# AN ABSTRACT OF THE DISSERTATION OF

Ryan C. Baumbusch for the degree of Doctor of Philosophy in Wildlife Science presented on March 14, 2023.

Title: Foraging Ecology of Barred Owls where they are Outcompeting the Threatened Northern Spotted Owl.

Abstract approved:

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Following European-American colonization of North America and associated landscape changes, barred owls (*Strix varia*) underwent a dramatic expansion of their historical range. The barred owl expanded across the previously tree-less Great Plains that had limited their distribution, and into the forests along the west coast. In these western forests they came into contact with and began to outcompete the congeneric and federally threatened northern spotted owl (*Strix occidentalis caurina*). The negative impacts of this competition contributed to further declines in northern spotted owl populations and prompted initiation of a large-scale lethal removal experiment of barred owls to assess whether this action could be used as a management strategy to conserve northern spotted owls. Collection of barred owls over several years at multiple study areas in the Pacific Northwest, USA provided specimens to investigate the foraging ecology and food-web interactions of this novel predator in its expanded range. Using 2,136 barred owl specimens collected near Cle

Elum, WA, Alsea, OR, and Roseburg, OR I characterized the diets of 1,329 owls by examining stomach contents and investigating factors associated with body condition of owls at the time of their collection. Diet composition of barred owls differed substantially from that of northern spotted owls in that prey species that typically comprise the majority (>50%) of spotted owl diets (e.g., flying squirrels (*Glaucomys* spp.), woodrats (*Neotoma* spp.), and tree voles (*Arborimus* spp.) comprised <10% of barred owl diets in WA and <3% of diets in OR. Yet, due to the estimated higher energetic demands of barred owls (greater body mass and larger brood sizes) and the fact that they achieve much higher densities than spotted owls, these prey species are likely consumed at much higher frequencies across the landscape as barred owls replace spotted owls. Mammalian insectivores – shrews (*Sorex spp.*), shrew moles (*Neurotrichus gibbsii*), and moles (*Scapanus* spp.) – along with salamanders were consumed at a high frequency by barred owls, suggesting these taxa may be at risk from invasive predator at high density. These prey, as well as arthropods, contribute little biomass to the diets of northern spotted owls, yet contributed 12-51% of the dietary biomass of barred owls in my study. Using a subsample of the barred owl specimens collected, I measured the proximate body composition of barred owls and developed models to estimate the percent fat of dry mass in a barred owl based on morphometrics, sex and time of year, and a fat score. The model that explained the most variation (adjusted $R^2 = 0.87$) in barred owl body condition used a body condition index of mass divided by foot-pad length, sex and time of year a female was collected (in relation to egg production), and a 4-level fat score. I used this model and one without a fat score covariate (adjusted $R^2 = 0.76$) to estimate the percent fat

of 96% of owls collected. Using estimates of percent fat, I assessed the influence of habitat quality and conspecific density on barred owl body condition. Habitat covariates previously associated with barred owl use had little influence on their body condition. Despite previous links between barred owl survival and increasing proportions of old forest habitat, intermediate proportions of old forest at a barred owl collection sites were associated with barred owls in the poorest physiological condition, and birds in the best condition collected at sites with lower or higher proportions of old forest. Mean elevation of collection sites had no effect on body condition, but relative topographic position (TPI) was negatively associated with percent body fat (i.e., owls collected from lowland valley bottoms were in better condition). In the Oregon Coast Range near Alsea, where territory occupancy rates prior to removals were the highest among study areas, barred owls showed evidence of negative density dependence. When more owls were collected close to each other in space and time, they were in poorer condition. However, in the other two study areas, where occupancy rates, and presumably barred owl density was lower, owls were in better body condition when collected from sites where many owls had been detected during surveys. This suggests negative density dependence was not yet occurring, and density at the time of collection was instead an indicator of site quality not accounted for by the habitat parameters I included in the analysis. The barred owl's broad diet and generalist habitat use has likely allowed this invasive species to expand throughout the range of the northern spotted owl and outcompete the threatened congeneric. While the threats posed by barred owls are pressing and complex, these threats are likely not limited to northern spotted owls alone, as a

variety of prey species may also be at risk from this new predator in the forests of the Pacific Northwest.

# Foraging Ecology of Barred Owls where they are Outcompeting the Threatened Northern Spotted Owl

by
Ryan C. Baumbusch

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Ryan C. Baumbusch, Author

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# DEDICATION

This thesis is dedicated to the honor and memory of Dr. Lowell V. Diller. Your dedication and enthusiasm to studying and protecting the animals and systems you cared about were an inspiration. I would certainly not be where I am today were it not for your mentorship and support. You were and still are my role model, and I hope to have a faction of the impact on science and conservation that you had in your career. More importantly, I am still in awe at the time and care you invested in the people around. We are all so much better off for having you touched our lives. The world lost you far too soon, and those who knew you miss you deeply.

# Chapter 1 - Introduction

Invasive species constitute a major threat to biodiversity worldwide, where populations of native fauna and flora can be negatively affected by predation or herbivory of an invasive species they have not evolved with (Mack et al. 2000, Pyšek et al. 2020). As native populations decline from the direct effects of consumption, these impacts can cascade down trophic levels and throughout foods webs, resulting in indirect effects to many other species in the ecological community (Wainwright et al. 2021). Traditionally, invasive species have been thought of as those that are introduced into a novel environment, intentionally or unintentionally, by humans (Elton 1958). A modification of this concept is that of the native invader; a species that shifts its range–possibly facilitated by human action–into a nearby ecological community that is not adapted for its presence, resulting in detrimental impacts on native species as the invasive species increases in abundance (Carey et al. 2012).

The barred owl (*Strix varia*) offers a dramatic case of a native invader. They are a medium-sized, territorial forest owl, historically restricted to eastern North America (Mazur and James 2020). The western extent of their distribution had been limited by the lack of forests in the Great Plains, partly maintained by Native Americans and Bison (*Bison* bison) through fires and herbivory, respectively (Livezey et al. 2009b). Yet, both were largely removed from the plains following European-American colonization across the continent, and in association with tree-planting policies associated with homesteading, allowed for tree growth to occur across the prairies. This may have helped facilitate a westward expansion of the barred owl's range, likely stemming from the northern Mississippi River valley in the late-19th century (Lizevey 2009b). Historic records of barred owl detections show a gradual expansion, where they reached the west coast of North America near the US-Canada border around the middle of the 20th century (Livezey 2009a). From there, they expanded northward into southeast Alaska and south into the forest of the US Pacific Northwest, where they encountered the closely related northern spotted owl (*Strix occidentalis caurina*; Long and Wolfe 2019).

Northern spotted owls are a medium-sized territorial forest owl that occurs from southern British Columbia throughout the Cascade Range and along the coastal mountains to the San Francisco Bay in California (Gutierrez et al. 2020). They require old growth forests for their survival and reproduction (Olson et al. 2004, Dugger et al. 2005, Franklin et al. 2020). Loss of these habitats through timber harvest caused historical population declines of spotted owls (Thomas et al. 1990). Those declines prompted the owl's listing under the endangered species act (USFWS 1990), enacting numerous protections of old-growth forests throughout the Pacific Northwest (USDA USDI 1994). While the focus of spotted owl conservation was focused on protection of old growth forest habitat, the listing decision acknowledged that the presence of the newly arrived and outwardly similar barred owl posed a potential, but as yet, unrealized threat (USFWS 1990).

In the years following the spotted owl listing and subsequent protections, the rate of range-wide population decline began to slow (Forsman et al. 2011). However, as barred owls expanded throughout the range of the northern spotted owl and became locally abundant, localized population declines of spotted owls began to spread and accelerate (Dugger et al. 2016, Franklin et al. 2021). Declines in annual survival and territory occupancy of spotted owls were linked to the presence of barred owls (Kelly et al. 2003, Olson et al. 2005, Dugger et al. 2011). It was hypothesized that the generalist life history characteristics of the larger, and more aggressive barred owl, including their use of old forest habitats (Singleton et al. 2010, Wiens et al. 2014), and prey resources that spotted owls rely upon (Hamer et al. 2001, 2007, Wiens et al. 2014), was allowing barred owls to outcompete spotted owls. In the revised recovery plan for northern spotted owls, the US Fish and Wildlife Service (2011) characterized barred owls as an "extremely pressing and complex" threat to northern spotted owls. Along with other conservation measures, USFWS (2011) strongly urged experimental removal of barred owls to establish a causative link between their presence and spotted owl population dynamics, and to assess if barred owl removal could benefit northern spotted owl conservation.

A pilot study of barred owl removal was first conducted on private timberlands in Northern California (Diller et al. 2014) and following those preliminary results, a large experiment was established on federal and tribal lands in Washington, Oregon, and California (USFWS 2013). Together, these studies demonstrated that barred owl populations could be reduced with subsequent positive benefit to northern spotted owls (Diller et al. 2016, Wiens et al. 2021). The question that wildlife and land managers currently face is whether lethal removal of barred owls should be implemented as a management action over large spatial scales to conserve northern spotted owls.

A historical focus on spotted owl-barred owl interactions may oversimplify the broader ecological dilemma barred owls present, as spotted owls are not the only species potentially at risk with the arrival and expansion of barred owls in the Pacific Northwest (Holm et al. 2016). Awareness of the impacts of competition between barred owls and northern spotted owls was largely recognized through long-term, large-scale demographic monitoring of northern spotted owl populations that incidentally detected barred owls as the species expanded its range and became locally abundant (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016, Franklin et al. 2021). The degree to which barred owls might impact other species in the food webs they invaded may largely depend upon the similarity of their foraging ecology to that of the northern spotted owls they are replacing in the Pacific Northwest.

While phylogenetically related and ecologically similar, barred owls appear to have a broader diet relative to northern spotted owls. In previous studies in Washington and Oregon, barred owls consumed all the same species as sympatric spotted owls (Hamer et al. 2001, Wiens et al. 2014), but also a variety of other prey that are rarely, if ever, reported in diets of spotted owls (Forsman et al. 1984, Cutler and Hays 1991, Zabel et al. 1995, Ward et al. 1998, Bevis et al. 1997, Forsman et al. 2001, Rosenberg et al. 2003, Forsman et al. 2004). This difference suggests that those species included in the more generalist diet of barred owls, but not in the relatively specialized diet of northern spotted owls, may be at risk from a novel predator that has reached high densities. The broader diet of barred owls may also be key in understanding how this species has thrived in the forests of the Pacific Northwest, where the northern spotted owl had struggled to persist and has required extensive conservation intervention.

The large-scale removal experiment recently completed in Washington, Oregon, and northwest California (Wiens et al. 2021) offered an opportunity to investigate the diets, foraging ecology and body condition of barred owls in different regions of their expanded range. Using the specimens collected during removal experiments in Oregon and Washington, I characterized barred owl diets by analyzing stomach contents. This provided information on both the variety of prey species that may be at risk from this novel predator and how barred owl diets varied among different study areas. The collected specimens also afforded an opportunity to investigate factors associated with the nutritional condition of individual barred owls (i.e., amount of stored fat), and how body condition varied over space and time. This information can help characterize the broader ecological impact of barred owls as novel predators, as well as to understand the underlying sources of their successful range expansion, which should be useful for resource professionals and decision-makers who must consider future management actions focused on this invasive species.

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# Chapter 2 Chapter 2 - Diet Composition of Barred Owls in the Range of the Northern Spotted Owl: Ecological Equivalent or Potential Food Web Disaster?

## Introduction

Ecological communities can be devasted by non-native species that reach high densities and become invasive, exerting negative effects on native species (Elton 1958, Mack et al. 2000, Pyšek et al. 2020) resulting in extinctions, extirpations (Doherty et al. 2016), and threats thereof (Dueñas et al. 2021). Impacts of invasive species are well-documented on islands where native fauna and flora often lack adaptations to cope with novel predation or herbivory (Jones et al. 2016, Spatz et al. 2017, Holmes et al. 2019), and across continents where their effects may take longer to materialize but can reach much larger scales (e.g., Keller et al. 2011, Bonesi and Palazon 2007, Doody et al. 2014, Phelps et al. 2017, Arismendi et al. 2009). As native populations decline from competition, herbivory, or predation from an invasive, the resulting impacts can cascade throughout food webs (Doherty et al. 2015, Walsh et al. 2016, Kotta et al. 2018, Liang et al. 2022, Wainright et al. 2021). Non-native species, however, are not always harmful (Vilà et al. 2010) and may serve ecological roles of native species lost from ecosystems (Lundgren et al. 2018).

Predicting which non-native species will become invasive is difficult (Kolar and Lodge 2001), and just because environmental damage is not observed does not mean it will not occur in the future (Essl et al. 2011, Bellard et al. 2021). Natural resource managers thus face a dilemma in deciding if, and when, to use limited conservation funds to control non-native species. Early action–especially before a non-native species undergo exponential population growth–can greatly minimize costs of control and may avert environmental damage (Myers et al. 2000, Kaiser and Burnett 2010, Simberloff et al. 2013), but also risks using limited resources to manage a non-native species that may never actually become invasive (Bonanno 2016). Alternative to controlling non-native species, some suggest allowing these species to persist under the notion they may fill roles of species already lost from ecosystems (Schlaepfer et al. 2010). In this case however, it should be imperative to verify non-native species pose no risks, even if they offer some benefit. One might expect that if a non-native species is replacing a closely related and outwardly similar congeneric already in decline, there would be little disruption to the broader ecological community and that the non-native may fill the vacated niche of its declining congener.

Following a range expansion across North America (Livezey 2009a, 2009b), barred owls (*Strix varia*) are now sympatric with and replacing the closely related and federally threatened northern spotted owl (*Strix occidentalis caurina*) throughout forests in the U.S. Pacific Northwest (see review by Long and Wolfe 2019). Loss and degradation of old-growth forest habitat from timber harvests originally prompted listing northern spotted owls under the Endangered Species Act (USFWS 1990). Despite extensive habitat conservation measures for spotted owls (see reviews by Spies et al. 2019), their populations continued to decline as invading barred owls outcompeted spotted owls for critical resources (Gutiérrez et al. 2007). Several options were proposed to address this new threat posed to spotted owls, ranging from no-action to the lethal removal of barred owls from habitats used by spotted owls (USFWS 2011). Recent experiments demonstrated the efficacy of removal (Diller et al. 2016, Wiens et al. 2021, Hofstadter et al. 2022), but also the dichotomy of early versus deferred action to control a non-native species. At the leading edge of expansion in California where their population density was still low, for example, only 76 barred owls were detected and subsequently removed over a 3-

year study period (Hofstadter et al. 2022). Conversely, in a well-established population at high density in Oregon, over 5-times as many barred owls were removed within a single year from an area 1/10th the size (Wiens et al. 2016). Responses of spotted owl populations differed likewise, where removals from well-established, high density barred owl populations simply arrested spotted owl declines (Wiens et al. 2021), whereas removals in recently established populations of barred owls reversed population declines spotted owls (Diller et al. 2016, Dugger et al. 2016), and removals at the leading edge of expansion with low barred owl densities took place largely before widespread impacts spotted owl populations had occurred (Hofstadter et al. 2022). Prospects of the lethal management of barred owls has spurred much debate (Le 2019, Batavia et al. 2020, Braun 2022, Odenbaugh 2022), which is often framed as "killing one owl to save another" (Livezey 2010a, 2010b). This view greatly oversimplifies the complexity of ecological and ethical dilemmas confronting natural resource managers (Lynn 2018), in that spotted owls may not be the only species under threat from this novel predator in the forests of the Pacific Northwest (Holm et al. 2016).

Northern spotted owl diets are well-studied, preying mainly on mammals (typically 85-98% of prey numbers; Forsman et al. 1984, Cutler and Hays 1991, Zabel et al. 1995, Ward et al. 1998, Bevis et al. 1997, Forsman et al. 2001, Hamer et al. 2001, Rosenberg et al. 2003, Forsman et al. 2004, Wiens et al. 2014), with 3 rodents–flying squirrels (*Glaucomys* spp.), woodrats (*Neotoma* spp.), and tree voles (*Arborimus* spp.)–accounting for the majority of the species' diet. Terrestrial voles (*Microtus* spp., *Myodes* spp.) and mice (*Peromyscus* spp.) in aggregate can contribute substantially to diets of spotted owls in some years, while small numbers of other mammals ranging from shrews (*Sorex* spp.) to snowshoe hares (*Lepus americanus*) and small amounts of non-mammalian prey such as insects and birds account for the remainder of their diet. In contrast, only 2 published studies examined barred owl diets in the range of the northern spotted owl, comparing them to co-occurring spotted owls in Washington (Hamer et al. 2001) and Oregon (Wiens et al. 2014). Mammals still constituted the majority of prey items, 76% in Washington and 66% in Oregon, but the types of mammals taken differed from spotted owls. Flying squirrels, woodrats, and tree voles all made up smaller shares, and insectivorous mammals–shrews, shrew moles (*Neurotrichus gibbsii*), and moles (*Scapanus* spp.)–were more common. Amphibians are almost entirely absent from diets of northern spotted owls, yet in barred owls frogs made up 6% of prey numbers in Washington and 1% in Oregon, while salamanders comprised 7% of the Oregon diet. Arthropods, while not contributing much nutrition (i.e., biomass), did make up 4% of prey numbers in Washington and 13% in Oregon. These disparities in owl diets raise concern that as barred owls replace northern spotted owls across Pacific Northwest forests, numerous species that were rarely or never preyed upon by spotted owls now have an entirely new nocturnal avian predator at high density.

Threats faced by northern spotted owls from barred owl competition grew slowly over decades after the newcomer arrived, and were recognized in part by the ongoing demographic monitoring of northern spotted owls that incidentally detected encroaching barred owls (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016, Franklin et al. 2021). Numerous studies investigated aspects of competitive interactions between the two owl species (Dugger et al. 2011, Van Lanen et al. 2011, Yackulic et al. 2014, Kroll et al. 2016, Jenkins et al. 2019), but studies of barred owl diets are uniquely capable of identifying other species possibly at risk from this new predator in the Pacific Northwest. To better understand the potential impacts of barred owls on the broader food web in their new range, I described their diets from stomach contents of individual owls lethally removed in Oregon and Washington during 2015 – 2020 (Wiens et al.

2021), and estimated the number of prey they consumed. Wildlife and land managers are confronted with a difficult decision in whether to implement lethal control of barred owls to prevent the extinction of the northern spotted owl. Understanding the diet of barred owls could inform whether this newly arrived bird of prey could serve as a functional replacement for its already threatened congener or if a host of new species beyond northern spotted owls may also be under threat.

## Methods

As part of an experiment to assess the efficacy of barred owl removal to benefit northern spotted owl conservation, barred owls were lethally removed and collected from 3 study areas between 2015-2019: Cle Elum, WA (CLE), Alsea, OR (COA), Roseburg, OR (KLA; Wiens et al. 2016, 2017). Each study area was a long-term northern spotted owl demographic monitoring site (see Anthony et al. 2006 for details) representing distinct ecological regions within the northern spotted owl's range. CLE was at high elevation on the eastern slope of the Cascade Range where winters are cold and most precipitation falls as snow, and summers are hot and dry. COA was in the Oregon Coast Range with cool and wet winters, little snow, and mild summers. KLA was at the base of the western Cascades where winters are cold, much of the precipitation falls as rain, and summers are hot and dry. Throughout all years in CLE and the first year in COA, collections occurred from September to mid-April. After the first year in COA, and for all years in KLA, removals occurred throughout the year, with the requirement that owls could not be collected if they had dependent young (Wiens et al. 2017).

Specially trained field technicians located barred owls for removal at night with electronic, conspecific broadcast calls in areas historically occupied by spotted owls. Once birds were lured within range, they were lethally removed with a 12 ga. shotgun and retrieved for later lab analyses. I removed barred owl stomach contents and identified and enumerated individual prey items using local reference collections (US Forest Service, OSU FWCS Wildlife Collection), taxonomic manuals (Verts and Carraway 1998, Jones et al. 2005), online resources (bugguide.net) and expert opinion. I identified taxa based on external characteristics or skeletal features, depending on the digestion stage. Salamanders were classified as "large" with femurs, humeri, or dentaries longer than ~1cm, and as "small" otherwise. Invertebrates smaller than ~5mm were excluded as secondary predation of insectivores also consumed. I excluded prey matter that appeared left over after pellet egestion, such as small tufts of fur or a few small bones.

I summarized the percent of total prey numbers for prey taxa found in barred owl diets by first calculating the percent of prey numbers for each taxon within each barred owl's stomach, and then averaged these percentages for each taxon across all the owls sampled within a given group. Only owls that had consumed prey (i.e., owls that did not have empty stomachs) were included in these summaries. Percent frequency was calculated for the owls sampled within each study area, and between breeding (March-August) and non-breeding (September-February) seasons. I also present percent occurrence as the proportion of stomachs (of both all owls and only among owls that had consumed prey) that contained at least 1 individual from a given prey taxon, for comparisons with studies that used molecular methods to detect presence but not abundance of prey species consumed by barred owls (e.g., Kryshak et al. 2022). Within each study area and season, I calculated dietary evenness with the inverse Simpson index ($1/q$; Simpson 1949, Levins 1968),

$$\frac{1}{q} = \frac{1}{\sum_{i}^{n} p_i^2}$$

where $q$ equals the sum of the proportions $p$ of each taxon $i$ squared for all taxa $n$. Inverse Simpson ranges from 1 if only one prey taxon is present, up to the total number of taxa found if each taxon is represented in equal proportion. I also calculated food-niche overlap between study areas and between seasons within study areas using Pianka's Index of Overlap ($O_{jk}$; Pianka 1973),

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}}$$

between groups (i.e., study areas or seasons) $j$ and $k$; $p_{ij}$ is the proportion of the $i$th prey taxon out of all prey items found in group j, while $p_{ik}$ represents this proportion for group $k$, and $n$ represents total number of prey taxa. Pianka's index ranges from 0 if no common resources are used between the two groups, to 1 if identical resources are used in the same proportions between the 2 groups.

Adapting methods from Forsman et al. (2004), I estimated the number of prey taken in each study area. First, I calculated the amount of biomass a breeding barred owl pair would consume in a year where each owl weighed 780g (average of male and female barred owl masses in my study), they produced 1.36 young per year (Wiens et al. 2014) that were fed for 4 months, and each owl consumed 12% of its mass per day (with the simplifying assumption that energetic needs of juveniles equal those of adults). Thus, over 1 year 83,911g of prey biomass are consumed on average by barred owls in one of their territories. The biomass consumed for each taxon in each study area was divided by the total biomass consumed in the study area (Chapter 3), yielding each taxon's proportional contribution to biomass. Multiplying each taxon's proportional contribution to biomass by the annual consumption of 83,911g, and dividing that value by the mass of an individual from the respective taxon yielded the average number of individuals consumed annually in a barred owl territory.

## Results

We analyzed the stomach contents of 1328 barred owls (228 from CLE, 625 from COA, and 475 from KLA), and identified a total of 4961 individual prey items (Appendix A). Individual barred owl stomachs contained an average of 3.92 prey items (SD = 6.84), with a maximum of 74 items in a single stomach, and 244 stomachs that were empty. Inverse Simpson indices ($1/q$) of prey diversity were relatively similar among study areas, with 6.87 in CLE, 5.86 in COA, and 5.39 in KLA, but the taxa contributing to this diversity varied among study areas with overlap indices of 0.31 between CLE and COA, 0.38 between COA and KLA, and 0.5 between CLE and KLA. Vertebrates were the majority of prey in CLE and COA areas, but not in KLA (Table 2.1). About half of all stomachs examined contained at least 1 mammal species (Table 2.2). In CLE, mammals were the most common class, comprised mainly of voles and mice, shrews, and flying squirrels (Table 2.1). In COA, amphibians, mostly small salamanders, were the most common prey in terms of frequency of occurrence in the diet (Table 2.1). In KLA where invertebrates outnumbered vertebrates, rain beetles (*Pleocoma* spp.) alone constituted 34% of total prey within that study area (Table 2.1). Few genera, and no taxa identified to species, comprised more than 10% of the diet in any of the study areas (Table 2.1).

Diet composition of barred owls collected in the breeding vs. nonbreeding season in CLE were similar (O = 0.87), with slightly less diversity in the non-breeding season (1/q = 5.13) than in the breeding season (1/q = 7.02) when fewer amphibians and mammalian insectivores were consumed but more arthropods were in the diet (Table 2.3). Likewise, the COA diet was similar between seasons (O = 0.85), with more diversity during the breeding season (1/q = 7.15) than non-breeding season (1/q = 4.41), where the proportion of salamanders in the diet remained relatively high year-round but was 50% higher in the wet non-breeding season, and the proportion of mammalian insectivores increased three-fold during the breeding season (Table 2.3). Seasonal diets were least similar in KLA (O = 0.23) with the highest diversity in the breeding season (1/q = 10.0) that dropped to the lowest diversity seen in the non-breeding season (1/q = 3.22) driven largely by the preponderance of rain beetles and Orthopterans in the fall (Table 2.3).

For several taxonomic groups I reported specimens to higher classifications (Table 2.1) but identified a wider diversity therein (Appendix A). Salamanders were often fully digested, and while their bones were easily distinguished from other taxa, without skin I could not identify them beyond Order. From the few specimens that included skin, I identified nearly every species of salamander that occurred in the study areas (*Ambystoma gracile*, *A. macrodactylum*, *Dicamptodon tenebrosus*, *Aneides ferreus*, *Ensatina eschscholtzii*), including toxic rough rough-skinned newts (*Taricha granulosa*; Clarke et al. 2021). Southern torrent salamanders (*Rhyacotriton variegatus*) were not identified, but they are small and their skin may not persist long after consumption. I did not differentiate between the 2 *Plethodon* species (*P.* dunni and *P. vehiculum*) since their markings are very similar and could not be distinguished with certainty after the onset of digestion.

We identified the remains of 61 individual birds in barred owl stomachs. Eleven were simply assigned a size class ranging from 10-550g, and another 21 specimens were assigned to Genus, Family, or Order. Nearly half the identified bird specimens were Passeriformes (n=26), 8 of which were Pacific wrens (*Troglodytes pacificcus*). Some of the larger birds found in barred owl stomachs were ruffed grouse (*Bonsa umbellus*), quail (Odontiphoridae), and band-tailed pigeons (*Patagioenas fasciata*). Several cases of intra-guild predation occurred with 4 western screech-owls (*Megascops kennicotii*), 1 northern pygmy-owl (*Glaucidium gnoma*), and notably, 1 large hawk (*Buteo* spp.). One stomach contained a white egg, similar in size to that of a barred owl, suggesting nest depredation of a conspecific or other mid-sized bird of prey.

We observed a wide diversity of arthropods in barred owl stomachs, but many could only be identified to higher classifications (Class, Order, Family), as identification keys rely on intact specimens to examine detailed features, and most of my specimens were degraded from digestion. Orthopterans were prevalent in all study areas, and the specimens I identified were primarily shield-backed katydids (Tettigoniidae). Lepidopterans were found as both adults, which could not be identified beyond Order, and caterpillars that were mostly identified as Geometridae or Noctuidae. Ants were the smallest prey found that I was certain were not secondary predation, as no insectivores occurred with some of them. The 5 occurrences of millipedes and 1 occurrence of *Juga* sp. snails may have been secondary predation, as these occurred with large salamanders, a predator of each.

Several taxa were notably absent from the diets. Some of the collected owls smelled of skunk, they were previously seen in barred owl pellets (Wiens et al. 2014), and predation on them has been observed (Tosa et al. 2022), but no skunks were found in barred owl stomachs. Predation of soft-bodied slugs and earthworms has been observed (Livezey et al. 2008), but they cannot be detected in pellets. I only found 1 possible occurrence for each taxon, where too little material was left to make a determination, suggesting detection of such taxa is better suited to molecular methods (Kryshak et al. 2022).

On average, the estimated number of prey taken over the course of a year in a barred owl territory was 1720 in CLE, 3442 in COA, and 3994 in KLA, with the number taken for each taxon in each area reflecting the area's overall diet composition (Table 2.4).

Table 2.1. Dietary composition (% of total prey numbers) of barred owl stomach contents expressed as mean and standard deviation averaged across barred owls collected in Cle Elum, Washington (CLE), Oregon Coast Range (COA), and southwestern Oregon (KLA) experimental study areas, 2015 – 2019. Only owls with prey in stomachs included in summary.

| | **CLE [a]** | | **COA** | | **KLA** | |
|---|---|---|---|---|---|---|
| **Prey Taxon** | **Mean %** | **SD** | **Mean %** | **SD** | **Mean %** | **SD** |
| Mammals | 40.8 | 39 | 25.4 | 34 | 19.2 | 31 |
| Flying Squirrels | 8.0 | 24 | 1.6 | 11 | 1.4 | 8.8 |
| Chipmunks | 2.0 | 13 | 1.3 | 7.9 | 0.2 | 2.6 |
| Douglas Squirrels | 2.2 | 14 | 1.4 | 9 | 0.4 | 4.0 |
| Gray Squirrels | | | | | 0.1 | 1.7 |
| Unidentified Squirrels | 0.7 | 7.2 | 0.2 | 4.2 | 0.1 | 2.7 |
| Woodrats | 1.0 | 9.9 | 0.3 | 3.8 | 0.5 | 6.3 |
| Red Tree Voles | | | 0.7 | 6 | 0.4 | 3.5 |
| Other/Unidentified Voles and Mice | 11.2 | 23 | 3.6 | 14 | 1.7 | 8.8 |
| Jumping Mice | 0.2 | 2.2 | 0.1 | 1.9 | <0.1 | 0.82 |
| Mountain Beaver | | | 0.1 | 3.3 | | |
| Pocket Gopher | 0.5 | 5.7 | 0.1 | 2.5 | | |
| Murid Rat | | | | | <0.1 | 2.0 |
| Unidentified Rodents | 0.2 | 5 | 0.2 | 3.8 | 0.1 | 3.0 |
| Shrew spp. | 9.5 | 20 | 10.1 | 20 | 6.9 | 17 |
| Shrew mole | 0.5 | 3.5 | 3.7 | 11 | 4.8 | 14 |
| Mole spp. | 0.7 | 5.8 | 1.1 | 7.3 | 1.6 | 9.1 |
| Hares, Rabbits, Pikas | 1.7 | 12 | 0.3 | 4.1 | 0.2 | 4.7 |
| Virginia Opossum | | | | | 0.2 | 3.8 |
| Bats | | | 0.1 | 2.1 | | |
| Unidentified Mammal | 2.5 | 12 | 0.5 | 6.2 | 0.7 | 6.8 |
| Amphibians | 16.4 | 30 | 39.5 | 36 | 12.4 | 23 |
| Small salamanders | 3.2 | 12 | 36.2 | 35 | 11.1 | 22 |
| Large salamanders | 0.2 | 5 | 2.3 | 7.9 | 0.3 | 2.1 |
| Frogs | 12.9 | 26 | 2.7 | 11 | 1.0 | 7.7 |
| Birds | 1.7 | 11 | 1.5 | 8.8 | 0.9 | 7.3 |
| Reptiles | 0.7 | 5.9 | 0.7 | 4.6 | 1.1 | 6.0 |
| Fish | 0.5 | 3.7 | <0.1 | 2.2 | | |
| Arthropods [b] | 38.1 | 39 | 21.1 | 28 | 62.3 | 39 |
| Katydids, Crickets, and Grasshoppers | 29.9 | 36 | 4.6 | 15 | 20.8 | 34 |
| Rain Beetles | | | | | 33.6 | 41 |
| Ground Beetles | | | 3.6 | 12 | 2.3 | 12 |
| Other and Unidentified Beetles | 1.5 | 6.9 | 2.3 | 8.6 | 1.0 | 6.4 |
| Moths and Butterflies | 0.5 | 7 | 2.1 | 11 | 1.0 | 7.5 |
| Caterpillars | 0.2 | 5 | 4.8 | 15 | 0.3 | 2.8 |
| Other and Unidentified Insects | 5.0 | 19 | 1.3 | 6.2 | 1.5 | 9.7 |
| Other and Unidentified Arthropods | 2.0 | 11 | 3.8 | 10 | 1.9 | 6.7 |
| Crayfish | 0.2 | 5.0 | 1.1 | 7 | 0.2 | 3.1 |
| Snails | | | 7.1 | 17 | 3.3 | 12 |
| Unidentified Prey | 0.2 | 5.0 | 0.2 | 4.1 | <0.1 | 2.0 |

[a] Sample sizes of owls: CLE = 164, COA = 527, KLA = 393; Sample size of prey items: CLE = 402, COA = 2077, KLA = 2482

[b] Values for Arthropods exclude crayfish.

Table 2.2. Percentage of all stomachs, and only stomachs with prey, containing at least 1 individual of a prey taxon from barred owls collected in Cle Elum, Washington (CLE), Oregon Coast Range (COA), and southwestern Oregon (KLA) experimental study areas, 2015 – 2019. Percentages of arthropods exclude crayfish.

| | **% with Empty Stomachs [a]** | | | **% without Empty Stomachs** | | |
|---|---|---|---|---|---|---|
| **Prey Taxon** | **CLE** | **COA** | **KLA** | **CLE** | **COA** | **KLA** |
| Mammals | 52.6 | 49.3 | 58.1 | 73.2 | 58.4 | 70.2 |
| Flying Squirrels | 14 | 5.4 | 6.7 | 19.5 | 6.5 | 8.1 |
| Chipmunks | 3.5 | 4 | 1.1 | 4.9 | 4.7 | 1.3 |
| Douglas Squirrels | 3.9 | 4.5 | 2.1 | 5.5 | 5.3 | 2.5 |
| Gray Squirrels | 0 | 0 | 0.6 | 0 | 0 | 0.8 |
| Unidentified Squirrels | 1.3 | 0.8 | 0.6 | 1.8 | 0.9 | 0.8 |
| Woodrats | 1.8 | 1.1 | 2.7 | 2.4 | 1.3 | 3.3 |
| Red Tree Voles | 0 | 2.4 | 2.1 | 0 | 2.8 | 2.5 |
| Other/Unidentified Voles and Mice | 15.8 | 10.6 | 8.6 | 22 | 12.5 | 10.4 |
| Jumping Mice | 0.4 | 0.3 | 0.2 | 0.6 | 0.4 | 0.3 |
| Mountain Beaver | 0 | 0.5 | 0 | 0 | 0.6 | 0 |
| Pocket Gopher | 0.9 | 0.2 | 0 | 1.2 | 0.2 | 0 |
| Murid Rat | 0 | 0 | 0.2 | 0 | 0 | 0.3 |
| Unidentified Rodents | 0.4 | 0.6 | 0.4 | 0.6 | 0.8 | 0.5 |
| Shrew spp. | 11.4 | 18.4 | 21.1 | 15.9 | 21.8 | 25.4 |
| Shrew mole | 0.9 | 9 | 18.1 | 1.2 | 10.6 | 21.9 |
| Mole spp. | 1.3 | 3.7 | 7.4 | 1.8 | 4.4 | 8.9 |
| Hares, Rabbits, Pikas | 3.1 | 1.1 | 1.3 | 4.3 | 1.3 | 1.5 |
| Virginia Opossum | 0 | 0 | 0.6 | 0 | 0 | 0.8 |
| Bats | 0 | 0.5 | 0 | 0 | 0.6 | 0 |
| Unidentified Mammal | 4.4 | 1.8 | 3.8 | 6.1 | 2.1 | 4.6 |
| Amphibians | 12.3 | 41.6 | 19.2 | 17.1 | 49.3 | 23.2 |
| Small salamanders | 3.5 | 36 | 16.6 | 4.9 | 42.7 | 20.1 |
| Large salamanders | 0.4 | 7.2 | 1.5 | 0.6 | 8.5 | 1.8 |
| Frogs | 10.5 | 6.4 | 2.1 | 14.6 | 7.6 | 2.5 |
| Birds | 3.1 | 4.6 | 4.6 | 4.3 | 5.5 | 5.6 |
| Reptiles | 0.9 | 2.2 | 5.5 | 1.2 | 2.7 | 6.6 |
| Fish | 0.4 | 0.2 | 0 | 0.6 | 0.2 | 0 |
| Arthropods[b] | 24.1 | 33 | 42.5 | 33.5 | 39.1 | 51.4 |
| Katydids, Crickets, and Grasshoppers | 18 | 10.1 | 19.6 | 25 | 12 | 23.7 |
| Rain Beetles | 0 | 0 | 11.6 | 0 | 0 | 14 |
| Ground Beetles | 0 | 6.2 | 3.6 | 0 | 7.4 | 4.3 |
| Other and Unidentified Beetles | 2.2 | 4.6 | 4.8 | 3 | 5.5 | 5.9 |
| Moths and Butterflies | 0.9 | 4.5 | 3.8 | 1.2 | 5.3 | 4.6 |
| Caterpillars | 0.4 | 6.9 | 1.5 | 0.6 | 8.2 | 1.8 |
| Other and Unidentified Insects | 3.9 | 2.9 | 4.6 | 5.5 | 3.4 | 5.6 |
| Other and Unidentified Arthropods | 3.1 | 11 | 7.8 | 4.3 | 13.1 | 9.4 |
| Crayfish | 0.4 | 2.7 | 1.3 | 0.6 | 3.2 | 1.5 |
| Snails | 0 | 11.7 | 9.9 | 0 | 13.9 | 12 |
| Unidentified Prey | 0.4 | 0.6 | 0.2 | 0.6 | 0.8 | 0.3 |

[a] Sample size of all owls: CLE = 228, COA = 625, KLA = 475; Sample sizes of only owls with prey in stomachs: CLE = 164, COA = 527, KLA = 393; Sample size of prey items found: CLE = 402, COA = 2077, KLA = 2482

[b] Values for Arthropods exclude crayfish.

Table 2.3. Percentage of total prey for taxa found in stomach contents of barred owls collected in Cle Elum, Washington (CLE), Oregon Coast Range (COA), and southwestern Oregon (KLA) experimental study areas, 2015-2019. The breeding season (B) was defined as March-August and non-breeding season (NB) as September-February. Percentages of arthropods exclude crayfish.

| | **CLE [a]** | | | | **COA** | | | | **KLA** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Breeding** | | **Non-breeding** | | **Breeding** | | **Non-breeding** | | **Breeding** | | **Non-breeding** | |
| **Prey Taxon** | **Mean %** | **SD** | **Mean %** | **SD** | **Mean %** | **SD** | **Mean %** | **SD** | **Mean %** | **SD** | **Mean %** | **SD** |
| Mammals | 37.1 | 40 | 41.9 | 38 | 31.1 | 35 | 20.5 | 32 | 40.2 | 37 | 10.8 | 23 |
| Flying Squirrels | 7.9 | 25 | 8 | 23 | 0.9 | 8 | 2.2 | 12 | 1.3 | 10 | 1.4 | 8.3 |
| Chipmunks | 1.1 | 11 | 2.2 | 14 | 0.6 | 4.8 | 1.9 | 9.8 | 0.4 | 4.1 | 0.1 | 1.6 |
| Douglas Squirrels | 3.4 | 18 | 1.9 | 13 | 0.4 | 5.2 | 2.2 | 11 | 0.4 | 4.6 | 0.4 | 3.7 |
| Gray Squirrels | | | | | | | | | | | 0.2 | 2 |
| Unidentified Squirrels | | | 1 | 8.2 | | | 0.4 | 5.7 | 0.3 | 4.3 | 0.1 | 1.7 |
| Woodrats | 2.2 | 15 | 0.6 | 8 | 0.1 | 2.3 | 0.5 | 4.7 | 1 | 8.4 | 0.3 | 5.3 |
| Red Tree Voles | | | | | 0.8 | 7 | 0.6 | 5 | 0.7 | 4.1 | 0.3 | 3.2 |
| Other/Unidentified Voles and Mice | 10.1 | 26 | 11.5 | 22 | 3.3 | 15 | 3.8 | 13 | 3.4 | 13 | 1.1 | 6.1 |
| Jumping Mice | 1.1 | 4.6 | | | | | 0.2 | 2.6 | 0.1 | 1.5 | | |
| Mountain Beaver | | | | | 0.2 | 4.6 | 0.1 | 1.7 | | | | |
| Pocket Gopher | 2.2 | 12 | | | | | 0.2 | 3.4 | | | | |
| Murid Rat | | | | | | | | | | | 0.1 | 2.4 |
| Unidentified Rodents | | | 0.3 | 5.7 | 0.2 | 3.7 | 0.3 | 3.8 | 0.3 | 5.3 | 0.1 | 1.2 |
| Shrew spp. | 4.5 | 7.5 | 10.9 | 22 | 17.5 | 25 | 3.8 | 12 | 17 | 25 | 2.9 | 11 |
| Shrew mole | | | 0.6 | 4 | 5.3 | 14 | 2.2 | 8.9 | 11.4 | 21 | 2.1 | 8.5 |
| Mole spp. | | | 1 | 6.6 | 0.8 | 6.2 | 1.3 | 8 | 3.4 | 14 | 0.9 | 6 |
| Hares, Rabbits, Pikas | 1.1 | 11 | 1.9 | 12 | 0.1 | 1.9 | 0.5 | 5.2 | 0.4 | 5.9 | 0.2 | 4.1 |
| Virginia Opossum | | | | | | | | | 0.1 | 2.6 | 0.2 | 4.1 |
| Bats | | | | | 0.2 | 2.1 | 0.1 | 2.1 | | | | |
| Unidentified Mammal | 3.4 | 16 | 2.2 | 11 | 0.6 | 6.9 | 0.4 | 5.6 | 1.1 | 8.5 | 0.6 | 6 |
| Amphibians | 3.4 | 13 | 20.1 | 32 | 31.2 | 31 | 46.7 | 38 | 18.7 | 27 | 9.9 | 20 |
| Small salamanders | 2.2 | 12 | 3.5 | 12 | 26.9 | 29 | 44.1 | 38 | 16.7 | 26 | 8.9 | 19 |
| Large salamanders | | | 0.3 | 5.7 | 2.4 | 7.3 | 2.1 | 8.4 | 0.4 | 3.2 | 0.3 | 1.5 |
| Frogs | 1.1 | 6 | 16.3 | 28 | 2.6 | 9.7 | 2.8 | 12 | 1.7 | 9.2 | 0.7 | 7 |
| Birds | 2.2 | 15 | 1.6 | 10 | 0.9 | 6 | 2 | 11 | 1.5 | 9.5 | 0.7 | 6.3 |
| Reptiles | 3.4 | 12 | | | 0.6 | 3.2 | 0.7 | 5.5 | 2.4 | 8.4 | 0.6 | 4.6 |
| Fish | | | 0.6 | 4.2 | | | 0.1 | 3 | | | | |
| Arthropods [b] | 50.6 | 42 | 34.5 | 37 | 22.6 | 28 | 19.9 | 28 | 27.2 | 32 | 76.4 | 32 |
| Katydids, Crickets, and Grasshoppers | 38.2 | 39 | 27.5 | 35 | 1.5 | 6.3 | 7.3 | 19 | 3.2 | 15 | 27.9 | 37 |
| Rain Beetles | | | | | | | | | 1 | 6.9 | 46.7 | 41 |
| Ground Beetles | | | | | 6.6 | 15 | 1.1 | 6.1 | 8 | 21 | 0.1 | 0.71 |
| Other and Unidentified Beetles | 3.4 | 12 | 1 | 4.3 | 3 | 9.9 | 1.7 | 7.3 | 2.9 | 11 | 0.3 | 2.4 |
| Moths and Butterflies | 1.1 | 11 | 0.3 | 5.7 | 3.3 | 14 | 1.1 | 5.9 | 2.7 | 13 | 0.3 | 2.6 |
| Caterpillars | | | 0.3 | 5.7 | 4.1 | 13 | 5.4 | 16 | 1 | 4.9 | 0.1 | 0.79 |
| Other and Unidentified Insects | 4.5 | 19 | 5.1 | 19 | 1.2 | 5.9 | 1.4 | 6.4 | 4.4 | 17 | 0.4 | 3.8 |
| Other and Unidentified Arthropods | 5.6 | 20 | 1 | 7.3 | 4.4 | 11 | 3.3 | 9.5 | 4.5 | 10 | 0.8 | 4.2 |
| Crayfish | 1.1 | 11 | | | 0.6 | 5.1 | 1.5 | 8.3 | 0.3 | 4.1 | 0.2 | 2.6 |
| Snails | | | | | 10.5 | 20 | 4.2 | 14 | 8 | 18 | 1.4 | 7.6 |
| Unidentified Prey | | | 0.3 | 5.7 | 0.1 | 3.2 | 0.3 | 4.7 | | | 0.1 | 2.4 |

[a] Samples size of owls: CLE breeding = 41, non-breeding = 123, COA breeding = 233, non-breeding = 294, KLA breeding = 202, non-breeding 191; Sample size of prey items: CLE breeding = 89, non-breeding = 313, COA breeding = 956, non-breeding = 1121, KLA breeding = 712, non-breeding 1770.

[b] Values for Arthropods excludes crayfish.

Table 2.4. Estimated average numbers of prey captured per year within each taxon in a barred owl territory in Cle Elum, Washington (CLE), Oregon Coast Range (COA), and southwestern Oregon (KLA) experimental study areas, 2015-2019.

| Prey Taxon | CLE | COA | KLA |
|---|---|---|---|
| Flying Squirrels | 140 | 59 | 56 |
| Chipmunks | 35 | 47 | 8 |
| Douglas Squirrels | 39 | 50 | 16 |
| Gray Squirrels | 0 | 0 | 5 |
| Unidentified Squirrels | 13 | 9 | 5 |
| Woodrats | 18 | 12 | 21 |
| Red Tree Voles | 0 | 26 | 18 |
| Other/Unidentified Voles and Mice | 197 | 129 | 71 |
| Jumping Mice | 4 | 3 | 2 |
| Mountain Beaver | 0 | 5 | 0 |
| Pocket Gopher | 9 | 3 | 0 |
| Murid Rat | 0 | 0 | 2 |
| Unidentified Rodents | 4 | 9 | 5 |
| Shrew spp. | 166 | 362 | 282 |
| Shrew mole | 9 | 131 | 194 |
| Mole spp. | 13 | 40 | 66 |
| Hares, Rabbits, Pikas | 31 | 12 | 10 |
| Virginia Opossum | 0 | 0 | 7 |
| Bats | 0 | 5 | 0 |
| Unidentified Mammal | 44 | 19 | 30 |
| Small salamanders | 57 | 1295 | 453 |
| Large salamanders | 4 | 81 | 13 |
| Frogs | 228 | 97 | 41 |
| Birds | 31 | 53 | 38 |
| Reptiles | 13 | 24 | 44 |
| Fish | 9 | 2 | 0 |
| Katydids, Crickets, and Grasshoppers | 525 | 166 | 846 |
| Rain Beetles | 0 | 0 | 1366 |
| Ground Beetles | 0 | 129 | 95 |
| Other and Unidentified Beetles | 26 | 83 | 43 |
| Moths and Butterflies | 9 | 76 | 39 |
| Caterpillars | 4 | 172 | 13 |
| Other and Unidentified Insects | 88 | 47 | 62 |
| Crayfish | 4 | 40 | 10 |
| Snails | 0 | 254 | 133 |
| Unidentified Prey | 0 | 2 | 0 |

## Discussion

Over half of the northern spotted owl diet is often comprised of either flying squirrels, wood rats, or tree voles, and almost always in combination (Ward et al. 1998, Forsman et al. 1984, Cutler and Hayes 1991, Zabel et al. 1995, Bevis et al. 1997, Forsman et al. 2001, Hamer et al. 2001, Rosenberg et al. 2003, Forsman et al. 2004, Wiens et al. 2014), yet together these 3 species amounted to less than 10% of the diet of barred owls in CLE, and less than 3% in COA and KLA. Furthermore, no taxonomic group lower than an Order made up more than 25% of the prey in any study area, except for rain beetles in KLA. Simpson indices from previous studies of spotted owls during the breeding season ranged from 2.4-4.5 (Forsman et al. 2004, Wiens et al. 2014), indicating a narrower dietary niche than I found for barred owls within any of the study areas (5.39-6.87), especially in comparison to breeding season diets (7.02-10.0). In my study, barred owls consumed insectivorous mammals, amphibians, and arthropods more frequently than what has been reported previously for spotted owls.

Between the study areas and seasons, I found barred owls consumed roughly the same suite of taxa but in different proportions. Two disparities between COA and KLA, which are only about 100 km apart, raise questions about how barred owls make their foraging decisions. Barred owls in KLA seemed to have a strong preference for rain beetles, constituting 34% of the annual diet, and 47% of the breeding season diet when they are primarily available. Despite rain beetles also being present within the COA study area, none were found there in the stomach contents. More surprising, I found fully digested, lethally toxic rough-skinned newts in the stomach contents of KLA owls (Clarke et al. 2021), but none in COA. While we would not expect barred owls to eat these newts anywhere, some of highest toxicity levels in newts occur around the COA study area (Hanifin et al. 2008), raising questions as to if and how barred owls actively avoid these highly toxic newts in COA where salamanders make up 39% of the diet, while consuming less toxic newts in nearby KLA as well as in California (Medina et al. 2018, Kryshak et al. 2022).

Arthropods and amphibians made up much larger portions of diets of barred owls presented here compared to previous descriptions (Hamer et al. 2001, Wiens et al. 2014). This may be reflective of true dietary differences or of possible methodological differences. Egested pellets, whether from barred or spotted owls, are primarily collected during the breeding season at nest and roost sites, while many owls I sampled were collected during the non-breeding season. Seasonal differences in prey availability or foraging preference may result in some differences, but I saw high overlap between breeding and non-breeding season diets in CLE and COA as seen previously (Wiens et al. 2014), where more arthropods were eaten during the breeding season. Amphibian consumption was higher in the non-breeding season in both areas. It was still relatively high in the COA breeding season, while in CLE few amphibians were consumed in the breeding season, but removals stopped in mid-April and more amphibians may have been consumed later in the breeding season as the snowpack melted. Arthropods and amphibians can be detected in owl pellets, but may need fur or feathers to help bind the pellets, where 31% of the stomachs with prey that I analyzed did not contain a bird or mammal. Pellets however can detect these taxa as they can occur, and in relatively high numbers in some cases (e.g., Smith et al. 1999), thus while arthropods and amphibians could be underrepresented in the barred owl pellet studies (Hamer et al. 2001, Wiens et al. 2014), I am confident they were not entirely missed in spotted owl diets.

Across Oregon, spotted owl pairs provisioning 2 young (well above contemporary estimated reproductive rates; Wiens et al. 2014, Franklin et al. 2021) were estimated to need

69,467 g of biomass per year, resulting in 706 prey items taken annually (Forsman et al. 2004), or about 5 times fewer prey items than I estimated barred owl pairs raising an average of 1.36 young would consume over a year in the Oregon study areas. This disparity is due both to the larger size of barred owls and their reliance on much smaller prey than spotted owls. Along the central coast of Oregon, the top prey spotted owls took annually were 100 red tree voles and 311 flying squirrels (adjusted for a breeding pair with 2 young; Forsman et al. 2004), while in COA I estimated a breeding barred owl pair would only take 26 red tree voles and 59 flying squirrels. However, barred owl home ranges can be 2-4 times smaller than spotted owls in the Oregon Coast Range (581 and 1,843 ha respectively; Wiens et al. 2014), and as much as 8 times smaller elsewhere (Singleton et al. 2010). Thus, over an area equivalent to a spotted owl home range, 4 barred owl pairs in COA would take a total of 13,768 prey items, with close to as many flying squirrels, 236, and slightly more red tree voles, 104, than a spotted owl pair raising 2 young. More concerning though, are the prey spotted owls do not rely upon. Breeding pairs of spotted owls in the central coast of Oregon would only take 7 shrews a year (Forsman et al. 2004), while I estimated 4 barred owl pairs would take 1,448 shrews over an equivalent area. Salamanders were never found among over 22,000 spotted owl prey items identified in Oregon (Forsman et al. 2004), yet I estimated that annually a single breeding pair of barred owls would take 466 salamanders in KLA and 1,376 in COA, which in the Coast Range equates to 5,504 salamanders taken over a spotted owl home range where none would have been consumed by the native owls. While these numbers seem staggering, the question remains as to whether barred owl predation impacts the populations of their prey.

Many prey species now experience dramatically increased, or an entirely new source of predation as barred owls replaced spotted owls, yet this does not necessarily mean the prey populations are at risk. Barred owls may consume relatively high numbers of invertebrates, but this likely matters little in comparison to other sources of predation, such as songbirds. Insectivorous mammals and salamanders, however, may warrant concern. Each can be found in relatively high numbers on the landscape (e.g., Gomez and Anthony 1996, Gomez and Anthony 1998), yet in the case of insectivorous mammals I was aware of no estimates of their population density or dynamics in the region, thus it would be difficult to establish if barred owls impact their populations. Salamanders can likewise be quite numerous but may be slow to mature with relatively low reproductive rates and some have extremely small distributions (e.g., Scott Bar and Shasta salamanders; *Plethadon asupak* and *Hydromantes shastae* respectively). Common northern spotted owl prey (flying squirrels, woodrats, tree voles) make up proportionally less of the barred owl diet but may be taken off the landscape at higher rates given the barred owl's smaller home range size and greater densities relative to spotted owls.

The staple prey for spotted owls–flying squirrels–presents a concerning case in that they constituted 12% of the barred owl diet between 2007-2009 (Wiens et al. 2014) in an area adjacent to COA where they were only 2% of the prey numbers between 2015-2018 in my study. This six-fold reduction in the share of the diet over time may be due to a decline in flying squirrel abundance itself. Given the proportion of biomass flying squirrels made up in the earlier study, I estimate 4 barred owl pairs would have eaten 862 flying squirrels a year, which would be in addition to any predation from spotted owls with overlapping territories. For a prey species that averages only about 1.5 individuals per hectare (Smith 2007), this could be an unsustainable rate of predation and the observed decrease from historical levels in the proportion of flying squirrels in the barred owl diet may be an early indicator of broader food web impacts. The diverse barred owl diet could diffuse their impacts over a broad range of prey species, however, prey with population dynamics able to absorb the extra predation may be creating a case of apparent competition (Holt 1977) where they support higher population densities of barred owls that in turn consume more of the other prey species that cannot sustain the extra predation.

My results, along with previous studies of barred owl diets (Hamer et al. 2001, Wiens et al. 2014, Kryshak et al. 2022) suggest some species may be at risk from barred owl predation, but again, I cannot say for certain their populations are threatened by the presence of barred owls. To do so for certain would at least require population estimates for species of concern prior to and after the arrival of barred owls locally. While these data may be available for some taxa, I know of no species other than northern spotted owls for which a link has been established between a population decline and the presence of barred owls in their expanded range. In the case of northern spotted owls, this causative link was recognized in part due to an already in-place, long-term, large-scale monitoring effort of their population dynamics that was able to incidentally detect the expanding competitor over many years and across the northern spotted owl range (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016, Franklin et al. 2021). However, waiting for evidence of a population decline in the prey of barred owls returns us back to the fundamental conundrum of invasive species management, we cannot know for certain if a non-native species will negatively impact the ecological communities it enters until those impacts are realized, and by that time management will be more difficult and there may already be irreparable damage done to the ecosystem (Simberloff 2003).

Given the disparities between barred and northern spotted owl diets, I strongly caution against considering the novel owl an ecological equivalent of the threatened congener it is replacing. These two owls are outwardly similar and closely related but interact with the food web differently. Furthermore, the utmost prudence should be used in considering whether a non-native species can fill the niche of a similar species missing from an ecosystem. It may seem tempting to isolate a perceived benefit of a non-native or invasive species as justification to maintain it within a novel environment (e.g., Lundgren et al. 2021), yet the well-intentioned recognition of a perceived benefit, and subsequent introduction of a non-native species has resulted in damaging and pervasive biological invasions (e.g., Shine 2010, Barun et al. 2011)

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# Chapter 3 - Dietary Biomass and Foraging Behavior of Barred Owls in their Expanded Range where they Outcompete Native and Threatened Northern Spotted Owls.

## Introduction

When novel species invade ecosystems, they do so in part by either exploiting unused resources–such as when predators arrive on predator-free islands–or by outcompeting native species for resources already being used (Perkins and Hatfield 2014). When an invasive species competes with a native species for space, the species with higher average fitness is expected to eventually extirpate the other (Chesson and Warner 1981). However, mechanisms that minimize fitness differences between competitors, increase the effects of intraspecific competition, or brief conditions that favor the inferior competitor can maintain both species in coexistence (Barabas et al. 2018, Ellner et al. 2019). Foraging can mediate this competition where one species excludes the other from resources, gathers a shared resource more efficiently while possibly limiting its availability, or distinctly different diets afford one species a fitness advantage. Barred owls (*Strix varia*) recently expanded their range throughout western USA (Livezey 2009a, b, Long and Wolfe 2019), and they consume a diverse range of prey types (Hamer et al. 2001, Wiens et al. 2014, Chapter 2). This diet diversity may give barred owls a competitive advantage over the native, congeneric northern spotted owl (*Strix caurina occidentalis*), resulting in the displacement and continued population decline of the spotted owl (UWFWS 2011, Franklin et al. 2021).

Barred and spotted owls are both medium-sized (barred owls being larger), territorial forest owls (Gutiérrez et al. 2020, James and Mazur 2020), creating the potential for competition that was recognized at the time northern spotted owls were listed as threatened under the US

Endangered Species Act (USFWS 1991). As barred owls expanded their range along the west coast of North America and became locally abundant, spotted owls tended to abandon historically used territories and avoided colonizing sites where their competitor was present (Kelly et al. 2003, Dugger et al. 2011, Yackulic et al. 2012, Jenkins et al. 2019, Franklin et al. 2021). Interference competition likely plays a role in these dynamics (Van Lanen et al. 2011, Gutiérrez et al. 2004, Jennings et al. 2011, Wiens et al. 2014), which can be alleviated when barred owls are removed, sometimes resulting in the former resident spotted owls reappearing (Diller et al. 2016, Wiens et al. 2021). Perhaps also important to explaining the nature of these competitive interactions is an understanding of how barred owls use the forested landscapes they have rapidly invaded, including old-growth forests conserved for northern spotted owls.

Old-growth forests are required for northern spotted owl survival and reproduction (Thomas et al. 1990), providing late-seral elements such as cavities and broken treetops for nesting (Forsman et al. 1984) and supporting their primary prey resources (e.g., flying squirrels, *Glaucomys* spp.; Smith 2007). Barred owls also use older forests but can also use a broader range of forest types, (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014). Where vital rates were estimated for both owl species in an area of sympatry, survival was comparable and highest for both species when territories contained high proportions of old forest, and survival decreased, but at a much greater rate for spotted owls, as the proportion of old forest declined (Wiens et al. 2014). In addition, barred owl reproductive rates were 4 times greater than spotted owls and equivalent to the highest reported historic reproductive rates for spotted owls in that area (Wiens et al. 2014). The use of more diverse types of forest likely contributes to barred owl success in western forests, and their generalist foraging behaviors likely facilitate these broader habitat associations resulting in their ability outcompete northern spotted owls.

Small mammals comprise nearly all the biomass northern spotted owls consume (≥ 94.5%), with either flying squirrels (*Glaucomys* spp; Forsman et al. 1984, Cutler and Hayes 1991, Bevis et al. 1997, Hamer et al. 2001, Forsman et al. 2001, Rosenberg et al. 2003, Forsman et al. 2004, Wiens et al. 2014) or woodrats (*Neotoma* spp.; Forsman et al. 1984, Cutler and Hayes 1991, Ward et al. 1998, Forsman et al. 2004) making up ca. half or more of total dietary biomass. The remainder of their dietary biomass comprises a mix of rabbits and hares, other squirrels, and a variety of smaller mammals, with any biomass from non-mammalian prey coming almost exclusively from birds; and while invertebrates can be consumed in high numbers their contributions to biomass are generally negligible (Forsman et al. 1984, Cutler and Hayes 1991, Bevis et al. 1997, Ward et al. 1998, Hamer et al. 2001, Forsman et al. 2001, Rosenberg et al. 2003, Forsman et al. 2004, Wiens et al. 2014).

In studies of barred owl diets–where spotted owl diets are predominated by flying squirrels–mammals comprised 89% of the biomass in Oregon (Wiens et al. 2014) and 75% in Washington (Hamer et al. 2001) with flying squirrels only contributing 24% and 18% of biomass in each respective area, while the variety of other small mammals generally each contributed more biomass to barred than spotted owl diets. Contributions from birds were comparable for both owls in Oregon (Wiens et al. 2014), but substantially higher for barred owls in Washington (Hamer et al. 2001), and a variety of other taxa rarely, if ever, seen in the diets of spotted owls (amphibians, crayfish, fish, snails) contributed small portions of biomass (0.2-4.7% each) to barred owl diets (Hamer et al. 2001, Wiens et al. 2014). Arthropods (other than crayfish) made up substantial shares of barred owl prey numbers but contributed minimally to biomass (≤0.1%; Hamer et al. 2001, Wiens et al. 2014). These few historical studies were limited to a few select areas early in the invasion process of this species, but suggested that barred owls utilize a broader range of prey resources than spotted owls to support their energetic demands.

To better understand the foraging ecology of barred owls and the variety of native prey species they derive dietary biomass from within the range of the northern spotted owl, I examined the stomach contents of barred owls that were lethally collected as part of a large-scale removal experiment (Wiens et al. 2021). Bird of prey diet studies typically rely on gathering egested pellets and prey remains near nest and roost sites (CITATIONS). This approach characterizes diets at specific locations and over broad timeframes (seasonal or annual). In contrast, stomach contents allow diets to be attributed to individuals, with specific characteristics (sex and age). Also, since owls were collected in the field, we know the date and approximate time of day prey were consumed. In contrast to diet studies based on pellets, samples from stomach contents allow for the direct measurement of meal sizes (including no meals when stomachs are empty), and identification of prey parts that were eaten. Thus, evaluating barred owl diets from their stomach contents can provide a unique perspective in the foraging ecology of a bird of prey and help us understand how barred owl populations are expanding in a novel landscape.

## Methods

Methods used to remove and collect barred owl carcasses from experimental study areas are described in detail by Wiens et al. (2016, 2017). Barred owls examined here were collected over 3-year periods near Cle Elum, WA (CLE; 2015-2018), Alsea, OR (COA; 2015-2018), and Roseburg, OR (KLA; 2016-2019). No collections took place from mid-April to late-August in 2016, but starting in 2017, collections took place during that time of year in COA and KLA with the stipulation that owls could not be collected if they possibly had dependent young (Wiens et al. 2018). Efforts to locate, lure, and collect barred owls began around dusk and carried on throughout the evening. Necropsy procedures and prey identification are described in Chapter 1. Upon opening the stomachs, I weighed all contents to the nearest 0.01 g.

We compared the preponderance of empty stomachs between the 3 study areas, males and females, and 3 age classes (first-year sub-adult: S1, second-year sub-adult: S2, and adult: A), as well as time since sunset and the time of year an owl was collected. Over the course of an evening, it appeared empty stomachs were more frequent in the early and late hours, and less frequent in the middle of the night, so I included a quadratic effect of time since sunset in some models. For time of year, I performed a circular transformation of the date an owl was collected, dividing the ordinal date by 365 and multiplying that by $2\pi$, then taking cosine of that value to use as my date covariate. Whether a stomach contained food (1) or was empty (0) was the binary response variable. I fit logistic regression models in Program R (R Core Team 2022) and using AICc values compared combinations of each predictor variable as additive, linear effects with the dredge function in the MuMin package (Bartoń 2020).

To assign live mass of prey taxa, I used values published by Wiens et al. (2014) and Forsman et al. (2004) to facilitate compatibility of my results with prior studies. Where taxa were listed with a mass range in those studies, I selected the midpoint of that range. For taxa absent in those studies, I used mass measurements from primary literature when available, or used the mass of similarly sized taxa when no published measurements were found (commonly for arthropods). For prey items that were not identified to species, I assigned masses from similarly sized taxa. Traditionally in diet studies the contribution of biomass from each prey taxon is calculated using whole mean mass of individual prey species (hereafter “live mass”) multiplied by the number of times it was found in the diet, making the assumption that no matter the size of the prey, it was entirely consumed. This assumption makes sense for pellet studies, as large prey are often shared between mates and young, or eaten over several meals. When pellets are gathered they typically represent a broad time frame (e.g., weeks to months of owl meals) and multiple parts of large prey are distributed throughout these pellets. Thus, large prey can be reconstructed to account for a single individual, and missing parts can be assumed to have been egested in pellets that were not found. I make the traditional calculation of biomass and refer to it as "captured biomass." However, because my analysis was based on stomach contents, making this calculation inflates the contribution of large prey items I assumed would have been entirely eaten by a mate or across multiple meals. Considering the sampling unit to be a single stomach, I made an additional biomass calculation restricting the contribution of large prey items to the maximum mass of stomach contents measured among sampled owls, which I refer to as "consumed biomass," with the assumption that this was the most that could be eaten from a large prey item in a meal. If large prey items truly constitute a large portion of overall dietary biomass as they are eaten across several meals or shared between pairs, then these taxa would occur more frequency in meals, increasing the probability of finding them in the stomachs sampled.

For most vertebrate prey I noted whether the item was eaten whole or in part and which parts were consumed. I assumed that most invertebrate prey would have been eaten whole. For larger prey (e.g., squirrels, woodrats, rabbits, hares) all major appendicular and axial bones needed to be present to consider the individual eaten whole. For smaller prey (e.g., voles, mice, shrews, shrew moles, large salamanders), I considered an individual entirely consumed if I found a skull or mandible with at least 1 front and 1 rear appendicular bone. Small salamanders were excluded from consideration here, since their appendicular bones were sometimes degraded beyond recognition and small enough to occasionally pass into the intestines. To determine the size of prey more likely to be partially consumed, I fit a logistic regression model using the glm function in R with whether a prey item was whole (1) or partially consumed (0) as the binary response variable and its live mass as the predictor variable. I then used the estimated slope and intercept with the logit link function to find the live mass at which a prey item had a 0.5 probability of being partially consumed.

Some owls were collected together as mating pairs, and for these I compared the similarity in their diets by finding the proportion of prey items that matched at least 1 prey item in the mate's stomach. For partially consumed prey, I examined if these items where shared between the pair.

To examine for potential resource partitioning between sexes and differences in foraging between age classes I compared the similarity in prey numbers of barred owl diets between groups in these factors using Pianka's Index of Overlap (Pianka 1973). This index is defined as:

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}}$$

where $Ojk$ is Pianka's index of niche overlap between groups (i.e., sex or age class) $j$ and $k$; $pij$ is the proportion of the $i$th prey taxon out of all prey items from $n$ taxa found in group $j$, while $pik$ represents this proportion for group $k$. Pianka's index ranges from 0 if no resources are shared between groups, to 1 if each group uses the same resources in identical proportions.

## Results

We analyzed the stomach contents of 1328 barred owls collected from CLE (n = 228), COA (n = 625), and KLA (n = 475). The number of sampled owls varied by month, with the most owls sampled from March, September, and October, and the fewest owls sampled in December, January, July, and August (Figure 3.1A). Barred owls sampled were collected, on average, 3.8 (sd = 1.8) hours after sunset, with very few collections occurring before sunset or more than 8 hours after sunset (Figure 3.1B). Of the owls sampled, 244 (18.4%) had empty stomachs. Average mass of stomach contents was 11.2 g (sd = 12.5 g), which did not vary much by study area: CLE 11.5 g (sd = 14 g), COA 10.6 g (sd = 11.9 g) and KLA 11.7 g (sd = 12.5 g). Excluding months with very low sample sizes, we see a general trend in average stomach content mass from a low in February with a gradual increase over the course of the year to a high in November (Figure 3.2A). Maximum stomach content mass was 68.11 g. I identified 4961 individual prey items from all owls (Chapter 1), where prey live masses ranged from 0.1 g for several arthropod taxa, up to 2850 g for Virginia Opossums, with most of the prey weighing less than 10 g (Figure 3.3). The total captured biomass of prey identified in each area was 19166.3g in CLE, 48654.9g in COA, and 51151.35g in KLA. When I restricted the contribution of large prey items to the maximum stomach content mass, the total consumed biomass was 8116.54g in CLE, 31767.15g in COA, and 22191.38g in KLA. The average captured biomass mass found in stomachs was 24 g (sd = 103.2 g), while the average consumed biomass was 12.5 g (sd = 19 g). The consumed biomass over the course of a year followed a similar pattern to stomach content mass with a low in February increasing over the year to a high in November, excluding the months with few owls sampled (Figure 3.4A).

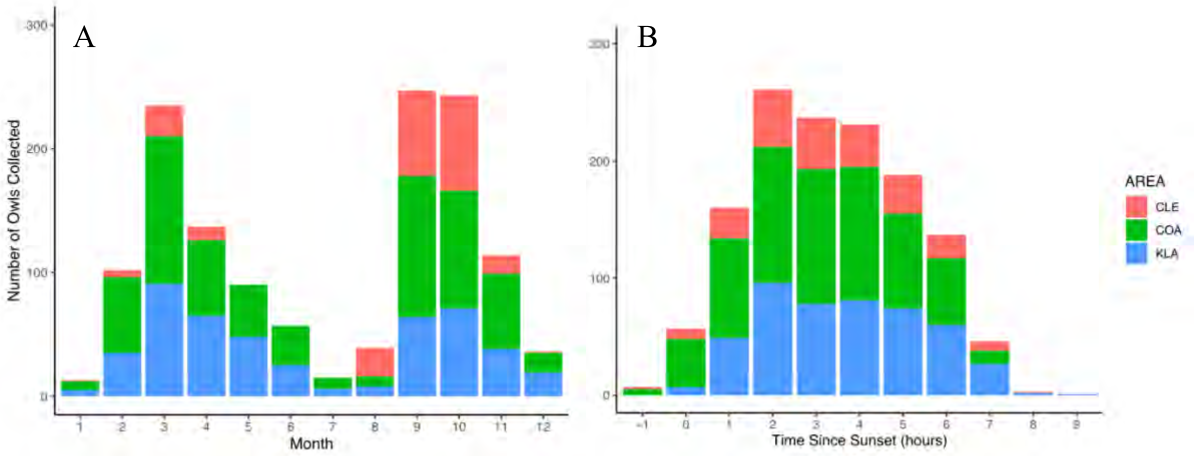

Figure 3.1. Numbers of barred owls with stomach contents analyzed by Month (A) and Hour (time since sunset; B) near Cle Elum, WA (2015-2018; CLE), Alsea, OR (2015-2018; COA), and Roseburg, OR (2016-2019; KLA) experimental study areas.

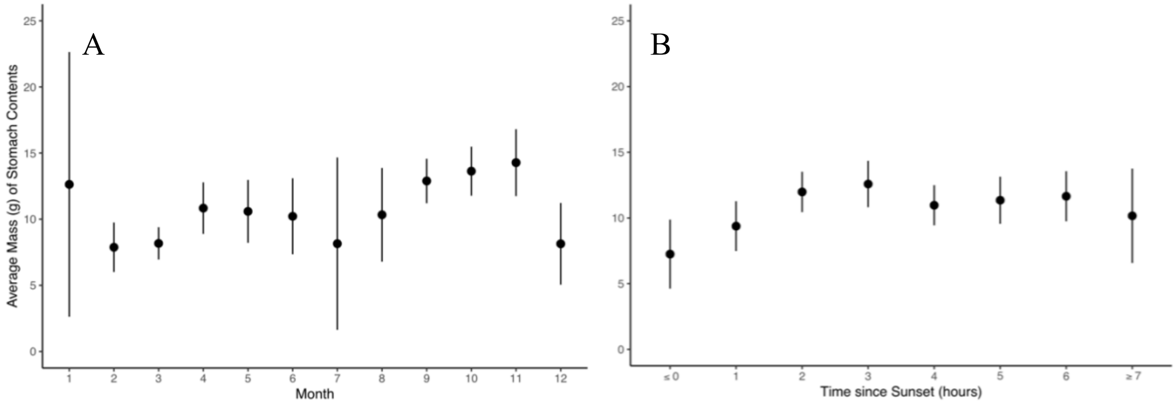

Figure 3.2. Mass of barred owl stomach contents by Month and Hour- The average (points) and 95% confidence intervals (lines) of barred owl stomach content mass by month (A) and hour since sunset (B) for owls collected near Cle Elum, WA (2015-2018), Alsea, OR (2015-2018), and Roseburg, OR (2016-2019).

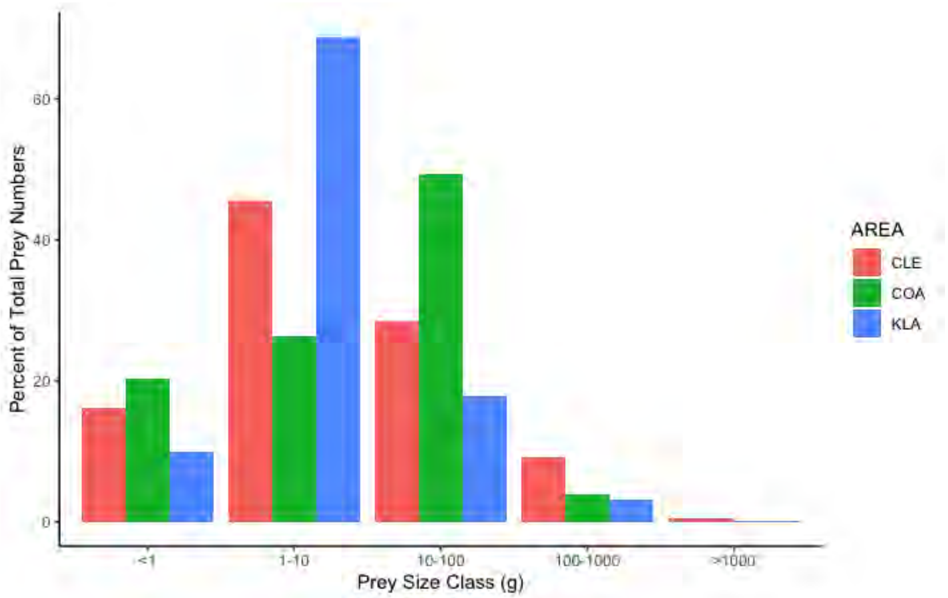

Figure 3.3. Prey Size Histogram - The distribution of prey live mass (g) found in the stomach contents of barred owls collected near Cle Elum, WA (2015-2018), Alsea, OR (2015-2018), and Roseburg, OR (2016-2019) combined.

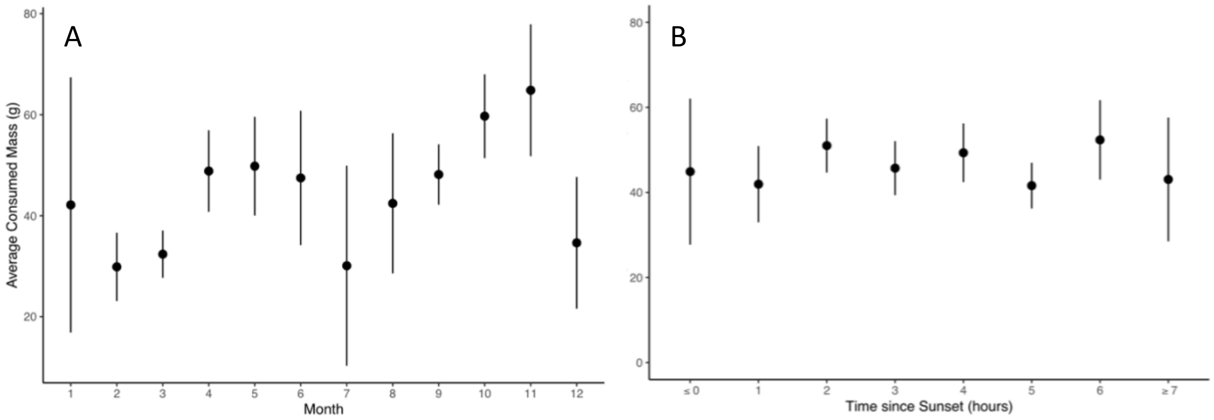

Figure 3.4. Consumed Mass by Month and Hour- The average (points) and 95% confidence intervals (lines) of consumed mass of prey by month (A) and hour since sunset (B) for barred owls collected near Cle Elum, WA (2015-2018), Alsea, OR (2015-2018), and Roseburg, OR (2016-2019). The consumed mass found in the stomach contents of each owl measured as the sum total of live masses for each prey item found in a stomach, where large prey items were restricted to the maximum stomach content mass measured (68.1g) to better represent prey species that were partially consumed.

In modeling factors affecting the occurrence of empty stomachs, the top (AICc model weight = 0.83) was the full model with effects for study area, age class, sex, circular transformed date, and a quadratic effect of time (

Table 3.1). The second ranked model had ΔAICc > 2 (

Table 3.1), and only the top 5 models had a model weight > 0.01. The intercept for the top model included effects for female adults collected in CLE. The percent of stomachs found empty varied between CLE, COA, and KLA was 28.1%, 15.7%, and 17.3% respectively, with coefficient estimates for COA ($\beta$= 0.83, SE = 0.19, 95% CI = 0.45 – 1.2) and KLA ($\beta$= 0.62, SE = 0.20, 95% CI = 0.23 – 1.0), both suggesting a higher probability in these areas that a barred owl was collected after having eaten something. We found 15.3% of females and 21.1% percent of males with empty stomachs, again reflected in the coefficient estimate for males ($\beta$ = -0.36, SE = 0.15, 95% CI = -0.66 – -0.072) suggesting a lower probability that males were collected after having eaten. The months with the highest frequency of stomachs found empty were December, January, and February (Figure 3.5A), and the circular transformed date estimated a lower probability that collected owls had eaten during this time of the year ($\beta$ = -0.70, SE = 0.16, 95% CI = -1.0 – -0.38). Owls were found more often with empty stomachs at the beginning and end of the evening (Figure 3.5B), and the quadratic effect of time since sunset ($\beta$= 053, SE = 0.15, 95% CI 0.25 – 0.82, $\beta$^2 = -0.62, SE = 0.018, 95% CI -0.098 – -0.026) received more support than a linear effect.

Table 3.1. AIC$_c$ model selection results for logistic models with AIC weight ($w$) $\geq$ 0.01 estimating the probability a barred owl had an empty stomach empty given its age class and sex, the study area it was collected in, date and time since sunset it was collected. Barred owls collected in study areas (Area) near Cle Elum, WA, Alsea, OR, and Roseburg, OR between 2015-2019.

| **Model**[a] | ***K*** | **log*L*** | **ΔAICc** | ***w*** |
|---|---|---|---|---|
| Area + Age + Sex + Date + Time + Time^2 | 9 | -596.5 | 0 | 0.83 |
| Area + Age + Date + Time + Time^2 | 8 | -599.49 | 3.95 | 0.12 |
| Area + Sex + Date + Time + Time^2 | 7 | -601.9 | 6.73 | 0.03 |
| Area + Age + Sex + Date | 7 | -603.01 | 8.97 | 0.01 |
| Area + Age + Sex + Date + Time | 8 | -602.2 | 9.37 | 0.01 |

[a] Key to terms: $K$ = number of parameters; log$L$ = log-likelihood; ΔAIC$_c$ = difference in AIC$_c$ score between given model and top model (AIC$_c$ = 1211.15 for top model); $w$ = AIC$_c$ model weight; Area = 3 factor categorical parameter for each study area, CLE, COA, KLA; Age = 3 factor categorical parameter for first-year subadults, second-year subadults, and adults; Sex = 2 factor categorical parameter for males and females; Date = circular transformation of ordinal date; Time = time since sunset; Time^2 = quadratic effect of time since sunset.

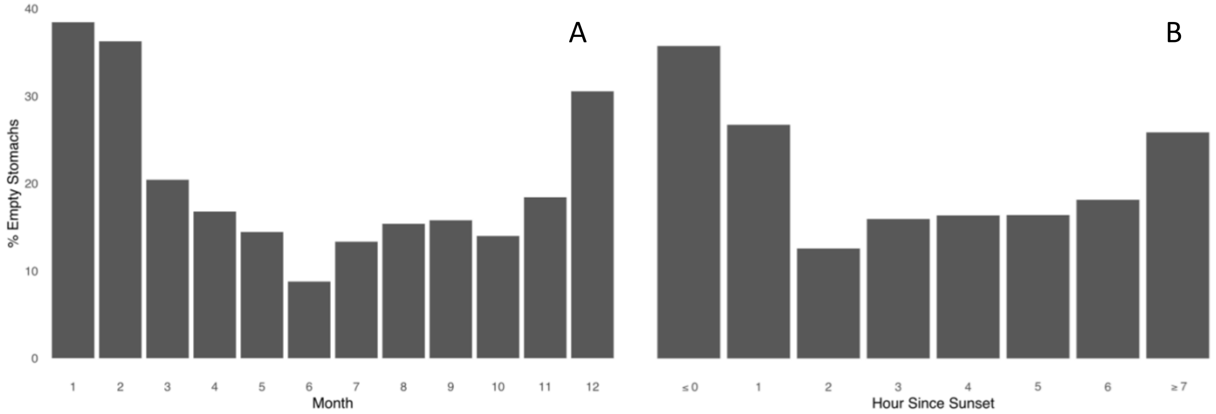

Figure 3.5. The percent of barred owls with empty stomachs over each month of the year (A) and over the course of an evening (B), collected near Cle Elum, WA (2015-2018), Alsea, OR (2015-2018), and Roseburg, OR (2016-2019). Times are hours relative to sunset in each area the day the owl was collected. Few owls were collected the hour before sunset or more than 8 hours after sunset, thus these owls were included with the adjoining hours.

As would be expected, restricting the contribution of large prey items to the maximum mass of stomach contents found in any owl (68.1g) reduced the proportional contributions of large prey while increasing the contributions of smaller prey (Table 3.2). Leporids and large squirrels were substantially reduced in importance in all three areas. The few opossums found in KLA went from 22.3% captured biomass down to 1.2% consumed biomass when I restricted their contribution. The live masses of flying squirrels (95g) and chipmunks (83g) were above the threshold, but in all areas their proportional contributions to biomass increased after the larger prey items were also restricted (Table 3.2). The contributions of amphibians approximately doubled in each area (Table 3.2). Slight increases were seen in the very small prey categories of shrews, shrew moles, and arthropods (Table 3.2). Considering the consumed biomass, mammals made up the largest share in CLE (83%) where a quarter of the biomass was flying squirrels and 14% were voles and mice (Table 3.2). The share of mammals was much lower in COA and KLA, where they only made up about half of the consumed biomass (Table 3.2). Flying squirrels contributed the most consumed biomass of any mammal in COA, but this was only 7% of the diet, and was closely followed by Douglas squirrels, chipmunks, terrestrial voles and mice, and moles, each at least about 5% of the consumed biomass (Table 3.2). In KLA, the 10% of consumed biomass that flying squirrels supplied was surpassed by moles that made up 12% biomass (Table 3.2). Amphibians (particularly small salamanders) made up substantial shares of the biomass, especially in COA where they amounted to 42% of the consumed biomass (Table 3.2).

Table 3.2. Percentage of total biomass contributions for prey taxa found in stomach contents of barred owl collected near Cle Elum, WA (2015-2018), Alsea, OR (2015-2018), and Roseburg, OR (2016-2019). Captured biomass values used the full, mean mass of individual prey taxa found within the diet, while the consumed biomass restricts the contribution of large prey items to the maximum mass of stomach contents found within a barred owl (68.11g). Percentages of arthropods exclude crayfish.

| | Caputred Biomass | | | Consumed Biomass | | |
|---|---|---|---|---|---|---|
| Prey Taxon | CLE | COA | KLA | CLE | COA | KLA |
| Mammals | 83.3 | 60.2 | 75.4 | 82.9 | 44.3 | 57.8 |
| Flying Squirrels | 15.9 | 6.6 | 6.3 | 26.9 | 7.3 | 10.4 |
| Chipmunks | 3.5 | 4.6 | 0.8 | 6.7 | 5.8 | 1.5 |
| Douglas Squirrels | 10.4 | 13.2 | 4.3 | 7.6 | 6.2 | 3.1 |
| Gray Squirrels | | | 2.6 | | | 0.9 |
| Unidentified Squirrels | 1.4 | 2 | 0.8 | 2.5 | 1.1 | 0.9 |
| Woodrats | 5.9 | 4.1 | 7.2 | 3.4 | 1.5 | 4.0 |
| Red Tree Voles | | 0.8 | 0.6 | | 1.2 | 1.3 |
| Other/Unidentified Voles and Mice | 6.1 | 3.5 | 2.1 | 14.4 | 5.4 | 4.8 |
| Jumping Mice | 0.1 | 0.1 | <0.1 | 0.3 | 0.2 | 0.1 |
| Mountain Beaver | | 2 | | | 0.6 | |
| Pocket Gopher | 1.1 | 0.4 | | 1.7 | 0.4 | |
| Murid Rat | | | 0.5 | | | 0.3 |
| Unidentified Rodents | 0.5 | 0.8 | 0.7 | 0.8 | 0.5 | 0.9 |
| Shrew spp. | 1.0 | 2.2 | 1.7 | 2.3 | 3.3 | 3.9 |
| Shrew mole | 0.1 | 1.4 | 2.1 | 0.2 | 2.2 | 4.8 |
| Mole spp. | 0.9 | 4.3 | 7.3 | 2.1 | 4.9 | 12.3 |
| Hares, Rabbits, Pikas | 15.8 | 6.8 | 5.6 | 5.9 | 1.5 | 1.8 |
| Virginia Opossum | | | 22.3 | | | 1.2 |
| Bats | | <0.1 | | | <0.1 | |
| Unidentified Mammal | 20.7 | 7.3 | 10.6 | 8.2 | 2.2 | 5.5 |
| Amphibians | 2.7 | 27.5 | 8.9 | 6.4 | 42 | 20.5 |
| Small salamanders | 1.0 | 22.4 | 7.8 | 2.3 | 34.3 | 18.0 |
| Large salamanders | 0.2 | 4.4 | 0.7 | 0.6 | 6.7 | 1.6 |
| Frogs | 1.5 | 0.7 | 0.3 | 3.5 | 1 | 0.8 |
| Birds | 11.2 | 5.4 | 7.2 | 5.2 | 4.3 | 4.8 |
| Reptiles | 1.6 | 2.7 | 3.9 | 2.5 | 2.9 | 6.2 |
| Fish | 0.5 | 0.1 | | 1.3 | 0.2 | |
| Arthropods | 0.6 | 0.3 | 2.9 | 1.4 | 0.5 | 6.7 |
| Crayfish | 0.1 | 1.1 | 0.3 | 0.3 | 1.7 | 0.6 |
| Snails | | 2.6 | 1.4 | | 4 | 3.2 |
| Unidentified Prey | | <0.1 | | | <0.1 | |

The proportional contributions of higher taxa remained relatively stable throughout the year, with some notable exceptions (Figure 3.6). Arthropods were found in great numbers in all study areas (20-62% of total prey; Chapter 1), but given their small size, contributed little to the consumed biomass, except during the fall in KLA (Table 3.2). Here I found that arthropods made up approximately 20-25% of the consumed biomass during October and November, driven largely by consumption of the 1.15g rain beetles (*Pleocoma* spp.; Figure 3.6). Between July and August in both COA and KLA, we see some large shifts in the biomass contributed by each taxon, but sample sizes were small in these months (less than 10 owls in each month in either area; Figure 3.6). Over the course of an evening, all major prey taxa first appeared in stomach contents within an hour and a half after sunset, but I observed some variation in the frequency different taxa occur in stomachs (Figure 3.7). During a single evening, I found that the mass of stomach contents measured in owls increased during the first few hours and then remained relatively stable (Figure 3.2B). However, the consumed mass appears to remain relatively stable throughout the evening (Figure 3.4B).

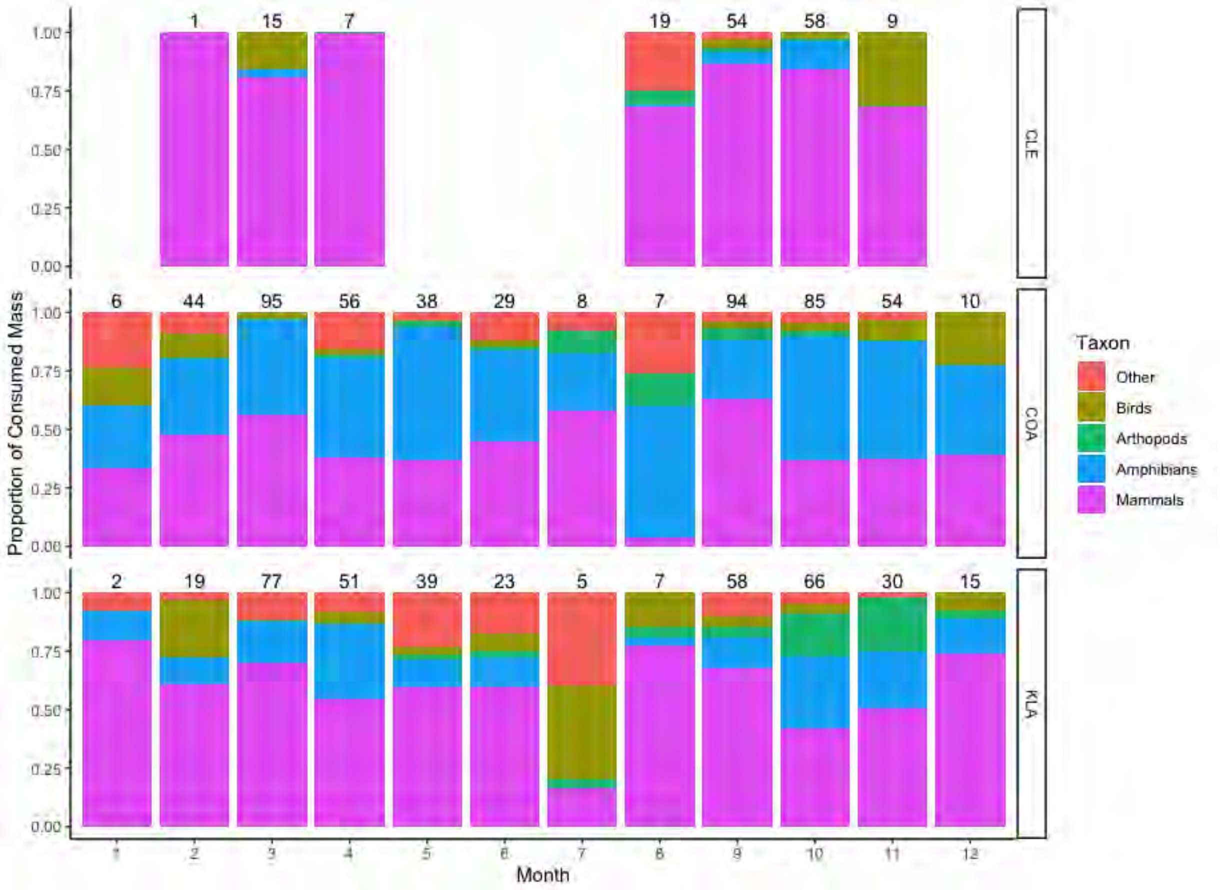

Figure 3.6. Biomass by Month Area - The proportional biomass contributions of higher taxa to the diets of barred owls collected near Cle Elum, WA (CLE; 2015-2018), Alsea, OR (COA; 2015-2018), and Roseburg, OR (KLA; 2016-2019). Values above columns indicate the number of owls sampled in each month in each area.

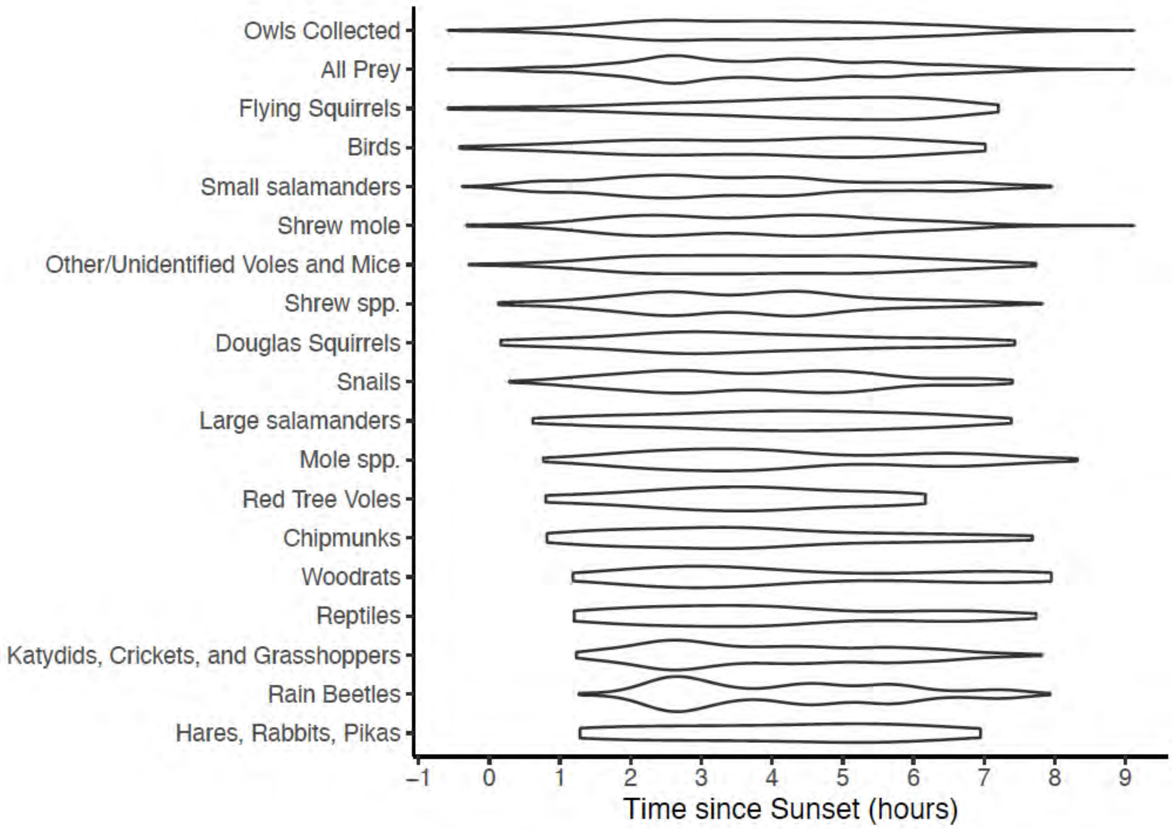

Figure 3.7. Taxa Since Sunset - Violin plots showing the distribution of prey taxa found in barred owl stomachs in relation to the time since sunset that the owl was collected. Owls collected near Cle Elum, WA (2015-2018), Alsea, OR (2015-2018), and Roseburg, OR (2016-2019).

The owls sampled ate 1482 vertebrates (excluding small salamanders), and of these 1259 had enough data to assess if they were partially consumed. Some of the smallest prey, 5g shrews, were found without heads, suggesting vertebrates of any size could be partially consumed. Only prey smaller than 285g woodrats were found entirely consumed, and the proportion of a taxon found entirely consumed increased as the mass of taxa decreased (

Table 3.3). The 37 unidentified mammals were each partially consumed and suspected to be larger prey taxa (average mass 341g), given the remains were primarily large unidentifiable bone fragments or a large volume of relatively long fur. The logistic regression of partial prey consumption found that prey heavier than 78.9g were more likely to be partially consumed.

Table 3.3. The percent (%) of vertebrate prey items (excluding small salamanders, taxa with < 3 individuals, higher taxonomic classifications with wide size ranges, i.e., unidentified squirrels, unidentified rodents, birds, and reptiles) found consumed whole in the stomach contents of barred owls collected near Cle Elum, WA (2015- 2018), Alsea, OR (2015-2018), and Roseburg, OR (2016-2019). Mass (g) is the average live mass of all items (n) assessed for partial consumption within the taxon.

| Prey Taxon | n | % | Mass (g) |
|---|---|---|---|
| Virginia Opossum | 4 | 0 | 2850 |
| Hares, Rabbits, Pikas | 20 | 0 | 460 |
| Gray Squirrels | 3 | 0 | 450 |
| Unidentified Mammal | 37 | 0 | 341 |
| Mountain Beaver | 3 | 0 | 325 |
| Woodrats | 23 | 0 | 285 |
| Douglas Squirrels | 41 | 7 | 221 |
| Pocket Gopher | 4 | 100 | 98 |
| Flying Squirrels | 90 | 17 | 95 |
| Mole spp. | 62 | 63 | 91 |
| Chipmunks | 34 | 47 | 83 |
| Large salamanders | 49 | 37 | 46 |
| Red Tree Voles | 23 | 100 | 26 |
| Jumping Mice | 3 | 100 | 24 |
| Other/Unidentified Voles and Mice | 138 | 99 | 24 |
| Shrew mole | 179 | 95 | 9 |
| Frogs | 78 | 99 | 6 |
| Shrew spp. | 375 | 96 | 5 |

We analyzed the stomach contents of 247 barred owl pairs collected together, containing 1982 prey items. In 12 (4.9%) pairs both mates had empty stomachs, and in 53 (21.5%) pairs one owl had an empty stomach. Only 8 (3.2%) pairs showed evidence of sharing prey, which were a Leporid, 2 Douglas' squirrels, 2 flying squirrels, a chipmunk, an unidentified squirrel, and a large salamander. The large salamander was the smallest shared prey item, and if we consider their 45.5g mass the minimum size a prey item could be shared, then 148 owls contained 162 prey items that were large enough to be shared but were not shared. However, for 42 of these owls (17% of pairs) with shareable prey items, their mates already had a full stomach (i.e., the mate's total consumed biomass exceeded 68.1), and only 18 owls (7% of pairs) with shareable prey had mates with empty stomachs. The overwhelming majority of prey items these owls consumed were simply too small to likely be shared. There were 814 prey items found where a matching taxon was in the stomach of the owl's mate, with an average 34.4% of prey items in owls matching what was found in their mates. Among these matching prey I did count 13 cases where vertebrate prey seemed similar but could not be identified to the same taxonomic level (i.e., one item identified to genus and the other to family) and likewise for 95 arthropods.

While I found relatively low dietary overlap between study areas (0.31-0.5; Chapter 1), within study areas I found near complete overlap between males and females in COA (0.97) and KLA (0.96), and fairly high overlap in CLE (0.78). Overlap in diets between age classes was always lowest when comparing adults to S1s (CLE = 0.8, COA = 0.9, KLA = 0.44), and fairly high between adults and S2s (CLE = 0.91, COA = 0.94, KLA = 0.85) as well as between S1s and S2s (CLE = 0.96, COA = 0.92, KLA = 0.79).

## Discussion

The biomass consumed by invasive barred owls illustrated their reliance upon a wide diversity of native prey, especially as compared to northern spotted owls. Whereas the biomass of spotted owl diets is almost entirely comprised of mammals, with about half or more from 1 of 2 species in any given study (e.g., Forsman et al. 2004, Wiens et al. 2014), mammals only accounted for about half of the consumed biomass in COA and KLA, and 83% of the biomass in CLE. Among the mammals, flying squirrels amounted to 27% of the consumed biomass in CLE, the highest proportion contributed by any mammal or single taxon identified to species, but flying squirrels represented a much smaller portion of the diet in COA and KLA. Perhaps the biggest disparity was in the contribution of amphibians, particularly salamanders in COA (41%) and KLA (20%), as here amphibians are very rarely reported from northern spotted owl diet studies. Arthropods occur in spotted owl diets but rarely in great enough numbers to meaningfully contribute to the biomass of their diets. However, arthropods made some contributions to the diets in CLE (1.4%) and COA (0.5%), but nearly 7% of the consumed biomass in KLA. Overall, if we consider all taxa that essentially contribute no biomass to northern spotted owl diets (amphibians, reptiles, arthropods – including crayfish – snails, and fish), the biomass accounted for by these taxa in barred owl diets were 12% in CLE, 51.3% in COA, and 37.2% in KLA. Furthermore, mammalian insectivores (shrews, shrew moles, and moles) only accounted for about 1% of spotted owl biomass in a single study conducted during the breeding season (1.2% moles, Rosenberg et al. 2003), whereas the total consumed biomass of this group in my study was 5% in CLE, 10% in COA, and 21% in KLA. There can be disparities in prey that can be detected in stomach contents and egested pellets (Chapter 1), but all prey considered here can be detected in pellets (Wiens et al. 2014), but are still largely absent from pellets of northern spotted owls. Thus, in effect, more than half of the biomass consumed by barred owls on 2 of the study areas is almost entirely unused by northern spotted owls.

Restricting mass contributions of large prey to the maximum mass of stomach contents measured (68.1 g), seems warranted considering prey with a live mass >78.9g were more likely to be partially consumed. The percentage of prey items eaten whole consistently increased as the size of prey items decreased. As would be expected, I observed that a smaller amount of an individual was consumed the larger its size (

Table 3.3). For leporids and large rodents (squirrels and woodrats) I found on several occasions that only a few vertebrae were eaten. Whereas with the smallest prey (voles, mice, shrews, and shrew moles) if they were partially consumed, only the head was missing. No prey with a live mass over 250 g (murid rat) was found consumed whole. In addition, the larger prey taxa consumed whole were likely smaller individuals and the restricted mass estimates of consumed biomass may have adjusted their contributions closer to the actual mass of the individuals consumed. Some mid-sized prey may be eaten in stages during a meal since some items (often moles) appeared split in half where one half was substantially digested and the other appeared freshly consumed and undigested.

Over the course of the year, the proportional contributions of higher taxa (i.e., birds, arthropods, amphibians, and mammals) remained relatively consistent, with some notable exceptions. While arthropods contributed some, but not much to the overall biomass of barred owl diets, in KLA arthropods comprised approximately 20% of the biomass in October and November, driven largely by the very high frequency of rain beetles in the diet. Salamanders remained a relatively consistent proportion of the COA diet throughout the year, and this consistency may reflect a seasonal shift in salamander species that are targeted in response to availability. Terrestrial salamanders will be more available during the wetter months of the year, while during the dry months they will remain underground. In contrast, aquatic salamanders would likely be more available to capture during the drier months of the year when stream flows are low, as opposed to the wetter months of the year when stream flows and water levels are high. While few owls were collected in December and January, we do see that in these months and also in February, barred owls in all 3 study areas were more likely to be collected with empty stomachs relative to the rest of the year.

Over the course of an evening, stomach content mass initially increased and peaked about 3 hours after sunset, then declined slightly as we would expect as digestible tissues are passed to the intestines. This pattern is also reflected in the proportions of empty stomachs, where most empty stomachs were observed in the first two hours after sunset. The increase in empty stomachs as the night progressed could reflect owls that ate early in the evening and egested a pellet before collection, since it takes them on average 9.85 (SD = 2.2) hours to egest a pellet after a meal (Duke et al. 1976). During dissections I observed that stomach tissue of some of the empty stomachs seemed stretched, as if it had recently contained food, while other empty stomachs seemed shrunken in comparison. The estimated consumed biomass varied little in relation to time since sunset. I also found little variation in when taxa first occurred over the course of an evening, as most major taxa appeared in stomachs collected within 1.5 hours after sunset. Flying squirrels, a nocturnal species, occurred in some owls collected very early in the evening, yet most flying squirrels were found in stomachs collected much later (~6 hours after sunset). Birds were also observed in stomachs early in the evening, likely because aside from the few small owls found in barred owl stomachs, all birds were diurnally active. In addition, most chipmunks occurred in stomachs ~ an hour after sunset, consistent with their diurnal habits. The two major arthropod taxa, rain beetles and shield-backed katydids, had some of the latest first occurrences (>1 hour after sunset). Caution should be used in interpreting these diel patterns, as the lack of occurrence early in an evening suggests a taxon may only be available later, yet any time a taxon occurred in a stomach it obviously had to be consumed at some point earlier in the evening. Similarly, if a taxon was primarily found in owls collected early in the evening, presumably this taxon would still be present in these stomachs if the owls had been collected later.

Barred owls do not appear to partition resources between sexes, with near complete dietary overlap between males and females in COA and KLA, and high overlap in CLE as well. However, males were found to have a higher occurrence of empty stomachs relative to females. In addition, while the proportion of females with empty stomachs remained relatively constant throughout the year, the months with a high proportion of empty stomachs (Figure 3.5A) were mostly the result of dramatic increases in the number of males collected with empty stomachs. It is possible that these sex-specific differences in empty stomachs are a result of males provisioning females during courtship and incubation, and delaying feeding themselves until later in the evening, as seen in barn owls (Durant et al. 2013). The dietary overlap between age classes is also quite high, with the largest disparities between adults and first-year sub-adults, possibly reflecting improved foraging ability as owls become more experienced with age.

The generalist foraging behaviors of barred owls may provide them with several advantages over spotted owls beyond greater prey availability. The broader diet may make finding and acquiring prey more efficient, resulting in barred owl home ranges that are 2-8 times smaller than those of northern spotted owls (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014), contrary to expectations given the barred owl's larger body size (McNab 1963, Schoener 1968). Greater foraging efficiency may also allow barred owls more time and energy for other necessary activities such as incubation, provisioning young, or territory defense. Stomach content mass and consumed biomass over the course of an evening both suggest that barred owls may meet their energetic needs early in the foraging period (i.e., within a few hours after sunset (Figure 3.2B). In addition, stomach content mass remains consistent through the evening (Figure 3.4B). Prey themselves are heterogeneous in nutritional quality both between (Hilton et al. 1999, Weathers et al. 2001), and within species (Taylor et al. 1991, Wilder et al.

2010). The amount of nutrition that can be derived from a meal is determined in part by gut volume (Whelan and Schmidt 2007), and the mammals and birds that spotted owls rely on constrain the amount of nutrients that can be consumed as undigested fur, feathers, and bones that need to be egested before more food can be consumed. Flying squirrels may be particularly disadvantageous given their bushy tails and patagia that have little soft tissue and a lot of fur. Spotted owls may occasionally discard these parts of their prey (Forsman et al. 2004), but I often found these parts in the stomach contents of barred owls. In contrast, the amphibians and invertebrates barred owls consumed had much less indigestible material, and as soft tissue is passed to the intestines more space is left to continue eating before pellet egestion is necessary.

Theory suggests that a demographically inferior species can co-exist with a competitor if the inferior species is relatively long lived and there are brief time periods where it holds a temporary fitness advantage over the superior species (Chesson 2000). With the relatively narrow, specialist diet of northern spotted owls, it is difficult to envision a scenario where they would temporarily obtain a dietary advantage over the generalist barred owls. Such an advantage seems even less likely given that barred owls eat everything that spotted owls eat in addition to opportunistically taken prey that are never eaten by spotted owls (e.g., rain beetles in KLA). Barred owls likely exploit short-term increases in spotted owl prey abundance as well. While I have not linked the diversity of barred owl diets directly to their increased fitness relative to spotted owls, this study better describes diet differences between the two species and outlines one likely mechanism by which barred owls are outcompeting the native forest owl in the Pacific Northwest.

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# Chapter 4 - Estimating Fat Content in Barred Owls (*Strix Varia*) with Predictive Models Developed from Direct Measures of Proximate Body Composition.

## Introduction

Energy storage is an important aspect of foraging ecology, where animals try to buffer future energetic demands against spatiotemporal variability in food resources (Brodin and Clark, 2007). Characterizing stored energy through body condition indices can inform relationships between individual fitness potential and habitat quality (Johnson, 2007), whereas other measures such as increased population density can suggest habitat quality is high when in fact, it is not (Van Horne, 1983, Bock and Jones, 2004, Marra et al., 2015). The importance of body condition has long been recognized and studied in birds (Nice, 1938), especially given the trade-offs they face between energetically demanding activities such as reproduction (Lindén and Møller, 1989) and migration (Lindström and Piersma, 1993) that benefit from larger fat reserves. Conversely, large fat reserves can degrade flight efficiency (Hedenström, 1992, Witter and Cuthill, 1993) and affect a bird's ability to forage (Houston and McNamara, 1993) or escape predation (Kullberg et al., 1996, Lind et al., 1999). A central challenge in avian body condition research is the ability to accurately and effectively characterize the amount of stored energy in live birds during field studies (Labocha and Hayes, 2012).

Avian body condition can be indexed by individual mass, whereby greater mass equates to more stored fat, however individual mass can be confounded by factors such as dehydration, recent meals, defecation (Green, 2001), or structural size with larger individuals simply weighing more than smaller individuals (Schulte-Hostedde et al., 2005). Numerous methods index or measure energy stores in birds to assess body condition while controlling these confounding variables (McWilliams and Whitman, 2013). Ideally, such methods are based on or verified against direct measures of lipid content from the species or population under consideration, (e.g., Salewski et al., 2009, Guglielmo et al., 2011). However, direct measures of lipids are not always taken because this requires chemical extraction of lipids from carcasses, raising questions about how well an unverified body condition index correlates with actual fat content (Schamber et al., 2009). For birds, this means direct measurements of stored lipids are often available for hunted or relatively abundant species (e.g., Schamber et al., 2009, Labocha and Hayes, 2012). In contrast, lethal sampling is often prohibited for rare and endangered species, such as many birds of prey, thus few studies have directly measured lipids among these birds (but see Gorney and Yom-Tov, 1994, Massemin and Handrich, 1997, DeLong and Gessaman, 2001). In the Pacific Northwest, USA, large-scale removal experiments conducted with barred owls (*Strix varia*) have presented an opportunity to obtain direct measures of lipids to develop verified body condition indices in a bird of prey, with immediate application for conservation and management.

Following a westward range expansion across North America (Livezey, 2009, Long and Wolfe, 2019), barred owls spread throughout the range of and are outcompeting threatened northern spotted owls (*Strix occidentalis* caurina; Franklin et al., 2021). Barred owls pose an “extremely pressing and complex” threat, prompting consideration of their lethal removal to protect northern spotted owls (USFWS, 2011). Several large-scale experiments assessed the efficacy of barred owl removal and demonstrated conservation value of this action for spotted owls (Diller et al. 2016, Wiens et al., 2021, Hofstadter et al., 2022). If broad-scale lethal removal is implemented for conservation of impacted native wildlife, barred owl management could be better informed by understanding their habitat quality.

Habitat associations of barred owls within their territories are well researched (e.g., Hamer et al. 2007, Singleton et al., 2010, Irwin et al., 2018, Jenkins et al., 2019), but few studies have assessed how habitat quality varies over the diverse range of landscapes they use in their expanded range (Wiens et al., 2014, Rossman et al., 2016). An accurate and easily implemented measure of barred owl body condition could be used in an adaptive management framework to assess body condition relative to the site-specific habitat conditions where they occurred. Such information could then guide future removal efforts on the highest quality habitats that have disproportionate benefits to barred owl fitness. Beyond this immediate application, a body condition index could aid in understanding the energetic patterns of this wide-ranging bird of prey to answer broader ecological and conservation questions.

Here we used barred owl specimens collected as part of a removal study in Washington and Oregon (Wiens et al., 2021) to: 1) directly measure the amount of lipid in a subsample of the owls collected, and 2) develop and evaluate linear models that rely on readily obtained information (morphometrics, sex, time of year, and fat scores) to estimate the percentage of lipid in individual barred owls. These models provide the ability to compare body condition of barred owls within and among populations that differ in available data, requiring only commonly used tools in ornithological studies (e.g., scales, rulers, and calipers).

## Methods

### Specimen collection

As part of a larger study, we lethally removed 2,249 barred owls between 2015-2019 from three study areas near Cle Elum, WA, Alsea, OR, and Roseburg, OR (Wiens et al., 2021), all of which were long-term northern spotted owl demographic study areas (Franklin et al., 2021). We collected barred owls using 12-gauge shotguns and non-lead ammunition during all times of the year. Collection methods and study areas are described in detail by Wiens et al. (2016, 2017). Removal and scientific collection of barred owls was conducted under protocols approved by Oregon State University's Institutional Animal Care and Use Committee and under federal and state Scientific Collection Permits. Upon collection in the field, we measured unflattened wing chord with a ruler to the nearest 1 mm, exposed culmen and foot-pad lengths with calipers to the nearest 0.1 mm, and mass of the whole bird including stomach contents (hereafter "field mass") with a Pesola scale (Pesola, Switzerland) to the nearest 5 g (Bildstein and Bird, 2007). We necropsied 1,327 owls of the collected owls, where we scored the amount of subcutaneous fat found on the breast, between the ventral feather tracts of each owl using criteria we developed based on observations during necropsies (Table 1; hereafter referred to as "fat score"). The wing pit has beenused to score fat in birds of prey (e.g., Delong and Gessaman 2001), however, we observed substantial variation in breast deposits that could be characterized by a small number of categories (Krementz and Pendleton 1990). We weighed stomach contents of each owl to the nearest 0.01 g and subtracted this from their field mass to obtain "carcass mass".

### Sample selection

Of the owls necropsied, 1,043 specimens possessed full data (morphometrics, sex, and fat score) and were free of severe gunshot damage. We grouped specimens based on sex, fat-score, and time of year a female was collected (breeding vs. non-breeding season) and either included all owls that were available in a group at the time of our study or for groups with large numbers of barred owls we randomly selected a maximum of 10 specimens from the group, resulting in a total of 77 barred owls included in the body composition analysis (Table 2). We grouped females into breeding (January-June) and non-breeding seasons (July-December) because body mass and composition can correlate with gonadal hypertrophy and rapid yolk development (Hirons et al. 1984). We found no females with enlarged gonads between July-December. Although testes also enlarge, we did not consider a seasonal effect in males, as testis growth seemed negligible to overall body composition.

### Aliquot preparation

We plucked all body and flight feathers, and trimmed feathers around the ears. Once defeathered, we used poultry shears to cut carcasses, including talons and beaks, into $\leq 2$ cm$^2$ pieces. Using a 1 hp tabletop meat grinder, we homogenized carcasses with at least 2 passes through a 4.76 mm die and thoroughly mixed this homogenate by hand. From the homogenate of each owl we took 3, approximately 10 g aliquots for body composition analyses.

### Body Composition Analysis

We adapted standard methods to analyze the proximate body composition of barred owls (Reynolds and Kunz, 2001, Dobush et al., 1985, Bligh and Dyer, 1959). Mass measurements were taken on a Mettler Toledo analytic balance to the nearest 0.0001g, which we calibrated daily. Aliquots and porous equipment that we weighed were first dried in an oven at 60 C overnight to minimize mass variation from absorbed water in the air due to changes in ambient humidity, with the exceptions that lean aliquots were stored in a desiccation cabinet prior to combustion and weighed directly from the furnace after combustion.

Aliquot wet mass (g) was the mass of the homogenate aliquot prior to drying. We dried each aliquot on an aluminum pan in an oven, until consecutive daily mass measurements were within 0.001 g or the sample mass increased from the previous day indicating that water content in the aliquot was at equilibrium with ambient humidity. This yielded aliquot dry mass (g), and water mass (g) was the difference between wet mass and dry mass. Once aliquots were dry, we ground them with a mortar and pestle, removed and weighed any shot pellets, then loaded the ground dry aliquot into a cellulose extraction thimble and plugged it with a cotton ball rinsed with extraction solvent. To extract lipids from dried aliquots we used a solvent composed of 7:2 hexanes and isopropyl alcohol in a Soxhlet apparatus, running extractions for 22-24 hours. This solvent is relatively safer to handle than common alternatives, but it will dissolve both structural (i.e., cellular membranes) and neutral (i.e., stored fat) lipids (Anthony et al., 2000). Lipid mass (g) was the difference in mass of loaded thimbles before and after extraction, and aliquot lean mass (g) was the mass of the loaded thimble after extraction minus the mass of thimble and cotton ball plug measured prior to extraction. We then transferred lean aliquots to ceramic crucibles and combusted them in a muffle furnace for at least 22 hours at 600 C. Bone mass (g) was the mass of the aliquot after combustion, and protein mass (g) was the difference between the lean mass in the crucible prior to combustion and the bone mass. We averaged all mass measurements across the 3 aliquots for each owl.

### Body Condition Indices and other covariates

Using the morphometric measurements taken in the field on each specimen (Table 3), we developed four continuous body condition indices (BCIs): 1) carcass mass, and carcass mass divided either by 2) wing chord, 3) exposed culmen, or 4) foot-pad length. There are a number of formulations to scale mass by body size (e.g. cube of linear measurement, scaled mass index), but in a post-hoc analysis the BCIs presented here outperformed these formulations. Fat score included 4 categories, ranked from 0 - 3 (Table 1). Sex was either male or female, and the sex-season parameter had 3 categories: 1) males, 2) females collected during the egg production (breeding) season from January-June, or 3) females collected outside of the egg production (non-breeding) season from July-December. Owls included in this body composition analysis were collected at all times of years, over a 4-year period at 3 different sites, and while this spatiotemporal variation may influence barred owl condition, it likely would not affect our ability to estimate the lipid content of barred owls (other than the aforementioned differences between breeding and non-breeding season females). Thus, we did not included covariates for year, time of year, or collection site in our models to estimate percent lipid.

## Statistical Analysis

We used percent lipid in dry mass as our primary response variable in all analyses. While percent lipid in wet mass may provide a more intuitive value relating to the field mass of an owl, uncontrolled variation in water loss between collection and body composition analysis can introduce unaccounted variance in the measurement of wet mass. Thus, percent lipid in dry mass provided a more reliable assessment of body condition in our case. Using the *glm* function in program R (R Core Team 2019) we fit linear models that estimated the percent lipid in dry mass of barred owls. Four univariate models each used one of the BCIs, and additional models used individual BCIs in combination with fat score and/or sex or sex-season, resulting in a set of 24 models (Table 4). We compared models with adjusted $R^2$ to develop predictive models that explained as much variance in our data as possible, rather than simply ranking models with a statistic such as AIC (Burnham and Anderson 2002).

To evaluate whether models produced different estimates of percent lipid from each other for a given population, we used each model to estimate the percent lipid of all necropsied owls with full data (n=1,043). We then performed an ANOVA to compare the estimates of percent lipid across all models and a post-hoc pairwise t-test with a Bonferroni *p*-value correction to compare estimates of percent lipid between models.

To provide a correction factor for studies that cannot remove stomach contents, we averaged the stomach content mass of all necropsied barred owls and evaluated how well this reduced bias from unmeasured stomach contents. Using our top model, we estimated 2 new sets of percent lipid for the 77 owls included in the body composition analysis, recalculating BCIs from 1) the field mass (rather than carcass mass) of each owl and 2) the field mass of each owl minus the average stomach content mass. We calculated the bias and mean squared error, and tested for differences with paired t-tests between the original percent lipid estimates of the top model based on carcass mass and each of the 2 new sets of estimates.

## Results

The average percent lipid in dry mass across the 77 owls measured was 27 % (+/- 14 SD, geometric mean 23.3 %, +/- 1.7 SD) and ranged from 8-56 %. The average standard deviation of the percent lipid of the 3 samples analyzed for each owl was 2.0 % (+/-2.0 SD). The average percent of protein in lean dry mass across all owls was 81 % (+/- 2.0 SD) and ranged from 76-86 %. The average stomach content mass of the 77 owls included in the analysis of body composition was 13.1 g (+/-13.6 SD) and ranged from 0.0-68.1g, while the average stomach content mass of all necropsied owls was 11.2 g (+/-12.5 SD, n = 1,327 stomachs). The average mass of shot pellets found in aliquots was 0.034 g (+/- 0.0083 SD), which on average constituted 0.33% of the measured wet mass.

All models explained a considerable amount of the variation in the percent lipid of barred owls with adjusted $R^2$ values ranging from 0.49 to 0.87 (Table 5). Under all parameter combinations (n=24 models total), models that included mass divided by foot-pad length explained the most variation in percent lipid, and mass divided by culmen explained the least (Table 5; Fig. 1). Including sex in the model almost always improved the amount of variation explained, and was further improved by separating females based on the season they were collected (Table 5). Models with fat scores explained more variation than models including only a sex effect (Table 5). The best model ($R^2 = 0.87$) included a BCI comprised of mass divided by foot-pad length with both fat score and sex-season (Table 5).

The percent lipid estimates for all necropsied owls with full data (n=1,043) differed only slightly between each model, with model estimate means for this population ranging from 23.5-25.8 % (ANOVA; F-statistic = 7.365, $p < 0.0001$). We excluded all models with culmen length, as they always explained less variation than a model that simply used mass. The post-hoc pairwise t-tests revealed that percent lipid estimates from BCI-only and BCI+fat score models differed statistically from the BCI+sex and BCI+sex-season models ($p < 0.05$ for each pairwise combination) for all but 2 combinations, but these results are likely not biologically meaningful given the small differences in means of model estimates.

Using field mass instead of carcass mass with our top model produced a slight bias (-0.0095, mean squared error = $1.8 \times 10^{-4}$) and statistical difference (t = -8.5806, $p < 0.001$) in model estimates of percent lipid. While this bias is small and likely negligible, subtracting the average stomach content mass of all necropsied owls, 11.17 g, from the field mass reduced bias (-0.0013, mean squared error = $9.49 \times 10^{-5}$) to the point that there was little difference (t = -1.2007, $p = 0.23$) between these model estimates and those using carcass mass.

## DISCUSSION

Our analysis and results demonstrated that a simple body condition index using mass or mass scaled with a basic morphometric measurement can provide accurate estimates of the percent lipid in barred owls. The adjusted $R^2$ values of the models we fit were comparable to, or better than, similar models fit for other bird species (see review by Labocha and Hayes, 2012). The efficacy of our models in estimating the percent lipid in barred owls was probably facilitated by the large sample of owls collected in a broad range of environmental conditions, which resulted in percent lipid of dry mass that ranged from 8-56%. By incorporating easily obtained field information such as the sex or the time of year a female was handled, we improved the accuracy of all models, regardless of the body condition index used. Furthermore, the fat score criteria we developed can substantially improve the accuracy of the BCIs in estimating percent lipid, especially when used in conjunction with sex or time of year (for females). Wing chord is a commonly recorded metric in ornithological studies, and routinely used to develop body condition indices (Labocha and Hayes, 2012), but our results suggest that foot-pad length is a better measurement for correcting mass by skeletal size in barred owls. Likewise, some models with mass-only effects explained more variation in precent lipid than mass divided by wing chord.

The upper limit of 56 percent lipid in dry mass was notably high relative to previous studies in birds, yet percent lipid in wet mass was 30% for this individual, which was more comparable to previous studies (Guglielmo 2018). Additionally, we selected our solvent for its safer handling properties, however it will dissolve structural lipids (e.g., cell membranes), whereas other common solvents only dissolve neutral lipids (e.g., stored fat; Anthony et al., 2000), resulting in slightly higher measures of lipids. Despite these minor methodological differences, we found relatively high measures of lipids in invasive barred owls compared to other birds of prey (Gorney and Yom-Tov, 1994, Massemin and Handrich, 1997, DeLong and Gessaman, 2001). Indeed, during necropsies we observed owls with substantial fat deposits, such that their abdominal cavities were filled with fat and a 2 cm thick layer of subcutaneous fat covered the breast and abdomen.

In general, female barred owls are larger than males (Mazur and James 2020), thus we see model coefficients for females were almost always negative compared to males, indicating that for an identical BCI value (especially mass-only) the estimated percent lipid will be higher in males than females. Similarly, coefficients for breeding season females were greater in magnitude (more negative) than the non-breeding season, indicative of a change in the proportion of protein to lipid between these seasons, as seen in other birds (e.g., Hohman, 1986). Fat scores explain more variation in percent lipid than just considering sex or sex-season, but there was considerable overlap in the percent lipid found across the fat score categories, as observed in other bird species (Krementz and Pendleton 1990, Scott et al. 1994), suggesting that these fat scores are better utilized in conjunction with the BCIs rather than as a standalone measure of body condition.

The data required to estimate percent lipid in barred owls with these models are easily and frequently collected on both live and dead birds, but there are limitations. These models estimate percent lipid in dry mass as a measure of body condition and should not be used to estimate the total fat mass in a whole barred owl. Mass divided by foot-pad length provided the best fitting models, but foot-pad length can be difficult to measure on live birds and impossible on museum study skins with closed feet. Mass divided by wing chord also provided reliable estimates of percent lipid, but wing chord cannot be used if the owl is molting or if the wing was flattened during measurement. Barred owl sex can often be determined through vocalizations (Odom and Mennill, 2010), but if sex is unknown then we recommend using mass divided by foot-pad length to estimate percent lipid if possible. If stomach content mass cannot be subtracted from field mass, then subtracting the average stomach mass of 11.2 g reduces the very slight bias of unmeasured stomach contents 7-fold. The exact impact of unaccounted for stomach contents varies depending on the model and individual, but for example, this correction factor (11.2 g) accounts for slightly less than a 1% difference in estimated lipids. Shot pellets constituted 0.33% of the homogenate wet mass, equating to about an extra 3 grams in our largest owls collected, less than the precision of our mass measurements (5 g). However, any study applying our models to barred owls not collected with a shotgun may wish to add .3 g per 100 g of owl or acknowledge this slight discrepancy.

Many studies of body condition only calculate a size-corrected mass BCI for within study comparison, preventing comparison of body condition across studies using different morphometrics. For instance, a female barred owl with a 335 mm wing chord, 67.1 mm foot-pad, and weighing 910 g would yield respective size-corrected mass BCIs of 2.72 and 13.6, affording no comparison. However, our BCI+sex models estimate the percent lipid as 31.8% and 32.1% respectively. Furthermore, the close agreement across all models in their averaged estimates of percent lipid (23.5-25.8%) for 1,043 owls gives us confidence that these models can facilitate comparison of barred owl body condition within and across studies using different morphometric data.

The ability to identify and map habitat quality for barred owls where they have become invasive may be a key component of effective management strategies for this species (Peery et al, 2018). The models we developed here could provide a valuable tool to understand how barred owls use forested landscapes of the Pacific Northwest and the implications of habitat use on their physical condition. Application of our models to estimate percent lipid in the large number of barred owls collected for the removal studies (Wiens et al., 2021, Hofstadter et al. 2022), as well as owls captured or collected during past and future research, could provide insight into the effect of landscape or forest structural features and population density on individual body condition. Understanding temporal and spatial patterns in barred owl energetics may inform the foraging ecology of this novel, generalist predator and how it interacts within the food web of the Pacific Northwest.

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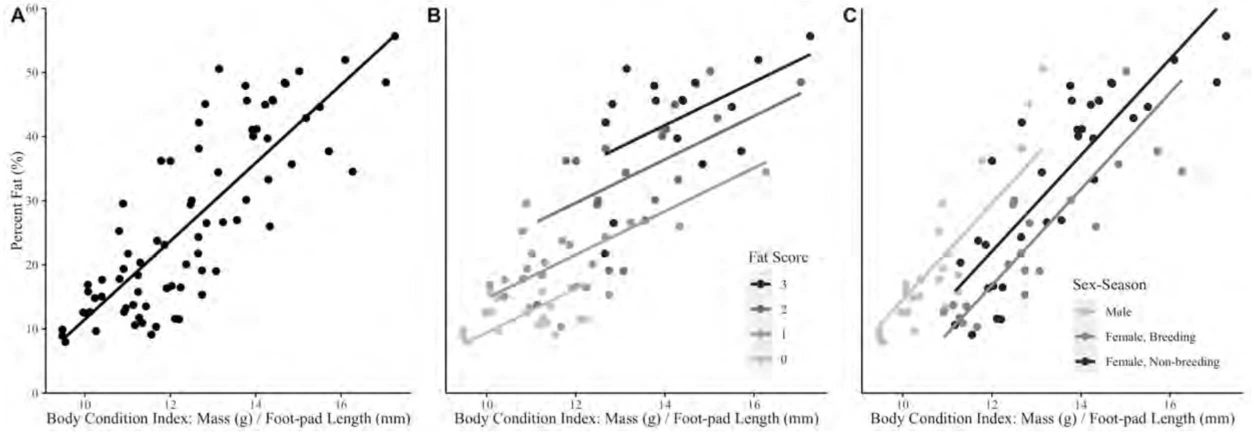

Figure 4.1. Predicted estimates of the percent lipid in the dry mass of barred owls as a function of the body condition index (BCI) calculated as the mass divided by foot-pad length from 3 linear regression models. Models shown include A) BCI only, B) BCI+fat score, and C) BCI+sex-season.

Table 4.1. Qualitative scoring criteria used to visually characterize the amount of subcutaneous fat on individual barred owls. The area between the 2 ventral feather tracts and the posterior and anterior edges of the rib cage is inspected and scored according to the following criteria. This region should be free of damage (e.g., from gunshot) that would obscure accurate scoring of the fat.

| Score | Definition |
|---|---|
| 0 | No fat visible under the skin, only muscle. |
| 1 | Some fat visible under the skin, but the breast is not entirely covered, and muscle can be seen. This could range from thin, faint deposits of fat flanking the sternum, to thick deposits of fat with one small patch of muscle still exposed. |
| 2 | Breast is completely covered with fat, and sternum can be felt through fat by gently placing a finger over the middle of the breast without pressing down. |
| 3 | Breast is completely covered with fat, and the sternum cannot be felt through fat by gently placing a finger over the middle of the breast without pressing down. |

Table 4.2. The number of barred owls analyzed for body composition within each group of fat score (0-3), sex (male and female), and time of year in relation to breeding cycle for females (BS: Jan-Jun, NBS: Jul-Dec).

| Fat Score | Males | Females BS | Females NBS |
|---|---|---|---|
| 0 | 10 | 4 | 4 |
| 1 | 10 | 5 | 9 |
| 2 | 2 | 7 | 10 |
| 3 | 2 | 5 | 9 |

Table 4.3. The mean+/-standard deviation and (minimum-maximum) values of all morphometrics used as a body condition index for male and female barred owl for which we directly measured lipid content. Mass was the total carcass mass of each owl after stomach contents were removed.

| Metric | Males (n = 24) | Females (n = 53) | Sexes combined (n = 77) |
|---|---|---|---|
| Mass (g) | 677+/-65 (575-830) | 877+/-109 (652-1170) | 815+/-134 (575-1170) |
| Wing (mm) | 315+/-7 (302-331) | 324+/-10 (304-347) | 321+/-10 (302-347) |
| Foot-pad (mm) | 62+/-2 (58.9-65.5) | 65+/-3 (57.7-69.3) | 64+/-3 (57.7-69.3) |
| Culmen (mm) | 24+/-1 (22.2-26.5) | 26+/-1 (22.8-29.6) | 26+/-2 (22.2-29.6) |

Table 4.4. Set of 24 models evaluated to estimate the percent lipid in barred owls. The body condition index (BCI) was a continuous variable that used either the mass of the owl or the mass divided by wing chord, foot-pad length, or exposed culmen. Fat score was a categorical variable with 4 levels characterizing the amount of subcutaneous fat on the breast. Sex was a categorical variable with 2 levels for males and females. Sex-season was a categorical variable with 3 levels for males, females collected between Jan.-Jun. and females collected between Jul.-Dec.

| **Model** |
|---|
| BCI |
| BCI+fat score |
| BCI+sex |
| BCI+sex-season |
| BCI+fat score+sex |
| BCI+fat score+sex-season |

Table 4.5. Adjusted $R^2$ values and parameter coefficients for all generalized linear models fit to estimate the percent lipid in barred owls. Parameters for each model are listed in left hand columns. For models with fat score and/or sex or sex-season, the intercept is for a fat score of 0 and males. For models with sex-season, Female, BS is for females collected during the breeding season (Jan.-Jun.) and Female, NBS is for females collected outside of the breeding season (Jul.-Dec.)

| Model Parameters | | | $R^2$ | Intercept | BCI | Fat Score | | | Sex | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Fat Score 0 Sex Male | | 1 | 2 | 3 | Female | Female, BS | Female, NBS |
| Mass/Foot | Fat Score | Sex-Season | 0.87 | -34.05 | 4.64 | 4.47 | 13.15 | 17.08 | | -11.37 | -5.35 |
| Mass | Fat Score | Sex-Season | 0.86 | -29.52 | 0.068 | 4.42 | 14.02 | 17.40 | | -13.47 | -7.09 |
| Mass/Wing | Fat Score | Sex-Season | 0.86 | -27.91 | 20.61 | 4.17 | 14.76 | 18.68 | | -11.99 | -5.27 |
| Mass/Culmen | Fat Score | Sex-Season | 0.83 | -20.09 | 1.28 | 5.27 | 17.98 | 22.38 | | -9.91 | -1.90 |
| Mass/Foot | Fat Score | Sex | 0.83 | -37.60 | 4.97 | 4.57 | 12.68 | 16.64 | -8.38 | | |
| Mass | Fat Score | Sex | 0.82 | -32.44 | 0.072 | 4.58 | 13.70 | 17.12 | -10.33 | | |
| Mass/Wing | Fat Score | Sex | 0.82 | -30.20 | 21.65 | 4.40 | 14.61 | 18.67 | -8.43 | | |
| Mass/Culmen | Fat Score | Sex | 0.77 | -19.73 | 1.25 | 5.92 | 18.39 | 23.24 | -5.07 | | |
| Mass/Foot | | Sex-Season | 0.76 | -60.53 | 7.50 | | | | | -12.73 | -7.45 |
| Mass | | Sex-Season | 0.74 | -54.44 | 0.11 | | | | | -16.05 | -10.27 |
| Mass/Wing | | Sex-Season | 0.70 | -52.74 | 34.48 | | | | | -13.15 | -6.80 |
| Mass/Culmen | | Sex-Season | 0.56 | -42.09 | 2.29 | | | | | -8.55 | 0.18 |
| Mass/Foot | | Sex | 0.74 | -62.79 | 7.72 | | | | -10.08 | | |
| Mass | | Sex | 0.72 | -56.50 | 0.12 | | | | -13.17 | | |
| Mass/Wing | | Sex | 0.67 | -54.68 | 35.40 | | | | -9.83 | | |
| Mass/Culmen | | Sex | 0.49 | -42.37 | 2.30 | | | | -3.34 | | |
| Mass/Foot | Fat Score | | 0.79 | -24.39 | 3.39 | 5.34 | 13.43 | 18.76 | | | |
| Mass | Fat Score | | 0.76 | -15.85 | 0.041 | 5.88 | 15.14 | 20.62 | | | |
| Mass/Wing | Fat Score | | 0.77 | -18.22 | 14.21 | 5.37 | 15.04 | 20.53 | | | |
| Mass/Culmen | Fat Score | | 0.76 | -14.46 | 0.97 | 6.16 | 17.66 | 23.27 | | | |
| Mass/Foot | | | 0.67 | -49.49 | 6.10 | | | | | | |
| Mass | | | 0.62 | -39.34 | 0.083 | | | | | | |
| Mass/Wing | | | 0.61 | -42.25 | 27.71 | | | | | | |
| Mass/Culmen | | | 0.49 | -38.68 | 2.10 | | | | | | |

# Chapter 5 - The Influence of Habitat Conditions and Conspecific Density on the Body Condition of Barred Owls in their Expanded Range

## Introduction

Characterizing a species' habitat requires identifying important resources necessary for successful reproduction and survival (i.e., fitness; Hall et al. 1997) and how those vital rates respond to variation in the quality of these resources across time and environmental gradients (Johnson 2007). Understanding variation in habitat quality for wildlife species is often critical for conservation and management. However, a species' population density can vary along a gradient of habitat quality, and the relationship between habitat and a species' vital rates may be difficult to understand if we do not account for increasing levels of intra-specific competition associated with increasing population density. Under the assumption of an ideal free distribution, high-quality habitat could attract and support large numbers of individuals, which in turn could reduce overall fitness through interference and resource competition, such that we measure little variation in habitat quality across a gradient that does indeed influence fitness (Fretwell and Lucas 1969). Alternatively, under an ideal despotic distribution a few highly competitive individuals could acquire and defend high-quality habitat, thereby forcing many less competitive individuals into low-quality habitat, which could be misleading if we consider population density an indicator of quality rather than the fitness of the individuals using the habitat (Van Horne 1983). Disentangling the effects of habitat and density on fitness of wildlife can be difficult, as experimental manipulation of population densities over environmental gradients is challenging. For species of conservation concern at low abundance, attention is often given to the negative effects of low rather than high density, such as difficulty in finding a mate (e.g., Lamberson et al. 1992) or inbreeding depression (Johnson et al. 2010). Yet, for other species that occur in high densities, such as invasives, it is worthwhile to understand how habitat quality varies over environmental gradients while accounting for the effects of density dependence. Such information can be used, for example, to focus management or control efforts most effectively on the landscape.

The conservation and management of northern spotted owls (*Strix occidentalis* caurina) has relied on an understanding of the relationship between population demographics and habitat quality. Demographic performance of this medium-sized, territorial, old-forest obligate owl is reduced when less old growth forest is available in their home range (Olson et al. 2004, Dugger et al. 2005). In the southern part of their range (southern Oregon and northern CA) they can benefit from a mosaic of old and young forests (Franklin et al. 2000), but old forest is critical for occupancy and survival of this species. Loss of old growth forest throughout the species' range due to timber harvest prompted listing of the northern spotted owl as threatened under the Endangered Species Act (USFWS 1990). This listing resulted in widespread protection of their habitat on federally managed lands through the Northwest Forest Plan (USDA USDI 1994) and some private lands through Habitat Conservation Plans (e.g., Simpson 1992, Plum Creek 2000). Despite the protection of old forest across their range, populations continued to decline in response to increased densities of a closely related, non-native competitor, the barred owl (*Strix varia*; Forsman 2011, USFWS 2011).

Barred owls are another medium-sized, territorial forest owl historically restricted to eastern North America, but their range has expanded westward across the continent likely following landscape changes from European-American colonization that facilitated dispersal across the Great Plains (Livezey 2009a, b). Barred owls arrived on the west coast of North America in the latter half of the 20th century and began to spread southward into the range of the northern spotted owl (Livezey 2009a, Long and Wolfe 2019). The presence of barred owls has been directly linked to declines in northern spotted owl vital rates and increased rates of population decline (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016, Franklin et al. 2021, Wiens et al. 2021). Barred owls are habitat generalists and will use a wide range of forest types, although some associations with older forests with bigger trees and lowland riparian stands have been reported (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014, Yackulic et al. 2014, Irwin et al. 2018, Jenkins et al. 2019). Barred owl survival in the Oregon Coast Range increased with increased amounts of old forests in barred owl territories (Wiens et al 2014). While barred owls use a variety of forest types, they do not appear to partition habitat such that competition with northern spotted owls is reduced, as barred owls successfully survive and reproduce in the old forest habitats critical to spotted owl survival and reproduction (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014, Yackulic et al. 2014, Irwin et al. 2018). Competition for habitat between these owls is exacerbated by barred owls maintaining home ranges that are 2-8 times smaller and overlap with home ranges of spotted owls (Singleton et al. 2010, Wiens et al. 2014). When barred owls are present spotted owls abandon their territories at higher rates, and fail to recolonize territories uninhabited by other spotted owls (e.g., Dugger et al. 2011, Yackulic et al. 2014, Mangan et al. 2019)

To determine if the increasing threat of barred owls to spotted owls could be reduced, barred owl removal experiments were first initiated on private timberlands in California (Diller et al. 2014) then later expanded to multiple sites across the range of the northern spotted owl (USWFS 2013). These studies were designed to establish a causative link between barred owl population growth and northern spotted owl population decline, and to assess whether lethal removal of barred owls could be used as a management strategy to achieve northern spotted owl recovery (USFWS 2011). Spotted owl populations stabilized (i.e., stopped declining) in areas where barred owls were lethally removed (Wiens et al. 2021), and even showed signs of growth at the leading edge of the barred owl expansion from north to south, where barred owl density was relatively low (Diller et al. 2016, Dugger et al. 2016). If wide-spread management of barred owls is implemented to recover spotted owls, understanding how barred owl habitat quality varies within Pacific Northwest forests could help guide this management effort. By removing and collecting barred owls across a range of forest types and conditions, the removal experiment offered a framework to assess variation in habitat quality and potential density dependent effects as barred owl populations expand.

Over the course of the removal experiments, far more barred owls were removed at some sites compared to others, owing to higher initial densities and more frequent recolonization by barred owls after removals, suggesting these seemingly preferred sites might offer higher quality habitats (Wiens et al. 2018, 2019, 2020). However, if barred owls reach high densities at these sites, their fitness may be reduced through intra-specific competition. Such competition can be mediated through resources if the local prey base is depleted, or through direct interactions associated with territory establishment and defense. Alternatively, the effects may be indirect if time and energy are diverted towards territorial defense that could otherwise be allocated to activities promoting fitness, such as foraging or nest attendance. Individual body condition (i.e., the amount of stored energy) can index habitat quality and the level of intra-specific competition experienced by individuals, as resource exploitation or con-specific interactions can affect the ratio of caloric intake to expenditure (Marra et al. 2015). In turn, individual condition can also correlate with fitness where individuals in poor condition may starve or make riskier foraging decisions, and every stage of avian reproduction can benefit from more stored energy (Martin 1987).

Here I evaluated the effect of habitat and site-level population density on the body condition of barred owls collected at 3 experimental removal study areas in Washington and Oregon during 2015-2019 (Wiens et al. 2021). Using previously developed models based on a subset of owls collected (Chapter 4) I estimated the percent of fat in the broader sample of the barred owls collected and then characterized intrinsic and extrinsic factors that contributed to variation in fat content among individuals. Repeated removals within and among years from the same sites within the three different study areas altered density over time and across environmental gradients. This study design allowed estimation of how habitat quality and population density may independently affect barred owl body condition. If habitat quality varies over the environmental gradients assessed, then barred owls collected from higher quality habitats should be in better body condition. In addition, if negative density dependence occurs within a population, then owls collected from sites with higher density should be in poorer body condition. The 3 study areas where barred owls were collected represent different ecoregions in the Pacific Northwest, over which barred owl body condition may also vary. I also characterized how condition varied between sex and age classes, as well as within and among years as the removal experiment progressed to provide insight into the basic foraging ecology of barred owls and account for intrinsic factors that influence body condition. Understanding how habitat quality varies for barred owls within the range of the spotted owl can have widespread management implications as resource managers attempt to save the northern spotted owl from extinction.

## Methods

Barred owl removals took place near Cle Elum, WA (CLE) and Alsea, OR (COA) between 2015-2019, and near Roseburg, OR (KLA) between 2016-2019. Study areas and barred owl survey, removal, and collection protocols are described in detail elsewhere (Wiens et al. 2016, 2017). Each experimental study area was divided into a gird of 500-ha hexagons (i.e., corresponding to the average size of a barred owl home range; Wiens et al. 2011, 2014) within which barred owl surveys and removals were conducted. I selected habitat parameters to associate with body condition based on past findings of barred owl habitat studies that suggested they used older forests and lowland valley bottoms with riparian forests more often than expected by chance (Singleton et al. 2010, Hamer et al. 2012, Wiens et al. 2014, Irwin et al. 2018). These parameters were summarized within each hexagon by calculating 1) the percent of a hexagon comprised of forests older than 80 years, 2) the mean elevation of a hexagon, and 3) the mean topographic position index (TPI) within a hexagon, which classified terrain into slope position (i.e., ridge, upper slope, flat and mid-slope, lower slope, and valley) with large positive values at ridge tops and large negative values at valley bottoms (Weiss 2001; Table 5.1).

Barred owls were surveyed using a multi-season occupancy framework where surveys took place between Mar-Aug of each year. The annual survey period was divided into 3, 2-month periods, wherein each hexagon was repeatedly surveyed for barred owls. Individual surveys consisted of visiting multiple locations within a hexagon in a single evening and broadcasting electronic, conspecific playback calls. Territorial barred owls were likely to respond either vocally or by flying into the broadcast location where they were visually detected (Wiens et al. 2011). While surveys were conducted in hexagons using an occupancy framework (detection/non-detection within a hexagon), surveyors also recorded the numbers of barred owls detected within a hexagon throughout the evening of a survey. The maximum number of owls detected during one of the three surveys within a year (hereafter “owls detected”) served as an approximation for local density (Table 5.1).

Removal of barred owls took place between September and mid-April during the first year in COA and all years in CLE, whereas after the first year in COA and for all years in KLA barred owls were removed year-round with the stipulation that any barred owls removed between mid-April and September could not have dependent young at the time of collection (Wiens et al. 2016, 2017). Removal efforts were guided by prior surveys, where electronic playback calls were broadcast at sites where barred owls had been previously detected in hexagons. When barred owls were lured into collection range they were located and lethally removed with a shotgun. In some cases, owls were located but could not be removed, so a follow-up attempt at removal would typically be made within a few days. Once all owls were removed from a hexagon, regular surveys were conducted and any recolonizing barred owls were removed if detected. The removals offered an alternative index of density with better temporal resolution than owls detected from the occupancy surveys. For every owl collected I tallied the number of other owls collected from the same hexagon within the 30 days before and after the focal owl’s collection (hereafter “owls removed”; Table 5.1). While owls detected offered a good estimate of the number of owls using a hexagon at a single time during the year, owls removed offered a more dynamic estimate of barred owls living proximate to each other in space and time. For logistical or detection reasons, not every owl present in a hexagon could be removed within a single evening, so this 30-day time window reflected the hexagon density given an asynchronous removal process.

At the time of collection, sex was determined through vocalizations, and age class [first-year subadult (S1), second-year subadults (S2), and adults (A)] was determined by identifying the loss of juvenile feathers as birds aged. Morphometric measurements were also taken on each carcass. For about half the owls collected, I performed laboratory dissections where I verified sex based on gonads, and I assigned a fat score (0-3) to most carcasses (Chapter 4). I estimated the percent fat in dry mass (hereafter "percent fat") of owls collected using one of two regression models (Chapter 4). Both models included coefficients for a body condition index (mass/foot-pad length) and for sex, with females further subdivided between breeding and non-breeding seasons (Chapter 4). One model also included an additional coefficient for owls with fat scores (Chapter 4). I was able to estimate the percent fat of 480 owls from CLE, 1,047 from COA, and 609 from KLA, which was 94%, 96%, and 98% of the owls collected in each area, respectively.

### Analysis

To understand the effects of habitat quality and conspecific density on barred owl body condition, I fit a variety of linear mixed-effects models using maximum-likelihood estimation with the estimated percent fat as the response variable and collection site (hexagon) as a random effect. I generated *a priori* model sets and compared models following an information-theoretic approach using Akaike's Information Criterion corrected for small sample size to evaluate models ($AIC_2$; Burnham and Anderson 2002). I conducted all analyses using Program R (R Core Team 2022). I used the *lme4* package to fit models with the *lmer* function (Bates et al. 2015), and the MuMIn package for model comparison (Bartoń 2020).

I first constructed a model set to account for intrinsic, life history factors of each owl including when and where it was collected, age class, sex, year, and study area as categorical variables, and day of year as a continuous variable. This initial model set included every combination of these parameters as additive effects. To evaluate the most parsimonious models and keep models sets as small as possible, I did not consider interactions between parameters. I observed a circannual cyclical pattern in the percent of fat, where owls collected around the beginning/end of the calendar year appeared to be in the best condition and those collected in the middle of the year were in the worst condition. While the reproductive cycle may seem like the obvious life history stages to subdivide this effect over (i.e., a binary breeding/non-breeding effect), several other biological and ecological mechanisms (e.g., prey availability, length of night, molting) may produce this pattern. Thus, I performed a circular transformation on the day of year, first dividing the ordinal date by 365 and multiplying that by $2\pi$, then taking the cosine of this value. Estimated coefficients for the day of year modified the amplitude of the cosine wave to match the magnitude of difference in percent fat in a cyclical trend across each year. The top model from this initial set of 32 models served as the base model to which I added the effects of habitat and conspecific density ("Build-up" approach to model set development; Morin et al. 2020).

To assess the effect of habitat and conspecific density on the body condition of barred owls, I modeled all combinations of these parameters (Table 5.1) as additive effects. TPI and elevation were not included in the same models (despite low correlation, <0.1), as I believed both these covariates represented the potential importance of lowland riparian habitat. Correlation between all habitat and density parameters did not exceed 0.5. In addition to linear effects of old forest, I also included models with quadratic effect of old forest to determine if there is an intermediate proportion of this parameter that supported better body condition in barred owls. For all habitat and density parameters, I ran a model set with owls from all study areas combined and no interaction terms (maintaining parsimonious models and small model sets), to assess for general trends across ecoregions. I then ran independent model sets for each study area to assess underlying differences in habitat and density between study areas that could produce differential effects in barred owl body condition.

If the parameters outlined above index habitat quality for barred owls (Table 5.1) and habitat quality is related to barred owl body condition, then I expect strong support for models containing these parameters. I considered models competitive, with strong support if $\Delta AIC_c \leq 2$, and strong support for covariates in these competitive models if 95% confidence intervals for model coefficients did not overlap zero. I predicted that barred owls would have better body condition (i.e., higher estimates of percent fat) when collected from hexagons with high-quality habitat. If negative density dependence is taking place within a barred owl population, then I expected that either or both density parameters (Table 5.1) would be included in competitive models with negative coefficients estimated precisely (i.e., non-zero; with 95% confidence intervals that do not overlap 0), such that as density increases, percent fat decreases. If a negative effect of owls detected is supported, this may indicate resource competition where a high number of barred owls living in a hexagon at one time in the year has depleted the prey base such that even when barred owl density is reduced at another time in the year, resident owls are still in poor condition. If a negative effect of owls removed is supported, this may indicate interference competition, such that when the number of owls living proximate to each other in both space and time is reduced they can achieve better body condition. Alternatively, we may see positive coefficients supported for the density parameters, which would strongly suggest that negative density dependence was not occurring in the population during the study through the hypothesized mechanisms (resource or interference competition). Alternatively, the density parameter may be an index of habitat quality over some gradient not accounted for by the habitat covariates I have developed.

Table 5.1. Parameter mean, standard deviations (in parentheses), and minimum-maximum values for barred owl survey and removal hexagons near Cle Elem, WA (CLE), Alsea, OR (COA), and Roseburg, OR (KLA).

| Parameter[a] | CLE | COA | KLA |
|---|---|---|---|
| Number Removed | 1.1 (1.2) 0-5 | 1.5 (1.5) 0-8 | 1.2 (1.4) 0-8 |
| Number Detected | 1.9 (1.2) 0-7 | 2.7 (1.6) 0-10 | 2.1 (1.4) 0-5 |
| Elevation (1000 m) | 1.2 (0.19) 0.73-1.6 | 0.32 (0.095) 0.16-0.84 | 0.56 (0.12) 0.34-1 |
| Topographic Position Index | 1.7 (46) -110-130 | 11 (37) -110-160 | 3.2 (39) -100-97 |
| % Old Growth | 36 (17) 2-71 | 21 (13) 0-45 | 20 (15) 1-70 |

[a] Key to Parameters: Number Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl was collected; Number Detected = maximum number of barred owls detected during repeated surveys each year; Elevation = mean elevation of a survey hexagon; Topographic Position Index = mean topographic position index of a survey hexagon; % Old Growth = the percentage of a survey hexagon comprised of forest older than 80 years.

## Results

I observed the most support (60% of $AIC_c$ weights;

Table 5.2) for a base model that included the additive effects of age, area, date, and sex, and all model coefficients were strongly supported with 95% confidence limits that did not overlap zero (Table 3). The second most-supported model was competitive ($AIC_c$ weight = 0.40; $\Delta AIC_c$ of 0.85; Table 2) and also included age, area, date and sex, but it also included the additive effect of year; however, model coefficients for each year had 95% confidence limits that overlapped 0, suggesting year effects were not well supported (estimated difference in percent fat from year to year was < 1%; Appendix Table 2). No other models carried any model weight (Appendix Table 1). The intercept from the top model (Table 3) represented the average percent fat for an adult female on CLE, collected 91 days before or after the new year. Relative to this baseline, males had lower average percent fat than females and S1 and S2 subadults had lower percent fat than adults, (Table 3). Owls from COA and KLA had higher mean percent fat than owls from CLE, although the mean difference was only ~2.5% (Table 3). Time of year had the largest effect on percent fat in owls, with the highest fat content observed for owls collected at the beginning/end of the calendar year (Table 3) relative to the middle of the year when percent fat was the lowest (Table 3, Fig. 1). Owls in the best body condition in the middle of the year were roughly equivalent in percent fat to owls in the worst condition at the beginning of the year (Figure 5.1). I carried all the covariates supported by the top model forward to evaluate the association between barred owl density and habitat quality on the percent fat of barred owls.

For analyses conducted on each study area separately, the maximum number of owls detected in a hexagon during a year was included in the top model (Table 2) and had a positive effect on percent fat for CLE and KLA, but owls detected was not in the top model for COA (Table 2) and when included in well-supported models it was not non-zero. The highest effect of owls detected on percent fat was ~5.5 and 3.5 in CLE and KLA, respectively, within hexagons where the most barred owls were detected. The top model when owls from all areas were combined also included owls detected (Tables 2), but the effect was negative and not strongly supported as 95% confidence limits widely overlapped zero (Table 2). The number of owls detected occurred in 2 out of 3 competitive models for CLE and all 6 competitive models for KLA (Table 2). The number of owls removed was included in all competitive models for COA (Table 2) and the negative association with percent fat was strongly supported with a precise model coefficient (Table 3). Owls removed from hexagons where 8 other owls were removed (highest value for this parameter; Table 1) were estimated to have a nearly 3% reduction in percent fat (Fig. 2). Owls removed was also in the top model for owls from all study areas combined and also included the negative effect of owls removed, but this effect was only weakly supported as model coefficients were imprecise (Tables 3).

When modeling effects of habitat within study areas, TPI was included in 2 of 3 competitive models in CLE and 2 of 6 competitive models in KLA (Table 2) but in all cases 95% confidence limits on the model coefficient for TPI widely overlapped zero (Appendix Tables 6, 10), and TPI was not included in any of the competitive models for COA (Table 2). The estimated difference in percent fat across the ranges of values was about 2.5, and owls were in the best condition at the lowest TPI values (Table 3). Conversely, the quadratic effect of old forest was in the top model in COA, as well as the competitive models (Table 2), and always estimated as non-zero (Tables S4, S8). Estimated percent fat was lowest at intermediate levels of old forest and highest at the lowest and highest proportion of old forest within a hexagon. However, the quadratic effect of old forest was not included in any of the competitive models for CLE or KLA (Table 2). A linear effect of old forest was included in the fourth ranked model from KLA, but the model coefficient was imprecise suggesting this effect was not important. An effect of elevation was not supported, only occurring in competitive models when owls from all areas were combined, or at CLE, but with imprecise model coefficients (Table 2). The top model with owls from all areas included mean topographic position index (TPI) and a quadratic effect of old forest (Table 3) in all competitive models (Table 2). As in COA, the estimated percent fat was higher for lower values of TPI, and at the highest and lowest values of old forest, with lower estimates of percent for owls collected from hexagons with intermediate values of old forest. The 95% confidence intervals for habitat coefficients included in the top model did not overlap 0.

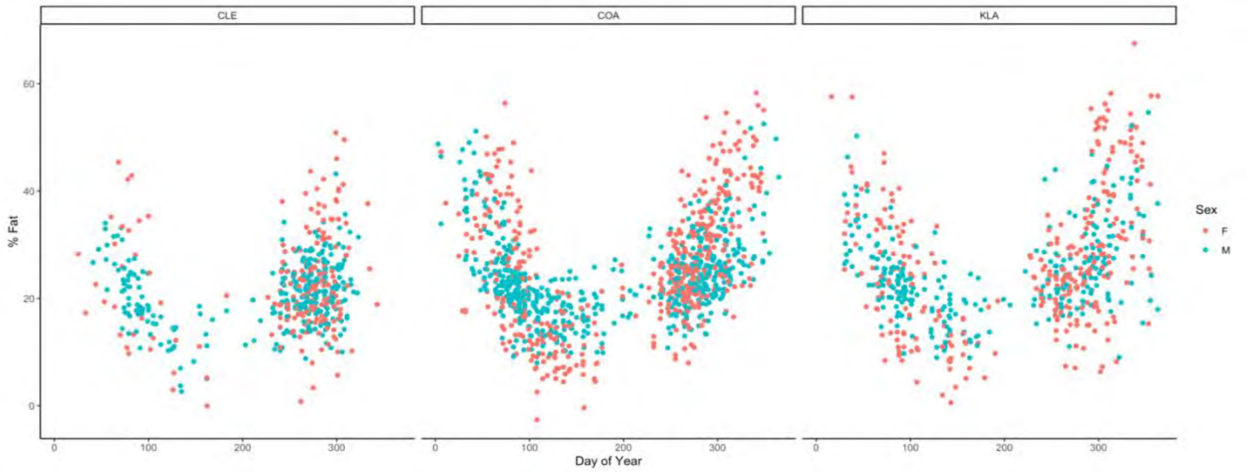

Figure 5.1. Percent fat estimates for barred owls collected near Cle Elum, WA (CLE), Alsea, OR (COA), Roseburg, OR (KLA) between 2015-2019 from models using a body condition index of mass/foot-pad length, sex and time of year females were collected, and a fat score (0-3) if the owl received one. Colors represent females (F) and males (M).

Table 5.2. Model selection results including model -2*log likelihood (-2log*L*) number of parameters (*K*), the difference between model AICc and AICc from the top model ($\Delta\mathrm{AIC}_c$), and $\mathrm{AIC}_c$ weights ($\mathrm{AIC}_c$ wt) for competitive ($\Delta\mathrm{AIC}_c \leq 2$) generalized linear mixed-effects models relating habitat and population density parameters to the percent fat of barred owls collected near Cle Elum, WA (CLE), Alsea, OR (COA), Roseburg, OR (KLA) between 2015-2019. Each model also included fixed effect additive terms for study area, sex, age, and date, and a random effect for survey hexagon where an owl was removed. Separate analyses were conducted on owls from each individual study area, and all areas combined (Total; with an individual study area parameter).

| **Model**[a] | ***K*** | **-2log*L*** | **$\Delta\mathrm{AIC}_c$**[b] | **$\mathrm{AIC}_c$ wt** |
|---|---|---|---|---|
| Total | | | | |
| Detected + Removed + TPI + % Old + % Old^2 | 14 | 14549.56 | 0 | 0.15 |
| Removed + TPI + % Old + % Old^2 | 13 | 14551.86 | 0.28 | 0.13 |
| TPI + % Old + % Old^2 | 12 | 14554.56 | 0.94 | 0.09 |
| Detected + TPI + % Old + % Old^2 | 13 | 14553 | 1.42 | 0.07 |
| CLE | | | | |
| Detected + TPI | 9 | 3151.5 | 0 | 0.2 |
| Detected | 8 | 3154.54 | 0.96 | 0.13 |
| Detected + Removed + TPI | 10 | 3150.46 | 1.05 | 0.12 |
| COA | | | | |
| Removed + % Old + % Old^2 | 10 | 7052.8 | 0 | 0.22 |
| Detected + Removed + % Old + % Old^2 | 11 | 7050.8 | 0.03 | 0.21 |
| Removed + Elevation + % Old + % Old^2 | 11 | 7052.26 | 1.51 | 0.1 |
| Detected + Removed + Elevation + % Old + % Old^2 | 12 | 7050.32 | 1.6 | 0.1 |
| KLA | | | | |
| Detected | 8 | 4261.92 | 0 | 0.18 |
| Detected + TPI | 9 | 4260 | 0.14 | 0.17 |
| Detected + Removed | 9 | 4261.6 | 1.73 | 0.08 |
| Detected + % Old | 9 | 4261.74 | 1.88 | 0.07 |
| Detected + Elevation | 9 | 4261.76 | 1.9 | 0.07 |
| Detected + Removed + TPI | 10 | 4259.72 | 1.92 | 0.07 |

[a] Number Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; Number Detected = maximum number of barred owls detected during one of three surveys each year; Elevation = mean elevation of a survey hexagon; Topographic Position Index = mean topographic position index of a survey hexagon; % Old Growth = the percentage of a survey hexagon comprised of forest older than XXX years.

[b] $\mathrm{AIC}_c$ score for each top ranked model: Total = 14577.76; CLE = 3169.87; COA = 7073.01; KLA = 4278.16

Table 3. Estimates of model coefficients ($\hat{\beta}$), standard errors (SE), and 95% lower (LCL) and upper (UCL) confidence intervals for top linear mixed-effects models estimating the percent fat in barred owls collected near Cle Elum, WA (CLE), Alsea, OR (COA), and Roseburg, OR (KLA) between 2015-2019. Base and Total models included all owls collected from all study areas, while CLE, COA, and KLA include only those owls collected from the specific study areas.

| **Parameter** [a] | **Base Model** | | | | **Total** | | | | **CLE** | | | | **COA** | | | | **KLA** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 25.5 | -0.4 | 24.6 | 26.3 | 26.4 | -0.68 | 25.1 | 27.8 | 23.8 | -0.9 | 22 | 25.6 | 29.9 | -0.73 | 28.4 | 31.3 | 27 | -0.8 | 25.2 | 28.3 |
| Age:S2 | -2.6 | -0.4 | -3.3 | -1.9 | -2.6 | -0.35 | -3.3 | -1.9 | -2.6 | -0.67 | -4 | -1.3 | -1.6 | -0.48 | -2.5 | -0.64 | -4 | 0.74 | -5.4 | -2.5 |
| Age:S1 | -8.4 | -0.5 | -9.3 | -7.5 | -8.2 | -0.48 | -9.1 | -7.3 | -6.8 | -0.93 | -8.7 | -5 | -7.6 | -0.66 | -8.9 | -6.3 | -9.2 | -1 | -11 | -7.3 |
| Sex:Male | -2.3 | -0.3 | -2.9 | -1.7 | -2.2 | -0.32 | -2.9 | -1.6 | -2.1 | -0.6 | -3.3 | -0.93 | -2.5 | -0.44 | -3.4 | -1.7 | -1.6 | -0.7 | -2.9 | -0.3 |
| Date | 11.2 | -0.3 | 10.5 | 11.8 | 11 | -0.34 | 10.3 | 11.7 | 7.8 | -0.77 | 6.3 | 9.3 | 11.6 | -0.46 | 10.7 | 12.5 | 12 | -0.6 | 10.5 | 13 |
| Area:COA | 2.4 | -0.4 | 1.6 | 3.2 | 2.3 | -0.46 | 1.4 | 3.2 | | | | | | | | | | | | |
| Area:KLA | 2.5 | -0.5 | 1.6 | 3.4 | 2.4 | -0.49 | 1.4 | 3.3 | | | | | | | | | | | | |
| Detected | | | | | 0.17 | -0.11 | -0.05 | 0.39 | 0.78 | -0.26 | 0.26 | 1.3 | | | | | 0.7 | -0.2 | 0.23 | 1.2 |
| Removed | | | | | -0.21 | -0.12 | -0.44 | 0.012 | | | | | -0.37 | -0.15 | -0.66 | -0.084 | | | | |
| TPI | | | | | -0.008 | -0.004 | -0.016 | -0.0005 | -0.01 | -0.008 | -0.03 | 0.002 | | | | | | | | |
| % Old | | | | | -0.082 | -0.032 | -0.15 | -0.019 | | | | | -0.22 | -0.068 | -0.35 | -0.083 | | | | |
| % Old^2 | | | | | 0.0012 | -0.0005 | 0.0002 | 0.0022 | | | | | 0.004 | -0.002 | 0.001 | 0.007 | | | | |

[a] Key to Parameters: Intercept includes the effect of females, adults, and CLE. Age = categorical parameter with 3 levels, adults, first-year subadults (S1), and second-year subadults (S2); Area = categorical parameter with 3 levels for each study area; Sex = categorical parameter with 3 levels for Females and Males; Date = cosine transformed circular date; Detected = maximum number of barred owls detected during one of three surveys each year; Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; TPI = mean topographic position index of a survey hexagon; % Old = the percentage of a survey hexagon comprised of forest older than 80 years; % Old^2 = quadratic effect of % Old.

## Discussion

My study is the first to evaluate temporal and spatial variation in body condition of an invasive species that has experienced rapid population growth in its expanded range. I found that age, sex, and timing within the annual cycle were important predictors of body condition, with impacts of habitat and population density more variable by study area. I found that on average, females carried slightly more body fat than males, and that adults were always in better condition than the younger age classes. I observed negative effects of density dependence on the body condition of barred owls in COA, but not in CLE or KLA. In addition, barred owl body condition was only weakly associated with habitat parameters previously associated with individual habitat use and increased fitness (Table 2). Circannual variation in percent fat of collected barred owls was strong, and birds were in the best condition on all study areas at the beginning and end of the calendar year.

The differences I observed in the effect of density dependence on barred owl body condition between study areas are likely attributable to differences in each area's underlying population density of barred owls. Through 2018, prior to the initiation of removals, barred owl occupancy in COA was likely at equilibrium with nearly every spotted owl territory occupied by barred owls (Franklin et al. 2021). Thus, the COA population appeared to be at levels where negative density dependent feedback was occurring. In contrast, the population in KLA was still increasing, as hexagon occupancy was <0.75 (Wiens et al. 2020, Franklin et al. 2021). Despite being the northern most site and likely colonized first by barred owls as they expanded their range southward, CLE had the lowest, most stable occupancy rate (<0.50) prior to removals (Franklin et al. 2021), likely related to the generally poor quality habitat at this northern study site (Yackulic et al. 2019). Estimated mean percent fat for owls from CLE was 2.5% lower than

COA and KLA, which were similar. This estimated difference in body condition in CLE incorporated differences in the timing of collections which did not occur at CLE during the late-breeding season, when percent fat appeared to be at its lowest point during the year in the other study areas (Fig. 1).

While I observed strong support for TPI when collected owls were combined across all study areas, the effect was poorly supported for owls within individual study areas (Table 2). The effect of TPI was always negative, such that barred owls collected in lowland riparian areas achieved better body condition than those collected in more upland habitats (Table 3), which was consistent with previous findings describing barred owl habitat use (Singleton et al. 2010; Wiens et al. 2014). In addition to TPI, the quadratic effect of habitat was supported in COA and also when all areas were modeled jointly (Table 2). However, the shape of this quadratic effect indicated that barred owls achieve better body condition at high and low proportions of old forest, but have poor body condition at intermediate levels. This is contrary to my predictions and previous research that has linked increased amounts of old forest with increased fitness for barred owls (Wiens et al. 2014, Rossman et al. 2016), so my results could be spurious or there is another mechanism generating this pattern that I did not identify. Elevation was also poorly supported with little evidence of an effect on barred owl body condition (Table 2).

The weak or contrary-to-predicted relationships I observed between barred owl body condition and habitat parameters may reflect their generalist habitat preferences and their ability to survive and reproduce in a variety of forest types. However, in CLE and KLA I found that barred owl body condition was better in hexagons where more owls had been detected and habitat parameters were supported in the top models on these areas (Table 2), suggesting there is some aspect of the habitat in these hexagons that the owls perceive and benefit from that I did not quantify.

Across age classes, study areas, and throughout the annual cycle, mean percent fat was slightly higher for females (ca. 2%) compared to males, which could be related to the energetic demands of reproduction. Females would need extra fat (and protein) to produce eggs, and additional stored energy would allow more time for nest attendance with fewer off incubation breaks that can reduce nest success in owls (Hirons 1985). Males in contrast, may benefit from lower fat stores and subsequent reduced wing loading to minimize energy expenditure while provisioning the nest (Witter and Cuthill 1993). Disparities in condition between age classes was substantial, especially between adults and first-year subadults (8.4% in base model; Table 3). These differences are likely related to multiple factors including barred owl biology and the design of the removal experiment. Long-term territorial adult owls may simply be more experienced, with more knowledge of where to find prey within their established territories and more capable of capturing that prey. In addition, the condition of long-term resident adults may be more closely linked to the habitat and density of the hexagons where they were collected since they would have been living under the influence of these factors for much longer than collected subadults. Also, first year subadults undergo natal dispersal, where they leave the territory on which they hatched to establish their own territory. Dispersal itself may be a large energy expenditure, and if an owl was removed shortly after this event their condition may be less a reflection of the habitat and density they were collected, and more a function of the dispersal process or the quality of their natal territory (Mikkelsen et al. *in press*). However, given the dynamic nature of body condition throughout the year, it may not take long for the condition of owls to respond to habitat quality and population density in the post-dispersal hexagons where they were collected.

My results support the strong effect of collection day during the year, with an estimated difference in percent fat of 22% between the high at the beginning/end of the calendar year and a low in the middle of the year (Fig 1, Table 3). This large difference in barred owl body condition was consistent for COA, KLA, and all areas combined (Table 3), but with a slightly lower difference on CLE (15%; Table 3), for which I had no samples between mid-April to September, which is when condition was at its lowest in the other areas. This circannual variation in condition could be a result of prey availability, yet the trend is consistent across study areas with very different diet compositions (Chapter 2) and biomass contributions (Chapter 3) between the study areas. Alternatively, as nocturnal predators barred owls would have more time to forage around the winter solstice when nights are the longest, than near the summer solstice when nights are shortest, possibly limiting the amount of food they can capture during a foraging period. Alternative, to an owl's caloric intake, their energy expenditure throughout the year may explain this trend. Collected owls were molting flight feathers from April to October (J.D. Wiens pers. Comm.), and this energetically demanding process corresponded with the lowest condition throughout the year. Finally, I cannot discount the energetic demands of reproductive cycle as an explanation of this strong annual trend in barred owl body condition. In the months leading up the breeding season, owls may store fat in preparation for the heightened energetic demands of reproduction, then as eggs are produced and the brood requires provisioning, energy stores are depleted until the young disperse and energy stores are replenished.

The differential effect of density on owl condition between study areas may suggest that once owls achieve high densities on the landscape, negative density dependence may start to regulate their populations. However, in many areas barred owl populations are still increasing (Franklin et al. 2021) and it may be some time before barred owl condition is negatively influenced by their own population density, as seen in COA. If barred owls do begin to achieve population densities across their range such that both interference competition and resource competition occurs, then we should be very concerned about the prey populations that would mediate this intra-specific competition (Chapter 1). If the effects of intraspecific competition outweigh those of interspecific competition, then in theory, two competing species can potentially coexist (Barabas et al. 2018, Ellner et al. 2019). Given that I found no evidence of negative density dependence between barred owls in 2 of the 3 study areas, and spotted owl populations have already been dramatically reduced through interspecific competition, it seems unlikely that intraspecific competition between barred owls would allow spotted owls to coexistence with barred owls. However, if lethal management of barred owls is implemented before populations reach equilibrium density levels, those removals would not increase the condition and fitness for remaining barred owls. Yet, if management is deferred until barred owl densities reach levels high enough to produce negative effects, removals in one area that result in reduced density in a neighboring area that is not managed, may benefit those owls left on the landscape by reducing intra-specific competition.

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# Chapter 6 - Conclusions

Barred owls impact the food web of the Pacific Northwest very differently than the native northern spotted owl. The broad, generalized diet of the barred owl places a variety of prey species at risk from a new predator as barred owls replace the northern spotted owl. Additionally, with the higher energetic requirements of barred owls (i.e., larger body size and larger broods; Wiens et al. 2014,Gutierrez et al. 2020, Mazur and James 2020) and their smaller territories (Singleton et al. 2010, Wiens et al. 2014) allowing for higher densities than spotted owls (Singleton et al. 2010, Wiens et al. 2014), shared prey with spotted owls (e.g., flying squirrels, wood rats, and tree voles) may now be removed at higher frequencies across the landscape despite making up a smaller percentage of the barred owl diet (Chapter 2). The risks posed to prey by either having a novel predator or increased rates of predation suggest that barred owls do not serve as an ecological equivalent for the northern spotted owl they are replacing.

More than half of the dietary biomass consumed by barred owls essentially goes unused by northern spotted owls (Chapter 3), and this broader diet may facilitate the barred owl's more general use of forested habitats, and subsequently allow them to achieve higher densities than spotted owls. Despite being larger birds, the disparities in the diet come primarily from barred owls foraging on much smaller prey items than northern spotted owls (Chapter 3), and the variation in barred owl diets across their expanded range likely explains differences in their expansion dynamics and equilibrium densities.

Barred owl occurrence in the Cle Elum, WA (CLE) study area prior to removals seemed stable at a much lower level than was estimated throughout the rest of the northern spotted owl range (Franklin et al. 2021). While barred owl body condition appeared comparable in the Oregon study sites, the percent fat of barred owls collected in CLE was estimated to be 2.5%

lower (Chapter 5). The diet in CLE contained the highest proportion of mammals and was most similar to spotted owl diets (Chapters 2, 3). These larger mammals certainly carry more nutrition per individual than arthropods or salamanders, but they may be much harder to come by on the landscape, since owls in CLE were more likely to be collected with empty stomachs (Chapter 3) and in poorer body condition (Chapter 5). In contrast, salamanders (and primarily small salamanders) comprised ca. 30-60% of the dietary biomass consumed by barred owls in the Oregon Coast Range (COA; Chapter 3). Small salamanders, along with the variety of other prey barred owls consumed, likely supported barred owls reaching equilibrium occupancy before the start of removals, where they were detected in nearly every spotted owl territory (Franklin et al. 2021). Owls collected near Roseburg, OR (KLA) during the fall consumed large numbers of arthropods (Chapter 3), which typically contribute negligible amounts of biomass to the spotted owl diet. While one might assume arthropods are lower quality prey than large vertebrates, the rain beetles and Orthopterans were primarily consumed during a time of the year where fat deposits were rapidly accumulated, presumably in preparation for reproduction (Chapter 5). In KLA, owls in the highest condition were collected shortly after the period when rain beetles occurred in the diet, when the percent of fat in dry mass was estimated to be around 50% (Chapter 5). Thus, after water was removed from the carcasses, barred owls had about as much fat in them as all other tissues combined. Energy stores of this magnitude leading into the breeding season may help explain why barred owls in the Oregon Coast Range fledged, on average, 4 times as many young as neighboring spotted owls (Wiens et al. 2014).

The decision to lethally manage populations of barred owls has been and continues to be difficult, and requires accounting for a multitude of social, ethical, and economic factors beyond the conservation value to northern spotted owls. Yet, in making this decision, my findings suggest this is not simply a question of killing one owl to save another. This novel predator is not an ecological replacement for spotted owls, and is likely impacting new prey species that may themselves be at risk if barred owls are not managed. If barred owls continue to increase in abundance throughout the forests of the Pacific Northwest, impacts on prey populations could cascade down trophic levels and throughout food webs to the variety of species that rely upon these species that now have a new predator.

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# Appendices

# Appendix A – Prey Taxa Identified in Barred Owl Stomach Contents.

Table A.1 - Mean mass and frequency of occurrence (n) of prey species identified in stomach contents of barred owls collected in Cle Elum, WA, Alsea OR, Roseburg, OR, USA, 2015–2019.

| Prey Taxon | Mean Mass (g) [a] | CLE | COA | KLA |
|---|---|---|---|---|
| Mammals | | 165 | 534 | 485 |
| Shrew (*Sorex* spp.) | 5 (1) | 38 | 210 | 172 |
| Shrew mole (*Neurotrichus gibbsii*) | 9 (1) | 2 | 76 | 118 |
| Flying squirrel (*Glaucomys oregonensis/sabrinus*) | 95 (1) | 32 | 34 | 34 |
| Deer mouse (*Peromyscus maniculatus*) | 22 (1) | 2 | 55 | 6 |
| Mole (*Scapanus* spp.) | 56-93 (1) | 1 | 22 | 40 |
| Douglas squirrel (*Tamiasciurus douglasii*) | 221 (1) | 9 | 29 | 10 |
| Unidentified beetle | 0.2-2.4 (1, 4) | 3 | 26 | 12 |
| Unidentified vole (*Microtus* spp.) | 20-30 (1) | 22 | 5 | 16 |
| Chipmunk (*Tamias* spp.) | 83 (1) | 8 | 27 | 5 |
| Unidentified mammal | 25-1200 (1, 2, 4) | 7 | 6 | 19 |
| Unidentified rabbit or hare | 475 (1) | 8 | 13 | 7 |
| Red tree vole (*Arborimus longicaudus*) | 26 (1) | | 15 | 11 |
| Unidentified vole or mouse | 20-171 (1, 2, 6) | 10 | 12 | 3 |
| Woodrat (*Neotoma* spp.) | 285 (1) | 4 | 7 | 13 |
| Creeping vole (*Microtus oregoni*) | 20 (1) | 8 | 2 | 8 |
| Western Red-backed Vole (*Myodes californicus*) | 23 (1) | | 5 | 10 |
| Unidentified squirrel (*Sciuridae*) | 83-221 (1) | 4 | 5 | 4 |
| Coast mole (*Scapanus orarius*) | 56 (1) | 3 | 1 | |
| Pacific jumpin mouse (*Zapus trinotatus*) | 24 (1) | 1 | 2 | 1 |
| Southern red-backed vole (*Myodes gapperi*) | 23.3 (6) | 4 | | |
| Virginia opossum (*Didelphis virginiana*) | 2850 (6) | | | 4 |
| Mountain beaver (*Aplodontia rufa*) | 325 (1) | | 3 | |
| Unidentified bat (*Microchiroptera*) | 1 (2) | | 3 | |
| Western gray squirrel (*Sciurus griseus*) | 450 (1) | | | 3 |
| Norther pocket gopher (*Thamomys talpoides*) | 102 (2) | 2 | | |
| Mazama pocket gopher (*Thomomys mazama*) | 95 (1) | | 2 | |
| Unidentified rat (*Rattus* spp.) | 250 (1) | | | 1 |
| Birds | | 7 | 31 | 23 |
| Unidentified bird | 9-550 (1, 2, 4) | 3 | 18 | 9 |
| Pacific wren (*Troglodytes pacificus*) | 9 (1) | | 4 | 4 |
| Varied thrush (*Ixoreus navius*) | 78 (1) | | 3 | 1 |
| Western screech owl (*Megascops kennicottii*) | 169 (1) | | 2 | 2 |
| Band-tailed pigeon (*Patagioenas fasciata*) | 392 (1) | | 2 | 1 |
| Ruffed grouse (*Bonasa umbellus*) | 514 (1) | 1 | | 1 |
| Norther flicker (*Colaptes auratus*) | 142 (1) | | | 2 |
| Clark's nutcraker (*Nucifraga columbiana*) | 135 (7) | 1 | | |

| | | | | |
|---|---|---|---|---|
| Hawk (*Buteo* spp.) | 1126 (7) | 1 | | |
| Unidentified swallow (*Hirundinidae*) | 16 (7) | 1 | | |
| Fox sparrow (*Passerella iliaca*) | 32 (2) | | 1 | |
| Northern pygmy owl (*Glaucidium gnoma*) | 68 (1) | | 1 | |
| Brown creeper (*Certhia americana*) | 8 (2) | | | 1 |
| Mountain quail (*Oreortyx pictus*) | 224 (1) | | | 1 |
| Unidentified egg | 45.5 (9) | | | 1 |
| Amphibians | | 66 | 854 | 309 |
| Small salamander (*Caudata*) | 14.5 (1) | 11 | 748 | 243 |
| Small frog (*Anura*) | 5 (5) | 43 | 50 | 22 |
| Large salamander (*Caudata*) | 45.5 (1) | 1 | 45 | 8 |
| Rough-skinned newt (*Taricha granulosa*) | 14.5 (1) | | | 33 |
| Pacific tree frog (*Pseudacris regilla*) | 5 (5) | 8 | 4 | 1 |
| Large frog (*Anura*) | 30 (1) | 1 | 2 | 2 |
| Long-toed salamander (*Ambystoma macrodactylum*) | 14.5 (1) | 2 | | |
| Ensatina (*Ensatina eschscholtzii*) | 14.5 (1) | | 2 | |
| Coastal giant salamander (*Dicamptodon tenebrosus*) | 45.5 (1) | | 1 | |
| Northwestern salamander (*Ambystoma gracile*) | 45.5 (1) | | 1 | |
| *Plethodon* spp. | 14.5 (1) | | 1 | |
| Reptiles | | 3 | 14 | 27 |
| Unidentified snake | 0.4-100 (1, 2) | 1 | 9 | 19 |
| Garter snake (*Thamnophis* spp.) | 100 (1) | 2 | 4 | 4 |
| Unidentified lizard | 22.5 (1) | | 1 | 3 |
| Ring-necked snake (*Diadophis puntatus*) | 10 (8) | | | 1 |
| Unidentified fish | 51 (1) | 2 | 1 | |
| Arthropods | | 154 | 443 | 1538 |
| Rain beetle (*Pleocoma* spp.) | 1.15 (10) | | | 833 |
| Shield-backed katydid (*Tettigoniidae*) | 1 (5) | 76 | 36 | 416 |
| *Orthoptera* | 0.3-2 (2, 4, 5) | 44 | 59 | 98 |
| Ground beetle (*Carabidae*) | 0.3 (1) | | 74 | 58 |
| Unidentified caterpillar (*Lepitoptera*) | 0.3 (4) | 1 | 73 | 8 |
| Unidentified moth or butterfly (*Lepidoptera*) | 0.2 (4) | 2 | 44 | 28 |
| Spider (*Areneae*) | 0.5 (3) | 2 | 32 | 19 |
| Unidentified insect | 0.1-0.3 (1, 4) | 9 | 19 | 16 |
| Unidentified beetle | 0.2-2.4 (1, 4) | | 1 | 2 |
| Centipede (*Chilopoda*) | 0.2 (5) | | 26 | 16 |
| Geometrid caterpillar (*Geometridae*) | 0.3 (4) | | 22 | |
| Unidentified Ant (*Formicidae*) | 0.1 (1) | 11 | 7 | 3 |
| Unidentified arthropod | 0.2 (4) | 4 | 12 | 4 |
| Weevil (*Curculionidae*) | 0.3 (1) | | 9 | 8 |
| Cicada (*Cicadidae*) | 0.4 (2) | | | 14 |
| Burying beetle (*Nicrophorus* spp.) | 0.3 (4) | | 7 | |
| Long-horn beetles (*Cerambycidae*) | 2.4 (1) | 3 | 1 | 2 |

| | | | | |
|---|---|---|---|---|
| Ponderosa borer beetle (*Trichonemis spiculatus*) | 2.4 (1) | | 5 | |
| Yellow-spotted millipede (*Harpaphe haydeniana*) | 0.4 (1) | | 5 | |
| Scorpion (*Scorpiones*) | 3 (2) | | | 5 |
| Unidentified arachnid | 0.5 (3) | 2 | | |
| Harvestman (*Opiliones*) | 0.1 (4) | | 2 | |
| Peppered moth caterpillar (*Biston betularia*) | 0.3 (4) | | 2 | |
| Camel cricket (*Pristoceuthophilus* spp.) | 0.3 (4) | | | 2 |
| Caterpillar (*Nadata* spp.) | 0.3 (4) | | 1 | |
| Grasshopper (*Acrididae*) | 0.5 (4) | | 1 | |
| Hover fly (*Syrphidae*) | 0.3 (4) | | 1 | |
| Noctuid caterpillar (*Noctuidae*) | 0.3 (4) | | 1 | |
| Saturnid caterpillar (*Saturnidae*) | 6 (5) | | 1 | |
| Stonefly (*Plecoptera*) | 0.1 (4) | | 1 | |
| Unidentified wasp (*Vespidae*) | 0.1 (1) | | 1 | |
| Cockroach (*Blattodea*) | 1 (2) | | | 1 |
| Crane fly (*Tipulidae*) | 0.1 (4) | | | 1 |
| Douglas fir borer (*Centrodera spruca*) | 0.5 (2) | | | 1 |
| Predaceous diving beetle (*Dytiscidae*) | 0.5 (5) | | | 1 |
| Unidentified fly larva (*Diptera*) | 0.1 (5) | | | 1 |
| Water scavenger beetle (*Hydrophilidae*) | 0.3 (4) | | | 1 |
| Signal crayfish (*Pacifastacus leniusculus*) | 23.8 (1) | 1 | 23 | 6 |
| Snails (*Gastropoda*) | 8.7 (1) | | 147 | 81 |
| Unidentified Prey | | 1 | 4 | 1 |

[a] 1 = Wiens et al. 2014; 2 = Forsman et al. 2004; 3 = Forsman et al. 1984; 4 = Mass based on estimate from similar sized taxa; 5 = Mass estimated from intact specimens.; 6 = Verts and Carraway 1998; 7 = Dunning 1993; 8 = Cox et al. 2018; 9 = Mazur and James 2021; 10 = Morgan 1987

# Appendix B – AIC$_c$ Model Selection Results for Empty Barred Owl Stomachs.

Table B.1. AIC model selection results for logistic models with AIC weight (w) > 0.01 estimating the probability a barred owl had an empty stomach empty given its age class and sex, the study area it was collected in, date and time since sunset it was collected. Barred owls collected in study areas (Area) near Cle Elum, WA, Alsea, OR, and Roseburg, OR between 2015-2019.

| **Model**[a] | ***K*** | **-2log*L*** | **ΔAICc** | **AIC$_c$ wt** |
|---|---|---|---|---|
| Area + Age + Sex + Date + Time + Time^2 | 9 | 1193 | 0 | 0.83 |
| Area + Age + Date + Time + Time^2 | 8 | 1198.98 | 3.95 | 0.12 |
| Area + Sex + Date + Time + Time^2 | 7 | 1203.8 | 6.73 | 0.03 |
| Area + Age + Sex + Date | 7 | 1206.02 | 8.97 | 0.01 |
| Area + Age + Sex + Date + Time | 8 | 1204.4 | 9.37 | 0.01 |
| Area + Date + Time + Time^2 | 6 | 1210.18 | 11.1 | 0 |
| Area + Age + Date | 6 | 1211.86 | 12.77 | 0 |
| Area + Age + Date + Time | 7 | 1210.4 | 13.35 | 0 |
| Age + Sex + Date + Time + Time^2 | 7 | 1211.38 | 14.32 | 0 |
| Area + Sex + Date | 5 | 1216.26 | 15.16 | 0 |
| Area + Sex + Date + Time | 6 | 1214.64 | 15.55 | 0 |
| Area + Age + Sex + Time + Time^2 | 8 | 1212 | 16.96 | 0 |
| Area + Sex + Time + Time^2 | 6 | 1217.58 | 18.49 | 0 |
| Area + Date | 4 | 1222.54 | 19.42 | 0 |
| Age + Date + Time + Time^2 | 6 | 1218.56 | 19.47 | 0 |
| Area + Date + Time | 5 | 1221.1 | 20 | 0 |
| Sex + Date + Time + Time^2 | 5 | 1221.32 | 20.21 | 0 |
| Area + Age + Time + Time^2 | 7 | 1218.08 | 21.03 | 0 |
| Age + Sex + Date | 5 | 1223.94 | 22.84 | 0 |
| Area + Time + Time^2 | 5 | 1223.94 | 22.85 | 0 |
| Age + Sex + Date + Time | 6 | 1222.5 | 23.41 | 0 |
| Date + Time + Time^2 | 4 | 1228.86 | 25.74 | 0 |
| Age + Date | 4 | 1231 | 27.89 | 0 |
| Sex + Date | 3 | 1233.32 | 28.2 | 0 |
| Age + Date + Time | 5 | 1229.7 | 28.6 | 0 |
| Sex + Date + Time | 4 | 1231.82 | 28.7 | 0 |
| Age + Sex + Time + Time^2 | 6 | 1229.14 | 30.06 | 0 |
| Sex + Time + Time^2 | 4 | 1234.18 | 31.07 | 0 |
| Area + Age + Sex + Time | 7 | 1228.76 | 31.7 | 0 |
| Area + Sex + Time | 5 | 1233.3 | 32.21 | 0 |
| Area + Age + Sex | 6 | 1231.68 | 32.6 | 0 |
| Area + Sex | 4 | 1236.18 | 33.06 | 0 |
| Date | 2 | 1240.8 | 33.67 | 0 |
| Date + Time | 3 | 1239.46 | 34.33 | 0 |

| | | | | |
|---|---|---|---|---|
| Age + Time + Time^2 | 5 | 1236.38 | 35.28 | 0 |
| Area + Age + Time | 6 | 1234.76 | 35.68 | 0 |
| Area + Age + | 5 | 1237.5 | 36.4 | 0 |
| Time + Time^2 | 3 | 1241.66 | 36.53 | 0 |
| Area + Time + | 4 | 1239.64 | 36.53 | 0 |
| Area + | 3 | 1242.32 | 37.19 | 0 |
| Sex + Time + | 3 | 1249.46 | 44.33 | 0 |
| Age + Sex + Time + | 5 | 1245.54 | 44.43 | 0 |
| Sex + | 2 | 1252.22 | 45.08 | 0 |
| Age + Sex + | 4 | 1248.32 | 45.2 | 0 |
| Age + Time + | 4 | 1252.68 | 49.56 | 0 |
| Time + | 2 | 1256.9 | 49.76 | 0 |
| Age + | 3 | 1255.3 | 50.18 | 0 |
| NULL | 1 | 1259.48 | 50.34 | 0 |

[a] Key to terms: $K$ = number of parameters; -2log$L$ = -2*log-likelihood; $\Delta\text{AIC}_c$ = difference in $\text{AIC}_c$ score between given model and top model ($\text{AIC}_c$ = 1211.15 for top model); $\text{AIC}_c$ wt = $\text{AIC}_c$ model weight; Area = 3 factor categorical parameter for each study area, CLE, COA, KLA; Age = 3 factor categorical parameter for first-year subadults, second-year subadults, and adults; Sex = 2 factor categorical parameter for males and females; Date = circular transformation of ordinal date; Time = time since sunset; Time^2 = quadratic effect of time since sunset.

# Appendix C – Model Selection Results and Coefficient Estimates for Models Estimating the Effects of Habitat Quality and Conspecific Density on Barred Owl Body Condition.

Table C.1. Model selection results from $AIC_c$ analysis for determining intrinsic parameters that influence the percent of fat in barred owls collected near Cle Elum, WA, Alsea, OR, and Roseburg, OR between 2015-2019. Generalized linear mixed-effects models used to estimate the percent fat in barred owls collected, where survey hexagon was fit as a random effect.

| **Model**[a] | ***K*** | **-2log*L*** | **$\Delta AIC_c$** | **$AIC_c$ wt** |
|---|---|---|---|---|
| Area + Age + Sex + Date | 9 | 14564.66 | 0[b] | 0.6 |
| Area + Age + Sex + Date + Year | 13 | 14557.44 | 0.85 | 0.4 |
| Age + Sex + Date | 7 | 14601.94 | 33.23 | 0 |
| Age + Sex + Date + Year | 11 | 14596.34 | 35.72 | 0 |
| Area + Age + Date | 8 | 14615.2 | 48.51 | 0 |
| Area + Age + Date + Year | 12 | 14607.8 | 49.2 | 0 |
| Age + Date | 6 | 14656.66 | 85.94 | 0 |
| Age + Date + Year | 10 | 14651.36 | 88.71 | 0 |
| Area + Sex + Date + Year | 11 | 14805.04 | 244.42 | 0 |
| Area + Date + Year | 10 | 14841.22 | 278.58 | 0 |
| Area + Sex + Date | 7 | 14861.24 | 292.53 | 0 |
| Sex + Date + Year | 9 | 14864.9 | 300.23 | 0 |
| Area + Date | 6 | 14896.86 | 326.15 | 0 |
| Sex + Date | 5 | 14904.18 | 331.45 | 0 |
| Date + Year | 8 | 14905.02 | 338.33 | 0 |
| Date | 4 | 14943.12 | 368.39 | 0 |
| Area + Age + Sex + Year | 12 | 15338.52 | 779.91 | 0 |
| Area + Age + Year | 11 | 15379.06 | 818.43 | 0 |
| Age + Sex + Year | 10 | 15390.22 | 827.57 | 0 |
| Age + Year | 9 | 15435.38 | 870.71 | 0 |
| Area + Age + Sex | 8 | 15450.58 | 883.9 | 0 |
| Area + Sex + Year | 10 | 15455.4 | 892.76 | 0 |
| Age + Sex | 6 | 15481.5 | 910.79 | 0 |
| Area + Year | 9 | 15487.62 | 922.96 | 0 |
| Area + Age | 7 | 15491.66 | 922.97 | 0 |
| Age | 5 | 15526.04 | 953.32 | 0 |
| Sex + Year | 8 | 15526.98 | 960.3 | 0 |
| Year | 7 | 15562.8 | 994.1 | 0 |
| Area + Sex | 6 | 15688.6 | 1117.89 | 0 |
| Area | 5 | 15719.48 | 1146.76 | 0 |
| Sex | 4 | 15727.98 | 1153.26 | 0 |
| NULL | 3 | 15761.78 | 1185.03 | 0 |

[a] Key to Parameters: *K*= number of parameter; log*L* = log-likelihood; $\Delta AIC_c$ = difference in score for Akaike Information Criterion corrected for small sample size between the top ranked model and the given model; $AIC_c$ wt = Akaike weight; Age = categorical parameter with 3 levels, adults, first-year subadults (S1), and second-year subadults (S2); Area = categorical parameter with 3 levels for each study area; Sex = categorical parameter with 3 levels for Females and Males; Date = cosine transformed circular date.

[b] $AIC_c$ score for top ranked model = 14582.75.

Table C.2. Estimates of model coefficients ($\hat{\beta}$), standard errors (SE), and 95% lower (LCL) and upper (UCL) confidence intervals linear mixed-effects models with $\Delta AIC_c \leq 2$, estimating the percent fat in barred owls collected near Cle Elum, WA (CLE), Alsea, OR (COA), and Roseburg, OR (KLA) between 2015-2019. Model selection to determine a base model accounting for intrinsic parameters that influence the percent fat in barred owls.

| | **Model Rank** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **1** | | | | **2** | | | |
| **Parameter [a]** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 25.5 | 0.44 | 24.6 | 26.4 | 25.6 | 0.57 | 24.5 | 26.7 |
| Area:COA | 2.4 | 0.41 | 1.6 | 3.2 | 2.4 | 0.41 | 1.6 | 3.2 |
| Area:KLA | 2.5 | 0.46 | 1.6 | 3.4 | 2.7 | 0.48 | 1.8 | 3.6 |
| Sex:Male | -2.3 | 0.32 | -2.9 | -1.7 | -2.3 | 0.32 | -2.9 | -1.7 |
| Age:S2 | -2.6 | 0.35 | -3.3 | -1.9 | -2.5 | 0.38 | -3.2 | -1.8 |
| Age:S1 | -8.4 | 0.47 | -9.3 | -7.5 | -8.1 | 0.5 | -9.1 | -7.1 |
| Date | 11.2 | 0.33 | 10.6 | 11.8 | 11 | 0.35 | 10.3 | 11.7 |
| Year:2016 | | | | | 0.59 | 0.62 | -0.6 | 1.8 |
| Year:2017 | | | | | -0.78 | 0.62 | -2.0 | 0.4 |
| Year:2018 | | | | | -0.27 | 0.64 | -1.5 | 1.0 |
| Year:2019 | | | | | -0.45 | 0.65 | -1.7 | 0.8 |

[a] Key to Parameters: Intercept includes the effect of females, adults, and CLE. Age = categorical parameter with 3 levels, adults, first-year subadults (S1), and second-year subadults (S2); Area = categorical parameter with 3 levels for each study area; Sex = categorical parameter with 3 levels for Females and Males; Date = cosine transformed circular date; Year = categorical parameter for each year of the study period.

Table C.3. Model selection results from $\text{AIC}_c$ analysis for determining habitat and density parameters that influence the percent of fat in barred owls collected near Cle Elum, WA, Alsea, OR, and Roseburg, OR between 2015-2019. Generalized linear mixed-effects models used to estimate the percent fat in barred owls collected, where survey hexagon was fit as a random effect.

| **Model**[a] | ***K*** | **-2log*L*** | **$\Delta\text{AIC}_c$** | **$\text{AIC}_c$ wt** |
|---|---|---|---|---|
| Detected + Removed + TPI + % Old + % Old^2 | 14 | 14549.56 | 0[b] | 0.15 |
| Removed + TPI + % Old + % Old^2 | 13 | 14551.86 | 0.28 | 0.13 |
| TPI + % Old + % Old^2 | 12 | 14554.56 | 0.94 | 0.09 |
| Detected + TPI + % Old + % Old^2 | 13 | 14553 | 1.42 | 0.07 |
| Removed + TPI | 11 | 14557.88 | 2.23 | 0.05 |
| Detected + Removed + % Old + % Old^2 | 13 | 14553.94 | 2.35 | 0.05 |
| Detected + Removed + TPI | 12 | 14556.08 | 2.47 | 0.04 |
| Removed + % Old + % Old^2 | 12 | 14556.22 | 2.61 | 0.04 |
| % Old + % Old^2 | 11 | 14558.7 | 3.06 | 0.03 |
| Detected + Removed + TPI + % Old | 13 | 14554.86 | 3.26 | 0.03 |
| TPI | 10 | 14560.94 | 3.28 | 0.03 |
| Removed + TPI + % Old | 12 | 14556.9 | 3.29 | 0.03 |
| Detected + % Old + % Old^2 | 12 | 14557.14 | 3.52 | 0.03 |
| Detected + Removed + Elevation + % Old + % Old^2 | 14 | 14553.66 | 4.09 | 0.02 |
| Removed | 10 | 14561.84 | 4.17 | 0.02 |
| Detected + TPI | 11 | 14559.84 | 4.2 | 0.02 |
| TPI + % Old + | 11 | 14559.9 | 4.26 | 0.02 |
| Removed + Elevation + % Old + % Old^2 | 13 | 14555.96 | 4.36 | 0.02 |
| Detected + Removed | 11 | 14560.06 | 4.42 | 0.02 |
| Elevation + % Old + % Old^2 | 12 | 14558.38 | 4.76 | 0.01 |
| Detected + TPI + % Old | 12 | 14558.58 | 4.97 | 0.01 |
| BASE[c] | 9 | 14564.66 | 4.99 | 0.01 |
| Detected + Removed + % Old | 12 | 14558.74 | 5.12 | 0.01 |
| Removed + % Old | 11 | 14560.78 | 5.15 | 0.01 |
| Detected + Elevation + % Old + % Old^2 | 13 | 14556.8 | 5.2 | 0.01 |
| % Old | 10 | 14563.54 | 5.89 | 0.01 |
| Detected | 10 | 14563.56 | 5.9 | 0.01 |
| Removed + Elevation | 11 | 14561.72 | 6.08 | 0.01 |
| Detected + Removed + Elevation | 12 | 14559.92 | 6.31 | 0.01 |
| Detected + % Old | 11 | 14562.22 | 6.57 | 0.01 |
| Elevation | 10 | 14564.54 | 6.87 | 0 |
| Detected + Removed + Elevation + % Old | 13 | 14558.74 | 7.14 | 0 |
| Removed + Elevation + % Old | 12 | 14560.78 | 7.17 | 0 |
| Detected + Elevation | 11 | 14563.4 | 7.76 | 0 |
| Elevation + % Old | 11 | 14563.54 | 7.9 | 0 |
| Detected + Elevation + % Old | 12 | 14562.2 | 8.58 | 0 |

[a] Key to Parameters: *K*= number of parameter; log*L* = log-likelihood; $\Delta\text{AIC}_c$ = difference in score for Akaike Information Criterion corrected for small sample size between the top ranked model and the given model; $\text{AIC}_c$ wt = Akaike weight; Number Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; Number Detected = maximum number of barred owls detected during one of three surveys each year; Elevation = mean elevation of a survey hexagon; Topographic Position Index = mean topographic position index of a survey hexagon; % Old = the percentage of a survey hexagon comprised of forest older than 80 years.

[b] $\text{AIC}_c$ score for top ranked model = 14577.76

[c] BASE model included in all models evaluated with parameters for study area, sex, age, and date.

Table C.4. Estimates of model coefficients ($\hat{\beta}$), standard errors (SE), and 95% lower (LCL) and upper (UCL) confidence intervals linear mixed-effects models with $\Delta AIC_c \leq 2$, estimating the percent fat in barred owls collected near Cle Elum, WA (CLE), Alsea, OR (COA), and Roseburg, OR (KLA) between 2015-2019. Model selection to determine habitat and density parameters that influence the percent fat in barred owls.

| | **Model Rank** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **1** | | | | **2** | | | |
| **Parameter** [a] | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 26.4 | 0.68 | 25.1 | 27.7 | 26.7 | 0.66 | 25.4 | 28.0 |
| Area:COA | 2.3 | 0.46 | 1.4 | 3.2 | 2.5 | 0.45 | 1.6 | 3.4 |
| Area:KLA | 2.4 | 0.49 | 1.4 | 3.4 | 2.4 | 0.49 | 1.4 | 3.4 |
| Sex:Male | -2.2 | 0.32 | -2.8 | -1.6 | -2.3 | 0.32 | -2.9 | -1.7 |
| Age:S2 | -2.6 | 0.35 | -3.3 | -1.9 | -2.7 | 0.35 | -3.4 | -2.0 |
| Age:S1 | -8.2 | 0.48 | -9.1 | -7.3 | -8.3 | 0.47 | -9.2 | -7.4 |
| Date | 11 | 0.34 | 10.3 | 11.7 | 11 | 0.34 | 10.3 | 11.7 |
| Removed | -0.21 | 0.12 | -0.45 | 0.025 | -0.19 | 0.11 | -0.41 | 0.026 |
| Detected | 0.17 | 0.11 | -0.046 | 0.39 | | | | |
| Elevation | | | | | | | | |
| TPI | -0.0083 | 0.004 | -0.016 | -0.00046 | -0.0083 | 0.004 | -0.016 | -0.00046 |
| % Old | -0.082 | 0.032 | -0.14 | -0.02 | -0.079 | 0.032 | -0.14 | -0.016 |
| % Old^2 | 0.0012 | 0.00051 | 0.00020 | 0.0022 | 0.0012 | 0.00051 | 0.00020 | 0.0022 |

| | 3 | | | | 4 | | | |
|---|---|---|---|---|---|---|---|---|
| | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 26.5 | 0.66 | 25.2 | 27.8 | 26.3 | 0.68 | 25.0 | 27.6 |
| Area:COA | 2.4 | 0.45 | 1.5 | 3.3 | 2.3 | 0.46 | 1.4 | 3.2 |
| Area:KLA | 2.4 | 0.49 | 1.4 | 3.4 | 2.4 | 0.49 | 1.4 | 3.4 |
| Sex:Male | -2.3 | 0.32 | -2.9 | -1.7 | -2.3 | 0.32 | -2.9 | -1.7 |
| Age:S2 | -2.6 | 0.35 | -3.3 | -1.9 | -2.6 | 0.35 | -3.3 | -1.9 |
| Age:S1 | -8.4 | 0.47 | -9.3 | -7.5 | -8.3 | 0.48 | -9.2 | -7.4 |
| Date | 11.1 | 0.33 | 10.5 | 11.7 | 11.1 | 0.33 | 10.5 | 11.7 |
| Removed | | | | | | | | |
| Detected | | | | | 0.14 | 0.11 | -0.076 | 0.36 |
| Elevation | | | | | | | | |
| TPI | -0.0081 | 0.004 | -0.016 | -0.00026 | -0.0081 | 0.004 | -0.016 | -0.00026 |
| % Old | -0.082 | 0.032 | -0.145 | -0.019 | -0.085 | 0.032 | -0.148 | -0.022 |
| % Old^2 | 0.0012 | 0.00052 | 0.00018 | 0.0022 | 0.0012 | 0.00052 | 0.00018 | 0.0022 |

[a] Key to Parameters: Intercept includes the effect of females, adults, and CLE. Age = categorical parameter with 3 levels, adults, first-year subadults (S1), and second-year subadults (S2); Area = categorical parameter with 3 levels for each study area; Sex = categorical parameter with 3 levels for Females and Males; Date = cosine transformed circular date; Detected = maximum number of barred owls detected during one of three surveys each year; Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; TPI = mean topographic position index of a survey hexagon; % Old = the percentage of a survey hexagon comprised of forest older than 80 years; % Old^2 = quadratic effect of % Old.

Table C.5. Model selection results from $\text{AIC}_\text{c}$ analysis for determining habitat and density parameters that influence the percent of fat in barred owls collected near Cle Elum, WA between 2015-2019. Generalized linear mixed-effects models used to estimate the percent fat in barred owls collected, where survey hexagon was fit as a random effect.

| **Model**[a] | ***K*** | **-2log*L*** | **$\Delta\text{AIC}_\text{c}$** | **$\text{AIC}_c$ wt** |
|---|---|---|---|---|
| Detected + TPI | 9 | 3151.5 | 0[b] | 0.2 |
| Detected | 8 | 3154.54 | 0.96 | 0.13 |
| Detected + Removed + TPI | 10 | 3150.46 | 1.05 | 0.12 |
| Detected + TPI + % Old | 10 | 3151.42 | 2.02 | 0.07 |
| Detected + Elevation | 9 | 3153.52 | 2.03 | 0.07 |
| Detected + Removed | 9 | 3153.88 | 2.39 | 0.06 |
| Detected + % Old | 9 | 3154.48 | 2.98 | 0.05 |
| Detected + TPI + % Old + % Old^2 | 11 | 3150.38 | 3.06 | 0.04 |
| Detected + Removed + TPI + % Old | 11 | 3150.42 | 3.1 | 0.04 |
| Detected + Removed + Elevation | 10 | 3152.96 | 3.55 | 0.03 |
| Detected + Elevation + % Old | 10 | 3153.52 | 4.11 | 0.03 |
| Detected + Removed + TPI + % Old + % Old^2 | 12 | 3149.5 | 4.29 | 0.02 |
| Detected + Removed + % Old | 10 | 3153.84 | 4.44 | 0.02 |
| Detected + % Old + % Old^2 | 10 | 3153.88 | 4.47 | 0.02 |
| Detected + Elevation + % Old + % Old^2 | 11 | 3152.9 | 5.6 | 0.01 |
| Detected + Removed + Elevation + % Old | 11 | 3152.94 | 5.63 | 0.01 |
| Detected + Removed + % Old + % Old^2 | 11 | 3153.34 | 6.02 | 0.01 |
| TPI | 8 | 3160.14 | 6.57 | 0.01 |
| BASE[c] | 7 | 3162.72 | 7.09 | 0.01 |
| Detected + Removed + Elevation + % Old + % Old^2 | 12 | 3152.44 | 7.23 | 0.01 |
| Removed + TPI | 9 | 3159.98 | 8.48 | 0 |
| Elevation | 8 | 3162.14 | 8.58 | 0 |
| TPI + % Old | 9 | 3160.14 | 8.64 | 0 |
| Removed | 8 | 3162.66 | 9.1 | 0 |
| % Old | 8 | 3162.72 | 9.15 | 0 |
| TPI + % Old + % Old^2 | 10 | 3159.62 | 10.22 | 0 |
| Elevation + % Old | 9 | 3162.04 | 10.55 | 0 |
| Removed + TPI + % Old | 10 | 3159.96 | 10.56 | 0 |
| Removed + Elevation | 9 | 3162.12 | 10.62 | 0 |
| % Old + % Old^2 | 9 | 3162.46 | 10.97 | 0 |
| Removed + % Old | 9 | 3162.66 | 11.17 | 0 |
| Removed + TPI + % Old + % Old^2 | 11 | 3159.5 | 12.19 | 0 |
| Elevation + % Old + % Old^2 | 10 | 3161.78 | 12.39 | 0 |
| Removed + Elevation + % Old | 10 | 3162 | 12.6 | 0 |
| Removed + % Old + % Old^2 | 10 | 3162.42 | 13.02 | 0 |
| Removed + Elevation + % Old + % Old^2 | 11 | 3161.76 | 14.46 | 0 |

[a] Key to Parameters: *K*= number of parameter; log*L* = log-likelihood; $\Delta\text{AIC}_\text{c}$ = difference in score for Akaike Information Criterion corrected for small sample size between the top ranked model and the given model; $\text{AIC}_\text{c}$ wt = Akaike weight; Number Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; Number Detected = maximum number of barred owls detected during one of three surveys each year; Elevation = mean elevation of a survey hexagon; Topographic Position Index = mean topographic position index of a survey hexagon; % Old = the percentage of a survey hexagon comprised of forest older than 80 years.

[b] $\text{AIC}_\text{c}$ score for top ranked model = 3169.87

[c] BASE model included in all models evaluated with parameters for study area, sex, age, and date.

Table C.6. Estimates of model coefficients ($\hat{\beta}$), standard errors (SE), and 95% lower (LCL) and upper (UCL) confidence intervals linear mixed-effects models with $\Delta \mathrm{AIC}_c \leq 2$, estimating the percent fat in barred owls collected near Cle Elum, WA between 2015-2019. Model selection to determine habitat and density parameters that influence the percent fat in barred owls.

| | **Model Rank** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1** | | | | **2** | | | | **3** | | | |
| **Parameter[a]** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 23.8 | 0.9 | 22.0 | 25.6 | 23.8 | 0.9 | 22.0 | 25.6 | 24 | 0.93 | 22.2 | 25.8 |
| Sex:Male | -2.1 | 0.6 | -3.3 | -0.92 | -2.1 | 0.6 | -3.3 | -0.92 | -2.1 | 0.6 | -3.3 | -0.92 |
| Age:S2 | -2.6 | 0.67 | -3.9 | -1.3 | -2.7 | 0.68 | -4.0 | -1.4 | -2.7 | 0.68 | -4.0 | -1.4 |
| Age:S1 | -6.8 | 0.93 | -8.6 | -5.0 | -6.9 | 0.93 | -8.7 | -5.1 | -6.9 | 0.93 | -8.7 | -5.1 |
| Date | 7.8 | 0.77 | 6.3 | 9.3 | 7.9 | 0.77 | 6.4 | 9.4 | 7.6 | 0.79 | 6.1 | 9.1 |
| Removed | | | | | | | | | -0.28 | 0.28 | -0.83 | 0.27 |
| Detected | 0.78 | 0.26 | 0.27 | 1.3 | 0.76 | 0.26 | 0.25 | 1.3 | 0.83 | 0.27 | 0.3 | 1.4 |
| TPI | -0.014 | 0.0078 | -0.029 | 0.0013 | | | | | -0.014 | 0.0077 | -0.029 | 0.0011 |

[a] Key to Parameters: Intercept includes the effect of females and adults. Age = categorical parameter with 3 levels, adults, first-year subadults (S1), and second-year subadults (S2); Area = categorical parameter with 3 levels for each study area; Sex = categorical parameter with 3 levels for Females and Males; Date = cosine transformed circular date; Detected = maximum number of barred owls detected during one of three surveys each year; Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; TPI = mean topographic position index of a survey hexagon.

Table C.7. Model selection results from $AIC_c$ analysis for determining habitat and density parameters that influence the percent of fat in barred owls collected near Alsea, OR between 2015-2019. Generalized linear mixed-effects models used to estimate the percent fat in barred owls collected, where survey hexagon was fit as a random effect.

| **Model**[a] | ***K*** | **-2log*L*** | **$\Delta AIC_c$** | **$AIC_c$ wt** |
|---|---|---|---|---|
| Removed + % Old + % Old^2 | 10 | 7052.8 | 0[b] | 0.22 |
| Detected + Removed + % Old + % Old^2 | 11 | 7050.8 | 0.03 | 0.21 |
| Removed + Elevation + % Old + % Old^2 | 11 | 7052.26 | 1.51 | 0.1 |
| Detected + Removed + Elevation + % Old + % Old^2 | 12 | 7050.32 | 1.6 | 0.1 |
| Removed + TPI + % Old + % Old^2 | 11 | 7052.8 | 2.04 | 0.08 |
| Detected + Removed + TPI + % Old + % Old^2 | 12 | 7050.8 | 2.08 | 0.08 |
| Detected + % Old + % Old^2 | 10 | 7055.84 | 3.03 | 0.05 |
| % Old + % Old^2 | 9 | 7059.08 | 4.23 | 0.03 |
| Detected + Elevation + % Old + % Old^2 | 11 | 7055.54 | 4.79 | 0.02 |
| Detected + TPI + % Old + % Old^2 | 11 | 7055.84 | 5.08 | 0.02 |
| Removed + % Old | 9 | 7060.74 | 5.91 | 0.01 |
| Elevation + % Old + % Old^2 | 10 | 7058.76 | 5.96 | 0.01 |
| Detected + Removed | 9 | 7060.96 | 6.12 | 0.01 |
| Detected + Removed + % Old | 10 | 7058.98 | 6.19 | 0.01 |
| TPI + % Old + % Old^2 | 10 | 7059.06 | 6.27 | 0.01 |
| Removed | 8 | 7063.24 | 6.37 | 0.01 |
| Removed + Elevation + % Old | 10 | 7060.3 | 7.5 | 0.01 |
| Detected + Removed + Elevation | 10 | 7060.32 | 7.53 | 0.01 |
| Removed + Elevation | 9 | 7062.52 | 7.67 | 0 |
| Removed + TPI + % Old | 10 | 7060.5 | 7.7 | 0 |
| Detected + Removed + Elevation + % Old | 11 | 7058.58 | 7.83 | 0 |
| Detected + Removed + TPI | 10 | 7060.64 | 7.84 | 0 |
| Detected + Removed + TPI + % Old | 11 | 7058.68 | 7.93 | 0 |
| Removed + TPI | 9 | 7062.98 | 8.14 | 0 |
| Detected | 8 | 7066.68 | 9.8 | 0 |
| Detected + % Old | 9 | 7064.78 | 9.94 | 0 |
| % Old | 8 | 7067.7 | 10.83 | 0 |
| BASE[c] | 7 | 7070.22 | 11.32 | 0 |
| Detected + Elevation | 9 | 7066.28 | 11.43 | 0 |
| Detected + TPI | 9 | 7066.34 | 11.5 | 0 |
| Detected + TPI + % Old | 10 | 7064.48 | 11.68 | 0 |
| Detected + Elevation + % Old | 10 | 7064.56 | 11.77 | 0 |
| TPI + % Old | 9 | 7067.48 | 12.63 | 0 |
| Elevation + % Old | 9 | 7067.48 | 12.64 | 0 |
| Elevation | 8 | 7069.76 | 12.88 | 0 |
| TPI | 8 | 7069.96 | 13.09 | 0 |

[a] Key to Parameters: *K*= number of parameter; log*L* = log-likelihood; $\Delta AIC_c$ = difference in score for Akaike Information Criterion corrected for small sample size between the top ranked model and the given model; *w* = Akaike weight; Number Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; Number Detected = maximum number of barred owls detected during one of three surveys each year; Elevation = mean elevation of a survey hexagon; Topographic Position Index = mean topographic position index of a survey hexagon; % Old = the percentage of a survey hexagon comprised of forest older than 80 years.

[b] $AIC_c$ score for top ranked model = 7073.01

[c] BASE model included in all models evaluated with parameters for study area, sex, age, and date.

Table C.8. Estimates of model coefficients ($\hat{\beta}$), standard errors (SE), and 95% lower (LCL) and upper (UCL) confidence intervals linear mixed-effects models with $\Delta AIC_c \leq 2$, estimating the percent fat in barred owls collected near Alsea, OR between 2015-2019. Model selection to determine habitat and density parameters that influence the percent fat in barred owls.

| | **Model Rank** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **1** | | | | **2** | | | |
| **Parameter[a]** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 29.9 | 0.73 | 28.5 | 31.3 | 30.4 | 0.82 | 28.8 | 32.0 |
| Sex:Male | -2.5 | 0.44 | -3.4 | -1.6 | -2.6 | 0.44 | -3.5 | -1.7 |
| Age:S2 | -1.6 | 0.48 | -2.5 | -0.66 | -1.7 | 0.48 | -2.6 | -0.76 |
| Age:S1 | -7.6 | 0.66 | -8.9 | -6.3 | -7.8 | 0.67 | -9.1 | -6.5 |
| Date | 11.6 | 0.46 | 10.7 | 12.5 | 11.6 | 0.46 | 10.7 | 12.5 |
| Removed | -0.37 | 0.15 | -0.66 | -0.076 | -0.34 | 0.15 | -0.63 | -0.046 |
| Detected | | | | | -0.2 | 0.14 | -0.47 | 0.074 |
| Elevation | | | | | | | | |
| % Old | -0.22 | 0.068 | -0.35 | -0.087 | -0.22 | 0.068 | -0.35 | -0.087 |
| % Old^2 | 0.0044 | 0.0015 | 0.0015 | 0.0073 | 0.0044 | 0.0015 | 0.0015 | 0.0073 |

| | **3** | | | | **4** | | | |
|---|---|---|---|---|---|---|---|---|
| | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 29.3 | 1.1 | 27.1 | 31.5 | 29.9 | 1.1 | 27.7 | 32.1 |
| Sex:Male | -2.5 | 0.44 | -3.4 | -1.6 | -2.6 | 0.44 | -3.5 | -1.7 |
| Age:S2 | -1.6 | 0.48 | -2.5 | -0.66 | -1.7 | 0.48 | -2.6 | -0.76 |
| Age:S1 | -7.6 | 0.66 | -8.9 | -6.3 | -7.8 | 0.67 | -9.1 | -6.5 |
| Date | 11.6 | 0.46 | 10.7 | 12.5 | 11.6 | 0.46000 | 10.7 | 12.5 |
| Removed | -0.38 | 0.15 | -0.67 | -0.086 | -0.35 | 0.15000 | -0.64 | -0.06 |
| Detected | | | | | -0.2 | 0.14000 | -0.47 | 0.074 |
| Elevation | 1.7 | 2.3 | -2.8 | 6.2 | 1.6 | 2.30000 | -2.9 | 6.11 |
| % Old | -0.21 | 0.067 | -0.34 | -0.079 | -0.21 | 0.068 | -0.34 | -0.08 |
| % Old^2 | 0.0044 | 0.0015 | 0.0015 | 0.0073 | 0.0044 | 0.0015 | 0.0015 | 0.0073 |

[a] Key to Parameters: Intercept includes the effect of females and adults. Age = categorical parameter with 3 levels, adults, first-year subadults (S1), and second-year subadults (S2); Area = categorical parameter with 3 levels for each study area; Sex = categorical parameter with 3 levels for Females and Males; Date = cosine transformed circular date; Detected = maximum number of barred owls detected during one of three surveys each year; Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; Elevation = mean elevation of a survey hexagon; % Old = the percentage of a survey hexagon comprised of forest older than 80 years; % Old^2 = quadratic effect of % Old.

Table C.9. Model selection results from $\text{AIC}_c$ analysis for determining habitat and density parameters that influence the percent of fat in barred owls collected near Roseburg, OR between 2016-2019. Generalized linear mixed-effects models used to estimate the percent fat in barred owls collected, where survey hexagon was fit as a random effect.

| **Model**[a] | ***K*** | **-2log*L*** | **$\Delta\text{AIC}_c$** | **$\text{AIC}_c$ wt** |
|---|---|---|---|---|
| Detected | 8 | 4261.92 | 0[b] | 0.18 |
| Detected + TPI | 9 | 4260 | 0.14 | 0.17 |
| Detected + Removed | 9 | 4261.6 | 1.73 | 0.08 |
| Detected + % Old | 9 | 4261.74 | 1.88 | 0.07 |
| Detected + Elevation | 9 | 4261.76 | 1.9 | 0.07 |
| Detected + Removed + TPI | 10 | 4259.72 | 1.92 | 0.07 |
| Detected + TPI + % Old | 10 | 4259.9 | 2.11 | 0.06 |
| Detected + TPI + % Old + % Old^2 | 11 | 4258.7 | 2.97 | 0.04 |
| Detected + % Old + % Old^2 | 10 | 4261.12 | 3.33 | 0.03 |
| Detected + Removed + % Old | 10 | 4261.4 | 3.61 | 0.03 |
| Detected + Removed + Elevation | 10 | 4261.46 | 3.67 | 0.03 |
| Detected + Removed + TPI + % Old | 11 | 4259.6 | 3.88 | 0.03 |
| Detected + Elevation + % Old | 10 | 4261.7 | 3.91 | 0.03 |
| Detected + Removed + TPI + % Old + % Old^2 | 12 | 4258.32 | 4.68 | 0.02 |
| Detected + Removed + % Old + % Old^2 | 11 | 4260.72 | 5.01 | 0.02 |
| Detected + Elevation + % Old + % Old^2 | 11 | 4260.96 | 5.25 | 0.01 |
| Detected + Removed + Elevation + % Old | 11 | 4261.38 | 5.67 | 0.01 |
| BASE[c] | 7 | 4270.36 | 6.39 | 0.01 |
| TPI | 8 | 4268.48 | 6.55 | 0.01 |
| Detected + Removed + Elevation + % Old + % Old^2 | 12 | 4260.62 | 6.97 | 0.01 |
| Removed | 8 | 4269.5 | 7.57 | 0 |
| Removed + TPI | 9 | 4267.66 | 7.8 | 0 |
| Elevation | 8 | 4270.34 | 8.41 | 0 |
| % Old | 8 | 4270.34 | 8.42 | 0 |
| TPI + % Old | 9 | 4268.48 | 8.61 | 0 |
| TPI + % Old + % Old^2 | 10 | 4267.3 | 9.52 | 0 |
| Removed + % Old | 9 | 4269.48 | 9.61 | 0 |
| Removed + Elevation | 9 | 4269.48 | 9.62 | 0 |
| Removed + TPI + % Old | 10 | 4267.66 | 9.86 | 0 |
| % Old + % Old^2 | 9 | 4269.76 | 9.9 | 0 |
| Elevation + % Old | 9 | 4270.32 | 10.47 | 0 |
| Removed + TPI + % Old + % Old^2 | 11 | 4266.36 | 10.65 | 0 |
| Removed + % Old + % Old^2 | 10 | 4268.78 | 10.99 | 0 |
| Removed + Elevation + % Old | 10 | 4269.46 | 11.68 | 0 |
| Elevation + % Old + % Old^2 | 10 | 4269.66 | 11.87 | 0 |
| Removed + Elevation + % Old + % Old^2 | 11 | 4268.74 | 13.02 | 0 |

[a] Key to Parameters: *K*= number of parameter; log*L* = log-likelihood; $\Delta\text{AIC}_c$ = difference in score for Akaike Information Criterion corrected for small sample size between the top ranked model and the given model; *w* = Akaike weight; Number Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; Number Detected = maximum number of barred owls detected during one of three surveys each year; Elevation = mean elevation of a survey hexagon; Topographic Position Index = mean topographic position index of a survey hexagon; % Old = the percentage of a survey hexagon comprised of forest older than 80 years.

[b] $\text{AIC}_c$ score for top ranked model = 4278.16

[c] BASE model included in all models evaluated with parameters for study area, sex, age, and date.

Table C.10. Estimates of model coefficients and standard errors in parentheses for generalized linear mixed-effects models with $\Delta AIC_c \leq 2$, estimating the percent fat in barred owls collected near Roseburg, OR between 2015-2019. Model selection to determine habitat and density parameters that influence the percent fat in barred owls.

| | **Model Rank** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1** | | | | **2** | | | | 3 | | | |
| **Parameter**[a] | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 26.8 | 0.78 | 25.3 | 28.3 | 26.8 | 0.78 | 25.3 | 28.3 | 26.7 | 0.8 | 25.1 | 28.3 |
| Sex:Male | -1.6 | 0.65 | -2.9 | -0.3 | -1.6 | 0.65 | -2.9 | -0.3 | -1.6 | 0.65 | -2.9 | -0.33 |
| Age:S2 | -4.0 | 0.74 | -5.5 | -2.5 | -4 | 0.74 | -5.5 | -2.5 | -4.00 | 0.74 | -5.5 | -2.5 |
| Age:S1 | -9.2 | 0.95 | -11.1 | -7.3 | -9.2 | 0.95 | -11.1 | -7.3 | -9.3 | 0.98 | -11.2 | -7.4 |
| Date | 11.8 | 0.64 | 10.5 | 13.1 | 11.7 | 0.64 | 10.4 | 13.0 | 11.8 | 0.64 | 10.5 | 13.1 |
| Removed | | | | | | | | | 0.14 | 0.24 | -0.33 | 0.61 |
| Detected | 0.71 | 0.24 | 0.24 | 1.2 | 0.71 | 0.24 | 0.24 | 1.2 | 0.69 | 0.24 | 0.22 | 1.2 |
| Elevation | | | | | | | | | | | | |
| TPI | | | | | -0.011 | 0.0083 | -0.027 | 0.0053 | | | | |
| % Old | | | | | | | | | | | | |

| | **4** | | | | **5** | | | | 6 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** | $\hat{\beta}$ | **SE** | **LCL** | **UCL** |
| Intercept | 27 | 0.92 | 25.2 | 28.8 | 27.4 | 1.7 | 24.1 | 30.7 | 26.7 | 0.8 | 25.1 | 28.3 |
| Sex:Male | -1.6 | 0.65 | -2.9 | -0.33 | -1.6 | 0.65 | -2.9 | -0.33 | -1.6 | 0.65 | -2.9 | -0.33 |
| Age:S2 | -4.0 | 0.75 | -5.5 | -2.5 | -4 | 0.75 | -5.5 | -2.5 | -4.0 | 0.74 | -5.5 | -2.5 |
| Age:S1 | -9.3 | 0.97 | -11.2 | -7.4 | -9.3 | 0.96 | -11.2 | -7.4 | -9.3 | 0.98 | -11.2 | -7.4 |
| Date | 11.8 | 0.64 | 10.5 | 13.1 | 11.7 | 0.64 | 10.4 | 13.0 | 11.8 | 0.64 | 10.5 | 13.1 |
| Removed | | | | | | | | | 0.13 | 0.24 | -0.3 | 0.6 |
| Detected | 0.72 | 0.24 | 0.25 | 1.2 | 0.71 | 0.24 | 0.24 | 1.2 | 0.69 | 0.24 | 0.2 | 1.2 |
| Elevation | | | | | -1.1 | 2.7 | -6.4 | 4.2 | | | | |
| TPI | | | | | | | | | -0.011 | 0.0083 | -0.027 | 0.0053 |
| % Old | -0.0094 | 0.022 | -0.1 | 0.0 | | | | | 26.7 | 0.8 | 25.1 | 28.3 |

[a] Key to Parameters: Intercept includes the effect of females and adults;. Age = categorical parameter with 3 levels, adults, first-year subadults (S1), and second-year subadults (S2); Area = categorical parameter with 3 levels for each study area; Sex = categorical parameter with 3 levels for Females and Males; Date = cosine transformed circular date; Detected = maximum number of barred owls detected during one of three surveys each year; Removed = number of barred owls removed from a survey hexagon within 30 days before or after a given owl; Elevation = mean elevation of a survey hexagon; TPI = mean topographic position index of a survey hexagon; % Old = the percentage of a survey hexagon comprised of forest older than 80 years.