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The Utility of Animal Behavior Studies in Natural Resource Management

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On the Ground

- Although research on the behavior of individual animals has been growing in recent years, the role that individual variation among animals may play in the outcome of species interactions in nature may be somewhat overlooked in natural resource management. Recognizing potential implications of individual behavioral variation can aid in developing more cost-effective and sustainable management techniques. Four illustrative examples are provided.
- Livestock foraging behaviors are important to understand, as they affect an animal's ability to locate and identify forage with nutritional qualities required for optimal growth. Studying the behavior of individual animals can help livestock producers anticipate and influence livestock grazing patterns to increase efficiency and productivity.
- Sage-grouse populations have declined dramatically in many areas, and managers are required to consider their needs in all management decisions where the species persists. Sage-grouse exhibit complex mating, nesting, and migratory behaviors that are important to recognize for management to be successful.
- Mountain lions were generally assumed to prey mainly upon mule deer, but recent studies have found that individual lions may specialize on alternate prey such as feral horses or bighorn sheep. The Bureau of Land Management spends millions of dollars each year to manage feral horse populations. Revelations surrounding prey switching in individual mountain lions may support management goals in which feral horse predation is occurring but may hinder bighorn sheep translocation efforts by wildlife managers.
- Many plants important to land managers, including grasses, shrubs, and trees, are dispersed by granivorous rodents that store seeds in scattered caches, and a growing body of literature reveals that the majority of seedling recruitment for some of these species is attributable to scatter-hoarding by rodents. This relationship can be utilized for restoration applications, and variation in seed preferences among individual animals may be valuable in this regard.

Keywords: individual variation, rangeland management, livestock, sage-grouse, mountain lions, granivorous rodents.

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Natural resource and land managers are aware of the value of population-level studies of wildlife, such as censuses and seasonal range use of game species populations. It is perhaps less appreciated that behavioral studies at the level of individual animals can also contribute valuable insights for management applications. Variation among individuals stems from variation in morphology, behavior, and physiology that influence an individual's ability to utilize alternative resources, resulting in distinct preferences and differences in how efficiently alternative resources can be used.[1] Understanding behavioral responses of individual animals and to what extent their preferences vary can aid in more efficiently and sustainably managing lands for multiple uses. By describing behavior at the individual level, we can understand the range of responses among animals within a population, allowing land managers to anticipate the needs of target species across space and time. When management plans are only based on the average behavior of the population, specialists or important demographic groups can get left out.[1]

Animal behavior often varies by age, body size, sex, learning ability, and previous experience, resulting in different responses among individuals of the same species given identical circumstances.[2] Moreover, the success or failure of management strategies may be affected by this variation.[2] With advancements in tracking and global positioning system (GPS) technology, researchers have been able to observe animal behavior on a much larger scale than was previously feasible. Observing responses of animals to conditions of their rangeland environments provides more applicable information directly to land managers than laboratory or small pasture studies. Here we highlight four very different examples of the utility of behavioral studies for management issues.

Livestock

Behavioral studies of livestock, such as documenting movement and foraging patterns in large pastures or on open rangelands (Fig. 1), are perhaps the most direct application of how knowledge of behavior can guide rangeland management. Information on how variation in management techniques and landscape variables influence livestock behavior can increase efficiency and returns for livestock producers. In herding animals it is important to recognize how individuals respond to one another. Variation in foraging behavior among individuals is partly the result of behaviors that are learned through an animal's own experience and also learned from social interactions and observation of other individuals.[3] In livestock, social facilitation, the increase in a behavior in response to observing others exhibiting the same behavior, has a large impact on an individual's inclination to consume new plants or food types.[4] Foraging behavior can be manipulated through aversive training to certain forage using small doses of chemicals that induce illness, such as lithium chloride, but the strong influence of social facilitation can reverse induced aversion when animals are grazed with non-averted individuals.[4] The behavior of peers and mothers have been found to influence diet in domestic cattle through influences on home-range or habitat use patterns and avoidance of toxic plants.[5] Mothers can greatly influence foraging behavior in calves, resulting in considerable individual variation by passing on food preferences through odors in their milk, and individuals may prefer the natal habitat chosen by their mothers.[3] Individual personalities that influence foraging behavior, such as a tendency for animals exhibiting more aggressive or bold behavior to explore new feeding sites, can also be passed between generations genetically.[3] In herbivores, certain individuals within the herd often act as leaders and are responsible for initiating movement toward water sources or new foraging locations.[3] Suites of correlated behaviors (i.e., "behavioral syndromes," which are analogous to animal personalities) may be associated with animal performance through variation in the use of rangelands.[6] Cows of one behavior type that covered more ground and went farther from a water source while foraging during the day were found to have higher weights, higher calf weaning weights, and a shorter period of postpartum anoestrus than cows that had a more concentrated search area and spent more time nearer to water.[6] Howery et al.[7] studied the habit at use and home ranges of individual cattle and found that most cows exhibited home range fidelity and suggested that selective culling of individuals that overused riparian areas could be a management strategy to minimize damage to sensitive habitats. Understanding how livestock select forage to meet nutritional needs in complex environments that vary spatially and temporally contributes to more efficient livestock management.

Research on individual behavior and learning can be applied through manipulation of foraging behavior. For example, cattle can learn to eat sagebrush and other sagebrush steppe vegetation, which can not only reduce feeding costs but was also found to increase grass and forb production with appropriately timed grazing.[8] Cattle can also learn visual cues and associate them with food quality, increasing the efficiency of grazing in heterogeneous rangelands.[2] Identifying how livestock perceive variation within their environment can help ranchers intervene to elicit desired behavior. Ganskopp[9] used GPS collars on cattle to compare responses to water and salt manipulation in an arid environment and found that patterns of foraging behavior and distribution can be manipulated by moving a water source, while salt placement had no effect. Cattle in this study also did not return to areas where they previously spent time, nor did they return to the previous location of the water station.[9] Strategic placement of

Figure 1. Free-ranging cattle in southern Nevada.

supplement blocks made of dehydrated molasses has also been found to entice cattle into rangelands that are underutilized.[10] Such information is especially important when livestock managers are trying to control grazing intensity and frequency in defined areas or move cattle to better forage as conditions change over time. Understanding the behavioral response of wild ungulates such as pronghorn (*Antilocapra americana*) to the presence of livestock or grazing by livestock can also help ranchers and land managers avoid or reduce competition.[11]

Sage-Grouse

In North America, sage-grouse populations have declined dramatically. The greater sage-grouse (*Centrocercus urophasianus*) now inhabits roughly 56% of the area it had occupied pre-settlement, and the Gunnison sage-grouse (*C. minimus*) only remains in 10% of its pre-settlement range.[12] Due to these declines, sage-grouse influence rangeland management in many sagebrush ecosystems in the western United States, and sage-grouse behavior informs conservation plans. Research on mating, nesting, and migratory behavior, as well as behavioral responses to disturbance, can help to identify habitat that is critical to sage-grouse survival. Radio telemetry equipment and techniques and GPS technology have made tracking sage-grouse movements easier, allowing researchers to observe these behaviors at the scale of individual birds (Fig. 2). The use of GPS collars is fairly new technology used for tracking sage-grouse, and although they are heavier than the VHF transmitters used for radio telemetry, the GPS collars do not appear to influence movement distances.[13] Collars with GPS technology can use solar power collecting information over long time periods and uploading location data to a satellite system, which is then available to researchers, allowing very detailed movement data to be collected on individual sage-grouse.[14]

Mating behavior can significantly affect genetic diversity within a population.[2] Male sage-grouse exhibit a mating behavior referred to as lekking, wherein males gather at a central location, a lek, and perform elaborate displays to attract females. Sage-grouse in general exhibit lek fidelity, but it is stronger in males than in females.[15] This is important in terms of management because when landscapes become more fragmented and habitats degrade, sage-grouse will likely continue to use leks even though the surrounding habitat might be less suitable or isolated, resulting in decreased reproductive output.[15] Fragmented landscapes can also cause females to travel longer distances from lek sites to nest sites,[15] likely increasing their risk of mortality. Although adults may show site fidelity despite habitat degradation and fragmentation, radio-marked chicks and yearling males and females avoided habitat disturbed by energy infrastructure.[16] Yearling males that were raised near energy infrastructure had reduced annual survival, as did those that avoided infrastructure when establishing leks, which also exhibited lower fecundity.[16] The avoidance of energy infrastructure by young sage-grouse will affect the formation of future lek sites by males, likely leading to abandonment of old lek sites and selection of new nesting sites by females, which will affect future habitat use.[16]

Female sage-grouse have varying habitat requirements throughout the stages of reproduction, from selecting nesting sites to laying and incubating to brood rearing.[17] Studying individuals can identify the variety of habitat types and attributes needed for successful reproduction. Dzialak et al.[17] tracked individual female sage-grouse and found that they selected areas with moderate sagebrush and avoided bare ground and mesic sites for nesting, but spent more time in habitats with moderate levels of bare ground during egg laying

Figure 2. Female sage-grouse with a radio telemetry collar.

and incubation. Although females avoid mesic areas during early brooding, in mid and late brooding phases they showed strong selection for mesic areas.[17] These behavioral patterns observed by tracking the movements of individuals illustrate that managing habitat for female sage-grouse is difficult and complex, as females require a variety of habitat traits at different times to successfully raise their young.[17]

Sage-grouse exhibit a great deal of individual variation in migratory behavior.[13,18] Populations that inhabit the same geographic area can generally exhibit three different migratory behaviors: non-migratory; one-stage migration, moving between two distinct seasonal ranges; and two-stage migration with movements among three distinct seasonal ranges.[18] However, Fedy et al.[13] tracked individual sage-grouse using both radio telemetry and GPS across Wyoming and found that migratory behavior was highly variable across sites or populations and between individuals, with certain individuals exhibiting flexible migratory behavior over time. Due to the high level of individual variation found, the authors concluded that it would be difficult to categorize populations by the three different migratory behaviors described.[13] Research tracking the timing of individual altitudinal migratory behavior during spring, summer, and fall transitions have found that migratory behavior was influenced by environmental conditions and might be more facultative than previously thought.[14] Populations that have both migratory and non-migratory grouse might be due to individuals experiencing differences in average environmental conditions, such as temperature and precipitation, as well as individual differences in reproductive status and habit used during the summer.[14] Understanding migratory behavior and habitat usage within and between years is essential to identifying the extent of land needed to maintain sustainable populations.

Natural resource extraction and grazing can affect wildlife in a variety of ways, and it is imperative to understand how sage-grouse respond to these disturbances to reduce impacts of these activities. One study that used radio transmitters found that females avoided nesting in landscapes dominated with edge habitat caused by human use, such as roads, oil well pads, croplands, and urban development. Areas closer to cropland and those with more urban development were also avoided by hens with broods.[19] Blickley et al.[20] used playback experiments to understand the behavioral responses of greater sage-grouse to anthropogenic noise from natural gas drilling and found that both road noise and drilling noise decreased attendance at leks. Following individual females using GPS during reproduction revealed that the risk of nest and brood failure is mainly driven by human modification of the landscape, such as the creation of low-elevation mesic habitats in arid areas where water from energy development discharge or agricultural water developments exists.[17] Grazing by livestock can negatively or positively affect sage-grouse habitat, depending on timing and intensity, and it appears that light to moderate grazing early in the season can increase forb availability and abundance.[21] Understanding individual grouse behavior during mating, nesting, and brood rearing and how individuals respond to human interactions such as creation of water resources, energy extraction, road building, and grazing is vital to successfully manage sage-grouse.

Mountain Lions

Land managers are often responsible for managing both predator and prey species, and knowledge of apex predator behavior can help facilitate more cost-effective practices. Under the 1971 Wild Free-Roaming Horses and Burros Act, the Bureau of Land Management has the authority to manage feral horse populations, which includes controlling population numbers to maintain sustainability on public lands.[22] The total expenditures for the Wild Horse and Burro Program for Fiscal Year 2016 were more than $78 million, with $3 million being spent on removal.[22] Efforts to control feral horse populations are not only expensive, but controversial. Mountain lions (*Puma concolor*) in the Great Basin have been found to prey on feral horses, including adult horses, and can play a significant role in limiting horse populations.[23,24] During an 11-year study that monitored feral horse population dynamics and monitored collared lions near the California and Nevada border, researchers found that at least 82% of foal deaths were due to mountain lion predation, which accounted for an average of ~45% of annual foal production.[23] The study concluded that mountain lions significantly affected feral horse population size, especially when compared with much higher foal survival rates observed at other sites.[23]

It has long been assumed that mule deer (*Odocoileus hemionus*) were the main large animal prey items in the diet of mountain lions, but recent studies of the behavior of individual mountain lions showed that some lions specialized almost exclusively on preying on horses (Fig. 3).[24] Research following 21 collared mountain lions found that mule deer were the most common prey for 13 individuals, but feral horses were the most common prey for 8 individuals and even accounted for 100% of the prey for 1 mountain lion.[24] Individual specialization on feral horses mainly occurred in a population of mountain lions that occupied a mountain range with abundant feral horses,[24] which are also the areas that managers focus on for herd reduction. Mountain lions in this particular mountain range preyed upon feral horses significantly more than expected based on proportions available compared with mule deer.[24] This specialization is thought to be driven by a decrease in mule deer populations in the Great Basin, causing lions to shift to a novel prey species despite the increased risk of injury associated with horse predation.[24]

In another study tracking over 50 GPS-collared mountain lions in Alberta, Canada, young feral horses were one of the main prey items for adult male lions, especially in the summer. However, subadults were never recorded preying upon horses, and female predation on horses was rare.[25] In a short-term, small-scale study that tracked six mountain lions in one mountain range in Wyoming and Montana, predation on feral horses was not observed, despite horses being available.[26] The lack of horse predation in this population could be due to

Figure 3. Mountain lion in northern Nevada during research on individual mountain lion behavior.

the small sample size, which makes it difficult to capture individual variation. Identifying populations of feral horses that experience significant levels of mountain lion predation can help land managers focus their removal efforts on populations that are expanding unchecked.

Individual mountain lion specialization has also been observed with other large prey such as bighorn sheep (*Ovis canadensis*). Predation by mountain lions has been found to negatively affect the success of bighorn sheep translocation projects,[27] so understanding predator behavior in these systems is imperative to successful bighorn sheep management. During a long-term study of bighorn sheep ecology and behavior, deaths of sheep due to mountain lions were insignificant during the first 11 years of the study.[2] However, during the last 2 years of the study a female mountain lion that had been collared for another unrelated study switched from hunting deer to hunting bighorn sheep and was responsible for a 20% reduction in the sheep population.[2] A similar case was observed at another site by the same researchers; an individual or a few individual lions were responsible for a 50% decline in the local bighorn population.[2] Another study of mountain lion prey composition found that all 16 bighorn sheep kills recorded over the course of a year were attributed to a single female lion.[26] In these circumstances, a management plan of generalized predator control would have likely failed; selective removal of the responsible predator would be both more cost-effective and more effective in achieving the desired result of reducing predator-induced mortality of bighorns.[2]

Rodents

Some animals, primarily rodents and birds to a lesser extent, exhibit food-storing behaviors like scatter-hoarding that can benefit plants. Scatter-hoarding is the superficial burial of seeds throughout an animal's home range, and when seeds are forgotten or surplus seeds are not recovered, they can germinate. Seed-caching rodents play an important role in seed dispersal and subsequent seedling recruitment for some economically important tree species and range plants. Seedling recruitment of Jeffrey pine (*Pinus jeffreyi*), a species used by the timber industry and also generally important to forestry management, is attributed to scatter-hoarding by yellow-pine chipmunks (*Tamias amoenus*).[28] Yellow-pine chipmunks were also responsible for nearly all recruitment of bitterbrush at a Sierra Nevada site,[29] and least chipmunks (*Tamias minimus*) as well as mice in the genus *Peromyscus* assume this role at lower elevations. Bitterbrush is an important dietary component for mule deer, bighorn sheep, and pronghorn during various seasons of the year.[30,31] Scatter-hoarding rodents also disperse *Ephedra* seeds in arid environments,[32] where *Ephedra* is an important seasonal component of pronghorn diets.[33]

Both sheep and cattle utilize Indian ricegrass (*Achnatherum hymenoides*) during winter grazing, a highly preferred winter forage for livestock, especially in salt desert habitats.[34] Scatter-hoards made by desert heteromyid rodents are responsible for the vast majority of seedling recruitment of Indian ricegrass.[35,36] Furthermore, scatter-hoarding has been shown to enhance longer-term survival of Indian ricegrass following seedling establishment, as the clumped seedlings that emerge from rodent caches have greater survival through summer heat and drought than seedlings growing singly.[37] An understanding of scatter-hoarding behavior has been applied experimentally in a study of "diversionary seeding," which utilizes the seed-caching services of these animals by offering a highly preferred, commercially available diversionary seed type to reduce the rate at which rodents recover the

Indian ricegrass caches that they have made.[38] Indian ricegrass seedling recruitment was significantly higher on plots where diversionary seeding was applied when compared with non-seeded plots.[38] The cost of diversionary seed treatments is minimal compared with direct seeding[38] and does not require the use of heavy equipment, which can damage native shrubs and create disturbance that invasive species can exploit. Studies of seed preferences by Merriam's kangaroo rats (*Dipodomys merriami*), an important dispersal agent for Indian ricegrass, have shown that individuals vary in their relative preference rankings of Indian ricegrass seeds versus alternate seeds tested as potential diversionary seed candidates (Fig. 4)[39]; thus, a mixture of diversionary seed types should yield the best results in terms of reducing the rate at which rodent populations recover and consume their Indian ricegrass caches.[39] Differences among individual Merriam's kangaroo rats in seed preferences are consistent with the findings of a more general study of behavior in this species, which found individual kangaroo rats to have distinct behavioral syndromes.[40,41] Understanding the scatter-hoarding behavior of rodents and how it varies spatially and temporally is central to managing for sustainable populations of many important rangeland and forest plant species.

Discussion

Darwin's[42] theory of evolution by natural selection provides the underlying framework for modern biology. However, despite the fact that selection operates on variation at the level of individual organisms, the simplifying (and generally unacknowledged) assumption that individuals of the same population or even the same species are uniform or that individual variation can be written off as statistical noise has been pervasive in much of the ecological, evolutionary, and behavioral literature.[1] The niche variation hypothesis, which suggested that relaxed interspecific competition resulted in expanded niche breadth due to increased individual variation, provided a relatively early counter argument.[43] Hayes and Jenkins[44] discussed the potential importance of individual variation in behavior and physiology among mammals and analytical approaches to studies of individual variation. A comprehensive review by Bolnick et al.[1] offers numerous examples from a wide diversity of animal taxa that niche breadth at the population level is often attributable to individual-level specialization. Another review by Searle et al.[3] highlighted the importance of variation in individual foraging behavior among herbivores for rangeland management and called for a more individual-based approach in future research. More recent recognition that individual behavioral patterns can yield pervasive effects at the population level has led to the study of behavioral syndromes.[6,40,45,46] While studies on population ecology and habitat use are undoubtedly important, it is often the case that behaviors drive variation in the number of individuals in a population, sex or age structure, or genetic diversity.[1] This is likely the result of individual variation in behavior having fitness consequences, as seen in cows that stayed close to water having longer times between estrous and lower weights,[6] and the use of man-made water sources by female sage-grouse that increased the risk of nest and brood failure.[17] Because natural selection acts at the level of the individual, variation in behavior among individuals, whether in relation to predator-prey relationships, foraging preferences, or selection of habitat for reproduction, can influence genetic diversity when there are fitness consequences to such behaviors.[1]

We would argue that behavioral studies at the level of individuals can also assist management. Studying how individuals behave can help ranchers manipulate and more efficiently raise cattle, identify human disturbance that decreases reproductive output for declining species such as sage-grouse, lead to novel discoveries that can have

Figure 4. Merriam's kangaroo rat with filled cheek pouches during a laboratory study on seed preferences of individuals.

management implications such as understanding prey specialization by mountain lions, and recognize natural species interactions that are important for the propagation of important range plants as with scatter-hoarding rodents. Management plans that are based on the average resource use by the population could negatively affect specialists and can even be less successful if individuals differ by age class and sex,[1] as seen in sage-grouse where females and males select for different habitat features throughout reproduction and the rearing of young. Research on animal behavior is critical to inform management decisions and can aid in more cost-effective, sustainable management practices that will benefit both livestock producers and native plants and animals. Considering animal behavior in management approaches can help cut costs by avoiding practices that unnecessarily replicate or conflict with natural plant and animal interactions, such as seed dispersal by scatter-hoarding rodents. Augmenting seed caching by scatter-hoarding rodents could be used in restoration efforts post-disturbance that are more cost effective and less invasive than direct seedings, allowing for the reestablishment of native plants important to other range species such as pronghorn, bighorn sheep, and mule deer. Once individual behaviors and their implications for ecological processes in nature are understood, land managers can utilize and sometimes even manipulate these behaviors to meet management goals for multiple uses in a more cost-effective manner. For example, identifying individual cattle on rangelands that tend to overuse or abuse riparian areas and removing them, using aversion training to deter certain foraging behaviors, or using supplements to lure livestock into underutilized habitat can potentially allow for more sustainable use of sensitive habitats and other rangelands by livestock without negatively affecting native herbivores and without resorting to costly habitat restoration projects. Acknowledging and understanding individual differences in animal behavior can lead to improved management of our natural resources.

References

1. Bolnick, D.I., R. Svanback, J.A. Fordyce, L.H. Yang, J.M. Davis, C.D. Hulsey, and M.L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161:1-28.
2. Festa-Bianchet, M., and M. Apollonio. 2003. Animal behavior and wildlife conservation. Washington, DC, USA: Island Press 380.
3. Searle, K.R., L.P. Hunt, and I.J. Gordon. 2010. Individualistic herds: individual variation in herbivore foraging behavior and application to rangeland management. *Applied Animal Behaviour Science* 122:1-12.
4. Ralphs, M.H., and F.D. Provenza. 1999. Conditioned food aversions: principles and practices, with special reference to social facilitation. *Proceedings of the Nutrition Society* 58:813-820.
5. Launchbaugh, K.L., and L.D. Howery. 2005. Understanding landscape use patterns of livestock as a consequence of foraging behavior. *Rangeland Ecology & Management* 58:99-108.
6. Wesley, R.L., A.F. Cibils, J.T. Mulliniks, E.R. Pollak, M.K. Petersen, and E.L. Fredrickson. 2012. An assessment of behavioural syndromes in rangeland-raised beef cattle. *Applied Animal Behaviour Science* 139:183-194.
7. Howery, L.D., F.D. Provenza, R.E. Banner, and C.B. Scott. 1996. Differences in home range and habitat use among individuals in a cattle herd. *Applied Animal Behaviour Science* 49:305-320.
8. Peterson, C.A., J.J. Villalba, and F.D. Provenza. 2014. Influence of experience on browsing sagebrush by cattle and its impacts on plant community structure. *Rangeland Ecology & Management* 67:78-87.
9. Ganskopp, D. 2001. Manipulating cattle distribution with salt and water in large arid-land pastures: a GPS/GIS assessment. *Applied Animal Behavior Science* 73:251-262.
10. Bailey, D.W., and G.R. Welling. 1999. Modification of cattle grazing distribution with dehydrated molasses supplement. *Journal of Range Management* 52:575-582.
11. Clary, W.P., and D.M. Beale. 1983. Pronghorn reactions to winter sheep grazing, plant communities, and topography in the Great Basin. *Journal of Range Management* 36:749-752.
12. Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S.D. Bunnell, J.W. Connelly, P.A. Deibert, S.C. Gardner, M.A. Hilliard, G.D. Kobriger, S.M. McAdam, C.W. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and S.J. Stiver. 2004. Distribution of sage-grouse in North America. *Condor* 106:363-376.
13. Fedy, B.C., C.L. Aldridge, K.E. Doherty, M. O'Donnell, J.L. Beck, B. Bedrosian, M.J. Holloran, G.D. Johnson, N.W. Kaczor, C.P. Kirol, C.A. Mandich, D. Marshall, G. McKee, C. Olson, C.C. Swanson, and B.L. Walker. 2012. Interseasonal movements of greater sage-grouse,migratory behavior, and an assessment of the core regions concept in Wyoming. *Journal of Wildlife Management* 76:1062-1071.
14. Pratt, A.C., K.T. Smith, and J.L. Beck. 2017. Environmental cues used by greater sage-grouse to initiate altitudinal migration. *The Auk: Ornithological Advances* 134:628-643.
15. Schroeder, M.A., and L.A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. *Wildlife Biology* 9:291-299.
16. Holloran, M.J., R.C. Kaiser, and W.A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. *Journal of Wildlife Management* 74:65-72.
17. Dzialak, M.R., C.V. Olson, S.M. Harju, S.L. Webb, J.P. Mudd, J.B. Winstead, and L.D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. *PLoS ONE* 6:e26273.
18. Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines to manage sage-grouse populations and their habitats. *Wildlife Society Bulletin* 28:967-985.
19. Aldridge, C.L., and M.S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat based approach for endangered greater sage-grouse. *Ecological Applications* 17:508-526.
20. Blickley, J.L., D. Blackwood, and G.L. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. *Conservation Biology* 26:461-471.
21. Crawford, J.A., R.A. Olson, N.E. West, J.C. Mosley, M.A. Schroeder, T.D. Whitson, R.F. Miller, M.A. Gregg, and C.S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2-19.
22. BLM. Bureau of Land Management Wild Horse and Burro Program Data. Available at: https://www.blm.gov/programs/wild-horse-and-burro/about-the-program/program-data Accessed 11/14/2017.
23. Turner, J.W., and M.L. Morrison. 2001. Influence of predation by mountain lions on numbers and survivorship of a feral horse population. *The Southwestern Naturalist* 46:183-190.

24. Andreasen, A.M. 2014. Source-sink dynamics and individual variation in prey selection and habitat selection of mountain lions in the Great Basin of Nevada. Available at: http://unr.idm.oclc.org/login?url=http://search.proquest.com/docview/1617974633?accountid=452 Accessed during the spring on 3/3/2017.
25. Knopff, K.H., A.A. Knopff, A. Kortello, and M.S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. *Journal of Wildlife Management* 75:1435-1447.
26. Blake, L.W., and E.M. Gese. 2016. Cougar predation rates and prey composition in the Pryor Mountains of Wyoming and Montana. *Northwest Science* 90:394-410.
27. Rominger, E.M., H.A. Whitlaw, D.L. Weybright, W.C. Dunn, and W.B. Ballard. 2004. The influence of mountain lion predation on bighorn sheep translocations. *Journal of Wildlife Management* 68:993-999.
28. Vander Wall, S.B. 1992. The role of animals in dispersing a "wind-dispersed" pine. *Ecology* 73:614-621.
29. Vander Wall, S.B. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. *Ecology* 75:1911-1926.
30. Wagner, G.D., and J.M. Peek. 2006. Bighorn sheep diet selection and forage quality in central Idaho. *Northwest Science* 80:246-258.
31. Hanley, T.A., and K.A. Hanley. 1982. Food resource partitioning by sympatric ungulates on Great Basin rangeland. *Journal of Range Management* 35:152-158.
32. Hollander, J.L., S.B. Vander Wall, and J.G. Baguley. 2010. Evolution of seed dispersal in North American *Ephedra*. *Evolutionary Ecology* 24:333-345.
33. Smith, C., R. Valdez, J.L. Holecheck, P.J. Zwank, and M. Cardenas. 1998. Diets of native and non-native ungulates in southcentral New Mexico. *Southwestern Naturalist* 43:163-169.
34. Cook, C.W., and L.E. Harris. 1968. Nutritive value of seasonal ranges. Utah State University, Logan, Utah, USA: Agricultural Experiment Station. *Bulletin* 472:43-44.
35. McAdoo, J.K., C.C. Evans, B.A. Roundy, J.A. Young, and R.A. Evans. 1983. Influence of heteromyid rodents on *Oryzopsis hymenoides* germination. *Journal of Range Management* 36:61-64.
36. Longland, W.S., S.H. Jenkins, S.B. Vander Wall, J.A. Veech, and S. Pyare. 2001. Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* 82:3131-3148.
37. Longland, W.S., and L.A. Dimitri. 2016. Can seed caching enhance survival of Indian ricegrass (*Achnatherum hymenoides*) through intraspecific facilitation? *Plant Ecology* 217:1523-1532.
38. Longland, W.S., and S.M. Ostoja. 2013. Ecosystem services from keystone species: diversionary seeding and seed-caching desert rodents can enhance Indian ricegrass seedling establishment. *Restoration Ecology* 21:285-291.
39. Longland, W.S., and L.A. Dimitri. 2016. Seed selection by desert rodents: implications for enhancing seedling establishment of Indian ricegrass (*Oryzopsis hymenoides*). *Western North American Naturalist* 76:253-258.
40. Dochtermann, N.A., and S.H. Jenkins. 2007. Behavioural syndromes in Merriam's kangaroo rats (*Dipodomys merriami*): a test of competing hypotheses. *Proceedings of the Royal Society B* 274:2343-2349.
41. Dochtermann, N.A., S.H. Jenkins, M.J. Swartz, and A.C. Hargett. 2012. The roles of competition and environmental heterogeneity in the maintenance of behavioral variation and covariation. *Ecology* 93:1330-1339.
42. Darwin, C. 1859; 1958. On the origin of species. Mentor edition. New York, NY, USA: New American Library.
43. Van Valen, L. 1965. Morphological variation and width of the ecological niche. *American Naturalist* 99:377-389.
44. Hayes, J.P., and S.H. Jenkins. 1997. Individual variation in mammals. *Journal of Mammalogy* 78:274-293.
45. Sih, A., A.M. Bell, J.C. Johnson, and R.E. Ziemba. 2004. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology* 79:241-277.
46. Bell, A.M. 2007. Future directions in behavioural syndromes research. *Proceedings of the Royal Society B* 274:755-761.