DIET COMPOSITION, NICHE AND GEOGRAPHIC CHARACTERISTICS, AND PREY SIZE PREFERENCE OF BARRED OWLS (*STRIX VARIA*) IN THE PACIFIC NORTHWEST

By

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A thesis

submitted in partial fulfillment

of the requirements for the degree of

Master of Science in Raptor Biology

Boise State University

August 2012

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BOISE STATE UNIVERSITY GRADUATE COLLEGE

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Thesis Title: Diet Composition, Niche and Geographic Characteristics, and Prey Size Preference of Barred Owls (*Strix varia*) in the Pacific Northwest

Date of Final Oral Examination: 11 June 2012

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ACKNOWLEDGMENTS

I first extend my genuine appreciation to my major advisor, Dr. Mark Fuller, of the U.S. Geological Survey Forest and Rangeland Ecosystem Science Center and Boise State University–Raptor Research Center. Mark was a thoughtful, challenging, and supportive mentor with dynamic strategies of helping me further advance my knowledge base in raptor biology and wildlife ecology research. I especially thank Mark for his dedicated time, patience, positivity, and willingness to reflect the many ideas and questions we formulated and subsequently addressed throughout this research. I am truly grateful to have worked with him and for his friendship. I extend my many thanks to Dr. Eric Forsman of the U.S. Forest Service Pacific Northwest Research Station. Eric was the first to encourage me to pursue this research by contacting Mark, and he has supported me throughout my degree while serving on my graduate committee. Eric also supported me during many years as an employer, mentor, and friend while researching Northern Spotted Owls and red tree voles. Both Mark and Eric have been invaluable to my wildlife research and management pursuits, and I thank them for their advice and guidance regarding fieldwork, data analysis, and manuscript writing that has, in turn, contributed to my research and academic development. I gratefully acknowledge Laura Bond of the Department of Biology at Boise State University who provided assistance with statistical methods associated with this research. In addition, I would like to thank other graduate committee members, Dr. James Belthoff of the Department of Biology at Boise State

University and Dr. Carl Marti of Boise State University–Raptor Research Center, for their support. Jim provided much assistance in the final review of this thesis. Carl passed away before this study was completed, and he is deeply missed. Although Carl did not live to see this manuscript completed, I am indebted to him for his extraordinary dedication to the feeding ecology of owls and extensive contribution to the literature from which I have learned throughout my own research.

Several dedicated biologists contributed to the central Coast Ranges of western Oregon field study. I thank J. David Wiens, Patrick Kolar, Kristian Skybak, James Swingle, Amanda Pantovich, and Justin Crawford for their field assistance. Kathy Bledsoe of the Raptor Research Center at Boise State University deserves special recognition for administrative and budget assistance. Special thanks to Dr. Eric Forsman for use of his local reference collection of mammal, bird, and reptile skeletons to identify prey remains in pellets. Thanks also to the Raptor Research Center at Boise State University and the Snake River Field Station of the U.S. Geological Survey Forest and Rangeland Ecosystem Science Center for loaning field and laboratory equipment and for providing me with office and laboratory space that I sincerely appreciated. Rita Claremont, Amy Price, and Martin Adams assisted with some of the laboratory work associated with this study. I thank Dr. Leslie Carraway for taking the time to train and share with Rita Claremont her highly specialized ability to identify shrew (*Sorex* spp.) individuals to the species level. Janice Reid provided helpful assistance with research logistics and radio-tracking activities. Douglas Barrett (Westside Ecological, Inc.) and Biological Information Specialists, Inc. provided this study with locations of incidental

detections of Barred Owls during concurrent Northern Spotted Owl surveys. I also thank the U. S. Bureau of Land Management (Eugene District Office), Roseburg Forest Products, Weyerhaeuser Company, Swanson Superior, and Plum Creek Timber Company for providing field crews access to their lands.

This project would not have been possible without the combined funding contributions from the U.S. Geological Survey Forest and Rangeland Ecosystem Science Center, Boise State University–Raptor Research Center, U.S. Fish and Wildlife Service, U.S. National Park Service, Oregon Department of Forestry, U.S. Forest Service Pacific Northwest Research Station, and U.S. Bureau of Land Management.

I am also grateful to the biologists who contributed efforts in the two Washington State study areas from where Barred Owl pellets were collected. I thank Peter Singleton, Danielle Clay, Marlene Farrell, John Meriwether, and Aja Woodrow who helped me collect pellets and for their efforts to locate, capture, and radio-track Barred Owls as part of the eastern Cascade Range, Washington Barred Owl study. Also, many thanks to Scott Gremel and his field crews for providing Barred Owl pellets collected from the Olympic National Park, Washington study area. Chapter two of this thesis would not have been possible without all of their field efforts.

Additionally, I am thankful to the enthusiastic biologists who provided assistance with Northern Spotted Owl feeding trials conducted in four Northern Spotted Owl demographic study areas in Oregon and Washington including: Steven Ackers, Sarah Hamilton, Jason Mowdy, Tim Plawman, Amy Price, Janice Reid, Thomas Snetsinger, Stan Sovern, James Swingle, and Margy Taylor. I particularly thank these participants

because feeding trials were performed in conjunction with normal Northern Spotted Owl survey protocol visits, thus increasing the challenge of their existing work load. I also thank Dr. Eric Forsman for his time and the use of his workshop for the construction of owl feeding platforms used for experiments. Supplemental funding for materials used for the prey size preference study was provided by the Idaho Department of Fish and Game, Rich Olendorff Idaho Wildlife Scholarship Award.

Most importantly, I convey my deepest gratitude to my family for their support. I am especially grateful to my brother, Greg Graham, for his sage advice and encouragement and to my fiancée, Danielle Clay, for exhibiting devoted love, patience, and wide-ranging support throughout my journey as a graduate student. Greg and Danielle acknowledged how important this research meant to me, and I am greatly indebted to them for allowing me the freedoms of growing as an individual and as a wildlife ecologist.

Lastly, this thesis is dedicated to a large band of wildlife and fisheries biologists, plant ecologists, and naturalists of whom I had the pleasure to work in the company of, supervise, and most importantly, learn from, and to the scientists and journeymen contractors that have employed me during my career. I have been able to achieve this research goal, in part, by Isaac Newton's words, "Standing upon the shoulders of giants." These giants deserve special thanks for their scientific knowledge and cumulative efforts.

ABSTRACT

This thesis comprises three chapters describing my investigations of dietary composition, niche and geographic characteristics, and prey size preference of Barred Owls (*Strix varia*) following their recent range expansion into the Pacific Northwest. In the first chapter, I examine annual, seasonal, within-breeding season, and local variation in the diet and evaluate reproductive success as a function of dietary composition in western Oregon during 2007–2009. Diets were based on 3,686 prey individuals identified in 1,127 regurgitated pellets collected from 26 owl family areas. Prey identified in pellets included ≥ 85 taxa (33 mammals, 25 birds, 4 reptiles, 4 amphibians, 1 fish, 3 gastropods, 1 diplopod, 1 collembolan, 12 insects, and 1 crustacean). Based on percent of prey numbers in pellets, owl diets comprised 64.8% mammals, 2.9% birds, 1.0% reptiles, 9.8% amphibians, 0.3% fish, 6.6% gastropods, 0.2% diplopods, < 1% collembolans, and 14.4% insects. Mean mass of prey in pellets was 55.8 g. Diets varied between years and seasons and among within-breeding season periods and owl family areas, but were generally dominated by coleopteran beetles, mammalian insectivores, and northern flying squirrels (*Glaucomys sabrinus*). Taxonomic richness of the diet provided an indication of the versatility of Barred Owls capable of preying on diverse kinds of prey in their expanding geographic range. Estimated food-niche breadths were generally narrow to moderate, indicating use of comparatively few to a variety of taxa in large numbers. Spatiotemporal variations in diet appeared to reflect this species' adaptation and

opportunistic feeding strategies in an area of range expansion. These results will enable ecologists and land managers to better understand the ecological role played by Barred Owls in their new environment, including potential effects such as competition for food with other native fauna of the Pacific Northwest, especially the threatened Northern Spotted Owl (*Strix occidentalis caurina*).

In the second chapter, I compare diet composition among three geographic populations of Barred Owls in the Pacific Northwest, including the central Coast Ranges in Oregon, Olympic National Park in northwest Washington, and eastern Cascades in central Washington during the breeding seasons of 2007–2009, 1997–2009, and 2004–2006, respectively. For this analysis, I examined 1,021 regurgitated pellets from 25 owl family areas in the central Coast Ranges, 48 pellets from 20 areas in Olympic National Park, and 57 pellets from 9 areas in the eastern Cascades. The estimated number and total biomass of prey in pellets was 3,463 prey and 192,951 g in the central Coast Ranges, 187 prey and 11,444 g in Olympic National Park, and 336 prey and 12,871 g in the eastern Cascades. The number of taxa owls used as prey differed among the study areas, with 81 taxa in the central Coast Ranges, 36 in Olympic National Park, and 32 in the eastern Cascades. Diets were similar between the central Coast Ranges and Olympic National Park areas in that diets mainly included forest mammals (64.3% and 71.7% of prey numbers, respectively), with a variety of shrews, coast moles (*Scapanus orarius*), and northern flying squirrels predominating in prey numbers and biomass. Owl diets differed in the eastern Cascades where insects were the most numerous taxa in the diet (47.0% of prey numbers), with beetles predominating by prey number (45.2%) followed by frogs

(18.8%) and flying squirrels (12.2%). Flying squirrels were the primary source of biomass across all areas (24.8% in the central Coast Range; 34.0% in Olympic National Park; 41.4% in the eastern Cascades) and occurred in pellets most of the time. Mean mass of individual prey was 55.7 g in the central Coast Ranges, 61.2 g in Olympic National Park, and 38.3 g in the eastern Cascades. Food-niche breadth values indicated that although many prey taxa were taken, the food-niche dimension for each population of Barred Owls was narrow. Factors contributing to differences in diet among geographic locales likely included disparities in prey distributions, differences in the number of pellets collected, and likely temporal and local variation in prey use and prey availability.

In the third chapter, I investigate prey size preference behavior by sympatric, wild Northern Spotted Owls and Barred Owls in Oregon and Washington. I describe a controlled experiment in which I used feeding experiments to test the hypothesis that owls will select a larger prey animal when given a simultaneous choice between a small prey animal (*Mus musculus*) and a larger prey animal (*Rattus norvegicus* or *Rattus rattus*). I performed 30 independent feeding trials with Northern Spotted Owls (11 females, 19 males) and 17 independent trials with Barred Owls (12 females, 4 males, 1 gender unknown) during 1 March–31 August 2008. Northern Spotted Owls preferred the smaller prey in 24 trials and the larger prey in 6 trials. Barred Owls preferred the small prey in 9 trials and the larger prey in 2 trials. Both species exhibited significant preference for the smaller-sized mice. There was no difference in prey size selection between female and male Northern Spotted Owls; both sexes preferred smaller prey. Sample sizes for Barred Owls were too small to test for sexual differences. There was no

interspecific difference in prey size selection between Northern Spotted Owls and Barred Owls. My results for Northern Spotted Owls were not expected because diets of Northern Spotted Owls are typically dominated by medium-sized mammalian prey such as northern flying squirrels and woodrats (*Neotoma cinerea* and *N. fuscipes*). Wild Barred Owls preferentially selected small prey during feeding trials, which is consistent with Barred Owl diet in different regions of North America, including the Pacific Northwest.

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CHAPTER ONE: DIET OF BARRED OWLS (*STRIX VARIA*) IN THE CENTRAL COAST RANGES OF WESTERN OREGON

Abstract

During the last century, Barred Owls (*Strix varia*) have expanded their distribution westward into the Pacific Coast region of the United States, entering the temperate rain forest and new biological communities (Dunbar et al. 1991, Kelly 2001, Livezey 2009a,b). Herein, I describe dietary composition and feeding-niche characteristics of Barred Owls, including annual, seasonal, within-breeding season, and local variation in diets, and I examine associations between diet composition and reproductive success of Barred Owls in western Oregon during 2007–2009. My description of diets was based on 3,686 prey individuals identified from 1,127 regurgitated pellets collected at 26 owl family areas. The diet based on evidence from only pellets included ≥ 85 taxa (33 mammals, 25 birds, 4 reptiles, 4 amphibians, 1 fish, 3 gastropods, 1 diplopod, 1 collembolan, 12 insects, and 1 crustacean). Based on percent of prey numbers in pellets, owl diets comprised 64.8% mammals, 2.9% birds, 1.0% reptiles, 9.8% amphibians, 0.3% fish, 6.6% gastropods, 0.2% diplopods, < 1% collembolans, and 14.4% insects (crustaceans not included). Mass of Barred Owl prey ranged from 0.02 g (pleurocerid snail; *Juga* spp.) to 1,200 g (snowshoe hare; *Lepus americanus*). The mean mass of individual prey was 55.8 g. Mammals were 64.8% of prey numbers and 87.9% of prey biomass. Of the mammalian prey, owls predominately captured small forest insectivores including moles (*Scapanus orarius*, *S. townsendii*, *Neurotrichus gibbsii*) and

a variety of shrews (*Sorex bendirii*, *S. sonomae*, *S. trowbridgii*, *S. trowbridgii/vagrans*, and *S. vagrans*). The comparably larger northern flying squirrel (*Glaucomys sabrinus*) was also common prey and was the primary source of biomass. Although beetles (Coleoptera spp.) were the most frequently captured prey, the biomass contribution of beetles was negligible. Other frequent prey included salamanders and Pacific sideband snails (*Monadenia fidelis*).

Diets varied between years, between breeding and nonbreeding seasons, among periods within the breeding season, and among family areas. Yearly differences in the percent of prey numbers and biomass were relatively small (i.e., < 5%) and coincided with year-to-year dietary shifts from one taxon to another or to a variety of prey taxa. Flying squirrels were the primary source of biomass during all seasons, but increased by frequency and biomass during the nonbreeding season, whereas predation on coast moles (*Scapanus orarius*) and insects was most prevalent during the breeding season. Predation on large prey (e.g., snowshoe hare) was largely restricted to the breeding season when small juveniles were available as prey. Flying squirrels were the primary prey biomass during each period of the breeding season and were generally the most common prey during the 2008 breeding season. However, the relative percentage of flying squirrels decreased as the season progressed, exceeded by higher proportions of small prey during the post-fledging period. Mean mass of individual prey captured by owls through three periods of the breeding period was 103.5, 51.8, and 56.1 g. Within the breeding season, prey ranged from < 1 g to > 160 g. However, there was a disproportionate distribution of prey, generally dominated by taxa in the 1–40 g and 81–160 g ranges. Local variation in diet composition and prey numbers among family areas primarily reflected differences in

the frequency with which owls captured different small-sized prey, whereas variation in diet composition and prey biomass primarily reflected differences in the frequency that owls consumed different mammalian taxa. Mammals predominated and contributed the most biomass to owl diets regardless of the nesting status or nesting success of the owls. Flying squirrels provided the most biomass to owls regardless of reproductive status. Although mammals dominated prey numbers of non-nesting owls and pairs with fledglings, non-nesting pairs captured comparatively fewer mammals and more birds, amphibians, gastropods, and insects. Because mammals, particularly medium-sized to large mammals, were important to both non-nesting pairs of owls as well as pairs that fledged young, it was unclear if diet composition was related to reproductive success. The taxonomic richness and spatial and temporal variation of the diet indicated considerable versatility for preying on diverse taxa. However, the estimated food-niche breadth value revealed that although many taxa were eaten, the owls most often selected a relatively small variety of mammalian prey among all taxa consumed. Food-niche breadths between years and seasons, and among breeding season periods and owl family areas, were narrow to moderate, indicating diets were generally dominated by relatively few to a variety of taxa used in large numbers. These results will enable ecologists and land managers to better understand the ecological role of Barred Owls in their new environment, including potential effects as predator of and competitor with other native fauna of the Pacific Northwest.

Introduction

Prior to the early 1900s, Barred Owls (*Strix varia*) were widely distributed residents of eastern North America (Bent 1938). During the last century, they have

expanded their range westward to the Pacific Coast and currently inhabit coniferous forests throughout much of western North America (Kelly 2001, Livezey 2007). This range expansion has been well documented (e.g., Taylor and Forsman 1976, Hamer et al. 1989, Dunbar et al. 1991, Mazur et al. 1997a, Takats 1998, Wright and Hayward 1998, Mazur and James 2000, Kelly 2001, Hobbs 2005, Gremel 2005, Schmidt 2005, Anthony et al. 2006, Steger et al. 2006), and several hypotheses have been formulated (Monahan and Hijimans 2007) and debated (Livezey et al. 2008a) about the chronology, distribution, and direction of the range expansion (e.g., Livezey et al. 2009a,b).

The first published record of Barred Owls in Oregon was of a pair observed in 1974 in the Blue Mountains in the northeast corner of the state (Taylor and Forsman 1976). Barred Owls were subsequently detected in 1981 in the Oregon Cascade Range (Nehls 1998), and between 1974 and 1987 in the Oregon Coast Ranges (Kelly 2001). Following an extensive examination of historical detections of Barred Owls in Oregon, Kelly et al. (2003) reported that yearly counts of incidental detections of Barred Owls increased rapidly between 1974 and 1998, and further provided a cumulative estimate that there were over 700 areas occupied by Barred Owls in one or more years during this period.

As the Barred Owl expanded its range westward it became sympatric with the closely related Northern Spotted Owl (*Strix occidentalis caurina*), a federally threatened subspecies (U.S. Fish and Wildlife Service 1990). The morphological and ecological similarity of the two species has led to concern that the Barred Owl might be a threat to the Northern Spotted Owl if the two species compete for space, habitat, or food resources (Dunbar et al. 1991, Leskiw and Gutiérrez 1998, Herter and Hicks 2000, Pearson and

Livezey 2003, Gremel 2005, Anthony et al. 2006, Gutiérrez et al. 2007, Singleton et al. 2010). Some morphological and behavioral relationships of the two species have been examined (e.g., Kelly et al. 2003, Courtney et al. 2004, Olson et al. 2005, Anthony et al. 2006, Buchanan et al. 2007, Gutiérrez et al. 2007, Hamer et al. 2007, U.S. Fish and Wildlife Service 2008, Bailey et al. 2009, Dugger et al. 2011, Forsman et al. 2011, Van Lanen et al. 2011), but their diets have been compared in only one area where they co-occurred (Hamer et al. 2001). There are numerous reports describing diets of Spotted Owls in many areas (e.g., Barrows 1980, Forsman et al. 1984, 2001, 2004, Richards 1989, Ward 1990). Barred Owl diets have not been studied in the Pacific Coast region of the United States, except for a single study by Hamer et al. (2001) who compared diets of Barred Owls and Northern Spotted Owls along the west slope of the Cascade Range of Washington. Because there is so little data on the diet of Barred Owls in the Pacific Northwest, more diet studies are needed to help managers and ecologists better understand the potential for competition with congeneric Northern Spotted Owls, and to develop a better understanding of the potential ecological impact of Barred Owls on their prey.

My objectives were to (1) describe dietary composition of and feeding-niche characteristics of Barred Owls, (2) compare differences in diets of Barred Owls between or among years, seasons, and owl family areas, and (3) examine associations between diet composition and reproductive success of Barred Owls. I discuss the importance of learning about Barred Owl diets in an area of relatively recent range expansion including the potential ecological implications of a new top-level predator on native wildlife in the Pacific Northwest. My data can be compared to Northern Spotted Owl food habits

collected during a simultaneous study on a shared study area (Wiens 2012). This information will assist ecologists and land managers to better understand the role played by Barred Owls in their new environment.

Methods

Study Area

My 745 km^2 Central Coast Ranges study area (CCR) was located in the central Coast Ranges of western Oregon, 30 km west of the city of Eugene in Lane County, Oregon, USA (Figure 1.1). The CCR was characterized by a mixture of federal, private, and state lands. Percentages in different ownerships were: U.S. Bureau of Land Management (48%), private timber companies (47%), Oregon Department of Forestry (3%), and other private ownerships (2%). The pattern of land ownership resembled a checkerboard, with 2.56 km^2 sections of federal or state land alternating with sections of private land.

Forest age and structure varied widely on the study area, mainly due to disturbance from logging, fire, and windstorms (Franklin and Dyrness 1973). Because of differing forest management practices on federal and non-federal ownerships, remnant stands of mature and old forest were restricted primarily to federal lands and young or recently cleared forests covered most private lands. Elevation within the study area ranged from 84–700 m, with the topography characterized by steep mountain slopes and with narrow ridgelines dissected by rivers and streams. Climate was maritime, with relatively warm, dry summers and wet winters (Franklin and Dyrness 1973).

Vegetation on the study area was predominantly composed of conifer forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western

redcedar (*Thuja plicata*). Patches or dense stands of bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) were often interspersed with conifers, especially in recently disturbed areas and riparian areas.

This CCR study area was selected based on a variety of factors, including a well-documented history of nest locations of Northern Spotted Owls, good forest road access to track movements of radio-marked owls year-round, and adequate numbers of sympatric Barred Owls. The CCR was bounded on the north and south by two long-term Northern Spotted Owl demographic study areas (Oregon Coast Ranges and Tyee; Figure 1.1) in which banded populations of Northern Spotted Owls had been monitored for 19 to 24 years (for reviews see Lint et al. 1999, Anthony et al. 2006, Forsman et al. 2011). Previous researchers in the CCR had documented at least 45 areas and nests occupied by Northern Spotted Owls (Forsman et al. 1984, Thrailkill et al. 1998). These sites provided a historical framework from which to begin fieldwork in 2007.

Study Design

My study was one component of a project to investigate interspecific relationships between sympatric Barred Owls and Northern Spotted Owls on a common study area in western Oregon. I collaborated with J. D. Wiens, Ph.D. graduate student at Oregon State University, who conducted a simultaneous study of competitive interactions and resource partitioning between Northern Spotted Owls and Barred Owls (Wiens 2012). My study was designed to describe dietary composition, prey use and size preference, and feeding-niche characteristics of Barred Owls. I participated in all field research activities including: (1) occurrence surveys to determine breeding areas and productivity of both owl species; (2) capturing and radio-marking owls to conduct the research; (3) radio-

tracking owls to monitor movements, habitat, and space use, and vital rates of owls; and (4) collecting regurgitated pellets of both owl species from beneath nest and roost locations of owls. This research was approved by the Institutional Animal Care and Use Committees at Boise State University (Study No. 692-07-004) and Oregon State University (Study No. 3516).

Barred Owl Occurrence Surveys and Monitoring

We conducted broadcast call and live-lure surveys to locate Barred Owls and determine occurrence of breeding areas. Survey methods and reproductive status determinations were consistent with standardized Northern Spotted Owl survey protocols (Lint et al. 1999, Reid et al. 1999), with minor modifications to target Barred Owls. Call survey locations were positioned approximately 1 km apart along forest roads and heavily used ungulate trails or human foot trails. Digital playback of Barred Owl vocalizations, including 8-note territorial and agitated calls (Mazur and James 2000, Odom and Mennill 2010), were broadcast for 20 min at each location using an amplified megaphone (Wildlife Technologies, Manchester, NH). Occasionally, live-lure techniques (Reid et al. 1999) were used in combination with broadcast calls to locate unresponsive Barred Owls. Although a combination of several day and nighttime visits were typically conducted to document occurrence and nesting status of Barred Owls, research crews attempted to complete at least three nighttime visits to each survey location between 1 March–31 August in 2007 and 2008.

Capturing, Radio-marking, and Tracking Barred Owls

After the presence of a pair of Barred Owls was confirmed, we attempted to capture and radio-mark both pair members at the breeding area. Barred Owls were

primarily captured using dho-gaza style traps (Bloom et al. 2007) and were lured into mist nets using a combination of simulated territorial calls (Elody and Sloan 1984, Hamer 1988, Singleton et al. 2010) and various types of bait, including a stuffed Barred Owl decoy, live mice, or an artificial mouse decoy. Less frequently, we captured Barred Owls with a neck snare pole (Forsman 1983), but this technique was usually ineffective because Barred Owls would not allow close approach by observers.

Captured owls were fitted with a U.S. Geological Survey aluminum leg band and a 12g backpack style radiotransmitter (Model RI–2CM, Holohil Systems Ltd., Carp, Ontario, Canada). Sex of owls was determined from vocalizations, nesting behavior, weight, morphological measurements, or the presence of a well-developed brood patch (Carpenter 1992). Transmitter mass averaged 1.8% and 1.5% of body mass for males and females, respectively. The backpack harness was constructed of 6 mm tubular Teflon® ribbon as described by Forsman et al. (1984), Snyder et al. (1989), and Guetterman et al. (1991). Transmitter lifespan ranged from 12–24 months, and units were equipped with motion sensors set to alter the transmission pulse rate following 12 hrs of inactivity. We used standard equipment and methods to estimate the locations of radio-marked owls (Guetterman et al. 1991, Kenward 2001), monitor their movements, and to identify roosts, nests, and foraging locations of owls from which evidence of diet were collected.

Radio-marked owls were relocated by triangulating with a hand-held two-element "H" antenna (Model RA-2AK, Telonics, Inc., Mesa, AZ) attached to a portable receiver (Model R–1000, Communication Specialists, Inc., Orange, CA). For each relocation, we obtained at least 3 azimuths from different locations in ≤ 20 min. After completing triangulations during the day or night, we frequently homed in on owls to obtain visual

confirmation of locations and to track radio-marked owls to nesting and roosting areas to search for and obtain dietary samples. Radio-marked owls were recaptured at the conclusion of the study to remove transmitters.

Owl Diets

I used the following definitions for discussing diet. Selection is the process by which owls choose a prey item, and usage of prey is the quantity consumed by owls in a predetermined period (Johnson 1980, McDonald et al. 2005). I estimated prey usage at two scales of hierarchy: diets of families at the study area (or geographical) scale, and diets of family members within the home range (Johnson 1980).

Obtaining Dietary Samples

Diets were estimated based on multiple sources of evidence, including three types of dietary samples: regurgitated entire pellets or individual fragmented pellets, observations of owls with recently killed prey, and uneaten prey remains. Although I collected three types of samples, the primary method used to describe diets was to examine the composition of prey in regurgitated pellets. Samples from all visits to each owl family area were cataloged into collections and partitioned by season and by year for spatial and temporal analyses. Dietary samples were collected year-round from March, 2007 through February, 2009. To ensure an accurate representation of the diet through space and time, I searched areas used by Barred Owls at weekly intervals to collect diet samples from the date of radio-marking throughout the study period. Initially in 2007, field efforts focused on locating, capturing, and radio-marking owls. Consequently, proportionately more samples were collected in 2008. Field crews often collected evidence of diet when relocating radio-marked owls three to four times each week.

Pellets and prey remains were cleared from areas occupied by owls prior to March, 2007, and I excluded old or weathered material that was believed to be from previous years from analyses. Similarly, all known roost and nest areas were cleared of pellets and prey remains between spring and summer months and fall and winter months to examine the potential for seasonal variation in prey selection.

Dietary samples were collected primarily from the ground below nest and roost trees within a 356 m mean radius of the nest trees of nesting pairs of owls and from below roost trees within home ranges of non-nesting pairs of owls. Unlike congeneric Northern Spotted Owls, a species known for infrequent diurnal movement (Sovern et al. 1994) and their repeated use of one or few roosts for long periods (e.g., Forsman 1976, Barrows 1981, Sovern et al. 1994), individual Barred Owls in my study used many disparate roost trees within a home range; therefore, dietary samples were collected from numerous locations within family areas. Evidence were found by: (1) tracking radio-marked owls to diurnal roost areas; (2) searching areas of concentrated use by radio-marked owls using observations of conspicuous whitewash or fecal matter to locate roosts; (3) searching occupied nest areas; (4) climbing to nest tree cavities used by radio-marked owls at the end of each breeding season; and (5) searching locations where samples were previously recorded and collected. The latter method was useful because pellets and uneaten prey remains were often not accompanied by whitewash or other sign.

By tracking radio-marked owls and collecting pellets from locations where the owls had roosted, I reduced the likelihood that pellets from one owl family area were confused with pellets of owls occupying adjacent family areas. Results of spatial interactions between radio-marked Northern Spotted Owls and Barred Owls by Wiens

(2012) indicated that the probability of a Northern Spotted Owl being located within a neighboring Barred Owl's home range was low ($\bar{x}$ = 0.15, SE = 0.03, range = 0.00 to 0.84) during the breeding season (1 March–31 August, 2007–2009). In addition, the probability of a Northern Spotted Owl being located within a neighboring Barred Owl's core area (or area of concentrated use) was essentially zero. Core area size for individual Barred Owls, which were generally centered on nest trees or regularly used roost trees, ranged in size from 40–334 ha (Wiens 2012). The mean radius from which I collected regurgitated pellets from Barred Owls (356 m) fell within this range. Family areas were identified based on occurrence of breeding areas used by non-nesting pairs or families of Barred Owls, many of which were radio-marked. Therefore, it is reasonable to assume that most regurgitated pellets from Barred Owl home ranges originated from that family of Barred Owls, in part because (1) spatial overlap of core use areas of neighboring Barred Owls was small; and (2) Northern Spotted Owls mostly avoided the core use areas of Barred Owls (Wiens 2012).

Each dietary sample was individually bagged and labeled in the field with codes for owl identification, transmitter frequency, owl species, collection date and season, family area name, nesting status, sex and age (if known), sample unit (e.g., individual, family area), time of pellet egestion (if observed), condition of evidence (e.g., pellet, remains) and location of sample (e.g., below roost), Universal Transverse Mercator (UTMs), and sample description (e.g., pellet morphology). The dimensions (length × width at the widest point) of intact pellets were measured in the field to the nearest 0.1 mm using an electronic digital caliper (Mitutoyo America Corp., Aurora, IL). Pellets were then air-dried or preserved frozen for subsequent dissection and prey identification.

The range, mean, and standard deviation were calculated for both pellet measurements, the estimated number of prey individuals, and prey taxa per pellet.

It proved difficult to assign most pellets to an individual because pair members and their offspring often shared roost trees, especially during the breeding seasons. As a result, I generally combined all data from each family area without trying to subdivide based on sex or age. Diet data obtained during the nonbreeding season (September–February) were assumed to be mostly from adults, based on the assumption that juvenile Barred Owls dispersed from natal areas (sensu Forsman et al. 2002).

I used information about the condition of evidence to determine if it was included in my analyses and how it contributed to the estimated use of prey (e.g., prey number, prey biomass, prey occurrence). In the field, the condition of evidence was divided into four categories: (1) entire pellet; (2) individual fragmented pellet; (3) observations of owls with recently killed prey; and (4) uneaten prey remains. I recorded condition of pellets because several factors can affect the size, shape, or number of parts (or fragments) associated with owl pellets (Andrews 1990, Terry 2004). These factors included: (1) prey composition and the digestive process; (2) local climate conditions and seasonality; (3) roost height in the forest canopy; and (4) the correlation between an owl's diurnal movement patterns and number of roost tree locations used. As a result of these factors, some entire pellets broke into fragments during or after falling to the ground. Fragmented pellets were collected and reconstructed as one individual pellet sample if they obviously originated from of an entire pellet. The reconstruction of fragmented pellets into entire pellets resulted in useful single pellet samples that were important for quantifying estimates of frequency of prey occurrence (proportion of pellets containing

each prey taxa) and building sample-based rarefaction and prey taxa sampling curves (see Prey Occurrence and Dietary Richness in Methods section).

Prey Taxa Identification

To identify and quantify prey in pellets, I teased the pellets apart with tweezers and separated the remains from fur, feathers, and other organic material. Then, I used dichotomous keys, illustrations from published sources, and a local reference collection of mammal, bird, and reptile skeletons obtained from the U.S. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA to identify prey remains to the lowest taxonomic level possible. I identified fish bones and arthropod remains (head capsules, mandibles, elytra, and exoskeleton fragments) by comparison with reference specimens. I identified uneaten bird remains by comparing feathers with specimens in the Vertebrate Museum in the Department of Biological Sciences at Boise State University. For some taxa I consulted with experts to determine the identity of specimens.

Mammals, birds, reptiles, gastropods, and three types of arthropods (diplopods, collembolans, and crustaceans) were identified primarily to the species level. Amphibians, fish, and insects were often not identifiable to the species level. Of these taxonomic categories, amphibians were identified to the ordinal level and salamanders (Caudata spp.) were placed into three size groups; large, medium, and small (see Appendix). Frog remains were lumped into one group (Frog spp.). Fish were identified to the superclass level (Osteichthyes spp.) and insects were identified to at least the ordinal level. Although beetles (Coleoptera spp.) were identified to the ordinal level and enumerated, beetles were further identified to the family, genus, and species levels using a sub-sample of pellets.

Dietary Composition Metrics

Regurgitated Pellets

I used all evidence identified from regurgitated pellets to compile a list of taxa captured by Barred Owls. I quantified dietary composition using percent of prey numbers, percent of prey biomass, and percent frequency of prey occurrence. These measures have been widely used in the literature to describe raptor diets (e.g., Korschgen and Stuart 1972, Marti 1974, 1988, Marti et al. 2007, Forsman et al. 1984, 2001, 2004, Trejo and Grigera 1998, Bertolino et al. 2001, Hamer et al. 2001, Booms and Fuller 2003).

Prey Numbers. To estimate the percent of prey numbers, I first estimated the number of individuals of each prey taxon in each pellet. Then, for each taxon, I calculated the proportion of that taxon in the diet by dividing the estimated minimum number of individuals by the total number of prey in the sample. This value of relative proportion of each taxon was then multiplied by 100 to produce the relative percent of numbers of each prey taxa in the diet.

I estimated the minimum number of individuals of vertebrate prey by enumerating skulls, mandibles, or bones of the appendicular skeleton, whichever gave the highest count. When skulls of vertebrate prey were highly fragmented or absent, paired sets of elements of each taxon were separated, and the highest number of elements of the right or left side was considered the number of individual prey animals from the dietary sample (Mollhagen et al. 1972).

I estimated the minimum number of gastropods by counting the number of different shell apexes (center of the gastropod shell). Occasionally, the apical whorls, or

protoconch, which represent the whorls that constitute the embryonic shell at the shell apex, were useful especially when this is clearly distinguishable from the later whorls of the shell, otherwise known as the teleoconch.

For most arthropod taxa (diplopods, collembolans, and insects), I estimated the minimum number of individuals of each taxon in each sample by counting the number of head capsules, mandibles, elytra, or fragments of exoskeleton, whichever gave the highest count. However, following an examination of preliminary field evidence, freshwater crustaceans (Signal crayfish; *Pacifastacus leniusculus*) were not quantified by estimating the minimum number of individuals in each pellet.

Empirical evidence suggested that Barred Owls regurgitated pellets that contained fragmented exoskeletons belonging to ≥ 1 entire individual crayfish or portions of individual crayfish (e.g., rostrum removed, 1 chela or both chelae removed and discarded prior to consumption). In a study of Eastern Screech-Owl (*Megascops asio*) diet, Ritchison and Cavanagh (1992) enumerated frequency by number of crayfish in the diet with the assumption that the presence of fragmented crayfish remains in pellets was equal to one individual. However, Barred Owls, which are comparatively larger than Eastern Screech-Owls (Mazur and James 2000), are capable of consuming multiple crayfish during a foraging bout. Therefore, the preceding method and assumption would not be applicable. Figueroa and Stappung (2003) used pairs of gastroliths (hardened calcium pellets) to quantify the number of crayfish in Great White Egret (*Ardea alba*) diets. Gastroliths are dynamic, calcified structures located in the anterior walls of the cardiac stomach of freshwater crayfish, some lobsters, and terrestrial crabs (Graf 1978) and contribute a calcium storage function during molting stages and regeneration (Stevenson

1985). Because not all crayfish are expected to have gastroliths (Dorn et al. 2008) and those bearing gastroliths become dissolved by enzymes in the foregut during the molt (Powers and Bliss 1983), Dorn et al. (2008) exercised caution when considering their usefulness for quantifying crayfish in avian diets. In fact, gastroliths were not present in all pellets containing crayfish remains during my study, and there are no reports of whether gastrolith incidence in signal crayfish is equivalent on the study area; thus, the efficacy of using gastrolith pairs to count the number of individual crayfish in Barred Owl diets was questionable. Therefore, with the absence of diagnostic features to accurately quantify the minimum number of individual crayfish in pellets and, because owls often consume only portions of crayfish, I did not estimate percent of crayfish numbers in the diet, but rather estimated percent frequency of occurrence and developed methods to estimate relative crayfish biomass for this study (see biomass determination below). One limitation to not calculating crayfish numbers is that diet diversity indices require the relative proportion of each identifiable taxa of the assemblage being investigated. Therefore, for the purpose of calculating food-niche breadth (a common measure of diversity), I estimated crayfish numbers by counting rostrums or chelae, whichever gave the highest count, or I applied a default value of one individual in cases where I could not document more than one individual in a pellet.

Prey Biomass. I estimated the percent of prey biomass in the diet by multiplying the estimated number of individuals of each prey taxon by the estimated mean mass of the prey taxon, or by estimating and summing the mass of each individual prey based on comparison with local reference specimens of known age and mass (Forsman et al. 2004). The estimated relative proportion of biomass of each prey taxon

was then divided by the total prey biomass in the sample and multiplied by 100 to produce relative percentages of prey biomass for each prey taxa. Mean mass of individual prey captured was estimated by dividing the total prey biomass in the sample by the total number of individuals in the sample.

For most prey taxa, I used estimates of mean mass to calculate estimates of total biomass of each prey taxon (Appendix). For a few of the larger prey such as rabbits and hares (*Sylvilagus bachmani*, *Lepus americanus*), mountain beaver (*Aplodontia rufa*), spotted skunk (*Spilogale gracilis*), and grouse (*Bonasa umbellus*, *Dendragapus obscurus*), I estimated the mass of each specimen based on comparisons of bones with specimens of known mass in the reference collection. This method was used to prevent overestimating biomass of large prey when almost all of these individuals found in pellets were small juveniles. Crayfish biomass was based on crayfish specimens collected from six segments along the upper mainstem Siuslaw River and tributary reaches in the study area. Live crayfish were weighed to the nearest 0.1 g using a portable digital scale (Model CS200, Ohaus Corp., Pine Brook, NJ) and stored frozen for laboratory procedures. Based on the live crayfish masses, I plotted a cumulative mass curve to aid in identifying size variation among crayfish in the study area (mean mass = 23.8 g, range = 5.1–73.5 g, n = 65). From the curve, I identified five live mass classes delineated by 10 g increments, from which I used a random sub-sample to represent each of the mass classes for further biomass determination.

In the laboratory, I re-weighed each entire crayfish specimen in the sub-sample before I removed portions of crayfish. Each specimen was weighed and recorded as each chela (or claw) was removed from the body. I derived four proportional masses: (1) entire

crayfish; (2) crayfish with left chela only; (3) crayfish with right chela only; and (4) crayfish with both chelae removed. Using a hot plate and a 1000 ml glass beaker filled with water, I boiled each specimen to aid in the removal of the internal anatomy and muscle tissue. Exoskeletons and chelae of gutted specimens were then placed under a basic laboratory hood, dried, and weighed.

I performed four regressions (PROC REG; SAS Institute Inc. 2001) that predicted crayfish live mass from dry mass (of exoskeleton with or without chelae) using the sub-sample of crayfish specimens. I evaluated scatterplots of the live masses in relation to dry masses of the sub-sample of specimens across size ranges. In all four regressions, live mass was positively related to dry mass (entire crayfish, $r^2 = 0.99$, $P < 0.0004$; crayfish with left chela only, $r^2 = 0.99$, $P < 0.0004$; crayfish with right chela only, $r^2 = 0.97$, $P < 0.0014$; crayfish with both chelae removed, $r^2 = 0.97$, $P < 0.0014$). Therefore, I concluded that it was reasonable to use linear regression to estimate crayfish biomass based on exoskeleton remains in pellets (Table 1.1). After separating crayfish remains from the contents of a pellet, I measured the mass of the crushed crayfish remains to the nearest 0.01 g using a fixed digital scale (Model TS4KD, Ohaus Corp., Florham Park, NJ) and applied the dry mass to one of the four models to estimate the live mass of the crayfish in each pellet. Crayfish elements, such as rostrum and chelae size, were also compared to locally collected specimens of known live mass to further evaluate the efficacy of each of the regression models. Estimated live crayfish masses were summed to estimate the total amount of crayfish biomass. The total amount of crayfish biomass was then divided by the total biomass of all prey taxa to further evaluate the relative contribution of crayfish to the Barred Owl diet.

Frequency of Prey Occurrence in Pellets. For each prey taxon, I calculated percent frequency of occurrence in the diet by dividing the estimated total number of pellets into the number of pellets in which the taxon was observed and multiplying by 100. Percent frequency of occurrence is a useful metric for comparison with other Barred Owl studies that used hair, feather, stomach analyses, or other analytical procedures in which it was not possible to estimate the number of individual prey (Coon 1917, Mendall 1944, Korschgen and Stuart 1972, Leder and Walters 1980).

Observations of Recently Killed Prey and Uneaten Prey Remains

I analyzed observations of recently killed prey and uneaten prey remains separately from pellets and did not combine them in the diet analysis. These dietary samples were not combined with pellets because of the differences in detectability among the different types of samples and because of the possibility of double-counting prey that might also have been found in a pellet (Marti et al. 2007). Uneaten prey remains were quantified by counting the minimum number of individuals based on feathers, bones, or fur. Single feathers were excluded from analysis because single feathers may have resulted from molting birds (Pyle 1997).

Dietary Richness and Diversity Metrics

Diversity is a representation of a community assemblage where taxonomic composition is characterized by richness, the total number of taxa present in a community, and the relative abundance of the taxa. In general, of the total number of taxa, a relatively small proportion might be abundant or dominant (based on large numbers of individuals) that bear high “importance” values, and a large proportion often are considered rare, having low “importance” values (Odum 1983). Dietary diversity,

commonly known as food-niche breadth (FNB), has two components, taxonomic richness (the total number of prey taxa or taxonomic groups in the diet) and evenness (how uniformly those taxa occur in the diet: Margalef 1958, Pielou 1966, Marti et al. 2007). I estimated diet richness based on the pellet data alone as well as all sources of data combined. To assess and compare diet richness and feeding-niche characteristics of owls at different spatial and temporal scales, I constructed prey taxa sampling curves and computed food-niche breadth (FNB), a simple index of diversity in the diet. These metrics of richness and diversity are comparable to other raptor diet studies in the literature (Marti 1988, Bosakowski and Smith 1992, Marti et al. 1993, Hamer et al. 2001, Forsman et al. 2004).

Dietary Richness

I produced prey taxa accumulation and rarefaction curves to evaluate whether a sufficient number of pellets had been examined to adequately describe richness of diet (Heck et al. 1975, Gotelli and Colwell 2001, Marti et al. 2007). I used “family area” as the unit for deriving taxa accumulation curves. I plotted the number of new prey taxa occurring in each pellet as it was added to the database, and I analyzed the curve as a function of the total sample size of pellets (Heck et al. 1975, Marti et al. 2007). I assumed that an adequate sample of pellets for assessing taxonomic richness of the diet was achieved when the curve reached an asymptote and few or no new taxa were added with the analysis of additional pellets.

Comparison of diet richness among owl families that occupy potentially different habitats supporting different prey taxa can be complicated by the fact that diversity indices typically vary as a function of sample size, independent of differences in dietary

composition and taxonomic richness (Colwell et al. 2004). To compensate for differences in taxonomic richness and the sample sizes of pellets collected among family areas or periods, I used sample-based rarefaction curves, which are a statistical representation of the corresponding accumulation curve; they generally entail repeated and random re-sampling of the collection of *N* samples and further plotting the average number of taxa represented by 1, 2, 3,…*N* samples (Gotelli and Colwell 2001). Because prey taxa accumulation curves are typically not smooth as a consequence of spatio-temporal patchiness, Colwell et al. (2004:2718) further described this random re-sampling procedure as "smoothing the prey taxa accumulation curve." Furthermore, rarefaction estimates the number of taxa that would be expected to be present in each smaller collection of *N* samples randomly drawn from the larger original collection of *N* samples. By performing this procedure, I avoided pitfalls associated with reducing all collections to the same sample size when calculating taxonomic richness (Heck et al. 1975). I used EstimateS version 7.5 (Colwell 2005) to compute rarefaction curves, randomizing the order in which pellets were analyzed 100 times and then plotting the mean cumulative number of prey taxa versus the number of pellets examined. I used the sample-based rarefaction curves and their approximate 95% confidence intervals (Colwell et al. 2004) to evaluate differences in observed taxonomic richness of the larger original collection of *N* pellets compared to the expected richness present in each smaller collection of the original pellets by family area, by year, and by season.

Food-niche Breadth

I estimated food-niche breadth (FNB) using Levins' (1968) reciprocal of Simpson's (1949) index of diversity: FNB = $1/\Sigma p_i^2$, where p_i = the relative proportion of

each prey taxa in the diet. This index generates values ranging from 1 to *n*, where *n* is the number of prey taxa in the diet, with higher values indicating a broader food-niche dimension with each taxa consumed in nearly equal numbers. For example, FNB is maximum when equal numbers of prey individuals occur in each prey taxa, thereby indicating the lack of discrimination among use of prey. I interpret index values that are near the middle third of the range of 1 to *n* (i.e., 14.29, range 1–28) to be "moderate" food-niche breadths, suggesting moderately selective use of a variety of prey. Conversely, FNB is minimum when the majority of numbers of prey individuals occur in only one or few taxa, thus indicating a narrow food-niche dimension caused by the birds selecting a small proportion of prey relative to all the taxa in the diet. I calculated FNB using the finest taxonomic level possible (see Prey Taxa Identification in Methods section).

For FNB comparisons among geographical areas within the study area and with the literature, I used Colwell and Futuyma's (1971) standardized food-niche breadth (FNB_{sta}), where $FNB_{sta} = (B_{obs} - B_{min})/(B_{max} - B_{min})$. In this formula, B_{obs} = observed FNB, $B_{min} = 1$ (the minimum niche breadth estimate), and $B_{max} = n$ (the maximum niche breadth estimate or number of taxa used in calculating B_{obs}). FNB_{sta} ranges from 0 to 1. I partitioned FNB_{sta} into three categories: narrow (0.00–0.33), moderate (0.34–0.66), and broad (0.67–1.00). This estimator is independent of the number of prey taxa used, thereby allowing for more useful comparisons of food-niche breadth among samples from different areas that differ in diet taxa number.

Diet Analysis

Annual Phenology

Diet data were collected year-round during the breeding (1 March–31 August) and nonbreeding (1 September–28 February) seasons. I further partitioned the breeding season into three periods that roughly corresponded to the incubation period (28–33 d), nestling period (30–37 d), and fledgling period (4–5 mo). Initiation of the incubation, nestling, and fledgling periods was estimated based on the date that radio-marked females were first observed in their nests. I also used observations of young owls in the nest tree (branchers) and young fledged from the nest tree to confirm the estimated chronology. Based on observation of radio-marked birds, the breeding phenology of Barred Owls in CCR was egg-laying and incubation (3 March–4 April); nestling and brancher (5 April–4 May); and post-fledging (5 May–August 31).

I used the estimated percent of prey numbers, prey biomass, and FNB to describe annual, seasonal, within-breeding season, and local variation in diet, and to determine whether diet composition was related to reproductive success. I collected pellets from 26 family areas from which the number of pellets by area varied between years and seasons, and in which the nesting status of owls included pairs that did not fledge young and those that successfully fledged young. Fledging success, a measure of reproduction, was determined when ≥ 1 young was observed away from the nest tree, as defined by Lint et al. (1999) during the breeding season. Using family areas that shared similar attributes, I had a sample of 15 family areas for evaluating spatial and temporal differences in diets of Barred Owls. I selected 18 as the minimum sample size of pellets for a family area.

Preliminary analyses with larger sample sizes (e.g., 30, 60) provided similar results in diet composition (percent of prey number and biomass) and taxonomic richness.

Annual Breeding Season Variation in the Diet

I examined annual variation in diet composition and feeding-niche characteristics using breeding season data from seven family areas that produced ≥ 1 young to fledging in both 2007 and 2008, and that had a minimum sample of 18 pellets in each breeding season. I selected these seven family areas because these same radio-marked owl pairs shared the same nesting status each year and to reduce biases in dietary analyses that can occur when pooling evidence of diet across individuals, family areas, or time periods that have unequal sample sizes or variations in nesting status. Thus, I computed the difference in percent of prey numbers and biomass for each prey taxa composing diets of each of the seven family areas. Between-year variation in diet was further evaluated by using paired samples *t*-tests to compare FNB and FNB_{sta}. Paired samples *t*-tests were applied to test whether the paired mean difference in FNB and in FNB_{sta} between years was significantly different from zero. For these comparisons, FNB data were presented as the mean difference ± SD, *n* was the number of family areas, and the significance level was set at $\alpha = 0.05$.

Seasonal Variation in the Diet

I described seasonal differences in diet and feeding-niche characteristics using data from the breeding season (1 March–31 August) and nonbreeding season (1 September–28 February). Due to small numbers of pellets obtained during the nonbreeding seasons, I combined pellets collected from each family area during the 2007 and 2008 nonbreeding seasons to be compared to the breeding seasons. Variation in diet

was further evaluated by computing and qualitatively comparing FNB and FNB_{sta} between seasons.

Within-Breeding Season Variation in the Diet

I examined within-breeding season diet composition and feeding-niche using the three previously described periods (see Annual Phenology) in 2008. I also developed frequency distributions of prey numbers by size and by breeding period in owl diets during the breeding season. Diet data obtained during the 2007 breeding season were excluded because of the small sample of pellets collected. Prey numbers were pooled for each prey size range. Prey size ranges included estimates of mean mass of prey taxa for this study (see Appendix), and all but one size range category (< 1 g) were taken from Hamer et al. (2001) to be used for comparison. Within-season variation in diet was further evaluated by computing and qualitatively comparing FNB and FNB_{sta} among the egg-laying and incubation, nestling and brancher, and post-fledging periods.

Local Variation in the Diet

I examined spatial differences in diet within the study area based on 15 family areas using the combined 2007 and 2008 breeding season data. Based on the results of little annual difference, I combined two breeding seasons into a single sample for each family, which allowed me to include additional families for this analysis and reduce the possibility of generating biased results associated with family areas with small samples of pellets carrying the same weight as areas with large samples. The combination of data also provided more complete accounting of the prey richness of Barred Owl diets. Diets were estimated separately for 15 family areas with a minimum of 18 pellets obtained for

a single breeding season and a minimum of 21 pellets obtained during the 2007 and 2008 breeding seasons combined.

I performed agglomerative hierarchical cluster analyses (Sneath and Sokal 1973) in program SAS 9.1 (SAS Institute Inc. 2001) to examine spatial differences in diet composition among 15 families of Barred Owls. Cluster analysis (CA) provided (1) an effective, quantitative toolset to sort families of owls into groups according to dissimilarities in dietary composition; and (2) a means to evaluate potential dissimilarities beyond the evaluation of the raw data tables alone. CA is a multivariate technique used to determine where discrete ecological clusters occur in multidimensional space (Sneath and Sokal 1973). CA was effective, in part, because Barred Owl diet during the breeding season was very rich (81), and this method groups similar sampling units (diets of owl family areas) together into hierarchical classes (Gauch 1982) based on the community of prey taxa revealed from pellets. CA was further useful in that this method clusters similar sampling units without requiring exact similarity (McGarigal et al. 2000). Therefore, families of owls were grouped based on their degree of shared similarity in diet composition and relative prey numbers or biomass. At least 81 prey taxa were used by the owls during the breeding season, but due to the predominance and high FNB importance of mammals to breeding season diets (64.3% of prey numbers and 87.7% of prey biomass), only mammalian prey are presented to family, generic, or species levels, whereas the remaining prey are presented to the class, superclass, or phylum level. Considering their high frequency, mammalian prey were presented in greater taxa detail to provide finer discrimination among owls' diets, whereas the remaining taxa were combined in higher taxa to provide an indication of the versatility of a family of owls

capable of predating on diverse kinds of prey. By pooling some prey taxa for this analysis, the taxonomic list of prey resulted in 23 taxa (rather than 81) being used for clustering.

I computed two matrices of Euclidean distances (ED) using relative percentages of prey numbers and prey biomass of each the 23 taxa captured by each family of owls. Specifically, the raw data matrix, containing 15 owl family areas (sampling units) and 23 prey taxa (variables), was converted into two dissimilarity matrices by computing the dissimilarity in (1) prey numbers (abundances) and (2) prey biomass contributions between every pair of owl family areas using the ED metric. Next, I performed two separate runs of cluster analysis (one with the dissimilarity in prey numbers matrix and one with the dissimilarity in prey biomass matrix) using Ward's (1963) minimum-variance linkage method to fuse clusters based on ED to produce two dendrograms. The two dendrograms reflected the degree of dissimilarity in the use of relative prey numbers and biomass among owl families. Ward's linkage is a hierarchical clustering method that agglomerates similar entities into homogenous groups by minimizing the within-group sum of squares. The distance between the clusters is measured by the between-group sum of squares. I chose Ward's method because after examining results using alternative linkage methods (e.g., average, flexible beta), Ward's method was more space-conserving, had less propensity to chain (McGarigal et al. 2000, McCune and Grace 2002), and produced the most effective illustration of the raw data and dietary results. Local variation in diet was further evaluated by computing and comparing FNB and FNB_{sta} among the 15 owl family areas using the finest taxa resolution possible (see Food-niche Breadth in Methods section).

Diet Composition Associated with Reproductive Success

To evaluate whether Barred Owl reproductive success was associated with diet composition, I examined differences in diet composition and feeding-niche characteristics between non-nesting pairs of owls and nesting pairs of owls that fledged young. Data used in this analysis originated from five owl family areas for which breeding parameters were monitored between egg-laying and juvenile dispersal with reproductive output (success) recorded by 31 August. Reproductive success was determined when nesting pairs fledged ≥ 1 young that was observed away from the nest tree (Lint et al. 1999). Non-nesting pairs occupied an area, attempted to breed based on pair formation and courtship behavior, but did not nest. Monitoring of non-nesting pairs did not indicate the laying or incubation of eggs, brooding of young, or detection of fledglings. As a consequence of cryptic behaviors by Barred Owls during visits to assess reproductive success, areas were searched many times to count and confirm the number of fledglings.

The nesting status of the five owl family areas differed by year, one year being a non-nesting pair, the other year a pair that fledged ≥ 1 young. I obtained a minimum of 18 pellets from each family area for each breeding season. I combined pellets collected from each family area that shared the same nesting status.

Variation in diet was further evaluated by using paired samples *t*-tests to compare the paired mean difference in FNB and in FNB_{sta} between non-nesting and nesting pairs. FNB data were presented as the mean difference ± SD, and the significance level was set at $\alpha = 0.05$.

Results

Dietary Composition and Richness

Diet data collected from 27 Barred Owl family areas included 1,127 pellets, 4 observations of owls with prey, and 90 uneaten prey remains. Prey from nest cavities were not included in the analysis because the remains were too fragmented to reconstruct into individual pellets and because I was concerned that remains in nests were not independent of remains in pellets. The Barred Owl diet, based on all evidence, had a richness of 89 taxa (Appendix).

Regurgitated Pellets

The 1,127 pellets were collected from 26 Barred Owls family areas. Mean length and width of 262 intact pellets were 48.3 ± 13.5 mm (range = 17.9−85.7 mm) and 25.8 ± 5.0 mm (range = 12.1−45.0 mm), respectively (Table 1.2). The mean number of prey individuals per pellet was 3.3 ± 3.1 (range = 1–43), not including crayfish and 3.4 ± 3.1, including crayfish. The number of prey taxa per pellet ranged from 1 to 10 (mean = 2.5 ± 1.6). The Barred Owl diet based only on evidence from pellets included 85 taxa (Table 1.3).

Prey Numbers and Biomass. I identified a total of 3,686 prey individuals from pellets that contributed an estimated 211,112 g of total prey biomass to owl diets (Table 1.3). Excluding crustaceans, owl diets comprised 64.8% mammals, 2.9% birds, 1.0% reptiles, 9.8% amphibians, 0.3% fish, 6.6% gastropods, 0.2% diplopods, < 1% collembolans, and 14.4% insects (Table 1.3). Prey size ranged from 0.02 g pleurocerid snails (*Juga* spp.) to 1,200 g adult snowshoe hares. The mean mass of individual prey was 57.3 g, not including crayfish, and 55.8 g including crayfish.

Mammals accounted for 64.8% of total prey numbers and 87.9% of total prey biomass (Table 1.3). Of the mammalian prey, owls captured predominately small forest insectivores, including moles (*Scapanus orarius*, *S. townsendii*), shrew-moles (*Neurotrichus gibbsii*), and a variety of shrews (*Sorex bendirii*, *S. sonomae*, *S. trowbridgii*, *S. trowbridgii/vagrans*, and *S. vagrans*; Table 1.3). Coast moles (*Scapanus orarius*) were the most common mammal in the diet and contributed the second highest amount of total prey biomass in the diet (Table 1.3). Although owls captured mainly small mammalian prey, the comparably large northern flying squirrel (*Glaucomys sabrinus*) was common in the diet (10.9% of total prey numbers) and was the primary source of biomass (Table 1.3). Other relatively common mammalian prey included seven species of arvicoline rodents, which combined contributed 8.2% of total prey numbers in the diet, most of which were red tree voles (*Arborimus longicaudus*; Table 1.3). The sixth most frequently captured mammal was the deer mouse (*Peromyscus maniculatus*; Table 1.3). Other important mammalian prey included Douglas' squirrels (*Tamiasciurus douglasii*) and woodrats (*Neotoma* spp.), which contributed the third and fourth highest amounts of prey biomass to the diet, respectively (Table 1.3). Lagomorphs, including brush rabbits and snowshoe hare, were 1.5% of total prey numbers in the diet. Mountain beavers and spotted skunks accounted for 0.7 and 0.3% of total prey numbers, respectively (Table 1.3). Lagomorphs, mountain beavers, and spotted skunks combined contributed 18.5% of prey biomass to the diet. Pocket gophers (*Thomomys mazama*), bats (*Myotis* spp.), black rats (*Rattus rattus*), Pacific jumping mice (*Zapus trinotatus*), and ermine (*Mustela erminea*) (< 0.1 to 0.9% of total prey numbers) formed the balance of mammalian prey (Table 1.3).

The second most frequently identified prey were insects, which were 14.4% of total prey numbers and contributed about 0.1% of total prey biomass. Twelve insect taxa comprised 531 prey individuals that were identified at least to the ordinal level, with coleopteran beetles and ants (Formicidae) being the most numerous insects consumed (Table 1.3). The remaining insect taxa were rare in the diet and generally composed ≤ 0.1% of total prey numbers.

Subsequent beetle identification using a sub-sample of pellets revealed that Barred Owls captured 10 coleopteran families that comprised 16 genera and at least 17 species (Table 1.4). Carabid beetles were the most frequently identified, with *Pterostichus lama* being the most common species followed by the curculionid beetle *Dyslobus lecontei*. Additionally, arachnids including two Acari families, Ixodidae (hard ticks) and Oribatidae (soil mites), were likely incidental prey consumed indirectly by Barred Owls. The small number of ticks and mites in the diet were likely incidental because these organisms parasitize and thrive in the skin and pelage of small mammals (Corn and Bury 1991).

Amphibian and gastropod taxa were the third and fourth most frequently used prey, constituting 9.8 and 6.6% of total prey numbers and 3.1 and 0.9% of total prey biomass, respectively. Amphibian taxa were mainly represented by medium-sized salamanders (5.0% of total prey numbers), also ranking fifth in frequency of prey among all taxa in the diet. Less common amphibians in the diet included small (3.1%) and large salamanders (1.2%). Frogs were rare in the diet composing 0.5% of total prey numbers. Gastropod taxa comprised two species of terrestrial snails (*Monadenia fidelis*,

Haplotrema vancouverense) and at least one species of freshwater pleurocerid snail (Table 1.3). Of nine pellets containing pleurocerid snails, one contained 43 individuals.

Birds comprised 2.9 % of total prey numbers and 5.7% of total prey biomass. Pacific Wrens (*Troglodytes pacificus*) were the most common bird in the diet, but Dark-eyed Juncos (*Junco hyemalis)*, Band-tailed Pigeons (*Patagioenas fasciata*), Stellar's Jays (*Cyanocitta stelleri*), and small owls were also fairly common (Table 1.3).

The remaining taxa that accounted for ≤ 1% of total prey numbers and ≤ 1.4% of total prey biomass in the diet included reptiles (*Coluber constrictor*, *Elgaria coerulea*, *Sceloporus occidentalis*, *Thamnophis* spp.), fish, yellow-spotted millipede (*Harpaphe haydeniana*), springtails (Entomobryidae spp.), and signal crayfish (Table 1.3).

Frequency of Prey Occurrence in Pellets. Percent frequency of prey occurrence in the total sample of pellets was 92.5% mammals, 8.9% birds, 3.2% reptiles, 17.4% amphibians, 0.6% fish, 11.4% gastropods, 0.7% diplopods, 0.1% collembolans, 20.7% insects, and 7.3% crustaceans (Table 1.3). Prey taxa identified in pellets that were numerically important in Barred Owl diets generally occurred in most pellets. More specifically, relative percentages of total prey occurrence of taxa such as Mammalia and Insecta generally paralleled those of total prey number from highest to lowest. However, there were notable exceptions at the ordinal and species levels. For example, coleopteran beetles were the most frequently identified taxa in the total diet by prey numbers, but they only occurred in 17.6% of pellets. Conversely, flying squirrels, the fourth most numerically important prey, had the highest frequency of occurrence in pellets (32.6%; Table 1.3). Coast moles, second numerically, occurred 28.0% of the time followed by Trowbridge's or vagrant shrews (*Sorex trowbridgii/vagrans*; 19.1% of total prey

occurrence). Douglas' squirrels and woodrats contributed 8.0 and 6.7% of total prey biomass to the diet but were identified less frequently (2.1 and 1.4% of total prey numbers), and their skeletal parts occurred in fewer pellets (6.6 and 4.4% of total prey occurrence) compared to other taxa (Table 1.3). Signal crayfish occurred in 7.3% of pellets.

Observations of Recently Killed Prey and Uneaten Prey Remains

Observations of Recently Killed Prey. Observations of Barred Owls with prey included one flying squirrel, one garter snake, one signal crayfish, and one unidentified squirrel (Sciurid spp.; Table 1.5). The 1st observation of predation occurred at 1251 on 8 May 2008 at the Lower Pugh Creek family area, 6 km south of Walton, Oregon, where I found a radio-marked female Barred Owl perched in a mature Douglas-fir about 10 m from her nest tree. I observed 2 nestlings on the rim of the nest cavity that were vocalizing begging calls and looking in the direction of the female. At 1315, the female turned her head and then her body about 180 degrees in the opposite direction of her nestlings. She flew downward into the multi-layered forest canopy and out of my view. About 15 m away, I heard scraping tree bark and flight feathers rustling among live foliage. Then, the owl flew about 6 m above me, carrying a flying squirrel in her beak at the base of the skull. The owl proceeded to the nest tree and placed the dead squirrel on a limb just below the rim of the cavity and in view of the nestlings. The adult female remained on the limb several minutes vocalizing contact calls and began to tug on the squirrel braced between her talons and the limb. Meanwhile, less than 1 m above, the nestlings began hopping along the rim of the nest cavity and continued begging calls.

Then, the female flew to her original perch, leaving the squirrel on the limb. I observed regurgitated pellets and old unidentifiable uneaten prey remains adjacent to the squirrel.

The 2nd observation was at 1530 on 12 May 2008 at the Lower Oat Creek family area, about 4 km southwest of Vaughn, Oregon, where I located the radio-marked female about 50 m from her nest. She flew upslope approaching the nest tree and perched in a mature Douglas-fir, where I observed a garter snake in her talons (Figure 1.2). The owl stared toward the nest cavity and vocalized two contact calls for several minutes before she flew higher into the forest canopy carrying the snake in her beak. She flew successively higher from perch to perch until she landed on the rim of the nest cavity and then descended into the cavity. I detected no nestlings during the delivery, but vocal and flight behavior of the adult female owl suggested that a prey delivery occurred as opposed to prey caching.

The 3rd observation occurred on 16 July 2008 along Russell Creek at Siuslaw Falls, about 6 km west of Lorane, Oregon. At 0530, a field crew member observed an adult female radio-marked owl fly from the water along the creek and then perch on a low log extending over the water. The crew member briefly, but clearly, observed the owl perched on the low log with an individual crayfish in her talons. This location was about 20 m from a creek-side roost tree with a Barred Owl feather and whitewash at the base and the same log where crayfish remains were observed and collected previously. Near the end of the low log, there was a barren spot situated on the top and middle of the log surrounded by a ring of crayfish remains (Figure 1.3). This owl feeding platform was within the Siuslaw Falls pair’s home range, and the radio-marked female owl was repeatedly relocated in the area throughout the study period.

The 4th direct observation was documented at 0810 on 12 December 2008 in the Camp Creek drainage, 1 km north of Alma, Oregon, when a crew member was tracking a radio-marked male perched about 4.6 m high in a conifer tree. He observed the owl capture and kill an unidentified squirrel. The crew member heard Douglas' squirrels begin vocalizing chirp calls, and then he observed the owl dive and capture a squirrel with its feet. The squirrel was medium-sized and had a squirrel-like bushy tail, but the crew member was not able to clearly identify the species of squirrel as it was handled by the owl.

Uneaten Prey Remains. I identified 84 prey individuals from 90 uneaten prey remains. The sample included 34 taxa (15 mammals, 17 birds, 1 gastropod, and 1 crustacean; Table 1.5). Excluding crustaceans, uneaten remains comprised 29 individual mammals, 42 birds, and 13 gastropods (Table 1.5). Uneaten mammalian and bird remains were mainly flying squirrels and Varied Thrushes (*Ixoreus naevius*; Table 1.5). Two samples with gastropod prey remains were entirely pleurocerid snails (7 and 6 individuals), which were associated with crayfish remains. My estimate of crayfish biomass was 1,577 g from 21 prey remains samples, which was lower than biomass estimates for both mammals (5,898 g) and birds (7,557 g).

Uneaten prey remains included taxa that were not identified in regurgitated pellets. These included two Northern Spotted Owls or Barred Owls (*Strix* spp.), one Belted Kingfisher (*Megaceryle alcyon*), one Crow or Raven (*Corvus* spp.), and one Red Crossbill (*Loxia curvirostra*), all of which were collected during the breeding season near Barred Owl nests or roost trees.

Dietary Richness and Diversity

Dietary Richness Based on Pellets

Results from regurgitated pellets revealed that Barred Owls in western Oregon have a rich diet, preying on at least 85 taxa (33 mammals, 25 birds, 4 reptiles, 4 amphibians, 1 fish, 3 gastropods, 1 diplopod, 1 collembolan, 12 insects, and 1 crustacean; Table 1.3) including numerous invertebrates. Of the 85 prey taxa in Barred Owl pellets, I identified 55 to the species level (Table 1.3).

I calculated prey taxa accumulation and rarefaction curves using 39 taxa from a sample of 60 pellets from the Iron Mountain family area and 33 taxa from 62 pellets from Kline Creek. These two owl families consumed 23 taxa in common, primarily mammals. In addition, Iron Mountain pellets revealed 16 unique taxa, and those for Kline Creek yielded 10 unique taxa. Prey taxa accumulation and rarefactions curves indicated that estimated taxonomic richness of the diet continually increased with increased number of pellets examined. As many as 62 pellets collected during the two years of fieldwork were not enough to describe the "complete" richness of a family diet. Rarefaction curves for increasing richness were similar by family area, by year, and by season, as evidenced by overlap of confidence intervals of the curves (see Figures 1.4 and 1.5). Furthermore, the trend in taxonomic richness was similar among the curves when estimated using various smaller numbers of pellets examined and at several points along these curves. In fact, the curves and their 95% confidence intervals indicated that there was no significant difference in taxonomic richness along the curves among family areas or periods despite unequal sample sizes among families and periods. Although prey taxa accumulation and

rarefaction curves did not become asymptotic, decreasing slopes suggested that the most common taxa were encountered with comparatively small samples of pellets.

Food-niche Breadth

The estimated food-niche breadth value was 16.67 based on the 85 prey taxa and their relative abundances in pellets. This value was near the lower range of possible values (1 to 85), indicating that although many prey taxa were taken, the food-niche dimension was relatively narrow. The narrow food-niche breadth of the diet indicated selection of a relatively small number of prey taxa in large numbers, which were primarily mammals. The standardized food-niche breadth value of 0.19 also was low in the range of possible values (0–1). Barred Owl diet breadth obtained from regurgitated pellets indicated that Barred Owl prey usage was comparatively high among a relatively small proportion of all the taxa consumed.

Annual Breeding Season Variation in the Diet

Diet composition during the breeding season varied between 2007 and 2008 at seven family areas. In most cases, yearly differences in the percent of prey numbers and biomass for any family area were < 5% (Figures 1.6 and 1.7). However, among some families, 14 taxa showed a difference in percent of prey numbers equal to or greater than 5% between years, and these taxa constituted ≥ 58.2% of the annual breeding season diets across the seven family areas (Table 1.6). Nine of these 14 taxa ranked among the 11 most frequently consumed in the two year sample. Mean masses of the most frequently caught prey in both years ranged from 0.3–134 g.

In both years, owls usually caught small prey including a variety of small forest mammals and unidentified beetles. The relative frequencies of predominate prey of some

families were similar between years while others differed. Coast moles were the most common both years at two of the seven family areas, and northern flying squirrels were most frequently captured both years at one family area. Diets of the remaining four family areas in each year were dominated by either Trowbridge's or vagrant shrews (*Sorex trowbridgii/vagrans*), Townsend's moles (*Scapanus townsendii*), flying squirrels, deer mice, or beetles. Percentages of flying squirrels and beetles were the most common taxa that differed ≥ 5% between years across family areas (Table 1.6).

Percentages of flying squirrels in diets were comparably lower in 2007 versus 2008 across all families except Fawn Creek (Table 1.6). Variation in flying squirrels was most notable at the Kline Creek family area between years (10.1%). The percent of beetles varied most notably between years (13.6%) at Upper Eames Creek (Table 1.6). The greatest between-year differences were a 19.2% decrease in the use of coast moles at Russell Creek and a 15.2% increase in deer mice at Iron Mountain. The percent of Townsend's voles (*Microtus townsendii*) in the diet varied dramatically between years at Fawn Creek and Iron Mountain (Table 1.6), but Townsend's voles did not occur in pellet collections from any other family areas.

The same taxa constituted the primary biomass in the diets each year at three family areas, but different taxa contributed primary biomass at the remaining four areas (Table 1.7). Douglas' squirrel was the most common prey that differed ≥ 5% between years. Percentages of biomass from Douglas' squirrels were lower in 2007 versus 2008 at five areas. Mean masses of taxa that contributed most to total biomass both years ranged from 56–650 g and included coast moles, Townsend's moles, brush rabbits, flying

squirrels, woodrats, and Townsend's voles, spotted skunks, and Band-tailed pigeons (Table 1.7).

Flying squirrels were the primary biomass both years at two of the seven family areas and Townsend's moles at one family area (Table 1.7). Three of the four remaining families shifted to flying squirrels in 2008, when the other shifted to spotted skunks. Flying squirrels were the secondary source of prey biomass in both years at one family area. In addition, flying squirrels were either the primary or secondary source of biomass each year at three areas, alternating with other prey biomass including, Townsend's moles, brush rabbits, woodrats, and Band-tailed Pigeons (Table 1.7).

Yearly differences in percentages of prey biomass were largely related to dietary shifts including: (1) a shift from one major taxon to another; (2) from one major taxon to several taxa; or (3) from two major taxa to a variety of taxa. The first type of dietary shift occurred at two of the four family areas where shifts were observed. At Kline Creek, owls shifted from woodrats to flying squirrels as their primary source of biomass between years (Table 1.7). This shift in source of biomass was associated with a 10.1% increase in the frequency of flying squirrels between years (Table 1.6). Similarly, at Upper Pugh Creek, Band-tailed Pigeons provided the most biomass in 2007 compared to flying squirrels in 2008 (Table 1.7), where the relative importance of flying squirrels increased by 29.5% and Band-tailed Pigeons decreased by 24.1%. I found evidence of Band-tailed Pigeons in the diet at only two owl family areas (Table 1.7).

The second type of dietary shift was exemplified in the Russell Creek family area (Table 1.7), where the primary source of biomass shifted from coast moles (55.3%) in 2007 to several taxa contributing 60.1% of the biomass in 2008 (21.2% spotted skunks,

19.7% flying squirrels, and 19.2% coast moles). Coast mole biomass decreased by 36.1% between years, which was the greatest percentage change among all family areas.

I observed the third type of dietary shift at Iron Mountain where Townsend's moles and Townsend's voles accounted for 30.2 and 26.3% of biomass in 2007, but in 2008, flying squirrels, woodrats, and Townsend's moles contributed 16.6, 13.3, and 12.2% of biomass. In this shift, Townsend's mole and Townsend's vole biomass decreased by 18.0 and 23.6%, while flying squirrels and woodrats, both absent from the diet in 2007, predominated in 2008 (Table 1.7).

Annual Breeding Season Variation in Food-niche Breadth

Estimates of FNB and FNB_{sta} of owls from seven family areas were narrow to moderate in the 2007 and 2008 breeding seasons (Table 1.6), indicating prey usage was comparatively high among a small to moderate proportion of all the taxa consumed. Five of the seven families exhibited higher FNB values in the 2008 breeding season compared to 2007. Also, FNB_{sta} of four family areas increased from 2007 to 2008 (Table 1.6). Russell Creek owls exhibited narrow FNB_{sta} in both years. Fawn Creek and Upper Eames Creek owls demonstrated a shift from a narrow FNB_{sta} in 2007 to moderate in 2008. Iron Mountain, Kline Creek, Lower Oat Creek, and Upper Pugh Creek owls exhibited moderate FNB_{sta} in both years (Table 1.6).

Between-year comparisons of FNB and FNB_{sta} for owls at the seven family areas produced similar results. In 2007, mean FNB_{sta} was 0.39 ± 0.17 (range = 0.18–0.58), while in 2008 mean FNB_{sta} was 0.42 ± 0.10 (range = 0.28–0.58). The mean difference in FNB between years was −3.28 ± 4.59 (range = −10.72 to 3.18, n = 7), and in FNB_{sta} the difference was −0.03 ± 0.16 (range = −0.23 to 0.19, n = 7), but these were not

significantly different from zero for either FNB (paired samples *t*-test, $t_6 = -1.89$, $P = 0.11$) or FNB_{sta} (paired samples *t*-test, $t_6 = -0.53$, $P = 0.61$). These results suggest that, although there was considerable variation in food-niche breadth among owl family areas (Table 1.6), food-niche breadth did not change substantially from one year to another.

Seasonal Variation in the Diet

I compared diet composition and feeding-niche characteristics using 1021 breeding season pellets representing 25 family areas and 106 nonbreeding season pellets from 21 family areas. I identified 3,463 prey individuals that contributed 192,951 g of biomass during the breeding season and 223 prey individuals that contributed 18,161 g of biomass during the nonbreeding season. Mean mass of individual prey during the breeding and nonbreeding seasons was 55.7 and 81.4 g, respectively.

Mammals predominated in owl diets during breeding (64.3% of prey numbers and 87.7% of prey biomass) and nonbreeding seasons (72.6% of prey numbers and 89.8% of prey biomass). Flying squirrels were the primary prey both seasons and increased from 10.3% in the breeding season to 20.6% during the nonbreeding season and increased in biomass from 24.8% to 33.9%. The proportion of birds in the diet also increased from 2.7% in the breeding season to 4.9% in the nonbreeding season. In contrast, the breeding season proportion of coast moles and insects (12.0 and 14.7%) declined during nonbreeding (5.8 and 10.3%, respectively). Contributions of amphibian and gastropod prey declined during the nonbreeding season, but reptile and crustacean numbers and biomass did not differ substantially between seasons.

Predation on large mammals was largely restricted to juveniles captured during the breeding season. For example, the 25 mountain beaver identified in pellets were all

small juveniles (100–550 g) captured during the breeding season. Of 54 brush rabbits and snowshoe hare in pellets, 49 (90.7%) were captured during the breeding season, and 43 (87.8%) were juveniles weighing ≤ 600 g.

Seasonal Variation in Food-niche Breadth

Food-niche breadth was 16.67 during the breeding season (range 1–81) and 14.29 during the nonbreeding season (range 1–45). Of the 85 taxa identified in pellets, 41 occurred in the diet during all seasons, 40 were unique to the breeding season, and 4 were unique to the nonbreeding season. The narrow FNB's indicated disproportionate usage of a few prey, primarily of beetles, coast moles, shrews, and flying squirrels. Standardized food-niche breadth (FNB_{sta}) was narrower during the breeding season than the nonbreeding season (0.20 vs. 0.30), indicating less even selection from the prey base during the breeding season.

Within-Breeding Season Variation in the Diet

Mammals predominated and contributed the most biomass to owl diets during all three periods of the breeding season (Table 1.8). Flying squirrels were the most frequently captured prey during egg-laying and incubation and nestling and brancher periods, whereas coast moles, shrews, and beetles were the most frequently captured prey during the post-fledging period (Table 1.8). Flying squirrels provided the primary source of prey biomass in all three periods of the breeding season (Table 1.8). Other major sources of biomass during egg-laying and incubation were spotted skunks (20.0%) and rabbits or hares (13.8%). During the nestling and brancher period, other major sources of biomass were Douglas' squirrels and spotted skunks (Table 1.8). During the post-

fledging period, other important sources of prey biomass were coast moles (12.6%) and Douglas' squirrels (8.2%; Table 1.8).

Insects, primarily beetles, were common in the diet and increased as the breeding season progressed (6.8%, 9.8%, and 13.7% of prey numbers). However, the percent biomass of insects was ≤ 0.1% in all periods of the breeding season. The frequency of gastropod and amphibian taxa varied the greatest among breeding periods, with highest proportions observed during the nestling and brancher period (19.3 and 12.3% of prey numbers, respectively). Pleurocerid snails and medium-size salamanders accounted for 13.2% and 6.1% of prey numbers during the nestling and brancher period, and were the second and fifth most frequently captured prey taxa during this period. The percent composition of birds and reptiles varied little among periods of the breeding season. Fish, diplopods, collembolans, and crayfish occurred only during the post-fledging period and contributed ≤ 0.2% of prey biomass.

Mean mass of prey consumed by owls during the three periods of the breeding season was 103.5, 51.8, and 56.1 g, respectively. During the 2008 breeding season, owls captured prey ranging in size from small pleurocerid snails and beetles (0.02–0.3 g) to adult snowshoe hare (≥ 1,200 g). The frequency with which owls ate different sized prey during each period of the breeding season was not evenly distributed across all size categories. Prey in the 1–40 g and 81–160 g size ranges were used disproportionately (Figure 1.8). Diets of owls during the egg-laying and incubation period were dominated by prey in the 1–10 g and 81–160 g ranges, accounting for 25.6% of prey numbers. In the 1–10 g range, prey included four of five shrew species (5–9 g) and shrew-moles (9 g). Prey in the 81–160 g range mainly included flying squirrels (134 g).

During the nestling and brancher period, the diet was dominated by taxa in the 11–40 g and < 1 g ranges (31.9% and 22.7% of prey numbers, respectively). The most common prey in the 11-40 g range included deer mice (22 g), western red-backed voles (*Myodes californicus*, 23 g), red tree voles (26 g), medium-sized salamanders (14 g), and Pacific sideband snails (11g; Table 1.8). Taxa in the < 1 g range included pleurocerid snails and beetles (Table 1.8).

During the post-fledging period, prey taxa in the 1–10 g range were the most frequently captured (25.6% of prey numbers), but the taxonomic richness of prey in the 1–10 g range for the post-fledging period was higher than in previous periods, and included more small birds (e.g., Pacific Wren; 9 g), small salamanders (4 g), and large insects (2–3 g), in addition to shrews and shrew-moles (Table 1.8).

Within-Breeding Season Variation in Food-niche Breadth

The number of taxa in the diet was 29 during egg-laying and incubation, 37 during nestling and branching, and 71 during post-fledging. There were 23 taxa that occurred in all three periods of the breeding season. There were 1-2 taxa that were unique to the egg-laying and incubation and nestling and brancher periods, and 33 taxa that were unique to the post-fledging period. Estimates of FNB during the three periods of the breeding season were 12.50 (range 1–29) in the egg-laying and incubation period, 12.50 (range 1–37) in the nestling and brancher period, and 16.67 (range 1–71) during the post-fledging period (Table 1.8). Estimates of standardized food-niche breadths became narrower as the breeding season progressed (egg-laying and incubation: $FNB_{sta} = 0.41$; nestling and brancher: $FNB_{sta} = 0.32$; post-fledging: $FNB_{sta} = 0.22$), mainly due to the

selective use of coast moles, shrews, beetles, and flying squirrels in the post-fledging period (Table 1.8).

Local Variation in the Diet

Differences in percent of prey numbers (Table 1.9) and biomass (Table 1.10) were evident among family areas and primarily reflected differences in the frequency among small-sized prey taxa (Table 1.9). In the cluster analysis of diet similarity based on percent of prey numbers, owl family areas clustered into three broad groups (Figure 1.9). Cluster 1 comprised five family areas that exhibited the lowest degree of dissimilarity (Semipartial r-squared [SPRSQ] value = 0.06) in diet from other areas, with slightly more than half (55.9–62.9%) of the diet consisting of mammals (Doe Hollow, Upper Eames Creek, Shitten Creek, Upper Pugh Creek, and Russell Creek in Table 1.9). These five family areas were similar in shared prey composition and exhibited the highest proportions of moles (*Scapanus* spp.), red tree voles, and arthropods in the diet compared to other areas. Cluster 2 comprised eight family areas that exhibited a moderate degree of dissimilarity (SPRSQ = 0.08) from other areas, with a slightly higher proportion of mammals (61.7–75.8%) than Cluster 1 (Fawn Creek, Kline Creek, Upper Wildcat Creek, Lower Buck Creek, Siuslaw Falls, Lower Oat Creek, High Point, and Iron Mountain in Table 1.9). These eight family areas were similar in shared prey composition and relative proportions of prey numbers, but were dissimilar to other areas mainly due to the absence of spotted skunks and comparatively higher proportions of shrews (*Sorex* spp.) and mountain beaver. Cluster 3 comprised the remaining two family areas, and was most dissimilar (SPRSQ = 0.10) to Clusters 1 and 2 and reflected mainly high use of mammalian prey taxa constituting 85.9 and 89.1% of prey numbers in Lower Pugh Creek

and Saragosa (Table 1.9), where diets included comparably fewer taxa, higher proportions of woodrats (6.1 and 4.7% of prey numbers), and an absence of arthropods.

The cluster analysis based on percent of prey biomass of 23 pooled prey taxa produced two broad groups (Figure 1.10). Cluster 1 comprised five family areas and exhibited the most dissimilarity from other areas (SPRSQ = 0.15). Dissimilarities were reflected by differences in primary and secondary sources of biomass. For example, the primary source of biomass in Doe Hollow and Saragosa included larger prey such as rabbits and/or hares followed by moles (Table 1.10). In contrast, the primary and secondary sources of biomass in Fawn Creek, Iron Mountain, and Russell Creek in Cluster 1 were moles and flying squirrels (Table 1.10). Cluster 2 exhibited the lowest degree of dissimilarity (SPRSQ = 0.11) in association with flying squirrels as the primary biomass (23.8 to 53.2%) for eight of ten family areas in Cluster 2. Cluster 2 partitioned into two smaller clusters largely due to differences in secondary sources of biomass; the first included three family areas in which mountain beaver or Douglas' squirrels were the secondary source of biomass, and the second, smaller cluster included four family areas in which moles were the secondary source of biomass (Table 1.10). Flying squirrels accounted for 22.6 and 18.0% of biomass at Upper Pugh Creek and Siuslaw Falls, but these were dissimilar to other areas because other taxa had higher values with birds contributing 22.8% of prey biomass at Upper Pugh Creek and other mammals (common muskrats [*Ondatra zibethicus*], 26.1%) contributing 27.9% of the prey biomass at Siuslaw Falls. Although flying squirrels were the primary source of biomass at the Lower Pugh family area, this area did not cluster with other areas within Cluster 2 because the richness of the diet (14) was relatively low compared to other areas in the cluster.

Local Variation in Food-niche Breadth

Standardized food-niche breadth (FNB_{sta}) at the 15 family areas ranged from 0.17 to 0.63 (mean = 0.39 ± 0.12). Twelve of the 15 family areas had $FNB_{sta} \geq 0.34$, thereby indicating that the majority of areas exhibited a moderate food-niche breadth (Table 1.9 and Figure 1.11).

Diet Composition Associated with Reproductive Success

I compared diets of non-nesting and nesting owls based on a collection of 112 pellets from five pairs of non-nesting owls and 159 pellets from five pairs that successfully fledged young. Prey obtained from the pellet samples included 316 prey individuals (prey biomass = 18,366 g) from non-nesting owls and 507 prey (30,301 g) from owls that nested successfully (Table 1.11). Of 61 taxa identified in the pellets, 7 were unique to non-nesting owls, 13 were unique to successful nesters, and 41 were shared in common.

Mammals predominated in the diet regardless of nesting status. However, nesting pairs had slightly higher proportions of mammals in the diet (70.6% of prey numbers and 92.9% of prey biomass) than non-nesting pairs (58.2% of prey numbers and 81.8% of prey biomass; Table 1.11). Non-nesting pairs captured comparatively fewer mammals and more birds, amphibians, gastropods, and insects than nesting pairs. Mean mass of prey was 60.0 ± 27.0 g (SD) for non-nesting owls and 60.8 ± 17.0 g for successful nesters. Because mammalian taxa, particularly medium-sized to large mammals, were energetically important to both non-nesting owls and nesting pairs that fledged young, it was unclear whether diet composition was related to reproductive success.

Food-niche Breadth Associated with Reproductive Success

Estimates of FNB and FNB_{sta} of non-nesting owls and owls that nested successfully were nearly identical (Table 1.11). Comparisons of FNB and FNB_{sta} for pairs of owls at five family areas where pairs did not nest in one year and nested successfully in the other year produced similar results (Table 1.12). Mean FNB_{sta} of the five non-nesting pairs was 0.47 ± 0.15 (range = 0.22–0.60) and mean FNB_{sta} for the five successful pairs was 0.43 ± 0.08 (range = 0.36–0.57). Paired comparisons of FNB and FNB_{sta} in the years when pairs did or did not nest indicated no difference based on nesting status for either FNB (paired samples *t*-test, $t_4 = 0.47$, $P = 0.67$) or FNB_{sta} (paired samples *t*-test, $t_4 = -0.75$, $P = 0.50$; Table 1.12). These results suggest that there was no consistent relationship between food-niche breadth and nesting status of owls.

Discussion

During the last 100 years, the range of the Barred Owl has expanded from eastern North America to western North America (Livezey 2009a). My results from 27 family areas occupied by Barred Owls in western Oregon revealed a rich diet including 89 taxa, but that prey usage varied spatially and temporally during the two-year study period. Some characteristics of the Barred Owl diet in this recent range appear to be different than the diets described from studies in other parts of the range. However, most other studies were based on fewer birds, often pooled from an unknown local distribution, and confined to one season. While these differences limit some comparisons, many of my results can be discussed in the context of studies conducted elsewhere in the species distribution.

Mean size of pellets collected in my study (48.3 ± 13.5 mm × 25.8 ± 5.0 mm) was slightly smaller than estimates from another study of Barred Owls in Montana (mean = 61.4 × 24.5 mm; Holt and Bitter 2007). In contrast, Dunstan and Sample (1972) reported that mean size of Barred Owl pellets collected in Minnesota was only 3.5 × 7.2 mm. The latter estimate of mean pellet size is so small that I suspect it is an error. I think the authors reported their measurements in mm when the measurements were actually in cm. If that is the case, then their estimate of mean pellet size is larger than in my study or the study by Holt and Bitter (2007). I could not find any studies that reported mean size of pellets from Northern Spotted Owls, so I could not compare size of pellets of Barred Owls to that of Northern Spotted Owls.

Wilson (1938) found that the mean number of prey in Barred Owl pellets in Michigan was 3.12. This result was virtually identical to mine (mean = 3.35 ± 3.07). I found no other studies of Barred Owl diet that estimated the mean number of individual prey per pellet. Forsman (1980) reported that the mean number of prey per pellet for Northern Spotted Owls in Oregon varied by season, from a low of 0.70 during fall and winter (September–February) to a high of 2.07 in summer (May–August). These estimates are considerably lower than for my Barred Owls, and probably reflect the fact that the diets of Barred Owls in my study included a much higher proportion of small prey (e.g., shrews, invertebrates) than did the diets of Northern Spotted Owls studied by Forsman (1980).

Diets of the Barred Owls studied by Wilson (1938) were also similar to the owls in my study in that owls in both studies consumed large numbers of small taxa such as shrews, voles, mice, and insects. The prevalence of small mammals and insects in Barred

Owl diets in these two widely disparate areas indicates Barred Owls are well adapted to feeding on small prey. The ability of Barred Owls to subsist on a wide variety of small mammals, birds, and invertebrates might be an important factor contributing to their successful westward range expansion.

Dietary Composition, Richness, and Diversity

Diets of Barred Owls in my study had high taxonomic richness. Prey taxa accumulation and rarefaction curves did not become asymptotic, even with collections as large as 62 pellets from individual family areas. However, the curves did exhibit decreasing slopes as the sample of pellets increased, and all but the rarest taxa were encountered with collections of ≥ 30 pellets, which usually contained > 100 individual prey items. Nevertheless, larger collections would undoubtedly provide a more complete picture of the diet. Because I described the diet based primarily on evidence from pellets, it is likely that soft-bodied invertebrates (e.g., earthworms, slugs) were underrepresented in my samples (Elderkin 1987, Livezey et al. 2008b). A combination of methods that included pellet data as well as information from direct observation of nests (i.e., Lewis et al. 2004) would be useful for developing a more complete taxonomic list of Barred Owl prey.

Although the diet in my study area had high taxonomic richness (≥ 85 taxa), the food-niche breadth was typically narrow to moderate, indicating that the owls obtained most of their prey biomass from a few taxa, especially small to medium-sized mammals. My estimate of standardized food-niche breadth was narrower than in most previous studies of Barred Owls (Table 1.13), but this result must be interpreted in light of the fact that dietary richness in all previous studies was much lower than in my study (Table

1.13). The disproportionate use of a small number of taxa (mainly mammals), is a recurring theme in most diet studies of Barred Owls (Bosakowski and Smith 1992, Marti et al. 1993). The one exception was a study on the west slope of the Cascade Range of Washington in which Hamer et al. (2001) found more equitable use of a broad range of small mammals (FNB_{sta} = 0.53).

Barred Owl diets in my study area included a large number of taxa ranging from insects to medium-size mammals. A large variety of taxa in diets of Barred Owls also is common in many other study areas in eastern North America (Errington and McDonald 1937, Wilson 1938, Korschgen and Stuart 1972, Devereux and Mosher 1984, Elderkin 1987, Bosakowski and Smith 1992) and western North America (Mazur et al. 1997b, Takats 1998, Hamer et al. 2001). Barred Owls are mainly nocturnal (Nicholls 1973, Fuller 1979), but diurnal movements and foraging are not uncommon (Caldwell 1972, Fuller 1979, this study). Diurnal foraging is also suggested by the fact that their diets include considerable number of diurnal mammals, birds, and reptiles (e.g., Douglas' squirrels, Townsend's chipmunks, most birds, reptiles). These results indicate that Barred Owls are generalist predators, capturing a wide variety of the local fauna, and enabling them to be opportunists, able to colonize previously unexploited habitat.

My study was similar to a study by Mazur et al. (1997b) in that diets of Barred Owls included relatively low proportions of birds (2.9 vs. 4.8%) and high proportions of beetles (11.7 vs. 15.2%). However, my findings contrast with Mazur et al. (1997b) because, in Saskatchewan, Canada, owls ate large numbers of frogs (63.6%), whereas diets in my study area were dominated by small to medium-sized mammals (62.2%).

Takats (1998) found that 78 Barred Owl pellets from west-central Alberta, Canada, contained 45.8% mammals, 25.2% birds, 24.5% wood frogs (*Rana sylvatica*), 0.6% gastropods, and 3.9% predacious diving beetles (*Dytiscus alaskanus*). My results were similar in that diets of Barred Owls in my study were dominated by small to medium-sized mammals, but differed in that Takats (1998) found much higher proportions of birds and frogs in the diet. High numbers of frogs in the diets of owls in the Canadian study areas suggest that frogs may have been more abundant in those areas than in my study area. The occurrence of fairly high numbers of amphibians in Barred Owl diets in many different areas (Mazur et al. 1997b, Takats 1998, Hamer et al. 2001, this study) indicates that Barred Owls frequently forage in riparian or wetland habitats (Bosakowski et al. 1987, Bosakowski and Smith 1992, Fuller 1996, Mazur and James 2000). More recently, several studies in the Pacific Northwest have also documented Barred Owls association with moist bottomland forests containing mixed riparian and varied spaces of wetland (Herter and Hicks 2000, Buchanan et al. 2004, Hamer et al. 2007, Singleton et al. 2010, Wiens 2012). Pellets containing freshwater pleurocerid snails and crayfish clearly indicate that Barred Owls in my study were wading in shallow water to obtain food, as these types of food would have been difficult to obtain without wading.

My findings included some notable differences and similarities with other studies of Barred Owl diets in the Pacific Northwest region of the United States. For example, the richness of the Oregon owl diet (≥ 85 taxa) was higher than on the west slope of the Cascade Range of Washington (≥ 20 taxa; Hamer et al. 2001). This could have been due to the difference in sample size in my study (n = 3,686 prey) and the Hamer et al. (2001) study (n = 265 prey). While diets at both locations were dominated by mammals, diets in

my study area included fewer flying squirrels and higher percentages of moles, shrews, and insects than in the Hamer et al. (2001) study. Hamer et al. (2001) also documented a higher proportion of birds (11.0%) than in my study (2.9%).

Generally, the diet of Barred Owls, based on my intensive study in central Oregon and in comparison with several other studies spanning the species' distribution, reveals diverse food habits of somewhat different species composition by locale, and a relatively narrow food niche, also differing among the species that are eaten most frequently and contribute the greatest proportion of biomass. In addition to variation in the occurrence of habitat and habitat use by Barred Owls, other important factors can cause regional differences in Barred Owl diets. These factors include annual, seasonal, within-breeding season, and local variation in owl food requirements.

Annual Breeding Season Variation in Diet

In my study, most year-to-year differences in dietary composition involved changes that were < 5% for individual taxa. Annual changes in usage that were ≥ 5% involved a few taxa, including coast moles, flying squirrels, deer mice, and beetles (Table 1.6 and Figure 1.6). Some family diets shifted from relatively large numbers of one species in one year (e.g., Townsend's voles) to several other taxa in another year. Prey taxa that constituted the primary percentages of biomass in the diets of each of the seven owl families were the same each year at three family areas, but shifted among taxa at the remaining four family areas (Table 1.7). Yearly differences in percentages of biomass by taxa resulted when a family diet shifted from one major taxon to another or from one or two major taxa to a few major taxa. These temporal shifts in the quantity of taxa used could be due to fluctuations in prey populations, prey availability, or selection or

preference behavior by the owls. Additionally, these data suggest that Barred Owls are capable of switching among prey types depending on prey abundance. The ability to take a broad range of prey and to switch among prey types depending on abundance may explain how Barred Owls have been able to rapidly expand their range across North America, inhabiting a broad range of forest types, from boreal forests in central Canada and southeast Alaska, to temperate rain forests in Washington and Oregon.

I found no published reports of annual variation in diets of Barred Owls. However, annual and seasonal variation in diets has been described for many other predatory birds. For example, Forsman et al. (2004) reported large annual variation in the proportion of flying squirrels and deer mice at some Northern Spotted Owl territories in Oregon, but found little annual variation at other territories. Korpimäki and Sulkava (1987) documented Ural Owls (*Strix uralensis*) shifting from their principal prey (*Microtus* spp.) to prey such as shrews, birds, and frogs during years when *Microtus* populations declined in Finland. Sahores and Trejo (2004) described Barn Owls (*Tyto alba*) switching from the bunny rat (*Reithrodon auritus*) to the Morgan's gerbil mouse (*Eligmodontia morgani*) after fires caused vegetation changes in Argentina. Olsen et al. (2008) found that Peregrine Falcons (*Falco peregrinus*) and Australian Hobbies (*F. longipennis*) switched from their primary prey, European Starlings (*Sturnus vulgaris*), to a variety of native bird species during years when European Starlings declined. Lastly, Steenhof and Kochert (1988) found that the proportion of Black-tailed jack rabbits (*Lepus californicus*) in diets of Golden Eagles (*Aquila chrysaetos*) decreased from 72% to 21% when jack rabbit numbers declined in southwest Idaho. When jack rabbit numbers were low, eagles used an alternative suite of prey including rodents and birds. Steenhof and

Kochert (1988) also reported that Red-tailed Hawks (*Buteo jamaicensis*) shifted to gopher snakes (*Pituophis melanoleucus*), kangaroo rats (*Dipodomys* spp.), and rabbits when their primary prey (Townsend's ground squirrel; *Spermophilus townsendii*) was at low density. These examples conform to optimal foraging theory that predicts diet breadth should expand when the abundance of the primary prey decreases and shrink when the primary prey increases (Pyke et al. 1977, Pyke 1984). I did not have data on prey abundance in my study area, so I could not test this hypothesis.

Seasonal Variation in the Diet

Few studies have reported the nonbreeding season or winter diet for Barred Owls in North America (Mazur and James 2000). In my study, predation on flying squirrels increased sharply during the nonbreeding season, while the use of lagomorphs and mountain beaver was mostly restricted to the breeding season when owls could take small juvenile lagomorphs, mountain beaver, and grouse. Prey that became largely unavailable during the nonbreeding season due to migration, hibernation, or periodic torpidity (e.g. migratory passerines, chipmunks, crayfish, insects, reptiles, some amphibians) were, to a large extent, absent in winter pellets and replaced with arboreal mammals that were available year-round. Crayfish that constructed burrows or burrow systems to elude predators or for hibernation were absent from the diet from about November–March.

Seasonal variation in diet of Barred Owls in my study was very similar to seasonal patterns in diets of Northern Spotted Owls in Oregon (Forsman 1980; Forsman et al. 1984, 2004) and in Washington (Forsman et al. 2001). For example, Forsman (1980) found that predation on lagomorphs and mountain beaver by Northern Spotted Owls was largely limited to juveniles captured during spring and summer. These results

suggest that adult snowshoe hare, brush rabbits, and mountain beaver are too large for Barred Owls and Northern Spotted Owls to capture easily, and are thus uncommon in the diet in all seasons. Seasonal use of juvenile lagomorphs has also been documented in other owls, including Barn Owls (Marti 1988), Great Horned Owls (*Bubo virginianus*; Rohner and Krebs 1996), Eagle Owls (*Bubo bubo*; Donázar and Ceballos 1989), Snowy Owls (*Bubo scandiacus*; Watson 1957), Northern Hawk Owls (*Surnia ulula*; Rohner et al. 1995), Great Gray Owls (*Strix nebulosa*), Tawny Owls (*Strix aluco*), Ural Owls (Mikkola 1983), and Long-eared Owls (*Asio otus*; Marks et al. 1994).

As in my study, Forsman (1980) and Forsman et al. (1984, 2001, 2004) also found that richness of Northern Spotted Owl diets declined in winter when many types of prey became less abundant or less available than during the breeding season. However, there were some differences between Barred Owls in my study and Northern Spotted Owls. One difference was that the proportion of birds in the diet of Northern Spotted Owls declined during the nonbreeding season (Forsman et al. 1984, 2001, 2004), whereas the proportion of birds in diets of Barred Owls increased during the nonbreeding season in my study.

Barred Owls have expanded their range into many areas of western North America including areas of western Montana (Shea 1974, Holt et al. 2001). In western Montana, Marks et al. (1984) reported that voles (*Microtus* spp.) accounted for 96.3% of the nonbreeding season or winter diet of Barred Owls. During another winter food habits study in western Montana, Holt and Bitter (2007) also found that the diet was largely comprised of *Microtus* (97.6% of prey numbers). These two studies stand in stark contrast with my study and most other studies of Barred Owls that have found high

species richness and generally moderate levels of food-niche breadth. Perhaps the almost total domination of the winter diet by a few species of *Microtus* in the Montana studies is just another example of the extremely adaptable nature of the Barred Owl regarding prey selection.

Diets of Barred Owls in areas of their historical range exhibited seasonal variation similar to what occurred in Oregon. Errington and McDonald (1937) revealed that during the breeding season, Barred Owl diets in Iowa and Wisconsin included a diversity of taxa. The diet was generally dominated by vertebrate prey including small fish, salamanders, frogs, garter snakes, a variety of common birds, juvenile eastern cottontail rabbits (*Sylvilagus floridanus*), voles, mice (*Peromyscus* spp.), moles, and invertebrate crayfish (*Cambarus* spp.) and beetles. During winter, Barred Owl diet in Iowa and Wisconsin shifted to more mammalian taxa, predominated by mice and shrews, with no evidence of adult cottontails. In addition, owls preyed on at least 10 resident or wintering bird species such as the Dark-eyed Junco and Eastern Screech-Owl.

Within-Breeding Season Variation in the Diet

Raptorial birds (Newton 1979) including owls (Mikkola 1983) partition their parental roles of provisioning young with food during the breeding season in a more marked way than most other bird taxa. Reversed sexual size dimorphism (RSD) is a trait in most diurnal and nocturnal raptors, including Barred Owls, and can be partially explained by several factors promoting hunting efficiency in males and egg production efficiency in females, or alternatively, to reduce intersexual competition for food (Snyder and Wiley 1976). In Barred Owls, the smaller-sized males provide the majority of food

for females from egg-laying to about the middle of the nestling period (Robertson 1959, Elderkin 1987, Mazur and James 2000).

My results agree, in part, with this RSD hypothesis. The relatively high frequency of small prey (< 1–40 g) in the diet during the egg-laying and incubation and nestling periods (when the female is on the nest most often) supported the hypothesis that predation by male Barred Owls was focused on delivery of small prey to the female and developing young. In addition, medium-sized prey (81–160 g) and some large prey (> 300 g) identified in the diet during the egg-laying and incubation period perhaps reflects some hunting by the female. However, the low frequency of large prey captured during the post-fledging period was not consistent with RSD theory.

Consequently, breeding period-specific variation in the diet could be unrelated to RSD, and possibly associated with seasonal availability of prey, or the lack of larger prey in the diet during the post-fledging period may reflect that there was little sexual difference in diet. If there were little intersexual difference in diet, my findings with Barred Owls would be consistent with those reported for Northern Spotted Owls studied by Forsman et al. (1984), who concluded that there was no difference in diet composition or prey size between the sexes. Gender-specific diet data are required to learn if male and female Barred Owls choose different size prey. During preference experiments with wild Barred Owls, no difference occurred in the frequency with which female Barred Owls captured prey by size compared to males, with both sexes exhibiting preference for small-sized prey (see Chapter Three).

Local Variation in the Diet

My cluster analysis of family area-specific diets based on percent of prey numbers partitioned 15 owl family areas into three clusters based on diet similarity. The main differences among these clusters were differences in the proportions of mammalian taxa in the diet. My analysis based on percent of prey biomass partitioned these family areas into two clusters. As with prey numbers, cluster analysis based on percent of prey biomass indicated differences primarily due to various mammalian taxa used among the family diets. One obvious explanation for much of the variation among family area-specific diets could be local variation in prey abundance. Prey abundance might reflect differences in taxonomic richness and prey numbers among family area diets. Therefore, I hypothesize that prey selection by pairs of owls is likely locality dependent, which in turn suggests that most owl families adapted their diet to the food supply locally available to them (i.e., that they forage as generalist opportunists). For example, several owl pairs that took large numbers of crayfish were located along the Siuslaw River where there were numerous shallow pools and streams that provided ideal crayfish habitat.

Diet Composition Associated with Barred Owl Reproductive Success

Although diet can be an important factor related to reproductive success in raptorial birds (Newton 1979, Arroyo 1998, Ward et al. 1998, Smith et al. 1999, Seamans and Gutiérrez 1999), I found no associations between diet and reproductive success in Barred Owls, regardless of whether I examined percent composition of the diet or FNB and FNB_{sta}. The lack of association between diet and reproductive success is interesting, but my data set of individual family areas (n = 5) was small. Future comparisons with larger samples might help to investigate relationships between diets and reproductive

output of Barred Owls. However, given that prey delivered to the female and young by nesting males may be biased towards large prey (Bull and Henjum 1990, E. Forsman pers. comm.), it is possible that dietary studies based on pellets may produce spurious results.

Conclusions and Implications

My results demonstrate that Barred Owls in west-central Oregon utilize a large number of prey taxa and feed heavily on many species of common terrestrial and arboreal mammals. This dietary flexibility is likely an important factor in this species' ability to dramatically extend its range westward across northern North America during the past 100 years. Small to medium-sized taxa predominated in Barred Owl diet and provided the majority of prey biomass. I found spatial and temporal differences in diet, suggesting that from the array of prey they eat, there is flexibility on a local and temporal basis to use some taxa more than others, including marked dietary shifts among taxa. Overall, the spatiotemporal variations in Barred Owl diet appear to reflect this species' adaptation and opportunistic feeding strategies in this area of range expansion. These results contribute to understanding the ecological role of Barred Owls in their new environment, including potential competition with native fauna of the Pacific Northwest, especially Northern Spotted Owls.

Barred Owl Diet and Predator–Prey Ecology

As a recent colonizer of western North America, and a species that likely feeds on more than 100 taxa there, Barred Owls directly affect many ecological communities (see Chapter Two). Small mammals are a predominant source of biomass in the northwest United States, and the importance of small mammals to Barred Owls was further

indicated by my finding that Barred Owls preferred small-sized mice to medium-sized rats (see Chapter Three). The ecological role of Barred Owls will be multifaceted, but one potential effect of the species' range expansion that has received special interest is competition with congeneric Spotted Owls, especially the Northern Spotted Owl subspecies, which is designated Threatened in the United States (U.S. Fish and Wildlife Service 1990) and Endangered in Canada (Harestad et al. 2004).

Information as to how Barred Owl range expansion might affect Northern Spotted Owls, including research and management responses to address such effects, has been summarized by numerous scientists (Buchanan et al. 2007, Gutiérrez et al. 2007). The background information has been based mainly on incidental detections of Barred Owls during Northern Spotted Owl monitoring studies (Anthony et al. 2006, Forsman et al. 2011), occupancy modeling (Olson et al. 2005, Bailey et al. 2009, Dugger et al. 2011) and recent Barred Owl home range studies (Singleton et al. 2010). In the Pacific Northwest, results from these studies suggest that Barred Owls are well adapted to and firmly established in their new range. The food habits of Barred Owls are an important factor in their ecological relationship to the Northern Spotted Owl and for the conservation of these two species in their sympatric range. David Wiens studied the potential for competition on our common Oregon study area. He compared food habits of the two species and evaluated their home range and habitat use. Here, I discuss generally my results in the context of previous findings about diet.

My research reveals that some taxa in Barred Owl diets also occur in diets of Northern Spotted Owls in nearby areas, and therefore present some potential for competition. There are differences in proportional Barred Owl usage of these taxa

documented by me and that by others for Northern Spotted Owls. For example, Barred Owls (this study) and Northern Spotted Owls (Forsman et al. 2004; Central Coast Region) captured various proportions of shrews (13.6 vs. 0.9%), moles (17.8 vs. 0.2%), flying squirrels (10.9 vs. 49.5%), deer mice (3.9 vs. 10.5%), woodrats (1.4 vs. 7.1%), red tree voles (4.0 vs. 12.7%), and salamanders (9.3 vs. 0.0%) in the central Coast Range of western Oregon. These proportions indicate that some prey that are important for Barred Owls do not appear to be so for Northern Spotted Owls, including shrews, moles, and salamanders. Important biomass in year-round Barred Owl and Northern Spotted Owl diets comes from flying squirrels (25.6 vs. 58.3%), moles (16.6 vs. 0.1%), Douglas' squirrels (8.0 vs. 1.2%), woodrats (6.7 vs.16.1%), and brush rabbits and/or snowshoe hare (10.9% vs. 9.9%). However, three larger mammal prey, the flying squirrel, woodrat, and lagomorphs contributed much biomass to the diets of both owl species; and of special interest are flying squirrels, on which the Northern Spotted Owl specializes (Forsman et al. 2004) in the central Coast Range of western Oregon.

Flying squirrels represented the most biomass in the year-round diet for both owl species, and the proportion of flying squirrel biomass in their respective diets (Forsman et al. 1984, 2001, 2004) is higher in the nonbreeding season than the breeding season. Therefore, with year-round, mutual use of flying squirrels by Barred Owls and Northern Spotted Owls, I hypothesize that the abundance of flying squirrels might be reduced in areas of owl sympatry resulting in a negative effect on the Northern Spotted Owl's primary prey resource (Forsman et al. 1984, 2001, 2004) numerically and by weight. In fact, Rosenberg and Anthony (1992) suggested that high predation on flying squirrels by Northern Spotted Owls (Forsman et al. 1984, Miller 1989) may affect squirrel abundance

on the west slopes of the central Cascade Range of Oregon, which is proximate to my study area. Additionally, flying squirrel populations persisting in low densities (Carey et al. 1992, Carey and Peeler 1995) also predominated in diets of Northern Spotted Owls (Forsman et al. 1984) at five study areas near the city of Roseburg in southwestern Oregon, three of which were bounded to the south of this study area. Consequently, I suspect high predation on flying squirrels by recently expanded Barred Owls may interfere with Northern Spotted Owl foraging and reduces the abundance of flying squirrels.

Barred Owls were abundant in my study area (0.60 owls detected/km^2; Wiens et al. 2011), and food habits likely have implications for small mammal communities and other predators' diets that overlap. For example, Barred Owls probably have dietary overlap with other co-occurring owls including Great Horned Owls, Western Screech-Owls (*Megascops kennicottii*), Northern Saw-whet Owls (*Aegolius acadicus*), Northern Pygmy Owls (*Glaucidium gnoma*), and some diurnal raptors such as Red-tailed Hawks, Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*A. cooperi*), and Northern Goshawks (*A. gentilis*). Bosakowski and Smith (1992) found that Barred Owls had moderate diet overlap with sympatric Eastern Screech-Owls and Red-tailed Hawks in New England, primarily due to shared use of shrews and mice. Therefore, because Barred Owls have prey-rich diets including high proportions of small prey taxa such as shrews and mice in this western study area, future research aimed to examine dietary overlap of sympatric forest raptors in this area would be valuable. The study of diet also provides a basis for future research of the long-term consequences of a new top-level predator in the community. After colonization, the effects of Barred Owls on prey populations likely

change as prey adapt to their presence and to the responses of other community members that are affected by the predator.

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Table 1.1. Predicted biomass conversions used for signal crayfish (*Pacifastacus leniusculus*) identified in regurgitated Barred Owl pellets collected from western Oregon, 2007-2009. In conversion models, predicted mass (M) and dry mass are in grams.

Crayfish proportions	Predicted biomass conversion (g)
Entire crayfish	M = 2.64002 + 4.33463 (dry mass*)
Crayfish with left chela only	M = 2.94676 + 5.58831 (dry mass*)
Crayfish with right chela only	M = 1.99055 + 0.92656 (Log of dry mass*)
Crayfish with both chelae removed	M = 2.47560 + 5.53214 (dry mass*)

* Dry mass of crayfish remains observed in pellets

Table 1.2. Dimensions (mm) of intact regurgitated pellets collected from beneath nest and roost locations of 21 Barred Owl family areas in western Oregon, 2007–2009. Mean length and width of all pellets in the sample was 48.3 × 25.8 mm (SD_{length} = 13.5; SD_{width} = 5.0). Pellets ranged in length from 17.9–85.7 mm and width from 12.1–45.0 mm.

		Length (mm)	Width (mm)
Family Area	*n* [a]	Mean ± SD	Mean ± SD
Alma	1	49.6 ± 0.0	28.4 ± 0.0
Doe Hollow	12	59.4 ± 13.8	27.4 ± 3.5
Elkhorn Creek	4	59.2 ± 18.4	26.9 ± 1.6
Fawn Creek	12	50.6 ± 11.0	24.1 ± 2.5
Gardner Creek	2	27.4 ± 5.0	19.7 ± 0.5
Hell Hollow	4	56.5 ± 3.3	27.1 ± 4.5
High Point	11	40.0 ± 13.1	21.2 ± 6.7
Iron Mountain	6	54.8 ± 8.4	30.5 ± 7.8
Kline Creek	15	43.7 ± 13.1	23.0 ± 5.2
Lower Buck Creek	13	48.6 ± 13.7	24.5 ± 2.9
Lower Oat Creek	30	52.8 ± 13.3	26.6 ± 4.5
Lower Pugh Creek	7	58.5 ±17.6	29.1 ± 4.2
Lower Wildcat Creek	2	50.2 ± 3.9	30.7 ± 1.1
Pataha Creek	5	58.1 ± 13.6	28.8 ± 7.3
Russell Creek	39	49.5 ± 14.9	26.5 ± 4.8
Saragosa	1	47.3 ± 0.0	23.5 ± 0.0
Shitten Creek	15	45.3 ± 10.4	26.0 ± 3.9
Siuslaw Falls	15	46.3 ± 11.9	23.3 ± 4.9
Upper Eames Creek	38	45.3 ± 11.0	26.2 ± 3.7
Upper Pugh Creek	29	41.7 ± 11.6	26.1 ± 6.4
Upper Wildcat Creek	1	58.0 ± 0.0	24.4 ± 0.0
All Pellets	262	48.3 ± 13.5	25.8 ± 5.0

[a] Number of entire, intact regurgitated pellets measured from each area used by Barred Owls.

Table 1.3. Prey taxa (*n* = 85), mean mass, and relative percentages of total prey numbers, prey biomass, and prey occurrence of each taxa identified from regurgitated pellets collected from 26 Barred Owl family areas in western Oregon, 2007–2009.

	Mean Mass	Number		Biomass		Occurrence	
Prey Taxa	g[a]	*n*[b]	(%)[c]	g	(%)[d]	*n*[e]	(%)[f]
Mammals							
Sorex bendirii	18	5	0.1	90	< 0.1	5	0.4
Sorex sonomae	9	73	2.0	657	0.3	57	5.1
Sorex trowbridgii	5	34	0.9	170	0.1	27	2.4
Sorex trowbridgii / vagrans	5	363	9.8	1815	0.9	215	19.1
Sorex vagrans	5	30	0.8	150	0.1	24	2.1
Neurotrichus gibbsii	9	154	4.2	1386	0.7	123	10.9
Scapanus orarius	56	428	11.6	23968	11.4	316	28.0
Scapanus townsendii	131	73	2.0	9563	4.5	69	6.1
Myotis spp.	6	3	0.1	18	< 0.1	3	0.3
Sylvilagus bachmani	350–650	14	0.4	7750	3.7	14	1.2
Lepus americanus	1075–1200	4	0.1	4475	2.1	4	0.4
Leporidae spp.	50–1100	36	1.0	10860	5.1	36	3.2
Aplodontia rufa	100–550	25	0.7	10000	4.7	25	2.2
Tamias townsendii	83	37	1.0	3071	1.5	35	3.1
Tamiasciurus douglasii	221	76	2.1	16796	8.0	74	6.6
Glaucomys sabrinus	134	403	10.9	54002	25.6	367	32.6
Unidentified Sciurid spp.	143	6	0.2	858	0.4	6	0.5
Thomomys mazama	95	18	0.5	1710	0.8	18	1.6
Peromyscus maniculatus	22	144	3.9	3168	1.5	113	10.0
Neotoma spp.	285	50	1.4	14250	6.7	50	4.4
Rattus rattus	250	1	< 0.1	250	0.1	1	0.1
Myodes californicus	23	61	1.7	1403	0.7	54	4.8
Arborimus longicaudus	26	147	4.0	3822	1.8	117	10.4
Microtus longicaudus	53	7	0.2	371	0.2	5	0.4
Microtus oregoni	20	49	1.3	980	0.5	44	3.9
Microtus townsendii	57	14	0.4	798	0.4	11	1.0
Microtus spp.	31	18	0.5	558	0.3	17	1.5
Ondatra zibethicus	1169	3	0.1	3507	1.7	3	0.3
Muridae spp.	25	54	1.5	1350	0.6	46	4.1
Zapus trinotatus	25	33	0.9	825	0.4	26	2.3
Mustela erminea	55	12	0.3	660	0.3	12	1.1
Spilogale gracilis	606	10	0.3	6060	2.9	10	0.9
Unidentified mammals	33–250	2	0.1	283	0.1	2	0.2
Mammals subtotal		**2387**	**64.8**	**185624**	**87.9**	**1042**	**92.5**
Birds							
Bonasa umbellus	25–576	4	0.1	2084	1.0	4	0.4
Dendragapus obscurus	1050	1	< 0.1	1050	0.5	1	0.1
Grouse spp.	350–576	1	< 0.1	350	0.2	1	0.1
Oreortyx pictus	224	3	0.1	672	0.3	3	0.3
Patagioenas fasciata	392	7	0.2	2744	1.3	7	0.6

Table 1.3. Continued.

Prey Taxa	Mean Mass g[a]	Number *n*[b]	Number (%)[c]	Biomass g	Biomass (%)[d]	Occurrence *n*[e]	Occurrence (%)[f]
Aegolius acadicus	83	7	0.2	581	0.3	6	0.5
Megascops kennicottii	169	5	0.1	845	0.4	5	0.4
Colaptes auratus	142	4	0.1	568	0.3	4	0.4
Dryocopus pileatus	287	1	< 0.1	287	0.1	1	0.1
Picoides villosus	66	1	< 0.1	66	< 0.1	1	0.1
Sphyrapicus ruber	49	2	0.1	98	< 0.1	2	0.2
Empidonax spp.	11	1	< 0.1	11	< 0.1	1	0.1
Cyanocitta stelleri	128	6	0.2	768	0.4	6	0.5
Perisoreus canadensis	73	1	< 0.1	73	< 0.1	1	0.1
Poecile rufescens	10	4	0.1	40	< 0.1	3	0.3
Sitta canadensis	10	3	0.1	30	< 0.1	3	0.3
Troglodytes pacificus	9	20	0.5	180	0.1	18	1.6
Catharus ustulatus	31	1	< 0.1	31	< 0.1	1	0.1
Ixoreus naevius	78	4	0.1	312	0.1	4	0.4
Turdus / Ixoreus spp.	78	2	0.1	156	0.1	2	0.2
Piranga ludoviciana	28	1	< 0.1	28	< 0.1	1	0.1
Pipilo maculatus	40	1	< 0.1	40	< 0.1	1	0.1
Junco hyemalis	18	9	0.2	162	0.1	9	0.8
Unidentified medium-sized	60–250	5	0.1	677	0.3	5	0.4
Unidentified small bird	5–59	12	0.3	261	0.1	11	1.0
Birds subtotal		**106**	**2.9**	**12114**	**5.7**	**100**	**8.9**
Reptiles							
Coluber constrictor	77	1	< 0.1	77	< 0.1	1	0.1
Elgaria coerulea	35	4	0.1	140	0.1	4	0.4
Sceloporus occidentalis	10	3	0.1	30	< 0.1	3	0.3
Thamnophis spp.	100	28	0.8	2800	1.3	28	2.5
Reptiles subtotal		**36**	**1.0**	**3047**	**1.4**	**36**	**3.2**
Amphibians							
Frog spp.	30	19	0.5	570	0.3	19	1.7
Large salamander	68	43	1.2	2924	1.4	41	3.6
Medium-size salamander	14	186	5.0	2604	1.2	121	10.7
Small salamander	4	115	3.1	460	0.2	69	6.1
Amphibians subtotal		**363**	**9.8**	**6558**	**3.1**	**196**	**17.4**
Fish							
Osteichthyes spp.	51	10	0.3	510	0.2	7	0.6
Fish subtotal		**10**	**0.3**	**510**	**0.2**	**7**	**0.6**
Gastropods							
Haplotrema vancouverense	7	50	1.4	350	0.2	41	3.6
Monadenia fidelis	11	134	3.6	1474	0.7	92	8.2
Juga spp.	0.02	60	1.6	1.2	< 0.1	9	0.8
Gastropods subtotal		**244**	**6.6**	**1825.2**	**0.9**	**128**	**11.4**
Arthropods							
Diplopods							
Harpaphe haydeniana	0.4	8	0.2	3.2	< 0.1	8	0.7
Diplopods subtotal		**8**	**0.2**	**3.2**	**< 0.1**	**8**	**0.7**
Collembola							
Entomobryidae spp.	0.1	1	< 0.1	0.1	< 0.1	1	0.1
Collembola subtotal		**1**	**< 0.1**	**0.1**	**< 0.1**	**1**	**0.1**

Table 1.3. Continued.

Prey Taxa	Mean Mass g[a]	Number n[b]	Number (%)[c]	Biomass g	Biomass (%)[d]	Occurrence n[e]	Occurrence (%)[f]
Insects							
Chlorochroa spp.	0.3	1	< 0.1	0.3	< 0.1	1	0.1
Brochymena affinis	0.3	1	< 0.1	0.3	< 0.1	1	0.1
Hemiptera spp.	0.3	3	0.1	0.9	< 0.1	3	0.3
Ergates spiculatus	3.0	4	0.1	12	< 0.1	4	0.4
Coleoptera spp.	0.3	433	11.7	129.9	0.1	198	17.6
Braconidae spp.	0.1	1	< 0.1	0.1	< 0.1	1	0.1
Ichneumonidae spp.	0.1	1	< 0.1	0.1	< 0.1	1	0.1
Formicidae spp.	0.1	66	1.8	6.6	< 0.1	27	2.4
Vespidae spp.	0.1	1	< 0.1	0.1	< 0.1	1	0.1
Hymenoptera spp.	0.1	2	0.1	0.2	< 0.1	2	0.2
Unidentified large insect	2.0	1	< 0.1	2	< 0.1	1	0.1
Unidentified small insect	0.3	17	0.5	5.1	< 0.1	17	1.5
Insects subtotal		**531**	**14.4**	**157.6**	**0.1**	**233**	**20.7**
Crustaceans							
Pacifastacus leniusculus	*	**	**	1273.8	0.6	82	7.3
Crustaceans subtotal				**1273.8**	**0.6**	**82**	**7.3**
Totals		**3686**	**100.0**	**211112.9**	**100.0**		

[a] See Appendix for common names and sources of mean mass of prey.
[b] Indicates the number of individual prey identified in Barred Owl pellets.
[c] Percent number of individual prey for each taxa, calculated by $n_i/n \times 100$ where n_i is the number of individuals in the *i*th category of prey divided by the total number of individual prey in the sample.
[d] Percent of prey biomass expressed as the proportion of each prey taxa contributed to the total biomass.
[e] Indicates the number of pellets in which ≥ 1 individual of each prey taxa occurred.
[f] Percent of prey occurrence, calculated by dividing the total number of pellets in the sample by the number of pellets in which each prey taxa was found.
[*] See predicted biomass conversions used for signal crayfish (*Pacifastacus leniusculus*; Table 1.1) and Prey Biomass in Methods section.
[**] indicates number and percent of prey number not estimated; see Prey Numbers in Methods section.

Table 1.4. Numbers of prey individuals (*n*) of coleopteran taxa identified to the family, genus, and species levels from a sub-sample of Barred Owl pellets collected from 26 family areas in western Oregon, 2007–2009.

Coleopteran Taxa	*n*	Coleopteran Taxa	*n*
Carabidae (ground beetles)		**Curculionidae (weevils / snout and bark beetles)**	
Calosoma spp.	1	*Dyslobus lecontei*	19
Cychrus tuberculatus	1	*Dyslobus segnis*	1
Omus audouini	9	*Dyslobus verrucifer*	1
Pterostichus lama	90	*Dyslobus* spp.	3
Pterostichus spp.	7	*Panscopus gemmatus*	1
Scaphinotus marginatus	1	*Sthereus horridus*	1
Carabidae spp.	6	Curculionidae spp.	14
Cerambycidae (longhorned beetles)		**Elateridae (click beetles)**	
Ergates spiculatus	1	*Ampedus phoenicopterus*	5
Plectrura spinicauda	1	**Lucanidae (stag beetles)**	
Cerambycidae spp.	1	*Sinodendron rugosum*	1
Chrysomelidae (leaf beetles)		**Phalacridae (shining flower beetles)**	
Brachypnoea puncticollis	1	Phalacridae spp.	1
Chrysomelidae spp.	8	**Silphidae (carrion beetles)**	
Coccinellidae (lady beetles)		*Heterosilpha ramosa*	1
Mulsantina picta	3	**Staphylinidae (rove beetles)**	
Psyllabora borealis	3	Staphylinidae spp.	6
Coccinellidae spp.	1		

Table 1.5. Prey composition identified from uneaten prey remains (*n* = 90 collections) and observations of prey (*n* = 4) recently killed by Barred Owls in western Oregon, 2007–2009.

	Type of Dietary Sample	
Prey Taxa	Uneaten Prey Remains	Observations of Recently Killed Prey
Mammals		
Sorex trowbridgii – Trowbridge's shrew	2	
Scapanus orarius – coast mole	3	
Scapanus townsendii – Townsend's mole	2	
Sylvilagus bachmani – brush rabbit	1	
Lepus americanus – snowshoe hare	1	
Aplodontia rufa – mountain beaver	2	
Tamias townsendii – Townsend's chipmunk	2	
Tamiasciurus douglasii – Douglas' squirrel	2	
Glaucomys sabrinus – northern flying squirrel	6	1
Unidentified Sciurid spp.	1	1
Neotoma spp. – unidentified woodrat	1	
Microtus spp. – unidentified vole	1	
Muridae spp. – unidentified vole / mouse	3	
Spilogale gracilis – spotted skunk	1	
Unidentified mammals	1	
Mammals subtotal	**29**	**2**
Birds		
Bonasa umbellus – Ruffed Grouse	5	
Grouse spp. – unidentified Grouse	1	
Patagioenas fasciata – Band-tailed Pigeon	4	
Aegolius acadicus – Northern Saw-whet Owl	1	
Megascops kennicottii – Western Screech-Owl	4	
Strix spp. – Spotted Owl or Barred Owl*	2	
Megaceryle alcyon – Belted Kingfisher*	1	
Picoides villosus – Hairy Woodpecker	1	
Sphyrapicus ruber – Red-breasted Sapsucker	1	
Cyanocitta stelleri – Stellar's Jay	3	
Perisoreus canadensis – Gray Jay	2	
Corvus spp. – unidentified Crow or Raven*	1	
Poecile rufescens – Chestnut-backed Chickadee	1	
Sitta canadensis – Red-breasted Nuthatch	4	
Catharus ustulatus – Swainson's Thrush	1	
Ixoreus naevius – Varied Thrush	9	
Loxia curvirostra – Red Crossbill*	1	
Birds subtotal	**42**	**0**
Reptiles		
Thamnophis spp. – garter snake spp.		1
Reptiles subtotal	**0**	**1**
Gastropods (Freshwater snails)		
Juga spp. – pleurocerid snail	13	
Gastropods subtotal	**13**	**0**
Crustaceans		
Pacifastacus leniusculus – signal crayfish	**	1
Crustaceans subtotal	**	**1**
Total	**84**	**4**

* indicates prey taxa not identified in regurgitated pellets.
** indicates prey number not estimated; see Prey Numbers in Methods section.

Table 1.6. Annual variation in breeding season diet of seven Barred Owl family areas in western Oregon. Numbers indicate the percent of total prey in each annual breeding season diet. Numbers in parentheses indicate the number of individual prey identified in pellets. FNB and FNB_{sta} were calculated using diet richness for each family, each year. Asterisks indicate the difference in percent of prey numbers are ≥ 5% between years. Of all taxa identified, only 14, in some families, changed ≥ 5% in prey numbers.

	FCr		IMo		KCr		LOCr		RCr		UECr		UPCr	
	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008
Prey Taxa	(24)	(114)	(51)	(141)	(66)	(89)	(52)	(149)	(192)	(246)	(231)	(182)	(158)	(175)
Sorex trowbridgii/vagrans	12.5	12.3	0.0	2.8	18.2*	6.7*	9.6	10.1	3.6	5.3	6.5	10.4	17.1*	11.4*
Sorex vagrans	0.0	0.9	7.8*	2.1*	0.0	1.1			0.5	1.2				
Scapanus orarius	16.7*	7.9*	7.8	5.7	9.1	10.1	13.5*	6.0*	39.1*	19.9*	11.7	14.3	10.1	10.3
Tamias townsendii	0.0*	6.1*			4.5	4.5	0.0	2.0	0.0	0.4	0.4	0.0	1.9	0.0
Tamiasciurus douglasii	0.0	1.8	0.0	2.1	1.5	0.0	1.9*	11.4*	0.0	0.8	0.0	4.4	2.5	0.6
Glaucomys sabrinus	8.3	6.1	0.0*	5.7*	4.5*	14.6*	15.4*	20.8*	4.7	8.5	10.8	14.3	5.1*	10.9*
Peromyscus maniculatus	0.0	2.6	3.9*	19.1*	7.6	4.5	9.6*	1.3*	0.5	0.8	1.3	2.2	6.3*	0.6*
Microtus townsendii	12.5*	0.0*	15.7*	2.1*										
Microtus spp.			2.0	0.0	0.0*	5.6*			0.0	0.8				
Medium-size salamander	0.0	3.5	0.0	2.8	4.5	5.6	0.0	3.4	9.4	10.2	4.8	3.3	1.9*	8.0*
Small salamander	0.0	3.5	7.8	7.1	3.0	3.4	1.9	1.3	2.1*	7.3*	4.8	0.5	1.3	4.6
Osteichthyes spp.	12.5*	0.9*												
Monadenia fidelis	0.0	3.5	5.9	1.4	7.6	9.0	1.9	4.0	9.4*	2.8*	2.6	6.0	2.5*	9.7*
Coleoptera spp.	8.3	12.3	23.5*	14.2*	12.1*	2.2*	7.7	10.1	8.9	8.1	25.1*	11.5*	9.5*	17.7*
Other Prey	29.2	38.6	25.6	34.9	27.4	32.7	38.5	29.6	21.8	33.9	32.0	33.1	41.8	26.2
Total %	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Richness	11	28	16	27	23	28	21	27	25	37	37	29	31	28
FNB	3.57	14.29	9.09	12.50	12.50	16.67	12.50	11.11	5.26	11.11	9.09	12.50	14.29	11.11
FNB_{sta}	0.26	0.49	0.54	0.44	0.52	0.58	0.58	0.39	0.18	0.28	0.22	0.41	0.44	0.37

Note: FNB and FNB_{sta} were calculated as described in the Methods section. Owl family areas are listed alphabetically. FCr, Fawn Creek; IMo, Iron Mountain; KCr, Kline Creek; LOCr, Lower Oat Creek; RCr, Russell Creek; UECr, Upper Eames Creek; UPCr, Upper Pugh Creek.

Table 1.7. Annual breeding season variation in prey biomass of seven Barred Owl family areas in western Oregon. Numbers indicate the percent of total prey biomass in each annual breeding season diet. Numbers in parentheses indicate annual estimates of total prey biomass (g). Asterisks indicate the difference in percent of prey biomass are ≥ 5% between years. Of all taxa identified, only 22, in some families, changed ≥ 5% in prey biomass.

	FCr		IMo		KCr		LOCr		RCr		UECr		UPCr	
	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008
Prey Taxa	(2215.8)	(7309.4)	(1734.4)	(6441.0)	(2829.4)	(4753.5)	(3476.1)	(13363.2)	(7599.7)	(14276.2)	(11521.0)	(10497.3)	(9741.2)	(6293.1)
Scapanus orarius	10.1	6.9	12.9	7.0	11.9	10.6	11.3*	3.8*	55.3*	19.2*	13.1	13.9	9.2*	16.0*
Scapanus townsendii	23.6	26.9	30.2*	12.2*	4.6	2.8	3.8	0.0	5.2	2.8	5.7	6.2	1.3*	14.6*
Sylvilagus bachmani	0.0*	7.7*			0.0*	11.8*			0.0	3.9	5.6*	0.0*		
Lepus americanus							0.0*	8.2*						
Leporidae spp.	0.0*	5.5*	0.0*	5.4*							12.8	8.1	1.2	0.0
Aplodontia rufa	13.5*	2.7*			11.5*	0.0*	15.8	11.2	7.2*	0.0*	2.6	0.0	8.7*	0.0*
Tamias townsendii	0.0*	7.9*			8.8	7.0	0.0	1.9	0.0	0.6	0.7	0.0	2.6	0.0
Tamiasciurus douglasii	0.0*	6.0*	0.0*	10.3*	7.8*	0.0*	6.4*	28.1*	0.0	3.1	0.0*	16.8*	9.1*	3.5*
Glaucomys sabrinus	12.1	12.8	0.0*	16.6*	14.2*	36.6*	30.8	31.1	15.9	19.7	29.1	33.2	11.0*	40.5*
Thomomys mazama			5.5*	0.0*	3.4	0.0			0.0	3.3	1.6	1.8		
Peromyscus maniculatus	0.0	0.9	2.5*	9.2*	3.9	1.9	3.2	0.3	0.3	0.3	0.6	0.8	2.3	0.3
Neotoma spp.	12.9	11.7	0.0*	13.3*	20.1*	6.0*			3.8	4.0	0.0	2.7	5.9	4.5
Microtus longicaudus			6.1*	0.8*			3.0	0.0						
Microtus townsendii	7.7*	0.0*	26.3*	2.7*										
Spilogale gracilis									0.0*	21.2*	5.3*	0.0*		
Bonasa umbellus							13.4*	0.0*	0.0	3.3	5.0*	0.0*		
Dendragapus obscurus													10.8*	0.0*
Patagioenas fasciata							0.0	2.9					24.1*	0.0*
Colaptes auratus			8.2*	0.0*					0.0	3.0				
Large salamander	0.0	1.9	0.0*	6.3*			3.9	0.5	0.0	1.9	1.2	1.9	2.1	1.1
Osteichthyes spp.	6.9*	0.7*												
Pacifastacus leniusculus	11.1*	0.5*			1.0	0.5	0.0	< 0.1	0.0	0.1	< 0.1	0.0	0.0	0.2
Other Prey	2.1	7.9	8.3	16.2	12.8	22.8	8.4	12.0	12.3	13.6	16.7	14.6	11.7	19.3
Total %	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Note: Owl family areas are listed alphabetically. FCr, Fawn Creek; IMo, Iron Mountain; KCr, Kline Creek; LOCr, Lower Oat Creek; RCr, Russell Creek; UECr, Upper Eames Creek; UPCr, Upper Pugh Creek.

Table 1.8. Within-breeding season variation in percent of prey numbers (Num) and prey biomass (Bio) from Barred Owl regurgitated pellets collected at nest and roost areas at 22 family areas during the 2008 breeding season in western Oregon. FNB and FNB_{sta} were calculated using diet richness for each breeding period.

	Breeding Period[a]					
	Egg-laying and Incubation		Nestling and Brancher		Post-fledging	
Prey Taxa	% Num	% Bio	% Num	% Bio	% Num	% Bio
Mammals						
Sorex bendirii			0.3	0.1	0.1	< 0.1
Sorex sonomae	0.9	0.1	0.3	0.1	2.4	0.4
Sorex trowbridgii	6.0	0.3	0.6	0.1	0.8	0.1
Sorex trowbridgii / vagrans	6.8	0.3	5.8	0.6	11.6	1.0
Sorex vagrans	4.3	0.2			0.6	0.1
Neurotrichus gibbsii	6.0	0.5	1.8	0.3	4.7	0.7
Scapanus orarius	2.6	1.4	2.1	2.3	12.7	12.6
Scapanus townsendii	1.7	2.2	0.9	2.3	2.5	5.8
Myotis spp.					0.2	< 0.1
Sylvilagus bachmani	0.9	4.6	0.3	3.3	0.3	3.5
Lepus americanus					0.2	4.6
Leporidae spp.	1.7	13.8			1.2	6.4
Aplodontia rufa					0.6	3.6
Tamias townsendii	1.7	1.4	1.5	2.5	0.9	1.4
Tamiasciurus douglasii	5.1	11.0	4.3	18.3	2.1	8.2
Glaucomys sabrinus	22.2	28.8	15.3	39.6	10.7	25.5
Unidentified Sciurid spp.					0.1	0.3
Thomomys mazama					0.6	1.0
Peromyscus maniculatus	6.0	1.3	7.7	3.3	3.6	1.4
Neotoma spp.	2.6	7.1	0.6	3.4	1.4	7.1
Myodes californicus	3.4	0.8	4.0	1.8	1.4	0.6
Arborimus longicaudus	2.6	0.6	5.2	2.6	3.3	1.5
Microtus longicaudus			0.3	0.3	0.1	0.1
Microtus oregoni	1.7	0.3	0.6	0.2	1.6	0.6
Microtus townsendii	1.7	0.9			0.1	0.1
Microtus spp.			0.6	0.4	0.6	0.3
Ondatra zibethicus					0.1	1.2
Muridae spp.	2.6	0.6	1.2	0.6	1.6	0.7
Zapus trinotatus	0.9	0.2	1.2	0.6	1.0	0.5
Mustela erminea					0.3	0.3
Spilogale gracilis	3.4	20.0	0.3	3.6	0.1	0.6
Mammals subtotal	**84.6**	**96.4**	**55.2**	**86.2**	**67.5**	**90.5**
Birds						
Bonasa umbellus					0.1	1.1
Oreortyx pictus	0.9	1.9	0.6	2.7		
Patagioenas fasciata			0.3	2.3		
Aegolius acadicus					0.2	0.3

Table 1.8. Continued.

	Breeding Period[a]					
	Egg-laying and Incubation		Nestling and Brancher		Post-fledging	
Prey Taxa	% Num	% Bio	% Num	% Bio	% Num	% Bio
Megascops kennicottii			0.3	1.0	0.1	0.4
Colaptes auratus					0.2	0.4
Dryocopus pileatus					0.1	0.3
Picoides villosus	0.9	0.5				
Sphyrapicus ruber			0.6	0.6		
Empidonax spp.					0.1	< 0.1
Cyanocitta stelleri					0.2	0.4
Poecile rufescens			0.6	0.1	0.1	< 0.1
Sitta canadensis	0.9	0.1			0.1	< 0.1
Troglodytes pacificus					0.3	0.1
Catharus ustulatus					0.1	< 0.1
Ixoreus naevius					0.2	0.2
Piranga ludoviciana					0.1	< 0.1
Pipilo maculatus					0.1	< 0.1
Junco hyemalis					0.2	0.1
Unidentified medium-sized			0.3	0.8	0.2	0.4
Unidentified small bird					0.4	0.1
Birds subtotal	**2.6**	**2.5**	**2.8**	**7.5**	**2.6**	**4.0**
Reptiles						
Coluber constrictor					0.1	0.1
Elgaria coerulea					0.1	< 0.1
Sceloporus occidentalis			0.3	0.1	0.1	< 0.1
Thamnophis spp.			0.3	0.6	0.9	1.6
Reptiles subtotal			**0.6**	**0.7**	**1.1**	**1.7**
Amphibians						
Frog spp.					0.3	0.2
Large salamander	0.9	0.6	1.8	2.4	0.9	1.1
Medium-size salamander	0.9	0.1	6.1	1.7	5.2	1.3
Small salamander			4.3	0.3	3.1	0.2
Amphibians subtotal	**1.7**	**0.7**	**12.3**	**4.4**	**9.5**	**2.7**
Fish						
Osteichthyes spp.					0.1	0.1
Fish subtotal					**0.1**	**0.1**
Gastropods						
Haplotrema vancouverense	0.9	0.1	1.2	0.2	1.4	0.2
Monadenia fidelis	3.4	0.4	4.9	1.0	3.4	0.7
Juga spp.			13.2	< 0.1	0.6	< 0.1
Gastropods subtotal	**4.3**	**0.4**	**19.3**	**1.2**	**5.4**	**0.8**
Diplopods						
Harpaphe haydeniana					0.1	< 0.1
Diplopods subtotal					**0.1**	**< 0.1**
Collembola						
Entomobryidae spp.					0.1	< 0.1
Collembola subtotal					**0.1**	**< 0.1**

Table 1.8. Continued.

	Breeding Period[a]					
	Egg-laying and Incubation		Nestling and Brancher		Post-fledging	
Prey Taxa	% Num	% Bio	% Num	% Bio	% Num	% Bio
Insects						
Ergates spiculatus					0.1	< 0.1
Coleoptera spp.	6.8	< 0.1	9.5	0.1	10.9	0.1
Braconidae spp.					0.1	< 0.1
Ichneumonidae spp.					0.1	< 0.1
Formicidae spp.					2.0	< 0.1
Hymenoptera spp.					0.1	< 0.1
Unidentified large insect					0.1	< 0.1
Unidentified small insect			0.3	< 0.1	0.4	< 0.1
Insects subtotal	**6.8**	**< 0.1**	**9.8**	**0.1**	**13.7**	**0.1**
Crustaceans						
Pacifastacus leniusculus					**	0.2
Crustaceans subtotal					**	**0.2**
Total %	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**
Number of Family Areas	14		16		22	
Number of Pellets	55		82		484	
Richness	29		37		71	
FNB	12.50		12.50		16.67	
FNB_{sta}	0.41		0.32		0.22	

[a] Breeding periods defined as: egg-laying and incubation (3 March–4 April 2008); nestling and brancher (5 April–4 May 2008); and post-fledging (5 May–31 August 2008). The number of prey individuals identified in pellets and estimated prey biomass was 117 and 12,105.4 g during the egg-laying and incubation period, 326 and 16,899.5 g during the nestling and brancher period, and 1,720 and 96,548.9 g during the post-fledging period, respectively.

** indicates percent of prey number not estimated; see Prey Numbers in Methods section.

Table 1.9. Variation in diet composition (% of prey numbers) among 15 Barred Owl family areas in western Oregon, 2007–2008. Numbers indicate the percent of total prey from the 2007 and 2008 breeding seasons combined. Numbers in parentheses indicate the number of individual prey identified in pellets. FNB and FNB_{sta} were calculated using diet richness for each family.

Prey Taxa[a]	DHo (143)	FCr (138)	HPo (115)	IMo (192)	KCr (155)	LBCr (186)	LOCr (201)	LPCr (99)	RCr (438)	SAR (64)	SCr (192)	SFa (187)	UECr (413)	UPCr (333)	UWCr (98)
MAMMALS	62.9	73.2	61.7	64.1	69.0	75.8	75.1	85.9	55.9	89.1	58.3	68.4	60.0	61.0	70.4
Sorex spp.	14.0	15.2	14.8	9.4	17.4	19.4	10.4	10.1	6.6	17.2	12.0	20.3	10.7	17.4	14.3
Neurotrichus gibbsii	4.9	3.6	5.2	1.6	5.2	7.5	5.0	3.0	0.9	10.9	1.0	2.1	5.8	4.5	4.1
Scapanus spp.	18.9	23.2	0.9	11.5	11.0	9.7	8.5	15.2	29.7	14.1	13.0	7.5	15.3	12.6	16.3
Leporidae spp.	3.5	1.4	1.7	0.5	0.6	1.1	0.5		0.2	7.8		2.1	2.2	0.3	1.0
Aplodontia rufa	0.7	1.4	2.6		0.6	1.6	2.5		0.2	1.6		0.5	0.2	0.9	2.0
Tamias townsendii		5.1	0.9		4.5		1.5	1.0	0.2			0.5	0.2	0.9	1.0
Tamiasciurus douglasii	1.4	1.4	1.7	1.6	0.6	0.5	9.0	2.0	0.5	4.7	2.1	2.1	1.9	1.5	3.1
Glaucomys sabrinus	7.7	6.5	11.3	4.2	10.3	16.1	19.4	32.3	6.8	7.8	10.9	9.6	12.3	8.1	13.3
Thomomys mazama			1.7	0.5	0.6				1.1			0.5	1.0		
Peromyscus maniculatus		2.2	7.8	15.1	5.8	7.0	3.5	6.1	0.7	7.8	3.1	2.7	1.7	3.3	7.1
Neotoma spp.	1.4	2.9	0.9	1.6	1.9	1.1		6.1	0.7	4.7	1.6	1.6	0.2	0.9	3.1
Myodes californicus	1.4	0.7	4.3	2.6		3.2	2.5	4.0	1.1	3.1	0.5	3.7	0.5	1.8	2.0
Arborimus longicaudus	5.6		4.3	1.0	2.6	4.3	4.5	3.0	2.7	1.6	10.4	2.7	5.1	6.3	1.0
Microtus spp.	2.1	2.9	2.6	10.4	3.2	2.2	4.0		2.1	4.7	1.0	5.3	0.2	0.3	
Zapus trinotatus		3.6		2.6	3.2	1.6	1.0				0.5	1.6	1.2	0.3	
Spilogale gracilis									1.1	1.6	0.5		0.2		
Other mammals	1.4	2.9	0.9	1.6	1.3	0.5	3.0	3.0	1.1	1.6	1.6	5.3	1.2	1.8	2.0
BIRDS	2.8	0.7	5.2	2.1	2.6	1.6	5.0	1.0	3.9	1.6	1.0	3.2	2.2	4.5	1.0
REPTILES	0.7		2.6			2.2			0.2			2.1	2.2	0.3	3.1
AMPHIBIANS	9.8	8.0	17.4	12.5	11.0	10.2	5.5	11.1	16.2	1.6	15.1	10.2	8.5	9.6	11.2
FISH		2.9										1.1			
GASTROPODS	2.8	3.6	6.1	3.1	9.7	6.5	3.5	2.0	6.2	7.8	9.9	4.3	4.4	8.4	5.1
ARTHROPODS	21.0	11.6	7.0	18.2	7.7	3.8	10.9		17.6		15.6	10.7	22.8	16.2	9.2
Total %	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Richness	31	30	33	33	32	30	35	16	44	22	29	50	45	39	25
FNB	11.11	12.50	16.67	12.50	16.67	12.50	12.50	6.67	8.33	14.29	12.50	16.67	11.11	14.29	14.29
FNB_{sta}	0.34	0.40	0.49	0.36	0.51	0.40	0.34	0.38	0.17	0.63	0.41	0.32	0.23	0.35	0.55

Note: Food-niche breadth (FNB) and standardized food-niche breadth (FNB_{sta}) were calculated as described in the Methods section. Owl family areas are listed alphabetically. DHo, Doe Hollow; FCr, Fawn Creek; HPo, High Point; IMo, Iron Mountain; KCr, Kline Creek; LBCr, Lower Buck Creek; LOCr, Lower Oat Creek; LPCr, Lower Pugh Creek; RCr, Russell Creek; SAR, Saragosa; SCr, Shitten Creek; SFa, Siuslaw Falls; UECr, Upper Eames Creek; UPCr, Upper Pugh Creek; UWCr, Upper Wildcat Creek.

[a] See Appendix for complete list of scientific and common names of pooled prey taxa.

Table 1.10. Variation in prey biomass among 15 Barred Owl family areas in western Oregon, 2007–2008. Numbers indicate the percent of total prey biomass in pellets from the 2007 and 2008 breeding seasons combined. Numbers in parentheses indicate estimates of prey biomass (g) in diets of owls in each family area.

Prey Taxa[a]	DHo (9651.6)	FCr (9525.2)	HPo (7315.1)	IMo (8175.4)	KCr (7582.9)	LBCr (9963.9)	LOCr (16839.3)	LPCr (8058.0)	RCr (21875.9)	SAR (6819.0)	SCr (8314.5)	SFa (13422.5)	UECr (22018.3)	UPCr (16034.3)	UWCr (6128.3)
MAMMALS	94.9	91.3	82.6	87.8	90.2	89.3	87.8	97.9	86.2	90.7	91.8	85.3	87.2	71.0	88.1
Sorex spp.	1.2	1.2	1.4	1.1	2.0	2.0	0.6	0.6	0.7	0.9	1.5	1.9	1.2	2.2	1.5
Neurotrichus gibbsii	0.7	0.5	0.7	0.3	0.9	1.3	0.5	0.3	0.2	0.9	0.2	0.3	1.0	0.8	0.6
Scapanus spp.	17.2	33.8	0.8	24.2	14.5	10.1	6.1	11.4	35.3	12.9	17.7	7.0	19.4	18.4	17.1
Leporidae spp.	42.2	10.1	12.4	4.3	7.4	2.8	6.5		2.6	25.2		7.0	13.5	0.7	2.9
Aplodontia rufa	4.1	5.2	22.6		4.3	16.6	12.2		2.5	5.9		3.5	1.4	5.3	7.3
Tamias townsendii		6.1	1.1		7.7		1.5	1.0	0.4			0.6	0.4	1.6	1.4
Tamiasciurus douglasii	4.6	4.6	6.0	8.1	2.9	2.2	23.6	5.5	2.0	9.7	10.6	6.6	8.0	6.9	10.8
Glaucomys sabrinus	15.3	12.7	23.8	13.1	28.3	40.3	31.0	53.2	18.4	9.8	33.8	18.0	31.0	22.6	28.4
Thomomys mazama			2.6	1.2	1.3				2.2			0.7	1.7		
Peromyscus maniculatus		0.7	2.7	7.8	2.6	2.9	0.9	1.6	0.3	1.6	1.6	0.8	0.7	1.5	2.5
Neotoma spp.	5.9	12.0	3.9	10.5	11.3	5.7		21.2	3.9	12.5	10.3	6.4	1.3	5.3	14.0
Myodes californicus	0.5	0.2	1.6	1.4		1.4	0.7	1.1	0.5	0.7	0.3	1.2	0.2	0.9	0.8
Arborimus longicaudus	2.2		1.8	0.6	1.4	2.1	1.4	1.0	1.4	0.4	6.3	1.0	2.5	3.4	0.4
Microtus spp.	0.6	2.0	0.8	11.2	2.0	1.0	1.3		0.9	0.9	0.6	2.0	0.1	0.1	
Zapus trinotatus		1.3		1.5	1.6	0.8	0.3				0.3	0.6	0.6	0.2	
Spilogale gracilis									13.9	8.9	7.3		2.8		
Other mammals	0.5	0.9	0.3	2.4	2.0	0.3	1.1	0.9	1.0	0.4	1.3	27.9	1.5	1.1	0.5
BIRDS	2.0	0.5	8.6	5.0	3.7	3.1	10.0	0.4	7.2	8.4	1.3	1.9	5.0	22.8	2.1
REPTILES	0.4		3.2			4.0			0.5			2.1	3.8	0.6	4.9
AMPHIBIANS	2.2	2.5	4.6	6.4	3.3	2.9	1.7	1.4	4.7	0.2	4.5	4.2	3.0	3.6	4.3
FISH		2.1										0.8			
GASTROPODS	0.4	0.5	0.7	0.8	2.1	0.2	0.5	0.3	1.3	0.6	2.3	0.4	0.9	1.7	0.6
ARTHROPODS	0.1	3.0	0.2	0.2	0.7	0.5	0.1		0.1		0.1	5.3	0.1	0.2	< 0.1
Total %	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100

Note: Owl family areas are listed alphabetically. DHo, Doe Hollow; FCr, Fawn Creek; HPo, High Point; IMo, Iron Mountain; KCr, Kline Creek; LBCr, Lower Buck Creek; LOCr, Lower Oat Creek; LPCr, Lower Pugh Creek; RCr, Russell Creek; SAR, Saragosa; SCr, Shitten Creek; SFa, Siuslaw Falls; UECr, Upper Eames Creek; UPCr, Upper Pugh Creek; UWCr, Upper Wildcat Creek.

[a] See Appendix for complete list of scientific and common names of pooled prey taxa.

Table 1.11. Variation in percent of prey numbers (Num) and prey biomass (Bio) between non-nesting pairs of Barred Owls and nesting pairs of Barred Owls that fledged young. Data are from regurgitated pellets collected at five owl family areas in western Oregon, 2007–2008. Numbers in parentheses indicate the number of individual prey identified in pellets and estimates of the biomass (g) of the prey in the samples. FNB and FNB_{sta} were calculated using diet richness for non-nesting pairs and nesting pairs that fledged young.

	Nesting Status[a]			
	Non-nesting pairs[b]		Nesting pairs that fledged young[c]	
Prey Taxa	% Num (316)	% Bio (18366.0)	% Num (507)	% Bio (30301.8)
Mammals				
Sorex sonomae	2.5	0.4	4.3	0.7
Sorex trowbridgii	1.9	0.2	0.8	0.1
Sorex trowbridgii / vagrans	10.4	0.9	9.9	0.8
Sorex vagrans	2.5	0.2	0.6	< 0.1
Neurotrichus gibbsii	3.2	0.5	4.5	0.7
Scapanus orarius	5.1	4.9	12.6	11.8
Scapanus townsendii	0.6	1.4	0.6	1.3
Sylvilagus bachmani	0.3	3.0	0.2	2.0
Lepus americanus			0.6	11.1
Leporidae spp.	0.9	3.4	1.0	3.4
Aplodontia rufa	0.9	8.6	1.0	8.6
Tamias townsendii	0.3	0.5	0.2	0.3
Tamiasciurus douglasii	0.9	3.6	2.0	7.3
Glaucomys sabrinus	10.1	23.3	12.0	27.0
Thomomys mazama	0.6	1.0	0.2	0.3
Peromyscus maniculatus	3.8	1.4	4.1	1.5
Neotoma spp.	2.2	10.9	0.8	3.8
Myodes californicus	1.3	0.5	3.4	1.3
Arborimus longicaudus	4.7	2.1	6.1	2.7
Microtus longicaudus			0.2	0.2
Microtus oregoni	1.9	0.7	1.8	0.6
Microtus spp.	0.6	0.3	0.8	0.4
Ondatra zibethicus	0.6	12.7	0.2	3.9
Muridae spp.	1.3	0.5	1.4	0.6

Table 1.11. Continued.

	Nesting Status[a]			
	Non-nesting pairs[b]		Nesting pairs that fledged young[c]	
Prey Taxa	% Num (316)	% Bio (18366.0)	% Num (507)	% Bio (30301.8)
Zapus trinotatus	0.9	0.4	0.8	0.3
Mustela erminea	0.3	0.3	0.4	0.4
Spilogale gracilis			0.2	2.0
Mammals subtotal	**58.2**	**81.8**	**70.6**	**92.9**
Birds				
Aegolius acadicus	0.6	0.9	0.4	0.5
Megascops kennicottii	0.6	1.8		
Empidonax spp.			0.2	< 0.1
Cyanocitta stelleri	0.3	0.7	0.2	0.4
Perisoreus canadensis	0.3	0.4		
Sitta canadensis	0.3	0.1	0.2	< 0.1
Troglodytes pacificus	0.6	0.1	0.2	< 0.1
Turdus / *Ixoreus* spp.			0.2	0.3
Piranga ludoviciana	0.3	0.2		
Junco hyemalis	0.3	0.1		
bird	0.3	1.4		
Unidentified small bird	0.3	0.2	0.2	0.1
Birds subtotal	**4.1**	**5.8**	**1.6**	**1.4**
Reptiles				
Coluber constrictor			0.2	0.3
Elgaria coerulea	0.3	0.2	0.2	0.1
Sceloporus occidentalis			0.2	< 0.1
Thamnophis spp.	1.3	2.2	0.8	1.3
Reptiles subtotal	**1.6**	**2.4**	**1.4**	**1.7**
Amphibians				
Frog spp.	1.3	0.7	0.2	0.1
Large salamander	1.9	2.2	1.0	1.1
Medium-size salamander	5.7	1.4	7.1	1.7
Small salamander	3.8	0.3	3.7	0.3
Amphibians subtotal	**12.7**	**4.5**	**12.0**	**3.1**
Fish				
Osteichthyes spp.	0.6	0.6		
Fish subtotal	**0.6**	**0.6**	**0.0**	**0.0**

Table 1.11. Continued.

	Nesting Status[a]			
	Non-nesting pairs[b]		Nesting pairs that fledged young[c]	
Prey Taxa	% Num (316)	% Bio (18366.0)	% Num (507)	% Bio (30301.8)
Gastropods				
Haplotrema vancouverense	1.9	0.2	2.0	0.2
Monadenia fidelis	5.4	1.0	1.0	0.2
Juga spp.	1.3	< 0.1	1.6	< 0.1
Gastropods subtotal	**8.5**	**1.2**	**4.5**	**0.4**
Diplopods				
Harpaphe haydeniana			0.2	< 0.1
Diplopods subtotal	**0.0**	**0.0**	**0.2**	**< 0.1**
Collembola				
Entomobryidae spp.			0.2	< 0.1
Collembola subtotal	**0.0**	**0.0**	**0.2**	**< 0.1**
Insects				
Coleoptera spp.	12.7	0.1	6.9	< 0.1
Braconidae spp.			0.2	< 0.1
Ichneumonidae spp.			0.2	< 0.1
Formicidae spp.	0.9	< 0.1	1.6	< 0.1
Hymenoptera spp.			0.4	< 0.1
Unidentified large insect			0.2	< 0.1
Unidentified small insect	0.6	< 0.1		
Insects subtotal	**14.2**	**0.1**	**9.5**	**< 0.1**
Crustaceans				
Pacifastacus leniusculus	**	3.7	**	0.3
Crustaceans subtotal	**	**3.7**	**	**0.3**
Total %	**100.0**	**100.0**	**100.0**	**100.0**
Richness	48		54	
FNB	16.67		16.67	
FNB_{sta}	0.33		0.30	

[a] A breeding parameter and determination used to adequately characterize reproductive success in owls, as described by Lint et al. (1999).
[b] Owl pairs (n = 5) that occupied an area, attempted to breed by pair formation/courtship but did not nest. Pair monitoring did not indicate the laying or incubation of eggs, brooding of young, or detection of fledglings.
[c] Owl pairs (n = 5) that nested and successfully fledged ≥ 1 young.

Table 1.12. Variation in FNB and FNB_{sta} between non-nesting pairs of owls (*n* =5) and nesting pairs of owls (*n* = 5) that fledged young in western Oregon, 2007–2008. FNB and FNB_{sta} were calculated using yearly diet richness for each family.

	Nesting Status[a]					
	Non-nesting pairs[b]		Nesting pairs that fledged young[c]		Paired difference[d]	
Family Area	FNB	FNB_{sta}	FNB	FNB_{sta}	FNB*	FNB_{sta}*
Doe Hollow	11.05	0.50	8.93	0.36	2.12	0.14
High Point	11.76	0.60	12.96	0.57	-1.20	0.03
Lower Buck Creek	13.52	0.52	10.71	0.44	2.81	0.08
Shitten Creek	11.49	0.52	10.77	0.43	0.72	0.10
Siuslaw Falls	7.28	0.22	17.04	0.37	-9.76	-0.16
Mean ± SD		0.47 ± 0.15		0.43 ± 0.08	−1.06 ± 5.10	0.04 ± 0.12
P					0.67	0.50

[a] A breeding parameter and determination used to adequately characterize reproductive success in owls, as described by Lint et al. 1999.
[b] Owl pairs that occupied an area, attempted to breed by pair formation/courtship but did not nest. Pair monitoring did not indicate the laying or incubation of eggs, brooding of young, or detection of fledglings.
[c] Owl pairs that nested and successfully fledged ≥ 1 young.
[d] Calculated difference in FNB and FNB_{sta} between non-nesting pairs of owls and nesting pairs of owls that fledged young by family area.
[*] Paired samples *t*-test: $t_4 = 0.47$, $P = 0.67$ for FNB and $t_4 = -0.75$, $P = 0.50$ for FNB_{sta}.

Table 1.13. Geographic locale, seasonality, taxonomic richness, and estimates of food-niche breadth (FNB) and standardized food-niche breadth (FNB_{sta}) from studies of Barred Owls.

Locale	Season	Richness	FNB	FNB_{sta}	Source
North America					
Western North America	Breeding and nonbreeding	28	11.84	0.40	Marti et al. 1993[a]
East Central North America	Breeding and nonbreeding	42	3.08	0.05	Marti et al. 1993[b]
Means of feeding-niche metrics for Barred Owls	Breeding and nonbreeding	14.8	3.49	0.18	Marti et al. 1993[c]
Eastern North America					
New England (New Jersey, New York, Conneticut)	Breeding	38	15.12	0.37	Bosakowski and Smith 1992
Pacific Northwest North America					
Central Coast Range of Western Oregon	Breeding and nonbreeding	85	16.67	0.19	This study
Central Coast Range of Western Oregon	Breeding	81	16.67	0.20	This study
Olympic National Park, Washington	Breeding	36	11.11	0.29	Graham, S. A., and S. A. Gremel (unpublished data)
West slope of the Cascade Range of Washington	Breeding	20	11.11	0.53	Hamer et al. 2001
East slope of the Cascade Range of Washington	Breeding	32	3.85	0.09	Graham, S. A., and P. H. Singleton (unpublished data)

[a] Estimates of food-niche breadths for Barred Owls in western North America. Original sources of data from Marks et al. (1984; Montana) and T. E. Hamer (unpublished data; Washington).
[b] Estimates of food-niche breadths for Barred Owls in east-central North America. Original sources of data from Errington (1932; Wisconsin), Wilson (1938; Michigan), Blakemore (1940; Minnesota), Hamerstrom and Hamerstrom (1951; Michigan).
[c] Means generated for North America by Marti et al. (1993) using data sources from [a] and [b] combined.
Note: Hamer et al. (2001) original work used the modified Simpson's Index to estimate diet diversity and the modified Hill Ratio to estimate evenness. For purposes of comparison, I recalculated the authors original data for diet diversity using Levins' reciprocal of Simpson's Index of diversity for FNB and Colwell and Futuyma's equation for FNB_{sta} (see Food-niche Breath in Methods section).

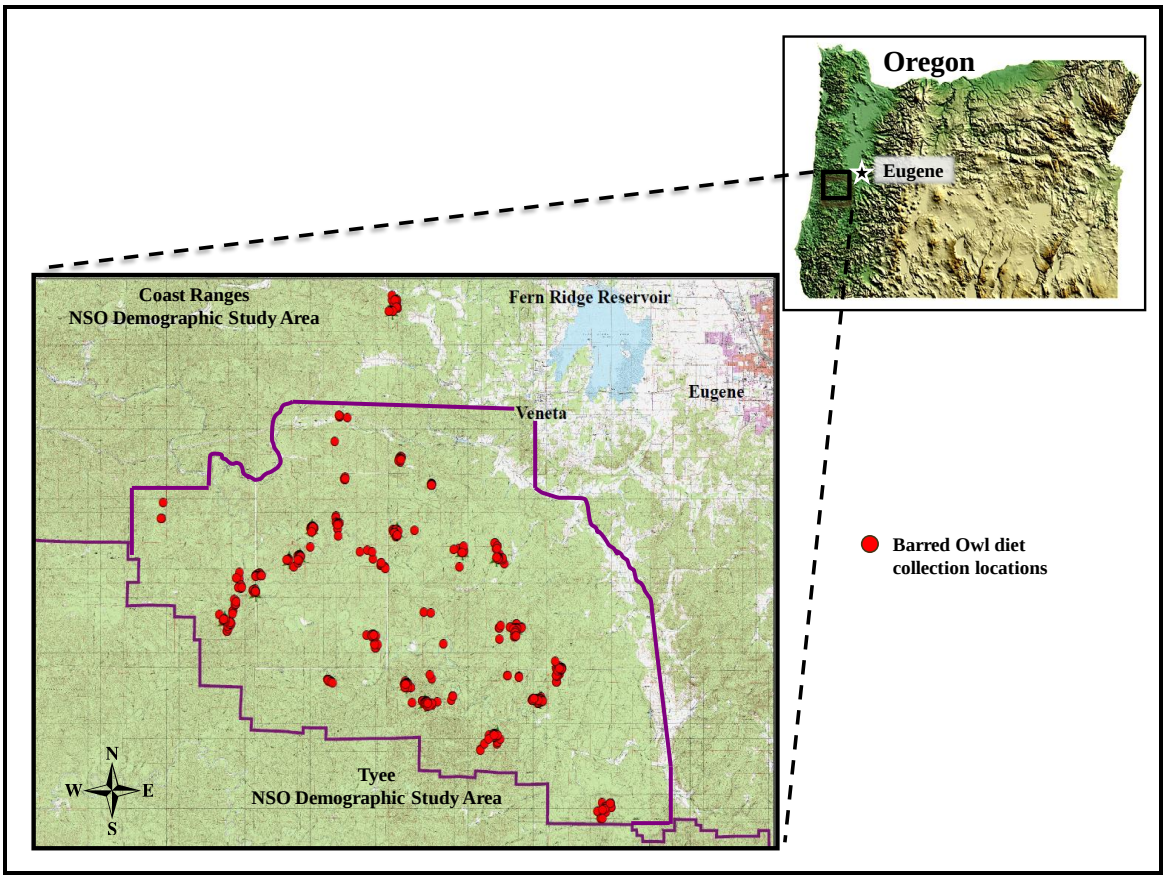


Figure 1.1. Map of the Barred Owl diet study area in the central Coast Range of western Oregon, and the distribution of family areas (*n* = 27) where evidence of diet were collected from March 2007 to February 2009. The study area was bounded on the north and south by two long-term Northern Spotted Owl (NSO) demographic study areas.

Figure 1.2. Photograph of a radio-marked adult female Barred Owl (*Strix varia*) with garter snake taken about 4 km southwest of Vaughn, Oregon at 1530 on 12 May 2008. The inset image magnifies the coiled-like snake in her feet and talons (Photo by S. Graham).

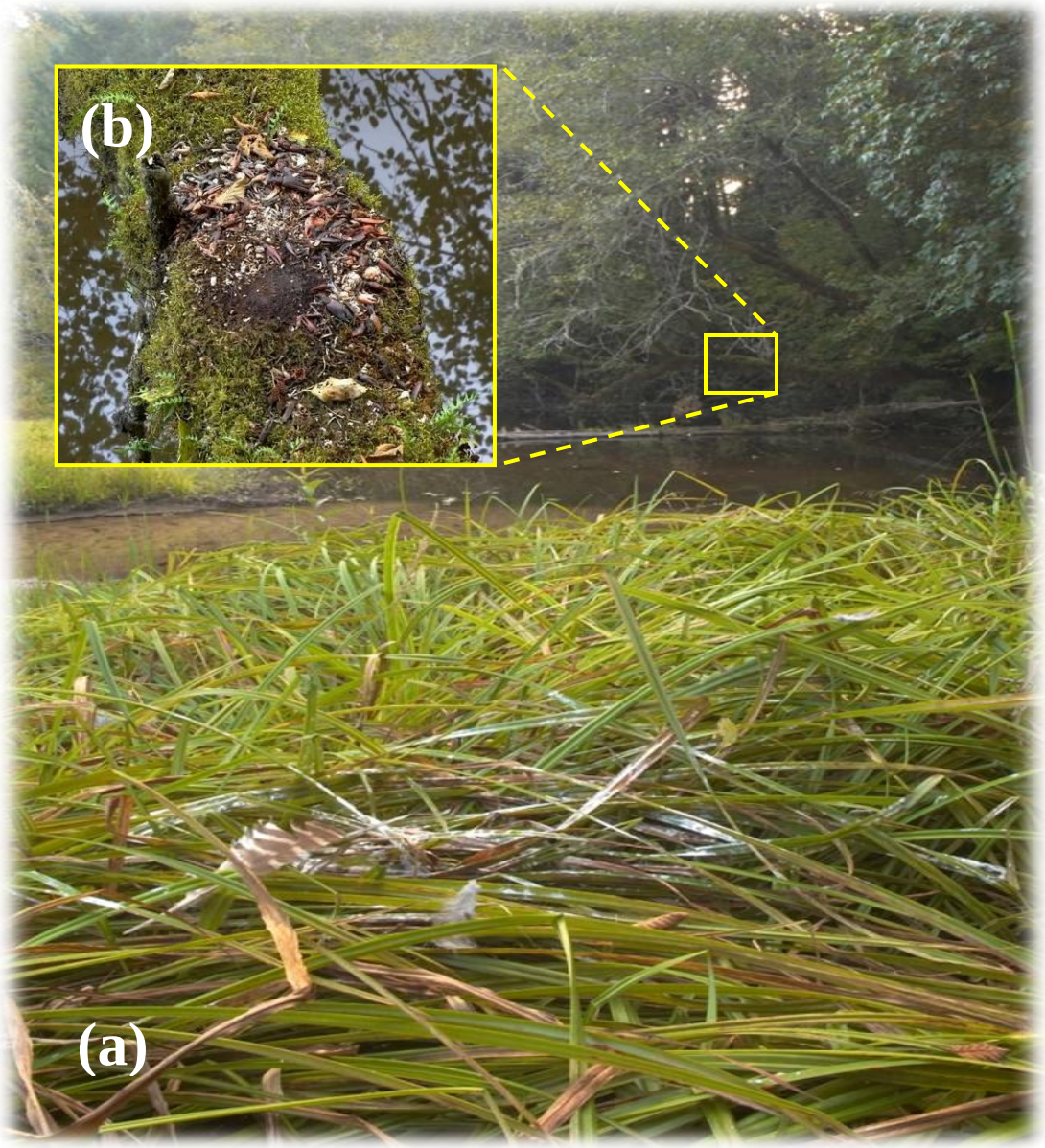


Figure 1.3. Photographs of a radio-marked adult female Barred Owl (*Strix varia*) roost (a) and feeding platform (b) along Russell Creek at Siuslaw Falls, about 6 km west of Lorane, Oregon, 17 September 2007. Photo (a) shows a molted or preened Barred Owl feather, owl excreta, by hidden crayfish remains under the roost tree. The inset (b) shows the owl feeding platform on a log, and a barren spot surrounded by a ring of crayfish remains including discarded chelae, rostrums, and exoskeleton (Photos by P. Kolar).

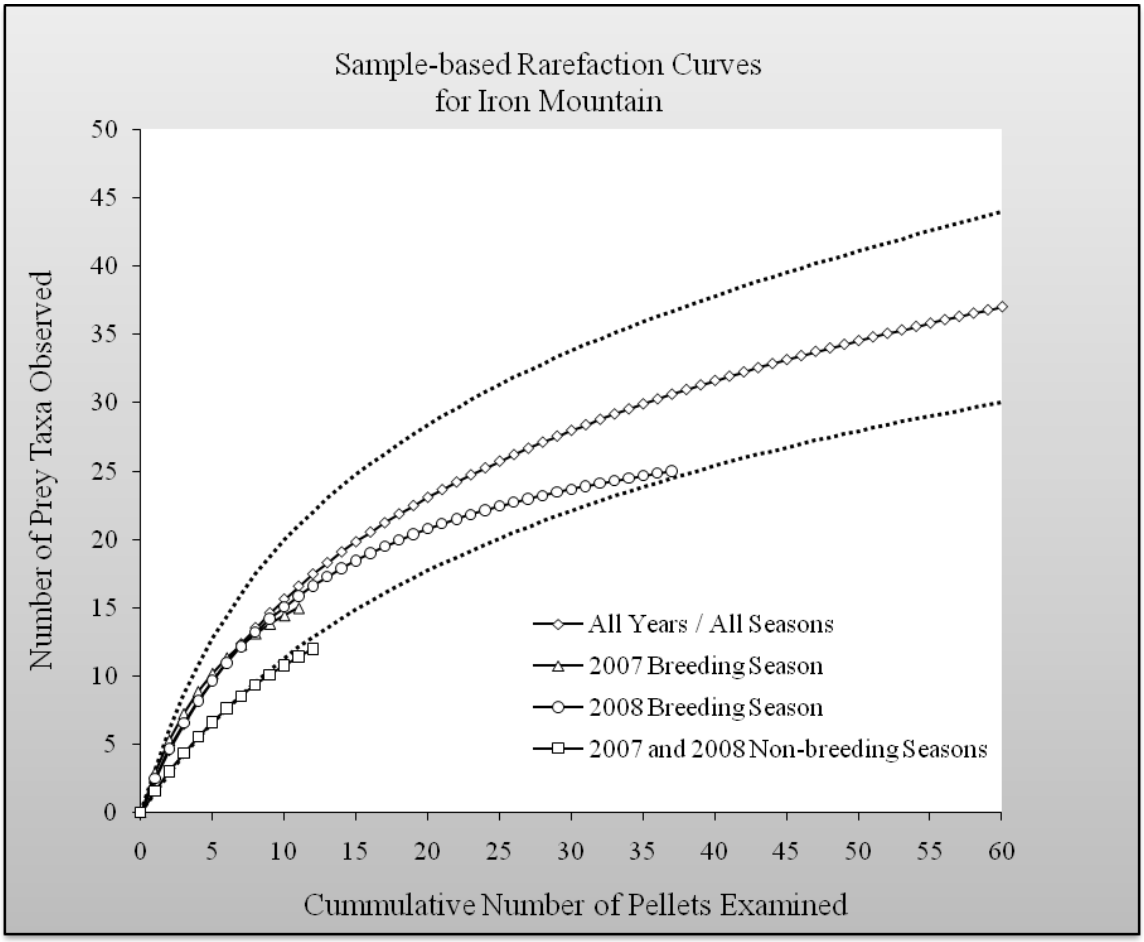


Figure 1.4. Rarefaction curves illustrate similarities in taxonomic richness of Barred Owl diet by year and by season using empirical diet data from pellets collected from the Iron Mountain family area in western Oregon, 2007–2009. Prey taxa rarefaction curves show the expected number of taxa observed relative to the number of pellets examined by year and by season. Dotted lines correspond to the 95% confidence intervals for the expected number of taxa based on pellets from both years. Confidence intervals on other curves overlapped in all cases and were omitted for clarity. Pellet sample accumulation order of all curves was randomized 100 times, and each point represents the mean of the resulting 100 estimates.

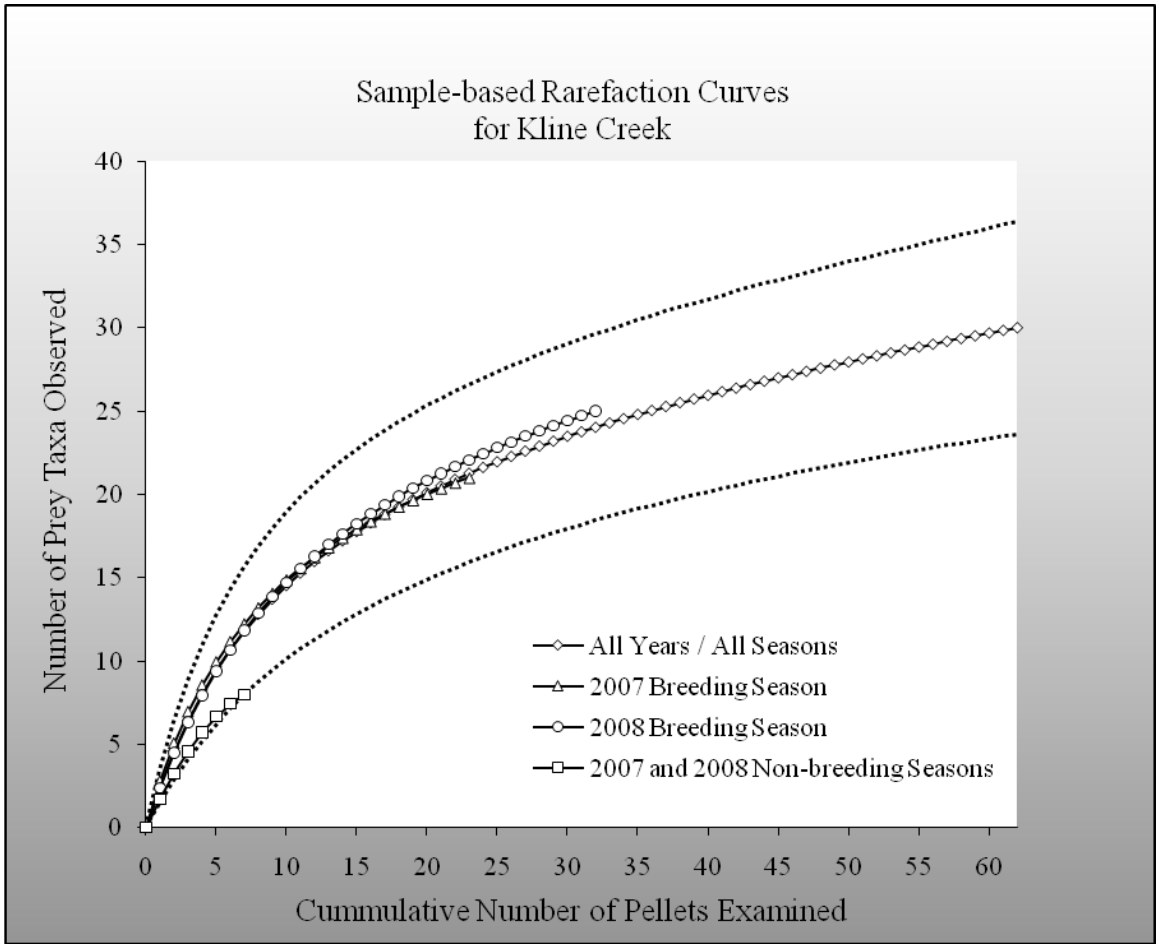


Figure 1.5. Rarefaction curves illustrate similarities in taxonomic richness of Barred Owl diet by year and by season using empirical diet data from pellets collected from the Kline Creek family area in western Oregon, 2007–2009. Prey taxa rarefaction curves show the expected number of taxa observed relative to the number of pellets examined by year and by season. Dotted lines correspond to the 95% confidence intervals for the expected number of taxa based on pellets from both years. Confidence intervals on other curves overlapped in all cases and were omitted for clarity. Pellet sample accumulation order of all curves was randomized 100 times, and each point represents the mean of the resulting 100 estimates.

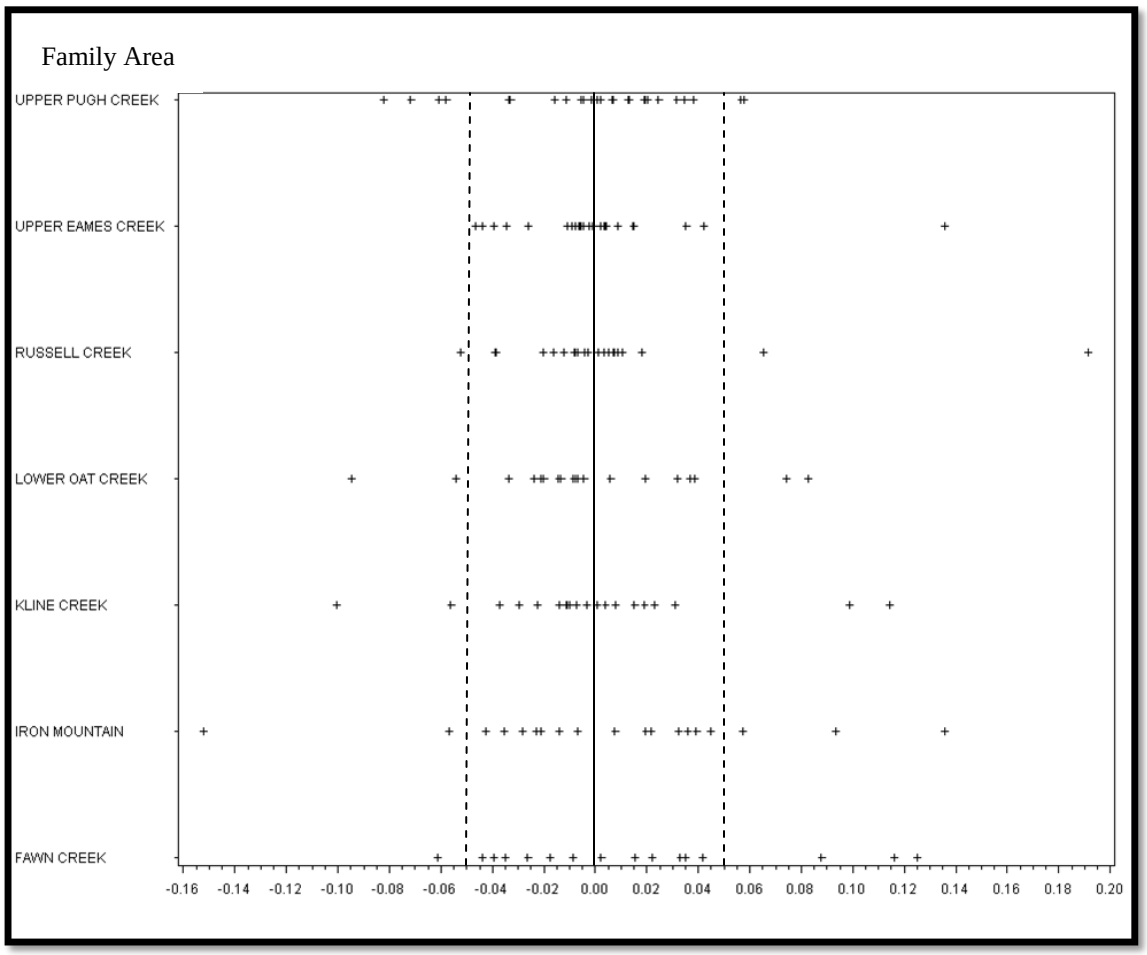


Figure 1.6. Annual variation in percentage of prey numbers based on evidence from pellets from seven Barred Owl family areas in western Oregon, 2007–2008. Plus symbols reported on the x-axis represent the between-year difference in percent of prey numbers for each taxa composing diets of the family areas. The solid line indicates zero difference between years. Dashed lines at ± 5% indicate the majority of differences in percent of prey numbers between years were ≤ 5%.

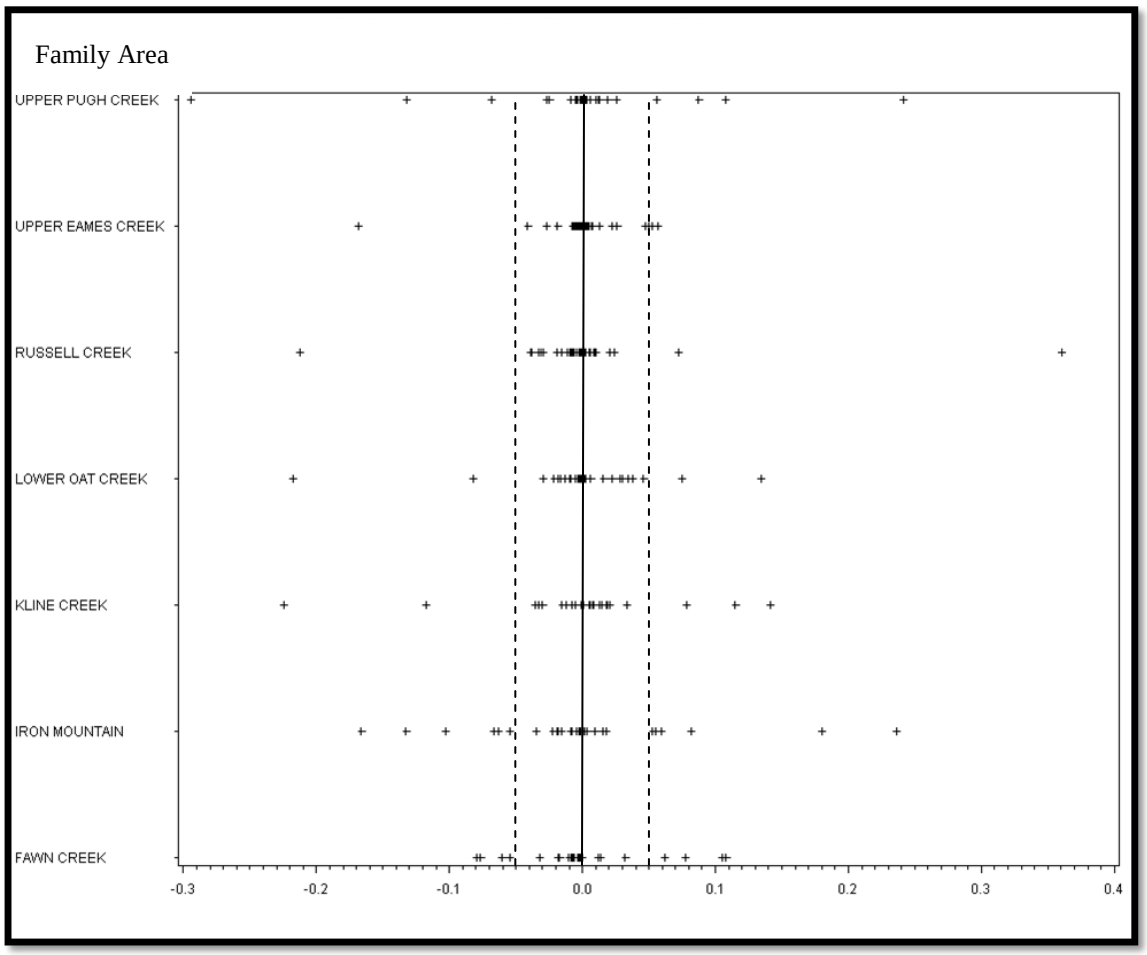


Figure 1.7. Annual variation in percentage of prey biomass based on evidence from pellets from seven Barred Owl family areas in western Oregon, 2007–2008. Plus symbols reported on the x-axis represent the between-year difference in percent of prey biomass for each taxa composing diets of the family areas. The solid line indicates zero difference between years. Dashed lines at ± 5% indicate the majority of differences in percent of prey biomass between years were ≤ 5%.

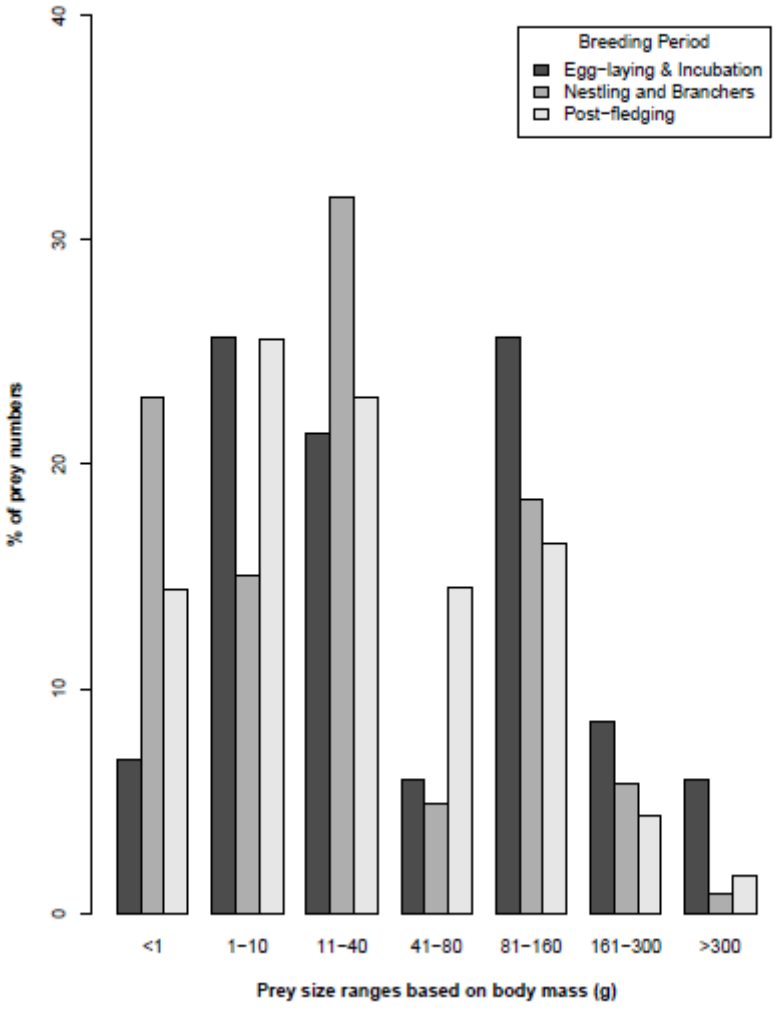


Figure 1.8. Frequency distributions of diet prey numbers (%) by prey mass categories and by breeding period of Barred Owls in western Oregon, 2008, based on pellet analysis. Prey number data are pooled from Table 1.8 for each prey mass range. Prey mass estimates are from Appendix. Breeding periods are: egg-laying and incubation (3 March–4 April 2008); nestling and brancher (5 April–4 May 2008); and post-fledging (5 May–31 August 2008).

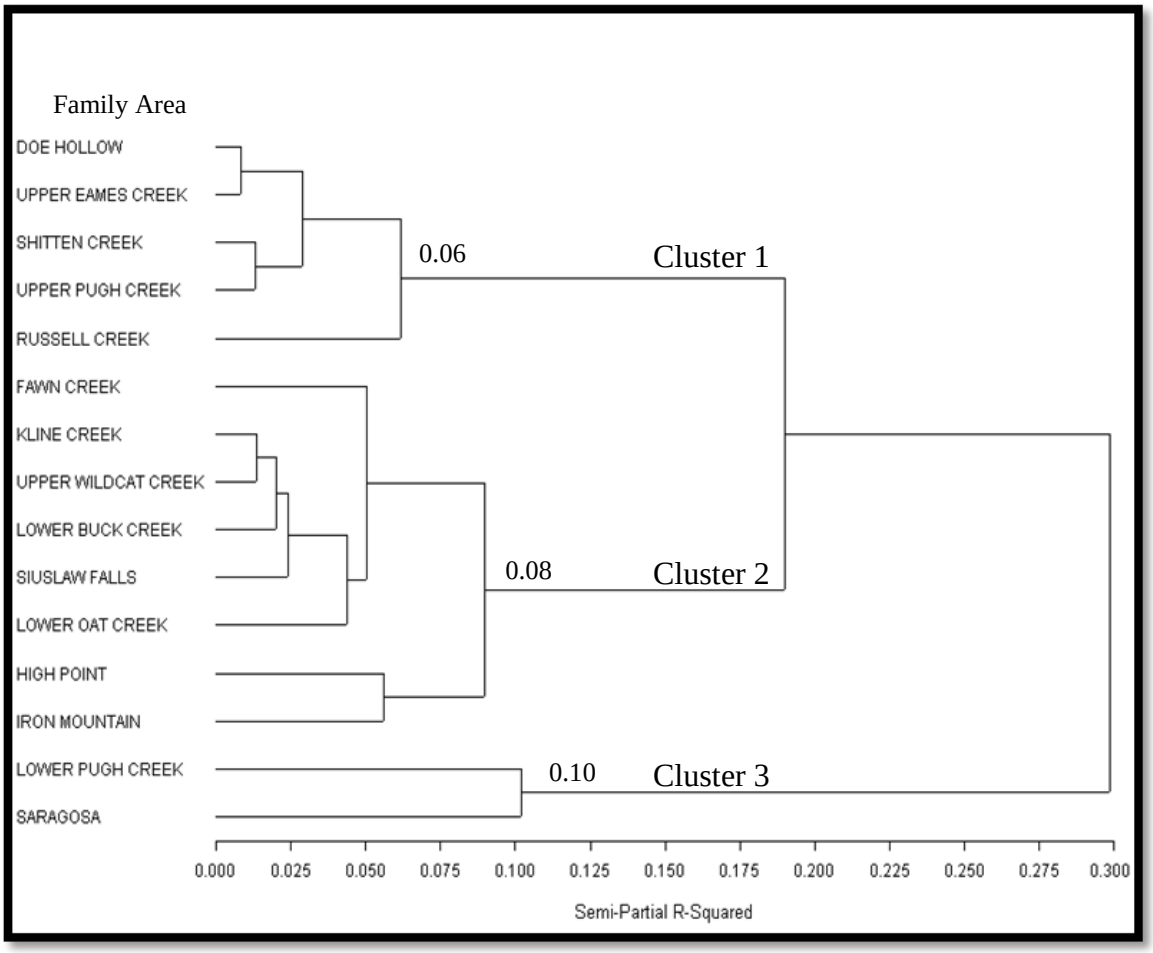


Figure 1.9. Dendrogram resulting from the cluster analysis of diet composition (% of prey numbers) based on pellets from 15 Barred Owl family areas in western Oregon, 2007–2008. Values of Ward's linkage are indicated at each cluster bifurcation. Dissimilarity measures are semi-partial r-squared. Cluster 3 comprised two family areas and was most dissimilar to Clusters 1 and 2 in diet composition and relative prey numbers.

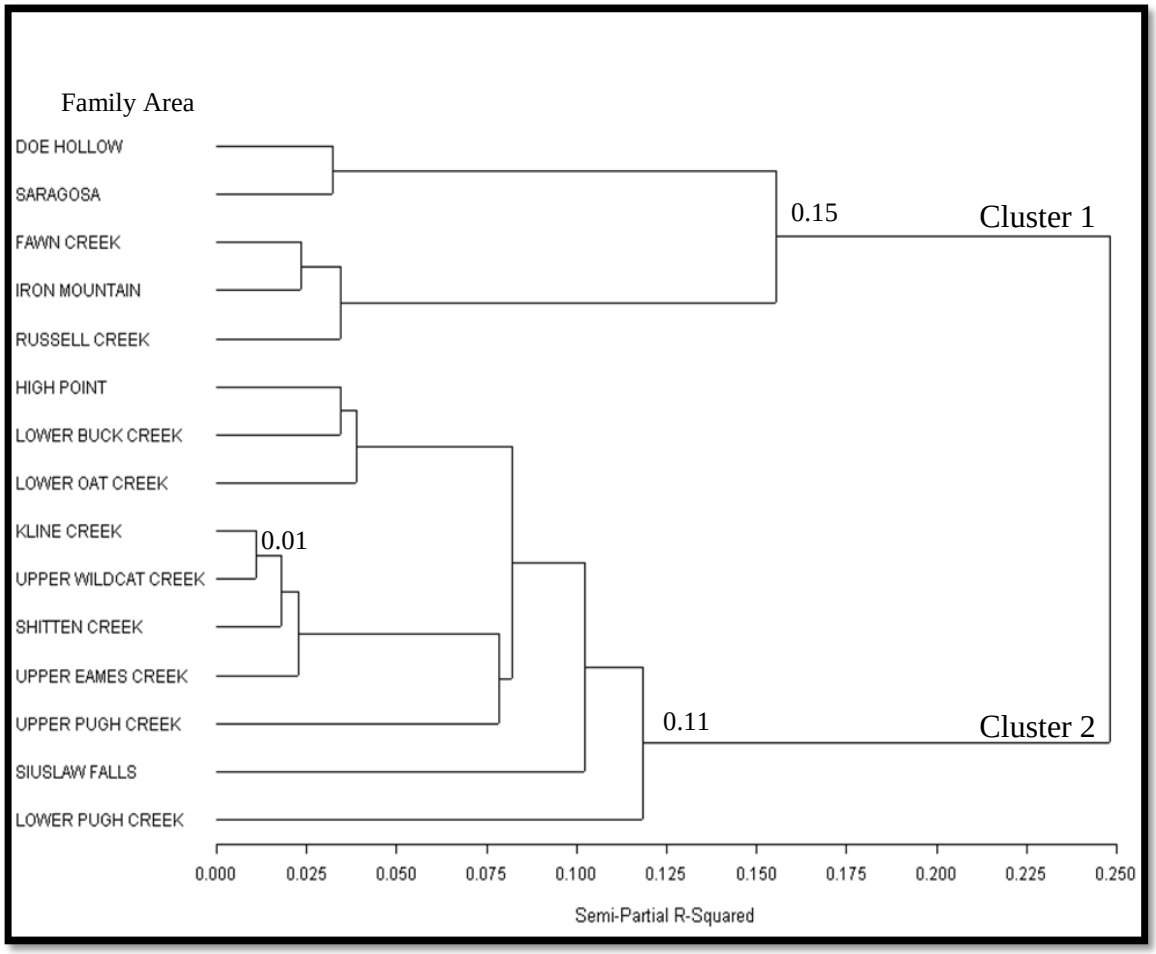
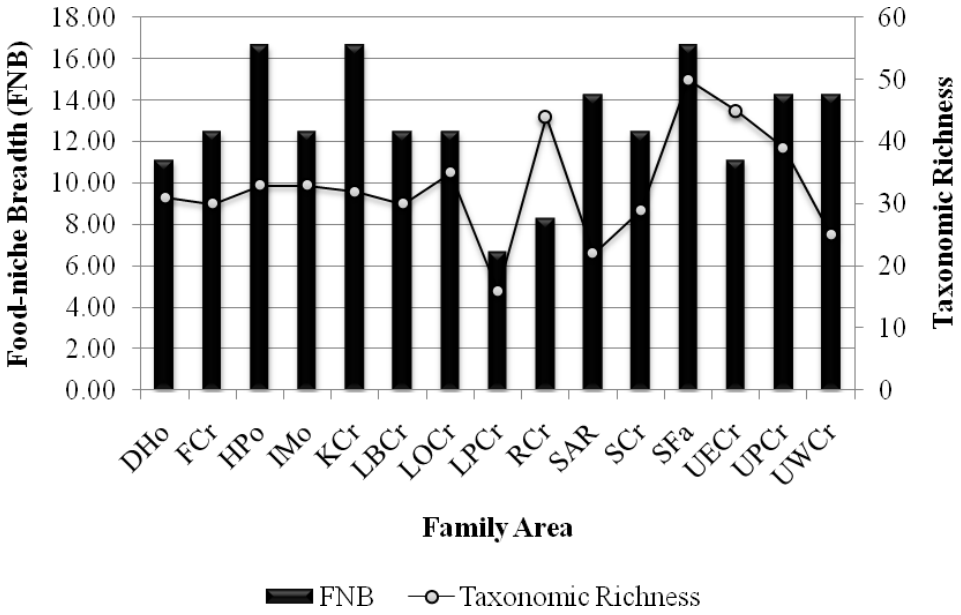


Figure 1.10. Dendrogram resulting from the cluster analysis of diet composition (% of prey biomass) based on pellets from 15 Barred Owl family areas in western Oregon, 2007–2008. Values of Ward's linkage are indicated at each cluster bifurcation. Dissimilarity measures are semi-partial r-squared. Cluster 1 comprised five family areas and exhibited the most dissimilarity from other areas in diet composition and relative prey biomass.

a)



b)

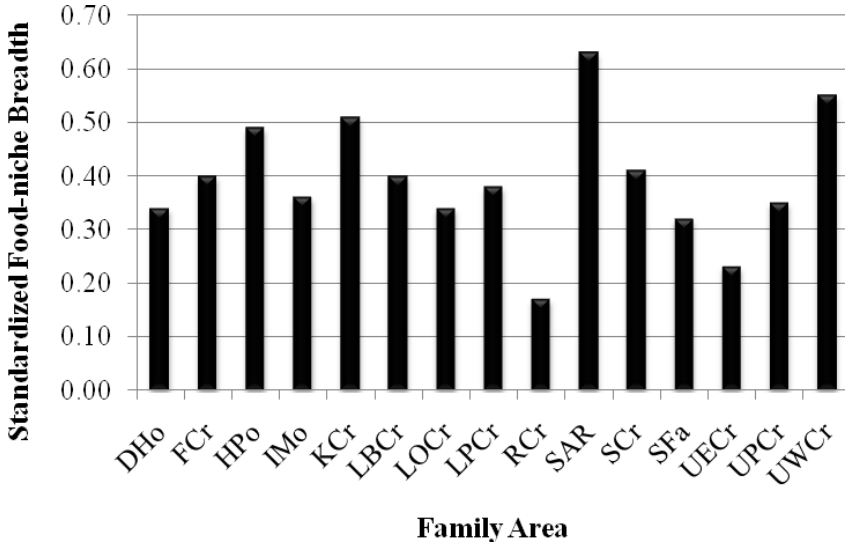


Figure 1.11. Pattern of food-niche breadth (FNB) among 15 Barred Owl family areas in western Oregon for 2007 and 2008 breeding seasons combined; a) FNB (solid bars) relative to taxonomic richness (solid line), and b) FNB_{sta}.

CHAPTER TWO: GEOGRAPHIC VARIATION IN DIETS OF BARRED OWLS (*STRIX VARIA*) DURING THE BREEDING SEASON: A COMPARISON OF THREE POPULATIONS IN THE PACIFIC NORTHWEST

Abstract

I compared diet composition and feeding-niche characteristics of three geographic populations of Barred Owls (*Strix varia*) in the Pacific Northwest United States, including the central Coast Ranges, Oregon, Olympic National Park, Washington, and eastern Cascade Range, Washington. I used evidence from 1,021 regurgitated pellets obtained from 25 owl family areas in the central Coast Ranges, 48 pellets from 20 areas in Olympic National Park, and 57 pellets from 9 areas in the eastern Cascade Range. The total sample was 3,463 prey and 192,951 g of prey biomass in the central Coast Ranges, 187 prey and 11,444 g in Olympic National Park, and 336 prey and 12,871 g in the eastern Cascades. The number of taxa in the diet was 81 in the central Coast Ranges, 36 in Olympic National Park, and 32 in the eastern Cascades. Diets were similar between the central Coast Ranges and Olympic National Park in that prey were mainly forest mammals (64.3% and 71.7% of prey numbers, respectively), with shrews (*Sorex* spp.), coast moles (*Scapanus orarius*), and northern flying squirrels (*Glaucomys sabrinus*) predominating in prey numbers and biomass. In the eastern Cascades, insects were numerically dominant in the diet (47.0%), with beetles (Coleoptera spp.) predominating by prey number (45.2%) followed by frogs (18.8%) and flying squirrels (12.2%). In the central Coast Ranges and Olympic National Park areas, beetles constituted 12.0% and

8.6% of prey numbers, respectively. Flying squirrels were the primary source of biomass across all areas (24.8% in the central Coast Ranges; 34.0% in Olympic National Park; 41.4% in the eastern Cascades). Estimated mean mass of individual prey was 55.7 g in the central Coast Ranges, 61.2 g in Olympic National Park, and 38.3 g in the eastern Cascades. Food-niche breadth values indicated that although many prey taxa were taken, the overall food-niche dimension in each study area was narrow. Factors contributing to differences in diet among geographic locales included disparities in prey distributions, differences in the number of pellets collected, and likely temporal and local variation in prey use and prey availability.

Introduction

The Barred Owl (*Strix varia*) had a historical range largely east of the Great Plains in the United States and Prairie Provinces of Canada, extending from southeastern Canada to montane Pacific slopes of western Mexico (Mazur and James 2000). During the past century, Barred Owls expanded their range westward through the southern Provinces of Canada to the Pacific Coast region of the United States. They currently inhabit coniferous forests throughout much of western North America (Livezey 2009a). A review and synthesis of Barred Owl literature conducted by Livezey (2007) revealed that Barred Owls occupy a variety of forested habitats and human-modified habitats, which might have facilitated their relatively rapid range expansion (Livezey 2009b).

Barred Owls are versatile predators and are considered to be primarily foraging generalists throughout their range in eastern North America (Errington and McDonald 1937, Wilson 1938, Korschgen and Stuart 1972, Devereux and Mosher 1984, Elderkin 1987, Bosakowski and Smith 1992) and western North America (Mazur et al. 1997,

Takats 1998, Hamer et al. 2001, [Graham Chapter One]), consuming terrestrial and arboreal prey, including numerous invertebrates and aquatic species. However, there is little data on the food habits of Barred Owls from western North America, where Barred Owls have recently expanded their range into the Pacific Northwest. My goal was to provide information about Barred Owl food habits from three different locales in the Pacific Northwest and to compare my results to the only previous study in the same region (Hamer et al. 2001).

In this report, I describe geographic variation in diets of Barred Owls during the breeding season, including differences and similarities in dietary composition and feeding-niche characteristics. These results will provide a better understanding of the ecological role of Barred Owls in their new environments, including the potential for competition for food resources with other native fauna and potential effects of a new top-level predator on prey populations.

Methods

Study Areas

My three study areas were the central Coast Ranges of western Oregon, Olympic National Park, Washington, and the eastern Cascade Range of Washington. The 745 km^2 central Coast Ranges study area was 30 km west of Eugene in Lane County, Oregon. Elevation ranged from 84–700 m, with topography characterized by steep mountain slopes and with narrow ridgelines dissected by rivers and streams. The mild maritime climate was characterized by warm, dry summers and wet winters with much of the winter precipitation accumulating as snow at higher elevations (Franklin and Dyrness 1973). Located within the western hemlock (*Tsuga heterophylla*) vegetation zone

(Franklin and Dyrness 1973), this region was covered by coniferous forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and western redcedar (*Thuja plicata*). Patches or dense stands of bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) were often interspersed with conifers and were often persistent early colonizers in recently disturbed areas and riparian bottomlands.

The central Coast Ranges study area included a mixture of lands managed by the U.S. Bureau of Land Management (48%), industrial timber companies (47%), Oregon Department of Forestry (3%), and private landowners (2%). The landscape was characterized by a checkerboard-like ownership pattern wherein 2.56 km^2 sections of federal or state land alternated with 2.56 km^2 sections of private land. Forest age and structure varied widely on the study area, mainly due to logging, fire, and windstorms (Franklin and Dyrness 1973). Variation in forest age was primarily due to differing forest management practices between federal and non-federal ownerships, which resulted in a mosaic of forest conditions on the landscape with predominantly mature and old forest covering federally managed lands and young or recently cleared forests covering industrial timber lands.

In the Olympic National Park study area, regurgitated pellets from Barred Owls were collected ancillary to studies of Northern Spotted Owls (*Strix occidentalis caurina*) that were conducted by the National Park Service in 1997–2009 (Gremel 2009, Forsman et al. 2011). Olympic National Park is on the Olympic Peninsula in northwest Washington and comprises 3,734 km^2, of which 3,059 km^2 were forested valleys naturally fragmented by the rugged high elevation peaks and ridges of the Olympic Mountains. Elevation in the study area ranged from near sea level to 2,428 m.

Much of Olympic National Park was covered by old forest, with the majority of forest stands greater than 100 years old. Also located within the western hemlock vegetation zone (Franklin and Dyrness 1973), the Olympic Mountains were characterized by marked differences in annual precipitation on the eastern and western halves of the peninsula (40–200 cm/yr vs. 360–480 cm/yr, respectively; Henderson et al. 1989). The comparatively dry eastern half of the peninsula was characterized by coniferous forests predominantly composed of Douglas-fir. Forests on the west side of the peninsula were mostly dominated by western hemlock, western redcedar, Sitka spruce (*Picea sitchensis*), and Pacific silver fir (*Abies amabilis*), with varied amounts of Douglas-fir (Franklin and Dyrness 1973).

The 309 km^2 eastern Cascades study area was located in Chelan County, Washington, near the town of Leavenworth on the Okanogan–Wenatchee National Forest (47°48’N, 120°35’W). In this study area, regurgitated pellets and uneaten prey remains were collected ancillary to a radio-telemetry study of Barred Owl movements during 2004–2006 (Singleton et al. 2010). Vegetation on the study area was mostly interior mixed-conifer forests of Douglas-fir, grand fir (*Abies grandis*), and ponderosa pine (*Pinus ponderosa*; Johnson and O’Neil 2001). Topography was mountainous with elevation ranging from 500–1,900 m (Singleton et al. 2010). The climate on this study area was characterized by warm, dry summers and cold, wet winters. Most precipitation occurred as snow during winter.

Barred Owl Diets

Pellet Collection

Regurgitated pellets were collected from roost and nest trees within owl family areas during 2007–2009 in the central Coast Ranges, 1997–2009 in Olympic National Park, and 2004–2006 in the eastern Cascades. Family areas were occupied by pairs of owls and routinely monitored by tracking radio-marked owls or by regularly surveying areas occupied by unmarked owls, generally in more than one year. I limited my analysis to the breeding season (March-August), when data were available from all three study areas. Pellets were individually bagged and labeled in the field and then air-dried or preserved frozen for subsequent dissection and identification of prey remains.

Prey Taxa Identification

Each pellet was teased apart by hand, and prey remains were separated from fur, feathers, and other organic material using tweezers and a probe. Skeletal remains were identified to the lowest taxonomic level possible using dichotomous keys (Maser and Storm 1970, Verts and Carraway 1998), illustrations from published sources (Duellman and Trueb 1994), and comparisons with specimens in a reference collection of mammal, bird, and reptile skeletons at the U.S. Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory in Corvallis, Oregon, USA. I identified fish bones, gastropod shells, and arthropod remains (head capsules, mandibles, elytra, and exoskeleton fragments) by comparison with reference specimens. Some uneaten bird remains were identified by matching feathers with specimens in the Vertebrate Museum, Department of Biological Sciences, Boise State University, Boise, Idaho, USA. Amphibians, fish, and insects that were not identifiable to the species level were

identified to the lowest taxonomic level possible, and, in the case of salamanders, were lumped into groups based on size.

Quantification of Diets

I quantified diets of Barred Owls in each study area using three standard measures, including percent composition of prey numbers and prey biomass, and frequency of occurrence of prey in pellets (Marti et al. 2007). All measures of diet were expressed as a percentage of the total prey numbers, biomass, and occurrence for each geographic locale for comparisons. I estimated the numbers of each prey taxon in each pellet by counting bones, gastropod shells, or fragments of arthropod exoskeleton. I estimated the minimum number of individuals of vertebrate prey by enumerating skulls, mandibles, or bones of the appendicular skeleton, whichever gave the highest count. Numbers of coiled and spiraled gastropods were estimated based on counts of shell apexes (center of the gastropod shell). Numbers of arthropods, including diplopods, collembolans, and insects were estimated based on the number of head capsules, mandibles, elytra, or fragments of exoskeleton, whichever gave the highest count. Freshwater crayfish (*Pacifastacus leniusculus*) were not quantified by estimating the minimum number of individuals in each pellet, but rather quantified using relative prey biomass and frequency of occurrence metrics (see Prey Numbers in Methods section of Chapter One for detailed description and rationale).

I estimated the total biomass of each prey taxon in each sample by either (1) multiplying the estimated number of individuals by the mean mass of the taxon, or (2) estimating and summing the biomass of each individual prey in the sample based on comparisons with bones of local reference specimens of known age and mass. The latter

approach was used only for large prey such as rabbits and hares (*Sylvilagus bachmani, Lepus americanus*), mountain beaver (*Aplodontia rufa*), spotted skunk (*Spilogale gracilis*), and grouse (*Bonasa umbellus, Dendragapus obscurus*) that would have been overestimated by using mean mass to estimate biomass (because almost all of those individuals taken by owls were small juveniles). Estimates of mean mass of mammals, birds, and reptiles were obtained from Verts and Carraway (1998), Forsman et al. (2004), Dunning (1993), and Steenhof (1983). Of the amphibians, I obtained mean mass estimates for frogs from Forsman et al. (2004) and for salamanders from several published sources including Johnston and Frid (2002), MacCracken (2005), Cardall et al. (2004), Alvarado (1967), Ray (1958), and Withers (1980). Because I could not identify most salamanders to species, I lumped all salamanders into three size groups (large, medium, small) based on evaluations of mass estimates and length of front and rear leg bones (Nebeker et al. 1994). For fish, I estimated average mass based on estimates from similar taxa at the superclass level using Behnke (2002). Average masses for gastropods were obtained from locally collected specimens or published sources (Forsman et al. 2004, Hawkins and Furnish 1987). For diplopods, collembolans, and insects, I used estimates of mean mass or masses of similar taxa from the literature (Cárcamo et al. 2000, Sarasola et al. 2003, Forsman et al. 2004). I elected not to use published estimates of crayfish biomass, but rather developed methods to estimate relative biomass of crayfish for the central Coast Ranges study area using locally collected specimens (see Prey Biomass in Methods section of Chapter One for detailed description and rationale).

I calculated frequency of prey occurrence in individual pellets by dividing the total number of pellets in which each taxon occurred by the total number of pellets in the sample and multiplying by 100.

Feeding-niche Characteristics

To compare feeding-niche characteristics among study areas, I computed food-niche breadth (FNB), a simple index of diversity in the diet. I estimated FNB using Levins' (1968) reciprocal of Simpson's (1949) index of diversity:

$$\mathrm{FNB} = 1/\Sigma p_i^2,$$

where p_i = the relative proportion of each prey taxa in the diet. This index produces values ranging from 1 to n, where n is the number of prey taxa in the diet, with higher values indicating a broader food-niche dimension with prey taxa nearly equally common in the diet. I considered index values that were near the middle third of the range of 1 to n (i.e., 14.29, range 1–28) to be "moderate" food-niche breadths, suggesting moderately selective use of a variety of prey. FNB is low when the majority of prey individuals occur in few taxa, thus indicating a narrow food-niche. For comparisons among geographical areas and the literature, I calculated a standardized food-niche breadth (FNB_{sta}) using Colwell and Futuyma's (1971) FNB_{sta} estimate:

$$\mathrm{FNB}_{sta} = (\mathrm{B}_{obs} - \mathrm{B}_{min}) / (\mathrm{B}_{max} - \mathrm{B}_{min}),$$

where B_{obs} = observed FNB, $\mathrm{B}_{min} = 1$, the minimum niche breadth estimate, and $\mathrm{B}_{max} = n$, the maximum niche breadth estimate (or number of prey taxa used in calculating B_{obs}). FNB_{sta} ranges from 0 to 1. I partitioned FNB_{sta} into three categories: narrow (0.00–0.33), moderate (0.34–0.66), and broad (0.67–1.00). Because this estimator was independent of

the number of prey taxa used in each study area, it was useful for comparisons among areas that differed in diet taxa number.

Results

Diet Composition and Prey Use

I obtained 1,021 pellets from 25 owl family areas in the central Coast Ranges, 48 pellets from 20 family areas in Olympic National Park, and 57 pellets and few discarded prey remains from 9 family areas in the eastern Cascade Range. The combined sample from all three study areas included 3,986 individual prey from 1,126 pellets, and included at least 94 prey taxa, including 40 mammals, 27 birds, 4 reptiles, 4 amphibians, 1 fish, 3 gastropods, 1 diplopod, 1 collembolan, 12 insects, and 1 crustacean (Table 2.1).

The estimated total number and biomass of prey was 3,463 and 192,951 g in the central Coast Ranges, 187 and 11,445 g in Olympic National Park, and 336 and 12,871 g in the eastern Cascades (Table 2.1). In the central Coast Ranges and Olympic National Park, diets included mostly forest mammals (64.3% and 71.7% of prey numbers, respectively), with a variety of shrews (*Sorex* spp.), coast moles (*Scapanus orarius*), and northern flying squirrels (*Glaucomys sabrinus*) predominating in prey numbers and biomass (Table 2.1). Other mammals that were common in owl diets in these two study areas included shrew-moles (*Neurotrichus gibbsii*), mice (*Peromyscus* spp.), and creeping voles (*Microtus oregoni*). Red tree voles (*Arborimus longicaudus*) were relatively common prey in the central Coast Ranges study area (3.9% of prey numbers), but did not occur in Washington. The diet sample from the eastern Cascades study area included large numbers of insects (47.0% of prey numbers), with beetles (Coleoptera spp.) being the most common taxon in the diet (45.2%), followed by frogs (18.8%), and northern

flying squirrels (12.2%). Beetles were much less common in diets in the central Coast Ranges and Olympic National Park study areas (Table 2.1).

Percent of prey biomass on all three study areas was dominated by northern flying squirrels, but the percent of prey biomass contributed by flying squirrels varied greatly among areas, ranging from 24.8% in the central Coast Ranges to 41.4% in the eastern Cascades (Table 2.1). In addition, frogs and snowshoe hare made up a large amount of the total prey biomass in the eastern Cascades (14.7% and 12.2%, respectively), but were comparatively uncommon in the diet in the central Coast Ranges and Olympic National Park study areas (Table 2.1).

Birds accounted for 2.7–6.4% of prey numbers and 5.8–17.4% of prey biomass (Table 2.1). The comparatively high proportion of bird biomass in the diet in Olympic National Park was mainly the result of predation on Blue Grouse, which contributed 9.2% of total prey biomass. Reptiles, fish, and gastropods generally accounted for ≤ 6.8% of prey numbers and ≤ 1.5% of prey biomass, with fish and gastropods absent from the diet in the eastern Cascades. Amphibians generally accounted for ≤ 10.1% of prey numbers and ≤ 3.2% of prey biomass; however, in the eastern Cascades study area, amphibians were comparably more common in the diet (22.6% of prey numbers and 15.5% of prey biomass) than on the other study areas. Crustaceans, including signal crayfish, only occurred in the diets of owls in the central Coast Ranges, contributing 0.6% of prey biomass.

Mean mass of individual prey was 55.7 g in the central Coast Ranges, 61.2 g in Olympic National Park, and 38.3 g in the eastern Cascades. The lower mean mass of prey

in the diet in the eastern Cascades was due to large numbers of insect prey in the diet in that region (Table 2.1).

Mammals had the highest frequency of occurrence in pellets in all study areas, and flying squirrels were the most frequently encountered prey in all areas, occurring in 31.7% of pellets in the central Coast Ranges, 41.7% of pellets in Olympic National Park, and 59.6% of pellets in the eastern Cascades. Insects were the second most frequently encountered prey taxa in pellets in all areas (Table 2.1). Amphibians or birds were generally the 3rd or 4th most commonly encountered taxa in pellets (Table 2.1). Other taxa that frequently occurred in pellets in the central Coast Ranges and Olympic National Park were shrews and coast moles. Conversely, other frequent taxa in the eastern Cascades included frogs and beetles (Table 2.1).

Feeding-niche Characteristics

Owls consumed 15 taxa, mainly mammals, which were common among the three study areas. Pellets from the central Coast Ranges revealed 37 taxa, primarily birds, consumed only there, whereas pellets from Olympic National Park and the eastern Cascades yielded two and eight unique taxa, respectively.

Estimated food-niche breadth (FNB) values based on diet richness and the relative abundance of prey used by Barred Owls for the three study areas were 16.67 (range 1–81) for the central Coast Ranges, 11.11 (range 1–36) for Olympic National Park, and 3.85 (range 1–32) for the eastern Cascades (Table 2.1). These values indicate that although many prey taxa were taken, the food-niche dimension was narrow in all study areas. This was due to the predominance of relatively few taxa, especially mammals in the central

Coast Ranges and Olympic National Park and beetles, frogs, and flying squirrels in the eastern Cascades.

Estimates of standardized food-niche breadth (FNB_{sta}) were also narrow across study areas (0.20, central Coast Ranges; 0.29, Olympic National Park; 0.09, eastern Cascades; Table 2.1). The comparatively broader FNB_{sta} for Barred Owls in Olympic National Park and central Coast Ranges indicated that prey captured in those areas were more evenly distributed among taxa than in the eastern Cascades study area.

Discussion

My results indicate that the Barred Owl in the Pacific Northwest, as elsewhere, is a generalist predator capturing prey ranging from small invertebrates to mammals as large as adult snowshoe hare, and including terrestrial, arboreal, aerial, and aquatic prey. This result was consistent with dietary results reported for Barred Owls on the west slope of the Cascade Range in northern Washington, where Hamer et al. (2001) found that Barred Owls most frequently preyed on small to medium-sized mammals, but also captured a variety of other prey, including birds, amphibians, fish, gastropods, and insects. Although mammals were the primary source of biomass used in all of my study areas, insects were numerically the most common prey in the eastern Cascades. The prevalence of insects in the latter area is likely associated with the dry forest environment in that region. Beetle infestations following drought or high-intensity fire damage in dry coniferous forests in the eastern Cascades (Hessburg et al. 1994, Lehmkuhl et al. 2007) might relate to their prevalence in the owl diet in this area. Results from my study and the study by Hamer et al. (2001) reveal that Barred Owls in the Pacific Northwest region

have a rich diet and readily adapt to use different prey in the different communities that occur within the region.

My estimates of standardized food-niche breadth (FNB_{sta}) of Barred Owls ranged from 0.09 in the eastern Cascades to 0.29 in Olympic National Park. These estimates were narrow compared to the moderate (FNB_{sta} = 0.53) estimate I derived from the original data presented in Hamer et al. (2001) for the west slope of the Cascade Range in Washington. These differences could reflect temporal variation since our studies were conducted many years apart, but could also reflect local variation in prey abundance and considerable flexibility in prey selection by Barred Owls.

Marti et al. (2007) suggested that samples containing about 100 prey individuals were reasonably adequate to describe diets of raptors. My samples were quite large (187−3,463), so they should have been adequate to identify all but the rarest items in the diet. However, the number of prey taxa identified in studies of raptor diets is sensitive to sample size, and larger samples are more likely to include rare prey taxa (Marti 1987). This may have explained the much larger number of prey taxa in the sample from the central Coast Ranges, Oregon study area, where my sample was 10−18 times larger than on the other areas I studied. However, it is also possible that the diversity of prey available to owls in the central Coast Ranges study area was higher than in the other study areas.

Barred Owls appear to be euryphagic throughout their range, and my results from the Pacific Northwest USA support that conclusion. In my three study areas and that of Hamer et al. (2001), the diets were rich. I found differences in the taxa eaten among areas, but relatively narrow food-niche breadths, indicating high dependence on a few

mammalian prey in each study area. I concluded that Barred Owls forage as generalist opportunists and are predators that have the ability to adapt to a wide range of prey as they move into new ranges in Oregon and Washington. My results indicate that study of additional areas and collections of several hundred or more pellets per site will be useful to determine adequacy of pellet sampling for describing Barred Owl diets in other areas of range expansion. Additional descriptions of Barred Owl food habits and foraging ecology will contribute to learning how Barred Owl expansion will affect the native fauna in the Pacific Northwest.

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Table 2.1. Geographic variation in breeding season diet composition, prey numbers (% Num), estimated prey biomass (% Bio), frequency of prey occurrence (% Occ), food-niche breadth (FNB), and standardized FNB (FNB_{sta}) of three populations of Barred Owls (*Strix varia*) in the Pacific Northwest. Numbers in parentheses indicate total number of prey individuals, estimates of total prey biomass (g) consumed by owls, and total number of regurgitated pellets obtained from each geographic locale.

	Central Coast Ranges, Oregon			Olympic National Park, Washington			Eastern Cascade Range, Washington		
Prey Taxa	% Num (3,463)	% Bio (192,951.1)	% Occ (1,021)	% Num (187)	% Bio (11,444.6)	% Occ (48)	% Num (336)	% Bio (12,871.0)	% Occ (57)
Mammals									
Sorex bendirii	0.1	< 0.1	0.5						
Sorex sonomae	2.1	0.3	5.5						
Sorex trowbridgii	0.9	0.1	2.4						
Sorex trowbridgii / vagrans	9.9	0.9	19.4						
Sorex vagrans	0.8	0.1	2.2						
Sorex spp.[a]				18.7	2.8	37.5	4.2	1.0	17.5
Neurotrichus gibbsii	4.3	0.7	11.7	3.7	0.6	12.5	0.6	0.1	3.5
Scapanus orarius	12.0	12.0	29.8	9.6	8.8	29.2	0.3	0.4	1.8
Scapanus townsendii[b]	2.1	4.8	6.6	2.1	4.6	8.3			
Myotis spp.	0.1	< 0.1	0.3						
Eptesicus fuscus							0.3	0.1	1.8
Sylvilagus bachmani[c]	0.3	3.0	1.0						
Lepus americanus	0.1	2.3	0.4	0.5	3.1	3.1	0.9	12.2	5.3
Leporidae spp.	1.0	5.5	3.4				0.3	3.3	1.8
Aplodontia rufa[b]	0.7	5.2	2.4	0.5	1.7	2.1			
Tamias townsendii[d]	1.0	1.4	3.0	0.5	0.7	2.1			
Tamias spp.[d]							1.2	1.8	5.3
Tamiasciurus douglasii	2.0	7.8	6.5	2.1	7.7	8.3	1.5	8.6	8.8
Glaucomys sabrinus	10.3	24.8	31.7	15.5	34.0	41.7	12.2	41.4	59.6
Unidentified Sciurid spp.	0.1	0.3	0.4						
Thomomys mazama[e]	0.4	0.7	1.5						
Thomomys talpoides[f]							0.3	0.8	1.8
Peromyscus maniculatus[g]	4.0	1.6	10.5				1.5	0.9	8.8
Peromyscus spp.[g]				3.7	1.3	12.5			
Neotoma cinerea[h]							0.3	2.2	1.8
Neotoma spp.[i]	1.3	6.6	4.4						
Myodes californicus[j]	1.6	0.7	4.9						
Myodes gapperi[k]				2.1	1.0	8.3	0.3	0.2	1.8
Phenacomys intermedius[k]							0.3	0.3	1.8
Arborimus longicaudus[j]	3.9	1.8	10.6						
Microtus longicaudus	0.2	0.2	0.5	0.5	0.5	2.1	0.3	0.4	1.8
Microtus oregoni	1.3	0.5	3.8	5.3	1.8	16.7	0.3	0.2	1.8
Microtus townsendii	0.4	0.4	1.1	2.1	2.3	8.3			
Microtus spp.	0.5	0.3	1.6				0.3	0.3	1.8
Ondatra zibethicus	0.1	1.8	0.3						
Muridae spp.	1.4	0.6	4.0	1.6	0.8	4.2	1.2	0.9	7.0

Table 2.1. Continued.

Prey Taxa	Central Coast Ranges, Oregon % Num (3,463)	% Bio (192,951.1)	% Occ (1,021)	Olympic National Park, Washington % Num (187)	% Bio (11,444.6)	% Occ (48)	Eastern Cascade Range, Washington % Num (336)	% Bio (12,871.0)	% Occ (57)
Zapus trinotatus	0.9	0.4	2.4	1.6	0.7	6.3			
Mustela erminea	0.3	0.3	1.1	0.5	0.5	2.1			
Spilogale gracilis	0.2	2.5	0.8	0.5	5.3	2.1			
Unidentified mammals							0.3	2.3	1.8
Mammals subtotal	**64.3**	**87.7**	**92.8**	**71.7**	**78.1**	**97.9**	**26.5**	**77.3**	**87.7**
Birds									
Bonasa umbellus	0.1	1.1	0.4						
Dendragapus obscurus	< 0.1	0.5	0.1	0.5	9.2	2.1			
Phasianidae spp.							0.3	2.3	1.8
Oreortyx pictus[j]	0.1	0.3	0.3						
Patagioenas fasciata	0.2	1.4	0.7						
Accipiter striatus							0.3	1.1	1.8
Aegolius acadicus	0.2	0.3	0.5						
Megascops kennicottii	0.1	0.4	0.4				0.3	1.3	1.8
Colaptes auratus	0.1	0.3	0.4						
Dryocopus pileatus	< 0.1	0.1	0.1						
Picoides villosus	< 0.1	< 0.1	0.1				0.3	0.5	1.8
Sphyrapicus ruber	0.1	0.1	0.2						
Empidonax spp.[l]	< 0.1	< 0.1	0.1						
Cyanocitta stelleri	0.2	0.4	0.6	0.5	1.1	2.1			
Perisoreus canadensis	< 0.1	< 0.1	0.1						
Poecile rufescens	0.1	< 0.1	0.3						
Sitta canadensis	0.1	< 0.1	0.3	0.5	0.1	2.1			
Troglodytes pacificus	0.5	0.1	1.4	1.6	0.2	6.3	0.3	0.1	1.8
Catharus ustulatus	< 0.1	< 0.1	0.1						
Ixoreus naevius	0.1	0.2	0.4	1.1	1.4	4.2			
Turdus / Ixoreus spp.	0.1	0.1	0.2						
Piranga ludoviciana	< 0.1	< 0.1	0.1						
Pipilo maculatus	< 0.1	< 0.1	0.1	0.5	0.3	2.1			
Junco hyemalis	0.2	0.1	0.6				0.6	0.3	1.8
Unidentified large bird				0.5	5.0	2.1			
Unidentified medium-sized bird	0.1	0.3	0.4						
Unidentified small bird	0.3	0.1	1.1	1.1	0.1	2.1	1.5	0.3	8.8
Birds subtotal	**2.7**	**5.8**	**8.7**	**6.4**	**17.4**	**20.8**	**3.6**	**5.9**	**19.3**
Reptiles									
Coluber constrictor[m]	< 0.1	< 0.1	0.1						
Elgaria coerulea	0.1	0.1	0.4						
Sceloporus occidentalis	0.1	< 0.1	0.3						
Thamnophis spp.	0.8	1.3	2.5	0.5	0.9	2.1	0.3	0.8	1.8
Reptiles subtotal	**1.0**	**1.5**	**3.3**	**0.5**	**0.9**	**2.1**	**0.3**	**0.8**	**1.8**
Amphibians									
Frog spp.[n]	0.4	0.2	1.5	4.8	2.4	10.4	18.8	14.7	22.8
Large salamander[o]	1.2	1.4	3.7						
Medium-size salamander[p]	5.2	1.3	11.5	0.5	0.1	2.1	3.9	0.8	10.5
Small salamander[q]	3.3	0.2	6.7	1.6	0.1	6.3			
Amphibians subtotal	**10.1**	**3.2**	**18.2**	**7.0**	**2.6**	**14.6**	**22.6**	**15.5**	**24.6**
Fish									
Osteichthyes spp.[r]	0.2	0.2	0.6	0.5	0.4	2.1			
Fish subtotal	**0.2**	**0.2**	**0.6**	**0.5**	**0.4**	**2.1**			

Table 2.1. Continued.

Prey Taxa	Central Coast Ranges, Oregon % Num (3,463)	% Bio (192,951.1)	% Occ (1,021)	Olympic National Park, Washington % Num (187)	% Bio (11,444.6)	% Occ (48)	Eastern Cascade Range, Washington % Num (336)	% Bio (12,871.0)	% Occ (57)
Gastropods									
Haplotrema vancouverense [b]	1.4	0.2	3.7	1.1	0.1	4.2			
Monadenia fidelis [b]	3.8	0.7	8.9	2.1	0.4	8.3			
Juga spp.[b]	1.7	< 0.1	0.8						
Gastropods subtotal	**6.8**	**0.9**	**12.1**	**3.2**	**0.5**	**12.5**			
Arthropods									
Diplopods									
Harpaphe haydeniana	0.2	< 0.1	0.8						
Diplopods subtotal	**0.2**	**< 0.1**	**0.8**						
Collembola									
Entomobryidae spp.	< 0.1	< 0.1	0.1						
Collembola subtotal	**< 0.1**	**< 0.1**	**0.1**						
Insects									
Mantis religiosa							0.3	< 0.1	1.8
Brochymena affinis	< 0.1	< 0.1	0.1						
Hemiptera spp.	0.1	< 0.1	0.3						
Ergates spiculatus	0.1	< 0.1	0.4				1.5	0.1	3.5
Coleoptera spp.	12.0	0.1	18.5	8.6	< 0.1	22.9	45.2	0.4	21.1
Braconidae spp.	< 0.1	< 0.1	0.1						
Ichneumonidae spp.	< 0.1	< 0.1	0.1						
Formicidae spp.	1.9	< 0.1	2.6	1.1	< 0.1	4.2			
Vespidae spp.	< 0.1	< 0.1	0.1						
Hymenoptera spp.	0.1	< 0.1	0.2						
Unidentified large insect	< 0.1	< 0.1	0.1						
Unidentified small insect	0.4	< 0.1	1.4	1.1	< 0.1	4.2			
Insects subtotal	**14.7**	**0.1**	**21.5**	**10.7**	**< 0.1**	**29.2**	**47.0**	**0.5**	**24.6**
Crustaceans									
Pacifastacus leniusculus	**	0.6	7.3						
Crustaceans subtotal		**0.6**	**7.3**						
Total %	**100.0**	**100.0**		**100.0**	**100.0**		**100.0**	**100.0**	
Richness		81			36			32	
FNB		16.67			11.11			3.85	
FNB_{sta}		0.20			0.29			0.09	

[a] Indicates either *Sorex bendirii*, *S. monticolus*, *S. palustris*, *S. trowbridgii*, or *S. vagrans* in Olympic National Park; and *S. cinereus*, *S. monticolus*, *S. palustris*, *S. trowbridgii*, or *S. vagran*s in the eastern Cascade Range, Washington study areas.
[b] Did not occur in the eastern Cascade Range, Washington study area.
[c] Did not occur in the Olympic National Park and eastern Cascade Range, Washington study areas.
[d] All *Tamias townsendii* except in the eastern Cascade Range, Washington study area where the diet included either *T. amoenus*, *T, minimus*, or *T. townsendii*.
[e] *T. mazama* in central Coast Ranges, Oregon and Olympic National Park, Washington.
[f] *T. talpoides* in eastern Cascade Range, Washington.
[g] All *P. maniculatus* except in the Olympic National Park, Washington study area where both *P. maniculatus* and *P. keeni* occur and could not be distinguished from skeletal identification.
[h] *N. cinerea* in Olympic National Park and eastern Cascade Range study areas of Washington.

Table 2.1. Continued.

[i] *N. cinerea* and *N. fuscipes* were present in the central Coast Ranges, Oregon study area and could not be separated based on skeletal identification.
[j] Occurs in central Coast Ranges, Oregon study area.
[k] Did not occur in central Coast Ranges, Oregon study area.
[l] Indicates either *E. difficilis*, *E. traillii*, or *E. hammondii*.
[m] Did not occur in Olympic National Park, Washington study area.
[n] Indicates either Pacific treefrog (*Pseudacris regilla*) or true frog (*Rana* spp.).
[o] Indicates either Pacific giant salamander (*Dicamptodon tenebrosus*) or Northwestern salamander (*Ambystoma gracile*).
[p] Indicates either larva or juvenile *D. tenebrosus* or *A. gracile* in the central Coast Ranges, Oregon and eastern Cascade Range, Washington study areas and larva or juvenile Cope's giant salamander (*Dicamptodon copei*) and *A. gracile* in Olympic National Park, Washington and roughskin newts (*Taricha granulosa*) in all areas.
[q] Indicates either long-toed salamander (*Ambystoma macrodactylum*), clouded salamander (*Aneides ferreus*), ensatina (*Ensatina eschscholtzii*), Dunn's salamander (*Plethodon dunni*), and western redback salamander (*Plethodon vehiculum*) in central Coast Ranges, Oregon. *A. macrodactylum*, Olympic torrent salamander (*Rhyacotriton olympicus*), *E. eschscholtzii*, *P. dunni*, Van Dyke's salamander (*Plethodon vandykei*), and *P. vehiculum* in Olympic National Park, Washington.
[r] Indicates unidentified bony small stream fish (e.g., coastal cutthroat trout [*Oncorhynchus clarki clarki*]).

CHAPTER THREE: PREY SIZE PREFERENCE BEHAVIOR BY SYMPATRIC NORTHERN SPOTTED OWLS AND BARRED OWLS IN OREGON AND WASHINGTON

Abstract

Controlled prey preference experiments provide a way to study raptor food choice and capture, and they can advance the interpretation of dietary evidence. I performed prey preference experiments with sympatric, wild Northern Spotted Owls (*Strix occidentalis caurina*) and Barred Owls (*Strix varia*) in Oregon and Washington during 1 March–31 August 2008. I tested the null hypothesis that, given a simultaneous choice between a small-sized prey animal (house mouse, *Mus musculus*) and a medium-sized prey animal (Norway rat, *Rattus norvegicus* or black rat, *Rattus rattus*), there is no difference in the frequency with which owls attempt to capture prey by size. Both species exhibited significant preference for the smaller-sized mice. There was no difference in prey size selection between female and male Northern Spotted Owls; both sexes preferred smaller prey. Sample sizes for Barred Owls were too small to test for sexual differences. There was no interspecific difference in prey size selection between Northern Spotted Owls and Barred Owls. Both species chose small-sized prey more frequently than medium-sized prey. My results for Northern Spotted Owls were not expected because diets of Northern Spotted Owls are typically dominated by medium-sized mammalian prey such as northern flying squirrels and woodrats (*Neotoma cinerea* and *N. fuscipes*).

Wild Barred Owls preferentially selected small prey during feeding trials, which is consistent with Barred Owl diets in North America, including the Pacific Northwest. These results add to our knowledge of feeding behavior and provide insight into the potential for food competition between Northern Spotted Owls and Barred Owls.

Introduction

Controlled experiments provide a way to study animal feeding, and they can advance the interpretation of dietary evidence of raptor diets based on pellets and prey remains, direct observations, or videography (Arroyo and Bretagnolle 1999, Dykstra et al. 2003, Meyer et al. 2004, Lewis et al. 2004, Marti et al. 2007). Some factors affecting raptor diet are food preferences, prey base, availability, vulnerability, and nutritional and energetic requirements, including those for foraging and food handling (Ellis et al. 1976, Krebs 1978, Houston and McNamara 1985, Rodgers 1990).

In the experiment described in this report, I tested for prey size preference in sympatric, wild Northern Spotted Owls (*Strix occidentalis caurina*) and Barred Owls (*Strix varia*). The preference for a food item is reflected by the likelihood of that item being chosen if offered when all items are equally available (Ivlev 1961, Ellis et al. 1976, Johnson 1980), and that one is selected more than the others. Prey preference also is an indication of what is important to an animal, and in turn, important for conserving a species. My procedure simulated traditional cafeteria-style trials (Pinowski and Drodz 1975) or food choice experiments documented in other birds, including Sharp-shinned Hawks (*Accipiter striatus*; Mueller and Berger 1970), a Red-tailed Hawk (*Buteo jamaicensis*; Snyder 1975), Eastern Screech-Owls (*Megascops asio*; Marti and Hogue

1979), and Northwestern Crows (*Corvus caurinus*; Willson and Comet 1993), whereby an animal is offered a choice of potential foods at equal availabilities.

However, I found no examples of field experiments of prey preference by free-ranging wild owls. Therefore, results of this experimental-field approach, together with diet compositions of the two co-occurring owl species, will complement one another and may be important because of competition between Barred Owls and the federally threatened Northern Spotted Owl in the Pacific Northwest (Wiens 2012).

Studies of Northern Spotted Owl diets indicate that the most common species in the diet in most areas are medium-sized small mammals, especially northern flying squirrels (*Glaucomys sabrinus*) and woodrats (*Neotoma cinerea* and *N. fuscipes*; Barrows 1980, Forsman et al. 1984, 2001, 2004, Gutiérrez et al. 1995, Ward et al. 1998). In contrast, numerous studies of small mammal abundance in the same areas clearly demonstrate that shrews (*Sorex trowbridgii*), mice (*Peromyscus maniculatus*), and terrestrial voles (*Microtus* spp., *Myodes* spp.) are more abundant than are squirrels or woodrats (Aubry et al. 1991, Corn and Bury 1991, West 1991, Carey et al. 1992, Rosenberg et al. 2003, Ward et al. 1998). This suggests that Spotted Owls may select for larger mammals when foraging (Barrows 1980, 1985, 1987, Forsman et al. 1984, Thrailkill and Bias 1989, Verner et al. 1992, Carey and Peeler 1995, Gutiérrez et al. 1995, Ward et al. 1998). An alternative hypothesis is that Northern Spotted Owls capture more squirrels and woodrats because those species are easier for the owls to capture (i.e., are more vulnerable). Unfortunately, there is no information about the comparative vulnerability of different types of prey to Northern Spotted Owls. Therefore, it has been difficult to determine if the diet data indicate selection of prey disproportionate to what

occurs or is available. Similarly, there exists no information about availability or occurrence of Barred Owl prey relative to the diet.

As described in Chapter One, Barred Owls in western Oregon appear to be opportunistic hunters, capturing and consuming a wide variety of prey across many taxa, with diet largely comprising mammals, including small mammals such as moles (*Scapanus orarius*), shrew-moles (*Neurotrichus gibbsii*), shrews (*Sorex bendirii*, *S. sonomae*, *S. trowbridgii*, *S. trowbridgii/vagrans*, and *S. vagrans*), red tree voles (*Arborimus longicaudus*), deer mice, and flying squirrels. Northern Spotted Owls generally use medium-sized small mammals (Gutiérrez et al. 1995). Size preference experiments will provide new behavioral information.

My objectives were to examine the level of (1) intraspecific variation in choosing different sized prey for each owl species, (2) sex-specific variation for different sized prey for each owl species, and (3) interspecific variation for choosing different sized prey.

Methods

Study Areas

Feeding trials were performed with free-ranging Northern Spotted Owls and Barred Owls on four study areas in western Oregon (Northern Coast Ranges, Central Coast Ranges, Tyee, and H. J. Andrews study areas) and one study area on the east slope of the Cascade Range in central Washington (Cle Elum study area; Figure 3.1). I conducted all feeding trials in the Central Coast Ranges. Trials on the other study areas were performed by biologists who were conducting long-term monitoring studies of Northern Spotted Owls (Anthony et al. 2006, Forsman et al. 2011), and who agreed to

participate in the study by sampling owls in their study areas. All of these study areas have been described by Forsman et al. (2011) and by Graham (Central Coast Ranges; Chapter One).

Field Procedure

I used cafeteria-style trials to determine if owls would preferentially select prey by size when simultaneously provided small and medium-sized animals within the normal range of sizes eaten by Northern Spotted Owls and Barred Owls. Feeding trials with Northern Spotted Owls were conducted by locating a owl in its roost tree during the day and then simultaneously presenting the owl with a live laboratory mouse (*Mus musculus*) and live laboratory rat (*Rattus norvegicus* or *Rattus rattus*) that were placed on separate elevated platforms that were 0.6 m apart in front of the owl. Platforms were small circular pieces of plywood (30 cm in diam) attached to the top of 1-m-long steel rods that were pushed into the ground so that the two platforms were about 0.6 m above the ground and clearly visible to the owl (Figure 3.2). To make sure that the focal owl was simultaneously exposed to both potential prey animals, I covered both potential prey with inverted bowls, and then removed the bowls at the same time. Then, I quietly walked away and observed the owl from a distance of 10-50 m, depending on topography and density of the vegetation. I used the same procedure for Barred Owls, except that I lured the owls in with playback calls until they were close enough to see the two alternative prey. All trials were conducted during the breeding season (1 March–31 August) in 2008. Individual owls were only sampled once in order to avoid lack of independence in the sample. The average minimum age of Northern Spotted Owls in the

sample was 10 (range = 1–17 yrs). Exact age of Barred Owls was unknown, but all were adults.

Average mass of mice and rats used in trials was 22.2 g (SD = 4.6, range = 10–35 g) and 191.8 g (SD = 64.8, range = 75–300 g), respectively. To reduce the amount of color variation in appearance of prey, I matched animals by color so that animals in each trial were similar in color (either white or dark). After each feeding trial, the observer completed a data form that included the owl site name, date and time of the trial, color and mass of each prey animal, information on which prey was taken, and activity level code of the rat and mouse (i.e., movement, no movement).

Statistical Analyses

I used 2 x 2 contingency tables in program SAS (SAS Institute Inc. 2001) to test the null hypothesis that Northern Spotted Owls and Barred Owls each selected small vs. medium-sized prey in equal proportions. Where sample sizes permitted, I conducted separate analyses to evaluate sex-specific differences and interspecific differences in prey size selection. I used chi-square (χ^2) tests to evaluate hypotheses when the expected cell frequency in each category was > 5 or Fisher's exact tests when cell frequencies were ≤ 5 (Manly et al. 1993, Zar 1999). I used $\alpha < 0.05$ as the criteria for statistical significance. This research was approved by the Institutional Animal Care and Use Committee at Boise State University (Study No. 692-07-004).

Results

My cooperators and I conducted 30 trials with Northern Spotted Owls (11 females, 19 males) and 17 trials with Barred Owls (12 females, 4 males, 1 gender unknown). The number of trials conducted on each study area was: Central Coast Ranges

(2 Northern Spotted Owls, 15 Barred Owls), Northern Coast Ranges (12 Northern Spotted Owls), Tyee (9 Northern Spotted Owls, 1 Barred Owl), H. J. Andrews (3 Northern Spotted Owls, 1 Barred Owl), and Cle Elum (4 Northern Spotted Owls). All 30 Northern Spotted Owl trials resulted in a bird choosing a prey, but only 11 (64.7%) of 17 Barred Owl trials were complete because some owls refused prey animals or approached the site, but quickly flew away.

Of the 30 Northern Spotted Owls tested, 24 (80%) chose the mouse and 6 (20%) chose the rat. Of the 11 Barred Owls tested, 9 (82%) chose the mouse and 2 (18%) chose the rat. In both species, the tendency to take smaller prey was significant (Northern Spotted Owls: $\chi^2 = 10.8$, $df = 1$, $P < 0.005$; Barred Owls: $\chi^2 = 4.46$, $df = 1$, $P < 0.05$). There was no difference in prey size selection between female and male Northern Spotted Owls (Fisher's exact test, $P = 0.638$); both sexes preferred smaller prey. Sample sizes for Barred Owls were too small to test for sexual differences. There was no interspecific difference in prey size selection between Northern Spotted Owls and Barred Owls (Fisher's exact test, $P = 1.000$).

Discussion

Northern Spotted Owls in my experiment preferred small prey, which was unexpected because their natural diets are dominated by larger prey such as flying squirrels and/ or woodrats (Barrows 1980, Forsman et al. 1984, 2001, 2004, Richards 1989, Ward 1990, Ward et al. 1998, Gutiérrez et al. 1995, Hamer et al. 2001), which are comparable in size with the rats that I used in the feeding trials. One possible explanation was that laboratory mice were more active and, therefore, more visible or attractive to the owls. However, a review of the data indicated that the activity level code for mice and

rats was identical in 77% of Northern Spotted Owl trials and 73% of Barred Owl trials. In contrast with Northern Spotted Owls, the Barred Owl preference for small prey is consistent with Barred Owl diets in regions of North America (see Mazur and James 2000) and with my results from the central Coast Ranges of western Oregon (see Chapter One). However, Barred Owls are capable of killing much larger prey than those offered in my experiments, including animals as large as adult snowshoe hare (*Lepus americanus*; see Chapter One).

As with my results, Eastern Screech-Owls (*Megascops asio*) also preferred smaller prey during laboratory experiments (Marti and Hogue 1979), and like Northern Spotted Owls and Barred Owls, they were capable of killing larger prey in the wild (Ritchison and Cavanagh 1992, Gehlbach 1995). Barred Owls and Screech-Owls have a comparatively rich diet base and forage on a range of large and small prey sizes (Mazur and James 2000, Gehlbach 1995).

Although it could be argued that my findings are consistent with the predictions of the dangerous prey hypothesis (Forbes 1989), that is unlikely because Northern Spotted Owl diets are normally dominated by squirrels and woodrats that are armed with formidable incisors and that are as large or larger than the rats used in my experiment. I also think that hypotheses regarding ease of capture or handling, or energy expended per gram captured (Schoener 1971, Pyke et al. 1977) are not likely for explaining my results because Northern Spotted Owls commonly capture and handle comparatively large prey, and the amount of energy needed to capture a rat in my experiment would have been little different than that needed to capture a mouse.

Another factor that could explain the selection for mice by Northern Spotted Owls was that many of the Northern Spotted Owls sampled in the demography study areas were familiar with taking live mice from researchers who used mice to locate nests and young of banded Northern Spotted Owls (Franklin et al. 1996). However, I doubt that this was a valid explanation for the observed behavior because I saw the same pattern in the sample of Northern Spotted Owls and Barred Owls in the central Coast Ranges study area where many owls had not been habituated to regular visits by researchers with mice. Nevertheless, feeding trials with naïve Northern Spotted Owls that have never been exposed to long-term behavioral conditioning with mice is an important consideration for future research. Additional research of prey size preference could be important for assessing competition between Northern Spotted Owls and Barred Owls because their diets overlap moderately in the Central Coast Ranges of western Oregon study area (42%; Wiens 2012) and substantially in northwestern Washington (76%; Hamer et al. 2001).

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Figure 3.1. Map showing the location of each study area in western Oregon (1, Central Coast Ranges; 2, H. J. Andrews; 3, Northern Coast Ranges; 4, Tyee) and in central Washington (5, Cle Elum) where feeding trials were conducted with wild Northern Spotted Owls and Barred Owls during 1 March–31 August 2008.

Figure 3.2. Photograph of feeding platforms (foreground) used for prey size preference experiments. Experimental prey animals were hidden under inverted bowls and then revealed and clearly visible to the owl (encircled in red in background) (Photo by P. Kolar).

APPENDIX

Prey Taxa, Common Names, Mean Mass of Prey, and Sources for Computing and Estimating Percent Prey Biomass of Barred Owl Diets in Western Oregon, 2007–2009

Appendix. Prey taxa, common names, mean mass of prey, and sources for computing and estimating percent prey biomass of Barred Owl diets in western Oregon, 2007–2009.

Prey Taxa	Mean Mass (g)	Source
Mammals		
Sorex bendirii – Pacific water shrew	18	Verts and Carraway 1998
Sorex sonomae – fog shrew	9	Verts and Carraway 1998
Sorex trowbridgii – Trowbridge's shrew	5	Verts and Carraway 1998
Sorex trowbridgii / vagrans – Trowbridge's or vagrant shrew	5	Verts and Carraway 1998
Sorex vagrans – vagrant shrew	5	Verts and Carraway 1998
Neurotrichus gibbsii – shrew-mole	9	Verts and Carraway 1998
Scapanus orarius – coast mole	56	Verts and Carraway 1998
Scapanus townsendii – Townsend's mole	131	Verts and Carraway 1998
Myotis spp. – unidentified myotis[a]	6	Verts and Carraway 1998; Mean of all species in this genus.
Sylvilagus bachmani – brush rabbit	350–650	Mass of each individual estimated based on comparison with reference specimens of known mass.
Lepus americanus – snowshoe hare	1075–1200	Mass of each individual estimated based on comparison with reference specimens of known mass.
Leporidae spp. – unidentified rabbit / hare	50–1100	Mass of each individual estimated based on comparison with reference specimens of known mass.
Aplodontia rufa – mountain beaver	100–550	Mass of each individual estimated based on comparison with reference specimens of known mass.
Tamias townsendii – Townsend's chipmunk	83	Verts and Carraway 1998
Tamiasciurus douglasii – Douglas' squirrel	221	Verts and Carraway 1998
Glaucomys sabrinus – northern flying squirrel	134	Verts and Carraway 1998
Unidentified Sciurid spp.	143	Mean of all species in this family.
Thomomys mazama – western pocket gopher	95	Verts and Carraway 1998
Peromyscus maniculatus – deer mouse	22	Verts and Carraway 1998
Neotoma spp. – unidentified woodrat[b]	285	Forsman et al. 2004
Rattus rattus – black rat	250	Forsman et al. 2004
Myodes californicus – western red-backed vole	23	Verts and Carraway 1998
Arborimus longicaudus – red tree vole	26	Verts and Carraway 1998
Microtus longicaudus – long-tailed vole	53	Verts and Carraway 1998
Microtus oregoni – creeping vole	20	Verts and Carraway 1998
Microtus townsendii – Townsend's vole	57	Verts and Carraway 1998
Microtus spp.– unidentified vole	31	Mean of all species in this genus.
Ondatra zibethicus – common muskrat	1169	Verts and Carraway 1998
Muridae spp. – unidentified vole / mouse	25	Mean of all species in this group.
Zapus trinotatus – Pacific jumping mouse	25	Verts and Carraway 1998
Mustela erminea – ermine	55	Verts and Carraway 1998
Spilogale gracilis – spotted skunk	606	Verts and Carraway 1998
Unidentified mammals	33–250	Mass of each individual estimated based on comparison with reference specimens of known mass.

Appendix. Continued.

Prey Taxa	Mean Mass (g)	Source
Birds		
Bonasa umbellus – Ruffed Grouse	25–576	Mass of each individual estimated based on comparison with reference specimens of known mass.
Dendragapus obscurus – Blue Grouse	1050	Mass of each individual estimated based on comparison with reference specimens of known mass.
Grouse spp. – unidentified Grouse	350–576	Mass of each individual estimated based on comparison with reference specimens of known mass.
Oreortyx pictus – Mountain Quail	224	Dunning 1993
Patagioenas fasciata – Band-tailed Pigeon	392	Dunning 1993
Aegolius acadicus – Northern Saw-whet Owl	83	Dunning 1993
Megascops kennicottii – Western Screech-Owl	169	Dunning 1993
Strix spp. – Spotted Owl or Barred Owl	610–717	Dunning 1993
Megaceryle alcyon – Belted Kingfisher	148	Dunning 1993
Colaptes auratus – Northern Flicker	142	Dunning 1993
Dryocopus pileatus – Pileated Woodpecker	287	Dunning 1993
Picoides villosus – Hairy Woodpecker	66	Dunning 1993
Sphyrapicus ruber – Red-breasted Sapsucker	49	Dunning 1993
Empidonax spp. – unidentified Flycatcher[c]	11	Mean of all species in this genus.
Cyanocitta stelleri – Stellar's Jay	128	Dunning 1993
Perisoreus canadensis – Gray Jay	73	Dunning 1993
Corvus spp. – unidentified Crow or Raven	823	Mean of all species in this genus.
Poecile rufescens – Chestnut-backed Chickadee	10	Dunning 1993
Sitta canadensis – Red-breasted Nuthatch	10	Dunning 1993
Troglodytes pacificus – Pacific Wren	9	Dunning 1993
Catharus ustulatus – Swainson's Thrush	31	Dunning 1993
Ixoreus naevius – Varied Thrush	78	Dunning 1993
Turdus / Ixoreus spp. – Robin / Thrush spp.	78	Mean of all species in this genus.
Piranga ludoviciana – Western Tanager	28	Dunning 1993
Pipilo maculatus – Spotted Towhee	40	Dunning 1993
Junco hyemalis – Dark-eyed Junco	18	Dunning 1993
Loxia curvirostra – Red Crossbill	36	Dunning 1993
Unidentified medium-sized bird	60–250	Mass of each individual estimated based on comparison with reference specimens of known mass.
Unidentified small bird	5–59	Mass of each individual estimated based on comparison with reference specimens of known mass.
Reptiles		
Coluber constrictor – racer	77	Steenhof 1983
Elgaria coerulea – northern alligator lizard	35	Forsman et al. 2004
Sceloporus occidentalis – western fence lizard	10	Forsman et al. 2004
Thamnophis spp. – garter snake spp.	100	Forsman et al. 2004

Appendix. Continued.

Prey Taxa	Mean Mass (g)	Source
Amphibians		
Frog spp. – unidentified frog spp.[d]	30	Forsman et al. 2004
Caudata spp. – unidentified salamander spp.		
Large salamander[e]	68	Nebeker et al. 1994, Johnston and Find 2002, MacCracken 2005
Medium-size salamander[f]	14	Cardall et al. 2004
Small salamander[g]	4	Ray 1958, Alvarado 1967, Withers 1980
Fish		
Osteichthyes spp. – unidentified bony fish[h]	51	Behnke 2002
Gastropods – terrestrial and freshwater snails		
Haplotrema vancouverense – robust lancetooth snail	7	Forsman et al. 2004
Monadenia fidelis – Pacific sideband snail	11	Estimated from locally collected specimens.
Juga spp. – pleurocerid snail[i]	0.02	Hawkins and Furnish 1987
Arthropods		
Diplopods – millipedes		
Harpaphe haydeniana – yellow-spotted millipede	0.4	Cárcamo et al. 2000
Collembola – springtails		
Entomobryidae spp. – unidentified springtail	0.1	Means based on estimates from similar species in this family.
Insects		
Chlorochroa spp. – stink bug	0.3	Forsman et al. 2004
Brochymena affinis – rough stink bug	0.3	Means based on estimates from similar species in the subfamily Pentatominae.
Hemiptera spp. – unidentified bugs	0.3	Means based on estimates from similar species in this order.
Ergates spiculatus – ponderous borer	3.0	Forsman et al. 2004
Coleoptera spp. – unidentified beetles	0.3	Forsman et al. 2004
Braconidae spp. – braconid wasp	0.1	Means based on estimates from similar species in this order.
Ichneumonidae spp. – ichneumon wasp	0.1	Means based on estimates from similar species in this order.
Formicidae spp. – ants	0.1	Forsman et al. 2004
Vespidae spp. – hornets and yellowjackets	0.1	Forsman et al. 2004
Hymenoptera spp. – unidentified ants, bees, or wasps	0.1	Means based on estimates from similar species in this order.
Unidentified large insect	2.0	Forsman et al. 2004
Unidentified small insect	0.3	Forsman et al. 2004
Crustaceans		
Pacifastacus leniusculus – signal crayfish	*	Estimated from locally collected specimens.

[a] Indicates either California myotis (*Myotis californicus*), long-eared myotis (*M. evotis*,) little brown myotis (*M. lucifugus*), or Yuma myotis (*M. yumanensis*).

[b] Indicates either bushy-tailed woodrat (*Neotoma cinerea*) or dusky-footed woodrat (*N. fuscipes*).

Appendix. Continued.

[c] Indicates either Pacific-slope Flycatcher (*Empidonax difficilis*), Willow Flycatcher (*E. traillii*), or Hammond's Flycatcher (*E. hammondii*).
[d] Indicates either Pacific treefrog (*Pseudacris regilla*) or true frog (*Rana* spp.).
[e] Indicates either Pacific giant salamander (*Dicamptodon tenebrosus*) or Northwestern salamander (*Ambystoma gracile*). Johnston and Find (2002) provided mass and femur lengths > 7 mm for Pacific giant salamanders. MacCracken (2005) and Nebeker et al. (1994) provided mass and leg lengths for Northwestern salamanders, respectively. Large salamanders ranged in mass from 23–114 g.
[f] Indicates Medium-size salamanders, including either larva or juvenile large salamanders and roughskin newts (*Taricha granulosa*; Cardall et al. 2004). Medium-size salamanders ranged in mass from 7–22 g.
[g] Indicates either long-toed salamander (*Ambystoma macrodactylum*; Alvarado 1967), clouded salamander (*Aneides ferreus*), ensatina (*Ensatina eschscholtzii*), and Dunn's salamander (*Plethodon dunni*; Ray 1958), and western redback salamander (*Plethodon vehiculum*; Withers 1980). Femur lengths averaged 2.0–4.9 mm. Small salamanders ranged in mass from 2–6 g.
[h] Indicates unidentified bony small stream fish (e.g., coastal cutthroat trout [*Oncorhynchus clarki clarki*]).
[i] Typical *Juga* individuals in the Pacific Northwest west of the Cascade crest also average 15 mm in length (Hawkins and Furnish 1987).
[*] See predicted biomass conversions used for signal crayfish (*Pacifastacus leniusculus*; Table 1.1) and Prey Biomass in Methods section.