

Context-Dependent Effects of Nutrition and Dam Behavior on Neonatal Survival in a  
Long-Lived Herbivore

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Nicole M. Bilodeau

Major Professor: Ryan A. Long, Ph.D.

Committee Members: E. Frances Cassirer, Ph.D.; Sophie L. Gilbert, Ph.D.;

Lisa A. Shipley, Ph.D.


Department Administrator: Lisette P. Waits, Ph.D.

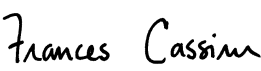
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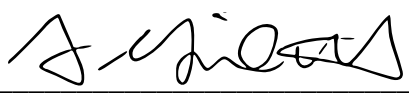
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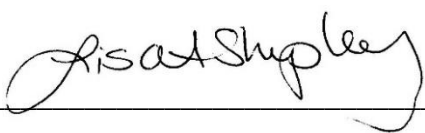
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Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor:  Date: 7/17/21  
Ryan A. Long, Ph.D.

Committee Members:  Date: 7/17/21  
E. Frances Cassirer, Ph.D.

 Date: 7/26/21  
Sophie L. Gilbert, Ph.D.

 Date: 7/26/21  
Lisa A. Shipley, Ph.D.

Department  
Administrator:  Date: 7/26/21  
Lisette P. Waits, Ph.D.

## Abstract

Behavior represents one of the primary mechanisms by which animals overcome environmental constraints on survival and reproductive success. Females in particular often exhibit plastic behavioral strategies for coping with the different nutritional demands and degrees of susceptibility to predation imposed by gestation, parturition and lactation. Previous studies have demonstrated a link between space-use behavior and important correlates of fitness and have highlighted the value of mechanistic nutritional approaches for understanding the fitness consequences of behavior. However, the mechanisms by which individual responses to variation in the nutritional landscape scale up to influence population performance remain unclear. We quantified relationships among the nutritional landscape (defined herein as spatiotemporal variation in forage biomass), dam behavior, and neonatal survival in bighorn sheep (*Ovis canadensis*). We conducted intensive vegetation sampling and used generalized additive modeling to map the nutritional landscapes available to sheep during summer (May–September) in three population ranges in Idaho: Owyhee River, East Fork of the Salmon River, and Lost River Range. We used GPS collars and lamb surveys to monitor ewe behavior and lamb survival in each study area, and used known-fate survival modeling to test for behaviorally mediated effects of nutrition on lamb survival. Relationships among the nutritional landscape, ewe behavior, and lamb survival were context dependent and varied among study sites. In the Lost River, where lamb survival was highest (83.9%), probability of lamb survival increased when ewes traded access to rugged terrain for access to higher forage biomass. We observed the opposite pattern in the East Fork (i.e., probability of lamb survival increased when ewes traded access to forage for access to rugged terrain), however, and in the Owyhee no metric of ewe behavior was significantly related to the probability of lamb survival. We also observed a strong, positive relationship between spring nutritional condition and probability of lamb survival across study sites. Our results highlight mechanistic links among habitat heterogeneity, individual space-use behavior, and reproductive success in bighorn sheep, and underscore the fundamental importance of nutrition as a driver of ungulate performance. Continuing to improve our understanding of such relationships will provide valuable insights for managers and conservationists, and will aid in accurately parameterizing models of population dynamics. Maximizing the usefulness of such models requires knowledge of the mechanisms that underpin variation in population

demographics, and nutritional-ecological approaches like those used in our study shed important light on those mechanisms.

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## CONTEXT-DEPENDENT EFFECTS OF NUTRITION AND DAM BEHAVIOR ON NEONATAL SURVIVAL IN A LONG-LIVED HERBIVORE

### **Introduction**

Understanding the complex mechanisms that drive variation in population abundance across space and time is a fundamental goal of population ecology and management (Krebs 2002). Many factors, both extrinsic and intrinsic, can influence reproduction, recruitment, and survival in wildlife populations (Caughley and Krebs 1983, Clutton-Brock and Pemberton 2004), and quantifying those factors is therefore critical for understanding and predicting patterns of population performance. For example, demographic variation can be influenced by population density, intra- and interspecific competition, predation, habitat quality, resource availability, disease, or climatic variation (Gaillard et al. 1998). Many of these factors are challenging to quantify, however, and the mechanisms that underpin their effects on wildlife populations are not always intuitive.

Nutrition integrates a variety of biotic and abiotic factors that influence fitness (Humphries et al. 2004, Parker et al. 2009), and thus nutritional ecology can provide important, mechanistic insights into the drivers of population dynamics. Nutritional condition is defined as the state of body components that are controlled by nutrition and in turn influence future survival and reproduction (Harder and Kirkpatrick 1994, Saltz et al. 1995). Nutritional condition can have a wide range of influences on the physiology and productivity of ungulates (Cook 2002), including effects on fecundity (Verme and Ullrey 1984; Cook et al. 2001, 2005; Tollefson et al. 2010; Morano et al. 2013), timing of parturition (Hass 1997, Cook et al. 2005), neonate birth mass and survival (Thorne et al. 1976, Côté and Festa-Bianchet 2001, Long et al. 2016), juvenile growth rate and mass (Cook et al. 1996), adult mass gain (Morgantini and Hudson 1989), and adult survival (Parker et al. 2009, Monteith et al. 2013). Nutrition can also modulate wildlife population dynamics via effects on life-history traits and patterns of behavior (Franzmann 1985, Harder and Kirkpatrick 1994). For example, Monteith et al. (2011) showed that individual traits such as age, reproductive status, and nutritional condition affected the timing of seasonal migration in mule deer.

Over the past several decades, researchers have developed a variety of methods for quantifying nutritional condition of ungulates based on measurements of body mass, fat reserves, protein reserves, or some combination of these (Stephenson et al. 1998, Cook et al.

2001a, Mysterud et al. 2001, Monteith et al. 2013). Cook et al. (2003) concluded that direct measurements of fat deposits are the most accurate and reliable method for estimating nutritional condition of ungulates. Accordingly, Cook et al. (2001a, 2010) developed and validated equations for predicting percent ingesta-free body fat (%IFBF) of ungulates from measurements of subcutaneous rump fat thickness (obtained using ultrasonography; Stephenson et al. 1998, 2002) and standardized palpation scores. Percent IFBF reflects the amount of stored energy reserves available to individual ungulates for allocation to growth, reproduction, immune function, etc., and is thus a useful metric for understanding the physiological causes and consequences of animal behavior (Parker et al. 2009).

Capital-breeding ungulates subsidize the cost of reproduction with energy stores accrued prior to the breeding season (Festa-Bianchet et al. 1998, Harrison et al. 2011). Allocation to reproduction, however, must be balanced against the need to retain adequate reserves for survival in stochastic environments, and is thus 'risk-sensitive' (Festa-Bianchet et al. 1998, Monteith et al. 2013). Risk-sensitive allocation is based on the premise that partitioning of endogenous energy reserves by an individual is state-dependent, and that there are seasonal thresholds of energy reserves that must be reached to facilitate investment in reproduction (Monteith et al. 2013). Accordingly, individuals entering the breeding season with greater reserves tend to have higher reproductive success, presumably because they have surplus energy to dedicate to breeding, gestation, and lactation (Cook et al. 2004, Stephens et al. 2009).

Nutritional condition reflects both the quality and quantity of available forage, and deficiencies in either of these traits on summer and autumn ranges can reduce population performance of ungulates. Nutrient deficiencies and concomitantly poor condition can inhibit ovulation and implantation (Bronson 1989, Frisch 1984, Gunn and Doney 1975, Kincaid 1988, Neville and Neathery 1974, Robbins 1983), and can potentially result in repeated cycling that may delay parturition. Several studies have shown that the probability of conceiving and carrying a fetus to term is strongly influenced by summer forage conditions and autumn body mass (Cameron et al. 1993, Gerhart et al. 1996, Pekins et al. 1998, Cook et al. 2004). Females in poor condition may also have lower milk production, resulting in slower neonatal growth (Oftedal 1985), which may predispose neonates to early death from a variety of sources (Rachlow and Bowyer 1991, Roffe 1993, Côté and Festa-Bianchet 2001, Long et

al. 2016). Even small differences in forage quality can have an outsized influence on animal performance via multiplier effects (White 1983). Cook et al. (2004) demonstrated such an effect in captive female elk and concluded that ruminants cannot compensate for low forage quality simply by eating more. Those authors' results revealed that even a moderate level of nutrition significantly delayed conception, and a low level of nutrition effectively precluded pregnancy of most females.

Behavior represents one of the primary mechanisms by which animals overcome environmental constraints on survival and reproductive success (Krebs and Davies 1997, Huey et al. 2003). Females in particular often exhibit plastic behavioral strategies for coping with the different nutritional demands and degrees of susceptibility to predation imposed by gestation, parturition and lactation (Long et al. 2009). Merems et al. (2020) revealed a significant relationship between use of the nutritional landscape and early-winter condition of female deer. They concluded that individuals who used, on average, areas that provided greater biomass of preferred forage plants during spring and summer entered winter in better nutritional condition. Another recent study demonstrated that selection for areas that provided relatively high-quality forage during autumn had a positive effect on the accumulation of fat reserves (i.e., nutritional condition) by lactating female elk (Long et al. 2016). Those authors highlighted the positive relationship between maternal nutritional condition in late winter and the probability of neonate survival. These studies add to the growing body of literature linking space-use behavior to important correlates of fitness and highlight the value of nutritional approaches to understanding the fitness consequences of behavior (Parker et al. 2009, Cook et al. 2010, Monteith et al. 2013, Long et al. 2016).

Bighorn sheep (*Ovis canadensis*) are an iconic species of the Rocky Mountains and are an important resource both ecologically and economically (Gordon et al. 2004). They are the largest herbivore in much of the habitat they occupy, and they have important effects on habitat structure. They also serve as an important source of prey for large predators (Festa-Bianchet 1999). Economically, bighorn sheep are a major resource for local communities and government agencies. In Idaho, harvest tags directly contribute hundreds of thousands of dollars to big game conservation, research, and management. Furthermore, indirect income is generated from sheep hunting activities, which includes monies spent by hunters on travel, food, lodging, outfitters and guides, and taxidermists (IDFG 2010). In addition to their



economic value, bighorn sheep are historically and culturally significant to Native Americans for tools, subsistence, and ceremonies (Demarchi et al. 2000).

In recent decades, populations of bighorn sheep have declined throughout North America largely due to infectious respiratory disease (Cassirer et al. 2017). The most prevalent disease among bighorn is pneumonia. Pneumonia is polymicrobial, but is typically initiated by the bacterium *Mycoplasma ovipneumoniae* (*M. ovi.*). *M. ovi.* is host-specific to Caprinae and is commonly carried by domestic sheep and goats without affecting their health (Foreyt and Jessup 1982). However, many bighorn sheep populations in the lower 48 U.S. states have experienced all-age die-offs after contracting the disease (Western Association of Fish and Wildlife Agencies Wild Sheep Working Group 2012). Once introduced, *M. ovi.* can persist in a bighorn sheep population for decades (Cassirer et al. 2017). Moreover, persistently infected populations have a high likelihood of prolonged periods of disease in lambs, which often reduces recruitment in subsequent years and limits population growth (Ryder et al. 1992; Enk et al. 2001; Smith et al. 2014, 2015).

All-age outbreaks are usually associated with significant population declines, but mortality rates from pneumonia vary widely, and factors influencing disease severity are not well understood (Hobbs and Miller 1992). Researchers continue to seek evidence of host genetic resistance, which might be expected in populations that are successful even in the long-term presence of pneumonia, but to date a genetic basis for resistance to pneumonia has not been identified (Gutierrez-Espeleta et al. 2001, Boyce et al. 2011, Cassirer et al. 2017). Wildlife management agencies have used a variety of strategies (e.g., population eradication, culling individuals observed with symptoms, translocations) to reduce the occurrence of respiratory disease outbreaks, but to date no specific strategy has successfully stopped an outbreak, and there is no evidence that intervention has consistently reduced morbidity, mortality, or spread of disease (Cassirer et al. 2017). Similarly, no vaccine or antibiotic treatment has successfully reduced infection or controlled the spread of disease in domestic or wild sheep (Cassirer et al. 2017). Inconsistencies in the frequency and severity of outbreaks, coupled with a lack of evidence for genetic resistance, suggest that there may be other underlying mechanisms (e.g., nutrition) contributing to the frequency and severity of die-off events from pneumonia.

One of the best-studied systems for shedding light on interactions among nutrition, disease, and immunity is the feral Soay sheep population in Scotland, which experiences periodic crashes of up to 50% due to the interactive effects of nutritional restriction during harsh winters (Clutton-Brock and Pemberton 2004) and gastrointestinal parasite loads (Coltman et al. 1999; 2001). Sheep that survive harsh winters may invest more in anti-parasite immunity, allowing them to slow the rate of decline in condition over winter relative to less-resistant conspecifics (Nussey et al. 2014). However, the benefits of increased immunity come at the expense of reduced reproductive performance following a harsh winter (Graham et al. 2010), highlighting the degree to which such tradeoffs can be mediated by nutrition.

The goal of our research was to evaluate the effect of (1) the nutritional landscape (defined herein as spatiotemporal variation in the availability of forage plants), and (2) inter-individual variation in how bighorn sheep use the nutritional landscape, on lamb survival. We aimed to provide managers with a dynamic model of relationships among the nutritional landscape, ewe behavior, and lamb survival that could be combined with data on adult survival and demographics to aid in effective management of bighorn sheep populations. We hypothesized that both spring nutritional condition of ewes and patterns of movement and space use during summer would influence probability of lamb survival during the first four months of life. Accordingly, we predicted that lambs born to ewes in good condition in spring would have a higher probability of surviving their first four months of life. Additionally, we predicted that lambs born to ewes that consistently used the best parts of the nutritional landscape (i.e., areas that provided high forage biomass) available to them would have a higher probability of surviving their first four months of life.

## Methods

### *Study Sites*

The Idaho Department of Fish and Game manages big game species in distinct Game Management Units (GMU) that are combined into Population Management Units (PMU) based on population movements, similarity of habitats, and management objectives. We selected three bighorn sheep PMUs as study sites (Fig. 1) based on their distinct bighorn sheep populations and the wide range of habitats they encompassed.

The first PMU included in our study was the Owyhee River (Owyhee), which is located in the southwest corner of Idaho near the border with Oregon and Nevada. The majority of the Owyhee River PMU is designated as wilderness by the Bureau of Land Management (BLM), and the entirety of the Owyhee River is protected under the National Wild and Scenic Rivers Act. The Owyhee is part of the Columbia Plateau and is bisected by the narrow, 150-300 m deep Owyhee River canyon. Portions of the canyon that are not shear-walled support sagebrush (*Artemisia spp.*) and bunchgrasses (*Festuca spp.*, *Pseudoroegneria spicata*), while the riparian areas support narrow bands of lush grasses, rushes (*Juncus spp.*), and sedges (*Carex spp.*). Habitat beyond the canyon rim consists of comparatively homogeneous sagebrush-steppe, which was expected to be of low nutritional value to bighorn sheep. Elevations range from 1,311 to 1,646 m. Our study site included ~604 km<sup>2</sup> of the 3,473-km<sup>2</sup> PMU and supported an estimated population of 158 bighorn sheep (IDFG 2017).

The East Fork of the Salmon River (East Fork) PMU is located in central Idaho between Stanley and Challis. The East Fork PMU encompasses predominately roadless land managed by the U.S. Forest Service (USFS) and includes the Wild and Scenic East Fork of the Salmon River corridor and three newly established (2015) wilderness areas (Boulder-White Cloud, Hemingway, and Jim McClure-Jerry Peak Wilderness). The East Fork is characterized by dry chalky cliffs along the river that rise to rocky peaks and spine ridges dotted with high-elevation mountain lakes. Habitat in the East Fork PMU varies from grasses (*Poa spp.*, *Festuca spp.*, *Achnatherum hyemoides*) and shrublands (*Artemisia spp.*, *Purshia spp.*, *Chrysothamnus spp.*) to high alpine forests (*Pinus spp.*) and meadows (*Antennaria spp.*, *Lupinus spp.*, *Phlox spp.*), and was expected to be of moderate to high nutritional value to bighorn sheep. Elevations range from 1,768 to 3,353 m. The East Fork PMU is roughly 1,994

km<sup>2</sup> (our study site included ~549 km<sup>2</sup>) and has an estimated population of 102 bighorn sheep (IDFG 2017).

Our third site was the Lost River Range (Lost River) PMU located in Central Idaho, which extends from east of Challis to Arco. The Lost River PMU spans the entire Lost River mountain range, which includes the tallest peaks in the state and consists almost entirely of USFS, BLM, and state lands. The Lost River is characterized by large sweeping valleys that quickly ascend to sagebrush steppe foothills, timbered slopes, and barren ridges that connect rugged peaks. Habitat types in the Lost River PMU are similar to the East Fork PMU, but there are a greater proportion of high-elevation habitats; the Lost River PMU was expected to be of moderate nutritional value to bighorn sheep. Elevations range from 1,676 to 3,859 m. The Lost River PMU encompasses 4,662 km<sup>2</sup>, of which ~3,186 km<sup>2</sup> were included in our study, and the area supports an estimated population of 256 bighorn sheep (IDFG 2017).

#### *Bighorn Sheep Capture, Sample Collection, and Body Condition*

During spring (Feb–March) of 2016–2018 we captured adult female bighorn sheep using a net gun fired from a helicopter (Krausman et al. 1985; Table 1). Typically, captured animals were suspended from a helicopter in sling bags and transported to a staging area for processing. We occasionally processed animals at the capture site if distance to the staging area was >5 km or if body temperature exceeded 41 °C. At the staging area we aged each sheep, collected biological samples (blood, fecal, and mucus swabs), and quantified nutritional condition and reproductive status using a combination of ultrasonography and manual palpation (Stephenson et al. 1998, 2002). We also fit each sheep with a GPS collar (Lotek: Iridium or Lifecycle Pro, Ontario, Canada; Vectronic Aerospace: Survey 1D, Berlin, Germany; Advanced Telemetry Systems, Minnesota, USA) programmed to record locations every 3 hours from the beginning of May to the end of August, and to remotely upload them 4 times per day. We affixed numbered, colored tags to the belting of each GPS collar to facilitate visual identification of ewes during field monitoring. We also ear-tagged each ewe with a small plastic tag inscribed with a unique ID number. We estimated age based on patterns of tooth eruption and replacement up to 4 years old (Mahon 1975, Lawson and Johnson 1982). This method is not reliable to age female bighorn sheep >4 years old without

extracting a tooth and counting cementum annuli (Turner 1977), so females estimated to be >4 years were aged as 4+.

We collected nasal and oral pharyngeal (OP) mucus swabs to test for disease, specifically *Mycoplasma ovipneumoniae*. Nasal swabs were inserted into both nostrils and gently rotated. A PVC tube was then inserted into the mouth to facilitate swabbing of the back of the throat while minimizing the likelihood of oral contamination. We also swabbed the ears of each ewe and visually inspected and scored them for scabies severity on a 0 to 4 scale, with 0 indicating no evidence of scabies and 4 indicating severe infestation. We collected blood samples using a 30-mL syringe with an 18 gauge  $\times$  25 mm needle inserted into the jugular vein, and samples were partitioned into 5 test tubes for subsequent DNA, disease, and pregnancy analysis. We also collected fecal samples to test for parasites.

We assessed body condition using ultrasonography and palpation scoring (Stephenson et al. 1998, 2002). A portable ultrasound (E.I. Medical Imagine, Ibex Pro) was used to measure maximum subcutaneous fat thickness immediately posterior to the cranial process of the tuber ischium (Maxfat), and maximum thickness of the longissimus dorsi between the 12th and 13th ribs (Stephenson et al. 1998, 2002). If no measurable subcutaneous fat was detected, we calculated body fat using overall body condition scores (BCS). Overall body condition was estimated using a scoring system similar to that described by Cook et al. (2001a). We palpated several key locations on the body and scored each on a scale of 0.5 to 6, in intervals of 0.5, where 0.5 = emaciated and 6 = obese. We calculated percent ingesta-free body fat (%IFBF) from BCS or Maxfat measurements using the equations of Stephenson et al. (2020). Percent IFBF is a measure of body condition that is directly related to the amount of stored energy available for allocation to growth, reproduction, immune function, and survival, and is thus a useful metric for understanding the physiological causes and consequences of animal behavior (Parker et al. 2009, Stephenson et al. 2020). Following processing, study animals were either released at the staging area or returned to the capture site as time and circumstances allowed. Capture and handling procedures followed methods established by the American Society of Mammalogists (Sikes et al. 2016) and were approved by the University of Idaho Institutional Animal Care and Use Committee (IACUC-2017-69).

### *Lamb Survival Surveys*

At the beginning of the lambing period (Owyhee: mid-April–May; East Fork and Lost River: mid-May–June) we conducted aerial surveys using a combination of visual observation and a high-definition infrared camera mounted to the plane to obtain an initial count of lambs born to collared ewes. An annual summary of the number of ewes monitored at each study site can be found in Table 1. In 2017 we conducted aerial surveys weekly during the first month of the lambing period in the East Fork and the Owyhee; the Lost River was only surveyed once in June and once in July due to weather constraints. During 2018 and 2019 we conducted aerial surveys weekly during the lambing period at all three study sites. After the initial survey period we attempted to locate and observe each collared ewe monthly from the ground through September. Each marked female was observed until it could be determined whether she was accompanied by a lamb. Confirmation required a direct observation of nursing or other behaviors indicative of close association (e.g., nuzzling, grooming, bedding together, etc.). Once a ewe was observed with a lamb we monitored the lamb status until late September or until the ewe was observed 3 consecutive times with no sign of a lamb. If a ewe was never observed with a lamb then we censored it for that year.

### *Forage Sampling*

During May–August of 2018–2019 we conducted intensive vegetation surveys to quantify biomass of forage available to bighorn sheep within our three study sites. We used the 30-m USDA Landfire Biophysical Settings Potential Vegetation Type (PVT) layer to stratify each study site into similar vegetation associations for sampling purposes (LANDFIRE 2008; Table 2). Potential vegetation types are comprised of similar biophysical characteristics (e.g., climate, aspect, and soil characteristics) that produce plant communities of similar composition, structure and function (Mueggler and Stewart 1980, Hansen and Hoffman 1988). Sampling locations within each PVT were selected using the Generalized Random Tesselation Stratified (GRTS) sampling method (Stevens and Olsen 2004). Sampled PVTs and the proportion of each study site comprised by each PVT are shown in Table 2.

We attempted to sample forage biomass during the peak of plant diversity, the timing of which we determined from a combination of visual observation and data from long-term vegetation phenology plots placed at each study site. We sampled during peak diversity

because it allowed observers to more accurately identify species and collect both annuals and perennials present on the landscape. Biomass plots consisted of a 100-m transect with 1-m<sup>2</sup> quadrats placed every 20 m, beginning at 20 m and ending at 100 m. Within each quadrat we identified all plants to species level or, in some cases, sub-species level. We then estimated forage biomass in each quadrat using a double-sampling approach (Bonham 1989). We began by visually estimating percent horizontal cover (% cover) of each plant species within each 1-m<sup>2</sup> quadrat to the nearest 1%. We then selected the 2 most species-rich quadrats along the transect and used standard clip-and-weigh methods to estimate dry biomass of each forage species within those quadrats (Bonham 1989, Butler and Wayne 2007, Proffitt et al. 2016). We clipped all plant species from 2 cm to 1.5 m in height (the approximate maximum foraging height of bighorn sheep), and we collected only leaves and current annual growth from shrubs and trees (all plant parts were collected for graminoids and shrubs). Clipped samples were placed in paper bags and dried in a forced-air convection oven at 100 °C for 24 hrs or until constant weight was achieved, typically within 3 days of collection. When samples could not be dried within this time frame they were stored in a dry, well-ventilated space until they could be processed. We weighed all samples using an Alaide jewelry scale (0.01g). Any samples weighing  $\leq 0.01$  g were assigned a trace value of 0.01 g. We sampled a total of 53 transects in the East Fork, 58 transects in the Lost River, and 19 transects in the Owyhee.

We used multiple linear regression (Neter et al. 1996) to fit species-specific predictive equations for estimating forage biomass in all unclipped quadrats as a function of % cover, Julian day, and the interaction between those variables. We did not include tree canopy cover as a covariate in biomass regressions because 70% of transects had 0% canopy cover, and average canopy cover was only 7.5% across transects that did include trees. We evaluated both linear and natural log-transformed terms for each predictor variable to test for potential non-linear relationships between covariates and forage biomass. We fit 8 competing models (see Appendix B) for each plant species for which we had obtained  $\geq 10$  paired biomass and % cover measurements. Many of our plant species ( $n = 86/353$ ) had consistently low (i.e.,  $< 1\%$ ) % cover values, making it impossible to fit a legitimate regression model to the cover/biomass data. In those instances we (1) calculated mean biomass of the species in all clipped quadrats where % cover was  $\leq 1\%$ , (2) assigned that mean biomass value to all unclipped quadrats

where % cover was  $\leq 1\%$ , and (3) upscaled (linearly) the average biomass value to unclipped quadrats where % cover was  $> 1\%$  (e.g., for a quadrat with 2% cover we multiplied average biomass by 2 and assigned the resulting value to the quadrat). Species with  $< 10$  paired biomass and % cover measurements were assigned to a growth-form group (evergreen shrubs, graminoids, tall forbs, short forbs, basal forbs, cacti, mid-tall shrubs, and evergreen trees) prior to fitting biomass regressions. Similarly, when the intercept-only model was the best-fitting model for an individual species with  $n \geq 10$ , or the adjusted  $R^2$  of the best model for a species was  $< 0.2$ , we assigned the species to the appropriate growth-form group prior to regression analysis. If inclusion of the species in the growth-form group either improved or did not significantly reduce ( $\leq 5\%$  reduction) the  $R^2$  of the best model then the species was retained, and the growth-form model was used to predict biomass of that species in all unclipped quadrats. If inclusion of the species in the growth-form group significantly reduced ( $\geq 5\%$  reduction) the  $R^2$  of the best model then the species was kept separate. We set the intercept of all biomass regressions equal to 0 (i.e., regression through the origin). Once the respective species- or group-form-specific biomass regressions were applied to all unclipped quadrats, final biomass (kg/ha) of each plant species at each transect location was estimated as the average biomass of the species across all 5 quadrats along the transect.

We did not have detailed site-specific data on bighorn sheep diets and were therefore uncertain what the most biologically meaningful metric of the nutritional landscape for sheep would be. Accordingly, we used plant species-specific biomass data to generate two candidate response variables for quantifying the nutritional landscape available to sheep: total forage biomass and accepted forage biomass. Total forage biomass was estimated as the summed biomass of all sampled forage plants. Accepted forage biomass was estimated as the summed biomass of plants likely to be selected or used in proportion to their availability (i.e., not avoided) by sheep. We used published diet data (Smith 1954, Johnson 1980, Miller and Gaud 1989, Wagner and Peek 2006, Whitaker 2010) together with expert recommendations (L. A. Shipley, Washington State University; T. R. Stephenson, California Department of Fish and Wildlife, personal communication) to determine which forage species were likely to be accepted by bighorn sheep in each study area (Appendix A). We then used spatiotemporally explicit estimates of total and accepted forage biomass at each transect location as response



variables in subsequent models of the nutritional landscape available to bighorn sheep at each study site.

### *Modeling the Nutritional Landscape*

We modeled spatiotemporal variation in total and accepted forage biomass within our three study sites as a function of remotely sensed covariates known to influence vegetation dynamics at broad scales. Candidate predictor variables included the enhanced vegetation index (EVI, an index of vegetation greenness; U.S. Geological Survey, Earthdata), PVT, snowmelt date (Snow Data Assimilation System), monthly total precipitation (ppt; TerraClimate), monthly soil moisture (soil; TerraClimate), monthly average maximum temperature (tmax; TerraClimate), monthly Palmer drought severity index (PDSI; TerraClimate), elevation, slope, aspect, and Julian day (Table 3). The EVI layer was filtered to correct for cloud cover. We also used the Gapfill package in R to predict missing values in the EVI layer introduced by cloud cover, missing orbits, sensor geometry artifacts, or other anomalies (Gerber et al. 2018).

We used Generalized Additive Models (GAMs) to predict spatiotemporal variation in the nutritional landscape (i.e., total or accepted biomass of forage) available to bighorn sheep in each of our three study areas in Idaho. For each study site we modeled variation in total biomass and accepted biomass separately. We followed the approach of Merems et al. (2020) and conducted model selection in two stages to (1) assess which spatiotemporally dynamic variables to retain, and (2) select the functional form of each model for each study site. Our goal was to maximize predictive strength of the best model for each study site. Accordingly, in the first stage of model selection we fit models that contained different combinations of smoothing terms for spatial (x-y coordinates) and/or temporal (Julian day, average maximum temperature, PDSI, total precipitation, soil moisture, or snowmelt date) covariates, combined with fixed effects for all uncorrelated spatial covariates (PVT, aspect [transformed with sine and cosine functions to measure eastness and northness, respectively], slope, and elevation). We fit cubic regression splines for each candidate smoothing term and used cross-validation to determine the optimal amount of smoothing (Zuur et al. 2009). We then used Akaike's Information Criterion corrected for small sample size (AICc) to determine the most parsimonious combination of smoothing term(s) to carry forward to the second stage of the

analysis (based on the model with the lowest AICc score). We limited the number of smoothing terms included in each model to a maximum of two (one spatial and one temporal smoother) to reduce model complexity and facilitate convergence, and because many of the time-dependent variables were highly correlated ( $r \geq 0.6$ ) and could not be included together in the same model.

In the second stage of the analysis we fit the following set of four models for each continuous covariate (all models also included the smoothing term/s brought forward from the first stage of analysis): (1) untransformed covariate; (2) covariate<sup>2</sup>; (3) ln(covariate); and (4) covariate removed. Each model thus specified a different functional form of the relationship between the covariate and forage biomass (except the last model, in which the covariate was absent). We used AICc to determine whether the covariate should be retained at all, and if so, whether a transformation was appropriate. Following selection of continuous covariates and their optimal functional form, we removed PVT, a categorical covariate with 6 levels in the Lost River and East Fork and 4 levels in the Owyhee (Table 2), from the model to determine whether PVT should be included in the final predictive model for each study site (based on whether inclusion of PVT resulted in a lower AICc score).

Following model selection we used the `gam.check` function in R to evaluate adherence of the final model to assumptions, and to identify outliers. Those diagnostics sometimes indicated that the assumption of homogeneity of variance was not satisfied, and that differences in variance among PVTs were the source of the problem (i.e., there was significantly more variation in forage biomass in some PVTs than others). When this occurred, we used the `varIdent` variance structure (Zuur et al. 2009) to calculate unique variance estimates for each PVT, and to fit a weighted GAM in which the inverse of the variance in forage biomass in each PVT was used as the weighting factor. We then repeated the second stage of the analysis with the weighted model. Lastly, we used the `CVgam` function in R to calculate cross-validation statistics for each of the six final models (see Table 3 for candidate predictor variables; see Table 4 for best models). Those models were then applied to the three study sites to calculate spatiotemporally explicit estimates of predicted total and accepted forage biomass available to bighorn sheep during the study from 2017–2019. We fit all models using the `mgcv` package in program R v4.0.2 (R Development Core

Team 2019; Wood 2006). We then compared the mean accepted and total forage biomass in PVTs that comprised >0.2% of each study site (Fig. 2).

We extracted model-predicted values of total and accepted forage biomass to both used (i.e., locations obtained from GPS-collared bighorn ewes) and random (i.e., locations that represented habitat availability) locations in each respective study site and year. We restricted our subsequent analyses of used locations to those that occurred in sampled PVTs (Table 2; 99%, 87%, and 91% of locations obtained in the East Fork, Lost River, and Owyhee study sites, respectively). To quantify variation in the availability of total and accepted forage biomass we generated random locations equal to the number of used locations we obtained from collared sheep ( $n = 118$ ) at each study site ( $n = 48,514$  in the Lost River, 40,807 in the East Fork, and 9,575 locations in the Owyhee, respectively). Random locations were generated within 100% minimum convex polygons (MCPs) derived from the complete sample of used locations at each study site. We used extracted values of total and accepted forage biomass at random locations to estimate the proportion of each study site that fell into each of four quartiles of habitat quality (Fig. 3; High  $\geq 705$  kg/ha, Mid-High = 423–704 kg/ha, Mid-Low = 246–422 kg/ha, Low  $\leq 245$  kg/ha). We also compared the distribution of predicted total and accepted biomass values between random locations and locations that were used by sheep at each study site (Fig. 4).

#### *Quantifying Individual Variation in Space Use*

We used the `adehabitatHR` package in R to estimate 95% fixed-kernel utilization distributions (UD) and associated home-range isopleths for individual ewes during summer of each year (Silverman 1986, Worton 1989). We used the ad hoc method for bandwidth selection, which is designed to prevent under-smoothing in kernel home-range analysis (Kie 2013). We estimated ad hoc bandwidths by incrementally reducing the reference bandwidth by 10% in successive steps until the 95% contour fragmented into two or more polygons (Berger and Gese 2007, Jacques et al. 2009). We excluded one (of 117) ewe from these analyses because we obtained <50 GPS locations during the period when she was collared.

We quantified the overall quality of each ewe's home range by casting random points within individual home range polygons and extracting the underlying values of total and accepted biomass to each point. We determined the minimum number of random locations

necessary to accurately represent available habitat in each home range using the methods of Long et al. (2014). Because access to rugged escape terrain is a well-known determinant of space use by bighorn sheep (Hansen 1980, Festa-Bianchet 1988, Smith et al. 1991, Rachlow and Bowyer 1998), we also extracted terrain ruggedness values to the random locations within each ewe's home range. We quantified terrain ruggedness using the methods outlined by Sappington et al. (2007). Briefly, this approach quantifies ruggedness by measuring the dispersion of vectors orthogonal to the terrain surface, which combines variation in slope and aspect into a single measure that provides a more accurate representation of terrain heterogeneity than indices based only on slope or elevation. The resulting values are low both in flat areas and in extremely steep areas, but values are high in areas that are both steep and variable. After total and accepted forage biomass and terrain ruggedness values had been extracted to all of the used and random locations within each home range, we calculated a series of descriptive statistics designed to represent (1) the overall 'quality' of each ewe's home range with respect to forage and escape terrain (descriptive statistics derived from random locations), and (2) variation in use of the nutritional landscape and escape terrain among individual ewes at each study site (descriptive statistics derived from used locations). For each variable (total forage biomass, accepted forage biomass, and terrain ruggedness) we calculated the mean, max, and coefficient of variation across random locations within each home range, and the mean and max values across used locations within each home range. Those metrics were then used as candidate predictor variables in subsequent models of lamb survival as a function of ewe space-use behavior.

### *Modeling Lamb Survival*

Our ultimate goal was to evaluate the influence of ewe behavior (i.e., use of the nutritional landscape and escape terrain) and nutritional condition on lamb survival during summer (May–September) at each of our three study sites. Accordingly, the unit of replication for our analyses was the ewe-year. Our GPS location dataset included 156 ewe-years from 2016–2019 derived from 97 unique individuals (some individuals were monitored for multiple years). We censored a ewe-year if that ewe was never observed with a lamb during a given year. We used the known-fate model in Program Mark (White and Burnham 1999) to model lamb survival at each study site as a function of the descriptive statistics representing use of

total biomass, accepted biomass, and terrain ruggedness by each ewe. We fit all possible combinations of candidate covariates in separate model sets for each study site with two exceptions: (1) correlated ( $|r| \geq 0.6$ ) pairs of variables were not included in the same model, and (2) descriptive statistics for total biomass and available biomass were never included in the same model. In addition, we fit separate model sets for evaluating the influence of landscape-scale behavioral choices (covariates derived from random locations within ewe home ranges) versus home-range scale choices (covariates derived from used locations) on lamb survival at each site. Models were ranked by AICc and inferences were based on models with  $\Delta\text{AICc} < 2$  (Burnham and Anderson 2002).

We were only able to obtain spring body condition measurements for a subset of our ewe-years ( $n = 77$ ), and thus we did not have sufficient sample size to include spring condition as a covariate in site-specific models of lamb survival. Therefore, we conducted a separate known-fate survival analysis in which we combined data across sites and modeled lamb survival as a function of spring condition.

## Results

### *Nutritional-Landscape Modeling*

Generalized additive models (GAMs) for explaining spatiotemporal variation in accepted or total forage biomass generally performed well for each of our three study sites, with adjusted  $R^2$  values ranging from 0.28 (East Fork total biomass model; Table 4) to 0.63 (Lost River accepted biomass model; Table 4). Top models for accepted biomass generally had higher predictive power (all Adj.  $R^2 > 0.49$ ) than top models for total biomass across study sites. Smoothing terms and spatial covariates included in top models varied considerably across sites and between response variables (i.e., between models of accepted versus total biomass; Tables 4 and 5). All top models for the Lost River and Owyhee study areas included a temporal smoother for Julian day, whereas neither Julian day nor any other temporal smoothing term were retained in top models for the East Fork (Table 5). The enhanced vegetation index (EVI, an index of vegetation greenness) or its square were included in 5 of the 6 top models across study sites, and EVI was always positively related to forage biomass (Table 5). In contrast, the influence of topography and potential vegetation type on forage biomass was more variable (Table 5). Top models of accepted versus total forage biomass in the Owyhee were nearly identical because these two measurements were equivalent at most transect locations (i.e., all sampled plants along most transects were classified as being acceptable to bighorn sheep; Table 4).

Predicted forage biomass varied among PVTs at each site but was more variable in the Lost River and East Fork (range  $\approx 375$ – $1,000$  kg/ha across PVTs) than in the Owyhee (range  $\approx 400$ – $800$  kg/ha; Fig. 2). With the exception of the Owyhee, where measurements of total and accepted biomass were typically equivalent, the proportion of each site classified as high- or mid-high-quality (top two quartiles) foraging habitat was greater based on total forage biomass than when accepted biomass was used as the metric of habitat quality (Fig. 3). Surprisingly, the proportion of each study site falling into the top two quartiles of total forage biomass was roughly equal across all three sites (Fig. 3). However, the relative proportion of high-quality habitat (based on total forage biomass) was higher in the East Fork and Lost River than in the Owyhee (Fig. 3). Also surprising was our observation that mean values of both accepted and total forage biomass were consistently lower at locations used by female sheep than at random locations generated within the boundaries of each study site (Fig. 4).

This result suggests that sheep at all three sites consistently used lower-quality (i.e., lower forage biomass) foraging habitat than was generally available. This trend was most pronounced in the Lost River and least pronounced in the Owyhee (Fig. 4).

#### *Effects of Nutrition on Lamb Survival*

Raw estimates of lamb survival probability were comparable to estimates derived from known-fate modeling (Fig. 5; see Appendix C for individual lamb survival by site) and were highest in the Lost River ( $83.9\% \pm 0.05 SE$ ), intermediate in the East Fork ( $61.0\% \pm 0.06$ ), and lowest in the Owyhee ( $51.5\% \pm 0.09$ ). At the home-range scale (i.e., locations used by GPS-collared sheep within their home ranges), use of the nutritional landscape by female sheep had a greater influence on lamb survival in the Lost River than at the other two sites, evidenced by the null model outperforming all other competing models of lamb survival in the East Fork and the Owyhee (Table 6). The top model for predicting summer lamb survival in the Lost River included a single nutritional covariate, max\_TB (maximum total forage biomass at locations used by sheep; Table 6). Moreover, that covariate was included in three of the top four models (models with  $\Delta AICc < 2$ ; Burnham and Anderson 2002; Table 6) for the Lost River, as was terrain ruggedness (either mean or maximum values of terrain ruggedness at locations used by female sheep; Table 6). Use of higher-quality foraging habitat (i.e., locations with higher maximum values of total forage biomass) in the Lost River was positively related to the probability of lamb survival, whereas use of more rugged terrain was negatively related to lamb survival (Table 7).

At the landscape scale, the overall quality of ewe home ranges (assessed based on random locations generated within each ewe's home range; see Methods) with respect to both the nutritional landscape (total forage biomass) and terrain ruggedness was related to the probability of lamb survival in the Lost River and East Fork, but the null model was once again the top model for the Owyhee (Table 8). The top model for predicting lamb survival as a function of home-range quality in the Lost River included mean\_TB (mean total forage biomass at random locations within sheep home ranges) and CV\_Ruggedness (the coefficient of variation for terrain ruggedness, considered to be a measure of terrain heterogeneity within sheep home ranges; Table 8). The top model in the East Fork included only mean\_TB, but the next-best model (the only other model in the set with  $\Delta AICc < 2$ ) included both mean\_TB and

CV\_Ruggedness (Table 8). Interestingly, the signs of the coefficients for these two covariates differed between the Lost River and the East Fork; mean\_TB was positively related to lamb survival in the Lost River but negatively related to lamb survival in the East Fork, whereas CV\_Ruggedness was negatively related to lamb survival in the Lost River and positively related to lamb survival in the East Fork (Table 9).

When we combined data across study sites for the subset of ewes for which we had estimates of spring nutritional condition (Appendix D), we found a strong, positive relationship between spring condition and probability of lamb survival (Fig. 6). Model results indicated that lambs born to ewes in relatively good condition (18% ingesta-free body fat) were roughly three times more likely to survive the summer months than lambs born to ewes in poor condition (3% ingesta-free body fat; Fig. 6).



## Discussion

Relationships among the nutritional landscape, behavior of female bighorn sheep, and lamb survival across 3 study sites in Idaho were context dependent. Although female sheep at all three sites consistently used lower-quality foraging habitat than was generally available, this trend was most pronounced in the Lost River. Yet, lamb survival was highest in the Lost River population, and this was the only site where use of the nutritional landscape by ewes at both the home-range and landscape scales positively influenced lamb survival (i.e., when ewes consistently used locations with greater forage biomass their lambs had a higher probability of survival). This result suggests that habitat heterogeneity plays a fundamental role in contextualizing relationships between behavior and fitness. Spatial variation in total forage biomass was much higher in the Lost River than at the other two sites, which likely led to the correspondingly greater variation in ewe behavior we observed at that site (Fig. 4). Consistently optimizing behavior is challenging for animals (Belovsky 1984, Kie 1999), and inter-individual variation in behavior often increases as habitat heterogeneity increases (Morales et al. 2005; van Beest and Milner 2013; Long et al. 2014, 2016). Our study, grounded in the principles and techniques of nutritional ecology, provides mechanistic support for the hypothesis that inter-individual variation in behavior can have important fitness consequences that could eventually scale up to influence population performance in heterogeneous landscapes (Stephenson et al. 2020).

Our results also suggest that sheep in alpine habitats exhibited context-dependent strategies for coping with tradeoffs between forage availability and vulnerability to predation. Probability of lamb survival in the Lost River increased when ewes consistently used locations that provided high forage biomass but reduced access to rugged escape terrain at both the home-range and landscape scales (although the specific metrics identified during model selection differed between scales; Tables 7, 9). In contrast, ewes in the East Fork that positioned their home ranges in areas that provided less forage biomass but greater access to heterogeneous escape terrain had higher lamb survival. Trade-offs between forage and predation risk are well-known in bighorn sheep (e.g., Festa-Bianchet 1988), but our results suggest that the nature and magnitude of such tradeoffs may be modulated by thresholds in the relevant risk factors (i.e., context-dependent variation in which factors are most limiting). Although escape terrain has consistently been identified as an essential component of habitat

for mountain sheep (Geist 1971, Krausman and Leopold 1986, Bleich et al. 1997), low overall risk of predation combined with a heterogeneous nutritional landscape may relax reliance of sheep on escape terrain while increasing the benefits of trading access to rugged terrain for access to forage. We had no data on predator densities at any of our study sites, but the high rate of lamb survival in the Lost River population suggests that that population is not currently limited by predation. Moreover, because the proportion of the nutritional landscape that fell into each quartile of total forage biomass was comparable between the Lost River and the East Fork (Fig. 3), differences between those sites in vulnerability of sheep to predation are more likely to explain our results than differences in forage availability. Empirical work designed to identify the conditions under which large herbivores like bighorn sheep begin to adjust their responses to tradeoffs between forage and perceived predation risk will be a fruitful avenue for future research.

We failed to detect any significant relationships among variation in the nutritional landscape, ewe behavior, and lamb survival in the Owyhee population at either the home-range or landscape scales. One simple explanation for this null result is our smaller sample size at that site ( $n = 54$  ewe-years in the Owyhee,  $\geq 40\%$  fewer than the East Fork and Lost River), which stemmed from a combination of inclement weather restricting capture operations and GPS-collar malfunctions. An alternative explanation, however, relates to the disease status of the Owyhee population and the potential for disease to have overridden more nuanced relationships among nutrition, behavior, and fitness. Lamb recruitment is severely affected by the presence of disease in bighorn sheep herds (Cassirer et al. 2017). In the Owyhee, an all-age pneumonia outbreak in 2015–2016 led to a large die-off of sheep in the canyon (Dennehy 2017). For example, one population (the Lower Owyhee River Canyon population) declined from 384 in 2015 to 111 in 2016, and most recently to 92 in 2019 (ODFW 2020). Accordingly, biologists are concerned about lingering effects of the outbreak related to chronic infection in adults and decreased lamb survival (Dennehy 2017). Our test results from captured sheep in the Owyhee in 2016–2018 resulted in two positive detections for exposure to *Mycoplasma ovipneumoniae*, although these results do not indicate whether or not a herd is currently infected (Appendix E). However, testing rates in the Owyhee were low (e.g., only 5 sheep were tested in the Owyhee in 2018 whereas 44 were tested in the Lost

River that year), and thus additional testing would be necessary to more accurately determine disease status of the Owyhee population.

Although relationships among the nutritional landscape, ewe behavior, and lamb survival were context dependent and varied among sites, when we combined data across sites we found a strong, positive relationship between spring condition of ewes and probability of lamb survival over summer. Indeed, within the range of nutritional condition observed in our study, maximizing nutritional condition in spring led to a threefold increase in the probability of lamb survival over summer. These results support our hypothesis and are consistent with previous studies that have shown wide-ranging effects of nutritional condition on the physiology and productivity of ungulates, including birth mass and neonatal survival (Thorne et al. 1976, Côté and Festa-Bianchet 2001, Monteith et al. 2014, Long et al. 2016). For example, in a recent study of bighorn sheep in particular, Stephenson et al. (2020) demonstrated that nutritional condition was directly related to the nutritional value of forage on occupied ranges and had pervasive effects on overwinter survival and reproductive success. Those authors also reported that nutritional condition of lactating ewes in autumn was positively associated with the finite rate of population increase ( $\lambda$ ), suggesting that individual-level response to the nutritional landscape and their associated effects on fitness components (e.g., nutritional condition and neonatal survival) do scale up to influence population performance.

One common criticism of studies of space-use behavior by animals is that they often fail to produce evidence that those behaviors have tangible fitness consequences (Morrison 2001). Our study was based on the premise that many potential fitness consequences of animal space-use and movement decisions should be energetically mediated, and that individuals that consume more forage should have more discretionary energy available to devote to reproduction (Monteith et al. 2013). Testing this hypothesis requires accurately quantifying spatiotemporal variation in the forage resources available to individuals, and our approach to accomplishing this goal combined intensive vegetation sampling with complex statistical modeling (following Merems et al. 2020). Although our models had relatively high predictive power, our approach was limited in several ways that are important to acknowledge. First, our approach focused on modeling variation in forage biomass rather than forage quality. It is possible that accounting for variation in energy and/or protein content of

forage would have improved our ability to link patterns of space use to lamb survival. Forage biomass tends to be more variable across space than forage quality, however, and Tveraa et al. (2013) suggested that variation in quantity (i.e., biomass) of forage was more critical to female reproductive success and offspring body mass than variation in forage quality (a notion also supported by Merems et al. 2020). Second, defining what constitutes ‘forage’ requires knowing which plant species an individual will consume when encountered, and we did not have site-specific diet composition data for any of our study populations. We attempted to overcome this limitation using expert opinion and previously published data for other bighorn sheep populations. However, nutritional landscape maps based on all sampled plants were more useful for linking ewe behavior to lamb survival than maps based on the subset of plants assumed to be eaten when encountered by sheep. This suggests that our attempts to classify forage plants as ‘accepted’ or ‘avoided’ were largely unsuccessful, and that future efforts to quantify population-specific patterns of diet composition are warranted. Finally, our approach assumed that sheep that used areas with higher predicted forage biomass did, in fact, consume more forage. There are several possible reasons why this assumption may have been violated. For example, Berger (1978) concluded that bighorn sheep forage less efficiently and interrupt foraging more frequently when foraging in small groups ( $n < 5$ ), and Rachlow and Bowyer (1998) reported similar results for Dall’s sheep. We were not able to account for group size in our analyses. Nevertheless, this limitation should, if anything, add noise to our data and reduce our ability to detect relationships between ewe behavior and lamb survival. Accordingly, we suggest that our results are more likely to be conservatively biased (i.e., higher probability of a type II error) than the alternative.

Another future consideration for wild sheep populations is the effects of climate change on population growth and sustainability. Current climate-change scenarios predict an increase in global air temperature of 1.1–3.3°C over the next century (Houghton 1996, Field et al. 1999). Warmer temperatures during the last 30 years have affected the function and composition of ecological communities and the phenology and distribution of many species (Walther et al. 2002). Population declines and local and global species extinctions have also been linked to this warming trend (McCarty 2001). As the climate warms, vegetation communities will likely shift in composition or distribution. High-elevation plant communities may decline in area, fragment, or vanish (Peters and Darling 1985). Climate-

mediated changes in habitat quality or availability may increase local extinctions and decrease the number of available habitat patches, conditions that can lead to extirpation of a metapopulation before all habitat becomes unsuitable (Hanski 1999). Our top models for predicting variation in the nutritional landscape in the Lost River included the Palmer drought severity index (PDSI), which uses air temperature and a physical water balance model to take into account the basic effect of climate warming through potential evapotranspiration to estimate relative dryness. The effects of variables like PDSI on forage quantity and/or quality may become increasingly pronounced as the climate continues to warm. Drought can increase mortality of bighorn sheep (Monson 1960), affect recruitment dynamics (Wehausen et al. 1987), and potentially lead to local extinction (Weaver and Mensch 1971). Indeed, changes in precipitation patterns, which are more difficult to predict than changes in temperature (Field et al. 1999), may often outweigh the effects of temperature change on animal populations because precipitation is more likely to be a performance-limiting factor in many ecosystems (Wehausen et al. 1987). Careful analyses of how variation in precipitation and temperature affect availability and quality of forage plants may improve future models of population persistence for large herbivores like bighorn sheep.

Our research helps to establish mechanistic links among habitat heterogeneity, individual space-use behavior, and reproductive success in bighorn sheep, and underscores the fundamental importance of nutrition as a driver of ungulate performance. Continuing to improve our understanding of such relationships will provide valuable insights for managers and conservationists, and will aid in accurately parameterizing models of population dynamics. Maximizing the usefulness of such models requires knowledge of the mechanisms that underpin variation in population demographics, and nutritional-ecological approaches like those used in our study shed important light on those mechanisms. Future efforts to build on our work with bighorn sheep would benefit from (1) collaring lambs at birth to monitor survival and cause-specific mortality at finer time scales, (2) measuring forage quality in addition to forage biomass, (3) quantifying diet composition of sheep using DNA metabarcoding, and (4) recapturing collared individuals at annual intervals to collect repeat measurements of nutritional condition.

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### Tables

Table 1. Number of female bighorn sheep captured and monitored from 2016–2019 in each of three bighorn sheep population management units in Idaho, USA (Owyhee, East Fork, and Lost River). Number of sheep monitored included some ewes that were captured in previous years and monitored for multiple years.

Year	Owyhee		East Fork		Lost River	
	Captured	Monitored	Captured	Monitored	Captured	Monitored
2016	16	12	25	23	0	0
2017	13	23	6	23	14	12
2018	5	15	17	27	44	42
2019	0	4	1	17	0	38
Total	34	54	49	90	58	92

Table 2. Potential vegetation types (PVTs) present in each of three bighorn sheep population ranges in Idaho, USA, and the percentage of each range comprised by each PVT.

Range	Potential vegetation type	ID code	% of range
Lost River	Barren-Rock/Sand/Clay <sup>a</sup>	Barren	4.1
	Inter-Mountain Basins Big Sagebrush Shrubland	IMB_Shrub	12.6
	Inter-Mountain Basins Big Sagebrush Steppe	IMB_Steppe	17.0
	Inter-Mountain Basins Mixed Salt Desert Scrub	IMB_Desert	1.7
	Inter-Mountain Basins Montane Sagebrush Steppe	IMB_MtnSteppe	12.7
	Middle Rocky Mountain Montane Douglas-fir Forest and Woodland <sup>b</sup>	MRM_MDFW	9.5
	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest <sup>b</sup>	NRM_Dry_MMCF	10.3
	Northern Rocky Mountain Subalpine Woodland and Parkland	NRM_SWP	6.8
	Perennial Ice/Snow <sup>a</sup>	Ice_Snow	0.4
	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	RMSM_Dry_SFW	11.2
Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland <sup>b</sup>	RMSM_Wet_SFW	0.8	
East Fork	Barren-Rock/Sand/Clay <sup>a</sup>	Barren	1.3
	Columbia Plateau Steppe and Grassland	CPS_Grassland	0.2
	Inter-Mountain Basins Big Sagebrush Shrubland	IMB_Shrub	2.6
	Inter-Mountain Basins Big Sagebrush Steppe	IMB_Steppe	2.4
	Inter-Mountain Basins Montane Sagebrush Steppe	IMB_MtnSteppe	12.6
	Middle Rocky Mountain Montane Douglas-fir Forest and Woodland <sup>b</sup>	MRM_MDFW	13.7
	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest <sup>b</sup>	NRM_Dry_MMCF	15.1
	Northern Rocky Mountain Subalpine Woodland and Parkland	NRM_SWP	18.6
	Perennial Ice/Snow <sup>a</sup>	Ice_Snow	1.3
	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	RMSM_Dry_SFW	25.0
Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland <sup>b</sup>	RMSM_Dry_SFW	1.6	
Owyhee	Columbia Plateau Steppe and Grassland	CPS_Grassland	1.4

Inter-Mountain Basins Big Sagebrush Shrubland	IMB_Shrub	50.3
Inter-Mountain Basins Big Sagebrush Steppe	IMB_Steppe	35.4
Inter-Mountain Basins Mixed Salt Desert Scrub	IMB_Desert	2.3

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<sup>a</sup>PVT lacks vegetation but was moderately used by bighorn sheep and so was included in analyses of sheep behavior.

<sup>b</sup>PVT was not sampled but was combined with RMSM\_Dry\_SFW for modeling analyses based on similarity of habitat.

Table 3. Sources of candidate predictor variables for modeling spatiotemporal variation in forage biomass.

Predictor variable	Source
Palmer Drought Severity Index (PDSI); Precipitation (monthly total, ppt); Soil moisture (soil); Max temperature (°C, tmax)	Climatology Lab. 2019. TerraClimate. < <a href="http://www.climatologylab.org/terraclimate.html">http://www.climatologylab.org/terraclimate.html</a> >. Accessed 20 July 2020.
Potential Vegetation Type (PVT)	LANDFIRE. 2008. Biophysical Settings Layer, LANDFIRE 1.1.0, U.S. Department of the Interior, Geological Survey. < <a href="http://landfire.cr.usgs.gov/viewer/">http://landfire.cr.usgs.gov/viewer/</a> >. Accessed 11 Oct 2017.
Enhanced Vegetation Index (EVI)	NASA LP DAAC MOD13Q1 MODIS/Terra Vegetation Indices 16-DAY 13 Global 250m SIN Grid V005. NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota < <a href="https://lpdaac.usgs.gov">https://lpdaac.usgs.gov</a> >. Accessed 6 Nov 2018.
Snowmelt date	National Operational Hydrologic Remote Sensing Center. 2004. Snow Data Assimilation System (SNODAS) Data Products at NSIDC, Version 1. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center. < <a href="https://doi.org/10.7265/N5TB14TC">https://doi.org/10.7265/N5TB14TC</a> >. Accessed 27 Aug 2020.
Aspect (cosAspect, sinAspect); Elevation (m); Slope (degrees)	Inside Idaho, < <a href="http://insideidaho.org/popular_data.html">http://insideidaho.org/popular_data.html</a> >. Accessed 7 June 2020.

Table 4. Generalized additive models (GAMs) used to predict spatiotemporal variation in the nutritional landscape (i.e., biomass of forage) available to bighorn sheep in each of three population ranges in Idaho, USA. For each population range we fit separate models for predicting total biomass (i.e., total dry mass [kg/ha] of all plant species) versus accepted biomass (i.e., total dry mass [kg/ha] of plant species ostensibly consumed by sheep) of forage. Spatial and temporal smoothing terms were fit using cubic regression splines, and cross-validation was used to determine the optimal amount of smoothing for each term. Model selection procedures are described in detail in the Methods section.

Range	Best model	Adjusted $R^2$	Deviance explained	GCV <sup>a</sup>
Lost River	Total biomass ~ s(JULIAN) <sup>b</sup> + s(UTM_X) + PVT <sup>c</sup> + sinAspect + Slope + Elevation + EVI <sup>2,d</sup> + PDSI <sup>e</sup>	0.49	62.6%	125,240
	Accepted biomass ~ s(JULIAN) + s(UTM_X, UTM_Y) + PVT + ln(Elevation) + EVI <sup>2</sup> + PDSI <sup>2</sup>	0.63	73.4%	90,971
East Fork	Total biomass ~ sinAspect + ln(Slope) + ln(ppt <sup>f</sup> )	0.28	31.9%	284,990
	Accepted biomass ~ s(UTM_Y) + PVT + sinAspect + ln(Slope) + EVI <sup>2</sup> + ln(ppt)	0.51	60.2%	213,590
Owyhee	Total biomass ~ s(JULIAN) + cosAspect + EVI	0.49	57.9%	109,110
	Accepted biomass ~ s(JULIAN) + cosAspect + EVI	0.49	57.3%	110,460

<sup>a</sup> Minimum generalized cross-validation score; <sup>b</sup> s( ) = smoothing term; <sup>c</sup> PVT = potential vegetation type; <sup>d</sup> EVI = enhanced vegetation index; <sup>e</sup> PDSI = Palmer drought severity index; <sup>f</sup> ppt = total precipitation; <sup>g</sup> soil = soil moisture.

Table 5. Regression coefficients and associated *SEs* and *P*-values for covariates included in the top generalized additive models (GAMs) for predicting spatiotemporal variation in the nutritional landscape (i.e., total or accepted biomass [kg/ha] of forage plants for bighorn sheep) in three population ranges in Idaho, USA, during summer (May-September), 2018–2019. Only *P*-values are shown for smoothing terms, which are denoted with an ‘s’. Potential vegetation type (PVT) was a categorical variable, and coefficients represent contrasts between each listed PVT and the reference PVT (IMB\_Shruh). See Table 1 for PVT definitions. EVI = enhanced vegetation index.

Range	Model	Parameter	Estimate	<i>SE</i>	<i>P</i>
Lost River	Total biomass	s(Julian)	-	-	0.041
		s(UTM_X,UTM_Y)	-	-	0.209
		PVT – IMB_Steppe	-183.052	158.739	0.255
		PVT – IMB_Desert	-247.195	197.390	0.217
		PVT – IMB_MtnSteppe	-220.035	243.104	0.371
		PVT – NRM_SWP	-648.605	314.320	0.045
		PVT – RMSM_Dry_SFW	-724.211	299.997	0.020
	Accepted biomass	Slope	-11.808	8.958	0.195
		Elevation	0.464	0.300	0.104
		EVI <sup>2</sup>	8407.301	2467.238	0.001
		s(Julian)	-	-	0.036
		s(UTM_X,UTM_Y)	-	-	0.003
		Intercept	322.820	77.440	<0.001
		EVI <sup>2</sup>	8829.820	2155.80	<0.001
East Fork	Total biomass	sinAspect	311.500	111.400	0.007
		ln(Slope)	-310.700	120.900	0.013
		ln(Total precipitation)	-339.500	113.300	0.004
	Accepted biomass	s(UTM_Y)	-	-	0.328
		PVT – CPS_Grassland	-77.850	249.010	0.756
		PVT – IMB_Steppe	32.200	261.240	0.903

		PVT – IMB_MtnSteppe	54.690	247.130	0.826
		PVT – NRM_SWP	-356.210	213.940	0.103
		PVT – RMSM_Dry_SFW	-583.340	222.720	0.012
		sinAspect	165.240	97.440	0.097
		ln(Slope)	-235.410	107.040	0.033
		EVI <sup>2</sup>	9899.120	2907.180	0.001
		ln(Total precipitation)	-412.600	96.950	<0.001
Owyhee	Total biomass	s(Julian)	-	-	0.648
		cosAspect	262.500	128.400	0.059
		EVI	7535.800	2393.100	0.007
	Accepted biomass	s(Julian)	-	-	0.613
		cosAspect	260.400	129.200	0.062
		EVI	7540.300	2407.900	0.007

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Table 6. Competing models ( $\Delta\text{AICc} < 2$ ) for explaining variation in the probability of lamb survival during summer (May–September) as a function of available forage biomass (total or accepted; see Methods) and terrain ruggedness at locations used by GPS-collared bighorn sheep in three population ranges in Idaho, USA from 2016–2019. The sheep-year (i.e., data from one GPS-collared sheep in one year) was considered the unit of replication for the analysis. Models were fit using the known-fate modeling framework in Program MARK and are ranked according to Akaike’s Information Criterion corrected for small sample size (AICc); model weights ( $w_i$ ) are also shown. Variable definitions are as follows: Max\_AB = Maximum accepted forage biomass; Mean\_AB = Mean accepted forage biomass; Max\_TB = Maximum total forage biomass; Mean\_TB = Mean total forage biomass; Max\_Ruggedness = Maximum terrain ruggedness; Mean\_Ruggedness = Mean terrain ruggedness.

Range	Model	AICc	$\Delta\text{AICc}$	$w_i$
Lost River	Max_TB	64.0	0.00	0.21
	Max_TB + Max_Ruggedness	64.3	0.32	0.18
	Max_TB + Mean_Ruggedness	64.9	0.88	0.14
	Max_Ruggedness	65.8	1.80	0.09
East Fork	Null	81.0	0.00	0.20
	Mean_AB	81.3	0.33	0.17
	Max_Ruggedness	82.7	1.69	0.09
	Mean_TB	82.7	1.71	0.09
	Max_TB	82.8	1.84	0.08
	Max_AB	82.8	1.86	0.08
	Max_AB + Mean_AB	82.9	1.97	0.08
Owyhee	Null	47.8	0.00	0.23
	Max_TB	49.3	1.45	0.11
	Mean_AB	49.3	1.50	0.11
	Mean_TB	49.4	1.51	0.11
	Max_AB	49.4	1.52	0.11

Table 7. Parameter estimates and associated *SEs* and 95% CIs for covariates included in one of four top models (see Table 6) for predicting bighorn sheep lamb survival as a function of forage availability and terrain ruggedness at locations used by sheep in the Lost River population range in Idaho, USA during summer (May-September), 2017–2019. Max\_TB = Maximum total forage biomass; Max\_Ruggedness = Maximum terrain ruggedness. The top used-location model for the East Fork and Owyhee population ranges was the null model, so no parameter estimates are presented for those ranges.

Range	Parameter	Estimate	<i>SE</i>	CI lower	CI upper
Lost River	Max_Ruggedness	-0.66	0.56	-1.76	0.45
	Max_TB	1.31	0.76	-0.18	2.80

Table 8. Competing models ( $\Delta\text{AICc} < 2$ ) for explaining variation in the probability of lamb survival during summer (May–September) as a function of available forage biomass (total or accepted; see Methods) and terrain ruggedness at random locations generated within the home ranges of GPS-collared bighorn sheep in three population ranges in Idaho, USA from 2016–2019. The sheep-year (i.e., data from one GPS-collared sheep in one year) was considered the unit of replication for the analysis. Models were fit using the known-fate modeling framework in Program MARK and are ranked according to Akaike’s Information Criterion corrected for small sample size (AICc); model weights ( $w_i$ ) are also shown. Variable definitions are as follows: Max\_AB = Maximum accepted forage biomass; Mean\_AB = Mean accepted forage biomass; CV\_AB = Coefficient of variation for accepted forage biomass; Max\_TB = Maximum total forage biomass; Mean\_TB = Mean total forage biomass; CV\_TB = Coefficient of variation for total forage biomass; Max\_Ruggedness = Maximum terrain ruggedness; Mean\_Ruggedness = Mean terrain ruggedness; CV\_Ruggedness = Coefficient of variation for terrain ruggedness.

Range	Model	AICc	$\Delta\text{AICc}$	$w_i$
Lost River	Mean_TB + CV_Ruggedness	56.3	0.00	0.65
East Fork	Mean_TB	76.6	0.00	0.25
	Mean_TB + CV_Ruggedness	77.1	0.54	0.19
Owyhee	Null	47.8	0.00	0.10
	CV_Ruggedness	48.3	0.41	0.08
	CV_AB	48.3	0.48	0.08
	CV_TB	48.4	0.52	0.08
	Mean_AB	49.1	1.23	0.05
	Mean_TB	49.1	1.24	0.05
	Max_TB	49.6	1.77	0.04
	Max_AB	49.6	1.78	0.04
	Mean_Ruggedness	49.7	1.88	0.04
	Max_Ruggedness	49.8	1.92	0.04

Table 9. Parameter estimates and associated *SEs* and 95% CIs for covariates included in top models (see Table 8) for predicting bighorn sheep lamb survival as a function of forage availability and terrain ruggedness at random locations within the home ranges of bighorn sheep in the Lost River and East Fork population ranges in Idaho, USA during summer (May–September), 2016–2019. Mean\_TB = Mean total forage biomass; CV\_Ruggedness = Coefficient of variation for terrain ruggedness. The top random-location model for the Owyhee population range was the null model, so no parameter estimates are presented for that range.

Range	Parameter	Estimate	<i>SE</i>	CI Lower	CI Upper
Lost River	Mean_TB	2.36	0.82	0.75	3.97
	CV_Ruggedness	-1.80	0.63	-3.02	-0.57
East Fork	Mean_TB	-0.87	0.32	-1.57	-0.18
	CV_Ruggedness	0.41	0.32	-0.23	1.04

## Figures

Figure 1. Bighorn sheep population ranges in Idaho, USA, where we conducted our study.

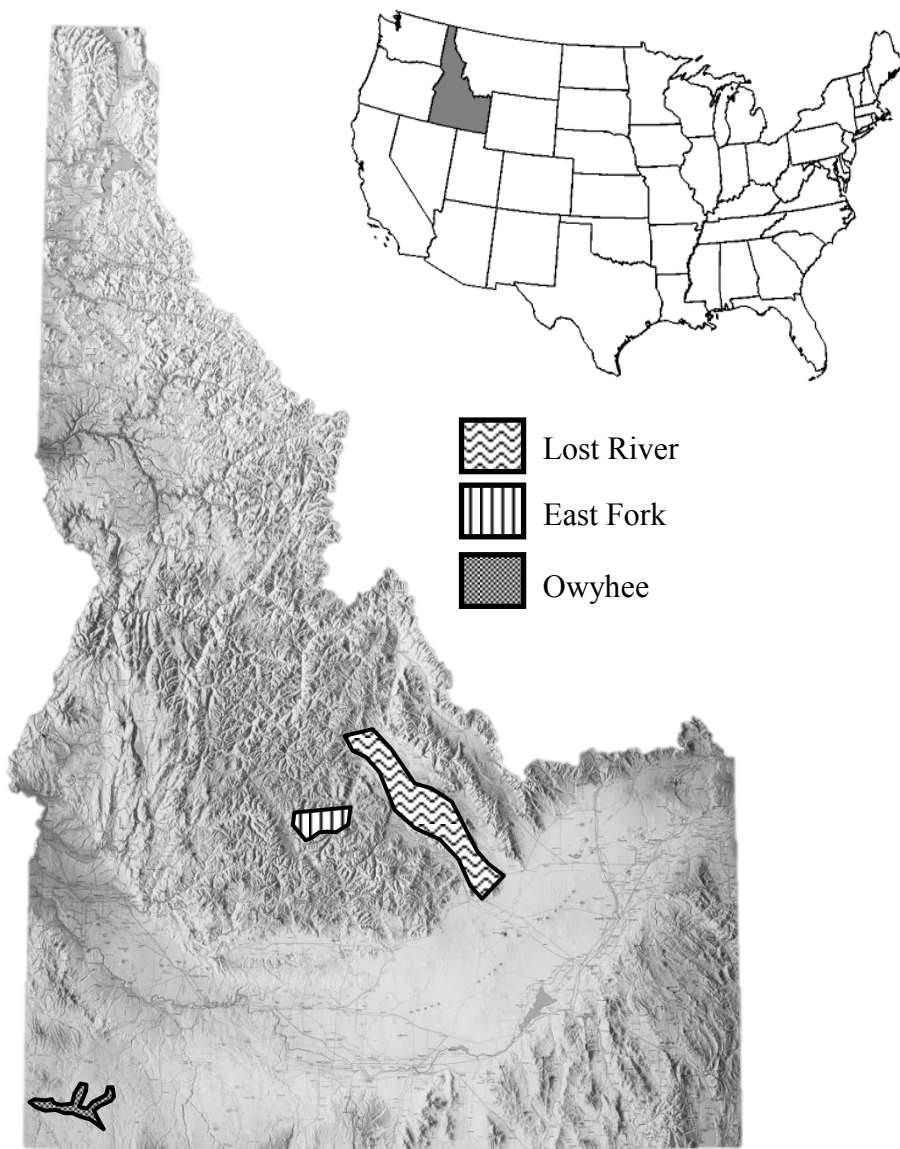


Figure 2. Mean ( $\pm 90\%$  CI) accepted and total biomass of forage (kg/ha) in potential vegetation types (PVTs) that comprised  $>0.2\%$  of three bighorn sheep population ranges in Idaho, USA during summer (May–September), 2018–2019. See Table 2 for PVT definitions.

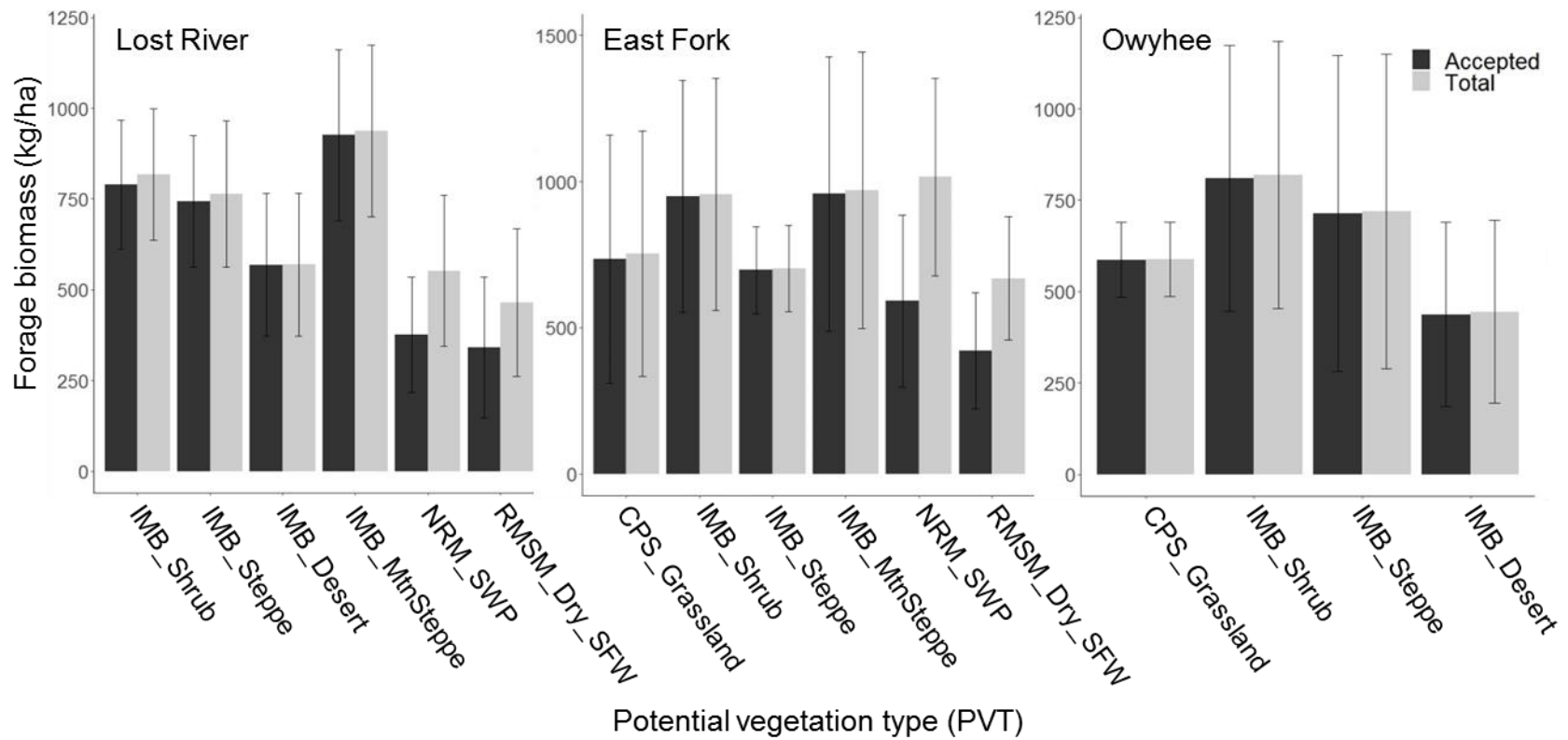


Figure 3. Proportion of randomly sampled locations in each of three bighorn sheep population ranges in Idaho, USA during summer (May–September) that fell into each of four quartiles of predicted forage biomass (accepted and total biomass) based on generalized additive models of the nutritional landscape (see Table 2; High  $\geq 705$  kg/ha, Mid-High = 423–704 kg/ha, Mid-Low = 246–422 kg/ha, Low  $\leq 245$  kg/ha).

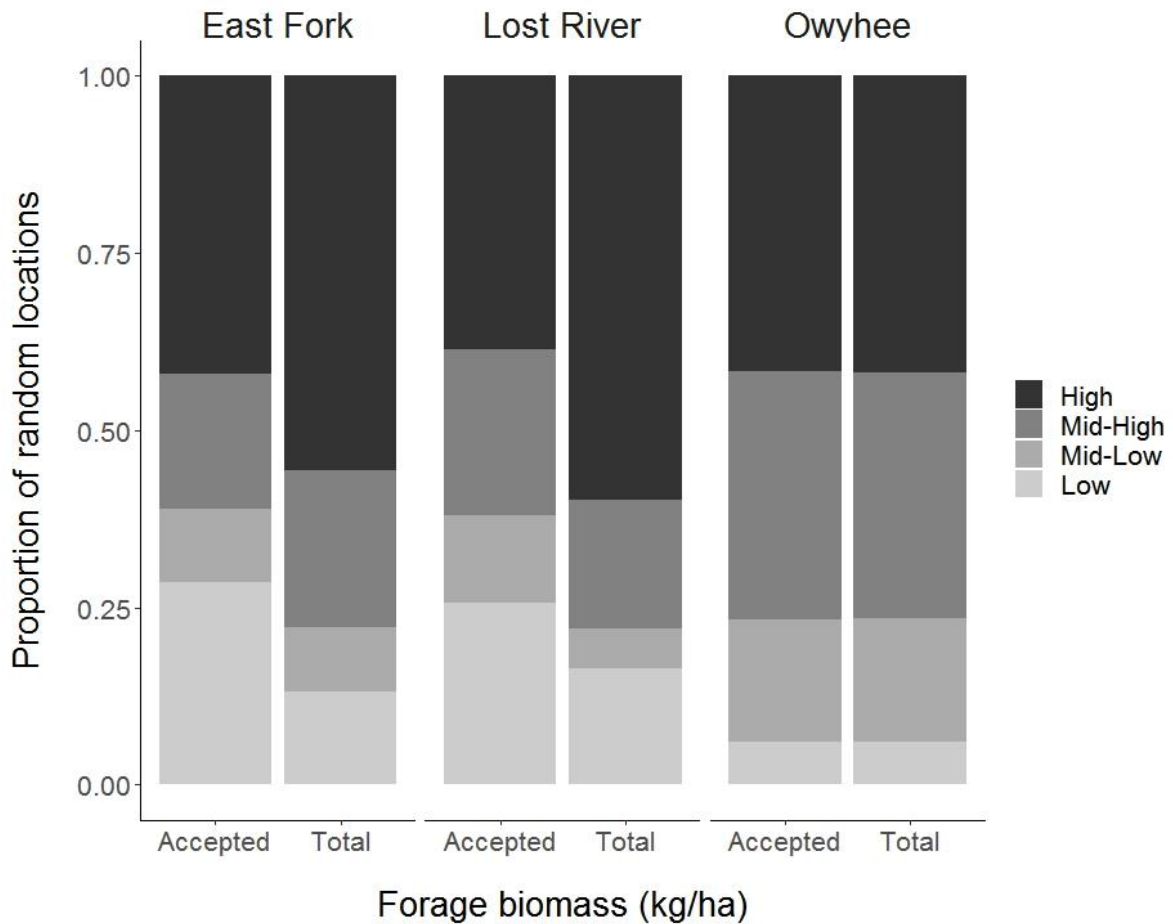


Figure 4. Boxplots of predicted (based on generalized additive models of the nutritional landscape; see Table 2) total and accepted forage biomass at random locations versus locations used by GPS-collared female bighorn sheep in each of three population ranges in Idaho, USA. GPS location data were collected during summer (May–September), 2016–2019.

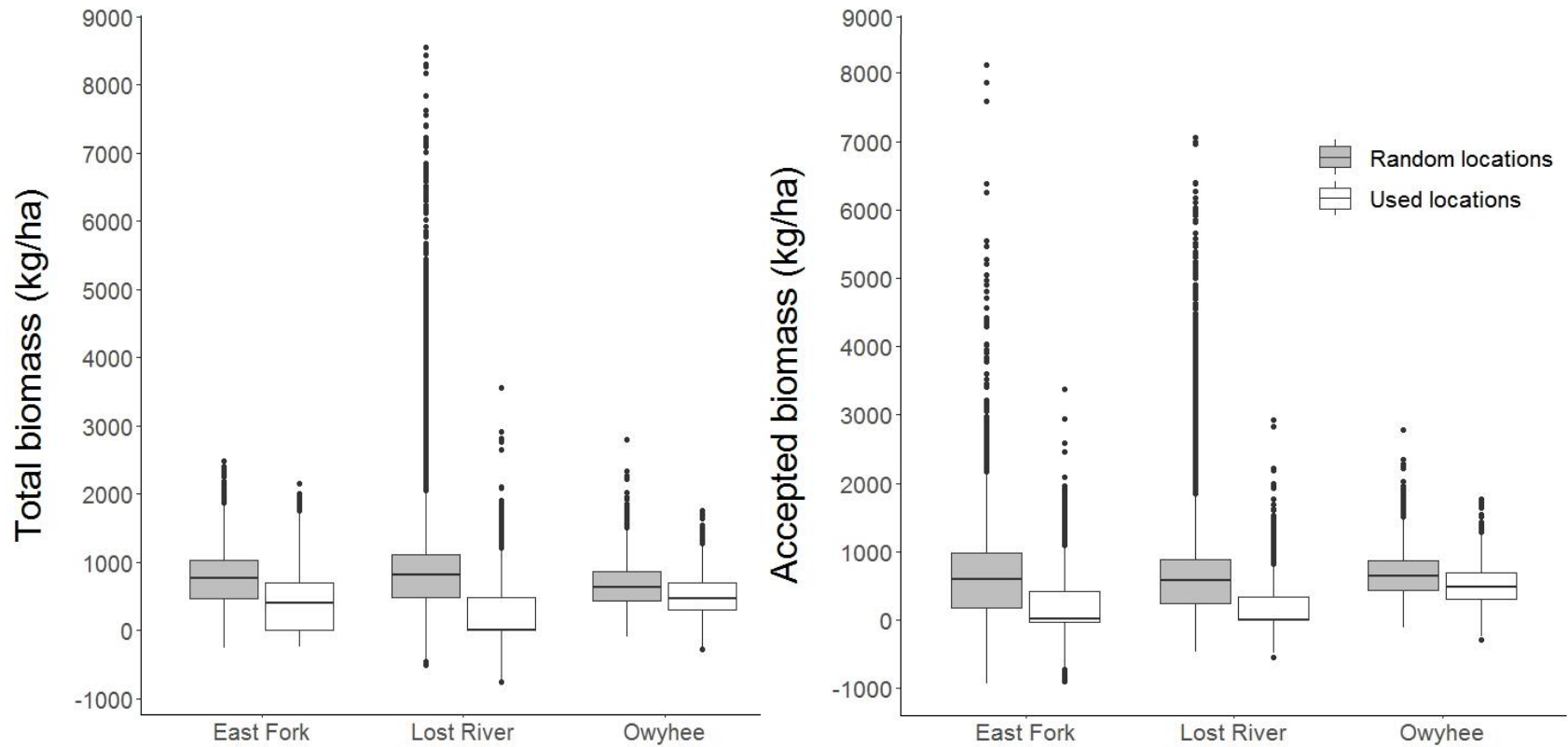




Figure 5. Estimated survival of bighorn sheep lambs in each of three population ranges in Idaho, USA during summer (May–September), 2016–2019. Panel A shows raw results for each combination of population range and year where >10 lambs were monitored. Panel B shows two sets of range-specific survival estimates ( $\pm 95\%$  CI) derived from the known-fate model in Program MARK (see Methods): (1) estimates derived from the best model of lamb survival where individual covariates were extracted from locations used by GPS-collared sheep; and (2) estimates derived from the best model of lamb survival where individual covariates were extracted from random locations within the home ranges of GPS-collared sheep.

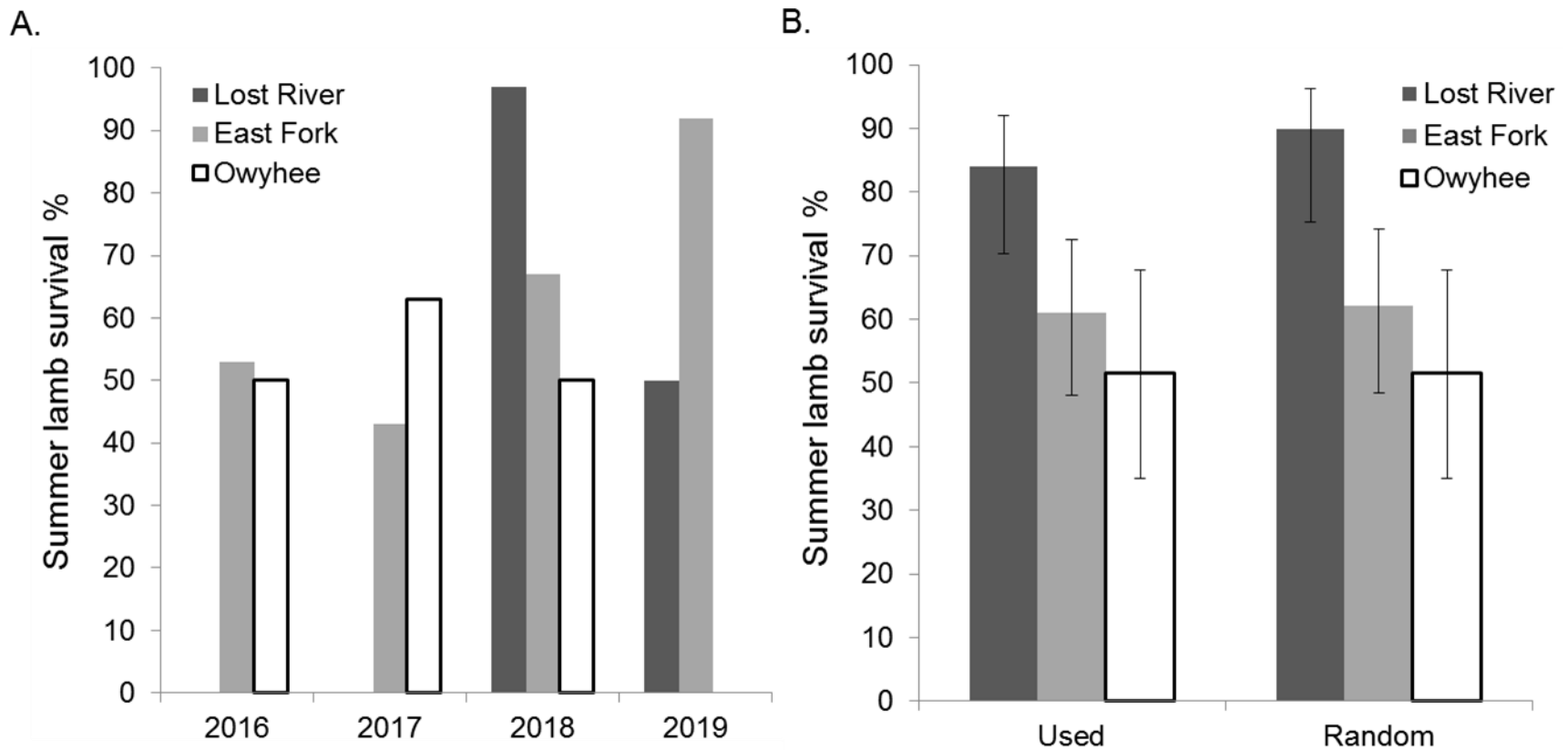
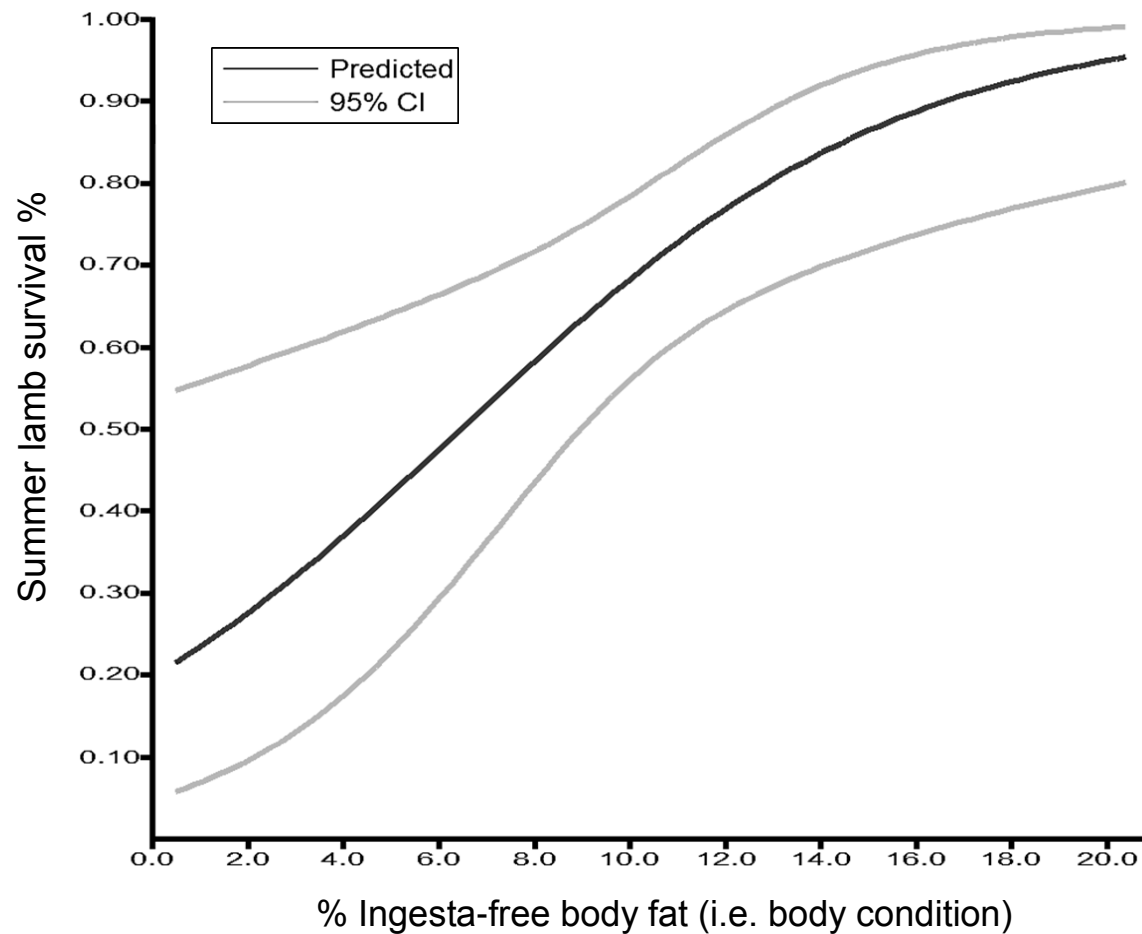


Figure 6. Relationship between summer (May–September) lamb survival and spring body condition (quantified by % ingesta-free body fat) of female bighorn sheep across three bighorn sheep population ranges in Idaho, USA during 2016–2018.



## Appendices

Appendix A. List of plant species sampled during our study (2017–2019) and the associated level of hypothesized selection by bighorn sheep. Level of selection by bighorn sheep was based on published and unpublished data provided by L. Shipley and T. Stephenson. Taxonomy: The PLANTS Database, USDA, NRCS, 2017 (<http://plants.usda.gov>, accessed 6/1/2017).

Plant code	Family	Scientific name	Common name	Level of selection
ABLA	Pinaceae	<i>Abies lasiocarpa</i>	Subalpine fir	Avoided
ACGL	Aceraceae	<i>Acer glabrum</i>	Rocky Mountain maple	Accepted
ACMI2	Asteraceae	<i>Achillea millefolium</i>	Common yarrow	Accepted
ACMIO	Asteraceae	<i>Achillea millefolium var. occidentalis</i>	Western yarrow	Accepted
ACHY	Poaceae	<i>Achnatherum hymenoides</i>	Indian ricegrass	Accepted
ACLEL	Poaceae	<i>Achnatherum lemmonii var lemmonii</i>	Lemmon's needlegrass	Accepted
ACLE9	Poaceae	<i>Achnatherum lettermanii</i>	Letterman's needlegrass	Accepted
ACNEN2	Poaceae	<i>Achnatherum nelsonii</i>	Columbia needlegrass	Accepted
ACTH7	Poaceae	<i>Achnatherum thurberianum</i>	Thurber's needlegrass	Accepted
AGAU2	Asteraceae	<i>Agoseris aurantiaca</i>	Orange agoseris	Avoided
AGGL	Asteraceae	<i>Agoseris glauca</i>	Pale agoseris	Avoided
AGGLL	Asteraceae	<i>Agoseris glauca var. laciniata</i>	False agoseris	Avoided
AGHE2	Asteraceae	<i>Agoseris heterophylla</i>	Annual agoseris	Avoided
AGCR	Poaceae	<i>Agropyron cristatum</i>	Crested wheatgrass	Accepted
AGHU	Poaceae	<i>Agrostis humilis</i>	Alpine bentgrass	Accepted
ALAC4	Amaryllidaceae	<i>Allium acuminatum</i>	Tapertip onion	Avoided
ALBR	Liliaceae	<i>Allium brandegeei</i>	Brandegee's onion	Avoided
ALBR2	Amaryllidaceae	<i>Allium brevistylum</i>	Shortstyle onion	Avoided
ALTO	Liliaceae	<i>Allium tolmiei</i>	Tolmie's onion	Avoided
ALIN2	Betulaceae	<i>Alnus incana</i>	Grey alder	Accepted
ALAL3	Brassicaceae	<i>Alyssum alyssoides</i>	Yellow alyssum	Accepted
ALDE	Brassicaceae	<i>Alyssum desertorum</i>	Desert madwort	Accepted

AMAL2	Rosaceae	<i>Amelanchier alnifolia</i>	Saskatoon serviceberry	Accepted
ANME	Boraginaceae	<i>Amsinckia menziesii</i>	Common fiddleneck	Accepted
ANSE4	Primulaceae	<i>Androsace septentrionalis</i>	Pygmy-flower rock-jasmine	Accepted
ANDR	Ranunculaceae	<i>Anemone drummondii</i>	Drummond's anemone	Avoided
ANMU	Ranunculaceae	<i>Anemone multifida</i>	Pacific anemone	Avoided
ANAL4	Asteraceae	<i>Antennaria alpina</i>	Alpine pussytoes	Avoided
ANDI2	Asteraceae	<i>Antennaria dimorpha</i>	Low pussytoes	Avoided
ANLA3	Asteraceae	<i>Antennaria lanata</i>	Woolly pussytoes	Avoided
ANME2	Asteraceae	<i>Antennaria media</i>	Rocky Mountain pussytoes	Avoided
ANMI3	Asteraceae	<i>Antennaria microphylla</i>	Tiny-leaved pussytoes	Avoided
ANRO2	Asteraceae	<i>Antennaria rosea</i>	Rosy pussytoes	Avoided
ANUM	Asteraceae	<i>Antennaria umbrinella</i>	Umber pussytoes	Avoided
AQCO	Ranunculaceae	<i>Aquilegia coerulea</i>	Colorado blue columbine	Accepted
AQFL	Ranunculaceae	<i>Aquilegia flavescens</i>	Yellow mountain columbine	Accepted
AQFO	Ranunculaceae	<i>Aquilegia formosa</i>	Western columbine	Accepted
ARCO	Brassicaceae	<i>Arabis cobrensis</i>	Sagebrush rockcress	Avoided
ARHI	Brassicaceae	<i>Arabis hirsuta</i>	Hairy rockcress	Avoided
ARHO2	Brassicaceae	<i>Arabis holboellii</i>	Holboell's rockcress	Avoided
ARLEL	Brassicaceae	<i>Arabis lemmonii</i> var. <i>lemmonii</i>	Lemmon's rockcress	Avoided
ARWIS	Brassicaceae	<i>Arabis williamsii</i> var. <i>saximontana</i>	William's rockcress	Avoided
ARDI2	Brassicaceae	<i>Arabis xdivaricarpa</i>	Spreadingpod rockcress	Avoided
ARUV	Ericaceae	<i>Arctostaphylos uva-ursi</i>	Kinnikinnick	Accepted
ARAC2	Caryophyllaceae	<i>Arenaria aculeata</i>	Prickly sandwort	Accepted
ARCO5	Caryophyllaceae	<i>Arenaria congesta</i>	Ballhead sandwort	Accepted
ARCO9	Asteraceae	<i>Arnica cordifolia</i>	Arnica cordifolia	Accepted
ARLA8	Asteraceae	<i>Arnica latifolia</i>	Broadleaf arnica	Accepted
ARLO6	Asteraceae	<i>Arnica longifolia</i>	Spearleaf arnica	Accepted
ARRY	Asteraceae	<i>Arnica rydbergii</i>	Rydberg's arnica	Accepted
ARSO2	Asteraceae	<i>Arnica sororia</i>	Twin arnica	Accepted
ARARA	Asteraceae	<i>Artemisia arbuscula</i> ssp. <i>arbuscula</i>	Low sage	Accepted

ARARL	Asteraceae	<i>Artemisia arbuscula ssp. longiloba</i>	Early sage	Accepted
ARART	Asteraceae	<i>Artemisia arbuscula ssp. thermopola</i>	Little sagebrush	Accepted
ARCA12	Asteraceae	<i>Artemisia campestris</i>	Field sagewort	Avoided
ARFR4	Asteraceae	<i>Artemisia frigida</i>	Prairie sagewort	Accepted
ARLU	Asteraceae	<i>Artemisia ludoviciana</i>	White sagebrush	Accepted
ARMI4	Asteraceae	<i>Artemisia michauxiana</i>	Lemon sagewort	Avoided
ARMI9	Asteraceae	<i>Artemisia minima</i>	Spreading sneezeweed	Avoided
ARTRT	Asteraceae	<i>Artemisia tridentata ssp. tridentata</i>	Basin big sagebrush	Accepted
ARTRV	Asteraceae	<i>Artemisia tridentata ssp. vaseyana</i>	Mountain big sagebrush	Accepted
ARTRW8	Asteraceae	<i>Artemisia tridentata ssp. wyomingensis</i>	Wyoming big sagebrush	Accepted
ARTR4	Asteraceae	<i>Artemisia tripartita</i>	Threetip sagebrush	Accepted
ASAL7	Fabaceae	<i>Astragalus alpinus</i>	Alpine milkvetch	Accepted
ASAT2	Fabaceae	<i>Astragalus atropubescens</i>	Hangingpod milkvetch	Accepted
ASAU4	Fabaceae	<i>Astragalus australis</i>	Indian milkvetch	Accepted
ASBE3	Fabaceae	<i>Astragalus beckwithii</i>	Beckwith's milkvetch	Accepted
ASCO11	Fabaceae	<i>Astragalus conjunctus</i>	Idaho milkvetch	Accepted
ASCU4	Fabaceae	<i>Astragalus curvicaarpus</i>	Curvepod milkvetch	Accepted
ASDO	Fabaceae	<i>Astragalus douglasii</i>	Douglas' milkvetch	Accepted
ASFI	Fabaceae	<i>Astragalus filipes</i>	Basalt milkvetch	Accepted
ASKET	Fabaceae	<i>Astragalus kentrophyta var. tegetarius</i>	Mat milkvetch	Accepted
ASLE8	Fabaceae	<i>Astragalus lentiginosus</i>	Freckled milkvetch	Accepted
ASOB4	Fabaceae	<i>Astragalus obscurus</i>	Arcane milkvetch	Accepted
ASPU9	Fabaceae	<i>Astragalus purshii</i>	Woollypod milkvetch	Accepted
ASWHW	Fabaceae	<i>Astragalus whitneyi var. whitneyi</i>	Balloonpod milkvetch	Accepted
ATCO	Chenopodiaceae	<i>Atriplex confertifolia</i>	Shadscale saltbush	Accepted
BAHO	Asteraceae	<i>Balsamorhiza hookeri</i>	Hooker's balsamroot	Accepted
BASA3	Asteraceae	<i>Balsamorhiza sagittata</i>	Arrowleaf balsamroot	Accepted
BEPA	Betulaceae	<i>Betula papyrifera</i>	Paper birch	Accepted
BLSC	Asteraceae	<i>Blepharipappus scaber</i>	Rough eyelashweed	Accepted

BROBO	Asteraceae	<i>Brickellia oblongifolia</i>	Narrowleaf brickellbush	Accepted
BRAR5	Poaceae	<i>Bromus arvensis</i>	Field brome	Accepted
BRER3	Poaceae	<i>Bromus erectus</i>	Meadow brome	Accepted
BRTE	Poaceae	<i>Bromus tectorum</i>	Cheatgrass	Accepted
BUAM2	Apiaceae	<i>Bupleurum americanum</i>	American thorrowax	Accepted
CAPU	Poaceae	<i>Calamagrostis purpurascens</i>	Purple reedgrass	Accepted
CARU	Poaceae	<i>Calamagrostis rubescens</i>	Pinegrass	Accepted
CANU3	Liliaceae	<i>Calochortus nuttallii</i>	Sego lily	Accepted
CALE4	Ranunculaceae	<i>Caltha leptosepala</i>	White marsh marigold	Accepted
CAMI2	Brassicaceae	<i>Camelina microcarpa</i>	Little false flax	Accepted
CASA2	Brassicaceae	<i>Camelina sativa</i>	False flax	Accepted
CAAB2	Cyperaceae	<i>Carex abrupta</i>	Abrupt-beaked sedge	Accepted
CADO2	Cyperaceae	<i>Carex douglasii</i>	Douglas' sedge	Accepted
CAEL3	Cyperaceae	<i>Carex elynoides</i>	Blackroot sedge	Accepted
CAFI	Cyperaceae	<i>Carex filifolia</i>	Threadleaf sedge	Accepted
CAGE2	Cyperaceae	<i>Carex geyeri</i>	Geyer's sedge	Accepted
CAHO5	Cyperaceae	<i>Carex hoodii</i>	Hood's sedge	Accepted
CALE9	Cyperaceae	<i>Carex leporinella</i>	Hare sedge	Accepted
CAMI7	Cyperaceae	<i>Carex microptera</i>	Small-wing sedge	Accepted
CAMU6	Cyperaceae	<i>Carex multicosata</i>	Manyrib sedge	Accepted
CAPA31	Cyperaceae	<i>Carex paysonis</i>	Payson's sedge	Accepted
CAPE42	Cyperaceae	<i>Carex pellita</i>	Woolly sedge	Accepted
CAPH2	Cyperaceae	<i>Carex phaeocephala</i>	Dunhead sedge	Accepted
CARO5	Cyperaceae	<i>Carex rossii</i>	Ross' sedge	Accepted
CASI2	Cyperaceae	<i>Carex simulata</i>	Analogue sedge	Accepted
CAVA3	Cyperaceae	<i>Carex vallicola</i>	Valley sedge	Accepted
CAME7	Ericaceae	<i>Cassiope mertensiana</i>	Western moss heather	Accepted
CAAN7	Scrophulariaceae	<i>Castilleja angustifolia</i>	Northwestern Indian paintbrush	Accepted
CAAP4	Scrophulariaceae	<i>Castilleja applegatei</i>	Wavyleaf Indian paintbrush	Accepted
CACO36	Scrophulariaceae	<i>Castilleja covilleana</i>	Coville's Indian paintbrush	Accepted

CAFL7	Scrophulariaceae	<i>Castilleja flava</i>	Yellow Indian paintbrush	Accepted
CAMIM6	Scrophulariaceae	<i>Castilleja minor</i>	Lesser Indian paintbrush	Accepted
CAOC4	Scrophulariaceae	<i>Castilleja occidentalis</i>	Western Indian paintbrush	Accepted
CAPA25	Scrophulariaceae	<i>Castilleja pallescens</i>	Pale Indian paintbrush	Accepted
CAPI3	Scrophulariaceae	<i>Castilleja pilosa</i>	Parrothead Indian paintbrush	Accepted
CAPIL	Scrophulariaceae	<i>Castilleja pilosa ssp. longispica</i>	Longspike Indian paintbrush	Accepted
CEST8	Asteraceae	<i>Centaurea stoebe</i>	Spotted knapweed	Accepted
CEAR4	Caryophyllaceae	<i>Cerastium arvense</i>	Field chickweed	Accepted
CENU2	Caryophyllaceae	<i>Cerastium nutans</i>	Nodding chickweed	Accepted
CELE3	Rosaceae	<i>Cercocarpus ledifolius</i>	Curl-leaf mountain mahogany	Accepted
CHDO	Asteraceae	<i>Chaenactis douglasii</i>	Douglas' dustymaiden	Accepted
CHDOA	Asteraceae	<i>Chaenactis douglasii var. achilleifolia</i>	Douglas' dustymaiden	Accepted
CHAN9	Onagraceae	<i>Chamerion angustifolium</i>	Fireweed	Accepted
CHLA13	Onagraceae	<i>Chamerion latifolium</i>	Broadleaf fireweed	Accepted
CHLE4	Chenopodiaceae	<i>Chenopodium leptophyllum</i>	Narrowleaved goosefoot	Accepted
CHUM	Pyrolaceae	<i>Chimaphila umbellata</i>	Prince's pine	Accepted
CHTW	Scrophulariaceae	<i>Chionophila tweedyi</i>	Tweedy snowlover	Accepted
CHTE2	Brassicaceae	<i>Chorispora tenella</i>	Purple mustard	Accepted
CHHU2	Asteraceae	<i>Chrysothamnus humilis</i>	Truckee rabbitbrush	Accepted
CHVI8	Asteraceae	<i>Chrysothamnus viscidiflorus</i>	Yellow rabbitbrush	Accepted
CHVIV2	Asteraceae	<i>Chrysothamnus viscidiflorus ssp. viscidiflorus</i>	Sticky leaved rabbitbrush	Accepted
CIAR4	Asteraceae	<i>Cirsium arvense</i>	Field thistle	Accepted
CICA6	Asteraceae	<i>Cirsium canovirens</i>	Graygreen thistle	Avoided
CICY	Asteraceae	<i>Cirsium cymosum</i>	Peregrine thistle	Avoided
CIFO	Asteraceae	<i>Cirsium foliosum</i>	Elk thistle	Accepted
CISC2	Asteraceae	<i>Cirsium scariosum</i>	Meadow thistle	Avoided
CIUN	Asteraceae	<i>Cirsium undulatum</i>	Wavyleaf thistle	Accepted
CIVU	Asteraceae	<i>Cirsium vulgare</i>	Common thistle	Accepted
CIUMU	Portulacaceae	<i>Cistanthe umbellata var. umbellata</i>	Mt. Hood pussypaws	Accepted
COPA3	Scrophulariaceae	<i>Collinsia parviflora</i>	Small-flowered blue-eyed Mary	Accepted

COGR4	Polemoniaceae	<i>Collomia grandiflora</i>	Grand collomia	Accepted
COLI2	Polemoniaceae	<i>Collomia linearis</i>	Tiny trumpet	Accepted
COTI2	Polemoniaceae	<i>Collomia tinctoria</i>	Staining collomia	Accepted
COSE16	Cornaceae	<i>Cornus sericea</i>	Red twig dogwood	Accepted
CRAC2	Asteraceae	<i>Crepis acuminata</i>	Tapertip hawksbeard	Accepted
CRAT	Asteraceae	<i>Crepis atribarba</i>	Slender hawksbeard	Accepted
CRMO4	Asteraceae	<i>Crepis modocensis</i>	Modoc hawksbeard	Accepted
CROC	Asteraceae	<i>Crepis occidentalis</i>	Largeflower hawksbeard	Accepted
CRIN9	Boraginaceae	<i>Cryptantha interrupta</i>	Elko cryptantha	Accepted
CRSO3	Boraginaceae	<i>Cryptantha sobolifera</i>	Waterton Lakes cryptantha	Accepted
CRT04	Boraginaceae	<i>Cryptantha torreyana</i>	Torrey's cryptantha	Accepted
CYCO4	Apiaceae	<i>Cymopterus corrugatus</i>	Wrinklewing spring-parsley	Avoided
CYNI3	Apiaceae	<i>Cymopterus nivalis</i>	Snow spring-parsley	Avoided
CYOF	Boraginaceae	<i>Cynoglossum officinale</i>	Gypsy flower	Avoided
DAIN	Poaceae	<i>Danthonia intermedia</i>	Mountain wild-oat grass	Accepted
DAUN	Poaceae	<i>Danthonia unispicata</i>	Onespike danthonia	Accepted
DAFR6	Rosaceae	<i>Dasiphora fruticosa</i>	Shrubby cinquefoil	Accepted
DEBI	Ranunculaceae	<i>Delphinium bicolor</i>	Little larkspur	Avoided
DEDE2	Ranunculaceae	<i>Delphinium depauperatum</i>	Slim larkspur	Avoided
DECE	Poaceae	<i>Deschampsia cespitosa</i>	Tuffed hair grass	Accepted
DEIN5	Brassicaceae	<i>Descurainia incisa</i>	Mountain tansy mustard	Avoided
DEPI	Brassicaceae	<i>Descurainia pinnata</i>	Western tansy mustard	Accepted
DEPIN	Brassicaceae	<i>Descurainia pinnata ssp. nelsonii</i>	Nelson's tansy mustard	Accepted
DESO2	Brassicaceae	<i>Descurainia sophia</i>	Flixweed	Accepted
DIUN	Fumariaceae	<i>Dicentra uniflora</i>	Steer's head	Avoided
DISP	Poaceae	<i>Distichlis spicata</i>	Saltgrass	Accepted
DOJE	Primulaceae	<i>Dodecatheon jeffreyi</i>	Sierra shooting star	Accepted
DOPU	Primulaceae	<i>Dodecatheon pulchellum</i>	Darkthroat shooting star	Accepted
DOID	Primulaceae	<i>Douglasia idahoensis</i>	Idaho dwarf primrose	Accepted
DRCR2	Brassicaceae	<i>Draba crassifolia</i>	Snowbed draba	Accepted



DRLO	Brassicaceae	<i>Draba lonchocarpa</i>	Lacepod draba	Accepted
DROL	Brassicaceae	<i>Draba oligosperma</i>	Fewseed draba	Accepted
DRSP2	Brassicaceae	<i>Draba sphaerocarpa</i>	Globe-fruit whitlow grass	Accepted
DRTR3	Brassicaceae	<i>Draba trichocarpa</i>	Stanley creek draba	Accepted
DRVE2	Brassicaceae	<i>Draba verna</i>	Common whitlow grass	Accepted
ELPA5	Cyperaceae	<i>Eleocharis parvula</i>	Common hairgrass	Accepted
ELAL5	Poaceae	<i>Elymus alaskanus</i>	Alaska wild rye	Accepted
ELEL5	Poaceae	<i>Elymus elymoides</i>	Squirreltail	Accepted
EPAN4	Onagraceae	<i>Epilobium anagallidifolium</i>	Pimpernel willowherb	Accepted
EPBR3	Onagraceae	<i>Epilobium brachycarpum</i>	Tall annual fireweed	Accepted
EPLA3	Onagraceae	<i>Epilobium lactiflorum</i>	Milkflower willowherb	Accepted
EQAR	Equisetaceae	<i>Equisetum arvense</i>	Field horsetail	Accepted
EQLA	Equisetaceae	<i>Equisetum laevigatum</i>	Smooth horsetail	Accepted
ERSP3	Polemoniaceae	<i>Eriastrum sparsiflorum</i>	Great basin woollystar	Accepted
ERNA7	Asteraceae	<i>Ericameria nana</i>	Dwarf goldenbush	Accepted
ERNA10	Asteraceae	<i>Ericameria nauseosa</i>	Rubber rabbitbrush	Accepted
ERSU13	Asteraceae	<i>Ericameria suffruticosa</i>	Singlehead goldenbush	Accepted
ERAP	Asteraceae	<i>Erigeron aphanactis</i>	Rayless shaggy fleabane	Accepted
ERAS	Asteraceae	<i>Erigeron asperugineus</i>	Idaho fleabane	Accepted
ERBL	Asteraceae	<i>Erigeron bloomeri</i>	Scabland fleabane	Accepted
ERCO4	Asteraceae	<i>Erigeron compositus</i>	Cutleaf daisy	Accepted
ERCO5	Asteraceae	<i>Erigeron corymbosus</i>	Longleaf fleabane	Accepted
ERFI2	Asteraceae	<i>Erigeron filifolius</i>	Threadleaf fleabane	Accepted
ERLA14	Asteraceae	<i>Erigeron latus</i>	Broad fleabane	Accepted
ERLE6	Asteraceae	<i>Erigeron leiomerus</i>	Rockslide fleabane	Accepted
ERLI	Asteraceae	<i>Erigeron linearis</i>	Desert yellow fleabane	Accepted
ERPE3	Asteraceae	<i>Erigeron peregrinus</i>	Subalpine fleabane	Accepted
ERPU2	Asteraceae	<i>Erigeron pumilus</i>	Shaggy fleabane	Accepted
ERCA8	Polygonaceae	<i>Eriogonum caespitosum</i>	Matted buckwheat	Accepted
ERFL4	Polygonaceae	<i>Eriogonum flavum</i>	Alpine golden buckwheat	Accepted

ERHE2	Polygonaceae	<i>Eriogonum heracleoides</i>	Parsnip-flower buckwheat	Accepted
ERME6	Polygonaceae	<i>Eriogonum meledonum</i>	Bridle buckwheat	Accepted
ERMI4	Polygonaceae	<i>Eriogonum microthecum</i>	Great basin buckwheat	Accepted
EROV	Polygonaceae	<i>Eriogonum ovalifolium</i>	Cushion buckwheat	Accepted
ERST4	Polygonaceae	<i>Eriogonum strictum</i>	Blue mountain buckwheat	Accepted
ERUM	Polygonaceae	<i>Eriogonum umbellatum</i>	Sulphur-flower buckwheat	Accepted
ERLA6	Asteraceae	<i>Eriophyllum lanatum</i>	Common woolly sunflower	Accepted
ERNA	Boraginaceae	<i>Eritrichium nanum</i>	Arctic alpine forget-me-not	Accepted
ERCA14	Brassicaceae	<i>Erysimum capitatum</i>	Sand-dune wallflower	Accepted
ERIN7	Brassicaceae	<i>Erysimum inconspicuum</i>	Shy wallflower	Accepted
FEBRB	Poaceae	<i>Festuca brachyphylla ssp. brachyphylla</i>	Alpine fescue	Accepted
FECA4	Poaceae	<i>Festuca campestris</i>	Rough fescue	Avoided
FEID	Poaceae	<i>Festuca idahoensis</i>	Idaho fescue	Accepted
FEOC	Poaceae	<i>Festuca occidentalis</i>	Western fescue	Avoided
FRVI	Rosaceae	<i>Fragaria virginiana</i>	Wild strawberry	Accepted
FRSP	Gentianaceae	<i>Frasera speciosa</i>	Elkweed	Accepted
FRAT	Liliaceae	<i>Fritillaria atropurpurea</i>	Spotted fritillary	Accepted
GAMU2	Rubiaceae	<i>Galium multiflorum</i>	Shrubby bedstraw	Accepted
GASE2	Rubiaceae	<i>Galium serpticum</i>	Northern bedstraw	Accepted
GAHU	Ericaceae	<i>Gaultheria humifusa</i>	Alpine spicy wintergreen	Accepted
GADI2	Onagraceae	<i>Gayophytum diffusum</i>	Spreading groundsmoke	Accepted
GARA	Onagraceae	<i>Gayophytum racemosum</i>	Blackfooted groundsmoke	Accepted
GARA2	Onagraceae	<i>Gayophytum ramosissimum</i>	Pinyon groundsmoke	Accepted
GEAF	Gentianaceae	<i>Gentiana affinis</i>	Pleated gentian	Avoided
GECA	Gentianaceae	<i>Gentiana calycosa</i>	Mountain bog gentian	Avoided
GEMA4	Rosaceae	<i>Geum macrophyllum</i>	Large-leaf avens	Accepted
GERO2	Rosaceae	<i>Geum rossii</i>	Alpine avens	Accepted
GETR	Rosaceae	<i>Geum triflorum</i>	Prairie smoke	Accepted
GIIN2	Polemoniaceae	<i>Gilia inconspicua</i>	Shy gilia	Accepted
GLST	Poaceae	<i>Glyceria striata</i>	Fowl mannagrass	Accepted

GRSP	Chenopodiaceae	<i>Grayia spinosa</i>	Spiny hopsage	Accepted
HADE	Boraginaceae	<i>Hackelia deflexa</i>	Nodding stickseed	Avoided
HAMI	Boraginaceae	<i>Hackelia micrantha</i>	Jessica stickseed	Avoided
HAPA	Boraginaceae	<i>Hackelia patens</i>	Spotted stickseed	Avoided
HAGL	Chenopodiaceae	<i>Halogeton glomeratus</i>	Saltlover	Avoided
HECO26	Poaceae	<i>Hesperostipa comata</i>	Needle and thread grass	Accepted
HECOI	Poaceae	<i>Hesperostipa comata ssp. intermedia</i>	Intermediate needle and thread grass	Accepted
HECY2	Saxifragaceae	<i>Heuchera cylindrica</i>	Roundleaf alumroot	Accepted
HEPA11	Saxifragaceae	<i>Heuchera parvifolia</i>	Little-leaf alumroot	Accepted
HICY	Asteraceae	<i>Hieracium cynoglossoides</i>	Hound's tongue hawksweed	Accepted
HOJU	Poaceae	<i>Hordeum jubatum</i>	Foxtail barley	Accepted
HYCA4	Hydrophyllaceae	<i>Hydrophyllum capitatum</i>	Ballhead waterleaf	Accepted
IOAL	Asteraceae	<i>Ionactis alpina</i>	Lava aster	Accepted
IPAG	Polemoniaceae	<i>Ipomopsis aggregata</i>	Scarlet gilia	Accepted
IPCO5	Polemoniaceae	<i>Ipomopsis congesta</i>	Ballhead ipomopsis	Accepted
IPCOP	Polemoniaceae	<i>Ipomopsis congesta ssp. palmifrons</i>	Ballhead gilia	Accepted
IPSP02	Polemoniaceae	<i>Ipomopsis spicata ssp. orchidaceae</i>	Orchid ipomopsis	Accepted
IVGO	Rosaceae	<i>Ivesia gordonii</i>	Gordon's ivesia	Accepted
JUAR2	Juncaceae	<i>Juncus arcticus</i>	Arctic rush	Avoided
JUBA	Juncaceae	<i>Juncus balticus</i>	Baltic rush	Accepted
JUDR	Juncaceae	<i>Juncus drummondii</i>	Drummond's rush	Accepted
JUEN	Juncaceae	<i>Juncus ensifolius</i>	Swordleaf rush	Avoided
JUME3	Juncaceae	<i>Juncus mertensianus</i>	Mertens' rush	Avoided
JUNE	Juncaceae	<i>Juncus nevadensis</i>	Sierra rush	Avoided
JUCO6	Cupressaceae	<i>Juniperus communis</i>	Common juniper	Avoided
JUOC	Cupressaceae	<i>Juniperus occidentalis</i>	Western juniper	Avoided
JUSC2	Cupressaceae	<i>Juniperus scopulorum</i>	Rocky mountain juniper	Avoided
KOMA	Poaceae	<i>Koeleria macrantha</i>	Prairie junegrass	Accepted
KRLA2	Chenopodiaceae	<i>Krascheninnikovia lanata</i>	Winterfat	Accepted
LASE	Asteraceae	<i>Lactuca serriola</i>	Prickly lettuce	Accepted

LARA	Asteraceae	<i>Lagophylla ramosissima</i>	Common hareleaf	Accepted
LAOC3	Boraginaceae	<i>Lappula occidentalis</i>	Flatspine stickseed	Accepted
LAGL5	Asteraceae	<i>Layia glandulosa</i>	White daisy tidytips	Accepted
LEGL	Ericaceae	<i>Ledum glandulosum</i>	Western Labrador tea	Avoided
LEPE2	Brassicaceae	<i>Lepidium perfoliatum</i>	Clasping pepperweed	Accepted
LEVI3	Brassicaceae	<i>Lepidium virginicum</i>	Least pepperwort	Accepted
LENU8	Polemoniaceae	<i>Leptosiphon nuttallii</i>	Nuttall's linanthus	Accepted
LESE17	Polemoniaceae	<i>Leptosiphon septentrionalis</i>	Northern linanthus	Accepted
LEKI2	Poaceae	<i>Leucopoa kingii</i>	Spike fescue	Accepted
LEPY2	Portulacaceae	<i>Lewisia pygmaea</i>	Pygmy bitterroot	Accepted
LERE7	Portulacaceae	<i>Lewisia rediviva</i>	Bitterroot	Accepted
LECI4	Poaceae	<i>Leymus cinereus</i>	Basin wildrye	Accepted
LIGR	Apiaceae	<i>Ligusticum grayi</i>	Gray's licorice-root	Accepted
LIPU11	Polemoniaceae	<i>Linanthus pungens</i>	Granite prickly phlox	Accepted
LILE3	Linaceae	<i>Linum lewisii</i>	Wild blue flax	Accepted
LIPA5	Saxifragaceae	<i>Lithophragma parviflorum</i>	Smallflower woodland star	Accepted
LIRU4	Boraginaceae	<i>Lithospermum ruderale</i>	Western stoneseed	Accepted
LOCO4	Apiaceae	<i>Lomatium cous</i>	Cous biscuitroot	Accepted
LOGR	Apiaceae	<i>Lomatium grayi</i>	Gray's biscuitroot	Accepted
LOMA3	Apiaceae	<i>Lomatium macrocarpum</i>	Bigseed biscuitroot	Accepted
LONU2	Apiaceae	<i>Lomatium nudicaule</i>	Bare-stem biscuitroot	Accepted
LOTR2	Apiaceae	<i>Lomatium triternatum</i>	Nineleaf biscuitroot	Accepted
LOIN5	Caprifoliaceae	<i>Lonicera involucrata</i>	Twinberry honeysuckle	Accepted
LUAR3	Fabaceae	<i>Lupinus argenteus</i>	Silvery lupine	Accepted
LULE2	Fabaceae	<i>Lupinus lepidus</i>	Prairie lupine	Accepted
LUSE2	Fabaceae	<i>Lupinus sellulus</i>	Donner lake lupine	Accepted
LUSE4	Fabaceae	<i>Lupinus sericeus</i>	Silky lupine	Accepted
LUWY	Fabaceae	<i>Lupinus wyethii</i>	Wyeth's lupine	Accepted
LUAR5	Juncaceae	<i>Luzula arcuata</i>	Curved wood rush	Avoided
LUSP4	Juncaceae	<i>Luzula spicata</i>	Spiked wood rush	Avoided

MACA2	Asteraceae	<i>Machaeranthera canescens</i>	Hoary tansyaster	Accepted
MAGR3	Asteraceae	<i>Madia gracilis</i>	Grassy tarweed	Avoided
MAST4	Liliaceae	<i>Maianthemum stellatum</i>	Starry false lily of the valley	Accepted
MADI6	Asteraceae	<i>Matricaria discoidea</i>	Wild chamomile	Avoided
MESP	Poaceae	<i>Melica spectabilis</i>	Purple oniongrass	Avoided
MEOF	Fabaceae	<i>Melilotus officinalis</i>	Sweet clover	Accepted
MEAR4	Lamiaceae	<i>Mentha arvensis</i>	Wild mint	Accepted
MEAL6	Loasaceae	<i>Mentzelia albicaulis</i>	Whitestem blazingstar	Accepted
MEDI	Loasaceae	<i>Mentzelia dispersa</i>	Bushy blazingstar	Accepted
MECA6	Boraginaceae	<i>Mertensia campanulata</i>	Idaho bluebells	Avoided
MEOB	Boraginaceae	<i>Mertensia oblongifolia</i>	Oblongleaf bluebells	Avoided
MIGR	Polemoniaceae	<i>Microsteris gracilis</i>	Slender phlox	Avoided
MINU4	Caryophyllaceae	<i>Minuartia nuttallii</i>	Nattall's sandwort	Accepted
MIOB2	Caryophyllaceae	<i>Minuartia obtusiloba</i>	Alpine stitchwort	Accepted
MYST2	Boraginaceae	<i>Myosotis stricta</i>	Blue forget-me-not	Accepted
NABR	Polemoniaceae	<i>Navarretia breweri</i>	Yellow pincushion	Accepted
NALE	Polemoniaceae	<i>Navarretia leucocephala</i>	White-flowered pincushion	Accepted
NEST5	Asteraceae	<i>Nestotus stenophyllus</i>	Narrowleaf goldenweed	Accepted
OECA10	Onagraceae	<i>Oenothera caespitosa</i>	Tufted evening primrose	Accepted
OPPO	Cactaceae	<i>Opuntia polyacantha</i>	Plains prickly pear	Accepted
ORAL4	Asteraceae	<i>Oreostemma alpigenum</i>	Alpine aster	Accepted
ORFA	Orobanchaceae	<i>Orobanche fasciculata</i>	Clustered broomrape	Accepted
PIEX4	Poaceae	<i>Oryzopsis exigua</i>	Little ricegrass	Accepted
OSCH	Apiaceae	<i>Osmorhiza chilensis</i>	Mountain sweet cicely	Accepted
OXSE	Fabaceae	<i>Oxytropis sericea</i>	White locoweed	Accepted
PACA15	Asteraceae	<i>Packera cana</i>	Woolly groundsel	Accepted
PADI11	Asteraceae	<i>Packera dimorphophylla</i>	Splitleaf groundsel	Accepted
PAST10	Asteraceae	<i>Packera streptanthifolia</i>	Rocky Mountain groundsel	Accepted
PASU40	Asteraceae	<i>Packera subnuda</i>	Buek's groundsel	Accepted
PASM	Poaceae	<i>Pascopyrum smithii</i>	Western wheatgrass	Accepted

PEGR2	Scrophulariaceae	<i>Pedicularis groenlandica</i>	Elephanthead lousewort	Accepted
PESI	Cactaceae	<i>Pediocactus simpsonii</i>	Mountain ball cactus	Accepted
PEAT3	Scrophulariaceae	<i>Penstemon attenuatus</i>	Sulphur penstemon	Accepted
PECY3	Scrophulariaceae	<i>Penstemon cyaneus</i>	Blue penstemon	Accepted
PEDE4	Scrophulariaceae	<i>Penstemon deustus</i>	Scabland penstemon	Accepted
PEER	Scrophulariaceae	<i>Penstemon eriantherus</i>	Fuzzy-tongue penstemon	Accepted
PEFR3	Scrophulariaceae	<i>Penstemon fruticosus</i>	Bush penstemon	Accepted
PEMOI2	Scrophulariaceae	<i>Penstemon montanus var. idahoensis</i>	Cordroot beardtongue	Accepted
PEPE12	Scrophulariaceae	<i>Penstemon perpulcher</i>	Minidoka beardtongue	Accepted
PEPR2	Scrophulariaceae	<i>Penstemon procerus</i>	Alpine beardtongue	Accepted
PEPU12	Scrophulariaceae	<i>Penstemon pumilus</i>	Salmon river beardtongue	Accepted
PERY	Scrophulariaceae	<i>Penstemon rydbergii</i>	Rydberg's penstemon	Accepted
PEWI	Scrophulariaceae	<i>Penstemon wilcoxii</i>	Wilcox's penstemon	Accepted
PHGL2	Hydrophyllaceae	<i>Phacelia glandulifera</i>	Sticky phacelia	Accepted
PHHA	Hydrophyllaceae	<i>Phacelia hastata</i>	Silverleaf phacelia	Accepted
PHLI	Hydrophyllaceae	<i>Phacelia linearis</i>	Threadleaf phacelia	Accepted
PHSE	Hydrophyllaceae	<i>Phacelia sericea</i>	Silky phacelia	Accepted
PHAL2	Poaceae	<i>Phleum alpinum</i>	Alpine timothy	Accepted
PHPR3	Poaceae	<i>Phleum pratense</i>	Timothy grass	Accepted
PHAU3	Polemoniaceae	<i>Phlox austromontana</i>	Mountain phlox	Accepted
PHDI3	Polemoniaceae	<i>Phlox diffusa</i>	Spreading phlox	Accepted
PHHO	Polemoniaceae	<i>Phlox hoodii</i>	Spiny phlox	Accepted
PHHOM	Polemoniaceae	<i>Phlox hoodii ssp. Muscoides</i>	Musk phlox	Accepted
PHLO2	Polemoniaceae	<i>Phlox longifolia</i>	Longleaf phlox	Accepted
PHMU3	Polemoniaceae	<i>Phlox multiflora</i>	Rocky mountain phlox	Accepted
PHPU5	Polemoniaceae	<i>Phlox pulvinata</i>	Cushion phlox	Accepted
PHCH	Brassicaceae	<i>Phoenicautis cheiranthoides</i>	Dagger pod	Accepted
PHEM	Ericaceae	<i>Phyllodoce empetriformis</i>	Pink mountain heath	Accepted
PHDI6	Brassicaceae	<i>Physaria didymocarpa</i>	Common twinpod	Accepted
PIEN	Pinaceae	<i>Picea engelmannii</i>	Engelmann spruce	Avoided

PIDE4	Asteraceae	<i>Picrothamnus desertorum</i>	Bud sagebrush	Accepted
PIAL	Pinaceae	<i>Pinus albicaulis</i>	Whitebark pine	Avoided
PICO	Pinaceae	<i>Pinus contorta</i>	Lodgepole pine	Avoided
PIFL2	Pinaceae	<i>Pinus flexilis</i>	Limber pine	Avoided
PIPO	Pinaceae	<i>Pinus ponderosa</i>	Ponderosa pine	Avoided
PLMA2	Plantaginaceae	<i>Plantago major</i>	Broadleaf plantain	Avoided
PLAQ2	Orchidaceae	<i>Platanthera aquilonis</i>	Northern green orchid	Accepted
POAR2	Poaceae	<i>Poa arctica</i>	Arctic bluegrass	Accepted
POBU	Poaceae	<i>Poa bulbosa</i>	Bulbous bluegrass	Accepted
POCO	Poaceae	<i>Poa compressa</i>	Canada bluegrass	Accepted
POCU3	Poaceae	<i>Poa cusickii</i>	Cusick's bluegrass	Accepted
POFE	Poaceae	<i>Poa fendleriana</i>	Muttongrass	Accepted
PONEI2	Poaceae	<i>Poa nemoralis ssp. interior</i>	Inland bluegrass	Accepted
POPA2	Poaceae	<i>Poa palustris</i>	Fowl bluegrass	Accepted
POPR	Poaceae	<i>Poa pratensis</i>	Kentucky bluegrass	Accepted
POSE	Poaceae	<i>Poa secunda</i>	Sandberg bluegrass	Accepted
POWH2	Poaceae	<i>Poa wheeleri</i>	Wheeler's bluegrass	Accepted
POPU3	Polemoniaceae	<i>Polemonium pulcherrimum</i>	Jacob's ladder	Accepted
POVI	Polemoniaceae	<i>Polemonium viscosum</i>	Sticky polemonium	Accepted
POBI6	Polygonaceae	<i>Polygonum bistortoides</i>	American bistort	Accepted
PODOJ2	Polygonaceae	<i>Polygonum douglasii ssp johnstonii</i>	Johnston's knotweed	Accepted
POPO4	Polygonaceae	<i>Polygonum polygaloides</i>	Milkwort knotweed	Accepted
POVI3	Polygonaceae	<i>Polygonum viviparum</i>	Alpine bistort	Accepted
POBA2	Salicaceae	<i>Populus balsamifera</i>	Balsam poplar	Accepted
POTR5	Salicaceae	<i>Populus tremuloides</i>	Quaking aspen	Accepted
POBR5	Rosaceae	<i>Potentilla brevifolia</i>	Sparseleaf cinquefoil	Accepted
PODI2	Rosaceae	<i>Potentilla diversifolia</i>	Mountain meadow cinquefoil	Accepted
POGL9	Rosaceae	<i>Potentilla glandulosa</i>	Sticky cinquefoil	Accepted
POOV2	Rosaceae	<i>Potentilla ovina</i>	Sheep cinquefoil	Accepted
PSSP6	Poaceae	<i>Pseudoroegneria spicata</i>	Bluebunch wheatgrass	Accepted

PSME	Pinaceae	<i>Pseudotsuga menziesii</i>	Douglas-fir	Avoided
PUTR2	Rosaceae	<i>Purshia tridentata</i>	Antelope bitterbrush	Accepted
PYEL	Pyrolaceae	<i>Pyrola elliptica</i>	Wax-flower shinleaf	Avoided
PYMI	Pyrolaceae	<i>Pyrola minor</i>	Snowline wintergreen	Avoided
RAAC3	Ranunculaceae	<i>Ranunculus acris</i>	Tall buttercup	Accepted
RAAN	Ranunculaceae	<i>Ranunculus andersonii</i>	Anderson's buttercup	Accepted
RAES	Ranunculaceae	<i>Ranunculus eschscholtzii</i>	Eschscholtz's buttercup	Accepted
RAGL	Ranunculaceae	<i>Ranunculus glaberrimus</i>	Sagebrush buttercup	Accepted
RATE	Ranunculaceae	<i>Ranunculus testiculatus</i>	Bur buttercup	Accepted
RIAU	Grossulariaceae	<i>Ribes aureum</i>	Golden currant	Accepted
RICE	Grossulariaceae	<i>Ribes cereum</i>	Wax currant	Accepted
RIHU	Grossulariaceae	<i>Ribes hudsonianum</i>	Northern black currant	Accepted
RIMO2	Grossulariaceae	<i>Ribes montigenum</i>	Gooseberry currant	Accepted
RILE2	Asteraceae	<i>Rigiopappus leptocladus</i>	Wireweed	Accepted
ROWO	Rosaceae	<i>Rosa woodsii</i>	Western wild rose	Accepted
RUAR9	Rosaceae	<i>Rubus armeniacus</i>	Himalayan blackberry	Accepted
RUUR	Rosaceae	<i>Rubus ursinus</i>	Pacific blackberry	Accepted
RUCR	Polygonaceae	<i>Rumex crispus</i>	Curly dock	Accepted
RUSA	Polygonaceae	<i>Rumex salicifolius</i>	Willow dock	Accepted
SAAR27	Salicaceae	<i>Salix arctica</i>	Artic willow	Accepted
SABE2	Salicaceae	<i>Salix bebbiana</i>	Bebb's willow	Accepted
SABO2	Salicaceae	<i>Salix boothii</i>	Booth's willow	Accepted
SAGE2	Salicaceae	<i>Salix geyeriana</i>	Geyer willow	Accepted
SALU	Salicaceae	<i>Salix lucida</i>	Shining willow	Accepted
SALU2	Salicaceae	<i>Salix lutea</i>	Yellow willow	Accepted
SAME2	Salicaceae	<i>Salix melanopsis</i>	Dusky willow	Accepted
SANI8	Salicaceae	<i>Salix nivalis</i>	Snow willow	Accepted
SAPL2	Salicaceae	<i>Salix planifolia</i>	Diamond leaf willow	Accepted
SAWO	Salicaceae	<i>Salix wolfii</i>	Wolf's willow	Accepted
SAVE4	Chenopodiaceae	<i>Sarcobatus vermiculatus</i>	Greasewood	Accepted



SAOC4	Saxifragaceae	<i>Saxifraga occidentalis</i>	Western saxifrage	Accepted
SARH2	Saxifragaceae	<i>Saxifraga rhomboidea</i>	Diamond-leaf saxifrage	Accepted
SCAR7	Poaceae	<i>Schedonorus arundinaceus</i>	Tall rye grass	Accepted
SEDE	Crassulaceae	<i>Sedum debile</i>	Orpine stonecrop	Accepted
SELA	Crassulaceae	<i>Sedum lanceolatum</i>	Spearleaf stonecrop	Accepted
SEHY	Asteraceae	<i>Senecio hydrophiloides</i>	Tall groundsel	Accepted
SEIN2	Asteraceae	<i>Senecio integerrimus</i>	Lambstongue ragwort	Accepted
SEME	Asteraceae	<i>Senecio megacephalus</i>	Large-headed ragwort	Accepted
SESE2	Asteraceae	<i>Senecio serra</i>	Tall ragwort	Accepted
SESP4	Asteraceae	<i>Senecio sphaerocephalus</i>	Ballhead ragwort	Accepted
SHCA	Elaeagnaceae	<i>Shepherdia canadensis</i>	Russet buffaloberry	Accepted
SIPR	Rosaceae	<i>Sibbaldia procumbens</i>	Creeping sibbaldia	Accepted
SIDO	Caryophyllaceae	<i>Silene douglasii</i>	Douglas's catchfly	Accepted
SIRE3	Caryophyllaceae	<i>Silene repens</i>	Creeping silene	Accepted
SIAL2	Brassicaceae	<i>Sisymbrium altissimum</i>	Tall tumble mustard	Accepted
SIID	Iridaceae	<i>Sisyrinchium idahoense</i>	Idaho blue eyed grass	Accepted
SMCA	Brassicaceae	<i>Smelowskia calycina</i>	Alpine smelowskia	Accepted
SOMI2	Asteraceae	<i>Solidago missouriensis</i>	Missouri goldenrod	Accepted
SOMU	Asteraceae	<i>Solidago multiradiata</i>	Rocky mountain goldenrod	Accepted
STCR	Caryophyllaceae	<i>Stellaria crassifolia</i>	Fleshy starwort	Accepted
STLO2	Caryophyllaceae	<i>Stellaria longipes</i>	Longstalk starwort	Accepted
STAC	Asteraceae	<i>Stenotus acaulis</i>	Stemless mock goldenweed	Accepted
STLA7	Asteraceae	<i>Stenotus lanuginosus</i>	Wooley mock goldenweed	Accepted
STTE2	Asteraceae	<i>Stephanomeria tenuifolia</i>	Narrow leaved wire lettuce	Avoided
SWPE	Gentianaceae	<i>Swertia perennis</i>	Star swertia	Accepted
SYOR2	Caprifoliaceae	<i>Symphoricarpos oreophilus</i>	Mountain snowberry	Accepted
SYAS3	Asteraceae	<i>Symphyotrichum ascendens</i>	Western aster	Accepted
SYEA2	Asteraceae	<i>Symphyotrichum eatonii</i>	Eaton's aster	Accepted
SYFOF	Asteraceae	<i>Symphyotrichum foliaceum</i>	Alpine leafy-bract aster	Accepted
SYPIC	Scrophulariaceae	<i>Synthyris pinnatifida</i> var. <i>canescens</i>	Cut-leaf kittentail	Accepted

TACA8	Poaceae	<i>Taeniatherum caput-medusae</i>	Medusahead	Avoided
TAOF	Asteraceae	<i>Taraxacum officinale</i>	Common dandelion	Accepted
TECA2	Asteraceae	<i>Tetradymia canescens</i>	Spineless horsebrush	Accepted
TEGR3	Asteraceae	<i>Tetranneuris grandiflora</i>	Old man of the mountain	Accepted
THOC	Ranunculaceae	<i>Thalictrum occidentale</i>	Western meadow rue	Avoided
THPL	Cupressaceae	<i>Thuja plicata</i>	Western red cedar	Avoided
TOAL	Asteraceae	<i>Townsendia alpigena</i>	Wyoming townsend daisy	Accepted
TRDU	Asteraceae	<i>Tragopogon dubius</i>	Western goats beard	Accepted
TRGY	Fabaceae	<i>Trifolium gymnocarpon</i>	Holly-leaf clover	Accepted
TRGYG	Fabaceae	<i>Trifolium gymnocarpon ssp. gymnocarpon</i>	Plummer's clover	Accepted
TRPL2	Fabaceae	<i>Trifolium plumosum</i>	Plumed clover	Accepted
TRPR2	Fabaceae	<i>Trifolium pratense</i>	Red clover	Accepted
TRRE3	Fabaceae	<i>Trifolium repens</i>	White clover	Accepted
TRSP2	Poaceae	<i>Trisetum spicatum</i>	Narrow false oat	Accepted
TRGR7	Liliaceae	<i>Triteleia grandiflora</i>	Wild hyacinth	Accepted
TRLA14	Ranunculaceae	<i>Trollius laxus</i>	American globeflower	Accepted
VASC	Ericaceae	<i>Vaccinium scoparium</i>	Grouse whortleberry	Avoided
VAAC	Valerianaceae	<i>Valeriana acutiloba</i>	Sharpleaf valerian	Accepted
VAACP	Valerianaceae	<i>Valeriana acutiloba var. pubicarpa</i>	Mountain valerian	Accepted
VETH	Scrophulariaceae	<i>Verbascum thapsus</i>	Common mullein	Avoided
VEWO2	Scrophulariaceae	<i>Veronica wormskjoldii</i>	American alpine speedwell	Avoided
VIAD	Violaceae	<i>Viola adunca</i>	Western dog violet	Accepted
VIPU4	Violaceae	<i>Viola purpurea</i>	Goosefoot violet	Accepted
VIPUV2	Violaceae	<i>Viola purpurea ssp. venosa</i>	Purple-marked yellow violet	Accepted
VIVA	Violaceae	<i>Viola vallicola</i>	Sagebrush violet	Accepted
WOOR	Dryopteridaceae	<i>Woodsia oregana</i>	Oregon woodsia	Accepted
ZIEL2	Liliaceae	<i>Zigadenus elegans</i>	Mountain death camas	Avoided
ZIVE	Liliaceae	<i>Zigadenus venenosus</i>	Meadow death camas	Avoided
ZIAQA2	Poaceae	<i>Zizania aquatica var. aquatica</i>	Annual wildrice	Accepted

Appendix B. Species-specific linear regressions of plant biomass against plant cover (%), sample date (i.e., Julian date), log transformations of plant cover and sample date, and interactions between plant cover and sample date with/without log transformations. Coefficients are shown for variables included in the best model for each species or growth-form group, along with the adjusted  $R^2$  value of the model. Species for which it was not appropriate to fit a regression model were assigned a species-specific mean biomass value (see Methods) in the species cover column. We used these models to estimate forage biomass in all unclipped quadrats in the Lost River, East Fork, and Owyhee bighorn sheep population ranges in Idaho, USA.

Plant Code	# of samples	Adj. $R^2$	Intercept	Plant cover	log(Plant cover)	Julian	log(Julian)	Plant cover: Julian	log(Plant cover): log(Julian)
ACMIO	18		0.00	1.14					
AGGL	24	0.98	-0.79	0.06		-0.01		0.03	
AGHE2	7		0.00	1.13					
ALAC4	21		0.00	0.33					
ALAL3	14		0.00	2.13					
ALBR	2		0.00	0.56					
ALDE	10		0.00	2.19					
ANDI2	16	0.40	0.68	1.69					
ANLA3	6		0.00	0.74					
ANMI3	24	0.36	1.28	2.70					
ARAC2	51	0.67	41.10	-35.87		-0.22		0.22	
ARARA	13	0.89	6.20		5.56		-0.97		-0.91
ARARL	14	0.59	90.16	-32.35		-0.51		0.23	
ARCO	9		0.00	0.57					
ARCO9	2		0.00	0.07					
ARHI	5		0.00	0.35					
ARHO2	32		0.00	0.40					
ARTRT	13	0.80	123.97	-10.92		-0.67		0.09	
ARTRV	20	0.89	-15.64	11.17		0.11		-0.04	

ARTRW8	67	0.78	22.76	-4.95		-0.10	0.06
ARWIS	2		0.00	0.87			
ASAU4	2		0.00	1.10			
ASLE8	2		0.00	1.02			
ASOB4	10		0.00	1.99			
ASPU9	15	0.97	-2.35	5.81			
BLSC	6		0.00	0.61			
BRTE	71	0.42	32.78	-40.13		-0.21	0.32
CAAN7	28		0.00	1.25			
CACO36	6		0.00	0.46			
CADO2	4		0.00	2.84			
CAFL7	3		0.00	1.63			
CAGE2	31	0.59	1.34		1.52		
CAMI2	2		0.00	0.66			
CAMI7	4		0.00	1.46			
CANU3	8		0.00	1.41			
CAPU	2		0.00	7.56			
CARU	3		0.00	4.42			
CHDOA	2		0.00	0.78			
CHVI8	14	0.54	1.61		0.69		
CIFO	4		0.00	1.61			
CIVU	4		0.00	2.84			
COPA3	43		0.00	0.61			
CRAC2	24		0.00	1.28			
CROC	20	0.50	-77.31	155.07		0.50	-1.00
CRSO3	3		0.00	1.29			
CYNI3	10		0.00	0.76			
DEBI	5		0.00	0.84			
DEIN5	12		0.00	0.12			
DRCR2	4		0.00	2.36			

DROL	3		0.00	3.95			
DRTR3	2		0.00	3.07			
DRVE2	14		0.00	0.34			
ELEL5	52	0.75	6.63	4.86	-0.04		
ERAS	16		0.00	1.16			
ERBL	8		0.00	0.30			
ERCO4	16	0.79	13.15	-19.46	-0.07		0.12
ERCO5	3		0.00	1.20			
ERLA14	2		0.00	0.54			
ERLE6	3		0.00	1.50			
ERNA10	16	0.90	54.73	-83.23	-0.37		0.61
EROV	23	0.93	-0.16	6.94	0.00		-0.02
ERSU13	7		0.00	1.35			
ERUM	10	0.47	1.06		1.47		
FEID	47	0.77	8.47		0.84	-1.32	
FRAT	3		0.00	0.12			
GADI2	16		0.00	0.19			
GARA2	3		0.00	0.43			
GERO2	4		0.00	2.27			
GETR	12	0.81	-0.29	4.39			
GLST	12	0.71	-86.18	171.78	0.42		-0.81
HAGL	2		0.00	1.28			
HAMI	2		0.00	4.75			
HECOI	20	0.84	1.31	4.96			
HEPA11	3		0.00	0.56			
HOJU	4		0.00	3.06			
IOAL	19	0.80	1.10	-17.08	-0.01		0.14
IPCO5	2		0.00	0.33			
LAOC3	7		0.00	0.37			
LASE	3		0.00	0.13			

LENU8	2		0.00	2.54				
LERE7	11		0.00	0.22				
LESE17	4		0.00	2.59				
LILE3	13		0.00	1.02				
LIPU11	13	0.57	-3.41	10.46				
LIRU4	4		0.00	1.28				
LOMA3	5		0.00	1.15				
LOTR2	5		0.00	0.76				
LUSE2	3		0.00	1.95				
LUSE4	30	0.83	-0.64	5.71				
MACA2	2		0.00	0.76				
MEDI	3		0.00	0.19				
MEOB	6		0.00	0.95				
MIGR	11		0.00	0.43				
OPPO	4		0.00	13.42				
PACA15	10	0.93	-4.66	9.42				
PASM	16	0.78	-0.95	8.60				
PEDE4	3		0.00	4.15				
PEER	17	0.84	-27.29	49.13	0.13			-0.23
PEMOI2	3		0.00	0.27				
PEPR2	33	0.54	-3.42	4.53	0.02			-0.02
PESI	3		0.00	9.24				
PHHA	9		0.00	1.16				
PHHOM	41	0.47	-12.74		1.64		2.81	
PHLI	3		0.00	0.46				
PHLO2	42	0.29	-1.40	4.76				
PHMU3	13	0.73	-68.03		95.26		13.12	-17.84
PODI2	6		0.00	1.75				
POPR	14	0.79	-62.61	139.47	0.30			-0.66
POSE	136	0.48	8.22	2.53	-0.04			

PSSP6	130	0.72	30.84	-9.01		-0.15	0.09
PYMI	2		0.00	0.16			
RAGL	13	0.96	1.48	2.78		-0.01	
RATE	3		0.00	0.41			
SARH2	5		0.00	1.98			
SEDE	2		0.00	2.46			
SELA	34	0.58	-2.81	7.46			
SESP4	4		0.00	0.79			
SIAL2	8		0.00	0.65			
SOMU	3		0.00	7.08			
STAC	16	0.52	9.63		-31.50	-1.60	6.36
SYOR2	11	0.59	0.12	2.44			
TAOF	9		0.00	0.49			
TOAL	3		0.00	1.15			
VIPU4	6		0.00	0.33			
VIVA	2		0.00	0.73			
ZIVE	3		0.00	1.89			
Basal forbs	208	0.58	7.99	0.19		-0.03	0.03
Short forbs	514	0.52	1.39	-3.46		0.00	0.04
Tall forbs	574	0.61	1.83	-1.37		0.00	0.03
Graminoids	639	0.59	15.59	-2.83		-0.07	0.05
Mid-tall shrubs	42	0.43	1.68		0.54		
Evergreen shrubs	209	0.68	2.04		0.73		
Evergreen-trees	17	0.88	2.34		1.01		

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Appendix C. Female bighorn sheep monitored during summer (May–September), 2016–2019 to estimate lamb survival in three population ranges in Idaho, USA. Ewe-Year values are a combination of individual identification number (before underscore) and the year a ewe’s lamb was monitored (after underscore). Lamb indicates whether or not an individual’s lamb survived the summer: Y = Yes, lamb did survive; N = No, lamb did not survive; C = Censored. Ewes were censored if they were never observed with a lamb or if they were not observed in late summer to evaluate lamb presence.

Owyhee		East Fork		Lost River	
Ewe-Year	Lamb	Ewe-Year	Lamb	Ewe-Year	Lamb
16265_2016	N	16270_2016	C	170007_2017	C
16279_2016	Y	16278_2016	Y	170008_2017	Y
16289_2016	Y	16288_2016	C	170009_2017	C
16324_2016	N	16297_2016	N	170010_2017	Y
16329_2016	Y	16323_2016	Y	170012_2017	C
16331_2016	C	16326_2016	Y	170013_2017	C
16363_2016	C	16327_2016	Y	170014_2017	C
16376_2016	N	16336_2016	Y	170016_2017	C
16382_2016	Y	16337_2016	Y	170019_2017	Y
16383_2016	N	16338_2016	Y	170023_2017	C
16386_2016	N	16366_2016	N	170027_2017	Y
16393_2016	Y	16369_2016	Y	170047_2017	C
16265_2017	Y	16370_2016	C	170007_2018	Y
16279_2017	Y	16374_2016	Y	170008_2018	Y
16324_2017	N	16379_2016	N	170010_2018	Y
16329_2017	Y	16385_2016	Y	170012_2018	Y
16331_2017	C	16388_2016	Y	170013_2018	Y
16376_2017	Y	16391_2016	C	170014_2018	Y
16382_2017	N	16392_2016	N	170016_2018	Y
16383_2017	Y	16396_2016	C	170019_2018	Y
16386_2017	N	16397_2016	N	170027_2018	Y



16393_2017	Y	16273_2017	N	170047_2018	Y
170028_2017	N	16278_2017	N	190060_2018	C
170031_2017	Y	16326_2017	Y	19051_2018	Y
170041_2017	Y	16327_2017	Y	19056_2018	Y
170042_2017	C	16336_2017	Y	19057_2018	Y
170046_2017	Y	16337_2017	N	19062_2018	Y
170052_2017	N	16338_2017	N	19064_2018	Y
170055_2017	Y	16366_2017	Y	19070_2018	Y
170057_2017	Y	16369_2017	N	19071_2018	Y
170031_2018	C	16373_2017	Y	19073_2018	Y
170039_2018	Y	16379_2017	N	19081_2018	Y
170041_2018	C	16385_2017	Y	19082_2018	N
170042_2018	N	16388_2017	N	19086_2018	Y
170045_2018	Y	16391_2017	Y	19087_2018	Y
170046_2018	N	16392_2017	Y	19088_2018	Y
170052_2018	Y	16397_2017	Y	19089_2018	Y
170055_2018	Y	170006_2017	N	19090_2018	Y
170057_2018	Y	170015_2017	N	19091_2018	Y
18857_2018	N	170020_2017	N	19094_2018	Y
18687_2018	C	170022_2017	N	19096_2018	Y
18689_2018	Y	170026_2017	N	19098_2018	Y
18687_2019	N	16278_2018	Y	19100_2018	Y
18689_2019	N	16336_2018	Y	19101_2018	Y
18699_2019	C	16337_2018	N	19103_2018	Y
18857_2019	Y	16338_2018	C	19104_2018	Y
		16366_2018	N	19105_2018	Y
		16367_2018	Y	19107_2018	Y
		16388_2018	N	19113_2018	Y
		16391_2018	Y	19114_2018	C
		16392_2018	Y	19119_2018	Y

16397_2018	Y	19120_2018	Y
170002_2018	Y	19121_2018	Y
170006_2018	Y	170007_2019	Y
170015_2018	Y	170008_2019	C
170020_2018	Y	170012_2019	Y
170022_2018	Y	170013_2019	Y
18856_2018	Y	170016_2019	N
19054_2018	Y	170019_2019	C
19067_2018	Y	170027_2019	C
19068_2018	N	170047_2019	C
19069_2018	C	190060_2019	Y
19075_2018	N	19051_2019	Y
19076_2018	N	19057_2019	Y
19077_2018	Y	19058_2019	N
19078_2018	Y	19062_2019	Y
16336_2019	Y	19064_2019	N
16369_2019	Y	19070_2019	N
16373_2019	C	19071_2019	N
16388_2019	N	19073_2019	Y
16392_2019	Y	19081_2019	C
16392_2019	Y	19082_2019	Y
16397_2019	Y	19086_2019	C
170022_2019	N	19087_2019	N
18856_2019	Y	19088_2019	Y
19054_2019	Y	19089_2019	Y
19061_2019	Y	19090_2019	N
19067_2019	Y	19091_2019	N
19068_2019	Y	19094_2019	N
19075_2019	Y	19096_2019	N
19076_2019	N	19100_2019	C

19077_2019	Y	19101_2019	C
19078_2019	N	19103_2019	Y
19080_2019	Y	19104_2019	N
		19105_2019	N
		19107_2019	Y
		19113_2019	C
		19114_2019	N
		19119_2019	Y
		19120_2019	N
		19121_2019	C

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Appendix D. Body condition measurements of female bighorn sheep from three population ranges in Idaho, USA during late-winter (February–March), 2016–2019. Ewe-Year indicates individual identification number (before underscore) and the year in which measurements were obtained (after underscore). BCS = Body condition score (0-6) measured via manual palpation (see Methods). MaxFat = Maximum subcutaneous fat thickness (cm) measured via ultrasound (See Methods). %IFBF = Percent ingesta-free body fat calculated from BCS or MaxFat measurements (see Methods).

Owyhee				East Fork				Lost River			
Ewe-Year	BCS	MaxFat	%IFBF	Ewe-Year	BCS	MaxFat	%IFBF	Ewe-Year	BCS	MaxFat	%IFBF
16265_2016	3.5	0.23	10.83	16270_2016	4	0.41	13.22	170008_2017	4	0.4	13.09
16279_2016	3	0.2	10.44	16297_2016	2	0	6.36	170010_2017	2	0.1	9.11
16289_2016	2.5	0	8.32	16323_2016	2	0	6.36	170019_2017	2	0	6.36
16376_2016	2.5	0	8.32	16326_2016	4	0.2	10.44	170027_2017	2	0	6.36
16382_2016	2.5	0.2	10.44	16336_2016	2.5	0.3	11.76	19051_2018	3.5	0	12.24
16383_2016	3	0.06	8.58	16338_2016	4	0.2	10.44	19056_2018	4	0.3	11.76
16386_2016	2.5	0	8.32	16366_2016	4	0.33	12.16	19057_2018	3.5	0.3	11.76
170028_2017	2	0	6.36	16369_2016	3	0.3	11.76	19062_2018	4.5	0.3	11.76
170031_2017	3	0.08	8.84	16374_2016	4	0.33	12.16	19064_2018	4	0.4	13.09
170041_2017	3.5	0.2	10.44	16379_2016	3.5	0.3	11.76	19070_2018	4	0.35	12.43
170046_2017	3.5	0.11	9.24	16385_2016	2	0	6.36	19071_2018	4.5	0.4	13.09
170052_2017	2.5	-	8.32	16388_2016	1	0	2.44	19073_2018	4.5	0.4	13.09
170055_2017	1	-	2.44	16392_2016	2	0	6.36	19081_2018	3	0.1	9.11
170057_2017	3.5	0.4	13.09	16397_2016	4	0.3	11.76	19082_2018	4	0.2	10.44
18689_2018	3	0.95	20.4	170006_2017	1.5	0	4.4	19086_2018	4	0.5	14.42
18857_2018	4	-	14.2	170015_2017	2	0	6.36	19087_2018	4	0.9	19.73
				170020_2017	1.5	0	4.4	19088_2018	5	0.6	15.75
				170022_2017	0.5	0	0.48	19089_2018	4.5	0.7	17.08
				170026_2017	1.5	0	4.4	19090_2018	4	0.4	13.09
				16385_2018	4.5	-	16.16	19091_2018	4.5	0.2	10.44
				16392_2018	4.5	-	16.16	19096_2018	3.5	0	12.24

170022_2018	3	0.15	9.77	19100_2018	4.5	0.4	13.09
18856_2018	4	0.3	11.76	19101_2018	3	0.6	15.75
19054_2018	4	0.3	11.76	19103_2018	4.5	0.45	13.76
19067_2018	5	0.9	19.73	19104_2018	4.5	0.8	18.4
19068_2018	4.5	0.45	13.76	19105_2018	2	0	6.36
19075_2018	4	0	14.2	19107_2018	2.5	0.2	10.44
19076_2018	5	0.3	11.76	19113_2018	4	0.45	13.76
19077_2018	3.5	0.25	11.1	19119_2018	4.5	0.65	16.41
19078_2018	4	0.1	9.11	19121_2018	4.5	0.9	19.73
16336_2019	2.5	-	8.32				

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Appendix E. Test results for detecting the bacterium *Mycoplasma ovipneumoniae* in serum and nasal swab samples collected from female bighorn sheep in three population ranges in Idaho, USA during 2016–2018. ELISA = enzyme-linked immunoassay and is a commonly used laboratory test to detect antibodies in blood serum. Polymerase chain reaction (PCR) testing was used to detect genetic material from a specific organism, such as a bacterium. Ewe-Year = Female sheep identification number (before underscore) and year sampled (after underscore). Site = East Fork (EF), Lost River (LR), or Owyhee (OH). PCR (Dry) = PCR test performed on a dry nasal swab after sampling female sheep. PCR (TSB) = PCR test performed on a nasal swab stored in tryptic soy broth (TSB) after sampling female sheep.

Ewe-Year	Site	ELISA	PCR (Dry)	PCR (TSB)
16265_2016	OH	Not Detected	–	Not Detected
16270_2016	EF	Detected	–	Not Detected
16273_2016	EF	Detected	–	Not Detected
16274_2016	EF	Detected	–	Detected
16278_2016	EF	Detected	–	Detected
16279_2016	OH	Not Detected	–	Not Detected
16288_2016	EF	Detected	–	Detected
16289_2016	OH	Not Detected	–	Not Detected
16297_2016	EF	Detected	–	Indeterminate
16322_2016	OH	Not Detected	–	Not Detected
16323_2016	EF	Detected	–	Not Detected
16324_2016	OH	–	–	Not Detected
16325_2016	OH	Not Detected	–	Not Detected
16326_2016	EF	Not Detected	–	Not Detected
16326_2018	EF	–	Not Detected	–
16327_2016	EF	Not Detected	–	Not Detected
16329_2016	OH	Not Detected	–	Not Detected
16331_2016	OH	Not Detected	–	Not Detected
16335_2016	OH	Detected	–	Not Detected
16336_2016	EF	Detected	–	Not Detected
16337_2016	EF	Detected	–	Not Detected
16338_2016	EF	Detected	–	Not Detected
16363_2016	OH	Not Detected	–	Not Detected
16366_2016	EF	Not Detected	–	Not Detected
16367_2016	EF	Detected	–	Indeterminate
16369_2016	EF	Indeterminate	–	Not Detected
16370_2016	EF	Detected	–	Not Detected
16373_2016	EF	Detected	–	Detected

16374_2016	EF	Indeterminate	–	Not Detected
16376_2016	OH	Not Detected	–	Not Detected
16379_2016	EF	Detected	–	Not Detected
16381_2018	OH	Not Detected	–	Not Detected
16382_2016	OH	Not Detected	–	Not Detected
16383_2016	OH	Not Detected	–	Not Detected
16385_2016	EF	Detected	–	Not Detected
16385_2018	EF	Detected	Not Detected	–
16386_2016	OH	Not Detected	–	Not Detected
16387_2018	LR	Detected	Detected	Not Detected
16388_2016	EF	Detected	–	Not Detected
16391_2016	EF	Detected	–	Detected
16392_2016	EF	Detected	–	Not Detected
16392_2018	EF	Detected	Not Detected	–
16393_2016	OH	Not Detected	–	Not Detected
16395_2016	OH	Not Detected	–	Not Detected
16396_2016	EF	Detected	–	Indeterminate
16397_2016	EF	Detected	–	Not Detected
170002_2017	EF	Detected	Not Detected	–
170006_2017	EF	Detected	Detected	–
170007_2017	LR	Not Detected	Not Detected	–
170008_2017	LR	Not Detected	Not Detected	–
170009_2017	LR	Detected	Not Detected	–
170010_2017	LR	Not Detected	Not Detected	–
170012_2017	LR	–	Not Detected	–
170013_2017	LR	Indeterminate	Not Detected	–
170014_2017	LR	Detected	Detected	–
170015_2017	EF	Detected	Detected	–
170016_2017	LR	Detected	Not Detected	–
170019_2017	LR	Detected	Not Detected	–
170020_2017	EF	Detected	Indeterminate	–
170022_2017	EF	Detected	Detected	–
170022_2018	EF	Detected	Not Detected	–
170023_2017	LR	Detected	Detected	–
170024_2017	LR	Detected	Not Detected	–
170026_2017	EF	Detected	Detected	–
170026_2018	EF	Detected	Detected	Detected
170027_2017	LR	Indeterminate	Not Detected	–
170028_2017	OH	Not Detected	Not Detected	–
170031_2017	OH	Not Detected	Not Detected	–
170032_2017	OH	Not Detected	Not Detected	–
170036_2017	LR	Not Detected	Not Detected	–
170039_2017	OH	Not Detected	Not Detected	–

170041_2017	OH	Detected	Detected	–
170042_2017	OH	Not Detected	Not Detected	–
170045_2017	OH	Not Detected	Not Detected	–
170046_2017	OH	Not Detected	Not Detected	–
170047_2017	LR	Detected	Not Detected	–
170052_2017	OH	Not Detected	Not Detected	–
170054_2017	OH	Not Detected	Not Detected	–
170055_2017	OH	Not Detected	Not Detected	–
170057_2017	OH	Not Detected	Not Detected	–
170059_2017	OH	Not Detected	Not Detected	–
18687_2018	OH	Not Detected	Not Detected	Not Detected
18689_2018	OH	Not Detected	Not Detected	Not Detected
18699_2018	OH	Not Detected	Not Detected	Not Detected
18856_2018	EF	Not Detected	Not Detected	–
18857_2018	OH	Not Detected	Not Detected	Not Detected
190060_2018	LR	Detected	–	Not Detected
19051_2018	LR	Not Detected	Not Detected	–
19053_2018	EF	Detected	Not Detected	–
19054_2018	EF	Detected	Not Detected	–
19056_2018	LR	Detected	Not Detected	–
19057_2018	LR	Detected	Not Detected	–
19058_2018	LR	Detected	–	Detected
19059_2018	LR	Detected	Detected	Detected
19061_2018	EF	Detected	Not Detected	–
19062_2018	LR	Not Detected	Not Detected	–
19064_2018	LR	Not Detected	Not Detected	–
19067_2018	EF	Not Detected	Not Detected	–
19068_2018	EF	Detected	Not Detected	–
19069_2018	EF	Detected	Not Detected	–
19070_2018	LR	Not Detected	Not Detected	–
19071_2018	LR	Indeterminate	Not Detected	–
19073_2018	LR	Not Detected	Not Detected	–
19075_2018	EF	Detected	Not Detected	–
19076_2018	EF	Detected	Not Detected	–
19077_2018	EF	Detected	Detected	Not Detected
19078_2018	EF	Detected	Detected	Detected
19080_2018	EF	Detected	Not Detected	–
19081_2018	LR	Indeterminate	Not Detected	–
19082_2018	LR	Not Detected	Not Detected	–
19085_2018	LR	Not Detected	–	–
19086_2018	LR	Indeterminate	Not Detected	–
19087_2018	LR	Indeterminate	Detected	Detected
19088_2018	LR	Detected	Not Detected	–



19089_2018	LR	Not Detected	Not Detected	–
19090_2018	LR	Not Detected	Not Detected	–
19091_2018	LR	Detected	Indeterminate	Detected
19092_2018	LR	Not Detected	Not Detected	–
19093_2018	LR	Not Detected	Not Detected	–
19094_2018	LR	Detected	Not Detected	–
19095_2018	LR	Detected	Detected	Detected
19096_2018	LR	Indeterminate	Not Detected	–
19097_2018	LR	Indeterminate	Not Detected	–
19098_2018	LR	Not Detected	Not Detected	–
19100_2018	LR	Detected	Not Detected	–
19101_2018	LR	Detected	Indeterminate	Detected
19102_2018	LR	Not Detected	Not Detected	–
19103_2018	LR	Detected	Not Detected	–
19104_2018	LR	Indeterminate	Not Detected	–
19105_2018	LR	Not Detected	Indeterminate	Not Detected
19106_2018	LR	Detected	Indeterminate	Detected
19107_2018	LR	Not Detected	Not Detected	–
19112_2018	LR	Not Detected	Not Detected	–
19113_2018	LR	Not Detected	Not Detected	–
19114_2018	LR	Detected	Indeterminate	Detected
19119_2018	LR	Not Detected	Not Detected	–
19120_2018	LR	–	Indeterminate	Detected
19121_2018	LR	Not Detected	Detected	Not Detected
19122_2018	LR	Not Detected	Detected	Detected
19123_2018	LR	Not Detected	Not Detected	–

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