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

A Thesis
Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science
with a
Major in Natural Resources
in the
College of Graduate Studies
University of Idaho
by
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.

August 2021

# Authorization to Submit Thesis

This thesis of Nicole M. Bilodeau, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Context-Dependent Effects of Nutrition and Dam Behavior on Neonatal Survival in a Long-Lived Herbivore," has been reviewed in final form. 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: __________
Ryan A. Long, Ph.D.

Committee Members: ________________________________________ Date: __________
E. Frances Cassirer, Ph.D.

________________________________________ Date: __________
Sophie L. Gilbert, Ph.D.

________________________________________ Date: __________
Lisa A. Shipley, Ph.D.

Department
Administrator: ________________________________________ Date: __________
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 (i.e., 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 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.

# Acknowledgments

The number of people to whom I owe the success of this project could be a chapter in and of itself. First, the support and collaboration between the University of Idaho and the Idaho Department of Fish and Game was instrumental in the success of this study. I was exceptionally fortunate to have Ryan Long as my major professor who bolstered my moral during times of frustration, expanded my critical thinking into the bigger picture, and inspired me with his passion for wildlife science. I would like to express my deepest appreciation to my committee members Frances Cassirer, Sophie Gilbert, Lisa Shipley, and Ryan Long for their exceptional expertise, their valuable project recommendations, and their constructive edits throughout the writing process. I would also like to extend my deepest gratitude to Mark Hurley who saw potential in me and took the time to mentor me over the years, which is how I got to where I am today. It was a privilege to be a part of the "Hurley Circus" and I learned more than I could have ever imagined including how valuable my weight is in jet fuel. I am extremely grateful to the entire bighorn sheep capture crew including but not limited to Paul Atwood, Curtis Hendricks, Bret Panting, Shane Roberts, Stacey Dauwalter, John Nelson, Josh Rydalch, Brett Stansberry, Jessie Shallow, Chris Gaughn, Chel Curtis, Katie Oelrich, Michelle Kemner, Brian Marek, Trent Brown, Nathan Borg, Sierra Robatcek, and Cindy McClellan. Your immense hard work, enthusiastic comradery, and endless humor made the 16 hour days just fly by! A special thanks to Hollie Miyasaki for being an excellent capture coordinator and providing a wealth of data. I must also thank Dr. Mark Drew for his uncompromising care for wildlife and for taking the time to teach. I'd also like to extend my gratitude to Tom Stephenson for assisting with capture, providing ultrasound training, and imparting his wisdom of all things sheep. I am deeply grateful to our helicopter pilot Tony Herby who not only made sure we all made it home safe every night, but also provided endless entertainment while on the road. I would like to extend my sincere thanks to Chel Curtis and Brett Stansberry for their invaluable insight and contribution to my project planning, logistics, sheep capture, and surveys. I must also thank Greg Painter, Dennis Newman, Michelle Kemner, and Curtis Hendricks for their help coordinating regional staff and assisting with lamb surveys. A special thank you to John Romero at Owyhee Air for being a smooth pilot, a great lamb spotter, and for bringing me breakfast cookies! Many thanks to two of the greatest botany extraordinaires, Lynn Kinter and Chris Murphy, for all of

your valuable insight, field training, and for inspiring me to love plants. A big thank you to the staff at the Wildlife Health Lab including but not limited to Stacey Dauwalter, Tricia Hebdon, and Shayla March for processing plant samples, letting me store endless amounts of equipment at the lab, making room for my mobile office, and for being awesome people to work with. I am deeply indebted to Doug Engemann and Morgan Fife at the Pahsimeroi Fish Hatchery for providing free housing, sample storage, and the perfect staging area for my summer field work. They were always welcoming and eager to help with inevitable equipment failures, and for that I will always be grateful! I owe a thank you to the Baker family and the Payne family for granting us permission onto your property to access bighorn sheep herds that would otherwise be nearly impossible to track. I would also like to thank Tony Folsom at the Clearwater Fish Hatchery for sharing the ever coveted freezer space with my hundreds of plant samples. Thank you to Jon Horne for letting me borrow your truck for unexpected and last minute transport trips as well as hosting great BBQs and providing invaluable R code assistance. I want to thank Dorah Mtui for going out of her way to help coordinate equipment storage space and laboratory access for me. My deepest appreciation goes to Lisa Shipley for her indispensable expertise and for teaching me how to run nutritional assays at WSU. I am particularly grateful to John Fluegel at the Steffen Center for tolerating the sound of a plant grinder for hundreds of hours and always letting me stay late. I also appreciate all the volunteer coordination and advice I received from Bill London and Zach Higgins at the Wild Sheep Foundation. I owe a big thank you to the countless volunteers who helped with lamb surveys all across the state, and while I didn’t get to meet all of you this project would not have been possible without you. In addition to all the volunteers, there were many IDFG staff members who spent long days hiking in rough sheep country to help complete surveys including Sarah Meronk, Ian Montgomery, Cathy Henry, Bret Stansberry, John Nelson, Morgan Pfander, Iver Hull, Brendon Oats, Paul Page, Dane Cook, Dustin Brewster, Tyler Rothe, and many more! I cannot begin to express my thanks to my technicians Andrea Gibbons, Liana Cabiles, Brendon Harker, Colby Slezak, Andy Landsem, Emily Holmes, Layne Saidnawey, and Conway LeBleu for your dedication and hard work in the field. I promise we really needed all those plants I made you pick! A special thanks to Matt Rafferty for working with me during the winter processing plants (which is quite possibly the most boring job ever) until all hours of the night and weekends! He is one of the most dedicated people I have ever met and his positivity is infectious—I couldn’t have done it without him. I am deeply indebted to my Long lab mates Sierra Robatcek, Jen Merems, Marc Wiseman, Paola Branco, Savannah Rodgers, Hallie Walker, Katey Huggler, Jeremy Van Driessche, and honorary member Matt Rafferty. They were tremendously helpful and supportive in every way and I can’t thank them enough for everything they have done! And to the lovely ladies I started grad school with we are the OG Long’s Ladies for life! I was fortunate enough to be a part of an extraordinary grad student community including Kayte Groth, John Guthrie, Eamon Harrity, Stacey Feeken, Austin Allison, Laura Ehlen, and so so many others. They are not only the greatest group of people to work with but also to hike, BBQ, and grab beers after work with. I wish you all the best of luck in your future endeavors, and if you’re ever in my neck of the woods lets go out for a beer. I would also like to offer a special thanks to Beth Waterbury, Gael Bissell, and Chris Hammond for taking a chance on me and hiring me for my first wildlife jobs. You inspired me, taught me, and sparked my passion for wildlife science. I am also extremely grateful to my family and friends for all your love and support over the years. It means a lot to have such amazing people in your corner cheering you on. A huge thanks to my parents for raising me to love the outdoors and for always encouraging me to pursue my passion. I am grateful to have found my niche in the world because of you. And finally, I would like to express my sincere gratitude to Haden Hussey my greatest adventure partner of all time. I am so thankful for your unwavering support, motivating encouragement, and wonderful humor. Thank you for always supporting me and pushing me to aim high for my goals.

# Table of Contents

## List of Tables

## List of Figures

# 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). A multitude of 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 impacts 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 negatively affect 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 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, etc.) 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 impact of (1) the nutritional landscape (i.e., 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 (*Artemesia 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 $km^2$ of the 3,473-$km^2$ 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 (*Artemesia 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

$km^2$ (our study site included ~549 $km^2$) 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 is about 4,662 $km^2$, of which ~3,186 $km^2$ were included in our study, and supports an estimated population of 256 bighorn sheep (IDFG 2017).

### *Bighorn Sheep Capture 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 ºC. At the staging area we weighed and aged each sheep, collected biological samples (blood, fecal, and nasal swabs), obtained morphological measurements (horn length, horn basal circumference, neck circumference, chest girth, and hind foot length), and quantified nutritional condition and reproductive status using a combination of ultrasonography and manual palpation (Stephenson et al. 1998, 2002). We weighed ewes in sling bags using a tripod with either a digital or spring scale, and true weight was calculated by subtracting the weight of the sling bag after removing the ewe. 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 rototag 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). It is not reliable to age bighorn ewes >4 years old without extracting a tooth and counting cementum annuli (Turner 1977), so ewes 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 × 1” 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 & Lost River: mid-May–June) we conducted aerial surveys using a combination of visual observation and a high-definition infrared (IR) 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.).

### *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). Sampling locations in each PVT were then 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 at each study site. Biomass plots consisted of a 100-m transect with 1-$m^2$ quadrats placed every 20 m, beginning at 20 m and ending at 100 m. Within each quadrat we identified all plants to species and assigned each species to one of the following phenological stages: newly emergent, flowering, fruiting, mature, or cured. 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-$m^2$ 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 ºC 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 ≤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 ≥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 ≤1%, (2) assigned that mean biomass value to all unclipped quadrats where % cover was ≤1%, and (3) upscaled (linearly) the average biomass value to unclipped quadrats where % cover was >1% (e.g., for a quadrat with 2% cover of the species 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 (≤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 (≥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 (AIC) 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 AIC 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) $\text{covariate}^2$; (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 AIC 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 AIC 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 ≥ 705 kg/ha, Mid-High = 423–704 kg/ha, Mid-Low = 246–422 kg/ha, Low ≤ 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 nutritional 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 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 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 ΔAICc < 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 ≈ 375–1,000 kg/ha across PVTs) than in the Owyhee (range ≈ 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 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) and were highest in the Lost River (83.9% ± 0.05 *SE*), intermediate in the East Fork (61.0% ± 0.06), and lowest in the Owyhee (51.5% ± 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, 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, ewe behavior, and lamb survival 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). It is challenging for animals to consistently optimize their behavior (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 dams consistently used locations that provided high forage biomass but reduced access to 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, ≥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 2015–16 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 2016–18 resulted in two positive detections for *Mycoplasma ovipneumoniae*, although these results do not indicate whether or not a herd is currently infected. 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 impacts 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, however, there were several limitations to our approach 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 are results are more likely to be conservatively biased (i.e., higher probability of a type II error) than the alternative.

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.

# References

Berger, K. M. 1978. Group Size, Foraging, and Antipredator Ploys: An Analysis of Bighorn Sheep Decisions. Behavioral Ecology and Sociobiology 4: 91–99.

Berger, K. M. and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76: 1075–1085.

Belovsky, G. E. 1984. Herbivore Optimal Foraging: New Data and a Comparison of Three Models. The American Naturalist 124: 97–115.

Bleich, V. C., R. T. Bowyer, and J. W. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134: 1–50.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons, New York, New York.

Boyce, W. M., M. E. Weisenberger, M. C. Penedo, and C. K. Johnson. 2011. Wildlife translocation: the conservation implications of pathogen exposure and genetic heterozygosity. BMC Ecology 11:5.

Bronson, F. H. 1989. Mammalian reproductive biology. The University of Chicago Press, Chicago, Illinois, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Butler, B. W., and C. Wayne. 2007. The fire environment – innovations, management, and policy; conference proceedings. Destin, FL. Proceedings RMRS-P-46CD. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 662p.

Cameron, R.D., W.T. Smith, S.G. Fancy, K.L. Gerhart, and R.G. White. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71: 480-486.

Cassirer, E. F., K. R. Manlove, E. S. Almberg, P. Kamath, M. Cox, P. Wolff, A. Roug, J. Shannon, R. Robinson, R. B. Harris, B. J. Gonzales, R. K. Plowright, P. J. Hudson, P. C. Cross, A. Dobson, and T. Besser. 2017. Pneumonia in bighorn sheep: risk and resilience. Journal of Wildlife Management 81:32-45.

Caughley, G., and C.J. Krebs. 1983. Are big animals simply little mammals writ large? Oecologia 59: 7–17.

Clutton-Brock, T. H., and J. M. Pemberton. 2004. Soay sheep: dynamics and selection in an island population. Cambridge University Press, Cambridge UK.

Coltman, D. W., J. G. Pilkington, J. A. Smith, J. M. Pemberton. 1999. Parasite-mediated selection against inbred soay sheep in a free-living, island population. Evolution 1259–67.

Coltman, D. W., K.Wilson, J. G. Pilkington, M. J. Stear, J. M. Pemberton. 2001. A microsatellite polymorphism in the gamma interferon gene is associated with resistance to gastrointestinal nematodes in a naturally-parasitized population of soay sheep. Parasitology 122(5):571–82.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. DelCurto, L. D. Bryant, and L. L. Irwin. 2005. Nutrition and Parturition Date Effects on Elk: Potential Implications for Research and Management. Pages 113-126 in M. J. Wisdom, editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Alliance Communications Group, Lawrence, Kansas, USA.

Cook, J.G., B.K. Johnson, R.C. Cook, R.A. Riggs, T. DelCurto, L.D. Bryant, and L.L. Irwin. 2004. Effects of summer and autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155: 1-60.

Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1996. Nutrition-grow relations of elk calves during late summer and fall. Journal of Wildlife Management 60:528–541.

Cook, R.C., D.L. Murray, J.G. Cook, P.Zager, and S.L. Monfort. 2001. Nutritional influences on breeding dynamics in elk. Canadian Journal of Zoology 79: 845-853.

Cook, R.C., J.G. Cook, and L.L. Irwin. 2003. Estimating elk body mass using chest-girth circumference. Wildlife Society Bulletin 31: 536-543.

Cook, R.C., J.G. Cook, D.L. Murray, P. Zager, B.K. Johnson, and M.W. Gratson. 2001a. Nutritional condition models for elk: which are the most sensitive, accurate, and precise? The Journal of Wildlife Management 65: 988-997.

Cook, R.C., J.G. Cook, R.A. Garrott, L.L. Irwin, and S.L. Monfort. 2002. Effects of diet and body condition of fecal progesterone excretion in elk. Journal of Wildlife Diseases 38: 558-565.

Cook, R.C., J.G. Cook, T.R. Stephenson, W.L. Meyers, S.M. Mccorquodale, D.J.Vales, L.L. Irwin, P.B. Hall, R.D. Spencer, S.L. Murphie, K.A. Schoenecker, P.J.Miller. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. Journal of Wildlife Management 74: 880-896.

Côté, S.D., and M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127: 230-238.

Demarchi, R. A., C. L. Hartwig, and D. A. Demarchi. 2000. Status of the Rocky Mountain bighorn sheep in British Columbia. Wildlife Bulletin No. B-99. British Columbia Ministry of Environment, Lands and Parks, Wildlife Branch. Victoria, British Columbia, Canada.

Dennehy, M. N. 2017. ODFW steps up disease monitoring in California bighorn sheep. Oregon Department of Fish and Wildlife News Releases 24 February. https://www.dfw.state.or.us/news/2017/02_feb/022417b.asp. Accessed on 16 April 2021.

Enk, T., H. Picton, J. Williams. 2001. Factors limiting a bighorn sheep population in Montana following a die-off. Northwest Science Journal 75: 280–290.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts of forage quality, forage quantity, and predator avoidance. Oecologia 75: 580-586.

Festa-Bianchet, M. 1999. Bighorn sheep. Pp. 348–350 in D Wilson, S Ruff, eds. The Smithsonian Book of North American Mammals. Washington, D.C.: The Smithsonian Institution Press.

Festa-Bianchet, M., J.Gaillard, and J.T. Jorgenson. 1998. Mass-and density-dependent reproductive success and reproductive costs in a capital breeder. The American Naturalist 152: 367-379.

Foreyt, W. J., and D. A. Jessup. 1982. Fatal pneumonia of bighorn sheep following association with domestic sheep. Journal of Wildlife Diseases 18:163–168.

Franzmann, A.W. 1985. Assessment of nutritional status. Pages 239–259 in R.J. Hudson and R.G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA.

Frisch, R. E. 1984. Body fat, puberty and fertility. Biological Review. 59:161-188.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores—variable recruitment with constant adult survival. Trends in Ecology and Evolution 13: 58–63.

Geist, V. 1971. Mountain Sheep: a study in behavior and evolution. The University of Chicago Press, Chicago, Illinois, USA.

Gerber, F., R. de Jong, M. E. Schaepman. 2018. Predicting missing values in spatio-temporal remote sensing data. IEEE Transactions on Geoscience and Remote Sensing 56(5):2841-2853.

Gerhart, K.L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Estimating fat content of caribou from body condition scores. Journal of Wildlife Management 60:713–718.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The Management of Wild Large Herbivores to Meet Economic, Conservation and Environmental Objectives. Journal of Applied Ecology 41:1021-1031.

Graham, A. L., A. D. Hayward, K. A. Watt, J. G. Pilkington, J. M. Pemberton, D. H. Nussey. 2010. Fitness correlates of heritable variation in antibody responsiveness in a wild mammal. Science 330(6004):662–665.

Gunn, R. G., and J. M. Doney. 1975. The interaction of nutrition and body condition at mating on ovulation rate and early embryo mortality in Scottish blackface ewes. Journal of Agricultural Science 85:465-470.

Gutierrez-Espeleta, G. A., P. W. Hedrick, S. T. Kalinowski, D. Garrigan, and W. M. Boyce. 2001. Is the decline of desert bighorn sheep from infectious disease the result of low MHC variation? Heredity 86:439–450.

Hansen, C. G. 1980. Habitat. Pages 64-79 *in* G. Monson and L. Sumner, editors. The desert bighorn, its life history, ecology, and management. University of Arizona Press, Tucson, AZ, USA.

Harder, J. D., and R. L. Kirkpatrick. 1994. Physiological methods in wildlife research. Pages 275-306 in T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, Maryland, USA.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80: 4-18.

Hass, C. C. 1997. Seasonality of births in bighorn sheep. Journal of Mammalogy 78:1251-1260.

Hobbs, N. T., and M. W. Miller. 1992. Interactions between pathogens and hosts: simulation of pasteurellosis epizootics in bighorn sheep populations. Pages 997–1006 in D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, Essex, UK.

Huey, R. B., P. E. Hertz, and B. Sinervo. 2003. Behavioral driver versus behavioral inertia in evolution: a null model approach. American Naturalist 161:357–366.

Humphries, M. M., J. Umbanhowar, and K. S. McCann. 2004. Bioenergetic prediction of climate change impacts on northern mammals. Integrative and Comparative Biology 44:152–162.

Idaho Fish and Game [IDFG]. 2010. Hollie Miyasaki. Bighorn Sheep Management Plan. <https://idfg.idaho.gov/old-web/docs/wildlife/planBighorn.pdf>. Accessed 15 July 2017.

Idaho Fish and Game [IDFG]. 2013. Hollie Miyasaki. Bighorn Sheep Statewide Report. <https://collaboration.idfg.idaho.gov/WildlifeTechnicalReports/Bighorn%20Sheep%20Statewide-2013.pdf>. Accessed 20 October 2018.

Idaho Fish and Game [IDFG]. 2017. Hollie Miyasaki. Bighorn Sheep Statewide Report. <https://collaboration.idfg.idaho.gov/WildlifeTechnicalReports/Bighorn%20Sheep%20Statewide%20FY2017.pdf>. Accessed 10 December 2018.

Jacques, C. N., J. A. Jenks, and R.W. Klaver. 2009. Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. Journal of Mammalogy 90:433–441.

Johnson, B. K. 1980. Bighorn sheep food habits, forage preferences, and habitat selection in alpine and subalpine communities. Dissertation, Colorado State University, Fort Collins, USA.

Kie, J. G. 1999. Optimal Foraging and Risk of Predation: Effects on Behavior and Social Structure in Ungulates. Journal of Mammalogy 80(4): 1114–1129.

Kie, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Animal Biotelemetry 1:13. doi: 10.1186/2050-3385-1-13.

Kincaid, R. 1988. Macro elements for ruminants. Pages 326-341 in D. C. Church, editor. The ruminant animal: digestive physiology and nutrition. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Krausman, P. R., and B. D. Leopold. 1986. Habitat components for desert bighorn sheep in the Harquahala Mountains, Arizona. Journal of Wildlife Management 50: 504–508.

Krausman, P. R., J. J. Hervert, and L. L. Ordaway. 1985. Capturing deer and mountain sheep with a net gun. Wildlife Society Bulletin 13:71–73.

Krebs, C. J. 2002. Two complementary paradigms for analyzing population dynamics. Transactions of the Royal Society of London B, Biological Sciences 357: 1211–1219.

Krebs, J. R., and N. B. Davies. (Eds.) 1997: Behavioural ecology: an evolutionary approach. Pages 464 in J. R. Krebs and N. B. Davies, editors (4th ed.). Blackwell Publishing. Oxford, UK.

Lawson, B., and R. Johnson. 1982. Mountain sheep. Pages 1036–1055 in J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America. Johns Hopkins University, Baltimore, Maryland, USA.

Long, R. A., J. G. Kie, R. T. Bowyer, M. A. and Hurley. 2009. Resource selection and movements by female mule deer Odocoileus hemionus: effects of reproductive stage. Wildlife Biology 15: 288–298.

Long, R.A., R.T. Bowyer, W.P. Porter, P. Mathewson, K.L. Monteith, and J.G. Kie. 2014. Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. Ecological Monographs 84: 513–532.

Long, R. A., R. T. Bowyer, W. P. Porter, P. Mathewson, K. L. Monteith, S. L. Findholt, et al. 2016. Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape. Oecologia 181: 709–720. doi: 10.1007/s00442-016-3604-7.

Mahon, C. 1975. Aging desert bighorn by teeth. Desert Bighorn Council Transactions 19:57.

Merems, J. L., L. A. Shipley, T. Levi, J. Ruprecht, D. A. Clark, M. J. Wisdom, N. J. Jackson, K. M. Stewart, and R. A. Long. 2020. Nutritional-landscape models link habitat use to condition of mule deer (Odocoileus hemionus). Frontiers in Ecology and Evolution 8:98. doi: 10.3389/fevo.2020.00098.

Miller, G. D., and W. S. Gaud. 1989. Composition and variability of desert bighorn sheep diets. Journal of Wildlife Management 53:597–606.

Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M. Conner, B. M. Pierce, and R. T. Bowyer. 2013. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. Journal of Animal Ecology 82: 377-388.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):47.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1–62.

Morales, J. M., D. Fortin, J. L. Frair, and E. H. Merrill. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. Landscape Ecology 20: 301–316.

Morano, S., K.M. Stewart, J.S. Sedinger, S.A. Nicolai, and M. Vavra. 2013. Life-history strategies of North American elk: trade-offs associated with reproduction and survival. Journal of Mammalogy 94: 162-172.

Morgantini, L. E., and R. J. Hudson. 1989. Nutritional significance of wapiti (Cervus elaphus) migrations to alpine ranges in western Alberta, Canada. Arctic and Alpine Research 21:288–295.

Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management 65:613–623.

Mysterud, A., N. G. Yoccoz, N. C. Stenseth, and R. Langvatn. 2001. The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. Proceedings of the Royal Society of London, Series B 268:911–919.

Neter, J., M. H., Kutner, W. Wasserman, and C. J. Nachsheim. 1996. Applied Linear Statistical Models. Fourth edition. McGraw-Hill, Boston, MA, USA.

Neville, W. E. Jr., and M. W. Neathery. 1974. Effect of temperature under field conditions on the reproductive performance of ewes. Journal of Reproduction & Fertility 36:423-426.

Nussey, D. H., K. A. Watt, A. Clark, J. G. Pilkington, J. M. Pemberton, A. L. Graham, T. N. McNeilly. 2014. Multivariate immune defenses and fitness in the wild: Complex but ecologically important associations among plasma antibodies, health and survival. Proceedings of the Royal Society B: Biological Sciences 281(1779):2013–2931.

Oftedal, O. T. 1985. Pregnancy and lactation. Pages 215-238 in R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA.

Oregon Department of Fish and Wildlife [ODFW]. 2020. California Bighorn Sheep Herd Size Estimates 2015-2019. ODFW Technical Report. Accessed 5 April 2021.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Pekins P. J., K. S. Smith, and W. W. Mautz. 1998. The energy costs of gestation in White-tailed Deer. Canadian Journal of Zoology 76:1091–1097.

Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart. 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. Ecological Applications 26:2156–2174.

Rachlow, J.L. and R.T. Bowyer. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. Journal of Mammalogy 72:487–492.

Rachlow, J.L. and R.T. Bowyer. 1998. Habitat selection by Dall’s sheep (Ovis dalli): maternal trade-offs. The Zoological Society of London 245: 457–465.

Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, USA.

Roffe, T. J. 1993. Perinatal mortality in caribou from the Porcupine herd, Alaska. Journal of Wildlife Diseases 29:295-303.

Ryder, R. J., E. S. Williams, K. W. Mills, K. H. Bowles, and E. T. Thorne. 1992. Effect of pneumonia on population size and lamb recruitment in Whiskey Mountain bighorn sheep. Biennial Symposium of Northern Wild Sheep and Goat Council. 8: 136–146.

Saltz, D., White, G.C., and Bartmann, R.M. 1995. Assessing animal condition, nutrition, and stress from urine in snow: a critical view. Wildlife Society Bulletin 23: 694–704.

Sappington, J. M., K. M. Lonshore, and D. B. Thompson. 2007. Quantifying land-scape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Diseases 71:1419–1426.

Sikes, R. S., and the Animal Care and Use Committee. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97: 663-688.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall (CRC Press), London.

Smith, D. R. 1954. The bighorn sheep in Idaho, its status, life history, and management. Idaho Department of Fish and Game Wildlife Bulletin 1: 1–154.

Smith, J. B., J. A. Jenks, T. W. Grovenburg, and R. W. Klaver. 2014. Disease and predation: sorting out causes of a bighorn sheep (Ovis canadensis) decline. PLoS ONE 9:e88271.

Smith, J. B., T. W. Grovenburg, K. L. Monteith, and J. A. Jenks. 2015. Survival of female bighorn sheep (Ovis canadensis) in the Black Hills, South Dakota. American Midland Naturalist 174:290–301.

Smith, T. S., J. T. Flinders, and D. S. Winn. 1991. Habitat evaluation procedure for Rocky Mountain bighorn sheep in the Intermountain West. Great Basin Naturalist 51(3): 205-225.

Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscope technique. Journal of Range Management 21: 264–265.

Stephens, P.A., I.L. Boyd, J.M. McNamara, and A.I. Houston. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90: 2057-2067.

Stephenson, T. R., D. W. German, E. F. Cassirer, D. P. Walsh, M. E. Blum, M. Cox, K. M. Stewart, and K. L. Monteith. 2020. Linking population performance to nutritional condition in an alpine ungulate. Journal of Mammalogy 101(5):1244-1256.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwarts, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

Stephenson, T. R., V. C. Bleich., B. M. Pierce., and G. P. Mulcahy. 2002. Validation of mule deer body composition using in vivo and post–mortem indices of nutritional condition. Wildlife Society Bulletin 30:557–564.

Stevens, D. L, and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99: 262-278.

Sudgen, L. G. 1961. The California bighorn in British Columbia with particular reference to the Churn Creek herd. The Queen’s Printer, Victoria, B. C.

Thorne, E.T., R.E. Dean, and W.G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. Journal of Wildlife Management 40: 330–336.

Todd, J. W. 1972. A literature review of bighorn sheep food habits. Colorado Division of Game, Fish and Parks and Cooperative Wildlife Research Unit. Special Report No. 27.

Tollefson, T.N., L.A. Shipley, W.L. Meyers, D.H. Keisler, N. Dasgupta. 2010. Influence of summer and autumn nutrition on body condition on body condition and reproduction in lactating mule deer. Journal of Wildlife Management 74: 974-986.

Turner, J. C. 1977. Cemental annulations as an age criterion in North American sheep. Journal of Wildlife Management 41:211–217.

Tveraa, T., A. Stien, B. J. Bardsen, and P. Fauchald. 2013. Population densities, vegetation green-up, and plant productivity: Impacts on reproductive success and juvenile body mass in reindeer. PLoS ONE 8(2):e56450.

van Beest, F. M., and J. M. Milner. 2013. Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. PLoS ONE 8(6):e65972.

Verme, L. J., and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91–118 in L. K. Halls, editor. White-tailed deer: ecology and management. Wildlife Management Institute, Stackpole Books, Harrisburg, Pennsylvania, USA.

Wagner, G. D., and J. M. Peek. 2006. Bighorn sheep diet selection and forage quality in central Idaho. Northwest Science 80(4):246–258.

Whitaker, J. M. 2010. Diet reconstruction of bighorn sheep (*Ovis canadensis*) using stable isotopes. Thesis, Brigham Young University, Provo, UT, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(1):S120-S139. doi: 10.1080/00063659909477239.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377– 384.

Wood, S. N. 2006. Generalized additive models: An introduction with R. Chapman and Hall (CRC Press), Boca Raton, FL, USA.

Worton, B. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in Ecology with R. Pages in M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, and W. Wong, editors. Statistics for Biology and Health. Springer Science+Business Media LLC. NewYork, NY, USA.

# 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.

| | Owyhee | | East Fork | | Lost River | |
|---|---|---|---|---|---|---|
| Year | 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[a] | 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[b] | MRM_MDFW | 9.5 |
| | Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest[b] | NRM_Dry_MMCF | 10.3 |
| | Northern Rocky Mountain Subalpine Woodland and Parkland | NRM_SWP | 6.8 |
| | Perennial Ice/Snow[a] | 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[b] | RMSM_Wet_SFW | 0.8 |
| East Fork | Barren-Rock/Sand/Clay[a] | 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[b] | MRM_MDFW | 13.7 |
| | Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest[b] | NRM_Dry_MMCF | 15.1 |
| | Northern Rocky Mountain Subalpine Woodland and Parkland | NRM_SWP | 18.6 |
| | Perennial Ice/Snow[a] | 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[b] | 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 |

[a] PVT lacks vegetation but was moderately used by bighorn sheep and so was included in analyses of sheep behavior.

[b] 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 forage biomass.

| Predictor variable | Source |
|---|---|
| Palmer Drought Severity Index (PDSI);<br>Precipitation (monthly total, ppt);<br>Soil moisture (soil);<br>Max temperature (ºC, tmax) | Climatology Lab. 2019. TerraClimate. <http://www.climatologylab.org/terraclimate.html>. 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. <http://landfire.cr.usgs.gov/viewer/>. Accessed 11 Oct 2017. |
| Enhanced Vegetation Index (EVI) | NASA LP DAAC MOD13Q1 MODIS/Terra Vegetation Indices 16-DAY l3 Global 250m SIN Grid V005. NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota <https://lpdaac.usgs.gov>. 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. <https://doi.org/10.7265/N5TB14TC>. Accessed 27 Aug 2020. |
| Aspect (cosAspect, sinAspect);<br>Elevation (m);<br>Slope (degrees) | Inside Idaho, <http://insideidaho.org/popular_data.html>. 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 [a] |
|---|---|---|---|---|
| Lost River | Total biomass ~ s(JULIAN)[b] + s(UTM_X) + PVT[c] + sinAspect + Slope + Elevation + EVI$^{2}$[d] + PDSI[e] | 0.49 | 62.6% | 125,240 |
| | Accepted biomass ~ s(JULIAN) + s(UTM_X, UTM_Y) + PVT + ln(Elevation) + EVI$^2$ + PDSI$^2$ | 0.63 | 73.4% | 90,971 |
| East Fork | Total biomass ~ sinAspect + ln(Slope) + ln(ppt[f]) | 0.28 | 31.9% | 284,990 |
| | Accepted biomass ~ s(UTM_Y) + PVT + sinAspect + ln(Slope) + EVI$^2$ + 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 |

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

Table 5. Regression coefficients and associated *SE*s 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_Shrub). See Table 1 for PVT definitions. EVI = enhanced vegetation index.

| Range | Model | Parameter | Estimate | *SE* | *P* |
|---|---|---|---|---|---|
| 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 |
| | | Slope | -11.808 | 8.958 | 0.195 |
| | | Elevation | 0.464 | 0.300 | 0.104 |
| | | EVI$^2$ | 8407.301 | 2467.238 | 0.001 |
| | Accepted biomass | s(Julian) | - | - | 0.036 |
| | | s(UTM_X,UTM_Y) | - | - | 0.003 |
| | | Intercept | 322.820 | 77.440 | <0.001 |
| | | EVI$^2$ | 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$^2$ | 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 |

Table 6. Competing models (ΔAICc < 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 | ΔAICc | $w_i$ |
|---|---|---|---|---|
| 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 5) 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 | *SE* | 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 (ΔAICc < 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 | ΔAICc | $w_i$ |
|---|---|---|---|---|
| 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 7) 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 | *SE* | 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.

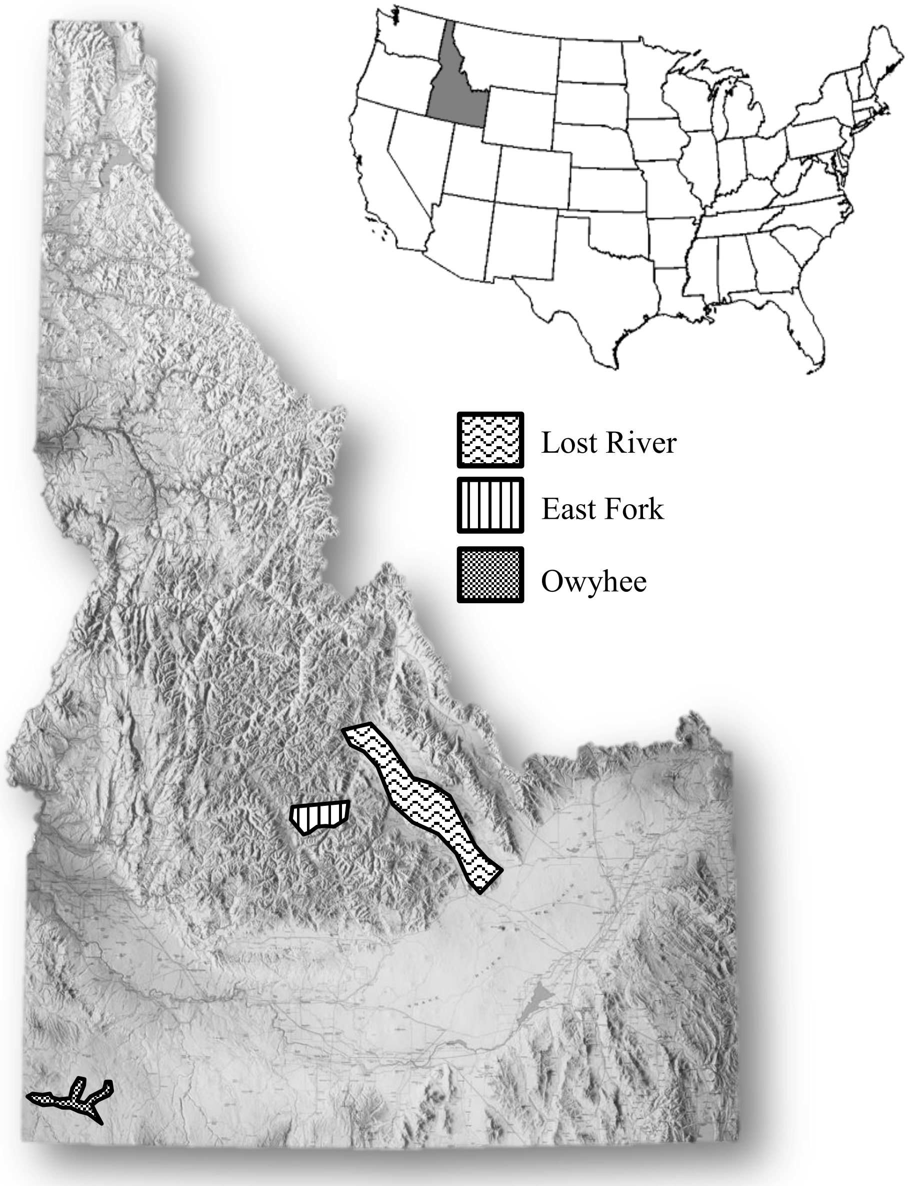


Figure 2. Mean (±90% CI) accepted and total biomass of forage (kg/ha) in potential vegetation types (PVTs) that comprised >0.2% of three bighorn sheep population ranges in Idaho, USA during summer (May–September), 2018–2019. See Table 2 for PVT definitions.

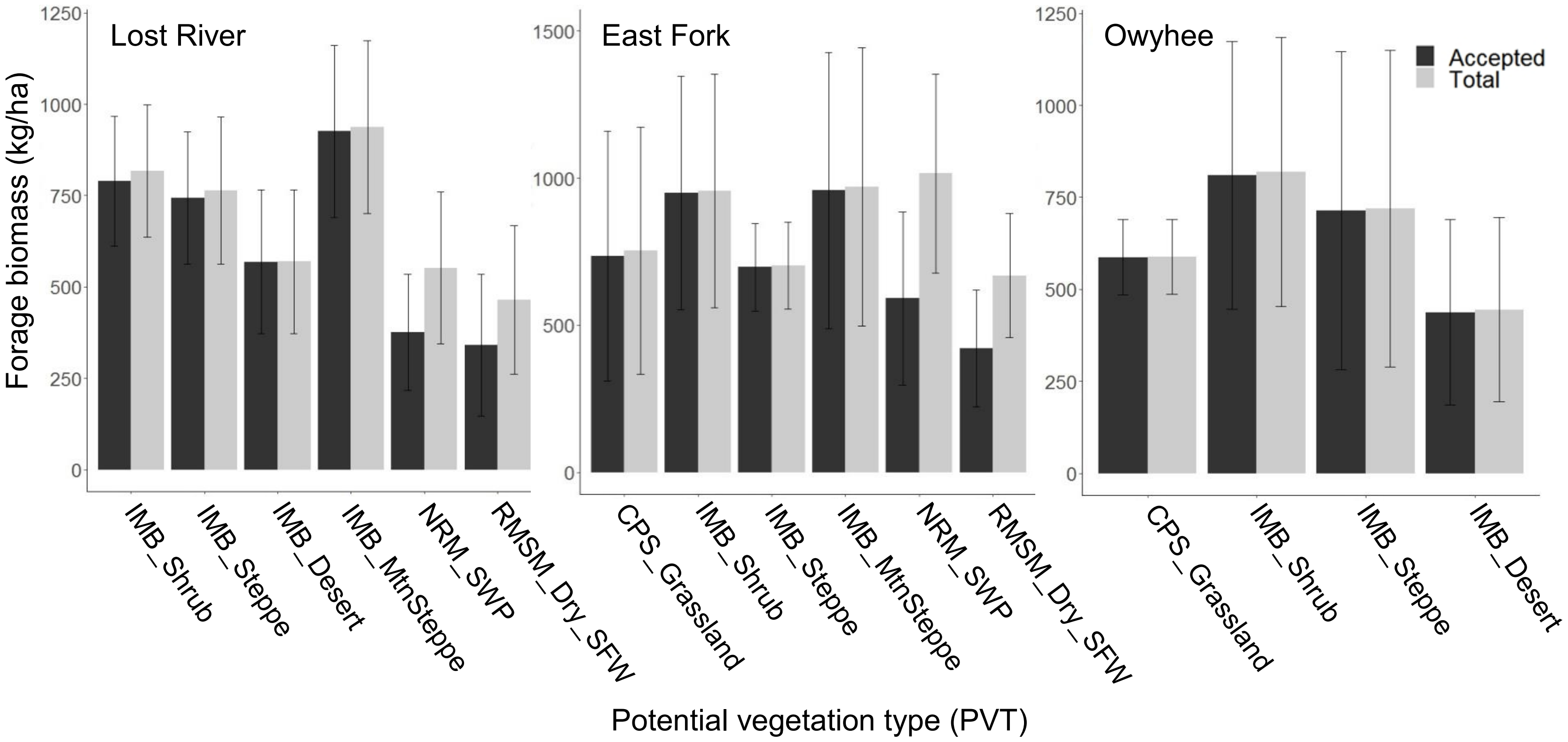


Figure 3. Proportion of randomly sampled locations in each of three bighorn sheep population ranges in Idaho, USA during summer (May–September) that fell into each of four quartiles of predicted forage biomass (accepted and total biomass) based on generalized additive models of the nutritional landscape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

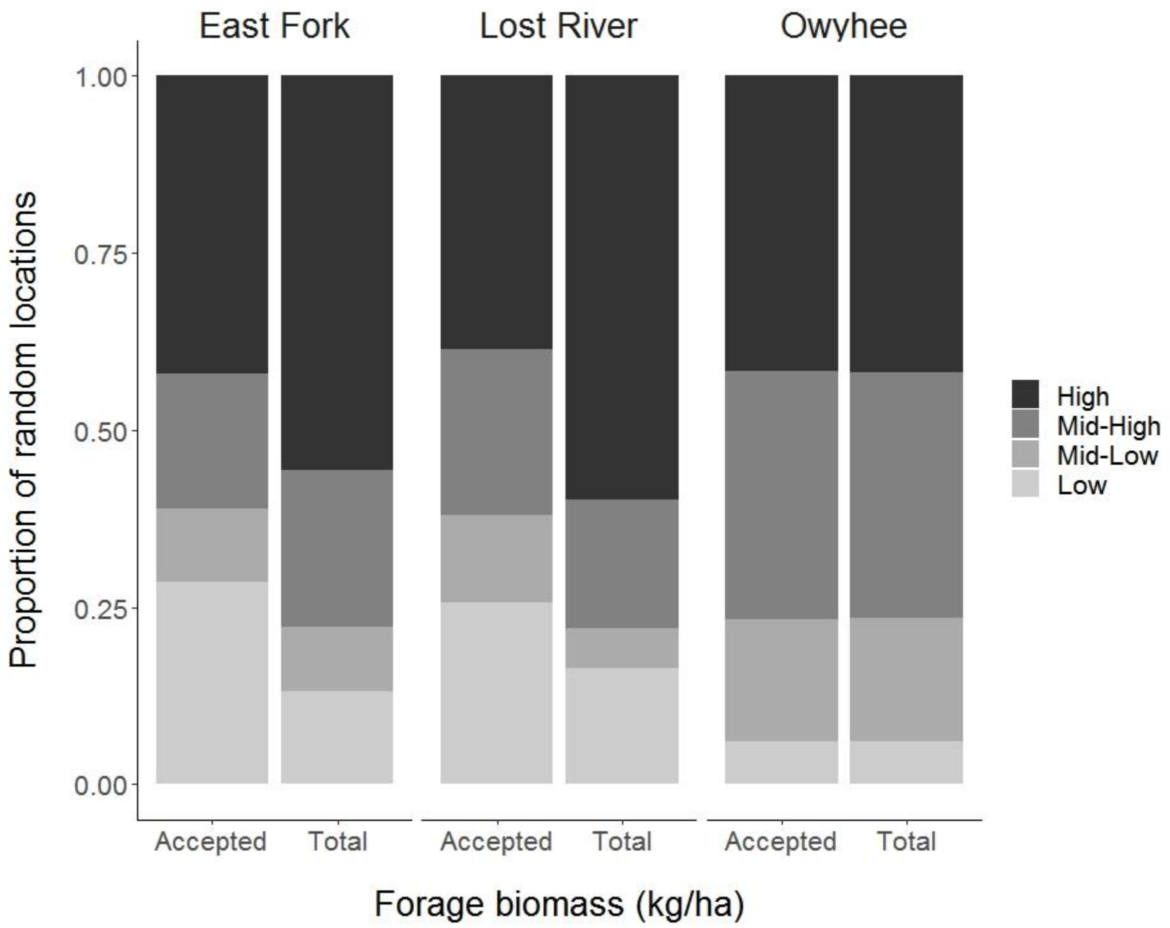


Figure 4. Boxplots of predicted (based on generalized additive models of the nutritional landscape; see Table 2) total and accepted forage biomass at random locations versus locations used by GPS-collared female bighorn sheep in each of three population ranges in Idaho, USA. GPS location data were collected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

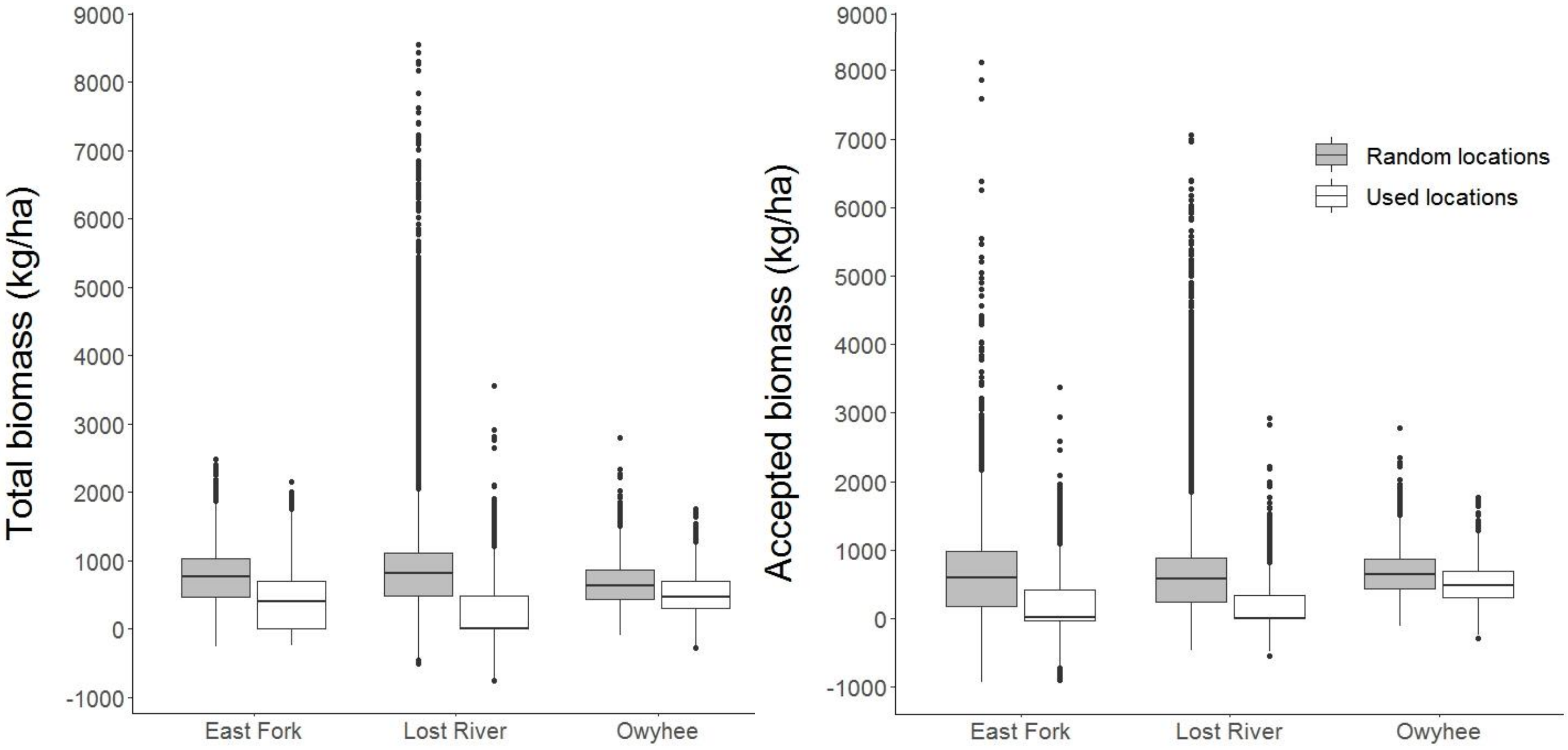


Figure 5. Estimated survival of bighorn sheep lambs in each of three population ranges in Idaho, USA during summer (May–September), 2016–2019. Panel A shows raw results for each combination of population range and year where >10 lambs were monitored. Panel B shows two sets of range-specific survival estimates (±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 range of each GPS-collared sheep.

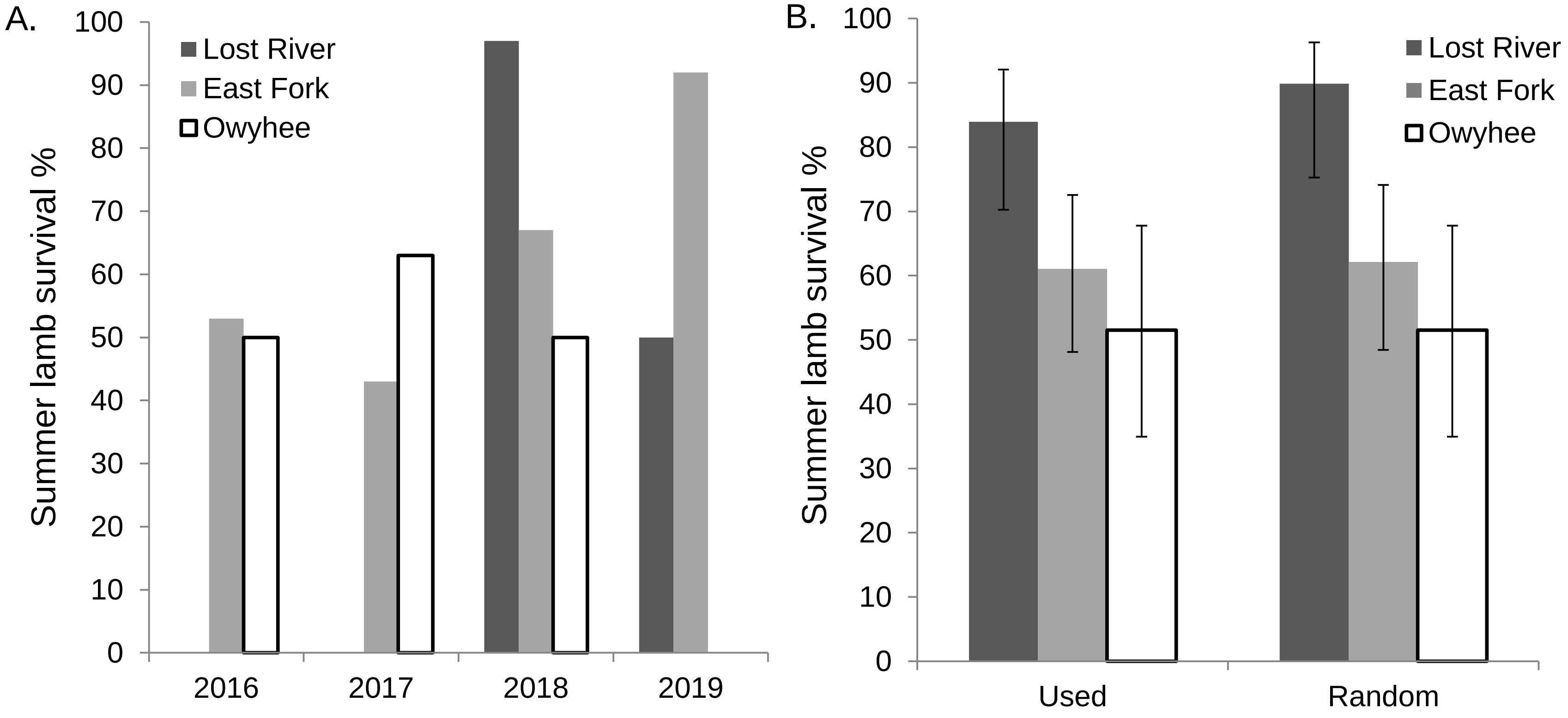
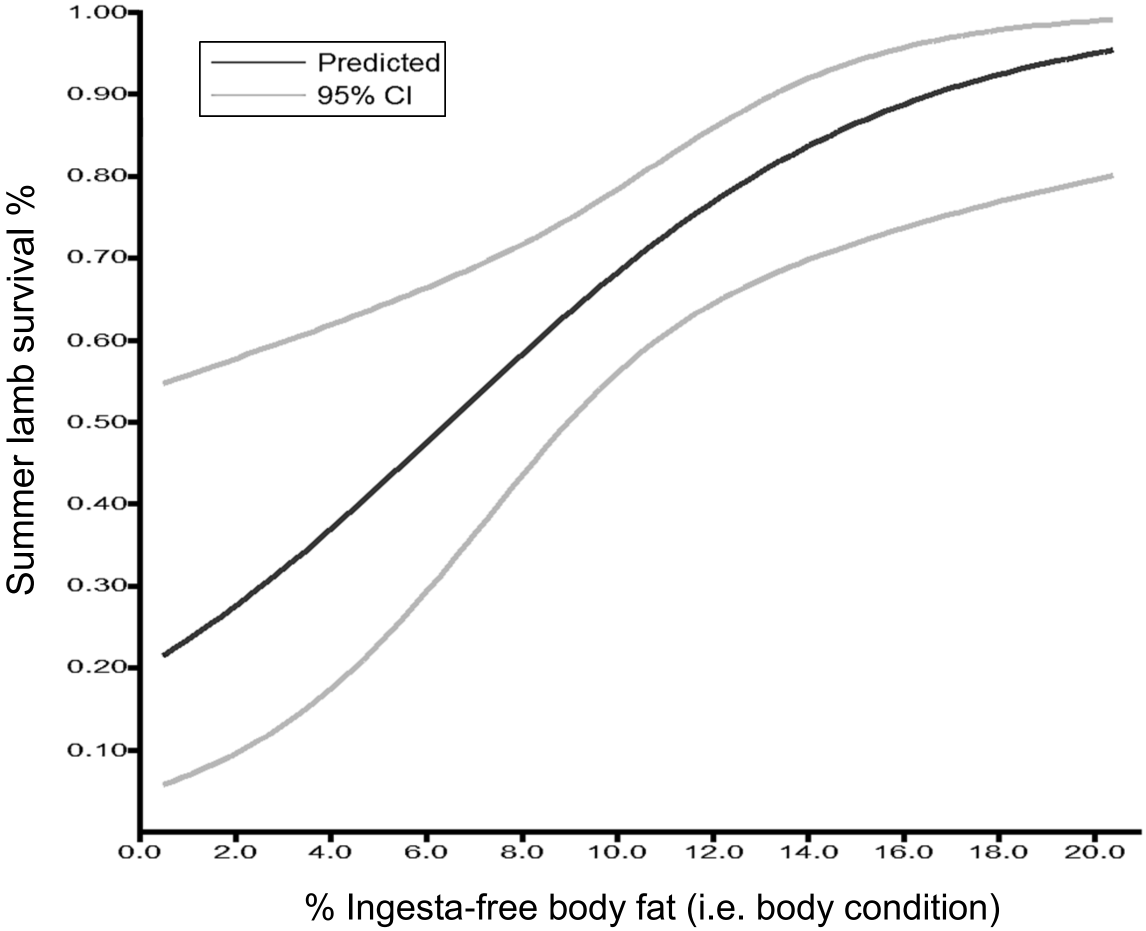


Figure 6. Relationship between summer (May–September) lamb survival and spring body condition (quantified by % ingesta-free body fat) of female bighorn sheep across three bighorn sheep population ranges in Idaho, USA during 2016–2018.



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

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

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

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

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

| | | | | |
|---|---|---|---|---|
| COGR4 | Polemoniaceae | *Collomia grandiflora* | Grand collomia | Accepted |
| COLI2 | Polemoniaceae | *Collomia linearis* | Tiny trumpet | Accepted |
| COTI2 | Polemoniaceae | *Collomia tinctoria* | Staining collomia | Accepted |
| COSE16 | Cornaceae | *Cornus sericea* | Red twig dogwood | Accepted |
| CRAC2 | Asteraceae | *Crepis acuminata* | Tapertip hawksbeard | Accepted |
| CRAT | Asteraceae | *Crepis atribarba* | Slender hawksbeard | Accepted |
| CRMO4 | Asteraceae | *Crepis modocensis* | Modoc hawksbeard | Accepted |
| CROC | Asteraceae | *Crepis occidentalis* | Largeflower hawksbeard | Accepted |
| CRIN9 | Boraginaceae | *Cryptantha interrupta* | Elko cryptantha | Accepted |
| CRSO3 | Boraginaceae | *Cryptantha sobolifera* | Waterton Lakes cryptantha | Accepted |
| CRTO4 | Boraginaceae | *Cryptantha torreyana* | Torrey's cryptantha | Accepted |
| CYCO4 | Apiaceae | *Cymopterus corrugatus* | Wrinklewing spring-parsley | Avoided |
| CYNI3 | Apiaceae | *Cymopterus nivalis* | Snow spring-parsley | Avoided |
| CYOF | Boraginaceae | *Cynoglossum officinale* | Gypsy flower | Avoided |
| DAIN | Poaceae | *Danthonia intermedia* | Mountain wild-oat grass | Accepted |
| DAUN | Poaceae | *Danthonia unispicata* | Onespike danthonia | Accepted |
| DAFR6 | Rosaceae | *Dasiphora fruticosa* | Shrubby cinquefoil | Accepted |
| DEBI | Ranunculaceae | *Delphinium bicolor* | Little larkspur | Avoided |
| DEDE2 | Ranunculaceae | *Delphinium depauperatum* | Slim larkspur | Avoided |
| DECE | Poaceae | *Deschampsia cespitosa* | Tuffed hair grass | Accepted |
| DEIN5 | Brassicaceae | *Descurainia incisa* | Mountain tansy mustard | Avoided |
| DEPI | Brassicaceae | *Descurainia pinnata* | Western tansy mustard | Accepted |
| DEPIN | Brassicaceae | *Descurainia pinnata ssp. nelsonii* | Nelson's tansy mustard | Accepted |
| DESO2 | Brassicaceae | *Descurainia sophia* | Flixweed | Accepted |
| DIUN | Fumariaceae | *Dicentra uniflora* | Steer's head | Avoided |
| DISP | Poaceae | *Distichlis spicata* | Saltgrass | Accepted |
| DOJE | Primulaceae | *Dodecatheon jeffreyi* | Sierra shooting star | Accepted |
| DOPU | Primulaceae | *Dodecatheon pulchellum* | Darkthroat shooting star | Accepted |
| DOID | Primulaceae | *Douglasia idahoensis* | Idaho dwarf primrose | Accepted |
| DRCR2 | Brassicaceae | *Draba crassifolia* | Snowbed draba | Accepted |

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

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

| | | | | |
|---|---|---|---|---|
| GRSP | Chenopodiaceae | *Grayia spinosa* | Spiny hopsage | Accepted |
| HADE | Boraginaceae | *Hackelia deflexa* | Nodding stickseed | Avoided |
| HAMI | Boraginaceae | *Hackelia micrantha* | Jessica stickseed | Avoided |
| HAPA | Boraginaceae | *Hackelia patens* | Spotted stickseed | Avoided |
| HAGL | Chenopodiaceae | *Halogeton glomeratus* | Saltlover | Avoided |
| HECO26 | Poaceae | *Hesperostipa comata* | Needle and thread grass | Accepted |
| HECOI | Poaceae | *Hesperostipa comata ssp. intermedia* | Intermediate needle and thread grass | Accepted |
| HECY2 | Saxifragaceae | *Heuchera cylindrica* | Roundleaf alumroot | Accepted |
| HEPA11 | Saxifragaceae | *Heuchera parvifolia* | Little-leaf alumroot | Accepted |
| HICY | Asteraceae | *Hieracium cynoglossoides* | Hound's tongue hawksweed | Accepted |
| HOJU | Poaceae | *Hordeum jubatum* | Foxtail barley | Accepted |
| HYCA4 | Hydrophyllaceae | *Hydrophyllum capitatum* | Ballhead waterleaf | Accepted |
| IOAL | Asteraceae | *Ionactis alpina* | Lava aster | Accepted |
| IPAG | Polemoniaceae | *Ipomopsis aggregata* | Scarlet gilia | Accepted |
| IPCO5 | Polemoniaceae | *Ipomopsis congesta* | Ballhead ipomopsis | Accepted |
| IPCOP | Polemoniaceae | *Ipomopsis congesta ssp. palmifrons* | Ballhead gilia | Accepted |
| IPSPO2 | Polemoniaceae | *Ipomopsis spicata ssp orchidaceae* | Orchid ipomopsis | Accepted |
| IVGO | Rosaceae | *Ivesia gordonii* | Gordon's ivesia | Accepted |
| JUAR2 | Juncaceae | *Juncus arcticus* | Arctic rush | Avoided |
| JUBA | Juncaceae | *Juncus balticus* | Baltic rush | Accepted |
| JUDR | Juncaceae | *Juncus drummondii* | Drummond's rush | Accepted |
| JUEN | Juncaceae | *Juncus ensifolius* | Swordleaf rush | Avoided |
| JUME3 | Juncaceae | *Juncus mertensianus* | Mertens' rush | Avoided |
| JUNE | Juncaceae | *Juncus nevadensis* | Sierra rush | Avoided |
| JUCO6 | Cupressaceae | *Juniperus communis* | Common juniper | Avoided |
| JUOC | Cupressaceae | *Juniperus occidentalis* | Western juniper | Avoided |
| JUSC2 | Cupressaceae | *Juniperus scopulorum* | Rocky mountain juniper | Avoided |
| KOMA | Poaceae | *Koeleria macrantha* | Prairie junegrass | Accepted |
| KRLA2 | Chenopodiaceae | *Krascheninnikovia lanata* | Winterfat | Accepted |
| LASE | Asteraceae | *Lactuca serriola* | Prickly lettuce | Accepted |

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

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

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

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

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

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

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

Appendix B. Species-specific linear regressions of p1ant 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 | | | | |