

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL

CHAPTER FOUR

Prey

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“The ecology of a predator cannot be understood without knowledge of the ecology of its primary prey”

Waters and Zabel 1995: 858

1 BACKGROUND

1.1 INTRODUCTION

Prey identity, abundance, distribution, and habitat associations have major effects on the habitat selection and demographic parameters of predator populations (Ranazzi et al. 2000). Indeed, there are many studies of the relationship of prey to the ecology of owls (see reviews in Mikkola 1983, Cramp 1985), including *Strix* owls (Southern 1970, Hirons 1982). In this section, we review and summarize current knowledge on the relationship between prey and Northern Spotted Owls. We do this in primarily with respect to information available at the time of listing and the information that has accumulated subsequent to listing. Specifically, we examine the interaction between diet, habitat associations, demographic parameters, and environmental effects. We will also summarize the available information on the different prey species (Appendices).

1.2 KNOWLEDGE AT THE TIME OF LISTING

At the time of listing, it was recognized that:

“Spotted owls are perch-and-dive predators and over 50 percent of their prey items are arboreal or semiarboreal species. Spotted owls subsist on a variety of mammals, birds, reptiles, and insects, with small mammals such as flying squirrels (*Glaucomys sabrinus*), red tree voles (*Arborimus longicaudus*) and dusky-footed woodrats (*Neotoma fuscipes*) making up the bulk of the food items throughout the range of the species (Solis and Gutiérrez 1982, Forsman et al. 1984, Barrows 1985).”

Federal Register 55: 26114

“It has been suggested that fluctuations in reproduction and numbers of pairs breeding may be related to fluctuations in prey availability (Forsman et al. 1984, Barrows 1985, Gutiérrez 1985).”

Federal Register 55: 26115

“The relative abundance of different prey in old-growth and in different kinds of young-growth has not been studied well enough for clear patterns to emerge...The Service agrees that the issue of prey abundance in different habitat warrants additional research.”

Federal Register 55: 26156

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“The Service concurs that recent summaries of prey abundance (Thomas et al. 1990) do not support a generalization that prey are more abundant in old than in younger forests. Rather, abundance of prey species by forest age varies with the species of prey, geographic region, and probably year. The fact remains that spotted owls forage disproportionately in older forests with the clear inference that they obtain prey in proportion to the time spent in the various age classes of forest.”

Federal Register 55: 26170

“The relationship of spotted owl reproduction to abundance of prey has not been well established. The reported positive association between reproduction and the frequency of large prey in spotted owl diets may represent either differential capture or differential transport of large prey to the nest; this issue is unresolved. The Ward and Gutiérrez (1989) study was unable to demonstrate differences in prey abundance between reproducing and nonreproducing owls by sampling prey at foraging sites used by the male owls (Thomas et al. 1990). Small mammal populations vary greatly from location to location and from year to year. It is not surprising, therefore, that investigators in different regions, and often in different years, report differing measures of abundance of the same or different species over a variety of forest types and age classes. “

Federal Register 55: 26171

As noted above, the primary summary of information on prey at the time of listing was Appendix J of the report by Thomas et al. (1990). This remained the most complete summary available for the development of the Final Draft Recovery Plan (USDI 1992), and the Northwest Forest Plan.

Major conclusions of Thomas et al. (1990) were:

- Spotted Owls eat a wide variety of prey, but nocturnal, arboreal or semi-arboreal small mammal species predominate in diets.
- At individual study sites, a high proportion of the diet is composed of just one or two species – typically Northern Flying Squirrels, Dusky-footed or Bushy-tailed Woodrats, and lagomorphs.
- Pocket Gophers, Red Tree Voles and Deer Mice may be regionally important.
- Flying Squirrels are the dominant prey in Western Hemlock/Douglas Fir forests; woodrats are more important in drier, mixed-conifer/mixed-evergreen forests.
- This association of prey use with habitat type is mirrored by geographic trends (Flying Squirrels predominating in diets from northern areas, woodrats in drier southern forests), local distribution (again woodrats predominating in more xeric forests), and (in some areas) elevational differences (Flying Squirrels being more abundant at higher elevations).
- Seasonal shifts in diet mirror shifts in prey abundance or vulnerability.
- Since most small mammal populations ‘fluctuate notoriously in abundance over time’, short-term studies will be insufficient to establish broad ecological relationships.

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- There was no conclusive association of flying squirrels with older forest types.
- Dusky-footed Woodrats are most abundant in early seral stages, when hardwoods were present and in riparian areas.
- Bushy-tailed Woodrats are associated with talus and outcrops.
- Red Tree Voles appear to be associated with older forests based on limited data.

We note that of the major hypotheses to explain the association of Northern Spotted Owls with old-growth habitat, proposed that owls selected prey that were more abundant in older forest (Carey 1985), or that they were more available to owls (Gutiérrez 1985).

1.3 INTRODUCTION TO PREY SPECIES

In the appendices, we review the current information on individual prey species, emphasizing studies carried out since the time of the Northern Spotted Owl listing in 1990. We report data for each species' ecology, abundance, habitat preference, and possible limiting factors of population, when available. Several main prey species have been identified - Northern Flying Squirrels, 2 species of woodrats, 2 species of Red-backed Voles, Red Tree Voles, 2 species of Deer Mice, and 2 species of lagomorphs. Although some species such as *Peromyscus* species and lagomorphs form only a small or seasonal component of the diet, they may be important to owl survival or reproduction.

Factors affecting the distribution and abundance will vary with species, season, biotic community (i.e., forest type and seral stage), geographic location, and sympatric species of competitors and predators. Indices of abundance indicate large fluctuations in species populations for several spotted owl prey species, which is not uncommon for small mammals.

Please refer to the Appendices for species descriptions and ecology.

1.4 PREDATION IN CONTEXT

Forests of the Pacific Northwest support one of the most diverse mammal faunas in the United States, with mammals comprising >25% of the vertebrate species in this area (>70 species of mammals on the Olympic Peninsula) (Corn and Bury 1991, Norse 1990, Songer et al. 1997). This diverse mammal community supports a prey base not only for Northern Spotted Owls, but for a variety of predators including coyotes (*Canis latrans*), foxes (*Vulpes vulpes* and *V. velux*), bobcats (*Lynx rufus*), martens, weasels and skunks (Mustelidae), hawks and other birds of prey (Falconiformes), and owls (e.g. Great Horned Owls) (Strigiformes). These predators all consume small mammals (see Ingles 1965, Maser et al. 1981, and Carey 1991 for overviews or Carey et al. 1992, Carey and Kershner 1996, Wilson and Carey 1996 and Watson et al. 1998 for specific examples, Carey et al. 1999c, Carey et al. 1999a, Martin and Anthony 1999). Hence, although Northern Spotted Owls are often regarded as quasi-specialist on larger small mammals, many other predators also take these same prey species in various proportions.

The prey species themselves have diverse dietary requirements. Some species are herbivores (e.g. Red Tree Voles, woodrats, lagomorphs), while others consume mostly fungi and lichens (Flying Squirrels). Therefore, it is probable that environmental factors affecting one prey species

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will act differently on other species. For instance, environmental factors affecting fungal fruiting body production are likely to differ from those affecting seed production. Prey species may also interact, directly or through competition for food and other resources.

Northern Spotted Owls occupy a niche in a complex web of interactions. However, it is not known whether this interaction web is composed of many diffuse relationships, with weak linkages between the abundance of different species, or a more structured system where each species is linked to the abundance and effects of a few key populations. However, numerous ecological studies suggest single-factor linear relationships are rare in temperate forests. As noted, although Northern Spotted Owls take many arboreal and semi-arboreal prey, these same species are also eaten by other flying, terrestrial (weasels), or arboreal predators. For instance, Northern Flying Squirrels are prey of mustelids (long-tailed weasels, fishers, and martens) and raptors, notably Great Horned Owls (*Carey pers. comm.*). Moreover, we know that Spotted Owls take many very small mammals, and more of them during high reproductive years (Rosenberg et al. 2003, Ward 2001). Therefore, while the Spotted Owl is a purported specialist, the dynamics of other species may be important to the owl as well. Hence, understanding the relationship between Northern Spotted Owls and prey populations must include all factors that effect prey populations, including predation. Given that Great Horned Owls are also a presumed major predator of Northern Spotted Owls, these interactions may be quite complex.

2 FORAGING ECOLOGY OF NORTHERN SPOTTED OWLS

Northern Spotted Owls usually forage at night, primarily on arboreal or semi-arboreal species (Anthony et al. 1998, *Carey 1993*, *Forsman Presentation 2004*, Forsman et al. 1984, 2001, 2004, Gutiérrez et al. 1995). Numerous studies of individual foraging behavior (e.g. Solis and Gutiérrez 1990) have shown that owls select among habitat types, and selection can be correlated with various vegetation variables (e.g. tree density, shrub cover). Solis and Gutiérrez found that canopy closure (as defined by the total cover of all plant growth forms above a point on the forest floor) was highest in roosting habitat, and lowest in areas infrequently used for foraging (typically on the edge of a home range). (Note that Carey et al. 1992 described roosting cover as being high overhead and lateral cover around the roosting owl and high foliage height diversity within the roosting stand.) Highest use areas were typically those areas with large conifers and high hardwood density. “Shrub and herb cover were highest in areas used infrequently for foraging” (Solis and Gutiérrez 1990:744). These results suggest, but do not demonstrate, that Northern Spotted Owls may respond behaviorally to structure of vegetation when selecting foraging areas. They hypothesized that maneuverability of the owl within a forest may be a significant factor affecting individual habitat selection. Solis and Gutiérrez noted that smaller males and larger female owls may forage in different habitats, perhaps in response to differing tree density that might differentially affect the flight capability of the different-sized sexes. An alternate explanation is this may allow a pair of owls to partition and more effectively track prey resources or allow the male to forage further from the nest grove.

The average prey size of the Northern Spotted Owl was 116 ± 6.5 g in Oregon, 111.4 ± 1.5 g on the Olympic Peninsula, 74.8 ± 2.9 g in the Western Washington Cascades, and 91.3 ± 1.7 g in the Eastern Washington Cascades, which is large when compared to the owl’s body mass (Forsman et al 2001, 2004, *Forsman Presentation 2004*). As noted in the *Federal Register*, Spotted Owls

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appear to select larger prey.

Tables 4.1 and 4.2 summarize data on diet of Northern Spotted Owls in different geographic areas. As noted above, Flying Squirrels and woodrats usually form the bulk of the diet. Indeed, Flying Squirrels are the most important prey (by biomass) in 16 of 17 studies in Table 4.2. However, other prey types, including a variety of small to medium sized mammals, are often a major component of diet (Forsman et al. 2004). Other prey items include birds, reptiles, amphibians, and insects, which usually comprise < 15% of the diet by frequency and < 5% of the biomass (Anthony et al. 1998, *Forsman Presentation 2004*, Forsman et al. 1984, 2001, 2004, Gutiérrez et al. 1995).

Forsman et al (2001, 2004), *Forsman (Presentation 2004)*, and Anthony et al. (1998) discuss variation in diet composition over time. For instance, Forsman et al. (2004:220) found that:

“Composition of the diet varied among years ($P < 0.05$) at 25 of 56 territories where we collected ≥ 20 prey in 2 or more years. In most cases, the differences were relatively small, but there were notable exceptions. For example, at two territories, the percent of tree voles and flying squirrels in the diet varied dramatically among years... At the Oak Creek territory, deer mice varied from 0% of the diet in one year to 79% of the diet in another year...”

In some cases there may have also been decreased use of voles, possibly due to declines in vole abundances or availability (Anthony et al. 1998).

Diet composition varies with distribution and abundance of prey, and habitat type. The data shown in Tables 4.1 and 4.2 essentially confirm patterns reported by Thomas et al. (1990):

- In any area, a few prey species predominate, typically Flying Squirrels and woodrats, but also Deer Mice, Red Tree Voles, Western Red-backed Voles, and lagomorphs (seasonally) in some areas.
- Flying Squirrels are the dominant prey in more mesic Western Hemlock/Douglas Fir forests; woodrats are more important in drier, mixed-conifer/mixed-evergreen forests.
- ‘Minor’ prey items, such as insects, may still occasionally be important (insects constitute 15.4% of the diet (by prey frequency) in the drier habitat of the eastern Cascades of Oregon).

Spotted Owl diet shows considerable variation regionally, seasonally, annually, and locally, which is likely in response to prey availability (Laymon 1988, Ganey 1992, Verner et al. 1992, Ward and Block 1995, Duncan and Sidner 1990, Forsman et al. 2001, *Carey 1993*). However *Carey (1993)* proposes that prey may be selected based on prey mass (100-400 g), a preference for arboreal or semi-arboreal prey, and social behavior. These characteristics may have more influence on the diet than either numerical abundance or total biomass (*Carey 1993*).

As noted by Thomas et al. (1990), there is a clear geographic pattern of diet, paralleling differences in habitat. While Northern Flying Squirrels and woodrats are usually the predominant prey both in biomass and frequency (Barrows 1980, Forsman et al. 1984, *Ward*

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1990, Bevis et al. 1997, Forsman et al. 2001, 2004, Forsman, Presentation 2004), these species have a general north-south trend, with Flying Squirrels comprising a large percentage of the diet in the north, while woodrats become an increasing portion of the diet in the southern range of the Spotted Owl (Table 4.1). Flying squirrels and woodrats are co-dominant in the diet through the southwest interior of Oregon (Table 4.1, Forsman et al. 2001, 2004).

Though their sample sizes were small, Cutler and Hays (1991) suggest small mammals notably voles (*Microtus* spp. and *Clethrionomys occidentalis*) are important prey items at higher elevation, as their abundance and seasonal availability to the owls in some areas may be greater than the generally selected prey species (Northern Flying Squirrel or woodrats). This is consistent with the results of Ganey (1988) for Mexican Spotted Owls in Arizona and Forsman et al (1984) in southwestern Oregon, except that western Red-backed Voles are more prevalent than *Microtus* spp. in Oregon (Cutler and Hays 1991). Increases in the presence of Red-backed Voles and gophers in the diet of Spotted Owls were positively correlated with elevation in Oregon Cascades (Forsman et al 2004). However, in the Central Cascades, predation on Red Tree Voles declines with increasing elevation; the occurrence of Red Tree Voles in the diet in other regions in Oregon was limited regardless of elevation (Forsman et al 2004). Note that if Northern Spotted Owls are displaced into higher elevation areas by Barred Owls (suggested by Gremel (presentation 2003) and others). This may cause changes in diet (see Chapter 7 on Barred Owls).

Relatively few studies have focused on the diet of Northern Spotted Owls outside of the breeding season. This is likely due to the necessity of radio-tracking owls during winter, which is time consuming and expensive. Owls expand their home ranges during winter and do not consistently roost in the same place, which makes pellets more difficult to find (Forsman et al. 1991, Carey et al 1992). Similar problems are associated with non-territorial owls (juvenile and sub-adult owls also known as the “floater” population). Therefore, little is known about their diet, and most of the data presented here are from territorial owls.

Studies that include fall and winter diet analysis have found that “species that hibernated or spent the winter under the snow (e.g. chipmunks, pikas) were absent from the diet from approximately October-March” (Forsman et al. 2001). Insects, terrestrial mammals, birds, and juvenile large mammals were also seasonal (mainly spring, summer and early fall for some species) (Forsman et al. 2001, 2004). Forsman et al. (2001, 2004) suggests adult large mammals and birds, like snowshoe hares, rabbits, mountain beavers, and grouse, are largely absent from the diet because they are difficult to capture due to their size. This increases predation pressure on other species still available to the owl, as revealed by a slight increase in the proportion of flying squirrels in the diet (Forsman et al. 2001).

Rosenberg et al. (2003) have discussed prey switching by Northern Spotted Owls. In their study area, the abundance of different prey species (small mammals) varied independently of each other, perhaps promoting switching in owls to the most abundant prey at any one season or year. Prey switching may occur in other owls when primary prey become rare (Wendland 1984, Petty 1999) or when secondary prey irrupt (Ward 2001).

2.1. ENERGETICS, DIET AND HOME RANGE

Energetic requirements have not been studied directly in the Northern Spotted Owl, although data are available for the similar Mexican and California Spotted Owls (Ganey et al. 1993, Weathers et al. 2001 respectively), and Ward et al. (1998) has extrapolated some of these data to calculate Northern Spotted Owl energetic costs. Note that Weathers et al. (2001) critiqued the calculations of Ganey et al. (1993), and that this criticism has apparently been accepted (*R. Gutiérrez pers. comm.*).

In calculating the effects of energetic needs on owl foraging behavior and biology, it is important to recognize that, for instance, average captures rates, which influence total energetic need, may be influenced by target prey species, habitat type, and stand age and structure. Additionally, Franklin et al. (2000) pointed out that the most energetically demanding season for owls may well be the breeding season rather than the winter (Wijnandts 1984, Meczewa 1986). Energetic stress due to reproductive effort will be additive with maintenance metabolic costs, increasing the risks of starvation. In addition, the male is providing food for both himself and his mate.

Forsman et al. (2004) estimated the average adult spotted owl needs 73.2g of prey per day (12% of its body mass of 610 grams) or 26,718g per year. Using the proportion of biomass of each species then dividing by the species mean mass, the number of prey items captured per year can be estimated. The East Cascades show the highest estimate of total prey captured per year because of the high proportion of insects and miscellaneous prey items that Northern Spotted Owls consume in that region. This may be an underestimate due to the remains of insects being less likely to be found in pellets compared to vertebrate remains (Ganey 1992). The estimated number of prey items that would be taken per year by owls in the south coast and southwestern interior regions of Oregon are 222.4 and 217.4, respectively (Forsman et al. 2004, *Forsman Presentation 2004*). (Estimated number of prey consumed by owls is also discussed in section 4 of this chapter.) This compares to the results of Weathers et al. (2001), who estimated that on average, California Spotted Owls feeding young can meet their own needs by consuming one Northern Flying Squirrel every 1.8 days or one Dusky-footed Woodrat every 3.7 days based on the FMR data, assimilated efficiency of 77% and the body composition of prey species. *Forsman (Presentation 2004)* estimated an average of 270.6 flying squirrels per year (0.7 squirrels a day) and 58 woodrats per year for a pair of owls with two young in Oregon. These estimates include the consumption of other prey in their average proportions. Non-nesting owls are estimated to capture an average 0.6-1.0 prey items per day, which includes the East Cascades where numerous insects are consumed relative to other areas in Oregon (Forsman et al. 2004).

Selection of large prey is energetically efficient, maximizing input over expenditure. Ward et al. (1998) estimate the energetic equivalency of alternative diet items. Ward et al.'s calculated energetic needs of a reproductive male owl (see above) are equivalent to 47 woodrats, 100 flying squirrels, 410 voles, 547 white-footed mice, or 2001 insectivores. While Northern Spotted Owls take many prey items, the hypothesized 'quasi-specialization' on large prey appears to make energetic sense.

Larger home ranges, especially at the northern extent of the range, suggest that when available prey density is low (Carey et al. 1992, Zabel et al. 1995) or there is an increased reliance on a

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single prey species (Northern Flying Squirrels), owls respond by increasing home range (and hence flight costs) (see habitat association section). Densities of Flying Squirrels generally tend to decrease toward the northern edge of the Spotted Owl's range (southern Coast Ranges and Western Cascades vs. Olympic Peninsula and North Cascades of Washington), with a few exceptions (Carey 1995a, 2000 Appendix X). Studies of the relationship between spotted owl home range size and prey requirements do support a general trend that prey abundance is negatively correlated with home range size (Carey et al. 1992).

Overall, the distribution of the Northern Spotted Owl does not encompass the entire range of some of its primary prey species. Northern Flying Squirrels range through parts of Canada and into Alaska. Deer Mice and Snowshoe Hares also occur over a wide region. Therefore, factors other than prey distribution must set limits to owl distribution. It is possible that the northern distribution limits of Northern Spotted Owls are set by energetic costs, since Spotted Owls likely have increased basic maintenance metabolic demands in those parts of the range; direct effects of temperature are, however, also a plausible limiting factor. *Forsman (pers. comm.)* has pointed out that Barred Owls (which must have somewhat similar metabolic needs to Northern Spotted Owls) have expanded rapidly into the interior mountain ranges of Idaho, Washington, Montana, British Columbia, and even into Alaska; this suggests that limits to the distribution of Northern Spotted Owls could be set by the relative abundance of preferred prey (such as flying squirrels). At this point, it can only be hypothesized that distribution may be affected by energetic needs, which increase with increased basal metabolic costs, and increased foraging costs (affected in turn by reduced prey diversity, reduced prey availability, forest fragmentation, and reduced habitat availability).

2.2. EFFECTS OF WEATHER AND CLIMATE ON OWL-PREY INTERACTIONS

Climate probably affects Spotted Owl population dynamics (see Demography chapter). Whether this effect is directly on the survival or reproductive success of the owl, an indirect effect through prey, or both is unclear. Reproductive success was reduced when weather was cold and wet during the late nesting period, while survival was negatively impacted by early nesting season precipitation (Franklin et al. 2000, *Olson et al. 2004*). These studies were from demographic study areas in Oregon and northern California. Therefore weather effects may be more pronounced in the northern parts of the range where seasonal variation is great, snow cover complicates prey acquisition, reduced prey availability, reduced prey diversity, and owls may be operating closer to their metabolic limits. Indirect effects could be through a reduction in prey abundance or availability, or through reducing the owl's hunting efficiency (Franklin et al. 2000). This appears to be the case for Northern Goshawks on the Olympic Peninsula where reproduction and survivorship were also reduced in cold, wet (la nina) years (Bloxtton 2002). Associated with these demographic costs were reductions in avian and mammalian prey and greater ranging behavior by radio-tagged hawks (Bloxtton 2002).

It is possible that noise from rain or wind may make it harder for Spotted Owls to hear their prey, thus directly influencing foraging success. Prey availability may also be a factor on foraging success. Flying Squirrels in North Carolina and Pennsylvania are known to delay nocturnal activity during high winds, mist and heavy rain (Weigl and Osgood 1974, Witt 1992). Flying

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Squirrels in Washington exhibit behaviors suggestive of minimization of exposure to cold and rain in the winter as well as predator avoidance (see Carey et al 1997, Carey 2000). Flying squirrels may reduce their on-the-ground foraging for truffles in the winter, when truffles may be scarce, and spend more time foraging on lichens in trees and remaining in their dens.

Weather undoubtedly affect prey abundance both on short (direct) and long-term (indirect) scales. For instance, severe weather conditions may cause increased prey mortality. After an ice storm, the abundance of most shrew species and two species of Deer Mice declined (*Risenhoover et al. 2002*). However, after this same ice storm, Northern Flying Squirrel abundance increased, perhaps due to habitat changes induced by the storm (*Risenhoover et al. 2002*). Therefore, different species may respond differently to environmental stresses.

Weather also affects prey reproduction. In Prairie Deer Mice, weather affects the sexual composition and size of litters, and weight of young (Myer et al. 1985). Warm temperatures in autumn or heavy rain during early pregnancy in any season decrease litter size of Prairie Deer Mice, while unusually warm temperatures during early pregnancy increase reproductive output (Myer et al. 1985). Whether this also applies to Deer Mice in the Pacific Northwest or other Spotted Owl prey remains untested. Although it has been demonstrated that weather may influence the survival and reproduction of some small mammals, there are few data regarding the effects of weather on any of the primary prey of Northern Spotted Owls.

Weather may also have indirect effects on prey abundance by altering food availability. Increased moisture tends to increase the abundance of mycorrhizal fungi, a source of food for several prey species including western Red-backed Voles and Flying Squirrels (Tallmon and Mills 1994, Mills 1995, Carey 1991, Maser et al 1978, Maser et al 1985, Carey 1995a, Carey et al 1999, Colgan et al 1999, Carey et al. 2002). Fungal species differ in the moisture, temperature and nutrients gained from the mineral soil and organic matter (Molina and Trappe 1982, Perry et al. 1989, Molina et al. 1992, Carey et al. 1999a). “Fungal production drops in summer with drought...” (Franklin and Dyrness 1973, USDC National Oceanic and Atmospheric Association 1981, Villa et al. 1999:40). “Lichen litterfall biomass increased with increasing stand complexity and moisture” (Lehmkuhl 2004:381). Lichens are used by “...small mammals (Maser et al., 1985; Rosentreter et al., 1997; Zabel and Waters, 1997), mainly during the winter when plant and fungal food sources are at low levels or unavailable under deep snow” (Lehmkuhl 2004:381). If lichens provide critical nutrients and energy when species are most food stressed, lichen diversity and abundance may affect survival and be one factor in determining population levels of small mammals. Precipitation also plays a role in moving the spores, yeasts, and bacteria from feces “...into the soil where the fungi colonize new [tree] roots” and “...enhance the ability of trees to absorb water and nutrients...” (Carey et al. 2002:148). Vegetation would also be expected to differ in growth rates and seed production. Despite indications that precipitation may adversely affect some small mammals, it also appears necessary for their survival.

Rosenberg et al. (2001, 2003) found a positive correlation between Northern Spotted Owl reproductive success and Deer Mice abundance. This is somewhat surprising in that Deer Mice are not a primary prey of Spotted Owls (less than 2% by biomass in the study area), and hence a strong linkage of the two species' populations was not predicted. One possibility may be that

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Deer Mice and owls responded similarly to weather and were simply correlated without direct causation. Alternatively, Deer Mice abundance may be correlated with that of presumed primary prey (whose densities are less easily measured with accuracy). Note that Fryxell et al. (1998) showed linkage of the abundance of many small mammal species (including Flying Squirrels and Deer Mice) over a 43-year period in eastern Canada. *Carey (pers. comm.)* speculates that such synchrony across the prey community could be driven by years of high conifer seed production, which triggers high reproduction in Douglas Squirrels and *Peromyscus*. In subsequent years, these elevated densities of seed eaters, lacking seeds, could compete heavily with mycophagous mammal species, resulting in community wide declines, and synchrony. This interesting hypothesis will require many more data to be adequately tested.

The interaction between Spotted Owls and their prey may be affected by weather in complex ways. Franklin et al. (2000) have shown that weather may interact with habitat characteristics. High territory quality, a function of habitat and other factors, can buffer the effects of bad weather on owls. Understanding such effects of weather (even though they cannot be controlled) may be critical to an understanding of viable population levels and in designing recovery strategies. The effects of weather may be exacerbated and confounded with diet and habitat differences, with complex consequences for owl reproductive success and survival.

Finally, we note that if weather affects prey and owl interactions, it is possible that systematic changes in weather, brought on by climate change (both long-term warming and cycling changes in temperature and precipitation characteristic of the Pacific coast), may affect Spotted Owls' survival and reproduction. This may be a fruitful area for exploration with predictive modeling— if and when adequate empirical data are available.

3 EFFECTS OF PREY ON SPOTTED OWLS

Predators are affected by the abundance and availability of their prey (e.g. Martin and Anthony 1999). “Numerous studies of strigids have shown positive correlations between prey abundance and either nest success or number of fledglings produced (reviewed by Verner et al. 1992)” (Ward et al. 1998). This suggests supplementing the spotted owl diet by increasing prey abundance may increase reproductive success as it has in many avian species including owls (Korpimäki 1989, Boutin 1990, Ward et al. 1998). Carey et al. (1992) provided empirical data on the effect of old-growth fragmentation and reduced prey abundance on stability and turnover in owl pairs. Carey and Peeler (1995) provide empirical evidence of the effects of forest fragmentation on spotted owl energetics in terms of prey base.

In the sections that follow we report information on the effects of prey on Northern Spotted Owl demographic performance and behavior. As noted above, prey type and availability also influence home range size, and interact with other factors to set limits of owl distribution (Carey et al. 1992).

Virtually all studies equate abundance with prey availability. However, factors other than prey abundance also affect availability, notably foraging opportunity. Some researchers have suggested that owls make less use of younger stands, because owls may be less maneuverable

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and, therefore, less able to catch prey there (Rosenberg and Anthony 1992, Zabel *et al.* 1993, Thome *et al.* 1999). Carey (1995b) disagrees with this interpretation, and suggests instead that lack of suitable perches limit foraging opportunities. This appears to agree better with data showing that owls use sapling stands, and densely vegetated riparian areas with woodrats (Carey *et al.* 1992, Carey and Peeler 1995 and others). It is reasonable to hypothesize that prey abundance is not a perfect predictor of availability; since we cannot currently measure availability (as opposed to density or abundance), many of our conclusions (for instance on relative prey availability) must remain tentative.

3.1 BREEDING AND REPRODUCTIVE SUCCESS

Several studies have examined relationships between Spotted Owl diet, breeding status, and reproductive success. Some have found a positive correlation between the proportion of large prey consumed and breeding success. For instance in some studies, owls that fledged young may have consumed higher proportions of large prey than those that did not fledge young (Barrows 1985, 1987, Laymon 1988, Thraillkill and Bias 1989, White 1996, also cited in Rosenberg *et al.* 2003, White 1996, Smith *et al.* 1999). Unsuccessful nesters consumed more small and medium prey, with small prey consisting of the largest proportion of the diet (White 1996) and their diet was more similar to non-nesters than successful nesters (Smith *et al.* 1999). “The diets of owls that successfully fledged young differed significantly in terms of prey size from the diet of owls that failed to fledge young ($\chi^2=14.78$, $df = 2$, $P<0.001$)” (White, 1996:234-235). However, other studies have not found a significant difference between owls that successfully fledged young, and those that did not, in the proportion of large prey consumed (Ward 1990, Ward *et al.* 1998, Forsman *et al.* 2001, see comments in Smith *et al.* 1999). In addition, Forsman *et al.* (2001, 2004) suggested that the higher proportion of large prey in pellets of nesting pairs of spotted owls could be the result of biased delivery of large prey to the female and young by nesting males. Bull *et al.* (1989) documented this type of bias by observing male great gray owls that were foraging during the day. Such biases are potentially serious and were not considered in many studies of Spotted Owls (E. Forsman, *pers. comm.*).

Smith *et al.* (1999) calculated using estimates by Ward *et al.* (1998) that energy costs increase by 276% when a male is providing for himself, a female, and one young from egg-laying through fledging. This estimate is similar to those made by Forsman (*Presentation 2004*) (a 266% increase in the number of prey for a pair with two young relative to estimates per owl). The energy cost of producing an egg is small compared to the energy required by a male to provide for itself, the female and young during the nesting period (Ward *et al.* 1998, Smith *et al.* 1999). Therefore, consumption of large prey, like woodrats, may influence nest success more than nest initiation (Smith *et al.* 1999).

Northern Spotted Owls do occasionally forage during the day. Sovern *et al.* (1994) and Forsman (1976) suggest these foraging events are limited and largely opportunistic. However, Miller (1974) and (Laymon 1988) suggest that those Spotted Owls that successfully fledge young frequently forage during the day (Sovern *et al.* 1994). Sovern *et al.* (1994) found that nesting owls were significantly more active during the day than non-nesting individuals; the proportion of time spent roosting vs. active behaviors, which included foraging, socializing, and moving, differed significantly depending on the time of day, with owls becoming more active after 18:00

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hours. However, the time spent in active behaviors did not differ between sexes. Nesting owls averaged 1.44 capture attempts per day, while non-nesting individuals averaged 0.24 (Sovern et al. 1994). Capture success rate averaged 22.2%, indicating nesting individuals might be expected to capture 0.32 animals/12-hr day. Chipmunks (*Tamias spp.*) and one unidentified small mammal were the diurnal prey that Spotted Owls targeted during this study. After fledging young, nesting pairs may double that rate (Sovern et al. 1994). Some diurnal prey (average of $3.3 \pm 0.2\%$ in Oregon; 8.5% in Washington) may appear in the diet; however, this does not necessarily indicate extensive diurnal movements as most capture attempts were made from the roost tree suggesting opportunistic foraging (Forsman et al. 2001, 2004, Sovern et al. 1994).

Whether it is diet composition, prey availability/abundance, selection, or both (return on foraging investment) that influences reproductive success is unclear (Ward et al. 1998, Smith et al. 1999). Seasonal diet differences and diet shifts following failures suggest selection plays a role (Smith et al. 1999) although such events may be following depletion of preferred prey or shifts in space use (Ward et al. 1998, Carey and Peeler 1995). Ward et al. (1998) showed that Spotted Owls select habitat with large prey, and selectively foraged in sites with greater abundance of large prey (particularly Dusky-footed Woodrats that are usually found in the edge ecotone region between late and early-seral areas in mixed-evergreen forest of northwestern California) as did Carey et al. (1992). Their study assumed that all night locations were foraging locations, which would exclude other typical activities. However, Carey et al (1989) concluded roosting and foraging sites were often synonymous (also see Carey et al 1992). Underestimates of availability of prey could affect estimates of selection, as could underestimates of abundance.

In the study of Ward et al. (1998), no prey species were significantly more abundant at foraging sites of nesting owls who successfully produced young, but the power of the test to detect relative differences was low because abundance varied greatly relative to sampling intensity (lack of power). However, there was a difference in abundances of woodrats in areas selected by breeders and non-breeders. Note that “Ward and Block (1995) found reproductive success of Mexican spotted owls...was not related to the abundance of a single prey species but rather by a suite of the more common prey” (Rosenberg et al 2001). Similarly, Rosenberg et al. (2001) noted that average reproductive performance might not be sensitive to flying squirrel abundance if Northern Spotted Owls switch prey. Spatial variability of primary prey may also influence owl’s reproduction (Ward et al. 1998). Relative abundance of woodrats and mice was significantly different among foraging areas within the same reproductive class - white-footed mouse abundance was similar among foraging areas where young owls were not produced compared to areas with young (Ward et al. 1998). Woodrat abundance did vary spatially with reproductive success. Hence, the data on prey effects on breeding and reproductive success are contradictory and no clear conclusions are available.

3.2 IMPORTANCE OF SECONDARY PREY SPECIES ON REPRODUCTION

Characteristics of spotted owl foraging behavior and densities of their prey suggest Spotted Owl populations are limited by prey (Forsman et al. 1984, Thomas et al. 1990, Carey et al. 1992, Rosenberg et al. 2003). As noted above, some studies have found evidence of a positive correlation linking reproductive success and the consumption of large prey (Barrows 1987,

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Laymon 1988, Thraillkill and Bias 1989, but see White 1996, Forsman et al. 2001, 2004). As Flying Squirrels are present throughout their range, and are a less patchy resource than woodrats, observational studies of reproduction have generally focused on them. Surprisingly, Rosenberg et al. (2003:1720) "...found only a weak relationship between flying squirrel abundance during fall and reproductive success the following spring". The measures that they considered, which included the proportion of nesting pairs, number of young per nesting attempt and overall number of young produced, may not be strongly affected by fall estimates of abundance because of over-winter changes in prey numbers. Prey switching would also reduce sensitivity of reproductive success to Flying Squirrel abundance. "The high spatial variability of prey abundance [such as Flying Squirrels, may influence reproductive success at the territory scale and] likely contributes to the spatial variation of reproductive success of the spotted owl (Ward et al. 1998)..." (Rosenberg et al. 2003:1721). However, lack of correlation with a primary prey species suggests that a different force may be driving reproduction (such as secondary prey, overall prey biomass, weather).

Some prey species may be critical to reproduction despite their limited frequency in the diet of Spotted Owls. For instance, Rosenberg et al. (2003) showed a striking correlation between annual reproductive success of owls and abundance of Deer Mice ($r^2 = 0.68$) despite the small contribution these make to the overall diet (less than 2%). Deer Mice abundance was most closely linked to the number of young per territory "relative to the proportion of pairs that attempted to nest... and the number of young per attempt..." (Rosenberg et al 2003:1720). This could be due to the influence of abundance or perhaps nutrient and energy value (Rosenberg et al. 2003). Alternatively, weather may simply affect both species, which could cause a correlation and not be direct causation (Rosenberg et al. 2003, See weather). Deer Mice in their study represented similar overall biomass as Northern Flying Squirrels, 160 ± 18.8 g/ha and 169 ± 13.9 g/ha respectively. However, Deer Mice had higher temporal variability (67.6% of process variation; spatial variation of 12.1%) with more than a 20 fold difference in abundance among years, while Flying Squirrels have greater spatial variability, which was year dependent (37.8%; 24.2% temporal variation) (Rosenberg et al. 2003). Great Gray Owls are known to deliver larger prey to nest and eat smaller food items thereby reducing foraging energy costs (Bull et al. 1989). Spotted Owls may have similar feeding behaviors; therefore, smaller prey items, like *Peromyscus*, may be underestimated in their importance in the diet of Spotted Owls (Forsman et al. 1984, 2001, 2004). Note that Ward (1990) also noted that mice were more abundant in areas selected for foraging by owls.

There is also evidence in Mexican Spotted Owls that reproductive success responds to a combination of prey instead of a single prey species (Ward and Block 1995). Ward (2001) found in Mexican Spotted Owls that reproductive success was most strongly correlated with abundance of small prey, despite an individual preference for large prey. Seamans and Gutiérrez (1999) also found evidence of an effect of white-footed mouse abundance on Mexican Spotted Owl reproductive success. Blakesley (*pers. obs.*) observed that a peak period of California Spotted Owl reproduction (including the production of triplets) coincided with a *Peromyscus* outbreak possibly due to a large Sugar Pine cone crop the previous fall. In California Spotted Owls in Kings Canyon National Park, L. Werner also noticed low reproduction rates in years with low small mammal capture rates in a nearby study area (*pers. comm. 2004*), perhaps indicating low abundance and availability of prey over a broad area. Overall low capture rates of small

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mammals may be indicative of synchronous fluctuations in the small mammal community, as found by Fryxell et al. (1998). However, without data to verify this, it remains speculation. Recent suggestions have been made that *Peromyscus* and perhaps other species (lagomorphs), which generally make up a small proportion of diet or are a seasonal resource, may influence reproductive success in Northern Spotted Owls (*minutes of March 2004 meeting*).

3.3 SURVIVAL

There are limited data on the influence of prey on Spotted Owl survival. As a predator, prey is essential and, obviously, is the ultimate factor determining survival. Juvenile rabbits and hares may supplement food resources during egg laying, incubation, brooding and early fledging, when the parents still provide for the young (mostly present in the diet March- September). However, juvenile Northern Flying Squirrels are weaned in mid-October to mid-November and may provide a good source of relatively naive prey for juvenile owls during a critical period of time for survival, represented by the dramatic increase of juvenile Flying Squirrels in the diet from September to early November (Carey 1991, Forsman et al. 1994).

Prey abundance is not generally measured on demographic study areas, and is not considered as a covariate in demographic analysis. The panel believes this is an important area for future investigation. We also recognize that these studies have not been done because of lack of funds rather than a failure of researchers to recognize the importance of these studies. European researchers routinely evaluate prey interactions in owl studies, but their systems are not as complex (low diversity of prey, cyclic rodents are easy to estimate relative abundance) as systems in the Pacific Northwest. Nevertheless, we feel this is a critical information gap that needs to be bridged. Meta-analysis of demographic parameters indicated low female survivorship may drive population change (Anthony et al. 2004). The analysis also indicates that populations at the northern distributional limit have lower survivorship. This may correlate with an increased reliance on a single prey species which is at a lower density compared to other areas in its range, and also to an increase in basic metabolic needs. This is consistent with the hypothesis that food availability or amount of food affects survival. Although this is ultimately true, we do not know if the lower survival of northern populations is related to prey or some other factor because there are no prey data (although see Carey et al. 1992 for demographic effects). Given the sensitivity of λ to small change in female survivorship, it is unlikely that there will be sufficient statistical power to detect the small, but critical changes that might result from changes in prey availability. Given these complex interactions, it is desirable that the effects of prey on demographic performance, including survival, be examined with a statistically well-designed research program.

4 THE EFFECTS OF NORTHERN SPOTTED OWLS ON PREY POPULATIONS

Spotted Owls have been suggested to depress prey populations (Rosenberg and Anthony 1992, Waters and Zabel 1995, Carey et al. 1992; Carey 2000a, Rosenberg et al 1996). Most of the support for this hypothesis comes from Northern Flying Squirrel studies, perhaps due to the extent to which that species has been studied relative to other prey species, but also perhaps due to the strong linkage between the two species in some regions. Flying Squirrels are the only prey

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species to account for more than 15% (by number) of the diet throughout the owl's range (Carey 1993, Forsman Presentation 2004, Forsman et al. 1984, 2001, 2004).

Only one study has been specifically designed to evaluate the effects of Spotted Owl predation on prey. Flying Squirrel densities before, during and after predation at different intensity levels support the hypothesis that heavy predation reduces population size by 50% with potentially long lasting effects (1-3 years) (Carey et al. 1992). Rosenberg and Anthony (1992), however, estimate only a 25% reduction in density based on the average Spotted Owl home range size of 1000 ha, two squirrels/ha (west slope of the Cascades, Oregon) and the consumption of 500 squirrels per year for one pair of owls (the percentage reduction could be larger in areas of low Flying Squirrel density). Forsman (*pers. comm.*) has pointed out that this estimate state to be based on a personal communication from him is in error. Forsman et al. (2004) found that, based on the actual composition of the diet in Oregon, Spotted Owls capture only 208 Flying Squirrels per year when not nesting and 271 per year when they were nesting. This would suggest lower overall prey depletion levels. Nevertheless, at least at local scales, Northern Spotted Owl predation appears to have the potential to depress Flying Squirrel populations.

By contrast, the woodrat literature contains only vague references that predation rates may be high. Substantial numbers of radio-tagged woodrats were killed by predators (both mammalian and raptor) in studies by Sakai and Noon (1993, 1997) in a northern California mixed-conifer mixed-evergreen forest (predators killed 50% of juveniles and 30% of adults (Sakai and Noon 1997)). In Douglas-fir transition forests, Bushy-tailed Woodrats experienced frequent local extinctions with variable prey abundance over time, which may be due to predation (Carey et al. 1992, Carey et al. 1999c, Carey 1991). Predators may be attracted to the clumped populations of Bushy-tailed Woodrats, which is a result of their social behavior (Escherich 1981, Carey et al. 1999c). The fact that woodrats are selectively preyed upon and experience local extinctions provides circumstantial evidence that high predation rates may depress populations for these species too.

5 INTERACTIONS BETWEEN SPOTTED OWLS, PREY AND HABITAT

As indicated above and in Chapter 5 (Habitat Associations), prey availability, numbers, and behavior may play a major role in determining habitat selection by Spotted Owls. Habitat type and structure directly influences prey species composition, abundance, and availability. Therefore, the composition of Spotted Owl diet may vary at the scale of individual territories as habitat varies.

Some prey species (e.g. Flying Squirrels, Red-backed Voles) are associated with forest structural complexity (including in old-growth, and in other forest types where this structure is maintained [e.g., old tree retention practices]). Other prey (notably Dusky-footed Woodrats) typically reach higher densities in younger forest, but are bimodal and more abundant in old growth and complex forest than in closed canopy young forests (Carey et al. 1997). Depending on the region and prey, stand structure and management may restrict or enhance prey abundance and availability to Spotted Owls. The ecology, including habitat association, of the primary prey species are described in the appendices.

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It has been suggested, based on empirical evidence, that Spotted Owls may select old-growth forest due to higher prey abundance (Forsman et al. 1982, 1984, Carey et al. 1990, Rosenberg and Anthony, 1992). Red-backed Vole abundance is higher in old-growth stands and in stands naturally regenerated from wildfire (such stands contained a large amount of coarse woody debris and snags that were “almost equivalent to old-growth stands” (Gillesberg and Carey 1991, Gilbert and Allwine 1991 and others)). However, studies on Flying Squirrels are more variable. While nearly all studies show higher squirrel densities in older forests, sometimes similar densities can be found in managed or second-growth stands (See Northern Flying Squirrel Appendix for details). Generally, older stands tend to have slightly higher, to much higher densities as stand age increases, but abundance among stands varies with inconsistent results (Carey 1995a, 2000; Rosenberg et al. 1996). Similar Flying Squirrel densities in both stand age-classes suggests that spotted owls avoid second-growth forests or use them in proportion to their occurrence because of low Flying Squirrel (prey) abundance (Forsman et al. 1984, Carey et al. 1990, Solis and Gutiérrez 1990, but see Carey and Peeler 1995).

Note however, that after intense foraging by breeding owls, prey densities in old growth can be reduced by up to 50%, while young forests with old growth legacies may hold high densities of flying squirrels. Both these effects will obscure differences between old growth and young forests (Rosenberg and Anthony 1992, Carey et al. 1992, Carey 1995a,b, 2000, Carey and Harrington 2002).

Differences in forest type also become important; for example Sitka spruce-western hemlock old growth may support fewer Flying Squirrels than Douglas-fir second growth. Douglas-fir dominated old growth may support twice as many Flying Squirrels (or more in the absence of owl predation) than does 40-70 year old second growth without legacies; however 80-100 year old young stands with substantial legacies may actually have the highest Flying Squirrel densities of all (Carey 1995a).

The relatively low use of young stands where woodrats are the primary prey (Sakia and Noon 1993, 1997), even though these young forest types have high woodrat abundance, also suggests that something other than prey abundance *per se* determines habitat selection. However, we note that the conclusions on relative prey abundance in different habitat types must be treated with caution. Empirical evidence (Carey et al. 1992, Rosenberg and Anthony 1992, Waters and Zabel 1995) suggests that Northern Spotted Owls may depress prey populations (see above), in which case local prey abundance may be expected to reflect predation pressure as well as prey-habitat associations. Hence failure to find an association of the abundance of a prey species with its expected preferred habitat is not necessarily strong evidence against such habitat preference (Carey, *pers. comm.*).

As noted above, foraging may be more easily carried out by Spotted Owls in some habitat types. “Radio-telemetry studies indicate that northern spotted owls are seldom located within brush stage clearcuts even though these habitats occur within or adjacent to the home ranges of most radio-tagged birds (Sisco 1990, Solis and Gutiérrez 1990, Carey et al. 1992, C. Zabel, U. S. Forest Service, *pers. comm.*)” (as cited by Sakai and Noon 1993:380). Note however Solis and Sisco commented on owls foraging along the edges of such clearcuts and old growth. Young

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forests have “low vertical diversity of vegetation and high canopy closure with few low structures beneath the canopy that would be suitable as hunting perches”, therefore are “structurally poor for sit-and-wait predators” (Carey et al. 1992:246). “Young second-growth forests often have high tree densities and homogeneous canopies which may impede flight and inhibit the ability of owls to capture prey” (Rosenberg and Anthony, 1992:165). Avoidance of such areas, even when they contain large numbers of a primary prey species (woodrats), is commonly attributed to the unavailability of prey to Spotted Owls (Carey et al. 1992, Rosenberg and Anthony 1992, Zabel et al. 1993, Thome et al. 1999 and others). In such areas, the effects of vegetation density, owl wing loading, and habitat use, mean that prey density is a poor predictor of prey availability.

In Southwestern Oregon, Spotted Owls sometimes selectively used young stands (Carey and Peeler 1995). Areas with high woodrat densities may attract Spotted Owls, based on pellets found in sapling/brushy poletimber stands (Carey et al. 1992, also Sakai and Noon 1993). “Because woodrats are arboreal (Linsdale and Tevis 1951), owls may also capture woodrats from trees in sapling/brushy poletimber type stands” (Sakai and Noon 1993:379). Occasional use of such young stands by Spotted Owls may be fostered by specific structure requirements, like remnant patches or available perches to hunt from (*Diller, minutes of March 2004 Meeting*).

In areas with woodrats, Spotted Owls might be expected to preferentially forage stands young enough to contain an abundance of woodrats, yet old enough to allow maneuverability (Thome et al. 1999). Some evidence suggests that 21-40 year-old redwood stands may have these characteristics (Thome et al. 1999). Indeed, territories in northwestern California with higher reproductive success had “lower proportions of the largest basal area class...and 61-80-year age class” and “higher proportions of 21-40-year-old stands” even though “spotted owl locations were characterized by lower proportions of 21-40-year-old stands compared to random locations” (Thome et al. 1999; 56-57). As this study focuses on redwood forests, result may not be applicable to other forest types or regions.

In some other areas, Spotted Owls select foraging areas around talus slopes (Forsman et al. 1984), or in riparian areas (Carey and Peeler 1995, Glenn et al. 2004), probably in response to Bushy-tailed Woodrat abundance. *Ward (1990)* showed that Northern Spotted Owls hunted in areas with higher abundance of both woodrats and mice. In the appendix we discuss the suite of factors that effect habitat selection by prey species.

Overall, there seems to be a strong effect of prey distribution on the selection of habitat by Northern Spotted Owl. Indeed, in the Klamath region at least, prey species identity is a better predictor of home-range size than is the proportion of older forest within the range (Zabel et al 1995).

5.1 HABITAT HETEROGENEITY, FRAGMENTATION AND EDGE EFFECTS

Areas where Spotted Owl diets contain large numbers of woodrats [or other non-old-growth species] may benefit from some level of forest heterogeneity. When woodrats were present, Spotted Owl foraging “site selection. . .was more pronounced at the ecotone between late and

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early seral stages” “where prey were more abundant” (Ward et al. 1998:89). Such results suggest that the spatial configuration and juxtaposition of forest types could have an important effect on prey species.

Lehmkuhl and Ruggiero (1991) estimated that less than 20% of original old-growth forests of the Pacific Northwest remained, with these remnants scattered over a fragmented landscape with successively decreasing patch sizes. They suggested that old-growth patches of 10 ha or less probably function entirely as edge with the loss of “essential old-growth attributes” (Lehmkuhl and Ruggiero 1991:37). However, Ruggiero et al. (1991) found complete biotic communities in small (10-40 ha) patches and field observation suggest many invertebrates and vertebrates with small ranges persist in even smaller patches (*Carey, pers. comm.*). Patches of old growth isolated by clearcuts eventually become legacies in second-growth forests, acting as refugia for species to colonize the second growth and promoting accelerated development of late-seral forest characteristics. There is no doubt that these patches are significant biological legacies, even if in themselves incapable of supporting spotted owls. Such forest fragmentation is regularly equated to habitat fragmentation, although the two terms are not equivalent (Franklin et al. 2002, *A. Franklin presentation 2004*). Fragmentation is often viewed to have negative connotations (reduced habitat cores, increased edge-effects, increased dispersal requirements, etc.)

Little attention has been focused on the effects of fragmentation on small mammal communities (Mills 1995, see review in Paton 1994, Rochele et al 1999) and, therefore, on the effect on predators of these small mammals. Effects associated with fragmentation and edge may include reduced functional size of remnant habitats, which further isolates small populations and increases the risk of extinction through factors of demographic, environmental, and genetic stochasticity and catastrophic events (reviewed by Lehmkuhl and Ruggiero 1991; Mills 1995). Edge effects also include increased susceptibility to edge-induced predation in birds (reviewed by Andrén and Angelstam 1988, Reese and Ratti 1988, Mills 1995) and presumably some small mammals (i.e. old-growth associated species such as Northern Flying Squirrels) (Mills 1995), cascading effects of the elimination of keystone species (see Northern Flying Squirrel section) (Lehmkuhl and Ruggiero 1991), interior and edge species competition (Anderson 1979, Askins and Philbrick 1987, Lehmkuhl and others 1991, Rosenberg and Raphael 1986, Lehmkuhl and Ruggiero 1991), changes in vegetation structure and composition (Lehmkuhl and Ruggiero 1991, reviewed by Saunders et al. 1991, see also Williams-Linera 1990, Mills 1995), and changes in microclimate including light, temperature and moisture that may affect the forest 50 meters to 160 meters from the forest edge (Lovejoy et al. 1986, Chen et al. 1992, Matlack 1993, Young and Mitchell 1994, Mills 1995).

Microclimatic changes at edges may include changes in light, moisture, and temperature which may in turn affect forest structure and prey food availability. Old growth may also act as a climatic buffer reflected by a high water-holding capacity (Franklin et al. 1981), increasing humidity used to maintain green foliage and access to chemically unbound water in the form of dew, rain, or condensation by fog (Meiselman and Doyle 1996, Carey 1991). In addition to the availability of water, increased moisture also tends to increase the abundance of mycorrhizal fungi, a source of food for several prey species including Red-backed Voles and Flying Squirrels (Slankis 1974, Tallmon and Mills 1994, Mills 1995, Carey 1991 and others). Truffles are also nearly absent from clearcuts and remnant edges (Mills 1995) unless coarse woody debris and

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ericaceous shrubs are retained in the clearcuts (Amaranthus and Perry 1994, Amaranthus et al. 1989, Perry et al. 1989). Edges also have increased quantities of coarse woody debris from fallen trees, blow downs and tree death associated with edge (Lovejoy et al. 1986, Williams-Linera 1990, Laurance 1991, Mills 1995). These fallen trees may not provide a short term benefit to species like Red-backed Voles (which show a preference for logs of advanced decay [Tallmon and Mills 1994, Mills 1995]). However, it is possible that over time, with increased decay, these may eventually prove beneficial.

California (Western) Red-backed Voles are “exceptionally rare in clearcuts” and their abundances were “strongly and negatively affected by clearcutting forests” which may have an effect for 10 to 60 years following clearcutting (Hooven and Black 1976; Taylor et al. 1988, Raphael 1988; Rosenburg et al. 1994, Mills 1995). The average number of unique individuals per trap in unlogged mature-to-old growth (more than 80 years old forests) was significantly greater than in clearcuts (Mills 1995). Overall, fewer individuals were captured in patches 0.6-2.5 ha (remnants) in size when compared to patches greater than 250 ha (control) but “the difference was only marginally significant ($p = 0.1$)” (Mills 1995:399). Remnant forest patches have high interior densities of Red-backed Voles that decrease toward the edge. Interior remnant densities may have six times as many Red-backed Voles compared to remnant edges and have higher densities than the control forests (Mills 1995). These density gradients mirror the effects seen in species confined to islands, due to limited emigration, and may “somewhat counteract” the negative effects of edge (Mills 1995). “...Small islands [or patches] will actually contain higher densities than larger ones... (review by Glicwicz 1980)” (Mills 1995:396). Results from DNA fingerprinting analysis showed that Red-backed Voles in remnants had lower genetic diversity in comparison to voles that were controls (i.e., those found in larger patches) (Mills 1993, 1995). Species associated with late-seral forest may follow a similar pattern to those of the Red-backed Vole.

Rosenberg and Raphael (1986) demonstrated that there was a decreasing frequency of Northern Flying Squirrel occupancy with decreasing stand size (Rosenberg et al 1996). 60-80% of stands that were >23ha were occupied, while there was <10% occupancy in stands <7ha (Rosenberg et al. 1996). As some prey species may go through periodic local extinctions, dispersal distances and barriers to dispersal need to be estimated to understand the likelihood of re-colonization and factors associated with isolation. Barriers to dispersal are plausibly species specific and may include restrictive landscape types, such as clearcuts and early seral habitat (Rosenberg et al. 1996)

In regions where Northern Flying Squirrels and other old-growth associated species are dominant in the diet, Northern Spotted Owls would be expected to show a negative effect of edge habitat (as compared to areas where woodrats predominate) (Anthony et al. 2002). Indeed, in fragmented Douglas-fir forests where flying squirrels are the predominant prey, Spotted Owl home ranges were larger compared to areas of “relatively intact forest of mixed-conifer” or areas with woodrats in the diet (Carey 1991, Carey et al. 1992, Ward et al. 1998).

By contrast, in areas where woodrats (or other prey associated with early-seral stages) are dominant in the diet of Northern Spotted Owl, (e.g. in the Roseburg area, Klamath Mountains), reproductive success was correlated with a high amount of edge between known Spotted Owl

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habitat and other habitat types (Anthony *et al.* 2002, Anthony *et al.* 2000, Franklin *et al.* 2000). This is consistent with high Dusky-footed Woodrat densities in early-seral habitat, where they have the opportunity to move into and through adjacent habitat types (Sakai and Noon 1993, 1997). Woodrats show no aversion to crossing sharp ecotones into old-growth, where they are more vulnerable to predation by Northern Spotted Owls (Sakai and Noon 1993). As woodrats may be unavailable to Spotted Owls in dense young forest (Forsman *et al.* 1984, Gutiérrez 1985, Carey *et al.* 1992, C. Zabel, U. S. For. Serv. pers. comm. cited in Sakai and Noon 1993, Rosenberg and Anthony 1992, Zabel *et al.* 1993), young stands may be important source areas for Spotted Owl prey. High availability of prey in edge ecotones may then increase Spotted Owl reproductive success. Radio-tagged woodrats were often killed by predators (both mammals and raptors) with many of the carcasses found in old forest adjacent to younger areas (Sakai and Noon 1993, 1997). Note that other studies show that in conifer/mixed evergreen zones, woodrats are abundant and resident in old growth (Carey *et al.* 1999, Raphael 1988, Rosenberg and Raphael 1986).

Zabel *et al.* (1995) verified a trend of a negative, linear relationship between home range size during the breeding season and the proportion of woodrats in the diet of Northern Spotted Owls. The proportion of Northern Flying Squirrels in the diet was positively correlated with home range. “Although many of the primary prey species are forest species, some edge habitats may benefit spotted owls because woodrats, rabbits, snowshoe hares, and pikas are common in non-forest types adjacent to forests” (Forsman presentation 2004).

Note that, while ecotones or forest edges may be important to Northern Spotted Owl foraging in some areas of the range, these same areas may also increase risks of Spotted owls from their own predators. See chapter 8 on Demography.

As we have shown, the effects of fragmentation or habitat heterogeneity varies with prey species and with geographic location. Given the additional complexities of multiple types of edges, it is unlikely that we will see any general pattern of fragmentation effects on Spotted Owl foraging or demographic success. For instance, fragmentation of Spotted Owl habitat in 40-48-year-old dense, closed canopy second growth Douglas fir or western hemlock stands without legacies and with little to no understory supports low numbers of woodrats, Flying Squirrels, hares, mice and vole. Clearly fragmentation in this type of habitat would produce the opposite effect as described above. It is therefore quite unlikely that results obtained in one habitat type or one part of the species range could be appropriately extrapolated to other areas, with different prey communities, forest structure, metabolic demands etc.

Given the complex interaction between forest structure, edge, and different prey species, we may expect both temporal and spatial variation in prey responses. For instance, in years of low woodrat abundance the net effect of edges on Spotted Owls might be negative in the southern part of the species' range. We may also expect different effects of heterogeneity at different spatial scales, depending on local prey composition and Spotted Owl territory size. This may be the case where prey populations become locally extinct (due to predation, fire or logging practices) and must be re-colonized from source populations.

6 COMPLEX INTERACTIONS AFFECTING NORTHERN SPOTTED OWLS AND THEIR PREY

Previous sections have shown that interaction between Spotted Owls and their prey may vary strongly, temporally, spatially, etc. It is also to be expected that other factors including weather, the presence of other predators, and forest management, will alter the interaction between Spotted Owls and their prey.

Northern Spotted Owls have been suggested to depress abundance of prey species (Carey et al. 1992). Therefore, it would be expected that some level of interspecific competition between Spotted Owls and other predators, including Barred Owls (see chapter 7), could affect Spotted Owl behavior and demographic parameters. For instance, long-tailed weasels (*Mustela frenata*) killed up to 32% of radio-marked Flying Squirrels in a winter in the Puget Trough (Wilson and Carey 1996, Carey 2000, 2002); other owls (e.g. *Bubo virginianus* and *S. varia*) and mustelids (*Martes americana* and *Martes pennanti*) also consume squirrels in large numbers (Carey 1991, Carey and Curtis 1996, Carey et al. 1996, Carey et al. 1999a, Carey 2000a). High predation rates by multiple predators have the potential of limiting prey populations. *Swingle and Forsman (2004)* followed 61 Red Tree Voles for an average of 70 days each. Twenty eight voles were eaten, 15 by weasels, three by owls, and 10 by other or unknown predators; these clearly indicate high levels of predation, which also could indicate competition between weasels and owls. Sakai and Noon (1997) followed 25 Dusky-footed Woodrats over a summer; six were killed by mammals and three by raptors. Spotted Owl behavior seems to track prey population size, avoiding depletion or areas of depletion with activities such as prey switching (Rosenberg et al 1996; Carey and Peeler 1995, also cited in Carey 2000a). “Multiple, abundant prey species allow spotted owls to use small home ranges (Carey et al. 1992) and may dilute predation pressure on any single species (or cause owls and other predators to focus on the most abundant and concentrated prey...)”(Carey et al. 1999c:76). Rosenberg et al. (2003) discuss for the possibility of switching behavior. Note that these are essentially options and hypotheses that are largely untested.

Complex interactions between trophic levels, are plausible, logically consistent, and perhaps important, but impossible to evaluate without a great deal of additional information. These interactions have a significant possibility of affecting diet choice, habitat use, demographic parameters and the application of forest management. Insight into this web of interactions will be time consuming, costly and difficult, but could alter management plans for the Spotted Owl.

7 MANAGEMENT EFFECTS ON FOREST STRUCTURE AND PREY

Sections below are in large part by the work of Carey. See appendix for the full document.

7.1 TIMBER HARVEST

“Timber harvest (clearcutting, partial cutting, and variable retention harvest systems) is a catastrophic disturbance with both short- and long-term effects on prey. Surprisingly

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many forest-floor small mammals respond positively to clearcutting in the short-term (Gunther et al. 1983). This is simply because any disturbance entails release of certain resources that then become available to various life forms, including small mammals. Cone- and seed-laden branches come to the forest floor to be exploited by diverse small mammals. With site preparation, these are often destroyed but colonization by grasses, forbs, and shrubs benefits diverse prey species (dusky-footed woodrats, deer mice, Oregon creeping voles [*Microtus oregoni*]) but the site might well be uninhabitable for a considerable period by the most arboreal rodents—red tree voles, flying squirrels, and Douglas’s squirrels. The degree to which legacies are retained during timber harvests is an important determinant of recolonization of the site by all life forms (Perry et al. 1989, Franklin et al. 2000), including the fungi that are the mainstay of the flying squirrel and California red-backed vole diets (*Clethrionomys californicus*) (Amaranthus et al. 1989). These legacies are diverse but include fungal mycelia (indeed intact forest floor microbial communities in patches of intact forest floor), coarse woody debris, intact vascular plants, and fungal and plant propagules. Intentional retention of legacies can accelerate the pace of ecosystem recovery (Franklin et al. 1997)—the rate of change in the new, self-organizing community will be rapid and prey species will be affected differentially. Dusky-footed woodrats are benefited by delayed recruitment of a dominant cohort of conifers and rapid recruitment by evergreen hardwoods; flying squirrels respond oppositely.

Perhaps the biggest consequence of conventional clearcutting comes not during the disturbance itself or the period of rapid reorganization, but later when the conifer canopy closes (the stem-exclusion or competitive exclusion stage, Oliver and Larson 1996, Carey et al. 1999c). Dense, closed-canopy second-growth without legacies can not only be devoid of exploitable prey populations (Carey 1995, Carey and Johnson 1995, Carey and Harrington 2001) but also poorly suited for owl roosting, foraging, or nesting (Carey et al. 1992). This period of low structural diversity can last >100 years (Carey et al. 1999c, Franklin et al. 2002) and can have profound effects on the capacity of the forest to develop biocomplexity in the future (Halpern et al. 1999, Carey 2003a). However, with legacy retention, patchy regeneration of multiple species including hardwoods, and natural disturbances during the periods following either a natural catastrophic disturbance by wind or fire or following partial cuts, the prey base can reach or exceed levels of diversity and abundance found in many old-growth stands and will be used for foraging and roosting by spotted owls (Carey et al. 1992, Rosenberg and Anthony 1992, Carey 1995, Glenn et al. 2004).”

(Carey 2004, see Appendix)

7.2 THINNING

“Thinning can be done in many ways and for many purposes and has differing and diverse consequences on the ecosystem including effects on the prey themselves, the plants that provide them with food and cover, the fungi that provide them with food, and the health and resilience of the forest (Waters et al. 1994; Carey et al. 1996, Colgan et al. 1999; Graham et al. 1999; Carey 2000b, 2001; Thysell and Carey 2000, 2001; Wilson

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and Carey 2000a, b, 2002b; Carey and Wilson 2001; Sullivan et al. 2001; Muir et al. 2002). All thinning has short-term negative effects on understory plants (mechanical destruction) and below-ground fungi (death of host trees and mechanical destruction). Heavy thinning in the Mixed Conifer/Mixed Evergreen Zone may benefit woodrats and deer mice in the mid-term, but to the detriment of flying squirrels. Conventional thinning in the Western Hemlock Zone may result in very low flying squirrel populations through negative effects on truffle production and arboreal travelways (Colgan et al. 1999, Carey 2000b) and reduced foraging by spotted owls (Meiman et al. 2003) for a long time while increasing numbers of forest-floor rodents (Wilson and Carey 2000). Conventional thinning, however, may result in uniform dense understories unfavorable to both flying squirrels and owl foraging in the midterm. Variable-density thinning, however, hold promise for acceleration of the development of spotted owl habitat and dense prey populations (Carey 1995, 2001, 2003a, Carey et al. 1999a,b; Carey and Wilson 2001; Muir et al. 2002) especially when appropriate attention is paid to decadence (snags, cavity trees, and coarse woody debris) (Bunnell et al. 1999; Carey et al. 1999a, b; Carey 2002). There maybe a short-term impact on truffle production, flying squirrel abundance, and owl foraging, the ecosystem recovers more quickly and begins to develop more quickly and completely than following conventional thinning. Variable-density thinning has all the positive effects of conventional thinning, such and increased growth of trees, crown differentiation, development of understory, and increased flowering and fruiting of understory plants (Harrington et al. 2002, Wender et al. 2004) that provide important ancillary foods to spotted owl prey (Carey 2000a) without the same extent of negative mechanical impacts, loss of canopy connectivity, loss of spatial heterogeneity, loss of woody plant diversity (variable-density thinning stresses multispecies management).” (Carey 2004, see Appendix)

Note that E. Forsman (*pers. comm.*) has expressed concern that regular thinning of young stands may make those stands unsuitable for Tree Voles. While there is no research that clearly documents the effects of thinning on Tree Voles, anecdotal evidence suggests thinning eliminates Tree Voles. Currently this relationship is not well documented.

7.3 FIRE SUPPRESSION

“Fires play different roles in different ecosystems (Franklin et al. 2002). Some forests and their fauna are well-adapted to fire—understory may be highly flammable, but quick to recover, and overstory trees may be quite fire resistant. This is true of the mixed-conifer forest of southwestern Oregon and northern California, where the old-growth is even more patchy and coarse-grained than the forests to the north, with the forest incorporating various evergreen hardwoods and hard-leaved shrubs especially supportive of dense woodrat populations. Forest to the north in western Oregon and Washington have increasing fire return intervals up through British Columbia where millennia might pass without catastrophic fire on some sites. Wind can be an important catastrophic disturbance in coastal forest, but intermediate disturbances due to wind, ice, snow, and disease may prove to be more important in forest developmental processes. East of the Cascades, forest historically appeared to have shorter, but spatially highly variable fire return intervals, often with frequent fires of low to moderate intensity. There, fire

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suppression has altered the ecology of the forests with fire-adapted understories of grasses, forbs, and low shrubs being replaced by flammable ladder fuels that may threaten catastrophic destruction of the forest when fire does occur. But eastside forests are diverse and conditions in dry site ponderosa pine (*Pinus ponderosa*) are too often generalized to other types. Furthermore, grazing and silviculture has compounded the changes in eastside forests (Graham et al. 1999). Franklin et al. (2002) point out the patterns in eastside forest are often misunderstood, with patches within late-seral forests interpreted as independent stands instead of part of the forest mosaic. The traditional forestry view of stands as homogeneous units of vegetation and the human tendency to reduce variability to one or two dimensions portend many management mistakes eastside. Researchers in interior forests have found that approaches to managing forest for diversity and support of top avian predators, like the goshawk (*Accipiter gentilis*) (Reynolds et al. 1992) entail much the same approach adopted by researchers seeking to solve the spotted owl/spotted owl prey base dilemma in Westside forests (Carey et al. 1992, 1999a, b, 2003a,b). The same will likely prove true in management of spotted owls and spotted owl prey eastside—spatial heterogeneity (patchiness) may prove to be the key to restoration of forest health and low intensity fire regimes while retaining patches of complex forests that benefit owls and their prey.” (Carey, see Appendix)

8 UNCERTAINTY

Though the overall quality of the currently available data is good, there are large gaps in the understanding of prey species ecology and their interactions with their environment, other small mammals, and predators. The lack of long term abundance estimates limits our ability to determine how abundance and availability changes over time and how these abundances affect reproductive success and survival in both territorial and “floater” owl populations. How the “floater” population interacts and competes for food with the breeding population and their foraging patterns are largely unknown. Although interactions between prey and owls are hypothesized to determine home range size, reproductive success, and limits to distribution, the details of such relationships are unknown. Results of present studies are habitat and species specific and have limited applicability throughout other parts of the range of the Northern Spotted Owl. The question of what is driving the system and what role intra- and interspecies competition plays is still uncertain.

One of the premises that run throughout the literature is to equate abundance with availability. The accuracy of this assumption is unknown and unlikely to be resolved as the question of how to measure true prey availability is probably unattainable.

Another major uncertainty concerns prey ecology and owl demography. A majority of the research effort has focused on flying squirrels and to a lesser extent woodrats. However, only a weak relationship between reproductive success and flying squirrel abundance has been shown. It is plausible that the answers lie in complex interactions of several prey species, and suggestions have been brought forward that perhaps the secondary prey may provide the essential nutrients and energy for reproduction. Prey species may also fluctuate in parallel affecting reproduction and survival (Bloxtton 2002, Fryxell et al. 1998). For now, these are just

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hypotheses that need to be examined. Currently, species other than Flying Squirrels and woodrats have received relatively little attention.

Little is also known about the factors that affect prey abundance, although it is known that their numbers fluctuate widely. How Spotted Owl diet changes in response to individual species fluctuations has not been assessed. As mentioned above, weather has been shown to affect prey litter size, sexual composition, and possibly mortality and reproductive success. Weather may also interact with other factors in a synergistic manner amplifying the effects on Spotted Owls. Interacting factors, such as weather and habitat heterogeneity, are likely to affect different prey species differently; the resulting effects on owls are likely to be complex and remain unknown.

9 SUMMARY AND CONCLUSIONS

In summary, Northern Spotted Owls feed mainly on forest small mammals, particularly arboreal and semi-arboreal species. The average prey size (74-116g) is relatively large compared to their body size. Though it has been suggested that there is a positive correlation between large prey and reproductive success, this relationship remains uncertain as there are conflicting results. There are also some results suggesting effects of secondary prey. Northern Flying Squirrels and woodrats comprise a bulk of the diet, but secondary species may be important for survival and reproduction. Deer Mice, Red Tree Voles, Red-backed Voles, and two species of lagomorphs are considered locally and/or seasonally important in the diet. Diet varies with the distribution and abundance of prey as well as with the type of habitat. Diet also varies locally, seasonally, and annually. Whether demographic variability in Northern Spotted Owls is affected by prey abundance, prey distribution or total prey biomass is unknown. Factors affecting the distribution and abundance of prey will vary with species, food source, season, biotic community (i.e., forest type and seral stage), geographic location, and sympatric species of competitors and predators. Weather may influence both owl and prey species directly and/or indirectly, though little data are available regarding its effect on prey. Interactions between Spotted Owls, prey and habitat are complex. Fragmentation or habitat heterogeneity affects prey species differently and is habitat and prey base specific. While habitat heterogeneity may benefit the owl in areas where woodrats are the primary prey, it has been shown to increase owl home range size in areas where Flying Squirrels dominate the diet. The extent to which these generalizations may be applied throughout the range of the owl is untested, and it is likely inappropriate to extrapolate the results from one area to another. The effects of fragmentation (both positive and negative) vary with prey species ecology and with temporal variation in abundance of species in the ecosystem. Further complexities include interactions amongst prey species, between predator and prey, and amongst predators that vary temporally, spatially, and with forest management. Overall there are large gaps in the information necessary to explain how prey species, weather, habitat, and forest management interact to affect Spotted Owl demography.

The basic conclusions set out in the 1990 listing of the Northern Spotted Owl are generally confirmed with recent information. The association of Spotted Owls with Northern Flying Squirrels and woodrats, their dominant prey items, is upheld, as are geographic differences in the importance of these prey types. Diet composition has remained relatively consistent, with annual and territorial variation as seen in previous studies.

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However, within these broad patterns, important new information has been brought forth. Prey species differ in their response to forest structure and conditions. It is clear that under some circumstances, habitat heterogeneity and presence of edge may be favorable for Spotted Owls by potentially increasing prey abundance and availability. The extent to which these result may be extrapolated is unknown at this time.

There is some evidence that suggests that secondary prey species influence Spotted Owls. However, this is speculative, and future research is needed to quantify their importance. Similarly, complex interactions between vegetation, prey species, Spotted Owls, other predators and weather are predicted to affect overall Spotted Owl population trends, but are not well understood at this point.

10 INFORMATION NEEDS

Information on some prey species and on complex interactions among the habitat-prey-predator communities is largely lacking despite the general acknowledgement that understanding prey ecology is essential when studying and managing a predator. The following is a brief list of information needs, which if these needs were met would be useful for future Status Reviews.

- Long-term, year round demographic studies of prey species, including abundance, ecology, limiting factors, weather effects, dispersal distances and local extinction characteristics, etc.
- Long-term seasonal diet variation in owls
- Diet and reproductive performance of owls at high elevation
- Individual territory and stand scale diet variation and their correlation to reproductive output of owls
- Foraging patterns and diet variation in the juvenile and “floater” population
- Weather effects on owl, owl behavior, and prey abundance at the territory scale
- Weather effects on prey species and Spotted Owls
- The effects of prey on demographic performance
- Influence of prey abundance and type during winter on subsequent Spotted Owl survival and reproduction
- Secondary prey species abundance and ecology
- Evaluating whether predator can limit or depress prey abundance
- Interspecific competition among prey species

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- Methods for increasing prey abundance and owl foraging in 2nd growth forests

Though Spotted Owl diets are well documented at broad regional scales, diet variation at the individual territory and stand scale are less well understood. Forsman et al. (2001) did compare diets at the territory scale, however, only 17 territories had sufficient sample size for the comparison and the sample size was too small to determine causes for individual prey use. Notably, “Ward et al. (1998) evaluated the relationship of Northern Spotted Owl reproduction with the abundance of prey at the level of the individual territory and found that because of the high spatial variability of prey abundance, they could not reliably estimate the abundance of prey at the scale of the individual owl” (Rosenberg et al. 2003). However, understanding diet variation at these scales will enhance our ability to directly correlate diet with reproductive success and survival. Along with general breeding season diet, non-breeding/winter diet and foraging patterns possibly determine nest initiation and survival. If Northern Spotted Owls are displaced to higher elevations by Barred Owl invasion, changes in diet and reproductive success may be needed to understand changes in demographic parameters, management strategies, extinction rates, and viable population estimates.

Currently, there are no long term, year-round demographic studies available on prey. This limits our ability to comprehend the influence of prey, both primary and secondary species, on owl demographics. We have no answers to questions like: What causes large prey fluctuations and how do they affect the Spotted Owl? Are there predictable patterns for different species? How do prey dynamics correspond with fluctuations in spotted owl reproduction? Do Spotted Owls depress prey? How do “floater” and juveniles use food resources and do they affect the breeding population? These questions are probably only answerable through long term monitoring and experiments like the Forest Ecosystem Study deliberately designed to test such hypotheses (Carey et al. 1999d). Long-term prey studies on owl demographic study areas could significantly increase our understanding of the interactions of the predator and its prey, leading to a substantial potential for changes in management plans. If management plans for prey species are to be developed to benefit owl populations, prey ecology needs to be examined. Factors limiting species abundance, such as weather, forest management effects, interspecies competition, dispersal distances and local extinction characteristics, will alter prey availability of the owl.

Currently, it is undetermined if weather affects owls directly, indirectly or both. It is plausible that weather may cause both owl and prey mortality and may affect the owl hunting efficiency. Different prey species may also react differently to various weather conditions. Investigations of the effect of weather on owls and a wide diversity of prey species at a territorial scale over broad regions should clarify these interactions and may explain some of the variation in owl reproductive success and survival. To this end, studies on climate change on weather and on metabolic demands may be useful.

Little attention has been focused on species other than Northern Flying Squirrels and to some extent woodrats, although some research in recent years has begun to focus on Red Tree Voles. It has long been thought that secondary prey species, a combination of prey species, or total prey biomass may affect owl reproductive success and survival. Secondary species may provide essential nutrients and energy required for reproduction.

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The ultimate question is ‘how do you manage a predator, like the Spotted Owl, without understanding and managing the species on which it depends?’ Habitat management may be sufficient, but at this point, we have a relatively poor understanding of the interactions between habitat, prey, and Spotted Owls. Ultimately, the question will boil down to: How does one manage for biocomplexity that provides multiple ecological services from spotted owl prey to spotted owls themselves to healthy, resilient forests.

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11 TABLES

Table 4.1: Percent composition of prey items †

	C Humboldt County, CA 850m-1340m	E South Coast Range, OR	A South-western OR 1350m-1740m	J Southwest Interior, OR	I Elliot Coast Range, OR	S Central Oregon Coast Range	H Central Coast Range, OR	F Blue River and McKenzie Ranger Districts, OR*	L Central Cascades, OR	M East Cascades, OR	D North-west Coast Range, OR	G North Coast Range, OR	K North Cascades, OR	B North-western WA, not Olympics 1840-1890 Oct. (Forest Area)	O Western Cascades, WA	P Eastern Cascades, WA	N Olympic Peninsula, WA	Q Sub-province N, Western Olympic Peninsula, WA** P<0.001	R Sub-province N, Eastern Olympic Peninsula, WA** P=0.001
Northern Flying Squirrel <i>Glaucomys sabrinus</i>	10.1	36	49.6	28.2	32.1	43.9	49.5	48.7	34.7	41.1	48.9	48.4	52.1	50.7	29.3	40.7	54.3	63.3**	45.2**
Bushy-tailed woodrat <i>Neotoma cinerea</i>			11.6		17.3			5.1			5.6			4.4	1.5	2.7	5.3	1.1**	9.6**
Dusky-footed woodrat <i>Neotoma fuscipes</i>	38.5																		
Woodrats		15.2		17.8		6.3	7.1		9.6	5.1	11.8	2.3							
Red tree vole <i>Arboreus longicaudus</i>	8.8	15.2		2.6			12.7	6.7	5.1		4.9								
Polioptila <i>polioptila</i>															3.7	0.8	0.2		
Red-Backed Toles <i>Captotriton</i>	2.1	2.8		6.8			2.2	12.8	10.7	12			26.9	6.8	10.3	6.4	5.8	12**	10.3**
Deer, Mice and Sice	6.8	6.2	3.9	4.9	10.4	10.9	10.5	4.9	6.4	4	13.9	17.3		20.6	17.2	6.5	11.3	15.6**	7.0**
Lepus spp - Rabbits and Hares		4.6		2.6	3.4	2.6	3.6	5.7	4.7	4.3	1	0.8		3	1.9	3.6	6.3	4.1	8.8
Lepus spp	10.7		20.9		17.2	13.3					3.4			0.7	4.7	3.9	1.7	0.9	2.6
Mammals	12.1	8	4.7	17.1	13.1	16.8	8.3	9.3	18.5	14.1	22.5	11.7	4.8	10	24.1	16.4	8.3	7.1	10
Undertified bird	4.6	3.6	1.6	5.7	6.1	4.8	3.9		4.1	3.9	3	3.6	13.9	2.8	6	4.4	6.4	6.4	5.3
Insect	7.6	2.4	0.8	4.3	0.5	1.4	2.1		3.1	15.4	1.8	1		1	2.5	10.6	0.4		
Miscellaneous				0.1			0.1		0.1	0.1		0.5		1			0.1	0.3	0.6

A Cutler and Hays, 1991 sampling dates: April-August, 1988 129 prey items (82 pellets), 4 territories

B 579 Hamer et al. 2001 sampling dates: mostly April-August 1986-1989 265 prey items, 28 territories

C Ward et al. 1997 sampling dates: March-September 1987-1988 495 prey item, 8 pairs, 1 single (9 territories)

D Anthony et al. 2000: 1992-1999 206 pellets

E Anthony et al. 2000: 1992-1999 318 pellets

F Rosenberg et al. 2003: 1987-1996, excluding 1993

*excluded, only spp >= 5% biomass in any given year.

G-M: Forsman Presentation 2004: 1970-2001

N-R: Forsman et al. 2001: 1983-96, after lumping territories with <20 prey N=64territories, O=12 territories, P=26 territories, Q,R=32 territories each.

S: Anthony et al. 1998: 1990-1995

†: Prey species greatly simplified from individual study reports. Standard errors, when reported, have been removed and species lists have compressed by added species totals together.

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Table 4.2: Percent biomass of prey items †

	C Humboldt county, CA. 850m- 1340m	I South Coast Range, OR	A South- eastern OR 1350m- 1750m	J Southwest Interior, OR	E Elliot Coast Range, OR	S Central Oregon Coast Range	H Centra l Coast Range, OR	F Blue River and McKenzie Ranger Districts, OR*	L Central Cascades, OR	M East Cascades, OR	D North coast, OR Coast Range	G North Coast Range, OR	K North Cascades, OR	B Northwest ern WA- not Olympics 244m- 1800m (forest area)	O Western Cascades, WA	P Eastern Cascades, WA	N Olympic Peninsula, WA
Northern Flying Squirrel <i>Glaucomys sabrinus</i>	9.3	38.6	53.5	30.1	30.2	46.1	58.2	48.8	45.7	56.3	57.5	52.4	74.5	58.1	45.3	52.5	58.6
Bushy-tailed woodrat <i>Neotoma cristata</i>			28.9		35.7			10.5			12.5			11.6	4.5	18.1	9.8
Dusky-footed woodrat <i>Neotoma fuscipes</i>	70.9																
Woodrats		37.1		48.7		14.5	16.1		20.7	12.4		24.9	5				
<i>Lifonocys</i> spp.	2.9		9.6		3.6	3.1					1			0.1	2.6	0.5	0.4
Red tree vole <i>Lepus sordidus</i>	1.7	4.2		0.6			3.8	3.7	2.3			1					
<i>Pipistrellus intermedius</i>															2	0.6	0.1
Red-backed Voles <i>Clethrionomys spp.</i>	0.4	0.6	1.5	1.3			0.5	5.5	2.7	3.5			8.2	1.6	3.6	2.2	1.2
Deer Mice and Mice	1.3	1.2	0.6	1	2.1	2.3	2.5	1.6	1.5	0.9	4.5	3.9		4.5	4.9	1.9	2.5
<i>Leporidae</i> Spp- Rabbits and Hares		11.6		5.9	13.9	12	9.9	10.7	12.5	12.7	4	2.2		13.4	8.9	9.4	16.3
Misc Mammals	11.5	4	4.8	8.8	11	17.9	5	9.6	11.7	10.9	17.7	10.4	1.7	9.3	22.7	10.6	6.2
Miscellaneous																	<0.05
Unidentified bird	2	2.8	1	3.5	3.5	4	3.9		2.8	2.4	1.8	4.3	10.7	1.4	5.5	3.5	4.8
Insect	0.1 TR		<0.1	0.1			0.1		0.1	0.9		0.1	0.50.05	<0.05		0.7	<0.05

A Cutler and Hays, 1991 sampling dates: April-August, 1988

B Hamer et al. 2001 sampling dates: mostly April-August 1986-1989 265 prey items, 28 territories

C Ward et al. 1997 sampling dates: March-September 1987-1988 495 prey item, 8 pairs, 1 single (9 territories)

D Anthony et al. 2000: 1992-1999 206 pellets

E Anthony et al. 2000: 1992-1999 318 pellets

F Rosenberg et al. 2003: 1987-1996, excluding 1993

*excluded, only spp >= 5% biomass in any given year.

G-M: Forsman Presentation 2004

N-R: Forsman et al. 2001: after lumping territories with <20 prey N=64territories, O=12 territories, P=26 territories, Q,R=32 territories each.

S: Anthony et al. 1998: 1990-1995

†: Prey species greatly simplified from individual study reports. Standard errors, when reported, have been removed and species lists have compressed by added species totals together.

SCIENTIFIC EVALUATION OF THE STATUS OF THE NORTHERN SPOTTED OWL