle distribution with salt and water in large arid-land
21 pastures: a GPS/GIS assessment. *Appl. Anim. Behav. Sci.* 73, 251-262.
22

- 1 Ganskopp, D., Bohnert, D.W., 2009. Landscape nutritional patterns and cattle distribution in
2 rangeland pastures. *Appl. Anim. Behav. Sci.* 116, 110-119.
- 3
- 4 Gonzalez, L.A., Bishop-Hurley, G.J., Handcock, R.N., Crossman, C., 2015. Behavioral
5 classification of data from collars containing motion sensors in grazing cattle. *Comp.*
6 *Electron. Agric.* 110, 91-102.
- 7
- 8 Grover, K.E., Thompson, M.J., 1986. Factors influencing spring feeding site selection by elk in
9 the Elkhorn Mountains, Montana. *J. Wildl. Manage.* 50, 466-470.
- 10
- 11 Hall, F.C., 1973. Plant communities of the Blue Mountains in eastern Oregon and southeastern
12 Washington. R6 Area Guide 3-1. USDA Forest Service, Pacific Northwest Region,
13 Portland, OR, USA, 62 pp.
- 14
- 15 Hanley, T.A., 1982. The nutritional basis for food selection by ungulates. *J. Range Manage.* 35,
16 146-151.
- 17
- 18 Hansen, R.M., Reid, L.D., 1975. Diet overlap of deer, elk, and cattle in southern Colorado. *J.*
19 *Range Manage.* 28, 43-47.
- 20
- 21 Hobbs, N.T., Baker, D.L., Bear, G.D., Bowden, D.C., 1996. Ungulate grazing in sagebrush
22 grassland: mechanisms of resource competition. *Ecol. Appl.* 6, 200-217.
- 23

- 1 IDFG, 2014. Idaho Elk Management Plan 2014-2024. Idaho Department of Fish and Game,
2 Boise, ID, USA, 168 pp.
- 3
- 4 Johnson, C.G. Jr., Clausnitzer, R.R., 1992. Plant associations of the Blue and Ochoco Mountains.
5 Technical Paper R6-ERW-TP-036-92. USDA Forest Service, Pacific Northwest Region,
6 Portland, OR, USA, 215 pp.
- 7
- 8 Jones, B., Kenward, M.G., 2003. Design and Analysis of Cross-Over Trials, second ed.
9 Chapman and Hall, London, England, UK, 408 pp.
- 10
- 11 Julander, O., Jeffery, D.E., 1964. Deer, elk, and cattle range relations on summer range in Utah.
12 Trans. N. Amer. Wildl. Conf. 29, 404-414.
- 13
- 14 Kenward, M.G., Roger, J.H., 2009. An improved approximation to the precision of fixed effects
15 from restricted maximum likelihood. Comp. Stat. Data Anal. 53, 2583–2595.
- 16
- 17 Lyon, L.J., Lonner, T.N., Weigand, J.P., Marcum, C.L., Edge, W.D., Jones, J.D., McCleery,
18 D.W., Hicks, L.L., 1985. Coordinating elk and timber management: final report of the
19 Montana cooperative elk-logging study. Montana Dept. Fish, Wildl. And Parks, Helena,
20 MT, USA, 53 pp.
- 21
- 22 Mackie, R.J., 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri
23 River Breaks, Montana. Wildl. Monog. 20, 1-79.

- 1 MFWP, 2004. Montana Statewide Elk Management Plan. Montana Department of Fish, Wildlife,
2 and Parks, Helena, MT, USA, 397 pp.
- 3
- 4 Morris, M.S., 1956. Elk and livestock competition. J. Range Manage. 9, 11-14.
- 5
- 6 NASS, 2016. National Agricultural Statistics Service, Statistics-by-State Reports. Various online
7 digital reports for 1 July calf crop from 9 western states (Arizona, Colorado, Idaho,
8 Montana, New Mexico, Oregon, Utah, Washington, and Wyoming).
9 http://www.nass.usda.gov/Statistics_by_State/ (accessed 19.05.2016).
- 10
- 11 Nelson, J.R., 1982. Relationships of elk and other large herbivores. In: Thomas, J.W., Toweill,
12 D.E. (Eds.), Elk of North America Ecology and Management. Stackpole Books,
13 Harrisburg, PA, USA, pp. 415-441.
- 14
- 15 Nelson, J.R., Burnell, D.G., 1975. Elk-cattle competition in central Washington. In: Roche, B.F.
16 (Ed.), Range multiple use management. Cooperative Extension Service, Washington
17 State Univ., Pullman; Oregon State Univ., Corvallis, Univ. of Idaho, Moscow, USA, pp.
18 71-83.
- 19
- 20 Neville, W.E., McCullough, M.E., 1969. Calculated energy requirements of lactating and non-
21 lactating Hereford cows. J. Anim. Sci. 29, 832-829.
- 22
- 23 Olson, O.A., 1943. Big game in multiple land use in Utah. J. Forestry 41, 792-797.

- 1 ODFW, 2003. Oregon's Elk Management Plan. Oregon Department of Fish and Wildlife,
2 Portland, OR, USA, 58 pp.
- 3
- 4 Parker, K.L., Gillingham, M.P., Hanley, T.A., Robbins, C.T., 1996. Foraging efficiency: energy
5 expenditure versus energy gain in free-ranging black-tailed deer. *Can. J. Zool.* 74,442-
6 450.
- 7
- 8 Rowland, M.M., Bryant, L.D., Johnson, B.K., Noyes, J.H., Wisdom, M.J., Thomas, J.W., 1997.
9 The Starkey Project: history, facilities, and data collection methods for ungulate research.
10 General Technical Report PNW-GTR-396. USDA Forest Service, Pacific Northwest
11 Research Station, Portland, Oregon, USA, 62 pp.
- 12
- 13 SAS, 2008. SAS/STAT® 9.2 User's Guide. SAS Institute Inc., Cary, NC, USA.
- 14
- 15 Scasta, J.D., Beck, J.L., Angwin, C.J., 2016. Meta-analysis of diet composition and potential
16 conflict of wild horses with livestock and wild ungulates on western rangelands of North
17 America. *Rangel. Ecol. & Manage.* 69, 310-318.
- 18
- 19 Sheehy, D.P., Vavra, M., 1996. Ungulate foraging areas on seasonal rangeland in northeastern
20 Oregon. *J. Range Manage.* 49, 16-23.
- 21

- 1 Skovlin, J.M., 1967. Fluctuation in forage quality on summer range in the Blue Mountains.
2 Research Paper PNW-44. USDA Forest Service, Pacific Northwest Forest and Range
3 Experiment Station, Portland, OR, USA, 20 pp.
4
- 5 Skovlin, J.M., 1968. The influence of cattle management on deer and elk. Trans. N. Amer. Wildl.
6 Conf. 33, 169-179.
7
- 8 Smith, G.A., 1930. The Sun River elk herd. J. Forestry 28, 644-647.
9
- 10 Stevens, D.R., 1966. Range relationships of elk and livestock, Crow Creek Drainage, Montana.
11 J. Wildl. Manage. 30, 349-363.
12
- 13 Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J., Johnson, B.K., 2002. Temporospatial
14 distributions of elk, mule deer, and cattle: resource partitioning and competitive
15 displacement. J Mammal. 83, 229-244.
16
- 17 Stewart, K.M., Bowyer, R.T., Kie, J.G., Dick, B.L., Ben-David, M., 2003. Niche partitioning
18 among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? Ecoscience 10,
19 297-302.
20
- 21 Torstenson, W.L.F., Mosley, J.C., Brewer, T.K., Tess, M.W., Knight, J.E., 2006. Elk, mule deer,
22 and cattle foraging relationships on foothill and mountain rangeland. Rangl. Ecol.
23 Manage. 59, 80-87.

- 1 Ungar, E.D., Henkin, Z., Gutman, M., Dolev, A., Genizi, A., Ganskopp, D., 2005. Inference of
2 animal activity from GPS collar data on free-ranging cattle. *Rangel. Ecol. Manage.* 58,
3 256-266.
- 4
- 5 Wang, Y., Nickel, B., Rutishauser, M., Bryce, C.M., Williams, T.M., Elkaim, G., Wilmers, C.C.,
6 2015. Movement, resting, and attack behaviors of wild pumas are revealed by tri-
7 accelerometer measurements. *Movement Ecol.* 2:1-12.
- 8
- 9 Westenskow-Wall, K.J., Krueger, W.C., Bryant, L.D., Thomas, D.R., 1994. Nutrient quality of
10 bluebunch wheatgrass regrowth on elk winter range in relation to defoliation. *J. Range*
11 *Manage.* 47, 240-244.
- 12
- 13 Wickstrom, M.L., Robbins, C.T., Hanley, T.A., Spalinger, D.E., Parish, S.M., 1984. Food intake
14 and foraging energetics of elk and mule deer. *J. Wildl. Manage.* 49, 1285-1301.
- 15
- 16 Yeo, J.J., Peek, J.M., Wittinger, W.T., Kvale, C.T., 1993. Influence of rest-rotation cattle grazing
17 on mule deer and elk habitat use in east-central Idaho. *J. Range Manage.* 46, 245-250.

Figure Captions

Figure 1. Foraging bout count responses (number of bouts animal-day⁻¹) by Rocky Mountain elk cows (dry) and beef cows (lactating) to habitat conditions during summer 2007 at the Starkey Experimental Forest and Range near La Grande, Oregon, USA.

Figure 2. Log-transformed foraging bout duration responses (log[sec + 1]) by Rocky Mountain elk cows (dry) and beef cows (lactating) to habitat conditions during summer 2007 at the Starkey Experimental Forest and Range near La Grande, Oregon, USA.

Figure 3. Daily travel distance responses (km) by Rocky Mountain elk cows (dry) and beef cows (dry) to habitat conditions during fall 2007 at the Starkey Experimental Forest and Range near La Grande, Oregon, USA.

Table 1. Classification performance, by behavior class and averaged across all classes, for a bootstrapped forest classifier applied to GPS tracking data acquired from Rocky Mountain elk cows (dry) during summer and fall at the Starkey Experimental Forest and Range near La Grande, Oregon, USA.

Behavior	Accuracy	Sensitivity	Specificity	F1 [†]	FDR [‡]
-----%-----					
Foraging	91.6	83.7	95.3	86.3	10.9
Stationary	91.9	95.0	87.5	93.3	8.33
Walking	99.6	75.5	99.9	83.5	6.54
Average	94.4	84.7	94.2	87.7	8.61

[†]F₁ score which is the harmonic mean of precision and recall.

[‡]False Discovery Rate.

Table 2. Classification performance, by behavior class and averaged across all classes, for a bootstrapped forest classifier applied to GPS tracking data acquired from lactating and dry beef cows during summer and fall, respectively, at the Starkey Experimental Forest and Range near La Grande, Oregon, USA.

Behavior	Accuracy	Sensitivity	Specificity	F1 [†]	FDR [‡]
	-----%-----				
Foraging	89.8	93.7	87.8	86.1	20.5
Stationary	90.4	85.9	95.6	90.6	4.24
Walking	99.1	77.6	99.9	85.4	4.98
Average	93.1	85.8	94.4	87.4	9.89

[†]F₁ score which is the harmonic mean of precision and recall.

[‡]False Discovery Rate.

1 Table 3. Least-squared means and 95% confidence limits for patch-scale behavioral responses by Rocky Mountain elk cows (dry) and
2 beef cows (lactating) to habitat conditions during summer 2007 at the Starkey Experimental Forest and Range near La Grande,
3 Oregon, USA.
4

Activity	Response	Elk			Cattle			DF [‡]	P-value
		Mean	LCL [†]	UCL	Mean	LCL	UCL		
Moving	Daily Travel Distance (km)	14.2[¥]	12.3	16.6	11.1	9.32	13.1	27.3	P < 0.0001
Stationary	Bout Counts	291	269	313	292	268	315	56.3	P = 0.8625
	Bout Durations (sec)	163	134	198	162	133	198	55.2	P = 0.7706
	Budget [§]	0.558	0.478	0.638	0.551	0.468	0.633	23.8	P = 0.5506
Foraging	Bout Counts	326	304	347	302	278	325	52.3	P < 0.0001
	Bout Durations (sec)	108	98.0	119	126	114	138	29.5	P < 0.0001
	Budget	0.405	0.316	0.494	0.440	0.349	0.532	19.4	P = 0.0054
	Path Lengths (m)	33.8	28.7	39.0	34.5	29.0	40.0	32.0	P = 0.5250
	Path Tortuosities (m/m)	5.20	4.93	5.45	5.34	5.11	5.57	31.1	P = 0.4169
	Velocity (kmh)	0.994	0.959	1.03	0.831	0.792	0.872	29.3	P < 0.0001

Walking	Bout Counts	31.4	5.47	161	9.50	0.769	61.3	29.3	P < 0.0001
	Bout Durations (sec)	80.2	59.4	108.3	72.1	52.9	98.0	27.4	P = 0.0348
	Budget	0.0347	0.0292	0.0405	0.00910	0.00520	0.0131	27.5	P < 0.0001
	Path Lengths (m)	86.8	65.3	115	71.2	53.4	94.7	23.5	P = 0.0031
	Velocity (kmh)	3.87	3.49	4.25	3.39	2.94	3.84	32.5	P < 0.0001

- 1
- 2 †LCL and UCL represent lower and upper 95% confidence limits, respectively.
- 3 ‡Denominator degrees of freedom used in the F-test of effect size.
- 4 §Budgets are expressed as the proportion of a 24-hr day during which animals were engaged in the corresponding activity type.
- 5 ¥Mean values printed in bold face and within the same row were significantly different at the 0.05 alpha level.

1 Table 4. Least-squared means and 95% confidence limits for patch-scale behavioral responses by Rocky Mountain elk cows (dry) and
2 beef cows (dry) to habitat conditions during fall 2007 at the Starkey Experimental Forest and Range near La Grande, Oregon, USA.

3

Activity	Response	Elk			Cattle			DF [‡]	P-value
		Mean	LCL [†]	UCL	Mean	LCL	UCL		
Moving	Daily Travel Distance (km)	12.4[‡]	10.6	14.1	10.4	8.65	12.1	30.7	P = 0.0002
Stationary	Bout Counts	296	246	345	282	232	331	26.7	P = 0.0002
	Bout Durations (sec)	167	121	230	184	133	254	19.1	P = 0.0030
	Budget [§]	0.571	0.514	0.629	0.601	0.544	0.659	23.2	P = 0.0110
Foraging	Bout Counts	311	263	359	299	250	347	18.2	P = 0.0138
	Bout Durations (sec)	118	95.6	140	111	88.3	133	31.5	P = 0.0023
	Budget	0.416	0.341	0.492	0.381	0.305	0.457	19.7	P = 0.0016
	Path Lengths (m)	35.9	25.8	46.5	29.2	18.4	40.0	31.8	P < 0.0001
	Path Tortuosities (m/m)	5.10	3.99	6.20	5.26	4.15	6.37	30.3	P = 0.4000
	Velocity (kmh)	0.950	0.898	1.00	0.844	0.795	0.894	31.1	P < 0.0001
Walking	Bout Counts	12.8	5.21	29.9	14.1	5.77	32.7	23.2	P = 0.5320

Bout Durations (sec)	60.1	42.9	84.0	72.9	52.0	102	32.9	P = 0.0271
Budget	0.0123	4.85E-5	0.0261	0.0172	0.00438	0.0316	30.3	P = 0.0570
Path Lengths (m)	72.4	1.79	143	79.7	6.39	153	32.8	P = 0.1390
Velocity (kmh)	4.00	3.41	4.59	3.40	2.80	4.01	3.07	P = 0.0079

- 1
- 2 [†]LCL and UCL represent lower and upper 95% confidence limits, respectively.
- 3 [‡]Denominator degrees of freedom used in the F-test of effect size.
- 4 [§]Budgets are expressed as the proportion of a 24-hr day during which animals were engaged in the corresponding activity type.
- 5 [¥]Mean values printed in bold face and within the same row were significantly different at the 0.05 alpha level.

Figure 1

Figure 2

Figure 3