Title

Environmental and managerial factors associated with pack stock distribution in high elevation meadows:
Case study from Yosemite National Park

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Abstract

Parks and protected areas are integral strategies for biological diversity conservation, and their management often involves balancing visitor use with resource protection. Effectively balancing these objectives requires data about how use is distributed within areas of interest and how management strategies and environmental conditions interact to minimize negative impacts. This study examined which environmental and managerial factors most influenced the distribution of domestic pack stock animals, a common visitor use-related activity, when released to graze in high elevation meadows. Using a species distribution modelling approach, MaxEnt, managerial factors were found to be among the top contributors to models. Pack stock animals concentrated use near the locations where they were released as well as portable enclosure fencing confining the lead animal even though the remainder were allowed to roam freely. Elevation was the environmental factor contributing most, with animals remaining at similar elevations to the meadow even if moving into nearby understory. Results highlight the importance of release point and fence locations to overall pack stock animal distribution and rotational or strategic placement can be a tactic for mitigating impacts to sensitive habitats.

Keywords

Horse; mule; maximum entropy; meadow; GPS tracking

1. Introduction

Biodiversity underpins healthy ecosystem function, provides ecosystem services, and supports human well-being. Parks and protected areas (PAs) represent a core component of biodiversity conservation strategies (Chape et al., 2005), with global agreements and efforts striving to increase the number and size of PAs to meet biodiversity conservation goals (Watson et al., 2014). In addition to conserving the resources within their boundaries, PA managing agencies may also have mandates to provide for compatible recreational opportunities. Balancing conservation and recreation needs can be challenging in light of recent estimates indicating terrestrial PAs around the world attract eight billion visits each year collectively (Balmford et al., 2015). Proactive management needs timely and accurate data about recreational use and environmental conditions to assess the magnitude, trends, and significance of recreation-associated disturbance. The purpose of this study is to identify environmental and managerial factors influencing the distribution of one type of visitor-related activity, use of pack stock animals (stock), to assess the influence of management tactics designed to minimize negative impacts.

In many PAs around the world, stock use is an established form of recreation, supports tourism operations, and is often part of the cultural heritage (Barros and Pickering 2015; Byers, 2009; Cole et al., 2004; Geneletti and Dawa, 2009; Newsome et al., 2002). The managing organization may also use stock to support administrative efforts. Stock use, which can include horses, mules, donkeys, yaks, or llamas, is one example of a visitor-related activity that can affect the ecological integrity of preserved ecosystems (Barros et al., 2015; Byers, 2009; Cole et al., 2004; Geneletti and Dawa, 2009). Impacts attributed to stock presence in alpine and mountainous landscapes include soil compaction, altering of hydrologic patterns, increases in erosion, and trampling (Barros et al., 2014; Byers, 2009; Kuhn et al., 2015; Ostojia et al., 2014). Research demonstrates horse trampling occurs at greater intensities than that of hikers (Weaver and Dale, 1978), and, in some cases, other hooved animals (Cole and Spildie, 1998). Additionally, transporting forage for stock may not always be feasible due to load sizes, geographic location, or invasive species concerns. Instead, stock may be released into meadows and adjacent areas to graze, with

estimates indicating an individual horse or mule consumes an average 14.8 kg of forage per night (Jacoby and The Society for Range Management, 1989).

Meadows are vital ecosystems supporting disproportionately high levels of biodiversity. In the western U.S., meadows also represent one of the most at-risk landscapes (Viers et al., 2013). Several studies reveal relationships between stock grazing and impacts to meadow ecosystem function. Overgrazing can decrease vegetation cover and meadow productivity, shift plant species composition through selective grazing of palatable species, change local soil chemistry and micro-climate conditions, increase bare ground cover, and facilitate the encroachment of invasive or woody species (Cole et al., 2004; Kuhn et al., 2015; McClaran and Cole, 1993; Moore et al., 2000; Olson-Rutz et al., 1996a, 1996b; Ostoja et al., 2014). Mitigating impacts from stock in PAs, while providing access for stock users, relies on understanding the interaction between stock and the environment (Moore et al., 2000). Research on the resistance and resiliency of grass, forb, and shrub-dominated habitats indicates proactive management is essential in limiting the propagation and proliferation of negative impacts (Cole et al., 2004; McClaran and Cole, 1993; Olson-Rutz et al., 1996b). Studies of grazing impacts in PAs are often based on inventories made before and after an animal has left the area, employing plots with varying levels of grazing treatments to measure ecosystem response, or observational studies of impacts to a variety of ecosystem components (Alzerreca et al., 2006; Cole et al., 2004; Holmquist et al., 2014; Kuhn et al., 2015; Ostoja et al., 2014).

How grazing intensity and environmental variables vary, however, has been identified as a research need within recreation ecology (Monz et al., 2010). Specifically, researchers and managers highlight a need to understand patterns of stock distribution and use during potential disturbance and how it is associated with environmental (e.g., vegetation composition, access to water) and managerial (e.g., fencing, stock release locations) factors, including overnight releases when direct supervision is less feasible (McClaran, 1989; Ostoja et al., 2014). Studies of stock resource use at the site level offer an opportunity to combine advances in data collection instruments, computing capacity, and statistical modeling methods from several disciplines interested in use-environment interactions to address this

research need (Brown et al., 2013; Gaylord and Sanchez, 2014; Jeltsch et al., 2013; Kays et al., 2015; Meijles et al., 2014; Rutter, 2007). The convergence of these advances have facilitated greater integration of animal distribution and movement data with environmental covariates (Kays et al., 2015).

1.1. Research objectives

The purpose of this study is to integrate data collection and analytical techniques from sub-disciplines of ecology to assess environmental and managerial variables influencing fine scale stock distribution and resource use. Specifically, this study:

- (1) Identifies which environmental and managerial factors contributed most to models of free-roaming stock distribution in meadows and adjacent areas during overnight release periods; and
- (2) Evaluates the accuracy of the models used to characterize stock distribution in relation to environmental and managerial factors.

2. Background Literature

To address the research objectives, three components were required: accurate spatio-temporal stock movement data, high-resolution environmental and managerial data, and a modelling method capable of addressing sampling limitations and quantifying model accuracy. This section reviews related work surrounding spatial use data and modelling use-environment interactions to identify which best address the research objectives.

2.1. Spatial use data

In the fields of recreation ecology, animal ecology, and movement ecology, global positioning system (GPS) data tracking visitor and animal movement are increasing in spatial and temporal accuracy, enhanced by expanding data collection capacity and environmental data captured by mobile and remote sensors (Handcock et al., 2009; Kays et al., 2015). Accuracy and capacity improvements are driven by reductions in GPS unit size, increases in battery longevity, and improved data retrieval options, rapidly increasing the amount and quality of tracking data available for analysis (Michelot et al., 2016). The development and application of statistical methods capable of garnering information from complex GPS

datasets represents a growing research focus, as data collection capacity has challenged computational capacity and traditional statistical assumptions about independence, and highlighted the need for user-friendly software (Long and Nelson, 2013; Michelot et al., 2016).

2.2. Modeling use-environment relationships

Distribution and movement models have also been employed to draw inference from species occurrence records (Edren et al., 2010). Species distribution models (SDMs) examine occurrence (or presence) records with surrounding environmental variables to determine habitat suitability. The underlying concept of SDMs is that species are more likely to be present in locations with conditions that suit their needs. Distribution models have used environmental envelopes, generalized linear models (GLM), generalized additive models (GAM), support vector machines, and boosted regression trees (BRT), to name a few, and have been applied to a diverse range of terrestrial and marine species to help inform conservation and management (Smith, 2013).

Key assumptions of SDMs, however, are that the presence records are independent from one another or representative of the species' distribution. When leveraging species data derived from GPS or telemetry methods, these assumptions are challenged and no systematic assessment of absences (i.e., where a species is not found) is inherent. Incorporating absence data is ideal for SDM and allows the prediction of presence probability using methods like logistic regression, without which model outputs should be interpreted as relative rates of occurrence (Merow et al., 2013). Lack of absence data is shared in SDMs derived from museum collections or opportunistic sampling of species locations common in plant and animal ecology and has received considerable attention in the last decade, especially following the development of the modelling tool, MaxEnt (Edren et al., 2010; Elith et al., 2006; Guillera-Aroita et al., 2015; Phillips et al., 2006).

MaxEnt is a machine-learning algorithm built on the principle of maximum entropy (Jaynes, 1957, 1982). The model compares covariate conditions at presence locations to the conditions at random locations in the greater area of potential occurrence (Elith et al., 2011; Phillips et al., 2006), and has been applied to GPS tracking data (Edren et al., 2010; Poor et al., 2012; van Gils and Kayijamahe, 2010;

Warton and Aarts, 2013). MaxEnt models examine patterns in the available data to make predictions based on the assumption of incomplete information (Jaynes, 1982), and insensitive to position errors and limited sample sizes (Elith et al., 2006). Research demonstrates that MaxEnt models are successful in modeling species distributions based on presence-only data when compared to other methods, including GLM and GAM (Elith et al., 2006). While often applied at regional scales, MaxEnt has also been successfully applied to finer scales (Smith et al., 2012).

Environmental predictors, termed features in MaxEnt, can be linear, quadratic, or cubic terms, or based on hinge or threshold functions. Coefficients are used to weight features, with iterative changes in the model determining the point at which coefficients converge on a probability distribution that maximizes the likelihood of use or probability of species occurrence (Braunisch et al., 2011). Benefits of MaxEnt models include the ability to integrate presence-only data with environmental data, incorporate continuous and categorical variables, employ methods to minimize overfitting, and evaluate each covariate's influence.

As with any model or method, MaxEnt is not without limitations. Critiques of MaxEnt discuss the potential for extreme values of environmental conditions not observed in the study area due to the use of an exponential probability model and sensitivity to sampling efforts (Elith et al., 2011; Phillips et al., 2006). These critiques recommend caution when interpreting model outputs and metrics (Yackulic et al., 2013). To address this concern, background selection should be ecologically informed and representative of a species distribution (Phillips and Elith, 2016). It is important to note that MaxEnt outputs are indices of habitat suitability (i.e., relative probability of presence) and reflective of potential biases in sampling (Royle et al., 2012). Options to minimize sampling biases include spatially filtering the number of occurrence records in oversampled locations, which can reduce the sample sizes needed for modelling, or corrective measures like choosing background data that reflect the same sampling bias as the occurrence data or bias correction files (Kramer-Schadt et al., 2013).

Additionally, Renner and Warton (2013) explored the mathematical similarities between Poisson regression, and therefore Poisson point process models (PPM), to MaxEnt. They found equivalencies

between the two methods depending on how model parameters are configured and analyzed. Renner and others (2015) demonstrated how MaxEnt could be used as a means for fitting a Poisson PPM, namely by retaining duplicate presence and examining the effect of the number of background points on the regularized training gain. For the purposes of this analysis, which examines distributions within a small scale to determine the influence of factors on observed distributions rather than predicting distributions in other environments, duplicate presence points were retained and the MaxEnt algorithm allowed to choose the best feature type (i.e., linear, quadratic, product, threshold, or hinge).

Use of MaxEnt with spatially and temporally autocorrelated GPS-derived position data also represents a challenge to modelling assumptions (Aarts et al., 2008; Baldwin, 2009; Gurarie et al., 2009). Solutions proposed to address this include modelling each species individually, using the home range as the background for model fitting, and comparing the percent contribution of each covariate for the individual model to determine which were most important (Baldwin, 2009). Subsampling also reduces autocorrelation and ensures no species contributes more positions to the model than another (Edren et al., 2010; Gschweng et al., 2012).

To evaluate model performance and address research objective 2, MaxEnt models assess the area under the curve (AUC) of the receiver operating characteristic (ROC), with values closer to one indicating better model performance. The ROC plots the percentage of correctly classified occurrence points against the percentage of correctly classified pseudo absence points, derived from available background points. Unlike model performance assessments when true absences are included, the AUC from a MaxEnt output should be interpreted as the ability of the model to correctly identify areas of high probability of occurrence from random background pixels, rather than suitable or unsuitable locations (Jalali et al., 2015; Yackulic et al., 2013).

3. Material and Methods

3.1. Study area

Yosemite National Park (YNP) is located in the Sierra Nevada mountain range of California. In 1890, it was one of the first National Parks established in the U.S. and was designated a United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage Site in 1984. The park, managed by the U.S. National Park Service (NPS), is known globally for its biodiversity, glacially created landforms, waterfalls, sequoia groves, and recreational opportunities. The park provides diverse habitats for over 400 species of vertebrates, including two potentially endemic species, in five biotic zones ranging from 600 to 4,000 m in elevation (UNESCO, 2016), and attracted over 4.1 million recreational visits in 2015 (USDI NPS, 2016a). Approximately 95% of the 3,027 sq. km park is federally designated wilderness, and two federally designated Wild and Scenic Rivers, the Merced and Tuolumne, flow within its boundaries.

Stock use is allowed in YNP, limited to 25 animals or less for NPS administrative functions, commercial trips, and private parties (Abbe and Ballenger, 2011). Commercial stock trips account for half of all overnight stock use in the park, with current management relying on permits and zoning to direct trail, camp, and meadow usage based on the number of stock use nights (e.g., number of animals at a site per night). Ostoja and others (2014) reported an average of 1,571 stock animal nights per year between 2004 and 2012. Meadows, some of which are located within a quarter mile of an NPS system trail, may be used for overnight grazing by stock animals, account for 3% of the total park area, and yet support disproportionate amounts of biodiversity and aesthetic and recreational opportunities for visitors (Viers et al., 2013).

Concerns about overuse impacts related to stock in YNP are documented as early as the 1930s (Sumner, 1935), with a call for monitoring in 1969 (Moore et al., 2000). Recent monitoring efforts of potential stock and visitor use impacts have been associated with management plan development for the Merced and Tuolumne Rivers, both of which require formal, dedicated management plans due to their status as Wild and Scenic Rivers (Ballenger et al., 2010; Ballenger et al., 2011; USDI NPS, 2014a,

2014b). These monitoring efforts also carried forward to inform the park's Wilderness Stewardship Plan (USDI NPS, 2016b).

As part of a greater NPS study, purposive sampling of stock meadow use in designated wilderness areas of the park was conducted during the summer months of 2014 by NPS staff using methods developed in collaboration with the authors. This paper compares two contrasting, graminoid-dominated meadow sites where similar number of animals were released for similar durations and managed with two common techniques. Techniques employed by management included changing the location at which the animals were released for free-range grazing (release point), and the use of a portable electric fencing (fence). When fences were used, the lead horse or horses were enclosed inside the fence and the remaining animals were allowed to roam freely. The two meadows included Castle Camp (CACA, UTM Zone 11N centroid at 293047.9, 4210568.4) and Upper Kerrick-North (UPKE, UTM Zone 11N centroid at 282509.2, 4221912.0). Animals were released for approximately 12 hours (i.e., release period) with differences in management techniques (Figure 1, Table 1). Both sites are subalpine meadow habitat, dominated by native grasses, with perennial stream channels and wetland complexes, surrounded by lodgepole pine (*Pinus contorta*) forest.

Figure 1 Location of release points and portable electric fences, when used, for both release periods in Castle Camp and Upper Kerrick-North meadows. Note: the release point in Upper Kerrick-North was the same for both release periods.

Table 1 General characteristics of the two study sites and stock management techniques.

Site Name (Abbreviation)	Area (ha)	Elevation (m)	Dominant Vegetation Associations ¹	Start Date (Time, PST) End Date (Time, PST)	Stock Management
Castle Camp (CACA)	2.9	2,677	DESCES, CALMUI	8/25/2014 (19:30)	Release Point : Animals released outside of meadow along the eastern boundary Fence: No fence used; All animals allowed to graze freely
				8/26/2014 (07:35)	
				8/26/2014 (19:30)	Release Point: Animals released outside of meadow approximately 50m closer to meadow boundary to the east Fence: Two horses enclosed in 643 sq. m. fence located in the NE of meadow
Upper Kerrick – North (UPKE)	21.4	2,858	STIKIN, CALMUI/OREA LP/VACCAE, DESCES, ELYTRA, HORBRA	9/22/2014 (18:15)	Release Point: Animals released at NW edge of meadow Fence: One horse enclosed inside 642 sq. m. fence located at north end of meadow approximately 150m NE of release point
				9/23/2014 (07:48)	
				9/24/2014 (18:20)	Release Point: Animals released from same location as previous release Fence: One horse enclosed inside 509 sq. m. fence located approximately 100m to the SE of the release point
				9/25/2014 (07:45)	
¹ Only the top five dominant vegetation associations are listed for general information on the plant communities present at each site (see Kuhn et al. 2015 for full inventory). Abbreviations include <i>Deschampsia cespitosa</i> (DESCES); <i>Calamagrostis muriana</i> (CALMUI); <i>Stipa kingii</i> (STIKIN); <i>Oreostemma alpigenum</i> (OREALP); <i>Vaccinium cespitosum</i> (VACCAE); <i>Elymus trachycaulus</i> (ELYTRA); and <i>Hordeum brachyanthemum</i> (HORBRA).					

Data for each night were analyzed separately to examine animal distribution under differing techniques, with outputs labeled by the meadow abbreviation and release number (e.g., CACA1 for release period starting the evening of August 25 and CACA2 for release period starting the evening of August 26). The trial at CACA included three horses and four mules, and the trial at UPKE included one horse and four mules.

3.2. Data collection and filtering

Stock performing administrative duties for the NPS were fitted with custom-built, professional-grade GPS units attached to the animal's halter when released to graze (Figure 2). Developed by Oregon State University, the GPS units used in this study contained the u-blox Max-7c module. Combined with a Pelican 1010 case for protection, the units weighed less than 1 kg to minimize influence or impact on the animal's comfort or behavior. During early pilot trials, one animal of the herd was not equipped with a unit so researchers could observe whether its presence affected behavior. For each pilot trial, the non-collared animal randomly varied. The presence of a unit did not appear to have an effect on animal behavior. For subsequent trials, including those at CACA and UPKE, all animals were equipped with units. Calibration testing of the units, conducted by Oregon State University under conditions similar to those of meadows, documented a circular error probability (CEP) of less than 6 m (D. Johnson and T. Kuhn, personal communication). CEP is the radius of a circle, calculated using the standard deviations of x and y coordinates, in which 50% of the values occur, and is a tested method for assessing the accuracy of GPS units (Frair et al., 2010; Graves and Waller, 2006; Lewis et al., 2007).

Figure 2 Stock animal wearing a custom GPS unit attached to its halter. Photo courtesy of T. Kuhn.

The GPS units recorded the animal's position every second for the duration of the release period, and differentially corrected in real-time to improve positional accuracy. NPS staff retrieved each unit at the conclusion of a release period and downloaded the data for later conversion to Environmental Systems Research Institute (ESRI) shapefiles for analysis. GPS data were examined for spatial and temporal errors and processed in Microsoft Excel to remove duplicate records and spatial or temporal outliers. Data filters available in MoveBank (www.movebank.org), an online database designed to manage and analyze movement data, confirmed outliers prior to their removal. Filtering excluded any points that indicated the animal was traveling at an improbable speed. Informed by research on horse gait analysis, a threshold of 13 meters per second (mps), which corresponds to the approximate mid-point of speeds achieved by a galloping horse, was used to remove outliers based on speed (Huang et al., 2013).

Studies of grazing animals indicate distributions can be influenced by environmental conditions like slope, distance to water, and forage quantity and quality (Bailey et al., 1996; Duncan, 1983).

Therefore, to address research objective 1, data sources relevant to this analysis included the U.S. Geological Survey (USGS) 3-meter resolution National Elevation Dataset ([NED] USGS, 2016), color infrared 1-meter resolution imagery from the U.S. Department of Agriculture (USDA) National Agricultural Imagery Program ([NAIP] USDA, 2016), USDA CALVEG vegetation survey data (USDA Forest Service, 2008), and a hydrology layer containing rivers and waterbodies obtained from the NPS and derived from 1992 USGS 1:24,000 topographic maps (USDI NPS and USGS, 2011). The NED was used to identify elevation at stock locations and to derive the slope (i.e., percent rise using a 3 x 3-pixel window) using the slope tool in ESRI ArcGIS 10.3.1 software.

NAIP images were cloud-free and color balanced using the mosaic color balance tool in ArcGIS 10.3.1 and used to calculate a Normalized Vegetation Difference Index (NDVI). NDVI is an indicator of surface greenness calculated by using two bands from spectral imagery, red and infrared. NDVI values range from -1 to 1, with greater positive values associated with more green vegetation. NAIP images used in the analysis for CACA were taken on August 15, 2014, 10 days prior to stock data collection in that area, and July 24, 2014 for UPKE, two months prior to stock data collection in that area. From the CALVEG vegetation survey, the regional dominance type was selected to classify land cover and indicates the primary (dominant) vegetation alliance in an area, as well as the secondary understory hardwood species in mixed cover types, based on procedures developed by the U.S. Forest Service (USDA Forest Service, 2008). Trimble Pro-XRT GPS receivers recorded the locations of the release point and fences, when used, and data were differentially corrected prior to inclusion in the model. Distance-to-release point, fencing, and hydrology raster layers were constructed using the near tool in ArcGIS.

3.3. Data analysis

We identified the potential area of stock use (i.e., background area of interest) to be the greatest distance to the release point for each animal by any animal based on GPS data during any release to the site. The overall maximum value for the site was rounded to the nearest 100 m to create the area of interest. The nearest 100 m was chosen as it would allow for consideration of GPS (in)accuracy and account for potentially visible yet not visited locations. The release point was then radially buffered by

this distance, and converted to a minimum-bounding polygon as the study area of interest (AOI) for analysis. AOI polygons included the meadow, as well as upland habitat, water bodies, and forested areas. This aligns with recommendations that the area from which unvisited sample points are taken (i.e., background points) reflect environmental conditions that are accessible to the species in question or have conditions of interest (Merow et al., 2013; Radosavljevic and Anderson, 2014).

The AOI is also directly relevant to management planning efforts focusing on the meadow and immediately adjacent area, including the area stock could reasonably travel during an overnight release. Additionally, this accounts for sampling bias as both presence and background samples represent the same conditions relevant to the research question, which is interested in a specific area's use rather than predicting to new locations (Yackulic et al., 2013). All data were clipped to the AOI using the extract by mask tool in ArcGIS at the coarsest resolution (3m).

Fourcade et al. (2014) found systematic subsampling of presence records to be among the top performing bias reduction methods for MaxEnt modelling when compared to three additional types of bias correction (i.e., bias files, restricted background, cluster sampling, and splitting datasets over large geographic regions). Although they selected their subsample to be distributed in a large region, they do note that this could underestimate the contribution of areas where species are found in high densities. Therefore, due to the small size of the AOIs in this study when compared to other MaxEnt studies, a systematic random subsample was selected following similar procedures outlined in Edren and others (2010) and Gschweng and others (2012). Gschweng and others (2012) identified the lowest number of locations for an individual animal as a threshold and subsequently randomly sampled other units to that threshold. Similarly, the total number of successful fixes for each GPS unit for all stock were examined. The fixed number for random sampling was determined by taking 30% of the unit with the least number of fixes and randomly sampling the remaining units to have the same number of fixes for the final sample.

The Maximum Entropy Species Distribution Modelling software, version 3.3.3k, fit MaxEnt models (<http://www.cs.princeton.edu/~schapire/maxent/>). Simplified to an n by two matrix, GPS tracking data contained X and Y UTM coordinates for data from all units. All predictors were included in model

fitting to allow the machine learning algorithm to determine which were important, through regularization (Phillips et al., 2006). Following a machine learning approach, high collinearity among predictors is less of an issue when compared with statistical methods (Elith et al., 2011), so long as results are interpreted as the predictive accuracy of the presences (Merow et al., 2013).

To fit the model, 30% of the data were randomly selected to be used as test points for cross-validation of the model, with 10 replicate runs using random seed subsampling (i.e., a different, randomly selected partition was selected for each run for the test/training partition and background sample). The regularization multiplier and maximum number of background points remained at the defaults of 1 and 10,000, respectively. The maximum number of iterations was set at 500, with a convergence threshold of 0.00001 (Phillips et al., 2006; Young et al., 2011). The software also created response curves and a jackknifing procedure was used to measure variable importance. The jackknife procedure examines the model, using AUC gain, without the specified variable and with only the specified variable, and compares it to the model with all variables included.

Model outputs ranked each predictor variable based on its contribution to the overall model. To evaluate the method and address research objective 2, predictive accuracy was assessed using AUC (Jalali et al., 2015). AUC scores above 0.5 indicate the model performs better than random and above 0.75 are considered acceptable for predictive accuracy (Phillips and Dudík, 2008; Richards and Friess, 2015), with >0.8 considered good and 0.9 considered excellent (Coppes and Braunisch, 2013).

4. Results

4.1. GPS tracking

A total of 267,538 and 250,825 location fixes were obtained from seven animals in CACA and five animals in UPKE, for both release periods. Of those records, 236,419 and 202,142 locations remained for CACA and UPKE, respectively, after removing points collected for periods of confinement if applicable. The remaining data for free-ranging animals were analyzed for duplicates and outliers, with 189,012 (80%) and 156,352 (77%) locations retained for CACA and UPKE, respectively. Successful fixes from the remaining sample ranged from 5,830 to 36,849 locations per unit in CACA and 7,174 to 46,199 per

unit in UPKE. To minimize the influence of varied fix rate success, a subsample of data was randomly selected from each unit, using a threshold of 30% of the total number of locations from the unit with the least number of fixes (i.e., 5,830). Thus, 1,750 records for each animal in each meadow were used for analysis.

4.2. AOI characteristics

Using the filtered full data sets (i.e., 189,012 in CACA and 156,352 in UPKE), the AOI for CACA was identified as 1100 m, as the furthest an animal traveled away from the release point during either release period was 1085 m. For UPKE, the AOI was 2100 m from the release point, as the furthest any animal traveled was 2044 m. The regional dominant vegetation alliances for both CACA and UPKE AOIs were predominately comprised of conifer species, with wet meadows representing only 0.66% and 6.48%, respectively (see Table S1 in the Supplementary Material for details on all vegetation alliances in the AOIs).

4.3. MaxEnt results

A MaxEnt model was fit for each of the four release periods, CACA1, CACA2, UPKE1, and UPKE2 (Table 2). The relative contributions of each variable to the MaxEnt model were examined in two ways. The first, percent contribution, is estimated by adding (or subtracting) the increase (or decrease) in regularized gain for each iteration of the training algorithm to rank variable importance. These values depend on the path taken to converge on a solution, with subsequent runs potentially yielding different values, and may indicate greater importance for highly correlated variables (Baldwin, 2009). Four additional iterations of the models with the same data yielded similar values, with the order of the top variables remaining constant.

As an alternative, permutation importance examines variable importance by reevaluating the model following a randomization of values for each variable separately and measuring the change in AUC as a normalized percentage. Unlike the percent contribution, the values are not dependent on the path taken to identify the optimal solution, but rather the values from the final model. Predictive accuracy as evaluated by the AUC indicates high accuracy (i.e., $AUC > 0.9$) for all four models.

Table 2 Percent contribution and permutation importance for variables by release period and meadow. The number 1 following the meadow abbreviation designates the first release period, with the second release period designated with the number 2. Bolded values indicate the variable is one of the top two factors contributing to the model for that area of interest.

	CACA1		CACA2		UPKE1		UPKE2	
	Percent Contribution	Permutation Importance (%)	Percent Contribution	Permutation Importance (%)	Percent Contribution	Permutation Importance (%)	Percent Contribution	Permutation Importance (%)
Distance to Fence (meters)	n/a	n/a	72.6	93.8	1.8	2.8	79.6	96.1
Distance to Release Point (meters)	82.4	93	24.4	1.7	67.7	80.1	1.4	0.3
Elevation (meters above sea level)	12.3	3.6	0.8	1.4	25.7	11.3	16.7	2.8
Distance to waterbodies (meters)	5.0	1.6	2.0	0.5	4.4	2.9	1.3	0.6
Regional dominant veg cover	0.1	0.8	0.1	0.4	0.3	1.1	0.2	0.1
Slope (percent rise)	0.1	1.0	0.2	2.1	0.1	1.9	0.8	0.2
NDVI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Average Test AUC (AUC Standard Deviation)	0.918 (0.0027)		0.947 (0.0022)		0.935 (0.0024)		0.961 (0.0020)	
Average Training AUC	0.9198		0.9465		0.9346		0.9617	

Response curves (Figure 3) illustrated how each variable influences the logistic prediction, with upward trends indicating positive associations. Response curves representing a separate MaxEnt model created with just the variable of interest are discussed below and are ‘clamped’ at the minimum and maximum values in the training data by the software to avoid errors due to extrapolation. The red line represents the MaxEnt run, with the blue area indicating plus or minus one standard deviation.

Distance to the release point was one of the top two variables in three of the four models based on percent contribution, contributing between 24% to 82%. The response curves illustrate dependence of the predicted occurrence at varying values of each factor. Greater values along the y-axis of a response curve indicates higher logistic probability of animal presence than lower values. For example, the model suggests a high probability of stock presence within 300 m for CACA and 500 m for UPKE of the release

point, with negative slope indicating declines beyond those values (Figure 3). A second peak near 450 m from the release point during the first release in CACA represents a cluster of points occurring in the SW of the meadow near the river.

Distance to fence was the variable contributing the most to the models for the second releases in both meadows, contributing over 70% of the model for each (Figure 3). A fence was used only during the second release period in CACA, and for both releases in UPKE, but placed in different locations of the meadow (Table 1, Figure 1). Stock presence is more likely within 200 m of the fence used during the second release period in CACA, and between 600 m and 400m for the first and second release periods in UPKE, respectively. The fence was not among the top variables during the first release period in UPKE, with elevation instead becoming a top contributing factor.

Elevation contributed as one of the top two variables in three of the four models, though its contribution was less than 25%. The response curves for elevation indicate the relative rate of occurrence increases at and around the elevation range of the meadow, approximately 2677 m for CACA and 2858 m for UPKE. Distance to a water body was often in the middle of the variable ranking and the regional dominant species also did not contribute much to the models. When examining the response curves independently from other variables, however, two specific dominant species did indicate greater relative probability of presence (i.e., logistic probability of presence greater than 0.4). Specifically, of the 12 dominant vegetation alliances identified in the AOI for CACA and 16 dominant vegetation alliances identified in the AOI for UPKE (see Table S1), results suggested an increased relative probability of presence (greater than 0.4 for all models) in lodgepole pine (*Pinus contorta*) and wet meadow areas. This corresponds also to the response curves from the NDVI variable, which although not contributing to the MaxEnt models independently, indicated higher relative probability of presence between values of 0.2 and 0.6. These NDVI values correspond to values associated with shrub, grasslands, and increasingly dense green vegetation (Figure 3).

Figure 3 Response curves for distance to release point, distance to fence and NDVI values for CACA1, CACA2, UPKE1, and UPKE2. The red line indicates the mean response of the 10 replicate MaxEnt runs and the blue line is plus and minus one standard deviation. Note the different scales between CACA and UPKE due to site extent differences.

Jackknife values compared a MaxEnt model without the specified variable in teal (i.e., what would the MaxEnt AUC be without the specified variable), a model created with only the specified variable in blue, and the full model with all variables in red (i.e., AUC values reported in Table 2). The length of the teal bar indicates how much is lost in AUC by excluding the variable. The length of the blue bar indicates the amount to which the specified variable contributes to the overall AUC by itself. For CACA meadow (Figure 4a), on the first night of release, the distance to release point, when modeled in isolation, contained the most useful information by itself (blue). Distance to the release point also decreased the gain the most when omitted from the model, indicating it contained information not present in the other variables. NDVI, by itself, achieved almost no gain, so the variable in isolation is not as useful for determining stock distribution. Similar results were found for the second night of release in CACA, although distance to fence contains the most useful information as well as information not contained by other variables for predicting distribution of occurrence data when measuring using AUC (Figure 4b).

Figure 4 Jackknife plots for AUC for (a) CACA1, (b) CACA2, (c) UPKE1, and (d) UPKE2. Fence, release point, and river/hydrology are distance-to variables.

For UPKE, the jackknife plots of AUC for the first night of release (Figure 4c) indicate that the release point distance contributes the highest gain when modeled by itself and therefore contains the most useful information in isolation, whereas elevation decreases the gain the most when omitted and therefore contains information that is not present in other variables. For the second night of release, UPKE2 (Figure 4d), distance to the fence contributes the highest gain and therefore most useful information by itself, and elevation again decreases the gain the most.

5. Discussion

The MaxEnt model results from the four release periods indicate the importance of managerial factors on the overall distribution of stock within and near meadows. For all release periods, a managerial variable was the top contributor to the model in terms of percent contribution, permutation importance, and jackknife variable importance when examined in isolation (i.e., contained the most useful information for the model as compared to the other variables). This included the release point, which was a top contributor in three of the four releases, with animals more likely to be present near the location of release. This is consistent with findings from an NPS pilot study incorporating 14 additional sites using the data collection procedures described in this paper and examining intensively used areas with kernel density estimates (Walden-Schreiner et al. 2015). Moving the location at which stock are released is a feasible tactic in landscapes where terrain is not a limiting factor. Further research on how this tactic influences distribution, especially in arid environments or locations where increasing numbers of tourists are leveraging stock to transport supplies in limited spaces, is needed.

The only instance where release point was not one of the top two variables in terms of percent contribution was during the second release in UPKE when the fence was 50 m further from the release point and became the top contributor to the model, with a permuted importance of 96.1%. The high permutation importance and model AUC gain by the fence variable as illustrated by the jackknife plot suggests that the release point did not contain additional information not already captured by other

variables. This suggests releasing animals away from sensitive habitats or in rotating locations may encourage grazing near the area of release and limit impacts.

Additionally, the use of an electric fence was also often an important factor, though the distance animals traveled varied between releases. Findings suggests additional conditions contributed to the effectiveness of the fence at limiting the distribution of the group and warrants further investigation of meadow size, fence visibility, and the social dynamics of the group. This was most noticeable during the first release in UPKE, as the fence was not among the top contributors to the model. Instead, the release point, which was the same location on both nights, became the top contributor to the model, with elevation and distance to a water body also ranking higher than distance to fencing. During the first night, the fence was approximately 50m closer to the release point and 200 m further north in the meadow than the second night. A potential explanation could include the fence being closer to the release point and not contributing as much new information to the model. However, the distance changes are relatively small at 50 m, and social dynamics within the group may also have contributed to differences. If directing stock grazing to smaller areas without overgrazing a particular location, the use of a fence to confine the lead animal may limit the dispersal of the other animals, but that social dynamics of the herd may also be important factors of animal dispersal. This finding is relevant for tourism operations that rely on the same animals who may have prior knowledge of grazing locations.

With respect to environmental variables, elevation was one of the top contributors to three of the four models. When considered in conjunction with land cover, animals were more often present at similar elevations as the meadow, even when outside of the meadow boundary. This may result from similar foraging opportunities associated with plant communities within the elevation gradient, or stock seeking resting locations not requiring traversing steep slopes. The relative logistic probability of presence dropped sharply to near zero at a slope of approximately five degrees (10% rise) or less. This parallels findings of studies of domestic grazing livestock (i.e., cattle, sheep) that also avoid steep slopes (see Bailey and Brown, 2011).

NDVI and dominant regional vegetation alliance consistently ranked as not contributing much new information, by themselves, to the models across all release periods. This is in slight contrast to Poor and others (2012) who found NDVI to be among the top two variables (and fencing among the least) contributing to a MaxEnt model of GPS-tracked pronghorn migration and suitable habitat in Montana, USA and Saskatchewan, Canada. However, the area of interest in this study is at the site level, as opposed to regional scale, and examines the distribution of domestic grazing animals within a natural environment. Thus, spatial and temporal scale could limit the opportunity for stock to experience a range of NDVI values. Additionally, while NDVI may not have contributed much new information to the model not contained in other variables, it is important to note that NDVI, by itself, achieved AUC values between 0.62 and 0.80 (i.e., better than random to fair model performance) as displayed in the jackknife plots. Response curves of the variable only, which enables interpretation free of correlations among predictor variables, indicate at which values of the predictor variable increased probability of presence was likely. In this site-scale study, lodgepole pine (*Pinus contorta*) and wet meadow regional vegetation alliances had a higher probability of stock presence than others. Further exploration of NDVI as a predictor variable in stock distribution is needed, especially in arid environments where stark contrasts may exist between meadows and adjacent areas.

5.1. Management Implications

Results highlight the importance of managerial factors in the distribution of stock. Managers tasked with mitigating impacts associated with stock use when animals are released to graze can consider the strategic placement of release points and portable fences. Encouraging release points in locations near quality forage and away from sensitive habitats, if available, may promote a concentration strategy, with stock remaining near the release location and away from areas more prone to impact. Conversely, rotating release points can promote a dispersal strategy at a broader spatial scale, spreading out grazing impacts over the course of a growing season and grazing area. How to implement strategies, concentration or dispersal, should be informed by area size, vegetation and hydrologic composition, number of stock use nights, and context of use.

Additionally, strategies can be used independently or together at different scales to accomplish resource protection goals. For example, a smaller site that is heavily used may choose a concentration strategy to minimize the area impacted. However, concentration relies on ample forage to support grazing in the area, otherwise animals will move further away to graze, reducing the influence of the release location. Stock in this study also concentrated use near portable electric fencing, when used during a release period. This tactic may also support both concentration and confinement strategies, depending on whether the fencing is moved systematically throughout the area, and may be best implemented in areas allowing for commercial or administrative stock use.

5.2. Limitations and Future Research

Due to the dynamic nature of pack stock trips, only a limited number of releases at the same site under similar conditions were available for analysis. Future research should select additional sites from which to develop a randomized study design, incorporating repeat visits that cover the same length of release, similar stock handling techniques, and pre-release activity and grazing. Additionally, incorporating more habitat heterogeneity and geographically diverse release points and fence locations may further explore distance-decay relationships related to stock distribution and managerial factors. Although the NDVI was not among the top contributors to the model, fine-scale vegetation mapping and phenology coupled with NDVI would examine fine-scale relationships between stock habitat use and vegetation. This would further elucidate how moving release points interacts with vegetation, as previous research in high elevation meadows in the Sierra Nevada indicated horses selected graminoids over forbs until foraging became limited within the area (Olson-Rutz et al., 1996b).

Finally, an important next step is to examine and incorporate stock behavior and group dynamics to expand the analysis of factors influencing distribution of stock when released to graze. Coupling direct observation with GPS tracking provides context for metrics (e.g., speed, turning angle) derived from GPS data that underpin the modelling of spatio-temporal behavior (Gurarie et al., 2016). Modelling group movement, which may help account for social dynamics, is also a growing area of research in movement ecology (Langrock et al., 2014). Modelling both behavior and group movement from data collected as

part of this study may further explain why top management variables identified in three models were not among the top variables in the fourth model and afford the opportunity to examine differences between administrative, commercial, and private stock use and behavior.

6. Conclusions

This study explored the importance of two management tactics (i.e., release locations and the use of portable electric fences) and environmental factors (i.e., elevation, slope, distance to water, dominant vegetation alliance cover, and NDVI) on stock distribution in two high elevation meadows using GPS tracking and MaxEnt modelling. Evaluation of the model's predictive success using AUC values indicated the models performed well ($AUC > 0.9$), suggesting MaxEnt offered an accessible method to generate distribution models for pack stock with respect to continuous and categorical data. The findings from this study, as well as the application of this modelling method to GPS tracking data of domestic animals when released to graze in natural areas, can help managers and planners in determining which tactics may be more effective in minimizing and mitigating impacts associated with free-range grazing in sensitive habitats.

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