TROPHIC ECOLOGY OF BURROWING OWLS IN NATURAL AND AGRICULTURAL HABITATS AND AN ANALYSIS OF PREDATOR COMMUNITIES USING STABLE ISOTOPES OF CARBON AND NITROGEN

by

Kathlyn Jean McVey

A thesis

submitted in partial fulfillment

of the requirements for the degree of

Master of Science in Raptor Biology

Boise State University

May 2011

BOISE STATE UNIVERSITY GRADUATE COLLEGE

DEFENSE COMMITTEE AND FINAL READING APPROVALS

of the thesis submitted by

Kathlyn Jean McVey

Thesis Title: Trophic Ecology of Burrowing Owls in Natural and Agricultural Habitats and an Analysis of Predator Communities using Stable Isotopes of Carbon and Nitrogen

Date of Final Oral Examination: 10 March 2011

The following individuals read and discussed the thesis submitted by student Kathlyn Jean McVey, and they evaluated her presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

James R. Belthoff, Ph.D.	Chair, Supervisory Committee
Peter Koetsier, Ph.D.	Member, Supervisory Committee
Mark R. Fuller, Ph.D.	Member, Supervisory Committee

The final reading approval of the thesis was granted by James R. Belthoff, Ph.D., Chair of the Supervisory Committee. The thesis was approved for the Graduate College by John R. Pelton, Ph.D., Dean of the Graduate College.

DEDICATION

I dedicate this thesis to my wonderful family and friends.

Thank you for all your support, kind words, and hours spent on the phone.

ACKNOWLEDGEMENTS

I would first like to thank the members of my family, both new and old, who provided me with support every step of the way during this long journey. I truly could not have completed my research and thesis without them. I wish to thank my advisor Dr. James Belthoff for his guidance, patience, and especially flexibility in allowing me to finish my thesis from afar. This thesis would not be complete without the thoughtful input and advice from my committee members Dr. Mark Fuller and Dr. Peter Koetsier whom I thank. I thank my fellow burrowing owl researchers, Matt Stuber and Justin Welty, as their help and camaraderie in the field was invaluable. And to the many other students, volunteers, and friends who offered their assistance in the field, classroom, or at happy hour, I appreciate your support. I would like to thank the Raptor Research Center for providing me a work space and use of vehicles for my thesis research. Thank you to the various sources who helped to fund my research including the USDA Cooperative State Research, Education, and Extension Service; Boise State University; and the Raptor Research Center. Finally, I thank the National Science Foundation GK-12 Fellowship program; the Foothills Learning Center in Boise, Idaho; AmeriCorps; and the US Fish and Wildlife Service for presenting me with opportunities and experiences that have helped shaped my thesis and my life.

ABSTRACT

Stable isotopes of carbon and nitrogen can provide powerful tools for estimating the trophic positions of animals and determining the source or the primary producer of a food web. I used stable isotopes analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to investigate the trophic position of burrowing owls (*Athene cunicularia*) in agricultural and natural habitats and trophic relationships of a community of vertebrate predators in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA), located in southern Idaho.

Burrowing owl populations have declined across much of North America owing to loss of habitat. However, burrowing owls show affinity for nesting near agriculture in some portions of their range, including s. Idaho. I used analysis of ^{13}C and ^{15}N to investigate burrowing owl food habits and trophic relationships in agricultural and natural habitats in the NCA. $\delta^{13}C$ did not differ between natural and agricultural habitats and indicated carbon sources in burrowing owl diet contained primarily C_3 plants. Conversely, $\delta^{13}C$ differed between nestling and adult owls, which may indicate that adults provisioned nestlings with a different diet than they consumed. Burrowing owl $\delta^{15}N$ values depended on both habitat (i.e., natural or agricultural) and group (i.e., samples from 20 day old juveniles, 30 day old juveniles, adult females or adult males), although owls nesting in natural habitat generally had higher $\delta^{15}N$ values than owls nesting in agricultural habitat. Owls in natural habitat potentially fed on more kangaroo rats (*Dipodomys ordii*), scorpions (*Hadrurus spadix*) and spiders (Infraorder

Mygalomorphae) and fewer montane voles (*Microtus montanus*) and crickets (*Gryllus* spp.), which may help explain elevated $\delta^{15}N$ values for owls nesting in natural habitat. My results corroborated Moulton et al. (2005, 2006), who used traditional food habits analysis and found that burrowing owls nesting in natural and agricultural habitats feed on different prey species in each habitat. As adults in natural areas had higher $\delta^{15}N$ values, this may be further evidence that adult owls consumed different prey than they used to provision nestlings. Food webs, of which burrowing owls are a part, for both natural and agricultural habitats were similar despite the introduction of irrigated agriculture into a naturally arid landscape.

I also examined trophic relationships of a community of vertebrate predators in the same area. The NCA has a rich diversity of predators, including sixteen raptor species and an array of mammalian predators. It presents a unique opportunity to examine trophic ecology of predators that may use the same prey resources. I compared my results from analysis of ^{13}C and ^{15}N with results from traditional food habit study methods from Marti et al. (1993). I collected 272 samples from 14 species of vertebrate predator. Predators had a relatively narrow range of $\delta^{15}N$ with only 2‰ separating the majority of the species; therefore, the vertebrate predators that I examined occupied a similar trophic position. The food web in the NCA is based on a combination of C_3 and C_4 plants and illustrates that a mixture of plant species is supporting a community structure of herbivores, omnivores, and predators, rather than a particular species of shrub, forbs, grass, or crop plant. My findings were consistent with the results from Marti et al. (1993), who found, when prey were identified to the class level, mean dietary overlap among vertebrate predators was 82%. As in Marti et al. (1993), results based on

stable isotopes analysis indicated that most species clustered into four principal groups, while two species (coyotes, *Canis latrans* and great horned owls, *Bubo virginianus*) were sufficiently dissimilar and were excluded from other groups. By pairing stable isotope technology with traditional food habit study methods, my study provides a more complete view of trophic relationships among vertebrate predators.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: STABLE ISOTOPES OF CARBON AND NITROGEN AND THEIR USE IN UNDERSTANDING TROPHIC ECOLOGY

Since their first uses in earth science research, applications of stable isotopes analysis in other disciplines, particularly ecology, have rapidly expanded. Stable isotopes of carbon and nitrogen can provide powerful tools for estimating the trophic positions of consumers in a food web and the carbon flow to such consumers (Kelly 2000, Post 2002, Fry 2006, Inger and Bearhop 2008). Furthermore, the ongoing advances in modeling techniques and laboratory approaches, the incorporation of additional isotopes (sulfur, oxygen, and hydrogen), and the relative decrease in cost of analysis have combined to greatly increase the number of studies using this technique. Stable isotopes analyses have been used extensively to investigate aquatic food webs, but their use in understanding terrestrial ecosystems is more recent. This chapter of my thesis provides an overview of how nitrogen and carbon stable isotopes are used in elucidating trophic ecology, which will facilitate understanding of the field studies that I describe in Chapters 2 and 3.

What Are Stable Isotopes?

Isotopes are chemical elements differing in the number of neutrons. Stable isotopes, unlike radiogenic isotopes, do not decay over time. Stable isotopes generally have one more neutron than a common form of the element and, thus, are heavier. Naturally occurring stable isotopes are found for biologically important elements, e.g., carbon, hydrogen, nitrogen, oxygen, and sulfur (Fry 2006, Inger and Bearhop 2008). The stable isotopes useful in trophic ecology are found in very low abundances. For instance,

of all the carbon in the world, 98.9% is ^{12}C (i.e., the common form), and only 1.1% is ^{13}C (Rundel et al. 1989). These differences in relative abundance of isotopes can be measured by mass spectrometry in the laboratory. Continuous-flow isotope-ratio mass spectrometers (CFIRMS) allow multiple isotopes to be analyzed simultaneously, which has greatly reduced the cost of analysis and makes this technique more practical (Inger and Bearhop 2008).

Stable isotope natural abundances are expressed as a delta (δ) in parts per mill (‰), where δ denotes the difference between a sample and an international standard. International standards for carbon, nitrogen, and hydrogen are Pee Dee Belemnite, atmospheric nitrogen (air), and Vienna Standard Mean Ocean Water (VSMOW), respectively. The expression for an isotope sample is:

$$\delta X = [(R_{SAMPLE} / R_{STANDARD}) - 1] * 1000$$

where X is the element of interest, R_{SAMPLE} = the ratio of heavy to light isotopes in the sample, and $R_{STANDARD}$ = the ratio of the heavy to light isotopes in the standard (Kelly 2000, Fry 2006, Inger and Bearhop 2008). Lighter isotopes are more quickly broken down than heavier isotopes and, as a result, many chemical and physical processes lead to isotopic fractionation. Carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are the two isotopes most frequently used in food habits analysis. Their analysis provides results that are useful in determining trophic structure and food webs for a wide variety of organisms and habitats.

Nitrogen

Nitrogen ($^{15/14}N$) shows predictable bioaccumulation of 2 - 4‰ per step upward in the food chain; thus, it is key to understanding trophic position of a species (Minagawa and Wada 1984, Post 2002). Bioaccumulation occurs as a result of differential

fractionation between the heavy and light isotopes. ^{14}N is more easily digested and excreted in waste products, whereas ^{15}N becomes incorporated into the tissues of the consumer (DeNiro and Epstein 1981, Fry 2006). Thus, a consumer's tissues tend to be enriched in^{15}N relative to the plants and animals in its diet. For example, if primary producers (plants) have a $\delta^{15}N$ value of 3‰, then one would expect primary consumers (herbivores) to have a $\delta^{15}N$ value of around 7‰. Secondary consumers (carnivores) would have a $\delta^{15}N$ value of around 11‰ (Figure 1.1, Bemis et al. 2003).

$\delta^{15}N$ bioaccumulation or isotopic enrichment factors are known for a variety of animals at many levels of presumptive food chains. Average fractionation of 3.4‰ is a robust and widely applicable assumption of the expected isotopic difference between animals of different trophic levels when applied to entire food webs with multiple pathways (Post 2002). However, choosing a specific enrichment factor between 2 and 4‰ will not dramatically affect the conclusions drawn from comparisons among organisms in the same food web. Comparing $\delta^{15}N$ values across food webs and habitats is generally appropriate when baseline measures of plants, litter, or soil are available to make inter-site comparisons (Nakagawa et al. 2007). Overall, analysis of bioaccumulation of $\delta^{15}N$ values allows one to assign trophic level and relative position in the food chain to a species (Fry 2006). For example, Hyodo et al. (2010) used analysis of nitrogen and carbon stable isotopes to examine trophic relationships of various animal consumers within a tropical rain forest in Malaysia. They found detritovores, omnivores, herbivores, and carnivores had distinct isotope values, and that herbivores derive most of their carbon from the forest canopy layer. O'Grady et al. (2010) studied several species of ants in a temperate limestone grassland. Using ^{15}N, they were able to tease apart

trophic structure of ant species and found $\delta^{15}N$ values for adult *Lasius flavus* were higher than expected, which suggested a more predatory diet than was implied in the literature. Thus, stable isotopes analysis led to new understanding of diets for coexisting species of ants.

Carbon

^{13}C shows less predictable bioaccumulation of between 0.7 - 1.3‰ (O'Leary 1988) and is more commonly used to determine the primary energy or source of carbon input at the base of the food web. Plant species use three different photosynthetic pathways: C_3, C_4, and CAM. C_3 and C_4 photosynthesis are the most common, and each pathway presents itself with a distinct ^{13}C range (Figure 1.2). The plants that use C_3 photosynthesis, mainly forbs, are characteristically more depleted in ^{13}C, with an average of -28‰. Grasses, such as corn (*Zea mays*) and cheatgrass (*Bromus tectorum*), are C_4 plants and are comparatively enriched in ^{13}C, with an average of -14‰ (Figure 1.2, O'Leary 1988, Rundel et al. 1989). There is very little overlap in the ^{13}C range for C_3 and C_4 plants; therefore, it is often possible to determine what types of plants are at the base of a food chain of interest (Figure 1.2, DeNiro and Epstein 1978, O'Leary 1988). Analysis of carbon isotopes can also determine from what habitat type an animal has been feeding, either marine or terrestrial (Figure 1.3, Hobson 1990, Inger and Bearhop 2008), or which types of plants were the most important to sustaining a food web (Wolf and Martínez del Rio 2003). ^{13}C and ^{15}N are often used in combination to examine food habits of an animal and can elucidate the primary energy source and species' relative trophic position for a food web.

Samples for Isotope Analysis

As plant and animal tissues have specific turnover rates, stable isotope values reflect the diet for specific periods of time depending on which tissue(s) are analyzed. Hobson and Clark (1992a) found that isotope values in whole blood of captive Japanese quail (*Coturnix japonica*) have a half-life of 11.4 days, so samples of isotopes from blood reflect recent diet. Isotopes in muscle have a slightly longer half-life of 12.4 days. Liver tissue has very short isotopic half-lives of 2.6 days, while bone collagen has a long half-life of about 173.3 days (Hobson and Clark 1992a). Miller et al. (2008) found that for deer mice (*Peromyscus maniculatus*) in a laboratory setting, nitrogen isotopes have a half-life of 19.8 days in whole blood and 24.8 days for muscle. However, Nagy (1987) suggested care be taken when extrapolating laboratory derived enrichment factors such as those just mentioned to wild populations. He found wild bird metabolic rates are often higher than the basal metabolic rates of caged animals.

Stable isotope analysis of fur, hair, and feathers can yield longer-term dietary information. Isotopes values from feathers in birds reflect the diet from when the feather was growing, as after a feather has emerged from the blood shaft, it is isotopically inert. The same is true with fur and hair in mammals. Therefore, it is important to know at what time and geographic location the fur or feather grew. For some bird species, it may be more than one year to complete one molt cycle, e.g., barn owls (*Tyto alba*) have a molt pattern of longer than two years. Therefore, they are a species where sampling two different primary feathers will yield two years of stable isotope values (Cramp 1985, Taylor 1994). When using stable isotopes analysis, it is important to define what time period one is trying to study and choose sample type according to that time frame.

Rates of assimilation or trophic enrichment values may differ based on sample type as well. Miller et al. (2008) found mean enrichment values for deer mice for blood and muscle to be -0.2‰ and -0.7‰ for carbon and 2.3‰ and 2.5‰ for nitrogen, respectively (no SE was reported). Hobson and Clark (1992b) studied peregrine falcon (*Falco peregrines*) blood and feather samples and found trophic enrichment values to be 0.2 ± 0.01‰ and 2.1 ± 0.08‰ for carbon and 3.3 ± 0.4‰ and 2.7 ± 0.5‰ for nitrogen, respectively. Tissues such as blood, muscle, and feathers are synthesized at different rates and potentially from different dietary components, as muscle and feathers are composed of protein, and blood is a mixture of sugars, protein, and other solutes. This makes it difficult to draw direct comparisons of isotope values across different tissues, as trophic enrichment factors can vary by tissue type (Inger and Bearhop 2008). However, Croxall et al. (1999) found isotope values derived from blood samples have an advantage of allowing comparisons among birds and mammals more easily than comparing isotope values derived from fur and feathers. Hobson and Clark (1992b) also found that for birds whose diet is animal protein, nitrogen fractionation values do not differ between young and adult birds.

How to Use Stable Isotopes

Mixing models based on stable isotopes analysis can be employed in some cases to further elucidate a species' position within an ecosystem and estimate percent of important prey species in a consumer's diet. However, complex systems with a diversity of species and sample types make it difficult to apply a mixing model (Kelly 2000, Post 2002, Fry 2006, Inger and Bearhop 2008). Many mixing models have specific requirements that can be hard to fulfill in a natural study. In addition to adequate

sampling of prey species (O'Grady et al. 2010) and temporal matching of diet and prey, mixing models usually require a low number of isotopically distinct nutrient sources and information on the isotopic heterogeneity of a species' diet or habitat (Inger and Bearhop 2008). Another complication of mixing models is that the output of these models corresponds to a set of possible solutions, rather than the real solution (Inger and Bearhop 2008).

Plots of $\delta^{13}C$ and $\delta^{15}N$ values and cluster diagrams are common methods to portray the results of food habits studies and trophic analyses based on isotopes. Carbon and nitrogen stable isotope values are traditionally displayed in a dual isotope plot with $\delta^{13}C$ on the x-axis and $\delta^{15}N$ on the y-axis (Figure 1.1, Figure 1.3). Isotope plots demonstrate trophic enrichment between food source and consumer and may elucidate differences in carbon source for species of interest (Figure 1.3). Additionally, cluster analysis of isotope values may be used to group species with similar dietary habits (Davenport and Bax 2002, Roth et al. 2007). Roth et al. (2007) used cluster analysis and found snowshoe hares (*Lepus americanus*), one of the most common prey items of Canada lynx (*Lynx canadensis*), were isotopically distinct from all other prey species. Some studies use an index or reference species with well-known dietary habits as a baseline to better interpret isotope values for species with less well-known food habits (see Herrera et al. 2003).

Perhaps the best approach to understanding diet is to combine stable isotopes analysis with traditional food habit study methods. Traditional approaches to understanding diet include analyses of stomach contents, fecal materials, or prey remains; direct observation; and, in some cases, examination of regurgitated pellets where partially

or undigested materials can be identified. While these methods can provide accurate taxonomic information about an animal's diet, they may not work well for animals that consume small prey items or forage a great distance from land. Isotope studies can offer novel insights into trophic relationships using a tool that is independent of traditional techniques (Evans Ogden et al. 2005).

Studying food habits using stable isotopes analysis may have some advantages over traditional food habits study methods. Most prominently, isotope samples are a reflection of not only what an animal eats, but what is assimilated and incorporated into the consumer. As animals 'are what they eat,' stable isotope values in a consumer's tissues reflect their diet, and consequently allow one to understand a consumer's food habits and trophic level within a habitat. Additionally, some samples for isotopes analysis such as feathers and fur can be collected non-invasively as they are shed throughout the year, while other sample types such as blood, toenail clippings, and muscle can be collected non-lethally. Samples collected during one trip to a nest or roost site can simultaneously yield information about an animal's recent and long-term diet, while only disturbing the animal once. Finally, while isotopes are weaker at providing taxonomic detail of diet and cannot typically distinguish diet contributions among trophically similar prey, they can provide better estimates of the role that soft-bodied prey items play in an animal's diet when compared to traditional methods. For instance, stable isotope analysis revealed differences in trophic level between seabirds living on two islands was caused by greater amounts of soft-bodied invertebrate prey consumed by birds on one of the two islands (Hobson et al. 2002).

Stable isotopes analysis can also be used to define trophic structure within an ecosystem and detect changes in diet that may occur across a group of individuals. Cherel et al. (2007) examined resource partitioning within a guild of air-breathing diving predators and demonstrated that guild structure did not change between summer and winter. Yi et al. (2006) used stable isotopes to categorize animals into trophic groups and found seasonal differences within omnivorous bird species occupying a Tibetan Plateau. Davenport and Bax (2002) investigated a marine ecosystem off the coast of Australia. They used cluster analysis of isotope values from fish species and produced groupings of trophic relationships that were supported by stomach contents analysis. Stable isotopes can also be a useful tool to study how alteration of natural landscapes can impact a species' food habits. Using stable isotopes analysis, Evans Ogden (2005) found that wintering dunlins (*Calidris alpine pacifica*) forage extensively in agricultural habitat.

Overview of Chapters 2 and 3

In Chapter 2 of this thesis, I report the results of my use of analyses of $\delta^{13}C$ and $\delta^{15}N$ to investigate western burrowing owl (*Athene cunicularia hypugaea*) food habits and trophic relationships in agricultural and natural habitats in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) in southern Idaho. Burrowing owl populations have declined across much of North America (Haug et al. 1993, Gervais and Anthony 2003). However, they show affinity for nesting near agriculture in some portions of their range (Rich 1986, Leptich 1994, DeSante et al. 2004, Conway et al. 2006, Moulton et al. 2006, Restani et al. 2008). Using analysis of $\delta^{13}C$ and $\delta^{15}N$, I found the food webs, of which burrowing owls are a part, in both natural and agricultural habitats were similar despite the introduction of irrigated agriculture into a naturally arid

landscape. For burrowing owls, carbon isotopes did not differ between natural and agricultural habitats and indicated carbon sources in burrowing owl diet contained primarily C_3 plants. However, $\delta^{13}C$ differed between nestling and adult owls, which may signify that adults provisioned nestlings with a different diet than they consumed. Burrowing owl $\delta^{15}N$ values depended on both habitat (i.e., natural or agricultural) and group (i.e., samples from 20 day old juveniles, 30 day old juveniles, adult females or adult males), although owls nesting in natural habitat generally had higher $\delta^{15}N$ values than owls nesting in agricultural habitat. Owls in natural habitat potentially fed on more kangaroo rats (*Dipodomys ordii*), scorpions (*Hadrurus spadix*), and spiders (Infraorder Mygalomorphae) and fewer montane voles (*Microtus montanus*) and crickets (*Gryllus* spp.), which may help explain elevated $\delta^{15}N$ values for natural habitat. My results corroborated Moulton et al. (2005, 2006), who found using traditional food habits analysis that burrowing owl nesting in natural and agricultural habitats feed on different prey species in each habitat. As adults in natural areas had higher $\delta^{15}N$, this may be further evidence that adult owls consumed different prey than they used to provision nestlings.

In Chapter 3 of this thesis, I examined trophic relationships of a community of vertebrate predators in s. Idaho. While the NCA has an array of mammalian predators, the diversity of avian predators and density of breeding raptors is unparalleled within North America. Sixteen raptor species regularly breed within the NCA and eight other species use the area while migration or wintering. This rich diversity of species presents a unique opportunity to examine relationships among a variety of vertebrate predators that may use the same prey resources. I compared my results from isotope analysis of

carbon (^{13}C) and nitrogen (^{15}N) with results from traditional food habit study methods in Marti et al. (1993). I collected samples from 14 species of vertebrate predator including five species of owl, two hawks, two falcons, three mammals, one reptile, and one additional bird species. Predators had a relatively narrow range of mean $\delta^{15}N$ with only 2‰ separating 13 of the 14 predators; therefore, the species of vertebrate predator that I examined occupied similar trophic positions. My findings were consistent with the results from Marti et al. (1993), who found, when prey were identified to the class level, mean dietary overlap among vertebrate predators was 82%. Pairing stable isotope technology with traditional food habit study methods may provide a more complete view of trophic relationships among vertebrate predators.

Figure 1.1. An example of trophic relationships among plants and categories of animals as illustrated by stable isotopes of carbon and nitrogen. Graph is modified from Bemis et al. (2003).

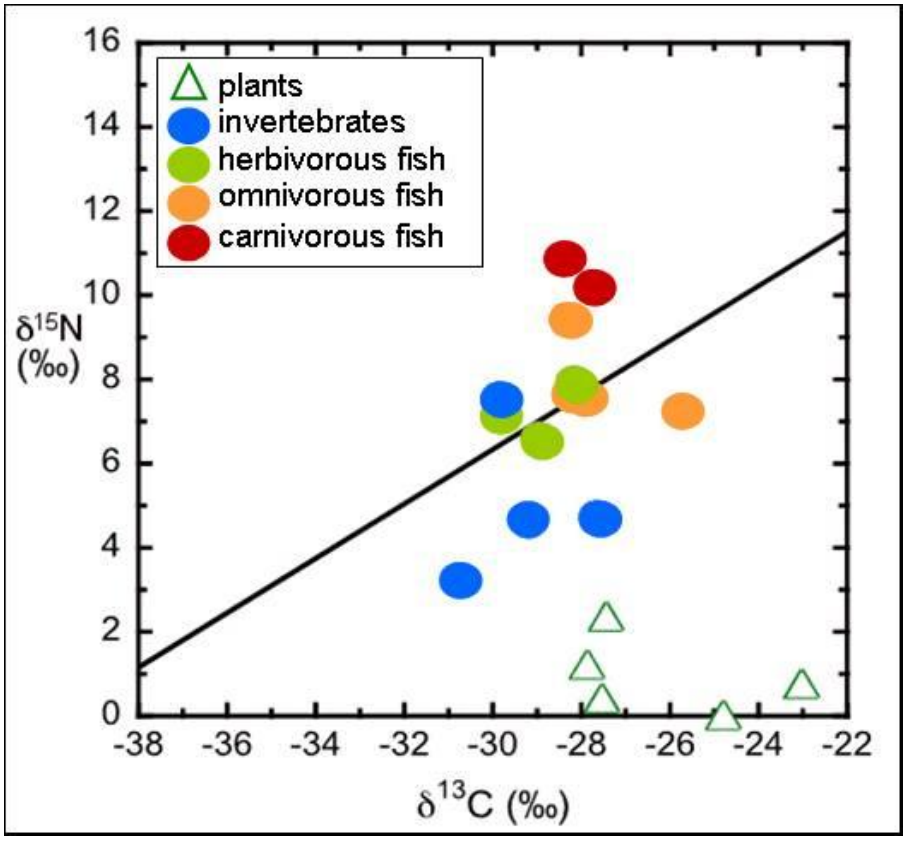


Figure 1.2. Carbon isotope distribution typical of plants species using C_3 or C_4 photosynthetic pathways. Graph is modified from O'Leary (1988).

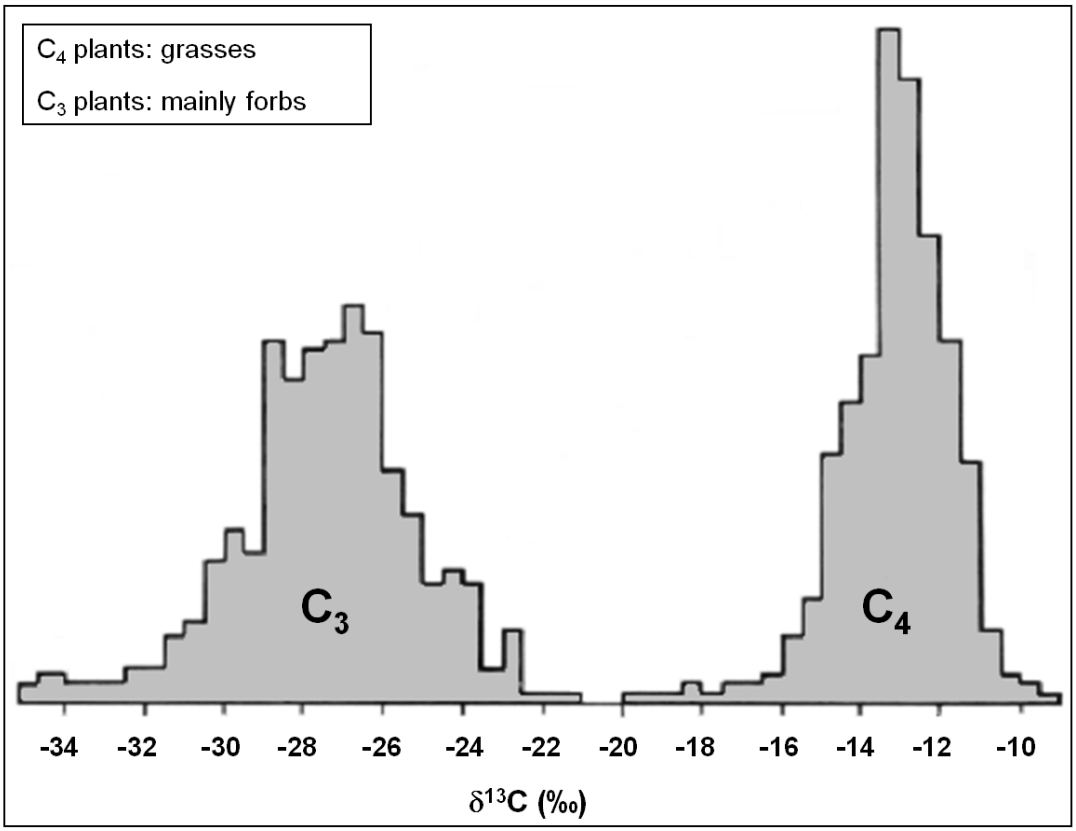
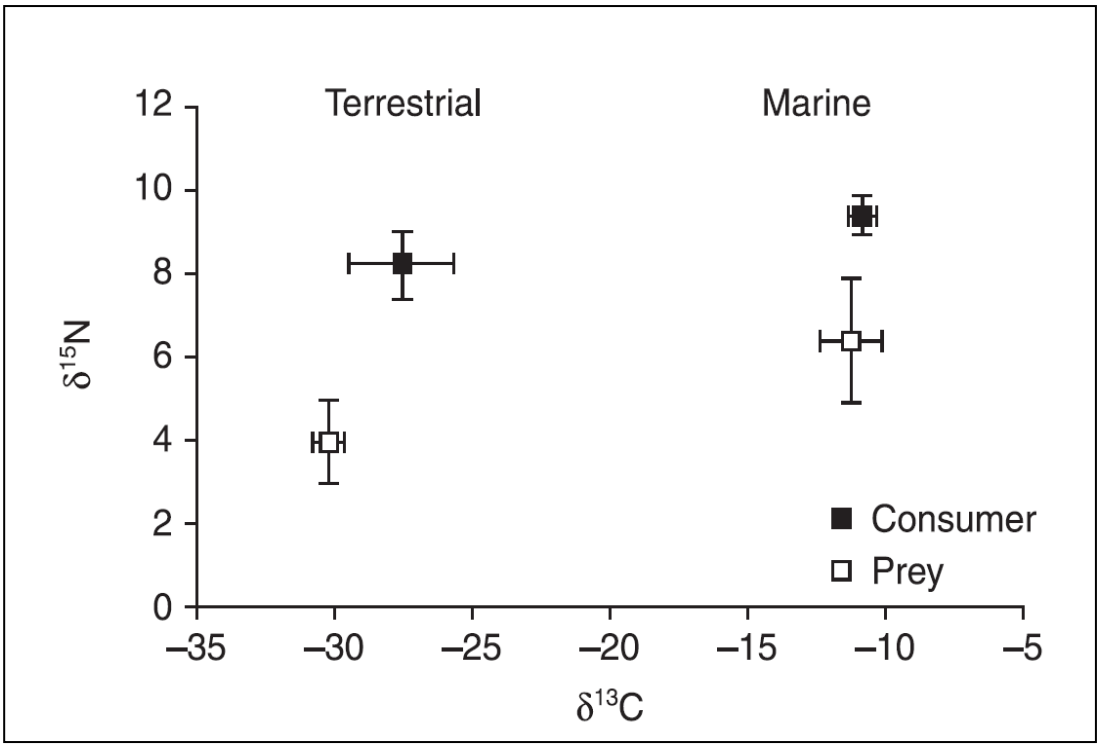


Figure 1.3. Conventional display of $\delta^{15}N$ and $\delta^{13}C$ in a dual isotope plot. This example, from Inger and Bearhop (2008), illustrates how consumers and prey can differ in $\delta^{15}N$ and how carbon sources can differ from terrestrial to marine inputs.



Literature Cited

Bemis, B.E., C. Kendall, S.D. Wankel, T. Lange, and D.P. Krabbenhoft. 2003. Isotopic evidence for spatial and temporal changes in Everglades food web structure. Poster presented at Greater Everglades Ecosystem Restoration Conference. Palm Harbor, Florida.

Cherel, Y., K.A. Hobson, C. Guinet, and C. Vanpe. 2007. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. Journal of Animal Ecology 76:826-836.

Conway, C.J., V. Garcia, M.D. Smith, L.A. Ellis, and J.L. Whitney. 2006. Comparative demography of burrowing owls in agricultural and urban landscapes in southeastern Washington. Journal of Field Ornithology 77:280-290.

Cramp, S. 1985. The Birds of the Western Palearctic. Vol. 4. Oxford University Press, Oxford.

Croxall, J.P., K. Reid, and P.A. Prince. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Marine Ecology-Progress Series 177:115-131.

Davenport, S.R. and N.J. Bax. 2002. A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Canadian Journal of Fisheries and Aquatic Sciences 59:514-530.

DeNiro, M.J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495-506.

DeNiro, M.J. and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341-351.

DeSante, D.F., E.D. Ruhlen, and D.K. Rosenberg. 2004. Density and abundance of burrowing owls in the agricultural matrix of the Imperial Valley, California. Studies in Avian Biology 27:116-119.

Evans Ogden, L.J., K.A. Hobson, D.B. Lank, and S. Bittman. 2005. Stable isotope analysis reveals that agricultural habitat provides an important dietary component for nonbreeding Dunlin. Avian Conservation and Ecology 1.3. http://www.ace-eco.org/vol1/iss1/art3/.

Fry, B. 2006. Stable Isotope Ecology. Springer, New York.

Gervais, J.A. and R.G. Anthony. 2003. Chronic organochlorine contaminants, environmental variability, and the demographics of a burrowing owl population. Ecological Applications 13:1250-1262.

Haug, E.A., B.A. Millsap, and M.S. Martell. 1993. Burrowing Owl (Athene *cunicularia*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/061doi:10.2173/bna.61.

Herrera, L.G., K.A. Hobson, M. Rodríguez, and P. Hernandez. 2003. Trophic partitioning in tropical rain forest birds: insights from stable isotope analysis. Oecologia 136:439-444.

Hobson, K.A. 1990. Stable isotope analysis of marbled murrelets: evidence for freshwater feeding and determination of trophic level. Condor 92:897-903.

Hobson, K.A. and R.G. Clark. 1992a. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor 94:181-188.

Hobson, K.A. and R.G. Clark. 1992b. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189-197.

Hobson, K.A., G. Gilchrist, and K. Falk. 2002. Isotopic investigations of seabirds of the North Water Polynya: contrasting trophic relationships between the eastern and western sectors. Condor 104:1-11.

Hyodo, F., T. Matsumoto, Y. Takematsu, T. Kamoi, D. Fukuda, M. Nakagawa, and T. Itioka. 2010. The structure of a food web in a tropical rain forest in Malaysia based on carbon and nitrogen stable isotope ratios. Journal of Tropical Ecology 26:205-214.

Inger, R. and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447-461.

Kelly, J. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1-27.

Leptich, D.J. 1994. Agricultural development and its influence on raptors in southern Idaho. Northwest Science 68:167-171.

Marti, C.D., K. Steenhof, M.N. Kochert, and J.S. Marks. 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. Oikos 67:6-18.

Miller, J.F., J.S. Millar, and F.J. Longstaffe. 2008. Carbon- and nitrogen-isotope tissue-diet discrimination and turnover rates in deer mice, *Peromyscus maniculatus*. Canadian Journal of Zoology 86:685-691.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48:1135-1140.

Moulton, C.E., R.S. Brady, and J.R. Belthoff. 2005. A comparison of breeding season food habits of burrowing owls nesting in agricultural and nonagricultural habitat in Idaho. Journal of Raptor Research 39:429-438.

Moulton, C.E., R.S. Brady, and J.R. Belthoff. 2006. Association between wildlife and agriculture: underlying mechanisms and implications in burrowing owls. Journal of Wildlife Management 70:708-716.

Nagy, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecological Monographs 57:111-128.

Nakagawa, M., F. Hyodo, and T. Nakashizuka. 2007. Effect of forest use on trophic levels of small mammals: an analysis using stable isotopes. Canadian Journal of Zoology 85:472-478.

O'Grady, A., O. Schmidt, and J. Breen. 2010. Trophic relationships of grassland ants based on stable isotopes. Pedobiologia 53:221-225.

O'Leary, M.H. 1988. Carbon isotopes in photosynthesis. BioScience 38:328-336.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Restani, M., J.M. Davies, and W.E. Newton. 2008. Importance of agricultural landscapes to nesting burrowing owls in the northern Great Plains, USA. Landscape Ecology 23:977-987.

Rich, T. 1986. Habitat and nest-site selection of burrowing owls in the sagebrush steppe of Idaho. Journal of Wildlife Management 50:548-555.

Roth, J.D., J.D. Marshall, D.L. Murray, D.M. Nickerson, and T.D. Steury. 2007. Geographical gradients in diet affect population dynamics of Canada lynx. Ecology 88:2736-2743.

Rundel, P.W., J.R. Ehleringer, and K.A. Nagy (eds.). 1989. Stable Isotopes in Ecological Research. Springer Verlag, New York.

Taylor, I.R. 1994. Barn Owls. Cambridge University Press, Cambridge, UK.

Wolf, B.O. and C. Martínez del Rio. 2003. How important are columnar cacti as sources of water and nutrients for desert consumers? A review. Isotopes in Environmental and Health Studies 39:53-67.

Yi, X., Y. Yang, and X. Zhang. 2006. Modeling trophic positions of the alpine meadow ecosystem combining stable carbon and nitrogen isotope ratios. Ecological Modelling 193:801-808.

CHAPTER 2: A COMPARISON OF TROPHIC RELATIONSHIPS OF BURROWING OWLS IN AGRICULTURAL AND NATURAL HABITATS USING STABLE ISOTOPES ANALYSIS

Abstract

I used stable isotopes analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to investigate burrowing owls food habits and trophic position in agricultural and natural habitats in the Morley Nelson Snake River Birds of Prey National Conservation Area, located in southern Idaho. I examined patterns of variation in $\delta^{13}C$ and $\delta^{15}N$ among nestlings, adult females and adult males between and within habitats and explored trophic relationships of a community of plants and animals that included burrowing owls in both natural and agricultural habitats. Food webs for both natural and agricultural habitats were similar in that species could be categorized into functional groups including primary producers, and primary, secondary, and higher-level consumers for each habitat. For burrowing owls, carbon isotopes did not differ between natural and agricultural habitats and indicated carbon sources in burrowing owl diet contained primarily C_3 plants. However, $\delta^{13}C$ differed between nestling and adult owls, which may signify that adults provisioned nestlings with a different diet than they consumed. Burrowing owl $\delta^{15}N$ values depended on both habitat (i.e., natural or agricultural) and group (i.e., samples from 20 day old juveniles, 30 day old juveniles, adult females or adult males), although owls nesting in natural habitat generally had higher $\delta^{15}N$ values than owls nesting in agricultural habitat. Owls in natural habitat potentially fed on more kangaroo rats (*Dipodomys ordii*),

scorpions (*Hadrurus spadix*) and spiders (Infraorder Mygalomorphae) and fewer montane voles (*Microtus montanus*) and crickets (*Gryllus* spp.), which may help explain elevated $\delta^{15}N$ values for natural habitat. My results corroborated Moulton et al. (2005, 2006), who found using traditional food habits analysis that burrowing owl nesting in natural and agricultural habitats feed on different prey species in each habitat. As adults in natural areas had higher $\delta^{15}N$, this may be further evidence that adult owls consumed different prey than they used to provision nestlings. Through the use of stable isotopes analysis, I investigated food habits of nestling and adult burrowing owls within natural and agricultural habitats in s. Idaho and was able to examine the broad scope of trophic relationships within each habitat.

Introduction

Agriculture has changed much of the landscape in the United States and, as such, many plant and animal communities have been affected. While agricultural practices can provide different types of habitat, such as windrows and fallow fields, they also drive degradation, fragmentation, and outright loss of habitat for wildlife (Carlson 1985, Murphy 2003, Teyssèdre and Couvet 2007). Agriculture can increase soil erosion and pollute surrounding areas (Carlson 1985, Gervais et al. 2000). Additionally, there are often increases in depredation and exposure to pesticides in species of wildlife that live near agriculture (Gervais et al. 2000). Many species of fish and wildlife have declined since the introduction of agriculture into their native habitats (Murphy 2003). Teyssèdre and Couvet (2007) argue that habitat degradation and destruction, caused mainly by agriculture expansion, are the main causes of current biodiversity decline. They contend

ecosystem conversions associated with agriculture expansion between 1990 and 2050 will greatly reduce the number of birds and bird species on the earth.

Despite a multitude of negative effects, some native species associate with agricultural areas and may even benefit because of them. For example, agricultural fields are important foraging grounds for some wintering bird species. Agricultural habitats contribute 38% to dunlin *(Calidris alpina pacifica)* wintering diet (Evans Ogden et al. 2005). Fields of corn *(Zea mays*) and alfalfa *(Medicago sativa)* provide important migration staging areas for the North American midcontinent population of Sandhill cranes *(Grus canadensis*, Krapu et al. 1984). Long-distance migratory pink-footed geese (*Anser brachyrhynchus*) and Greenland white-fronted geese (*Anser albifrons flavirostris*) also show affinity for agricultural fields and use them as both resting and wintering sites (Fox et al. 2005). Williams et al. (2000) reported red-tailed hawk (*Buteo jamaicensis*) and Northern harrier (*Circus cyaneus*) densities were higher in cropland than in rangeland in Kansas. Finally, Chimango caracaras (*Milvago chimango*) occurred more often than expected by chance on agricultural lands in Western Pampas of Argentina (Goldstein and Hibbitts 2004).

Western burrowing owls (*Athene cunicularia hypugaea*) can also occur in agricultural areas in certain portions of their range (Orth and Kennedy 2001, DeSante et al. 2004, Rosenberg and Haley 2004, Conway et al. 2006, Moulton et al. 2006, Bartok and Conway 2010), and they frequently nest in higher densities in agricultural landscapes (Rich 1986, York et al. 2002, Rosenberg and Haley 2004). In southern Idaho, burrowing owls are the only species of raptor to show a positive association with agricultural habitat (Leptich 1994). My study was one component of multidisciplinary research that

investigates the effects of the introduction of irrigated agriculture into naturally arid landscapes and the effects of such habitat change on burrowing owls. Specifically, I focused on burrowing owl food habits and explored trophic relationships for owls nesting near agriculture and in more natural landscapes.

As burrowing owl populations have declined across much of North America (Haug et al. 1993, Gervais and Anthony 2003), they are now considered a sensitive species in many western states, federally endangered in Canada, and threatened in Mexico (Klute et al. 2003). Habitat destruction and increased exposure to pesticides, both of which occur from various forms of agriculture, have contributed to burrowing owl declines (Haug et al. 1993, Gervais et al. 2000, Gervais and Anthony 2003). Why then are burrowing owls seemingly attracted to agricultural areas, and how does their position within a community differ when owls nest in natural versus agricultural habitat?

Moulton et al. (2005, 2006) examined why burrowing owls in s. Idaho are attracted to irrigated agriculture areas for nesting. The three hypotheses they evaluated revolved around: (1) greater availability of suitable burrows in agricultural habitat, which provides more nesting opportunities for owls, (2) fewer predators in agricultural habitat, so owls nest in agricultural areas to avoid depredation, and (3) more or better foraging opportunities in agricultural habitat. Burrow availability and predation were not the driving forces behind greater abundance and higher nesting densities in agricultural areas. Instead, prey diversity and availability appeared to alter burrowing owl nesting behavior, resulting in greater owl nesting abundance in agricultural areas (Moulton et al. 2006).

As a follow up to Moulton et al.'s (2006) study, I investigated the food habits, trophic position, and food web dynamics of burrowing owls nesting in natural and

agricultural habitats. Based on traditional food habits methods (e.g., examination of regurgitated pellets and prey remains), Moulton et al. (2005) found burrowing owl diet, by biomass, consisted of 75.8 ± 2.6% and 79.1 ± 3.5% vertebrates and 24.2 ± 2.6% and 20.9 ± 3.5% invertebrates in agricultural and natural habitats, respectively. Moreover, burrowing owls nesting in agricultural areas consumed seven species of rodents, of which more than 5% of biomass in burrowing owl diet comprised five species (Figure 2.1). In natural areas, owls ate three species of rodents that each contributed more than 5% of biomass (Figure 2.1; see Moulton et al. 2005, 2006). Montane voles (*Microtus montanus)* provided substantial biomass for burrowing owl diet in agricultural areas, but owls did not prey on montane voles in natural habitat primarily because this rodent occurred mainly in agricultural habitat. The biomass contributed by Great Basin pocket mice (*Perognathus parvus),* which lived in both habitat types, also differed between habitats and was greater in natural habitat (Figure 2.1). Likewise, there were differences for invertebrate prey between habitats. Burrowing owls in agricultural areas consumed more crickets (*Gryllus* spp.), and owls in natural areas consumed more scorpions (*Hadrurus spadix*) and sunspiders (Solpugida, Family Eremobatidae; Figure 2.1).

Although Moulton et al. (2005, 2006) and other burrowing owl studies (Tyler 1983, Brown et al. 1986, Haug et al. 1993, York et al. 2002, Rosenberg and Haley 2004, Hall et al. 2009) have quantified food habits, each of these studies based analyses on regurgitated pellets, stomach contents, or prey remains, which are traditional methods for studying diet. Traditional food habits study methods may not work well for predators that include insects and other invertebrates in their diet (Marti 1974, Marti et al. 2007) because pellets comprising invertebrate materials break down rapidly. Plumpton and

Lutz (1993) indicate discrepancies between pellet casting and prey remains analysis. They found mice and beetles more often in pellet castings, while prey remains indicated a greater occurrence of moths, amphibians, passerines, and other small mammals in the diet. Thus, for a predator such as burrowing owls, pellet casting and prey remains results alone may not capture the full variability and scope of the diet. Therefore, I used an alternative method for investigating food webs for burrowing owls in natural and agricultural habitats, stable isotopes analysis of carbon and nitrogen (Kelly 2000, Post 2002, Inger and Bearhop 2008), to build upon the understanding of burrowing owl diet that Moulton et al. (2005, 2006) provided. As it is frequently difficult to assign castings to individuals at a nest (i.e., to distinguish between those castings produced by nestlings or by adults tending a nest), an added advantage of stable isotopes analysis is that it allowed me to examine the diet of adult males, adult females, and nestlings separately at each nest.

Stable isotopes of carbon and nitrogen can also provide data for estimating the trophic positions of and carbon flow to consumers in food webs (Kelly 2000, Post 2002, Fry 2006, Inger and Bearhop 2008). Nitrogen (^{15}N) shows predictable step-wise bioaccumulation of 2 - 4‰ and is useful for determining at what step an animal fits in a food web (Minagawa and Wada 1984, Post 2002). Carbon (^{13}C) is useful in determining the source or the primary producer of a food web. This can be accomplished because plants use different types of photosynthesis, C_3 and C_4 photosynthesis, which have distinct carbon isotope ranges (O'Leary 1988, Rundel et al. 1989). For example, Hyodu et al. (2010) used stable isotopes analysis to elucidate the food web in a tropical rain forest in Malaysia. They examined four consumer trophic groups (detritovores,

herbivores, omnivores, and predators) in relation to canopy and understory leaves. Herrera et al. (2003) investigated trophic partitioning of 23 bird species in southeastern Mexico and found most species fed on C_3 based foods. Nitrogen stable isotope analysis separated bird into trophic levels, which contained species whose diet included plants, insects, or a combination of both food sources.

Given the advantages offered by stable isotopes analyses, my goal was to further investigate burrowing owl food habits in both agricultural and natural habitats. Using stable isotopes analysis of carbon (^{13}C) and nitrogen (^{15}N), I also wanted to understand relative trophic positions of burrowing owls and their food webs in each habitat, including elucidating primary producers and primary, secondary, and higher-level consumers.

Objective 1: Compare Burrowing Owl Food Habits Between Habitats and Among Groups

My first objective was to determine if burrowing owls occupied similar trophic positions in agricultural and natural habitats, and to compare findings based on stable isotopes analysis to those from traditional food habit studies. I predicted burrowing owls nesting in natural habitats would have higher $\delta^{15}N$ value, which would be indicative of a higher trophic level. My prediction was based on the fact that while burrowing owls in both habitats eat a similar proportion of vertebrates, owls in natural areas eat more scorpions and solpugids (Moulton et al. 2005). These latter prey items are secondary consumers and, therefore, likely have increased $\delta^{15}N$ values. Ultimately, increased $\delta^{15}N$ values of prey would be reflected in burrowing owls who consumed these items. Additionally, I compared $\delta^{13}C$ and $\delta^{15}N$ to investigate patterns among 20 day old

nestlings, 30 day old nestlings, adult females and adult males between and within habitats. These comparisons are important because foraging theory predicts that adults should select higher quality prey for provisioning nestlings. Predators that can carry only one prey item, such as burrowing owls, are likely to deliver large prey items to the nest, while feeding themselves on a much broader range of prey sizes (Newton 1979, Orians and Pearson 1979, Rudolph 1982, Sonerud 1992, Davoren and Burger 1999).

Objective 2: Establish Food Webs for Agricultural and Natural Habitats

My second objective was to illuminate a food web for animal communities within agricultural and natural habitats using burrowing owls as a focal species. Using $\delta^{13}C$ and $\delta^{15}N$ values of plant, predator, and prey species to illustrate food webs, I explored the broad scope of animal food habits in both habitat types and commented on differences in ecosystem dynamics that may have been established because of the introduction of irrigated agriculture.

Study Species

Burrowing owls inhabit prairies, grasslands, steppes, and other open areas (Haug et al. 1993, Poulin et al. 2005, Lantz et al. 2007). Although they frequently nest in well-drained areas, they can also show affinity for nesting near irrigated agriculture (Rich 1986, Leptich 1994, DeSante et al. 2004, Conway et al. 2006, Moulton et al. 2006, Restani et al. 2008), as well as in fragmented suburban and urban areas (Trulio 1995, Conway et al. 2006, Mrykalo et al. 2009). These relatively small owls nest underground in burrows previously made by prairie dogs (*Cynomys* spp.), ground squirrels (*Spermophilus* spp.), American badgers (*Taxidea taxus*), and other fossorial mammals (Gleason and Johnson 1985, Rich 1986, Green and Anthony 1989, Poulin et al. 2005,

Lantz et al. 2007, Tipton et al. 2008). However, burrowing owls also nest in artificial burrows installed by researchers and wildlife managers (Henny and Blus 1981, Trulio 1995, Smith and Belthoff 2001, Todd et al. 2003, Smith et al. 2005, Barclay 2008). Artificial burrows typically consist of an underground nesting chamber (e.g., a bucket, tub, or valve box) with a tunnel leading to the surface (Smith and Belthoff 2001).

Female burrowing owls typically lay 8 - 12 eggs per clutch and incubate while their mates provision them. Pairs produce, on average, 0.9 to 4.9 nestlings per nesting attempt (Haug et al. 1993, Kaufman 1996, Smith et al. 2005, Wellicome 2005, Conway et al. 2006, Griebel and Savidge 2007, Welty 2010). Male burrowing owls are the principal food provider during the egg laying, incubation, and early nestling periods (Haug et al. 1993, Plumpton and Lutz 1993, Kaufman 1996, Poulin and Todd 2006). Female burrowing owls contribute the majority of invertebrate prey later in the nestling period and are more likely to forage diurnally and closer to the nest site than their male counterparts (Haug et al. 1993, Poulin and Todd 2006). York et al. (2002) found male burrowing owls have a broader food-niche breadth, consuming more Araneida, Coleoptera, Dermaptera, Isopoda, and Orthoptera than females. They speculated males build a broader collection of search images related to greater time spent foraging during the breeding season, and this allows male owls to key in on a greater variety of prey items than females.

Burrowing owls occur from British Columbia and Saskatchewan southward into Mexico and are annual migrants in the northern portions of their range (Haug et al. 1993). Migration routes for Idaho burrowing owls remain relatively unknown (Haug et al. 1993,

King and Belthoff 2001); however, a small number of band returns indicate that at least some Idaho burrowing owls may overwinter in California (Belthoff, unpublished data).

Study Area

I examined trophic ecology of burrowing owls in and near the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) located in s. Idaho during 2007 - 2008. This 195,325 ha area was established in 1993 by Congress (Public Law 103-64) for the conservation, protection, and enhancement of raptor populations and habitats (Sharpe and van Horne 1998). Precipitation averages 31.7 cm annually (N.O.A.A. 2002), with 12.1 cm occurring during the burrowing owl breeding season (March through July). The topography in the NCA is mainly flat to rolling with a number of rock outcrops, isolated buttes, and small canyons. The NCA is not intensively farmed, but approximately 5% is irrigated agriculture where the main agricultural crops include alfalfa, corn, sugar beets (*Beta vulgaris*), and mint (*Mentha L.*). The NCA was historically dominated by shrub-steppe (Hironaka et al. 1983), but human disturbances and fires have converted much of the area to disturbed grassland, dominated by invasive annual plants species, such as cheatgrass (*Bromus tectorum*) and tumble mustard (*Sisymbrium altissimum*). Plant communities in areas adjacent to agricultural fields are reasonably similar to those in natural habitat. Cattle and sheep grazing occur in the NCA, primarily during winter (USDI 1996, Moulton et al. 2005).

There are approximately 350 artificial burrow sites available for burrowing owls for nesting or roosting within the NCA (Smith and Belthoff 2001, Belthoff and Smith 2003, Moulton et al. 2006, Welty 2010). Artificial burrows allow researchers to readily count, capture, and mark young and adult owls and collect cached prey items. Since

1997, burrowing owl pairs occupied 30 - 60 of the artificial burrows within the NCA each year for nesting (Belthoff and Smith 2003, Belthoff, unpublished data). Burrowing owls nest in many portions of the NCA but are particularly common in regions with irrigated agriculture.

Methods

To examine food webs and trophic relationships of burrowing owls in natural and agricultural habitats, I obtained tissue samples for stable isotopes analysis from owls (nestlings and adults), their prey (vertebrates and invertebrates), their potential predators, and vegetation within the study area. I obtained samples in both 2007 and 2008 during standard monitoring of burrowing owl nests as part of long-term research in the NCA, roadway and walking surveys designed to locate animal carcasses from which tissue samples could be harvested, and vegetation and invertebrate sampling. I collected samples from March - July, which represented the breeding period for burrowing owls, at all levels of the presumptive food chain (e.g., primary producers, and primary, secondary, and higher-level consumers). I recorded the species, portion of carcass collected, and location (agricultural or natural habitat) for each sample. As burrowing owls frequently cached prey in nest and roost burrows, I was also able to obtain prey samples from these caches. Ultimately, samples were subjected to analysis by mass spectrometry to determine isotopic ratios for both carbon and nitrogen.

Burrowing Owl Sample Collection and Nest Monitoring

I obtained burrowing owl blood for stable isotopes analysis via venipuncture of a wing vein after capture of owls during regular monitoring of nests. As all nests used for my study were in artificial burrows, I was able to capture juveniles and adult females by

hand after excavating nest chambers. I captured adult males at or near their artificial burrow nests using a variety of trapping techniques (see King 1996, Moulton et al. 2005, Welty 2010). I collected blood from juveniles within each nest at 20 days after hatching and again at 30 days after hatching. For both 20 day and 30 day samples, to minimize the amount of blood needed from each nestling within a nest, I pooled blood from all nestlings within a nest to generate one 20 day and one 30 day sample for each nest. When possible, I also obtained blood from each adult tending a nest. Thus, for each nest, I analyzed up to four samples as follows: (1) pooled sample from nestlings at 20 days, (2) pooled sample from nestlings at 30 days, (3) sample from the adult female, and (4) a sample from the adult male. I hereafter refer to these as 20 day, 30 day, female, and male samples for a nest. Samples containing 0.3 to 0.5 ml of owl blood were stored frozen at -20 °C in 1.5 ml micro-centrifuge tubes until subjected to stable isotopes analysis.

Each owl received a United States Geological Survey (USGS) aluminum leg band (size 4) and 3 colored plastic leg bands (Foy's Pigeon Supplies, Beaver Falls, PA) for visual identification in the field. Adult owls with brood patches were classified as females, but I could not determine sex of the nestlings in the field because juvenile burrowing owls are not sexually dimorphic (Haug et al. 1993). Taylor (2005) found burrowing owl offspring sex ratio did not differ from the 0.50 proportion male that would be expected through random segregation of chromosomes at meiosis; therefore, the samples that I pooled from juveniles within each nest likely contained both male and female nestlings.

Haug and Oliphant (1990) and Rosenberg and Haley (2004) measured the typical range of foraging burrowing owls during the breeding season to be 600 m. Therefore, to

facilitate comparisons of burrowing owl diet between agricultural and natural habitat, I considered nests that were < 600 m from an irrigated agricultural field to be in 'agricultural habitat,' as owls within this distance had high potential to be foraging within irrigated agricultural fields or in areas directly influenced by such fields. I classified nests that were > 1500 m from agriculture as being in 'natural habitat' and assumed that owls from these nests rarely if ever foraged in agricultural areas. I excluded nests from analysis if they were 600 - 1500 m from agriculture to avoid potential ambiguity about their habitat status that may arise by including them.

Plants

I collected leaf or whole plant samples of native, non-native, and/or crop plants from around burrowing owl nest sites in both agricultural and natural habitats. I sampled plants that use C_3 photosynthesis (C_3 plants) and plants that use C_4 photosynthesis (C_4 plants). Cheatgrass and tumble mustard were the dominant form of ground cover near many burrowing owl nests irrespective of habitat type. Russian thistle (*Salsola* spp.) and halogeton (*Halogeton glomeratus*) were common in both natural and agricultural habitats. Tracks of big sagebrush (*Artemisia tridentata*) and other small shrubs were located in some natural areas. The dominant agricultural crop grown under irrigation during my study was alfalfa. I pressed plant samples and stored them dry until analysis.

Invertebrates

Invertebrate samples were collected by hand or netted while afield and retrieved from nest or roost burrows after burrowing owls had cached them as prey. I collected samples of as many invertebrate prey items that burrowing owls consume as possible, including herbivorous crickets, grasshoppers, and darkling beetles (*Eleodes* spp.) and

carnivorous spiders (Infraorder Mygalomorphae) and scorpions. I also collected carrion beetles (*Nicrophorus* spp.) from carcasses that I found during roadway surveys. I placed invertebrates in glass vials with ethanol and stored them at room temperature until analysis.

Vertebrate Samples Collected from Burrowing Owl Nest Sites

Remains of rodents and other vertebrate prey cached at nest sites served as the primary source of tissue for stable isotopes analysis. From cached mammalian, amphibian, and reptilian prey, I collected a portion of the hind limbs or the rear half of the animal. For avian prey cached by owls, I collected a sample of feathers or muscle tissue. I stored all muscle tissue/limb samples in glass vials and froze them at -20 °C and placed feathers in individual paper envelopes until analysis.

Vertebrate Samples Collected from Roadway Surveys

I opportunistically collected tissue samples from species known to prey on burrowing owls and other vertebrates from carcasses I located along roads in the study area. I obtained samples from American badgers, coyotes (*Canus latrans*), gopher snakes (*Pituophis catenifer*), black-tailed jackrabbits (*Lepus californicus*), and Piute ground squirrels (*Spermophilus mollis*). I stored all muscle tissue samples in glass vials and froze them at -20 °C until prepared for stable isotopes analysis.

Stable Isotopes Analysis

In preparation for analysis, I first thawed blood and other frozen samples. For invertebrates, entire animals were analyzed, whereas for vertebrates I dissected a small section of muscle and used that for analysis. Feathers were washed with liquid detergent and distilled water to remove external contaminants (Mizutani et al. 1992). Samples

were loaded into 30 mm aluminum weigh pans and oven dried for 48 hr at 60 °C (Cherel et al. 2007). All dried samples were ground into fine powder using a mortar and pestle or cut into small fragments using stainless steel scissors.

I ultimately sent 420 samples to the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University, Flagstaff, AZ for carbon and nitrogen stable isotope analysis. There, samples were weighed into tin capsules and analyzed on a Carlo Erba NC 2100 elemental analyzer connected to a DeltaPlus Advantage isotope ratio mass spectrometer (Thermo Finnigan) through the Conflo III interface (Thermo Finnigan). Carbon and nitrogen stable isotope ratios were analyzed simultaneously for each sample. Repeat analysis of an international laboratory standard (National Institute of Standards and Technology, NIST 1547-peach leaves) was precise to ± 0.06‰ for $\delta^{13}C$ and ± 0.10‰ for $\delta^{15}N$ (n = 175). Standards for carbon and nitrogen were Pee Dee Belemnite and atmospheric nitrogen (air), respectively. Stable isotope natural abundances were expressed as a delta (δ) in parts per mill (‰), where δ denoted the difference between a sample and an international standard. The standard expression for an isotope sample is: $\delta X = [(R_{SAMPLE} / R_{STANDARD}) - 1] * 1000$: where X is the isotope in question, R_{SAMPLE} = the ratio of heavy to light isotopes in the sample and $R_{STANDARD}$ = the ratio of the heavy to light isotopes in the standard (Kelly 2000, Post 2002, Fry 2006, Inger and Bearhop 2008).

Statistical Analysis

I used general linear models and restricted maximum likelihood estimation to examine effects of habitat (agriculture vs. natural) and group on burrowing owl stable isotope ratios, where the levels of group were 20 day (pooled sample from nestlings at 20

days), 30 day (pooled sample from nestlings at 30 days), female (a sample from adult female), and male (a sample from the adult male). Group was considered a repeated measure in each analysis, as samples from nestlings and adults were derived from the same nests and therefore not independent. When I detected significant effects, I used follow-up pairwise comparisons (Least Significant Difference tests) between or among factor levels judged at alpha = 0.05. To evaluate trophic position of burrowing owls and to determine if and how trophic structure differed between natural and agricultural habitat, I plotted $\delta^{13}C$ and $\delta^{15}N$ for the plant and animal groups that I was able to sample. I conducted all analyses in JMP (version 8.0.2, SAS Institute, Inc., Cary, NC). Means ± SE are presented unless indicated otherwise.

Results

I collected and analyzed 172 burrowing owl samples from 65 nests: 20 day (n = 61), 30 day (n = 37), female (n = 47), and male (n = 27). There were 38 nests from agricultural habitat and 27 nests from natural habitat. I collected 59 plant samples from 10 species, 79 samples from six species of mammalian prey, and 66 samples from a wide variety of both primary and secondary consumer invertebrates that burrowing owls include in their diet (Table 2.1). In addition, I collected and analyzed four species of reptiles, Woodhouse's toads (*Bufo woodhouseii*), horned larks (*Eremophila alpestris)*, and American badgers and coyotes, the latter two of which are mammalian predators (Table 2.1).

Food Habits: Differences Between Habitats and Among Burrowing Owl Groups

Overall, the burrowing owl samples that I analyzed from these 65 nests had $\delta^{13}C$ that averaged -20.05 ± 0.15‰ and ranged from -23.44 to -13.97‰ (n = 172). For $\delta^{13}C$,

there was no habitat by group interaction (REML Anova, $F_{3, 103.52} = 1.97$, $P = 0.12$), and $\delta^{13}C$ did not differ between agricultural and natural habitat ($F_{1, 64.3} = 1.18$, $P = 0.28$). However, $\delta^{13}C$ differed significantly among levels of group ($F_{3, 103.50} = 12.07$, $P < 0.0001$). Adult males and females were more enriched in $\delta^{13}C$ than each of the nestling age classes (Figure 2.2).

$\delta^{15}N$ averaged 10.43 ± 0.07‰ and ranged from 7.47 to 12.37‰ (n = 172). I found that habitat and group interacted for $\delta^{15}N$ (REML Anova, $F_{3\ 103.40} = 8.56$, $P < 0.0001$); thus, differences between agricultural and natural habitat depended on which group was considered (Figure 2.3). Within both agricultural and natural habitat, there was no difference between 20 day and 30 day nestlings (Figure 2.3). In agricultural habitat, females were more enriched than males and 20 day and 30 day nestlings (Figure 2.3). In natural habitat, males were significantly more enriched than females, and females were significantly more enriched than 20 day and 30 day nestlings (Figure 2.3). For both sexes of adults, $\delta^{15}N$ was also significantly greater in natural habitat than in agricultural habitat (Figure 2.3). While 20 day and 30 day juveniles were slightly more enriched in natural habitat as well, the difference was not statistically significant (Figure 2.3).

Food Webs for Agricultural and Natural Habitats

To evaluate trophic position of burrowing owls and determine if and how trophic structure differed between natural and agricultural habitat, I examined $\delta^{13}C$ and $\delta^{15}N$ isotope values for the plant and animal groups that I sampled (Figure 2.4; Table 2.1). With the exception of horned larks and black-tailed jackrabbits, other animal groups, including burrowing owls, had $\delta^{13}C$ averages that ranged from -19.00 to -23.00‰;

therefore, the food web in both agricultural and natural habitats was based primarily on C_3 plants (Figure 2.4). In addition, distinct groups of plants and animals could be visualized for each habitat in accordance with increasing $\delta^{15}N$ values. Functional groups for both natural and agricultural habitat included primary producers, primary, secondary, and higher-level consumer groups, (Figure 2.4), as I describe below.

Primary Producers

Irrespective of habitat, C_3 plants and C_4 plants showed $\delta^{13}C$ values that reflected the characteristic differences between them; that is, C_3 plants were depleted, and C_4 plants were more enriched (Figure 2.4). C_4 plants had greater $\delta^{15}N$ values than C_3 plants, and C_3 plants tended to be more enriched in $\delta^{15}N$ in agricultural habitats (Figure 2.4, Table 2.1).

Primary Consumers

Primary consumers included black-tailed jackrabbits, rodents, and invertebrate herbivores, such as crickets and grasshoppers (Family Acrididae); these animals are typically herbivores or granivores. $\delta^{15}N$ and $\delta^{13}C$ for primary consumers were $7.91 \pm 0.16‰$ and $-22.12 \pm 0.29‰$ ($n = 118$ for each isotope), respectively. Rodents and invertebrates that are primary consumers had $\delta^{13}C$ and $\delta^{15}N$ values that were similar in both agricultural and natural habitat (Figure 2.4). $\delta^{13}C$ values suggest that C_3 plants formed the base of the food web for rodents and invertebrate herbivores. In contrast, $\delta^{13}C$ for black-tailed jackrabbits differed between habitats. Rabbits in agricultural habitats were more depleted in $\delta^{13}C$ than all other primary consumers. In fact, they were the most depleted in $\delta^{13}C$ and the most similar to the C_3 plants of all animal species that I analyzed (Figure 2.4).

The horned larks that I sampled from agricultural habitat had $\delta^{15}N$ and $\delta^{13}C$ values similar to primary consumers. However, larks from natural habitat had much higher $\delta^{15}N$ and were much more enriched in $\delta^{13}C$. Within natural habitat, lark $\delta^{13}C$ values indicated a relatively heavier reliance on C_4 plants. Values of $\delta^{15}N$ for larks in natural areas were more similar to burrowing owls and other secondary consumers than to larks in agricultural areas (Figure 2.4).

Secondary Consumers

There were 13 species that I classified as secondary or higher-level consumers and whose putative diet included primarily animals (Table 2.1). The $\delta^{15}N$ average for secondary consumers, excluding burrowing owls, was $10.97 \pm 0.21‰$ ($n = 63$). I divided this large group into two sub-groups, secondary and higher-level consumers, based on relative trophic position as established by $\delta^{15}N$ values (Figure 2.4, Table 1).

Burrowing owls and four species of reptile had similar $\delta^{15}N$ values and constituted the lower of the two groups of predators in the food web (Table 2.1, Figure 2.4). $\delta^{13}C$ values indicated that primarily C_3 plants formed the base of the food web for secondary consumers. However, burrowing owls were more enriched in $\delta^{13}C$ than other secondary and higher-level consumers (Figure 2.4).

Mammalian predators (American badgers and coyotes) and secondary invertebrates, including scorpions and spiders, had among the highest $\delta^{15}N$ values (Figure 2.4); thus, these consumers were near the top of this food web and comprised the group of higher-level consumers. Woodhouse's toads were only sampled in agricultural habitat but had the highest $\delta^{15}N$ values (Figure 2.4). As with primary consumers and the

previously described secondary consumers, $\delta^{13}C$ values indicated that primarily C_3 plants formed the base of the food web for this group of higher-level consumers (Figure 2.4).

Discussion

Although burrowing owls are characterized as generalist predators, location, habitat, and season can cause differences in diet among burrowing owls (Marti 1974, York et al. 2002, Moulton et al. 2005, Poulin and Todd 2006, Littles et al. 2007, Williford et al. 2009). Poulin and Todd (2006) and York et al. (2002) found sex-based differences in owl foraging behavior and owl diet, respectively. Few studies have investigated trophic relationships among burrowing owl nestlings and adults. Fewer still have examined what plants form the base of the food webs of burrowing owls. Isotopic values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) can be used to elucidate dietary differences among habitats and among species. Additionally, isotopes are useful for comparisons of diet among age classes and sexes within a single species. Hobson et al. (2002) found trophic level differences among seabird species living on two different islands in Canada. Black-legged kittiwakes (*Rissa tridactyla*) and thick-billed murres (*Uria lomvia*) nesting on Hakluyt Island occupied a lower trophic level (based on decreased $\delta^{15}N$ values) than birds of the same species nesting on Coburg Island. Hakluyt and Cobug islands are located on either side of the North Water Polynya in northern Baffin Bay. Water around Hakluyt Island warms earlier in the year and may have larger invertebrate populations as compared to Coburg Island. In this aquatic ecosystem, invertebrate prey have lower $\delta^{15}N$ values than the preferred prey, Arctic cod (*Boreogadus saida*). Stable isotopes analyses helped to identify that populations of kittiwakes and murres nesting on two nearby islands occupy different trophic levels (Hobson et al. 2002).

Similarly, Alisauskas and Hobson (1993) examined dietary habits of lesser snow geese (*Chen caerulescens caerulescens*) wintering in three different habitats: coastal marsh, rice agriculture, and corn agriculture. While geese could not be assigned to a specific habitat with 100% confidence, Alisauskas and Hobson argued that geese wintering in rice fields were more enriched in ^{15}N than geese in other habitats. Geese in rice fields were also consuming weed seeds, and these weeds seeds had among the highest $\delta^{15}N$ values of all plants sampled in their study. Thus, geese could be linked to a specific wintering habitat based on stable isotope analysis of the geese and the plant species available for consumption in each habitat.

I used stable isotopes analysis of ^{13}C and ^{15}N to investigate burrowing owl trophic position in agricultural and natural habitats in the NCA and examined trophic relationships of a community of plants and animals in both habitats. Burrowing owls in natural habitat generally had higher $\delta^{15}N$ values than owls nesting in agricultural habitat. A difference in owl diet, which potentially included more Ord's kangaroo rats (*Dipodomys ordii*), scorpions and spiders and fewer montane voles and crickets, may explain elevated $\delta^{15}N$ values for burrowing owls in natural habitat. Furthermore, as adults in natural areas had higher $\delta^{15}N$ values than nestlings, it appears that adult owls consumed different prey than they used to provision nestlings. Nestling and adult burrowing owls had $\delta^{13}C$ values that differed only slightly, but $\delta^{13}C$ values indicated that C_3 plants formed the base of food webs in both natural and agricultural habitats. Overall, my results suggest the food webs in both natural and agricultural habitats within s. Idaho were similar and contained herbivorous, omnivorous, and carnivorous species. The

majority of species that I sampled from both habitats held equivalent trophic positions in each habitat.

Food Habits: Differences Between Habitats and Among Burrowing Owls

As $\delta^{13}C$ did not differ between habitats for burrowing owls, owls nesting in agricultural and natural habitats were part of a food web that was based on both C_3 and C_4 plants. Correspondingly, the burrowing owl prey species that I sampled from both habitats reflected primarily C_3 components in their $\delta^{13}C$ values. However, both C_3 and C_4 plants were common in natural habitat and areas adjacent to agricultural fields in my study. There were, however, group differences. Nestlings had slightly but significantly more depleted $\delta^{13}C$ than both males and females. Such a result could occur if adults did not provision nestlings with the same diet as they consumed. Analysis of ^{13}C and ^{15}N in seabirds found differences in diet between adults and young of the same species in some populations (Hobson et al. 2002, Wilson et al. 2004), so this pattern of difference between parental and self-care is not unusual.

The trend toward higher $\delta^{15}N$ in natural habitat was consistent with my prediction in that burrowing owls in natural areas may have consumed a larger proportion of scorpions and spiders and fewer crickets in their diet, similar to the results Moulton et al. (2005) reported. Crickets are small, nocturnal herbivores. They were abundant in and around agricultural fields but were scarce in natural areas (pers. observ.). In addition, crickets had the second lowest $\delta^{15}N$ value of all animal species I sampled (Table 2.1). Scorpions and spiders are carnivores that had enriched $\delta^{15}N$ values (Table 2.1). Therefore, burrowing owls whose diet contained more spiders and scorpions in natural

habitats would have higher $\delta^{15}N$ values than owls eating an abundance of crickets in agricultural areas.

Possible differences in rodent prey are another factor that may have contributed to differences in $\delta^{15}N$ for burrowing owls between habitats. Montane voles were common prey items that I found in owl nests within agricultural habitat. These voles had lower $\delta^{15}N$ than all of the other species of rodents irrespective of habitat (see Table 2.1). While I obtained Ord's kangaroo rats from owl nests in both habitats, they were available for collection from more nests in natural habitat. Kangaroo rats from natural habitat had higher $\delta^{15}N$ values than rats from agricultural habitat (Table 2.1). Moreover, Moulton et al. (2005) found different rodent species accounted for approximately 20% of burrowing owl diet by biomass in each habitat; montane voles were proportionately more important in agricultural habitat, whereas kangaroo rats predominated in natural habitat (Figure 2.1). Therefore, it is possible that the burrowing owl $\delta^{15}N$ values I obtained reflect such diet differences relative to voles and kangaroo rats between habitats. Hobson et al. (2002) also found differences in $\delta^{15}N$ values of populations of seabirds nesting on two islands in Baffin Bay, Canada. They speculated diet differences, which included an increase of herbivorous invertebrate prey and a decrease of carnivorous Arctic cod in seabird diet, led to lower $\delta^{15}N$ values of birds nesting on the islands. Lavin et al. (2003) investigated red fox (*Vulpes vulpes*) diet between urban and agricultural habitats and in relation to coyote occurrence. Foxes in urban areas had lower $\delta^{15}N$ values than foxes in agricultural areas. Lavin et al. (2003) hypothesized that intensely farmed agricultural areas may hold fewer herbivorous prey, such as rabbits, and that foxes in agricultural areas may have higher $\delta^{15}N$ values because of the consumption of a wider variety of prey,

which is likely to contain herbivores, omnivores, and carnivores. Burrowing owls do inhabit areas of intensive agriculture where irrigation practices make the land inhospitable to mammals (e.g., York et al. 2002), but this was not the case in my study area as only about 5% of the NCA is irrigated agriculture, and these lands frequently harbor suitable prey for owls (Moulton et al. 2005, 2006).

Adult burrowing owls tended to be more enriched for $\delta^{15}N$ than nestlings in both natural and agricultural habitat; this suggests that they occupied a relatively higher trophic position than nestlings. Adult males in natural habitat were also more enriched than females. Foraging theory predicts that adults should select higher quality prey for offspring provisioning. Furthermore, animals that are single prey loaders are likely to deliver large prey items to their young, while maintaining themselves on a much broader range of prey sizes (Newton 1979, Orians and Pearson 1979, Rudolph 1982, Sonerud 1992, Davoren and Burger 1999). Wilson et al. (2004) found common guillemot (*Uria aalge*) adults consume smaller fish, while they deliver larger fish to the nest site to be consumed by guillemot young. Hobson et al. (2002) found black-legged kittiwake and thick-billed murre adults were selectively feeding fish to their young while consuming more invertebrates themselves. Adult breeding dippers (*Cinclus cinclus cinclus*) consume smaller prey than nestlings (Ormerod 1985). Chiu et al. (2009) suggest that while adult brown dippers (*Cinclus pallasii*) may consume their prey when captured, they carry larger prey items to compensate for the flight costs between foraging sites and the nest.

Birds of prey that are central place foragers often eat smaller prey items at the capture site and transport large items back to the nest site (Newton 1979, Rudolph 1982,

Sonerud 1992). Thus, it is possible that adult burrowing owls, especially males, consumed small prey items at the capture site and delivered the larger prey items to the nest site. Crickets were likely the smaller prey items for owls in agricultural areas, while scorpions and spiders may have been in natural habitat. Such a pattern of foraging behavior could have enriched $\delta^{15}N$ values for adults in natural habitat.

Finally, male burrowing owls that nested in natural areas were the most enriched in $\delta^{15}N$ of any group of owls in my study. Poulin and Todd (2006) reported that male burrowing owls were crepuscular in their foraging whereas females were more likely to forage diurnally for insects. Male owls may move up to 600 m from the nest site in search of food. As a consequence, they likely encounter a wider variety of food items and have a broader array of search images than females, who spend more time near the nest incubating and brooding young and therefore may forage nearer the nest more frequently (Haug et al. 1993, York et al. 2002). Male burrowing owls therefore may have increased $\delta^{15}N$ values when compared to the female and nestlings. However, I did not see this pattern in both habitat types. Moreover, in agricultural areas, males were relatively depleted in $\delta^{15}N$ as compared to females. This shift may be a result of male owls in agricultural areas foraging closer to the nest site than males in natural habitat. Moulton et al. (2005, 2006) reported burrowing owls may nest near agriculture because of increased availability of prey. Rosenberg and Haley (2004) suggest, in some cases, agricultural fields may provide quality foraging habitat for burrowing owls. Conversely, male owls in natural habitat may have to forage farther from the nest to find food. While agricultural fields are primarily a monoculture, owls foraging in natural habitat likely encounter a more varied landscape that harbors different prey items, including small

omnivores or carnivores that adult owls consume at the capture site rather than deliver to the nest site. Thus, a combination of increased prey in agricultural areas and increased habitat variation in natural areas may account for different $\delta^{15}N$ values that I observed in male burrowing owls.

Establish Food Webs Using Stable Isotopes Analysis

To further understand the ecology of burrowing owls, I also investigated food web relationships for broad taxonomic groups of plants and animals within agricultural and natural habitats using stable isotopes analysis of carbon and nitrogen. Differences in habitat and land use may cause trophic level changes among animals living in s. Idaho. Landscape scale conversion of native shrub-steppe habitat to disturbed grassland has increased fire frequency and changed much of the habitat in the NCA (USDI 2008). Within the NCA, burrowing owls nest near irrigated agricultural fields, in grazed areas, and in more natural habitat. Irrigated agriculture may impact soil depth, ground moisture levels, plant communities, and the amount of human disturbance to an area, in addition to the potential changes caused by use of fertilizers and pesticides.

Annual natural precipitation for my study area averages approximately 12 cm during the burrowing owl breeding season (N.O.A.A. 2002). Alfalfa, the main crop grown in the NCA, requires 1 - 5 cm of additional water per week depending on ambient temperature, wind and humidity (Bauder 1997). Thus, agricultural habitat receives more water than natural habitat. Although some plant and animal species were sampled from only natural or agricultural habitat, I found increased water in agricultural habitat did not appear to drive great changes in the trophic relationships among species. Species

sampled from both natural and agricultural habitats have similar isotope values and therefore occupied similar trophic positions in both habitats.

Nitrogen-based fertilizers and other agricultural enhancements have artificially increased soil nitrogen for some agricultural ecosystems (Kelly 2000, Post 2002). Isotope studies indicate it is important to look at base levels of $\delta^{15}N$ and $\delta^{13}C$ when comparing different habitats to ensure isotope values reflected in consumers are not an artifact of different values at the base of the food web (Cabana and Rasmussen 1994, 1996, Post 2002). In my study, $\delta^{15}N$ values from plants in agricultural areas were generally greater than plants from natural habitat. However, of the five plant species I sampled in both natural and agricultural habitats, two had higher $\delta^{15}N$ levels within natural habitats. Therefore, if soil nitrogen enrichment were occurring, it was not in a regular or consistently detectable fashion in the areas I sampled for my study.

In addition to enriching soils with fertilizers, agriculture may change soil depth, add pesticides to the system, and increase the amount of human activity. While I did not investigate changes of soil depth or use of pesticides, agricultural habitat was proximal to paved roadways, and farm personnel and their vehicles were common in such areas. Dirt, two-track roads occurred in natural habitat; however, I encountered vehicles far less frequently in natural areas than in agricultural habitat. Despite such potential differences in soils, pesticides, and human activity between natural and agricultural habitat, food webs for both habitats were similar, and I was able to categorize species into functional groups, including primary producers, and primary, secondary, and higher-level consumers for each habitat.

Primary producer composition (i.e., plant species) surrounding agricultural fields was reasonably similar to plants that occurred in natural habitat, although the presence of sagebrush and kochia (*Kochia scoparia*) were two exceptions. Sagebrush uncommonly grew in agricultural areas, whereas kochia thrived in or near irrigated agricultural areas (pers. observ.). Both habitats contained plant species that used C_3 or C_4 photosynthesis; thus, food webs in natural and agricultural habitats both had the potential to be based on C_3 and C_4 plants. The animal species that I sampled in both habitats had $\delta^{13}C$ values reflective of primarily C_3 plant input in their diets. Cerling et al. (2003) reported dietary preferences for 37 species of African bovids and used $\delta^{13}C$ to document dietary preferences for C_3 browse plants or C_4 grasses. They found $\delta^{13}C$ values could be used to provide a quantitative measure of C_4 plants in bovid diet. Herrera et al. (2003) investigated trophic partitioning of 23 birds species in southeastern Mexico and found most species fed on C_3 based foods. Similarly, C_3 plants were the main source of carbon input for an alpine meadow ecosystem in the Tibetan Plateau (Yi et al. 2006). However, in both of these studies, isotope analysis of C_4 plants was not reported. In habitats that included a mixture of C_3 and C_4 plants such as in s. Idaho, it is possible that the basis of the animals' diets is a combination of C_3 and C_4 plants.

Primary consumers such as rodents, crickets, and grasshoppers had $\delta^{13}C$ values that were similar in both natural and agricultural habitat and reflected primarily C_3 plants in their diets. Black-tailed jackrabbits that I sampled from agricultural areas were more depleted in $\delta^{13}C$ than all other species, which indicated that they consumed more C_3 plants than other herbivores. Alfalfa, the dominant agricultural crop in the NCA, is a C_3 plant and had the most depleted $\delta^{13}C$ value of any species I analyzed (Table 2.1).

Therefore, it is possible that rabbits living in agricultural areas were closely tied to alfalfa crop fields. Jackrabbit diet is highly variable depending on what forage species are available (Johnson and Anderson 1984). Jackrabbits frequently select plants that can fulfill their water needs and are known to damage agricultural crops including alfalfa (Best 1996). Knick and Dyer (1997) found that black-tailed jackrabbits in the NCA were more likely to use land that included agriculture but only during winter months or when rabbit populations were below average densities.

Primary consumers including jackrabbits, rodents, crickets, and grasshoppers had the lowest $\delta^{15}N$ levels of the animals I sampled. Yi et al. (2006) also reported voles, other rodents, and rabbits to have the lowest $\delta^{15}N$ values of animals in their study of trophic relationships in an alpine meadow in the Tibetan Plateau. Primary consumers in my study were enriched in $\delta^{15}N$ by 2.5‰ as compared to plants. This difference is consistent with literature values of 2 - 4‰ for nitrogen enrichment and indicated an increase of one trophic level between primary producers and primary consumers (Minagawa and Wada 1984, Rundel et al. 1989, Hobson 1990, Hobson and Clark 1992, Hobson et al. 1994).

Horned larks had remarkable $\delta^{13}C$ and $\delta^{15}N$ values. These small passerine birds have omnivorous food habits. As in many other passerines, during the breeding season adults consume a preponderance of seeds (73%), while they feed young almost exclusively insects (Beason 1995). I found that horned larks that lived in agricultural habitat had similar $\delta^{13}C$ and $\delta^{15}N$ values as the primary consumer group (rodents, crickets, and grasshoppers). Horned larks from natural areas, however, were enriched in $\delta^{13}C$ and $\delta^{15}N$ (Figure 2.4, Table 2.1). Lark $\delta^{13}C$ values were more similar to C_4 plants;

however, all of the C_4 plants I sampled (Russian thistle, halogeton, and kochia) were located in both agricultural and natural habitats. Therefore, larks in natural habitat may have relied more heavily on C_4 plants as a food source. Horned larks in natural areas boasted a $\delta^{15}N$ value comparable to burrowing owls and other generalist predators. Although it is not clear what caused this difference, it may be that larks who consumed C_4 plant species also had enriched $\delta^{15}N$, as C_4 plants were more enriched in $\delta^{15}N$ than C_3 plants. Another possible explanation is my sample of larks in natural areas may have included hatch-year birds that were recently fed primary and secondary consumer insects and thus had elevated $\delta^{15}N$ values, as a diet consisting of animals rather than plants would be enriched in $\delta^{15}N$. However, Yi et al. (2006) reported a lower $\delta^{15}N$ value for nestling horned larks than for adults in an alpine meadow ecosystem; thus lark diet may fluctuate greatly with season and location.

There were many species from a broad range of taxa that qualified as secondary consumers. Thus, I divided the category into two groups: secondary and higher-level consumers. I considered burrowing owls and reptiles as secondary consumers because they eat a wide variety of small animals, including one another. Burrowing owls from both agricultural and natural habitats were relatively enriched in $\delta^{13}C$ compared to all other secondary consumers. For owls nesting within agricultural habitat, this was somewhat surprising as montane voles, which were common in burrowing owl diet within agricultural habitat, were relatively depleted in $\delta^{13}C$ (Table 2.1). The literature shows burrowing owls are generalist predators with a broad diet (Marti 1974, York et al. 2002, Moulton et al. 2005, Poulin and Todd 2006, Littles et al. 2007, Williford et al. 2009). My results were consistent with the literature, and $\delta^{15}N$ values among burrowing

owls suggested that they were within the same relative trophic position in the food web for both natural and agricultural habitats.

I considered mammalian predators, including American badgers and coyotes, to be in the higher-level consumer category because they eat both primary and secondary consumers, and each has few natural predators. Consistent with this classification, mammalian predators were more enriched in $\delta^{15}N$ than burrowing owls and reptiles. Although the difference was not sufficient to indicate two distinct trophic levels, it confirmed that badgers and coyotes were positioned relatively higher in natural and agricultural food webs than both burrowing owls and reptiles (Figure 2.4). Azevedo et al. (2006) summarized the diet of prairie carnivores, including badgers and coyotes, and found badgers regularly consume a wide variety of rodents and supplement their diet to a lesser extent with eggs, amphibians, birds, and wheat seeds. Coyotes rely more heavily on deer (*Odocoileus* spp.) and birds, while they consumed rabbits, eggs, wheat seeds, and insects less often. Thus, my finding indicating that badgers and coyotes are higher-level consumers in both agricultural and natural habitats was consistent with the literature based on traditional approaches to food habits analysis for these two species.

Woodhouse's toads presented the highest $\delta^{15}N$ values of any organism in my study. They are nocturnal foragers that eat a variety of small terrestrial invertebrates including isopods, scorpions, mites, spiders, beetles, and ants (Sullivan 2005). These amphibians commonly occur in agricultural areas and the backwaters of the Snake River, Idaho (Idaho Digital Atlas 2010). Moulton et al. (2005) noted that toads were only recorded as burrowing owl prey within agricultural habitat. Indeed, I was only able to collect toad tissue samples from agricultural habitat. I collected other secondary

invertebrates, including scorpions and spiders, from both natural and agricultural habitat, and I also considered these species as higher-level consumers based on their enriched $\delta^{15}N$ values. It was rather surprising that toads, spiders, and scorpions held slightly higher positions in the food web compared to burrowing owls. Therefore, stable isotopes analysis can help delineate where predators fit within a food web despite a researcher's preconceived notions based on traditional food habit studies.

Conclusions

Stable isotopes analysis provides a picture of an animal's diet over time and can be used to establish its place in a food web. This is especially true for insectivorous raptors, where traditional pellet analysis to establish diet can be misleading (Marti 1974, Marti et al. 2007). I used analysis of $\delta^{13}C$ and $\delta^{15}N$ to gain new information on burrowing owl food habits, food webs, and ecosystem dynamics and compared natural and agricultural habitats. I found that burrowing owls nesting within natural habitat fed on slightly different prey than owls in agricultural habitat and that adult owls may be eating small prey at the capture site and delivering a different diet to nestlings. I also found that both habitats had a suite of primary producers, and primary, secondary, and higher-level consumers. The introduction of agriculture into a small proportion of the NCA did not alter the trophic position of burrowing owls, although the suite of species in each food web differed slightly.

Figure 2.1. Burrowing owl diet delineated by habitat (revised from Moulton et al. 2005).

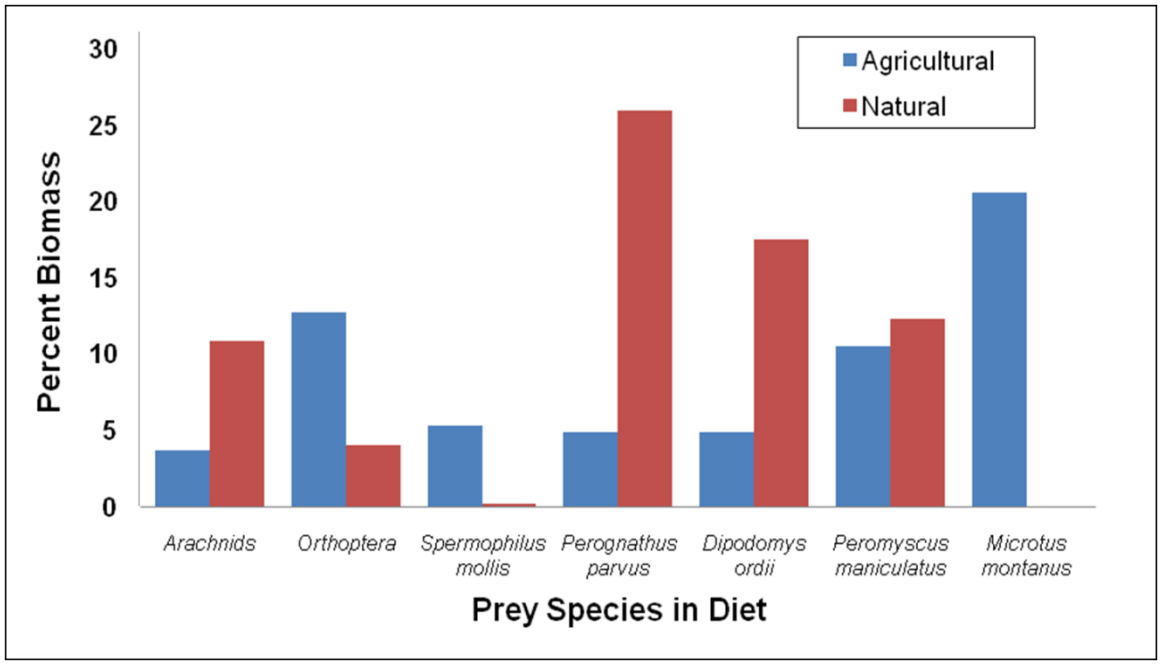


Figure 2.2. Burrowing owl δ^{13}Carbon values (mean ± SE). Values not sharing the same letter differ significantly.

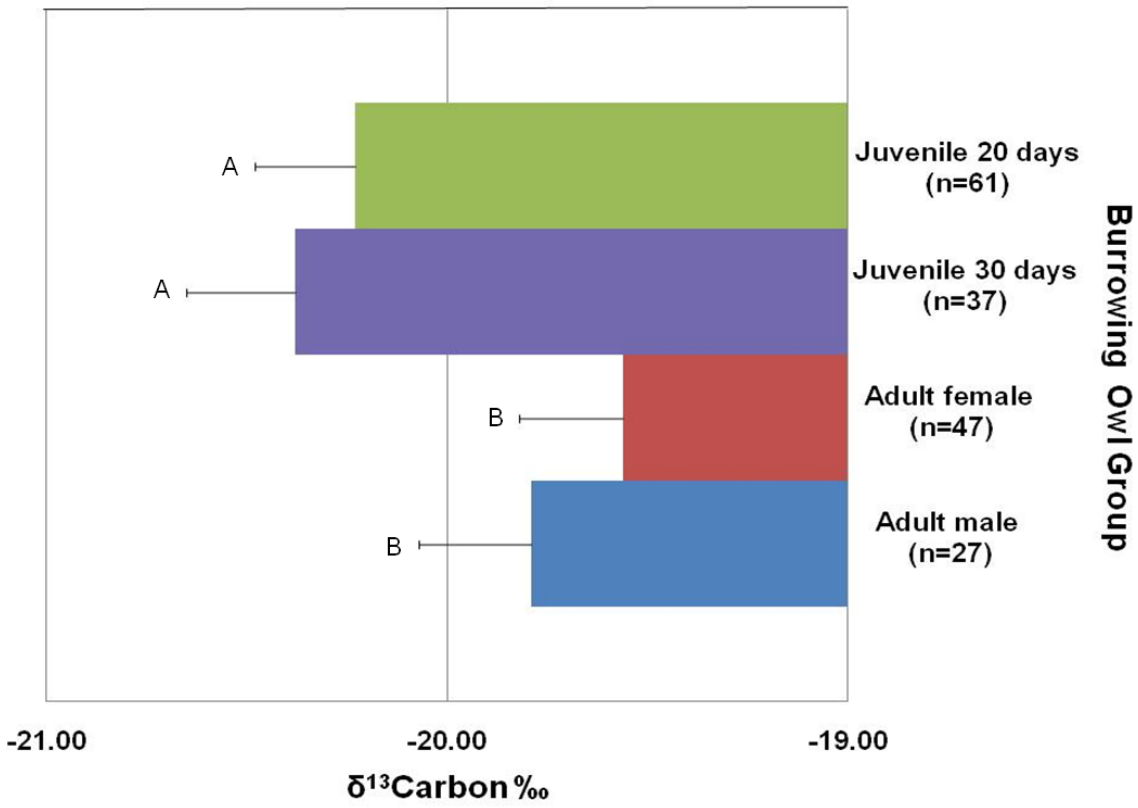


Figure 2.3. Burrowing owl δ^{15}Nitrogen values (mean ± SE). Values not sharing the same letter are significantly different.

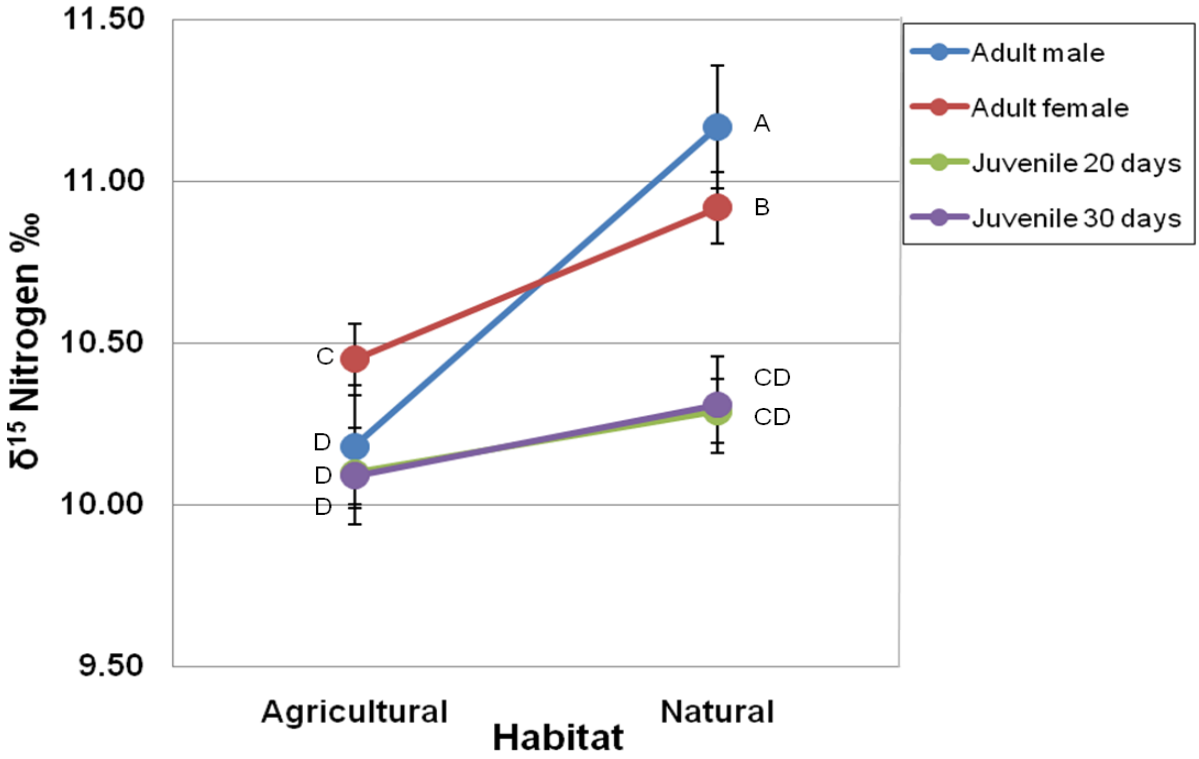


Figure 2.4. δ^{15}Nitrogen and δ^{13}Carbon isotope values for the presumptive food web of burrowing owls in natural and agricultural habitats. Mean ± SE are listed for each group or species (see text). Triangles represent samples from natural habitat, and squares represent samples from agricultural habitat. Primary Producers - green circles; Primary Consumers - red circle; Secondary Consumers - blue circle; Higher-level consumers - black circle.

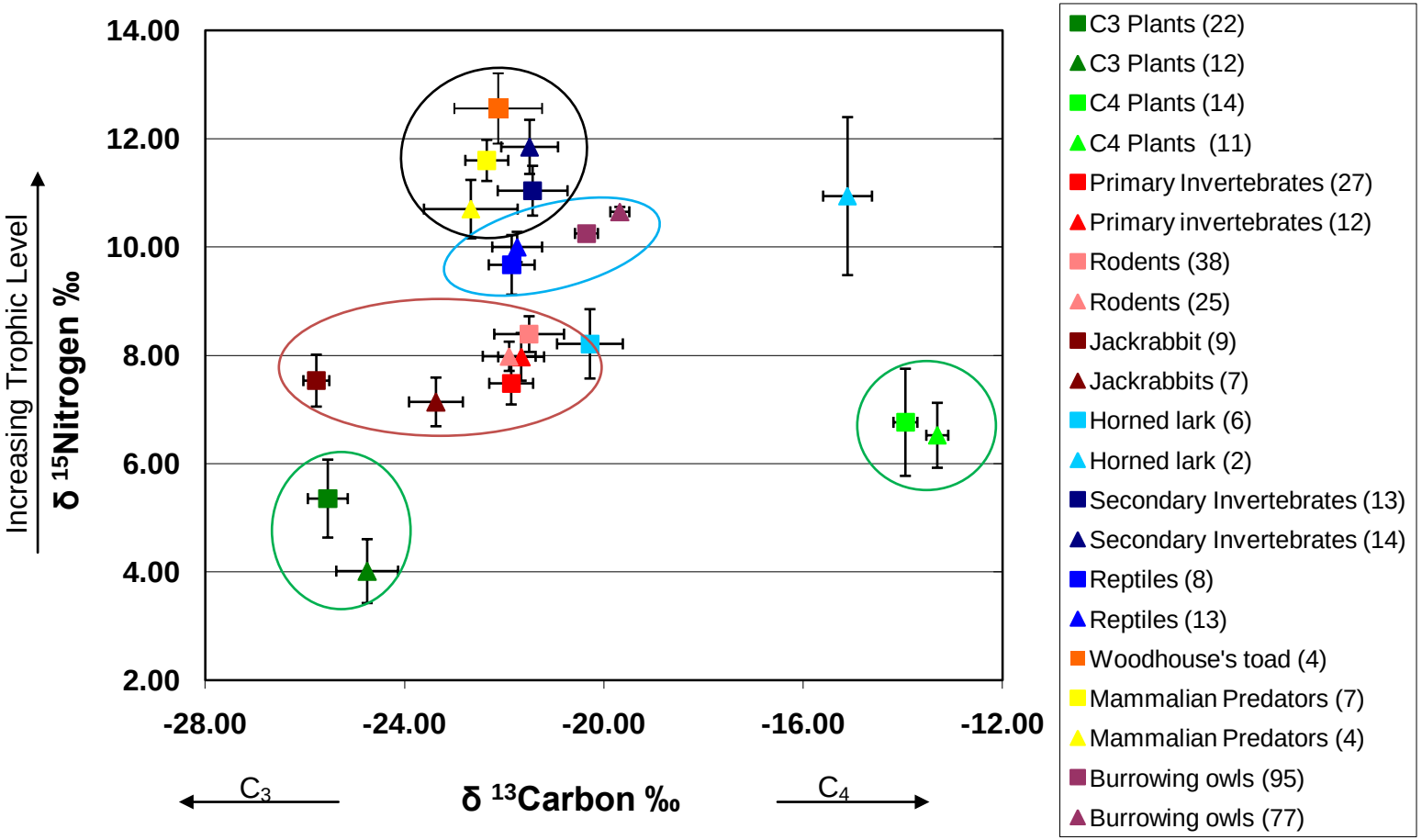


Table 2.1. Species sampled in both natural and agricultural habitats for stable isotopes analysis. Mean ± SE are presented for each isotope within each habitat. Group headings or species listed in Figure 2.4 are in grey, and species below each group heading constitutes group members.

Common Name	Scientific Name	Agricultural Habitat			Natural Habitat		
		N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$
C_3 Plants							
Alfalfa	*Medicago sativa*	7	-27.49 ± 0.44	5.92 ± 0.91			
Big sagebrush	*Artemisia tridentate*				3	-24.09 ± 0.34	2.39 ± 0.66
Cheatgrass	*Bromus tectorum*	6	-24.89 ± 0.43	4.11 ± 0.87	3	-23.06 ± 0.60	2.72 ± 1.03
Clasping pepperweed	*Lepidium perfoliatum*	1	-25.76	3.54			
Oats	*Avena sativa*	1	-26.09	13.25			
Globemallow	*Sphaeralcea* spp.				2	-27.95 ± 1.17	4.96 ± 0.21
Tumble mustard	*Sisymbrium altissimum*	7	-24.03 ± 0.45	4.98 ± 1.44	4	-24.93 ± 1.09	5.71 ± 0.96
C_4 Plants							
Halogeton	*Halogeton glomeratus*	4	-12.11 ± 0.37	5.78 ± 0.81	5	-12.95 ± 0.33	8.05 ± 0.56
Kochia	*Kochia scoparia*	5	-14.62 ± 0.27	8.51 ± 2.15	2	-13.55 ± 0.34	6.70 ± 1.27
Russian thistle	*Salsola* spp.	5	-13.96 ± 0.32	5.77 ± 1.64	4	-13.65 ± 0.37	4.51 ± 0.39
Primary Invertebrates							
Cricket	*Gryllus* spp.	7	-22.45 ± 0.67	6.91 ± 0.85			
Darkling beetle	*Eleodes* spp.	7	-21.19 ± 0.61	8.98 ± 0.29	7	-21.43 ± 0.28	8.83 ± 0.43
Grasshopper	Family Acrididae	6	-21.79 ± 0.70	5.82 ± 0.79	5	-21.98 ± 1.08	6.76 ± 0.53
Lepidoptera larvae	Order Lepidoptera	2	-22.91 ± 0.54	7.18 ± 1.7			
Moth	Order Lepidoptera	5	-21.64 ± 2.00	8.29 ± 0.69			

Common Name	Scientific Name	Agricultural Habitat			Natural Habitat		
		N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$
Rodents							
Deer mouse	*Peromyscus maniculatus*	11	-16.76 ± 1.14	10.49 ± 0.54	1	-20.45	8.28
Great Basin pocket mouse	*Perognathus parvus*	7	-20.64 ± 0.92	7.99 ± 0.48	3	-20.61 ± 3.07	8.48 ± 0.99
Montane vole	*Microtus montanus*	11	-25.93 ± 0.36	7.15 ± 0.45			
Ord's kangaroo rat	*Dipodomys ordii*	5	-22.21 ± 0.50	7.38 ± 0.50	14	-20.98 ± 0.44	8.00 ± 0.42
Piute ground squirrel	*Spermophilus mollis*	4	-23.00 ± 0.96	8.01 ± 0.86	7	-24.49 ± 0.55	7.68 ± 0.28
Black-tailed jackrabbit	*Lepus californicus*	9	-25.77 ± 0.26	7.53 ± 0.48	7	-23.37 ± 0.54	7.14 ± 0.45
Horned lark	*Eremophila alpestris*	6	-20.28 ± 0.66	8.21 ± 0.64	2	-15.11 ± 0.49	10.94 ± 1.46
Secondary Invertebrates							
Common desert centipede	*Scolopendra polymorpha*	2	-20.72 ± 0.64	9.84 ± 2.05	1	-24.14	11.37
Carrion beetle	*Nicrophorus* spp.	5	-23.73 ± 0.75	12.01 ± 0.64			
Desert hairy scorpion	*Hadrurus spadix*	3	-20.22 ± 1.54	10.48 ± 1.11	8	-21.04 ± 0.89	10.86 ± 0.62
Solifugid	Family Eremobatidae	3	-19.31 ± 0.83	10.78 ± 0.30	1	-22.32	14.28
Trapdoor spider	Infraorder Mygalomorphae				4	-21.52 ± 0.71	13.36 ± 0.36
Reptiles							
Desert horned lizard	*Phrynosoma platyrhinos*				1	-19.71	11.3
Gopher snake	*Pituophis catenifer*	7	-22.14 ± 0.42	9.41 ± 0.56	6	-22.85 ± 0.62	9.73 ± 0.48
Racer	*Coluber constrictor*				3	-21.76 ± 0.63	9.96 ± 0.30
Side-blotched lizard	*Uta stansburiana*	1	-19.88	11.51	3	-20.17 ± 1.00	10.18 ± 0.61
Woodhouse's toad	*Bufo woodhousii*	4	-22.12 ± 0.88	12.56 ± 0.65			
Mammalian Predators							
American badger	*Taxidea taxus*	5	-22.77± 0.74	11.37±0.52	4	-22.68 ± 0.94	10.70 ± 0.54
Coyote	*Canis latrans*	2	-21.29 ± 0.52	12.17 ± 0.44			

Literature Cited

Alisauskas, R.T. and K.A. Hobson. 1993. Determination of lesser snow goose diets and winter distribution using stable isotope analysis. Journal of Wildlife Management 57:49-54.

Azevedo, F.C.C., V. Lester, W. Gorsuch, S. Larivière, A.J. Wirsing, and D.L. Murray. 2006. Dietary breadth and overlap among five sympatric prairie carnivores. Journal of Zoology 269:127-135.

Barclay, J.H. 2008. A simple artificial burrow design for burrowing owls. Journal of Raptor Research 42:53-57.

Bartok, N.D. and C.J. Conway. 2010. Factors affecting the presence of nesting burrowing owls in an agricultural landscape. Journal of Raptor Research 44:286-293.

Bauder, J. 1997. Irrigated alfalfa production agronomy notes. No. 103. Montana State University Extension. http://agnotes.org/AgNotes/docs/103.htm.

Beason, R.C. 1995. Hornes Lark (*Eremophila alpestris*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/195.

Belthoff, J.R. and B.W. Smith. 2003. Patterns of artificial burrow occupancy and reuse by burrowing owls in Idaho. Wildlife Society Bulletin 31:138-144.

Best, T.L. 1996. *Lepus californicus*. Mammalian Species. No. 530.

Brown, B.A., J.O. Whitaker, T.W. French, and C. Maser. 1986. Note on food habits of the screech owl and the burrowing owl of southeastern Oregon. Great Basin Naturalist 46:421-426.

Cabana, G. and J.B. Rasmussen. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372:255-257.

Cabana, G. and J.B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences 93:10844-10847.

Carlson, C.A. 1985. Wildlife and agriculture: can they coexist? Journal of Soil and Water Conservation 40:263-266.

Cerling, T.E., J.M. Harris, and B.H. Passey. 2003. Diets of east African bovidae based on stable isotope analysis. Journal of Mammalogy 84:456-470.

Cherel, Y., K.A. Hobson, C. Guinet, and C. Vanpe. 2007. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. Journal of Animal Ecology 76:826-836.

Chiu, M.C., M.H. Kuo, C.S. Tzeng, C.H. Yang, C.C. Chen, and Y.H. Sun. 2009. Prey selection by breeding brown dippers *Cinclus pallasii* in a Taiwanese mountain stream. Zoological Studies 48:761-768.

Conway, C.J., V. Garcia, M.D. Smith, L.A. Ellis, and J.L. Whitney. 2006. Comparative demography of burrowing owls in agricultural and urban landscapes in southeastern Washington. Journal of Field Ornithology 77:280-290.

Davoren, G.K. and A.E. Burger. 1999. Differences in prey selection and behavior during self-feeding and chick provisioning in rhinoceros auklets. Animal Behaviour 58:853-863.

DeSante, D.F., E.D. Ruhlen, and D.K. Rosenberg. 2004. Density and abundance of burrowing owls in the agricultural matrix of the Imperial Valley, California. Studies in Avian Biology 27:116-119.

Evans Ogden, L.J., K.A. Hobson, D.B. Lank, and S. Bittman. 2005. Stable isotope analysis reveals that agricultural habitat provides an important dietary component for nonbreeding Dunlin. Avian Conservation and Ecology 1.3. http://www.ace-eco.org/vol1/iss1/art3/.

Fox, A.D., J. Madsen, H. Boyd, E. Kuijken, D.W. Norriss, I.M. Tombre, and D.A. Stroud. 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. Global Change Biology 11:881-893.

Fry, B. 2006. Stable Isotope Ecology. Springer, New York.

Gervais, J.A. and R.G. Anthony. 2003. Chronic organochlorine contaminants, environmental variability, and the demographics of a burrowing owl population. Ecological Applications 13:1250-1262.

Gervais, J.A., D.K. Rosenberg, D.M. Fry, L. Trulio, and K.K. Sturm. 2000. Burrowing owls and agricultural pesticides: evaluation of residues and risks for three populations in California, USA. Environmental Toxicology and Chemistry 19:337-343.

Gleason, R.S. and D.R. Johnson. 1985. Factors influencing nesting success of burrowing owls in southeastern Idaho. Great Basin Naturalist 45:81-84.

Goldstein, M.I. and T.J. Hibbitts. 2004. Summer roadside surveys in the western pampas of Argentina. Journal of Raptor Research 38:152-157.

Green, G.A. and R.G. Anthony. 1989. Nesting success and habitat relationships of burrowing owls in the Columbia Basin, Oregon. Condor 91:347-354.

Griebel, R.L. and J.A. Savidge. 2007. Factors influencing burrowing owl reproductive performance in contiguous shortgrass prairie. Journal of Raptor Research 41:212-221.

Hall, D.B., P.D. Greger, and J.R. Rosier. 2009. Regional and seasonal diet of the western burrowing owl in south central Nevada. Western North American Naturalist 69:1-8.

Haug, E.A. and L.W. Oliphant. 1990. Movements, activity patterns, and habitat use of burrowing owls in Saskatchewan. Journal of Wildlife Management 54:27-35.

Haug, E.A., B.A. Millsap, and M.S. Martell. 1993. Burrowing Owl (Athene *cunicularia*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/061doi:10.2173/bna.61.

Henny, C.J. and L.J. Blus. 1981. Artificial burrows provide new insight into burrowing owls nesting biology. Journal of Raptor Research 15:82-85.

Herrera, L.G., K.A. Hobson, M. Rodríguez, and P. Hernandez. 2003. Trophic partitioning in tropical rain forest birds: insights from stable isotope analysis. Oecologia 136:439-444.

Hironaka, M., M.A. Fosberg, and A.H. Winward. 1983. Sagebrush–grass habitat types of southern Idaho. Forest, Wildlife and Range Experiment Station, University of Idaho, Bulletin 35, Moscow, USA.

Hobson, K.A. 1990. Stable isotope analysis of marbled murrelets: evidence for freshwater feeding and determination of trophic level. Condor 92:897-903.

Hobson, K.A. and R.G. Clark. 1992. Assessing avian diets using stables isotopes I: turnover in ^{13}C in tissues. Condor 94:181-188.

Hobson, K.A., J.F. Piatt, and J. Pitocchelli. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786-798.

Hobson, K.A., G. Gilchrist, and K. Falk. 2002. Isotopic investigations of seabirds of the North Water Polynya: contrasting trophic relationships between the eastern and western sectors. Condor 104:1-11.

Hyodo, F., T. Matsumoto, Y. Takematsu, T. Kamoi, D. Fukuda, M. Nakagawa, and T. Itioka. 2010. The structure of a food web in a tropical rain forest in Malaysia based on carbon and nitrogen stable isotope ratios. Journal of Tropical Ecology 26:205-214.

Idaho Digital Atlas. 2010. *Bufo woodhousii* (Woodhouse's Toad). http://imnh.isu.edu/digitalatlas/bio/amph/main/amphmnfr.htm.

Inger, R. and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447-461.

JMP. 2009. Version 8.0.2, SAS Institute, Inc., Cary, NC.

Johnson, R.D. and J.E. Anderson. 1984. Diets of black-tailed jack rabbits in relation to population density and vegetation. Journal of Range Management 37:79-83.

Kaufman, K. 1996. Lives of North American Birds. Houghton Mifflin Company. New York.

Kelly, J. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1-27.

King, R.A. 1996. Post-fledging dispersal and behavioral ecology of burrowing owls in southwestern Idaho, M.S. Thesis, Boise State University, Idaho.

King, R.A. and J.R. Belthoff. 2001. Post-fledging dispersal of burrowing owls in southwestern Idaho: characterization of movements and use of satellite burrows. Condor 103:118-126.

Klute, D.S., L.W. Ayers, M.T. Green, W.H. Howe, S.L. Jones, J.A. Shaffer, S.R. Sheffield, and T.S. Zimmerman. 2003. Status assessment and conservation plan for the western burrowing owl in the United States. U.S. Department of Interior, Fish and Wildlife Service, Biol. Tech. Publ. FWS/BTP-R6001-2003, Washington, D.C., USA.

Knick, S.T. and D.L. Dyer. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. Journal of Wildlife Management 61:75-85.

Krapu, G.L., D.E. Facey, E.K. Fritzell, and D.H. Johnson. 1984. Habitat use by migrant sandhill cranes in Nebraska. Journal of Wildlife Management 48:407-417.

Lantz, S.J., C.J. Conway, and S.H. Anderson. 2007. Multiscale habitat selection by burrowing owls in black-tailed prairie dog colonies. Journal of Wildlife Management 71:2664-2672.

Lavin, S.R., T.R. Van Deelen, P.W. Brown, R.E. Warner, and S.H. Ambrose. 2003. Prey use by red foxes (*Vulpes vulpes*) in urban and rural areas of Illinois. Canadian Journal of Zoology 81:1070-1082.

Leptich, D.J. 1994. Agricultural development and its influence on raptors in southern Idaho. Northwest Science 68:167-171.

Littles, C.J., D. Williford, M.K. Skoruppa, M.C. Woodin, and G.C. Hickman. 2007. Diet of western burrowing owls wintering in southern Texas. Journal of Raptor Research 41:307-313.

Marti, C.D. 1974. Feeding ecology of four sympatric owls. Condor 76:45-61.

Marti, C.D., M. Bechard, and F.M. Jacksic. 2007. Raptor food habits studies. *In* Raptor Research and Management Techniques (D.M. Bird and K.L. Bildstein, eds.). Hancock House Publishers, Blaine, WA.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48:1135-1140.

Mizutani, H., M. Fukuda, and Y. Kabaya. 1992. ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. Ecology 73:1391-1395.

Moulton, C.E., R.S. Brady, and J.R. Belthoff. 2005. A comparison of breeding season food habits of burrowing owls nesting in agricultural and nonagricultural habitat in Idaho. Journal of Raptor Research 39:429-438.

Moulton, C.E., R.S. Brady, and J.R. Belthoff. 2006. Association between wildlife and agriculture: underlying mechanisms and implications in burrowing owls. Journal of Wildlife Management 70:708-716.

Mrykalo, R.J., M.M. Grigione, and R.J. Sarno. 2009. A comparison of available prey and diet of Florida burrowing owls in urban and rural environments: a first study. Condor 111:556-559.

Murphy, M.T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk 120:20-34.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, SD.

N.O.A.A. (National Oceanic and Atmospheric Administration). 2002. Divisional normals and standard deviations of temperature, precipitation, and heating and cooling degree days 1971-2000. Climatography of the United States No. 85.

O'Leary, M.H. 1988. Carbon isotopes in photosynthesis. BioScience 38:328-336.

Orians, G.H. and N.E. Pearson. 1979. On the theory of central place foraging. *In* Analysis of Ecological Systems (D.J. Horn, R.D. Mitchell, and G.R. Stairs, eds.). Ohio State University Press, Columbus, OH, p.154-177.

Ormerod, S.J. 1985. The diet of breeding dippers (*Cinclus cinclus*) and their nestlings in the catchment of the River Wye, mid-Wales: a preliminary study by fecal analysis. Ibis 127: 316-331.

Orth, P.B. and P.L. Kennedy. 2001. Do land-use patterns influence nest-site selection by burrowing owls (*Athene cunicularia hypugaea*) in northeastern Colorado? Canadian Journal of Zoology 79:1038-1045.

Plumpton, D.L. and R.S. Lutz. 1993. Prey selection and food habits of burrowing owls in Colorado. Great Basin Naturalist 53:299-304.

Post, D. 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83:703-718.

Poulin, R.G. and L.D. Todd. 2006. Sex and nest stage differences in the circadian foraging behaviors of nesting burrowing owls. Condor 108:856-864.

Poulin, R.G., L.D. Todd, K.M. Dohms, R.M. Brigham, and T.I. Wellicome. 2005. Factors associated with nest- and roost-burrow selection by burrowing owls (*Athene cunicularia*) on the Canadian prairies. Canadian Journal of Zoology 83:1373-1380.

Restani, M., J.M. Davies, and W.E. Newton. 2008. Importance of agricultural landscapes to nesting burrowing owls in the northern Great Plains, USA. Landscape Ecology 23:977-987.

Rich, T. 1986. Habitat and nest-site selection of burrowing owls in the sagebrush steppe of Idaho. Journal of Wildlife Management 50:548-555.

Rosenberg, D.K. and K.L. Haley. 2004. The ecology of burrowing owls in the agroecosystem of the Imperial Valley, California. Studies in Avian Biology 27:120-135.

Rudolph, S.G. 1982. Foraging strategies of American kestrels during breeding. Ecology 63:1268-1276.

Rundel, P.W., J.R. Ehleringer, and K.A. Nagy (eds.). 1989. Stable Isotopes in Ecological Research. Springer Verlag, New York.

Sharpe, P.B. and B. van Horne. 1998. Influence of habitat on behavior of Townsend's ground squirrels (*Spermophilus townsendii*). Journal of Mammalogy 79:906-918.

Smith, B.W. and J.R. Belthoff. 2001. Effects of nest dimensions on use of artificial burrow systems by burrowing owls. Journal of Wildlife Management 65:318-326.

Smith, M.D., C.J. Conway, and L.A. Ellis. 2005. Burrowing owl nesting productivity: a comparison between artificial and natural burrows on and off golf courses. Wildlife Society Bulletin 33:454-462.

Sonerud, G.A. 1992. Functional responses of birds of prey: biases due to the load-size effect in central place foragers. Oikos 63:223-232.

Sullivan, B.K. 2005. *Bufo woodhousii*. *In* Amphibian Declines: The Conservation Status of United States Species (M. Lannoo, ed.). Regents of the University of California, University of California Press.

Taylor, N.A. 2005. Burrowing owl offspring sex ratios: long-term trends and a test of the Trivers and Willard hypothesis. MS Thesis, Boise State University, Boise, ID.

Teyssèdre, A. and D. Couvet. 2007. Expected impact of agriculture expansion on the world avifauna. Comptes Rendus Biologies 330:247-254.

Tipton, H.C., V.J. Dreitz, and P.F. Doherty, Jr. 2008. Occupancy of mountain plover and burrowing owl in Colorado. Journal of Wildlife Management 72:1001-1006.

Todd, L.D., R.G. Poulin, T.I. Wellicome, and R.M. Brigham. 2003. Post-fledging survival of burrowing owls in Saskatchewan. Journal of Wildlife Management 67:512-519.

Trulio, L.A. 1995. Passive relocation: a method to preserve burrowing owls on disturbed sites. Journal of Field Ornithology 66:99-106.

Tyler, J.D. 1983. Notes on burrowing owl (*Athene cunicularia*) food habits in Oklahoma. Southwestern Naturalist 28:100-102.

U.S. Department of the Interior. 1996. Effects of military training and fire in the Snake River Birds of Prey National Conservation Area. BLM/IDARNG Research Project Final Report. U.S. Geological Survey, Biological Research Division, Snake River Field Station, Boise, Idaho, USA.

U.S. Department of the Interior. 2008. Snake River Birds of Prey National Conservation Area Resource Management Plan and Record of Decision. Bureau of Land Management Boise District Office, Idaho, USA.

Wellicome, T.I. 2005. Hatching asynchrony in burrowing owls is influenced by clutch size and hatching success but not by food. Oecologia 142:326-334.

Welty, J. 2010. Costs and benefits of variable nesting density in burrowing owls. M.S. Thesis, Boise State University, Boise, ID.

Williams, C.K., R.D. Applegate, R.S. Lutz, and D.H. Rusch. 2000. A comparison of raptor densities and habitat use in Kansas cropland and rangeland ecosystems. Journal of Raptor Research 34:203-209.

Williford, D.L., M.C. Woodin, M.K. Skoruppa, and G.C. Hickman. 2009. Rodents new to the diet of the western burrowing owl (*Athene cunicularia hypugaea*). Southwestern Naturalist 54:87-90.

Wilson, L.J., F. Daunt, and S. Wanless. 2004. Self-feeding and chick provisioning diet differ in the common guillemot *Uria aalge*. Ardea 92:197-207.

Yi, X., Y. Yang, and X. Zhang. 2006. Modeling trophic positions of the alpine meadow ecosystem combining stable carbon and nitrogen isotope ratios. Ecological Modelling 193:801-808.

York, M.M., D.K. Rosenberg, and K.K. Sturm. 2002. Diet and food-niche breadth of burrowing owls (*Athene cunicularia*) in the Imperial Valley, California. Western North American Naturalist 62:280-287.

CHAPTER 3: TROPHIC RELATIONSHIPS AMONG VERTEBRATE PREDATORS IN THE MORLEY NELSON SNAKE RIVER BIRDS OF PREY NATIONAL CONSERVATION AREA

Introduction

The Morley Nelson Snake River Birds of Prey National Conservation Area (NCA), located in southern Idaho, was established in 1993 by Congress (Public Law 103-64) for the conservation, protection, and enhancement of raptor populations and habitats (Sharpe and van Horne 1998). While the NCA has an array of mammalian predators, the diversity of avian predators and density of breeding raptors is unparalleled within North America. Sixteen raptor species regularly breed within the NCA and eight other species use the area for migration or wintering (USDI 1996, 2008). This rich diversity presents a unique opportunity to examine relationships among vertebrate predators that may use the same prey resources. Marti et al. (1993) examined the food habits of 17 vertebrate predators that reside within the NCA, including data that 19 primary researchers collected during 1971 to 1987. They investigated community structure of predators by analyzing trophic characteristics, including diet composition, dietary overlap, food-niche breath, and prey size. Diet overlap was greater for predators that forage during the same period of day than for predators that forage at different times. Prey items were from nine taxonomic classes, and mammalian prey constituted the majority of diet by biomass for all 17 species of vertebrate predators (Marti et al. 1993).

Food is often a limiting resource for animals, and the food an animal consumes will help shape its interactions with conspecifics and other species. Therefore, a predator's dietary needs contribute to community structure, and these dietary needs underlie trophic relationships among predators. Marti et al. (1993) defined four feeding guilds within the suite of vertebrate predators inhabiting the NCA (Figure 3.1). A ground squirrel-eating guild was formed by western rattlesnakes (*Crotalus viridis*), prairie falcons (*Falco mexicanus*), ferruginous hawks (*Buteo regalis*), red-tailed hawks (*Buteo jamaicensis*), and American badgers (*Taxidae taxus*), while golden eagles (*Aquila chrysaetos)* and coyotes (*Canis latrans*) constituted a jackrabbit-eating guild. An arthropod/mammal-eating guild contained burrowing owls (*Athene cunicularia*) and common ravens (*Corvus corvax*). Lastly, northern harriers (*Circus cyaneus*), western screech-owls (*Megascops kennicottii*), barn owls (*Tyto alba*), long-eared owls (*Asio otus*), great horned owls (*Bubo virginianus*), and gopher snakes (*Pituophis catenifer*) formed a small-rodent guild. Marti et al. (1993) excluded northern saw-whet owls (*Aegolius acadicus*) and American kestrels (*Falco sparverius*) from any of the aforementioned guilds (Figure 3.1). Northern saw-whet owls were closely related to the small-rodent guild; however, these owls were not included as a member because they consumed prey from a single family, Muridae, within the class Mammalia (Marks and Doremus 1988). Although, American kestrels shared similar diet characteristics to common ravens and burrowing owls, including feeding heavily on arthropod prey, kestrel diet was different enough to exclude them from any guild (Marti et al. 1993).

Traditional approaches to understanding diet have included analyses of stomach contents, fecal materials, or prey remains; direct observation; and, in some cases,

examination of regurgitated pellets where partially or undigested materials can be identified. Marti et al. (1993) used traditional food habit study methods to report on predator diets within the NCA. Stable isotopes analysis is a newer method for studying animal dietary habits, trophic relationships, and ecosystem dynamics, as examination of stable isotopes of carbon and nitrogen can provide powerful tools for estimating the trophic positions of consumers in a food web and the carbon flow to such consumers (Kelly 2000, Post 2002, Fry 2006, Inger and Bearhop 2008). Nitrogen (^{15}N) shows predictable step-wise bioaccumulation of 2 - 4‰ among successive trophic levels and is therefore useful for determining at what step an animal fits in a food web (Minagawa and Wada 1984, Post 2002). Carbon (^{13}C) is useful in determining the source or the primary producer of a food web. This can be accomplished because plants use different types of photosynthesis, C_3 and C_4 photosynthesis, which have distinct carbon isotope ranges (O'Leary 1988, Rundel et al. 1989). Moreover, isotope samples reflect not only what an animal eats, but what is assimilated and incorporated into the consumer; thus, this approach may have an advantage over traditional methods in capturing the broad scope of diet even with a single sample (Fry 2006, Inger and Bearhop 2008).

I used stable isotope analysis of carbon (^{13}C) and nitrogen (^{15}N) to investigate the food web and trophic relationships for a community of vertebrate predators within the NCA. I compared my results from isotope analysis with results from traditional food habit study methods in Marti et al. (1993), which also allowed me the opportunity to assess changes in community structure that may have occurred since the time that Marti et al. (1993) worked in the NCA. Pairing stable isotope technology with traditional food habit study methods may provide a more complete view of trophic relationships among

vertebrate predators. Furthermore, isotope analysis might prove a useful way to uncover previously unknown relationships within food webs and do so less invasively and with fewer samples than traditional methods (see Chapter 1).

Methods

The NCA was historically dominated by shrub steppe (Hironaka et al. 1983), but human disturbances and fires have converted much of the area to disturbed grassland. In the past 30 years alone, over 121,000 ha of native shrub communities were lost to an increasing number of wildfires. Current NCA management focuses on restoring habitat and plant communities in an effort to stabilize and increase small mammal populations (USDI 2008). The topography in the NCA is mainly flat to rolling with a number of rock outcrops, isolated buttes, and small canyons. Precipitation averages 31.7 cm, with 12.1 cm March through July, annually (N.O.A.A. 2002). Cattle and sheep graze portions of the NCA, primarily during winter (USDI 1996, Moulton et al. 2005). Approximately 5% of the NCA is irrigated agriculture, and the main agricultural crops include alfalfa *(Medicago sativa)*, corn (*Zea mays*), sugar beets (*Beta vulgaris*), and mint (*Mentha L.*).

To examine trophic relationships among vertebrate predators, I obtained tissue samples during monitoring of raptor nests and via roadway and foot surveys designed to locate carcasses within the study area during 2007 - 2008. For many raptor species, I obtained feathers from young within nests and stored the feathers within individual paper envelopes until analysis. As burrowing owls were the focus of a concurrent study (see Chapter 2), I obtained up to 50 ul of blood (via venipuncture of a wing vein) during routine monitoring of nests. Samples were stored frozen in 1.5 ml micro-centrifuge tubes. I obtained samples of muscle or feathers from carcasses of vertebrate predators

that I located during surveys. Muscle samples were collected from the hind limbs or rear half of an animal. I stored all muscle tissue samples in glass vials and froze them at -20 °C until prepared for stable isotopes analysis. Ultimately, all feather, blood, and muscle tissue samples were subjected to analysis by mass spectrometry to determine isotopic ratios for both carbon and nitrogen. Samples from potential prey species were also collected and processed for isotopes analysis using the methods outlined in Chapter 2 of this thesis.

Stable Isotopes Analysis

In preparation for analysis, feathers were washed with liquid detergent and distilled water to remove external contaminants (Mizutani et al. 1992). I thawed frozen blood and muscle samples. A small section of muscle was dissected and rinsed with distilled water. Samples were loaded into 30 mm aluminum weigh pans, oven dried for 48 hr at 60 °C (Cherel et al. 2007), and ground into fine powder. I ultimately sent samples to the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University, Flagstaff, AZ for carbon and nitrogen stable isotope analysis. There, samples were weighed into tin capsules and analyzed on a Carlo Erba NC 2100 elemental analyzer connected to a DeltaPlus Advantage isotope ratio mass spectrometer (Thermo Finnigan) through the Conflo III interface (Thermo Finnigan). Carbon and nitrogen stable isotope ratios were analyzed simultaneously for each sample. Repeat analysis of an international laboratory standard (National Institute of Standards and Technology, NIST 1547-peach leaves) were precise to ± 0.06 ‰ for $\delta^{13}C$ and ± 0.10 ‰ for $\delta^{15}N$ (n = 175). Standards used for carbon and nitrogen were Pee Dee Belemnite and atmospheric nitrogen (air), respectively. Stable isotope natural abundances were expressed as a delta

(δ) in parts per mill (‰), where δ denoted the difference between a sample and an international standard. The standard expression for an isotope sample was: $\delta X = [(R_{SAMPLE} / R_{STANDARD}) - 1] * 1000$: where X is the isotope in question, R_{SAMPLE} = the ratio of heavy to light isotopes in the sample, and $R_{STANDARD}$ = the ratio of the heavy to light isotopes in the standard (Kelly 2000, Post 2002, Fry 2006, Inger and Bearhop 2008).

Statistical Analysis

To evaluate trophic position of vertebrate predators, I plotted $\delta^{13}C$ and $\delta^{15}N$ for the species I was able to sample. I used cluster analysis (Ward's minimum variance method, JMP version 8.0.2, SAS Institute, Inc., Cary, NC) of mean $\delta^{15}N$ and $\delta^{13}C$ values for each species to elucidate trophic relationships within the vertebrate predator community. Means ± SE are presented unless indicated otherwise.

Results and Discussion

I collected 84 samples from 13 species of vertebrate predator (Figure 3.2), including four species of owl, two hawks, two falcons, three mammals, one reptile, and one additional bird species. Furthermore, I obtained 188 samples from burrowing owls (See Chapter 2). While I was unable to obtain samples from all of the species studied in Marti et al. (1993), I collected samples from three additional species that Marti et al. (1993) did not include: short-eared owl (*Asio flammeus*), Swainson's hawk (*Buteo swainsoni*), and long-tailed weasel (*Mustela frenata*).

The vertebrate predator species that I sampled in the NCA had $\delta^{13}C$ values reflective of C_3 and C_4 plant inputs at the base of their diets, although C_3 plants may be more important to some species than others (Figure 3.2). Both C_3 and C_4 plants were common throughout the portions of the NCA in which I collected plants (See Chapter 2,

Figure 2.4, and Table 2.1). Cerling et al. (2003) reported dietary preferences for 37 species of African bovids and used $\delta^{13}C$ to document dietary preferences for C_3 browse plants or C_4 grasses. They found $\delta^{13}C$ values could be used to provide a quantitative measure of C_4 plants in bovid diet. Herrera et al. (2003) investigated trophic partitioning of 23 birds species in southeastern Mexico and found most species fed on C_3 based foods. Similarly, C_3 plants were the main source of carbon input for an alpine meadow ecosystem in the Tibetan Plateau (Yi et al. 2006). The fact that the predator food web in the NCA is based on a combination of C_3 and C_4 plants illustrates a mixture of plant species is supporting a community structure of herbivores, omnivores, predators, rather than a particular species of shrub, forb, grass, or crop plant.

Predators in the NCA had a relatively narrow range of mean $\delta^{15}N$, and only 2‰ separated the majority of the species (Figure 3.2). Coyotes were the most enriched in $\delta^{15}N$, and they were 0.95‰ greater than the closest species. Furthermore, coyotes' $\delta^{15}N$ value was > 2.5‰ more enriched than six species of predator; this may mean coyotes occupied a different tropic level than other vertebrate predators within the NCA (Figure 3.2). Nitrogen increases of 2 - 4 ‰ indicate an increase of one trophic level (Minagawa and Wada 1984, Rundel et al. 1989, Hobson 1990, Hobson and Clark 1992, Hobson et al. 1994). Therefore, $\delta^{15}N$ results from the samples I collected indicated the majority of predator species occupied a similar trophic position. Jaksić (1983) investigated sympatric assemblages of hawks and owls in five geographic locations and found trophic structure was also similar among locations, although he noted trophic relationships may vary according to availability of food resources. My findings were consistent with the results from Marti et al. (1993), who found, when prey were identified to the class level, mean

dietary overlap among vertebrate predators was 82%. An overlap of this magnitude indicates many of the vertebrate predators in the NCA are consuming prey from the same sources, although prey resources may be partitioned differently based on prey size, predator size, or the predators' activity periods (Marti et al. 1993).

Cluster analysis of $\delta^{13}C$ and $\delta^{15}N$ values for vertebrate predators (Figure 3.3) had similarities to guild structure established by Marti et al. (1993, Figure 3.1). As in Marti et al. (1993), results based on stable isotopes analysis indicated that many species clustered into four principal groups, while two species were each sufficiently dissimilar to be placed in a group by themselves (Figure 3.3). Six species (Northern saw-whet owls, short-eared owls, Swainson's hawks, ferruginous hawks, prairie falcons, and gopher snakes) formed the largest cluster (Figure 3.3). These vertebrate predators were the most depleted in $\delta^{15}N$, which indicates that they occupied a relatively lower trophic position. Consequently, the diet of these predators is likely to include a greater portion of herbivores. Studies based on traditional methods of examining diet (Diller and Johnson 1988, Marti et al. 1993, Bechard and Schmutz 1995, Steenhof 1998, Wiggins et al. 2006, Rasmussen et al. 2008, Bechard et al. 2010) indicate that members of this cluster prey primarily on small rodents, including ground squirrels (*Spermophilus* spp.), voles (*Microtus* spp.), kangaroo rats (*Dipodomys* spp.), and mice (*Peromyscus* spp.). Within this larger group, prairie falcons and gopher snakes may form a smaller sub-group (Figure 3.3), as these species were slightly more depleted in $\delta^{13}C$ than others in this cluster. Prairie falcons and gopher snakes may have consumed a larger portion of ground squirrels or rabbits in their diet than other predators within this cluster, which could have led to their slightly more depleted $\delta^{13}C$. Marti et al. (1993) did not include Swainson's

hawks and short-eared owls in their analyses of trophic relationships among predators in the NCA because they had no dietary data for these species nesting in Idaho. Therefore, the samples that I gathered from nests and roadway surveys add new understanding of tropic relationships among vertebrate predators within the NCA and indicated that short-eared owls shared a similar diet with other small rodent-eating predators. While Swaninson's hawks are insectivorous during the non-breeding season (Bechard et al. 2010), my results suggested they relied heavily on mammalian prey during the breeding season in s. Idaho.

Common ravens and American kestrels also clustered based on analysis of stable isotopes of C and N (Figure 3.3). These two species were somewhat more enriched in $\delta^{15}N$ when compared to the species I described above and had a diet that likely included herbivorous, omnivorous, and carnivorous prey. Marti et al. (1993) found kestrels, ravens, and burrowing owls shared a similar diet in that each species consumes a large number of arthropod prey. However, analysis of regurgitated pellets may not be the best diagnostic tool for predators that include insects and other invertebrates in their diet (Marti 1974, Marti et al. 2007) as pellets that comprised invertebrate materials break down rapidly. Therefore, my results based on isotopes analysis may provide a more accurate description of trophic relationships for predators, such as ravens, kestrels, and burrowing owls that consume a large number of arthropods.

Boarman and Heinrich (1999) also reinforced the need for additional methods to study raven diet. They explain, "one mouse would leave hard parts detectable in a pellet whereas hundreds of pounds of meat from a moose (*Alces americana*), consumed without ingestion of hair or bones, would be undetectable." Additionally, Marti et al. (1993)

noted ravens were one of only two species in their study to include plant materials in their diet. Stable isotopes analysis could provide an alternative method for detecting dietary components such as plant and invertebrate materials, and soft-bodied prey and carrion in raven diet. Consuming plant materials would result in lower $\delta^{15}N$, as plants are producers and are likely to have lower $\delta^{15}N$ values than consumers (Post 2002, Inger and Bearhop 2008). Many of the raven samples I collected were from nestlings that still depended on adult birds for food. It is possible that raven $\delta^{15}N$ values in my study reflected a diet enriched in animal proteins and depleted in plant materials, as it may be difficult to carry plant materials, such as grain seeds, to a nest site. Steenhof and Kochert (1982) noted that adult ravens delivered lizards, snakes, rodents, and bird eggs, but not plant materials during observation of raven nests in the NCA. Although I could not estimate dietary input from plants or carrion in raven diet, if prey sources are isotopically distinct, nutrient input from these sources is reflected in the isotope values of consumers.

A third cluster that appeared included burrowing owls and western screech-owls (Figure 3.3). These species had $\delta^{15}N$ values similar to ravens and kestrels, which may indicate they fed upon herbivorous, omnivorous, and carnivorous prey. However, relatively more enriched $\delta^{13}C$ values distinguished burrowing owls and western screech-owls from raven and kestrels (Figure 3.2), which may indicate that these small owls included more avian prey in their diets. The bird species I sampled that were potential prey items were the most enriched in $\delta^{13}C$ of all the groups of prey (Figure 3.2, Appendix 1). Marti et al. (1993) reported avian prey constitutes 18.1% and 29.3% of diet by biomass for burrowing owls and western screech-owls, respectively. However, some more recent studies (Rains 1997, 1998, Moulton et al. 2005, 2006) found that avian prey

constituted a smaller amount of owl diet by biomass (2.2 ± 0.8% for burrowing owls and 2.7% for screech-owls). The stable isotopes values that my study provided suggest that burrowing owls and western screech-owls may have consumed more avian prey items than other predators included in my study, and it is possible that the changing role of avian prey in the diets of these owls is related to changes in the availability of mammalian prey. That is, in years when mammal prey (e.g., voles and mice) are abundant, there tends to be fewer remains of birds in burrowing owl nest burrows (pers. observ.). In contrast, when mammalian prey appear scarcer, we notice increases in avian prey among remains in artificial burrows. It is possible that western screech-owls respond in a similar fashion to changes in the availability of mammalian prey.

American badgers and long-tailed weasels formed an additional two-species cluster (Figure 3.3). These mammalian predators were more depleted in $\delta^{13}C$ than all of the other species of vertebrate predators. As I found that $\delta^{13}C$ values for Piute ground squirrels (*Spermophilus mollis*) were among the most depleted of all the species I sampled (see Chapter 2), it follows that badgers and weasels likely included a large portion of ground squirrels in their diets. This finding agrees with Marti et al. (1993), who placed badgers within the ground squirrel guild, although they did not include long-tailed weasels in their study because no data on weasel diet were available. Sheffield and Thomas (1997) describe long-tailed weasels as a generalist predator that consumes a wide variety of prey including ground squirrels and other small mammals. The weasel's slender body shape allows it to easily enter ground squirrel burrows and may help it access this fossorial prey source. In the NCA, long-tailed weasels also prey on burrowing owl nests and may eat eggs or young nestlings (King 1996, Moulton et al. 2006). I was

able to collect only one long-tailed weasel sample. While a single sample can help elucidate a species' place within the trophic structure of vertebrate predators in the NCA, additional samples would be needed to more completely investigate a possible trophic relationship between burrowing owls and weasels.

Coyotes and great horned owls had $\delta^{13}C$ and $\delta^{15}N$ values that were different enough from all other species to suggest that each belonged to a unique group. Great horned owls were the most enriched in $\delta^{13}C$, and this appeared to be the predominant reason why each clustered into a group by itself. Nonetheless, the great horned owl samples that I collected had substantial variation in $\delta^{13}C$ (Figure 3.2). On the other hand, coyotes had the greatest mean $\delta^{15}N$. Coyotes consume a very wide variety of prey ranging from deer and elk, ground nesting birds, and small mammals to fish and other aquatic animals, and they often include plants in their diet (Bekoff 1977). Within s. Idaho, Marti et al. (1993) found coyotes clustered with golden eagles for which jackrabbits were an important part of the diet. Although I was unable to collect golden eagle samples, stable isotope analyses suggested coyotes consumed a large portion of omnivorous and carnivorous prey (likely with elevated $\delta^{15}N$ values) in their diet, much like would be expected of eagles. Had coyotes consumed a substantial proportion of plants, they likely would have had much lower $\delta^{15}N$ than I observed.

Summary and Conclusions

The rich diversity of vertebrate predators in the NCA in s. Idaho presents a unique opportunity to examine relationships among species that use the potential prey base in the community. The results I presented from stable isotope analysis of carbon and nitrogen from samples collected in 2007 and 2008 generally corroborated with Marti et al. (1993),

who summarized diet studies conducted from 1971 to 1987 that were based on traditional food habit study methods. As in Marti et al. (1993), results based on stable isotopes analysis indicated that most species clustered into four principal groups, while two species were sufficiently dissimilar and were excluded from other groups (Figure 3.3). $\delta^{15}N$ results indicated the majority of predator species I sampled occupied a similar trophic position. Northern saw-whet and short-eared owls, ferruginous and Swainson's hawks, prairie falcons and gopher snakes had the lowest $\delta^{15}N$ values and have a diet based on herbivorous mammalian prey. Common ravens, American kestrels, burrowing owls and western screech-owls may include more species that are omnivores and carnivores in their diet. American badgers and long-tailed weasels may favor a diet rich in ground squirrels. Coyotes occupied the highest trophic position among vertebrate predators. My study also provided insight into the relationships of three additional species (Swainson's hawks, short-eared owls, and long-tailed weasels) in the community structure of vertebrate predators in the NCA.

The NCA is in a state of rapid change. The effects of human activities have grown substantially since the time when Marti et al. (1993) performed their studies, and wildfires and the invasion of exotic plants continue to modify shrub communities and alter or eliminate important habitat for small mammals that are the primary prey for many of these vertebrate predators. Current NCA management goals include restoring habitat and plant communities in an effort to stabilize and increase small mammal populations (USDI 2008). Continued loss of native vegetation, effects of climate change, or further introduction of C_4 crop plants, such as corn, could adjust baseline $\delta^{13}C$ and ultimately alter trophic relationships among species. Further monitoring of vertebrate predator

species combined with ongoing isotopes studies would be useful for determining the efficacy of restoration activities, documenting effects of any further habitat declines on trophic relationships of raptors, and for detecting important community level changes among predators within the NCA that would affect their persistence.

Figure 3.1. Guild structure of vertebrate predators in southwestern Idaho by prey identified to species/genus level (from Marti et al. 1993:12). Avian predator name abbreviations correspond to the American Ornithologists' Union abbreviations as follows: NOHA = northern harrier, RTHA = red-tailed hawk, FEHA = ferruginous hawk, GOEA = golden eagle, AMKE = American kestrel, PRFA = prairie falcon, BANO = barn owl, WESO = western screech-owl, GHOW = great horned owl, BUOW = burrowing owl, LEOW = long-eared owl, NSWO = northern saw-whet owl, and CORA = common raven. Abbreviations for mammals and reptiles are based on scientific names: CALA = coyote, TATA = badger, PIME = gopher snake, and CRVI = western rattlesnake. See text for scientific names.

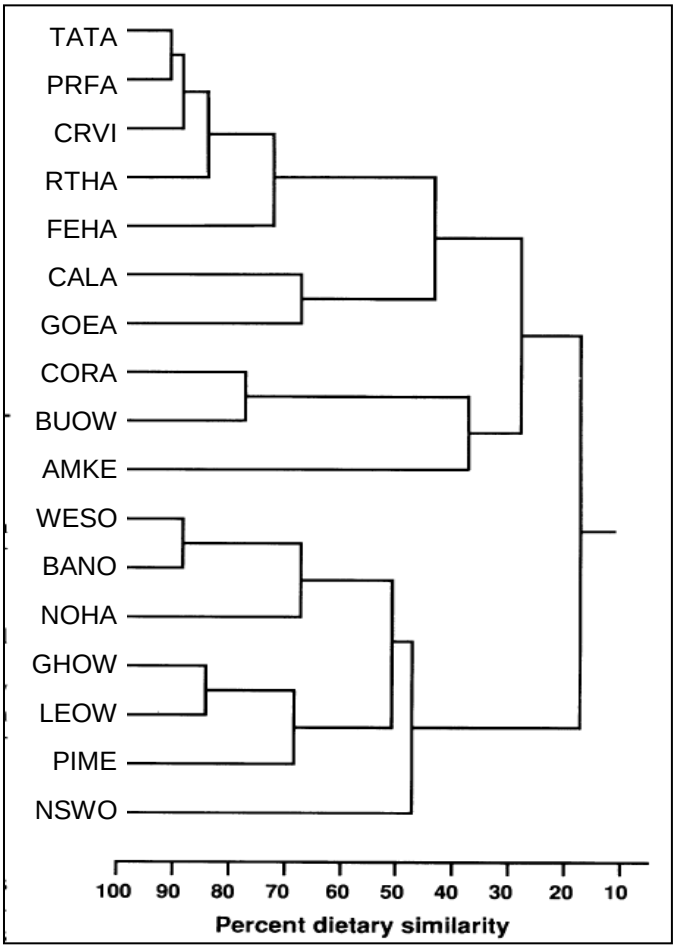


Figure 3.2. Mean (± SE) δ^{15}Nitrogen and δ^{13}Carbon for species of vertebrate predator in the Morley Nelson Snake River Bird of Prey National Conservation Area. Number of samples for each group or species is in parentheses. Mean (± SE) δ^{15}N and δ^{13}Cvalues for groups of potential prey species are shown in grey (See Chapter 2 for methods related to prey species isotopes and Appendix for a list of species within each group of prey species.

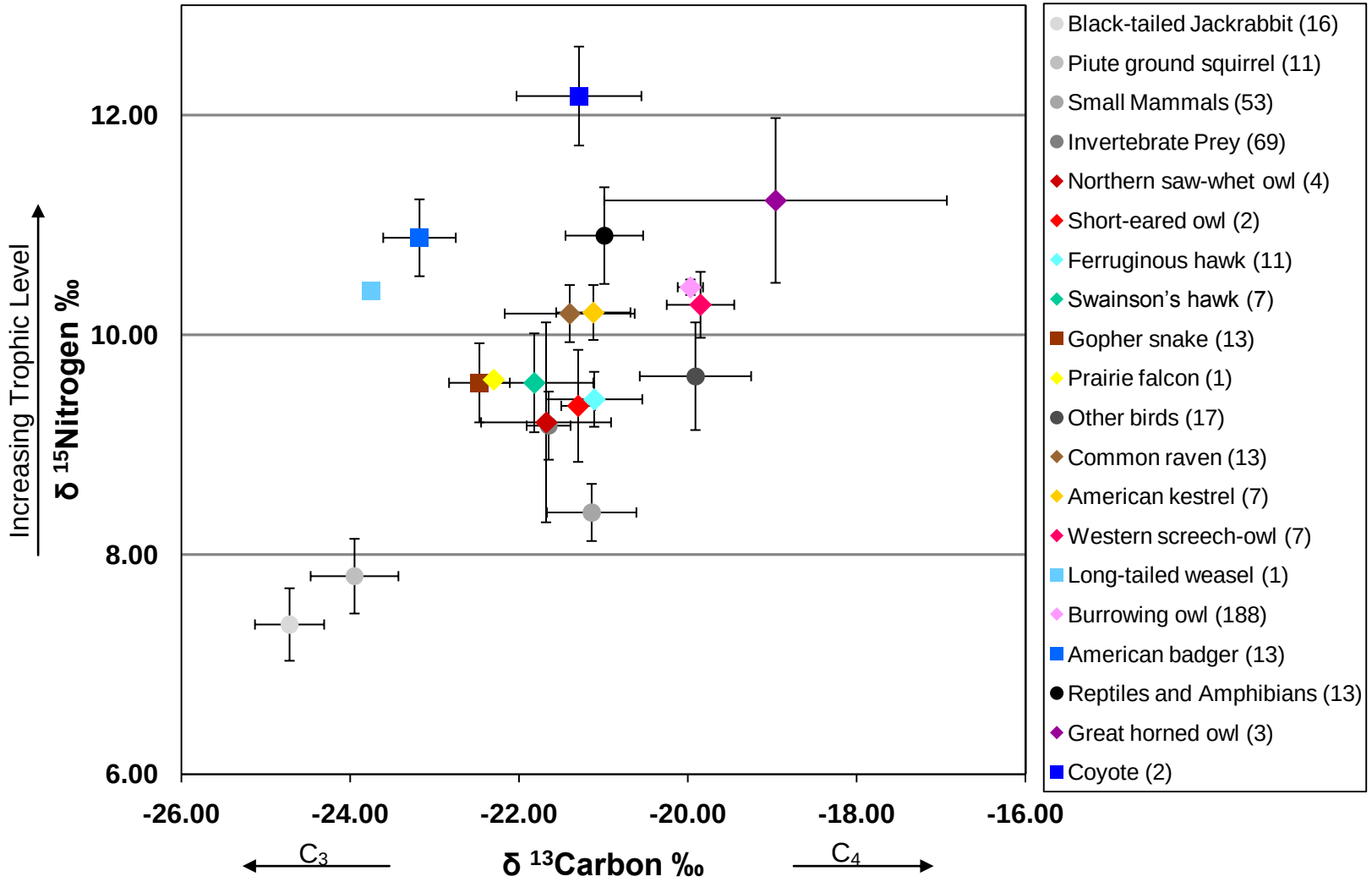
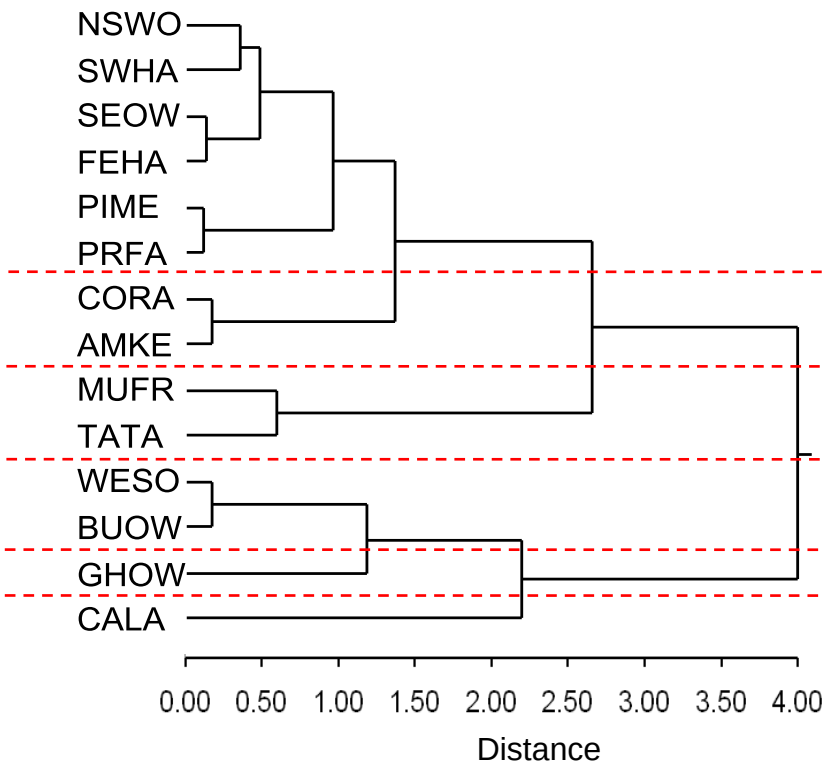


Figure 3.3. Hierarchical clustering (Ward's method, dendrogram distance scale) of δ^{15}Nitrogen and δ^{13}Carbon results for the vertebrate predator community in the Morley Nelson Snake River Bird of Prey National Conservation Area. Red lines separate the resulting clusters. Avian predator name abbreviations correspond to the American Ornithologists' Union abbreviations as follows: FEHA = ferruginous hawk, RTHA = red-tailed hawk, AMKE = American kestrel, PRFA = prairie falcon, WESO = western screech-owl, GHOW = great horned owl, BUOW = burrowing owl, SEOW = short-eared owl, NSWO = northern saw-whet owl, and CORA = common raven. Abbreviations for mammals and reptiles are based on scientific names: CALA = coyote, TATA = badger, MUFR = long-tailed weasel, and PIME = gopher snake. See text for scientific names.



Literature Cited

Bechard, M.J. and J.K. Schmutz. 1995. Ferruginous Hawk (*Buteo regalis*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/172doi:10.2173/bna.172.

Bechard, M.J., C.S. Houston, J.H. Sarasola, and A.S. England. 2010. Swainson's Hawk (*Buteo swainsoni*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/265doi:10.2173/bna.265.

Bekoff, M. 1977. *Canis latrans*. Mammalian Species. No. 79.

Boarman, W.I. and B. Heinrich. 1999. Common Raven (*Corvus corax*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/476doi:10.2173/bna.476.

Cerling, T.E., J.M. Harris, and B.H. Passey. 2003. Diets of east African bovidae based on stable isotope analysis. Journal of Mammalogy 84:456-470.

Cherel, Y., K.A. Hobson, C. Guinet, and C. Vanpe. 2007. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization diving predators from the Southern Ocean. Journal of Animal Ecology 76:826-836.

Diller, L.V. and D.R. Johnson. 1988. Food habits, consumption rates, and predation rates of western rattlesnakes and gopher snakes in southwestern Idaho. Herpetologica 44:228-233.

Fry, B. 2006. Stable Isotope Ecology. Springer, New York.

Herrera, L.G., K.A. Hobson, M. Rodríguez, and P. Hernandez. 2003. Trophic partitioning in tropical rain forest birds: insights from stable isotope analysis. Oecologia 136:439-444.

Hironaka, M., M.A. Fosberg, and A.H. Winward. 1983. Sagebrush-grass habitat types of southern Idaho. Forest, Wildlife and Range Experiment Station, University of Idaho, Bulletin 35, Moscow, USA.

Hobson, K.A. 1990. Stable isotope analysis of marbled murrelets: evidence for freshwater feeding and determination of trophic level. Condor 92:897-903.

Hobson, K.A. and R.G. Clark. 1992. Assessing avian diets using stables isotopes I: turnover in ^{13}C in tissues. Condor 94:181-188.

Hobson, K.A., J.F. Piatt, and J. Pitocchelli. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786-798.

Inger, R. and S. Bearhop. 2008. Applications of stable isotope analysis to avian ecology. Ibis 150:447-461.

Jaksić, F.M. 1983. The trophic structure of sympatric assemblages of diurnal and nocturnal birds of prey. American Midland Naturalist 109:152-162.

JMP. 2009. Version 8.0.2, SAS Institute, Inc., Cary, NC.

Kelly, J. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1-27.

King, R.A. 1996. Post-fledging dispersal and behavioral ecology of burrowing owls in southwestern Idaho. M.S. Thesis, Boise State University, Boise, Idaho.

Marks, J.S. and J.H. Doremus. 1988. Breeding-season diet of northern saw-whet owls in southwestern Idaho. Wilson Bulletin 100:690-694.

Marti, C.D. 1974. Feeding ecology of four sympatric owls. Condor 76:45-61.

Marti, C.D., K. Steenhof, M.N. Kochert, and J.S. Marks. 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. Oikos 67:6-18.

Marti, C.D., M. Bechard, and F.M. Jacksic. 2007. Raptor food habits studies. *In* Raptor research and management techniques (D.M. Bird and K.L. Bildstein, eds.). Hancock House Publishers, Blaine, WA.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48:1135-1140.

Mizutani, H., M. Fukuda, and Y. Kabaya. 1992. ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. Ecology 73:1391-1395.

Moulton, C.E., R.S. Brady, and J.R. Belthoff. 2005. A comparison of breeding season food habits of burrowing owls nesting in agricultural and nonagricultural habitat in Idaho. Journal of Raptor Research 39:421-430.

Moulton, C.E., R.S. Brady, and J.R. Belthoff. 2006. Association between wildlife and agriculture: underlying mechanisms and implications in burrowing owls. Journal of Wildlife Management 70:708-716.

N.O.A.A. (National Oceanic and Atmospheric Administration). 2002. Divisional normals and standard deviations of temperature, precipitation, and heating and cooling degree days 1971-2000. Climatography of the United States No. 85.

O'Leary, M.H. 1988. Carbon isotopes in photosynthesis. BioScience 38:328-336.

Post, D. 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83:703-718.

Rains, C. 1997. Comparison of food habits of the Northern Saw-whet Owl (*Aegolius acadicus*) and the Western Screech-Owl (*Otus kennicottii*) in southwestern Idaho. *In* Biology and conservation of owls of the Northern Hemisphere: 2nd International Symposium; Winnipeg, MB. (Duncan, J. R., D. H. Johnson, and T. H. Nicholls, eds.) USDA Forest Service, General Technical Report NC-190, St. Paul, MN.

Rains, C. 1998. Niche overlap and nearest-neighbor distances of northern saw-whet owls (*Aegolius acadicus*) and western screech-owls (*Otus kennicottii*) in southwestern Idaho. M.S. Thesis. Boise State University, Boise, ID.

Rasmussen, J.L., S.G. Sealy, and R.J. Cannings. 2008. Northern Saw-whet Owl (*Aegolius acadicus*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/042doi:10.2173/bna.42.

Rundel, P.W., J.R. Ehleringer, and K.A. Nagy (eds.). 1989. Stable Isotopes in Ecological Research. Springer Verlag, New York.

Sharpe, P.B. and B. van Horne. 1998. Influence of habitat on behavior of Townsend's ground squirrels (*Spermophilus townsendii*). Journal of Mammalogy 79:906-918.

Sheffield, S.R. and H.H. Thomas. 1997. *Mustela frenata*. Mammalian Species. No.570.

Steenhof, K. 1998. Prairie Falcon (*Falco mexicanus*), The Birds of North America Online (A.Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/346doi:10.2173/bna.346.

Steenhof, K. and M.N. Kochert. 1982. Nest attentiveness and feeding rates of common ravens in Idaho. Murrelet 63:30-32.

U.S. Department of the Interior. 1996. Effects of military training and fire in the Snake River Birds of Prey National Conservation Area. BLM/IDARNG Research Project Final Report. U.S. Geological Survey, Biological Research Division, Snake River Field Station, Boise, Idaho, USA.

U.S. Department of the Interior. 2008. Snake River Birds of Prey National Conservation Area Resource Management Plan and Record of Decision. Bureau of Land Management Boise District Office, Idaho, USA.

Wiggins, D.A., D.W. Holt, and S.M. Leasure. 2006. Short-eared Owl (*Asio flammeus*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/062doi:10.2173/bna.62.

Yi, X., Y. Yang, and X. Zhang. 2006. Modeling trophic positions of the alpine meadow ecosystem combining stable carbon and nitrogen isotope ratios. Ecological Modelling 193:801-808.

APPENDIX

Listing of species and $\delta^{13}C$ and $\delta^{15}N$ values from groups of species found in Figure 3.2.

Common Name	Species	N	$\delta^{13}C$	$\delta^{15}N$
			mean ± SE	mean ± SE
Small Mammals				
Deer mouse	*Peromyscus maniculatus*	13	-17.25 ± 1.01	10.42 ± 0.50
Great Basin pocket mouse	*Perognathus parvus*	10	-20.63 ± 1.01	8.14 ± 0.42
Montane vole	*Microtus montanus*	11	-25.93 ± 0.36	7.15 ± 0.45
Ord's kangaroo rat	*Dipodomys ordii*	19	-21.31 ± 0.37	7.83 ± 0.34
Invertebrates				
Cricket	*Gryllus* spp.	7	-22.45 ± 0.67	6.91 ± 0.85
Darkling beetle	*Eleodes* spp.	15	-21.33 ± 0.30	8.78 ± 0.27
Grasshopper	Family Acrididae	11	-21.88 ± 0.59	6.25 ± 0.49
Lepidoptera larvae	Order Lepidoptera	2	-22.91 ± 0.54	7.18 ± 1.70
Moth	Order Lepidoptera	5	-21.64 ± 2.00	8.29 ± 0.69
Blue leg centipede	*Scolopendra polymorpha*	3	-21.86 ± 1.20	10.35 ± 1.29
Carrion beetle	*Nicrophorus* spp.	6	-23.92 ± 0.64	11.37 ± 0.83
Giant hairy scorpions	*Hadrurus spadix*	12	-20.54 ± 0.73	10.74 ± 0.47
Solifugid	Family Eremobatidae	4	-20.06 ± 0.95	11.65 ± 0.90
Trapdoor spider	Infraorder Mygalomorphae	4	-21.52 ± 0.71	13.36 ± 0.36
Other Birds				
Black-billed magpie	*Pica pica*	2	-19.6 ± 1.61	11.53 ± 2.07
Horned lark	*Eremophila alpestris*	9	-19.04 ± 0.87	8.92 ± 0.62
Long-billed curlew	*Numenius americanus*	3	-19.61 ± 12.22	11.24 ± 0.75
Western kingbird	*Tyrannus verticalis*	2	-21.54 ± 1.26	9.6 ± 0.85
Western meadowlark	*Sturnella neglecta*	1	-25.95	7.30
Reptiles and Amphibians				
Desert horned lizard	*Phrynosoma platyrhinos*	1	-19.71	11.30
Racer	*Coluber constrictor*	3	-21.76 ± 0.63	9.96 ± 0.30
Side-blotched lizard	*Uta stansburiana*	5	-19.88 ± 0.59	10.05 ± 0.63
Woodhouse's toad	*Bufo woodhousei*	4	-22.12 ± 0.88	12.56 ± 0.65