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DIETS AND FORAGING BEHAVIOR OF NORTHERN SPOTTED OWLS IN OREGON

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ABSTRACT.—We describe local, regional, and annual variation in diets of northern Spotted Owls (*Strix occidentalis caurina*) in Oregon based on 24 497 prey collected at 1118 owl territories in 1970–2003. The sample included 91.5% mammals, 4.3% birds, 4.1% insects, and 0.1% other prey. The diet included ≥131 species, including 49 mammals, 41 birds, 3 reptiles, 1 frog, 1 crayfish, 1 scorpion, 2 snails, and 33 species of insects. On average, 91.9 ± 0.3% (SE) of prey in the diet were nocturnal animals, 3.3 ± 0.2% were diurnal, and 4.8 ± 0.2% were active both day and night. Of the prey captured, 50.5 ± 0.8% were arboreal, 18.7 ± 0.7% were scansorial, 4.8 ± 0.2% were aerial, and 26.0 ± 0.7% were terrestrial. Mean mass of prey was 116.6 ± 6.5 g. Diets varied among owl territories, geographic regions, and years; but were generally dominated by four to six species of nocturnal mammals, including northern flying squirrels (*Glaucomys sabrinus*), woodrats (*Neotoma fuscipes* and *N. cinerea*), red tree voles (*Arborimus longicaudus*), western red-backed voles (*Clethrionomys californicus*), deer mice (*Peromyscus maniculatus*), or gophers (*Thomomys* spp.). Estimates of dietary evenness were low, indicating diets dominated by a few species of mammals. Forest management practices that produce healthy populations of arboreal and scansorial mammals such as flying squirrels, woodrats, and red tree voles should benefit northern Spotted Owls in Oregon and Washington.

KEY WORDS: *northern Spotted Owl*; Strix occidentalis caurina; *diet; prey selection*; *northern flying squirrel*; Glaucomys sabrinus; *red tree vole*; Arborimus longicaudus.

DIETA Y COMPORTAMIENTO DE FORRAJEO DE *STRIX OCCIDENTALIS CAURINA* EN OREGON

RESUMEN.—Describimos la variación local, regional y anual en la dieta de *Strix occidentalis caurina* en Oregon en base a 24 497 presas colectadas en 1118 territorios de los buhos para el reúodo 1970–2003. La muestra incluyó 91.5% de mamíferos, 4.3% de aves, 4.1% de insectos y 0.1% de otras presas. La dieta incluyó ≥131 especies, incluyendo 49 mamíferos, 41 aves, 3 reptiles, 1 rana, 1 pez, 1 escorpión, 2 caracoles y 33 especies de insectos. En promedio 91.9 ± 0.3% (SE) de las presas en la dieta fueron animales nocturnos, 3.3 ± 0.2% fueron diurnos y 4.8 ± 0.2% fueron activos durante el dia y la noche. De las presas capturadas, 50.5 ± 0.8% fueron arboreas, 18.7 ± 0.7% fueron scansorial, 4.8 ± 0.2% fueron aereas y 26.0 ± 0.7% fueron terrestres. La media de la masa de las presas fue de 116.6 ± 6.5 grm. Las dietas variaron entre los territorios de los buhos, las regiones geográficas y los años; pero fueron generalmente dominadas entne cuatro a seis especies de mamíferos nocturnos, incluyendo a ardillas voladoras (*Glaucomys sabrinus*), ratas (*Neotoma fuscipes* y *N. cinerea*) y *ratones (Arborimus longicaudus, Clethrionomys californicus, Peromyscus maniculatus,* y *Thomomys* spp.). Las estimaciones de la uniformidad de la dieta fueron bajos, indicando que la dieta fue dominada por unas pocas especies de mamíferos. Las prácticas forestales que producen poblaciones saludables de mamíferos como ardillas voladoras, ratas y ratones deben favorecer a los buhos en Oregon y Washington.

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Home-range areas, population cycles, and behavior of owls are greatly influenced by the distribution, density, and behavior of their prey. To understand these relationships, biologists need detailed information on the diet of the predator, including data on local and regional variation. Examination of the diet can provide many clues regarding foraging behavior, habitat selection, and degree of dietary specialization. This information is particularly important for understanding which types of prey are most important to a predator in different regions, and for understanding the numeric impact of the predator on its prey.

There have been numerous studies of northern Spotted Owls (*Strix occidentalis caurina*) in Oregon, Washington, and California. The earliest of these studies focused primarily on distribution, basic life history attributes, dispersal, and habitat selection of the species (e.g., Gould 1977, Barrows 1980, Forsman et al. 1984, Miller 1989, Carey et al. 1992, Miller et al. 1997, Zabel et al. 1995, Thrailkill et al. 1997). These pioneering efforts have been followed by nearly 20 yr of demographic studies, in which researchers used mark-recapture methods to estimate population trends of the owl (e.g., Burnham et al. 1994, Forsman et al. 1996, Franklin et al. 2000). During many of these studies, investigators routinely collected pellets from Spotted Owl roost areas to determine the composition of the diet. Some of these data have been published (e.g., Forsman et al. 1984, Barrows 1980, Thomas et al. 1990, Ward 1990, Zabel et al. 1995), but most of the data from Oregon have never been published. In 1996–2003, we contacted most of the researchers who have studied Spotted Owls in Oregon and solicited their assistance in compiling all of the available information on the diet of the Spotted Owl in Oregon. Here, we summarize results of that effort, compare regional, local, and annual variation in the diet; and estimate annual number of prey captured by individual Spotted Owls in different regions.

STUDY AREA

The study area included western Oregon and the eastern slopes of the Cascades Range (Fig. 1). With the exception of the lowland interior valleys of western Oregon, this region is characterized by mountainous terrain covered by coniferous forests. Forest composition is predominantly Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) in the Coast Ranges and western Cascades Range, mixed-conifer or mixed-evergreen forests in southern Oregon, and mixed conifer forests on the east slope of the Cascades (Franklin and Dyrness 1973). For our analysis we subdivided the study area into seven geographic regions (Fig. 1). Regional boundaries followed county lines, except that we used Interstate Highway 5 to subdivide samples from the Coast and Cascades ranges (Fig. 1). The eastern edge of the study area corresponded with the eastern limits of the range of the Spotted Owl in Oregon (Fig. 1).

METHODS

Pellets were collected below owl roosts, air-dried, and stored in labeled plastic bags until they could be analyzed. Some pellets were obtained from radio-marked owls during fall and winter (Forsman et al. 1984, Miller et al. 1997), but most were collected during the breeding season (March–August) when we visited historic nest areas to locate and band owls. With the exception of a few radio-marked owls (Forsman et al. 1984), no attempt was made to sample different individuals or territories randomly or systematically, although many territories were sampled in multiple years. Territories were identified based on occupancy by pairs of Spotted Owls, many of which were banded or radio-marked.

We based all analyses on the estimated number of prey or biomass of prey in each sample. We estimated the number of prey in each sample by counting skulls, mandibles, bones of the appendicular skeleton, or pieces of exoskeleton, whichever gave the highest count. In a few cases we also used hair or feathers to identify prey. To avoid double counting remains of large prey that appeared in several pellets, we combined remains from multiple pellets or pellet fragments found at the same roost on the same date. We used dichotomous keys (Maser and Storm 1970, Verts and Carraway 1984) and a reference collection of bird and mammal skeletons to identify remains in pellets.

We estimated biomass by multiplying the number of individuals of each species in a sample by the mean mass of the species, or by estimating and summing the unique mass of each prey item in the sample. The latter method was used only for large prey such as snowshoe hare (*Lepus americanus*), brush rabbits (*Sylvilagus bachmani*), and mountain beaver (*Aplodontia rufa*), because those prey types were mostly represented in our samples by small juveniles, and would have been overestimated if we used mean mass from museum specimens. For these species, we estimated mass based on comparisons of bones with specimens of known mass in our reference collection and we made the simplifying assumption that mass was linearly correlated with the size of bones in pellets. Estimates of mean mass for birds and mammals were obtained from Dunning (1993) and Verts and Carraway (1998; Appendix). For invertebrates, snakes, lizards, and amphibians, we used estimates of mean mass from local specimens or from similar species in the published literature (Smith and Murphy 1973; Appendix).

To evaluate when and where owls were foraging, we subdivided prey into groups based on their primary period of activity (nocturnal, diurnal, or both), and their primary activity zone (terrestrial, arboreal, scansorial, or aerial; Appendix). These classifications were based on information in Verts and Carraway (1998) as well as our own observations of animals in our study areas. For this analysis we classified mammals as arboreal if they nested

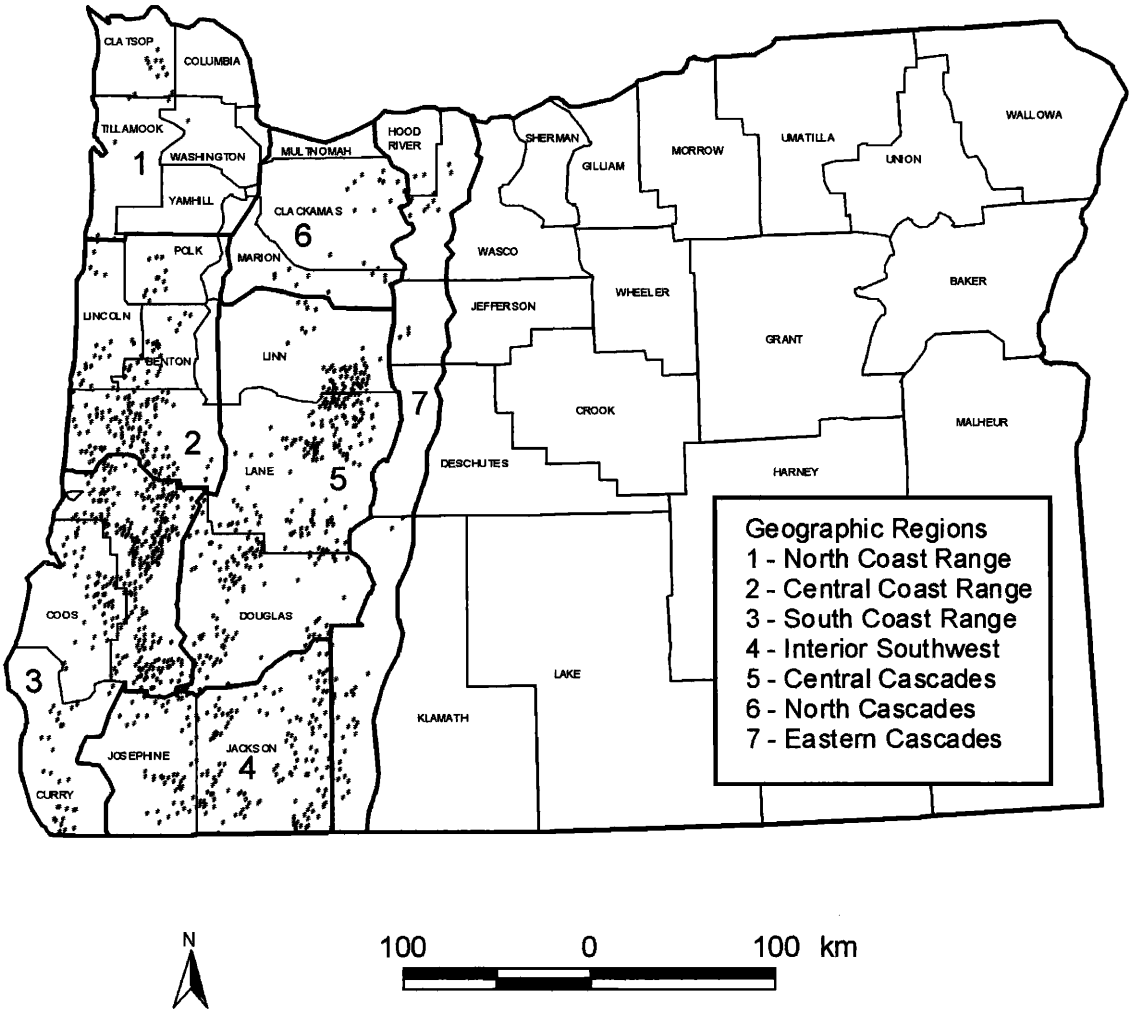

Figure 1. The Oregon study area, illustrating locations of 1118 northern Spotted Owl territories from which we collected data on owl diets, and seven geographic regions that we used for regional comparisons of diet. Boundaries of geographic regions followed county lines except that we used Interstate Highway 5 to divide samples from the Coast Ranges and Cascades Mountains north of Josephine County (solid dark line bisecting Douglas, Lane, Linn, Marion, Clackamas, and Multnomah counties).

primarily in trees, and scansorial if they spent much of their time climbing in trees but often nested on the ground (Appendix). This analysis provided a general measure of the amount of owl foraging that occurred in different time periods or activity zones, as we knew from field observations that prey were not always captured in their primary activity periods or activity zones (Sovern et al. 1994).

We used all prey remains to compile a list of species captured by northern Spotted Owls (Appendix). We estimated mean dietary composition by computing the diet in each owl territory, and averaging across territories to get the mean and SE for each prey category. Estimates of means were based on a subset of owl territories from which we obtained samples of $\geq$10 prey items, regardless of the number of years in which pellets were collected at a particular territory. We selected 10 as the minimum sample size for analysis after exploratory analyses with larger sample sizes (i.e., 20, 50) indicated that the choice of minimum sample size made little difference to our conclusions. We estimated mean mass of prey captured by each pair of owls by dividing the total biomass in the sample by the number of prey in the sample. Regional means were then estimated by averaging among pairs.

For comparisons of dietary composition among and within regions we subdivided the diet into 18 prey cate-

gories and used one-way analysis of variance to compare mean proportions of each prey type in the diet. Statistical tests of proportional data were based on arcsine transformations to better meet the assumptions of the tests (Sokal and Rohlf 1969). However, the results were virtually identical regardless of whether the data were transformed or not, so we present the untransformed data in all tables and figures.

To compare the evenness of the diet in different regions we used the reciprocal of Simpson's Index (Hill 1973). Simpson's Index (q) is equal to the sum of the squared values of the proportional abundances of all species (or groups) in a sample (Hill 1973). For a given sample, the range of q is from $1/N$ (all species equally abundant) to 1 (only one species in diet). Conversely, the reciprocal of Simpson's Index ($1/q$) ranges from 1–N, where 1 indicates a diet composed entirely of one species, and N is a diet composed of more than one species with all species equally represented in the diet. In our case, minimum and maximum values of $1/q$ were 1 and 18, where 1 indicted a diet composed entirely of 1 species, and 18 indicated a diet in which all 18 prey groups were equally represented. We estimated the mean $1/q$ for each region as $(\Sigma^N\ 1/q)/N$, where N = the number of territories in the sample.

We used χ^2 tests to examine among-year variation in the diet at individual territories that had samples of $\geq$20 prey in 2 or more years. For this analysis we lumped prey into seven groups: (1) Lagomorphs (*Lepus americanus, Sylvilagus bachmani*), (2) northern flying squirrels (*Glaucomys sabrinus*), (3) deer mice (*Peromyscus maniculatus*), (4) woodrats (*Neotoma fuscipes, N. cinerea*), (5) western red-backed voles (*Clethrionomys californicus*), (6) red tree voles (*Arborimus longicaudus*), and (7) all other prey.

We used linear regression to examine relationships between elevation and the numeric proportion of several species of small mammals in the diet. For this analysis we used a single estimate of the overall diet at each territory, regardless of when pellets were collected, and we used a single estimate of elevation at each owl territory, based on the elevation at the nest site or primary roost area. We determined elevations with altimeters, topographic maps, or a 30-m-resolution digital elevation map.

We estimated the number of prey captured per year by individual owls based on the assumption that a Spotted Owl of average mass (610 g) consumes 12% of its body mass (73.2 g) of food per day, or 26 718 g/yr. The number of each species captured per year was then estimated by multiplying the proportional biomass of each species in the diet by 26 718 and dividing by the mean mass of the species. The critical assumption in this analysis was the amount of food consumed per day. We could have used a more conservative estimate of 56–59 g/d (Weathers et al. 2001), but we chose to use a slightly higher estimate because we wanted to allow for the fact that Spotted Owls often discard stomachs, intestines, tails, and other parts of the prey that they capture. Thus, we felt that our estimate of 12% of body mass was a reasonable measure of the amount of prey captured per day, especially considering other data on food consumption of Spotted Owls (Forsman 1980) and other owls (Graber 1962). To estimate the number of prey captured per year in each owl territory we multiplied the number of prey captured per owl by 2.0 for non-nesting pairs, and 2.6 for nesting pairs with two young. Estimates of prey capture for adults with young assumed that nesting pairs fed their young for ca. 4 mo (Forsman et al. 1984), and that the mean biomass consumed per day was the same for juveniles and adults. The latter assumption was a simplification of the actual rate of daily food intake by juveniles, which was small at first, and then increased as juveniles matured.

All statistical analyses were conducted with Program SPSS (Version 11.5, SPSS Inc., Chicago, IL U.S.A.). We set the significance level for statistical tests at $\alpha = 0.05$. All means are expressed as $\bar{x} \pm 1$ SE.

RESULTS

Attributes of Prey. We identified 24 497 prey items from 1118 owl territories, including 547 territories with $N > 10$ (Fig. 1). The total sample included 91.5% mammals, 4.3% birds, 4.1% insects, and 0.1% other prey (Appendix). The sample included at least 131 species; 49 mammals, 41 birds, 3 reptiles, 1 frog, 1 crayfish, 1 scorpion, 2 snails, and 33 insects (Appendix). On average, 91.9 ± 0.3% of prey in the diet were nocturnal animals, 4.8 ± 0.2% were active both day and night, and 3.3 ± 0.2% were diurnal (N = 547). Of the prey captured, 50.5 ± 0.8% were arboreal, 26.0 ± 0.7% were terrestrial, 18.7 ± 0.7% were scansorial, and 4.8 ± 0.2% were aerial (N = 547). The percent of prey that were either arboreal or scansorial was 70.8% in the North Coast, 74.8% in the Central Coast, 77.8% in the South Coast, 64.8% in the Interior Southwest, 59.2% in the Central Cascades, 56.7% in the North Cascades, and 64.3% in the East Cascades. Mean mass of prey ranged from 91–142 g in the seven regions, and was 116.6 ± 6.5 g overall (Table 1).

Dietary Evenness. Mean estimates of dietary evenness ($1/q$) for all regions were near the lower end of the scale of possible values, indicating diets dominated by a few species in all regions (Table 2). Diets were most even in the Central Cascades, Interior Southwest, South Coast, and Eastern Cascades regions, and least even in the North Cascades, North Coast, and Central Coast regions (Table 2).

Regional Differences in Diet. Composition of the diet differed among regions for 16 of the 18 prey categories in Table 2 (P-values < 0.05). The only two categories that did not differ among regions were the "Bats" category ($P = 0.70$) and the category "Other," which included miscellaneous prey such as molluscs, snakes, lizards, and scorpions ($P = 0.21$). In some cases, differences among

Table 1. Mean mass (g) of prey captured by northern Spotted Owls in different regions of Oregon, 1970–2003. *N* is the number of owl territories sampled in each region.

REGION	*N*	MEAN ± SE	RANGE	95% CI
North Coast Region	9	123.6 ± 10.3	75–173	100–147
Central Coast Region	90	112.8 ± 3.2	41–213	106–119
Southern Coast Region	180	131.4 ± 2.7	55–317	126–137
Interior Southwest	75	142.1 ± 5.0	25–242	132–152
Central Cascades	154	108.5 ± 2.7	44–209	103–114
North Cascades	4	90.7 ± 14.1	67–130	46–136
East Cascades	35	106.7 ± 7.3	11–247	92–121
All areas[1]	7	116.6 ± 6.5		

[1] Grand mean of seven regional means.

regions were expected because some prey species, such as American pikas (*Ochotona princeps*) and red tree voles did not occur in all regions. In most cases, however, there were no obvious *a priori* reasons to expect regional variation in prey composition.

Although there was considerable variation among regions, the diet in all areas was composed mainly of four to six species of nocturnal mammals, including northern flying squirrels, woodrats, red tree voles, western red-backed voles, deer mice, or gophers (*Thomomys* spp.; Tables 2–3). Northern flying squirrels were the most common animal in the diet in most regions, averaging 28–52% of prey numbers and 30–74% of prey biomass (Tables 2–3). Woodrats comprised 11.7 ± 3.3% of prey numbers, 24.9 ± 5.3% of prey biomass, and were most

Table 2. Mean percent (±1 SE) of prey numbers in diets of northern Spotted Owls in seven different geographic regions of Oregon, 1970–2003. Sample size (number of owl territories with ≥10 prey items) is in parentheses. "T" indicates trace amount (<0.05%).

PREY[a]	NORTH COAST (9)	CENTRAL COAST (90)	SOUTH COAST (180)	INTERIOR SOUTHWEST (75)	CENTRAL CASCADES (154)	NORTH CASCADES (4)	EASTERN CASCADES (35)
Shrews	1.8 ± 1.4	0.9 ± 0.2	1.2 ± 0.2	2.8 ± 0.6	1.9 ± 0.3	2.5 ±2.5	1.5 ± 0.5
Moles		0.2 ± 0.1	0.1 ± 0.0	2.8 ± 0.6	1.0 ± 0.2		1.2 ± 0.5
Bats		0.2 ± 0.1	0.5 ± 0.1	0.3 ± 0.2	0.4 ± 0.1		0.3 ± 0.2
Rabbits/hares	0.8 ± 0.4	3.6 ± 0.5	4.6 ± 0.4	2.6 ± 0.4	4.8 ± 0.4		4.5 ± 0.8
American pika				0.1 ± 0.1	0.9 ± 0.2		0.3 ± 0.2
Douglas' squirrel	1.3 ± 0.8	0.6 ± 0.2	0.3 ± 0.1	0.1 ± 0.1	0.4 ± 0.1		0.1 ± 0.1
Chipmunks	2.1 ± 1.4	0.7 ± 0.2	0.6 ± 0.1	1.5 ± 0.3	1.4 ± 0.2	2.3 ± 2.3	1.3 ± 0.5
N flying squirrel	48.3 ± 3.6	49.5 ± 1.6	36.0 ± 1.2	28.2 ± 2.0	34.6 ± 1.2	52.1 ± 8.7	38.9 ± 3.1
Gophers	2.6 ± 1.3	0.6 ± 0.2	0.1 ± 0.1	5.4 ± 0.9	4.9 ± 0.6		6.5 ± 1.7
Deer mouse	17.3 ± 5.4	10.5 ± 1.1	6.2 ± 0.6	4.9 ± 0.6	6.1 ± 0.7		2.9 ± 0.7
Woodrats	11.1 ± 2.8	7.1 ± 0.8	18.2 ± 0.9	27.8 ± 2.4	9.5 ± 1.0	2.3 ± 2.3	8.2 ± 1.8
W red-backed vole		2.2 ± 0.4	2.8 ± 0.3	6.8 ± 0.7	11.0 ± 0.7	26.9 ± 8.7	10.4 ± 1.6
Red tree vole	4.8 ± 2.7	12.7 ± 1.1	18.2 ± 0.9	2.6 ± 0.7	7.7 ± 0.8		
Microtus spp.		1.2 ± 0.3	1.5 ± 0.2	2.5 ± 0.5	2.6 ± 0.4		1.1 ± 0.3
Other mammals	3.8 ± 1.8	3.9 ± 0.5	3.7 ± 0.3	1.4 ± 0.3	5.1 ± 0.4		3.9 ± 0.8
Birds	3.8 ± 1.2	3.9 ± 0.4	3.6 ± 0.3	5.7 ± 0.9	4.1 ± 0.3	13.9 ± 6.1	4.3 ± 0.8
Insects	1.0 ± 0.6	2.1 ± 0.7	2.4 ± 0.3	4.3 ± 1.2	3.5 ± 0.6		14.5 ± 3.1
Other	0.4 ± 0.4	0.1 ± 0.0	T	0.1 ± 0.1	0.1 ± 0.1		0.1 ± 0.1
Sum (%)	100.0	100.0	100.0	100.0	100.0	100.0	100.0
$1/q$[b]	3.1 ± 0.2	3.2 ± 0.1	3.9 ± 0.1	3.9 ± 0.2	4.5 ± 0.1	2.4 ± 0.2	3.7 ± 0.3

[a] See appendix for complete list of common and scientific names of prey.

[b] $1/q$ = reciprocal of Simpson's Index.

Table 3. Mean percent (±1 SE) of prey biomass in diets of northern Spotted Owls in seven different geographic regions of Oregon, 1970–2003. Sample size (number of owl territories with ≥10 prey items) is in parentheses. "T" indicates trace amount (<0.05%).

PREY[a]	NORTH COAST (9)	CENTRAL COAST (90)	SOUTH COAST (180)	INTERIOR SOUTHWEST (75)	CENTRAL CASCADES (154)	NORTH CASCADES (4)	EASTERN CASCADES (35)
Shrews	0.1 ± 0.1	0.1 ± T	0.1 ± T	0.1 ± 0.1	0.1 ± T	0.2 ± 0.2	0.1 ± 0.1
Moles		0.1 ± T	T	1.3 ± 0.3	0.6 ± 0.1		0.7 ± 0 3
Bats		T	T	T	T		T
Rabbits/hares	2.2 ± 1.1	9.9 ± 1.3	11.6 ± 1.0	5.9 ± 1.1	12.9 ± 1.1		12.3 ± 2 6
American pika				0.1 ± 0.1	1.4 ± 0.3		0.5 ± 0.3
Douglas' squirrel	1.9 ± 1.1	1.2 ± 0.3	0.5 ± 0.1	0.3 ± 0.2	0.7 ± 0.2		0.3 ± 0.2
Chipmunks	1.7 ± 1.1	0.5 ± 0.1	0.4 ± 0.1	1.2 ± 0.2	1.2 ± 0.2	1.4 ± 1.4	1.2 ± 0 5
N. flying squirrel	52.3 ± 3.9	58.3 ± 1.6	38.6 ± 1.6	30.2 ± 2.5	45.5 ± 1.7	74.5 ± 4.5	50.7 ± 4 2
Gophers	2.5 ± 1.3	0.5 ± 0.2	0.1 ± T	4.3 ± 0.7	4.8 ± 0.6		7.5 ± 2 3
Deer mouse	3.8 ± 1.5	2.5 ± 0.3	1.2 ± 0.1	1.0 ± 0.1	1.4 ± 0.2		0.7 ± 0.2
Woodrats	25.8 ± 4.7	16.1 ± 1.5	37.1 ± 1.6	48.5 ± 3.4	20.7 ± 1.8	5.0 ± 5.0	18.2 ± 3.4
W. red-backed vole		0.5 ± 0.1	0.6 ± 0.1	1.3 ± 0.2	2.7 ± 0.2	8.2 ± 3.3	2.8 ± 0 6
Red tree vole	1.0 ± 0.6	3.7 ± 0.5	4.2 ± 0.3	0.6 ± 0.2	2.2 ± 0.3		
Microtus spp.		0.3 ± 0.1	0.4 ± 0.1	0.6 ± 0.1	0.9 ± 0.1		0.4 ± 0 1
Other mammals	4.2 ± 2.4	2.4 ± 0.4	2.4 ± 0.3	0.9 ± 0.4	1.9 ± 0.2		1.0 ± 0 3
Birds	4.3 ± 2.3	3.9 ± 0.5	2.8 ± 0.3	3.5 ± 0.6	2.8 ± 0.3	10.7 ± 5.9	2.9 ± 0.9
Insects	T	T	T	0.1 ± 0.1	0.1 ± T		0.7 ± 0.4
Other	0.1 ± 0.1	T	T	T	T		T
Sum (%)	100.0	100.0	100.0	100.0	100.0	100.0	100.0

[a] See appendix for complete list of common and scientific names of prey.

important in the diet in the Interior Southwest and South Coast regions (Tables 2–3). Red tree voles comprised 6.6 ± 2.6% of prey numbers, and were most common in the diet in the South and Central Coast regions (Tables 2–3). Western red-backed voles were uncommon in the diet in all coastal regions, but comprised 7–27% of prey numbers in the Cascades and Interior Southwest regions (Table 2). Deer mice comprised 6.8 ± 2.1% of prey numbers, with the highest occurrence in the Central and Northern Coast ranges (Table 2). Gophers comprised 5–6% of prey numbers in the Interior Southwest, Central Cascades and Eastern Cascades regions, but were comparatively rare or uncommon in the diet in all coastal regions (Table 2). Chipmunks (*Tamias* spp.) and Douglas' squirrels (*Tamiasciurus douglasii*) together comprised 1–3% of prey numbers.

Brush rabbits and/or snowshoe hare comprised 1–5% of the prey captured and 2–13% of the biomass in the diet (Tables 2–3). Of 1010 rabbits or hares found in pellets, 826 (81.8%) were juveniles, 63 (6.2%) were subadults, 114 (11.3%) were adults, and 7 (0.7%) were of undetermined age. The estimated mean mass of individual rabbits and hares in pellets was 340 ± 6 g (range = 50–1400 g). American pikas occurred only in the Cascades and Interior Southwest regions, where they averaged less than 1% of prey numbers (Table 2).

Bats (Chiroptera), shrews (*Sorex* spp.), and moles (*Scapanus* spp.) were uncommon in the diet in all areas except the Interior Southwest Region, where the average diet included 5.6% shrews and moles (Table 2). The category "Other mammals" in Tables 2–3 included small mammals that we could not identify to species as well as a variety of small and medium-sized mammals that were uncommon in the diet. These included weasels (*Mustela ermınea, M. frenata*), heather voles (*Phenacomys intermedius*), white-footed voles (*Arborimus albipes*), mountain beaver, western gray squirrels (*Sciurus griseus*), ground squirrels (*Spermophilus beecheyi, S. lateralis*), spotted skunks (*Spilogale gracilis*), ringtails (*Bassariscus astutus*), and jumping mice (*Zapus trinotatus, Z. princeps*; Appendix).

Of 56 mountain beaver in pellets, 55 were juveniles, 1 was a small subadult, and 48 (85%) were captured in June or early July, when juvenile mountain beaver first began to emerge from their natal dens (Lovejoy 1972). The five ringtails found in

pellets were all small juveniles with estimated mass = 200–400 g. The only spotted skunk was a subadult, with estimated mass ca. 500 g.

Birds averaged 5.6 ± 1.4% of prey numbers and 4.4 ± 1.1% of prey biomass (Tables 2–3). Most small or medium-size birds that occurred in the forests of western Oregon were taken at least occasionally (Appendix). Of 540 birds identified to species or family, the most common were jays (17.6%), small owls (23.0%), woodpeckers (12.8%), grouse and quail (3.7%), and Varied Thrushes (*Ixoreus naevius*) or American Robins (*Turdus migratorius*) (24.4%). In most cases we could not differentiate between skeletons of Varied Thrushes and American Robins, so we combined them for analysis.

Insects were generally uncommon in the diet, except in the Eastern Cascades Region (Table 2). Of 1005 insects identified, the two most common species were the great grig (*Cyphoderris monstrosa*), a large scansorial cricket (41.0%), and the ponderous borer (*Ergates spiculatus*), a large woodboring beetle (24.8%). Great grigs occurred only in the Cascades Range, where we commonly heard them on summer nights, as they stridulated from elevated perches on tree trunks or tree limbs. Adult ponderous borers were noisy, clumsy fliers that frequently crashed into limbs while flying through the forest at night.

Other items in the diet included frogs (*Rana* spp.), snakes (*Thamnophis ordinoides, T.* spp.), lizards (*Sceloporus occidentalis, Elgaria coeruleus*), terrestrial snails (*Haplotrema vancouverense, Monedenia fidelis*), crayfish (*Pacifastacus leniusculus*), and scorpions (*Uroctonus mordax*). All of these were rare in the diet (<0.1% of total prey; Appendix).

Local and Annual Variation in Diet. Composition of the diet was highly variable among owl territories within regions (all *P*-values <0.05). While some of this variation was probably the result of small sample size, we found similar results even when we limited the analysis to territories with samples >50 (data not presented). This suggested that dietary variation among territories was due to factors other than sample size.

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 (Table 4). At the Oak Creek territory, deer mice varied from 0% of the diet in one year to 79% of the diet in another year (Table 4).

Table 4. Annual variation in diet at two different northern Spotted Owl territories in Oregon. Numbers indicate percent of total prey in each annual sample. Annual sample sizes are in parentheses.

	Oak Creek				Brummet	
Species/group	1970 (174)	1972 (89)	1973 (34)	1974 (95)	1990 (45)	1991 (47)
Rabbits/hares	1	2		2		2
N. flying squirrel	5	37	29	6	47	15
Deer mouse	8	15		79	5	8
Woodrats	2	8	3		13	9
W. red-backed vole		3				
Red tree vole	66	10	44	11	33	60
Other prey	18	25	24	2	2	6
Total %	100	100	100	100	100	100

Variation in Diet with Changing Elevation. In the Cascades Mountains (Central Cascades, North Cascades, East Cascades regions), predation on red-backed voles and gophers was positively correlated with elevation (red-backed vole $F_{1,191} = 27.7$, $P < 0.001$, $R^2 = 0.127$; gophers $F_{1,191} = 17.66$, $P < 0.001$, $R^2 = 0.085$). In the Central Cascades Region, predation on red tree voles was negatively correlated with elevation ($F_{1,152} = 32.6$, $P < 0.001$, $R^2 = 0.177$). Further examination of the data from the Central Cascades Region revealed that tree voles comprised only 2.3 ± 0.6% of the diet at territories above 975 m elevation ($N = 51$), compared to 10.3 ± 1.1% of the diet at territories below 975 m ($N = 103$). The analysis of elevational limits of tree voles was limited to the Central Cascades Region because tree voles were uncommon or absent in the diet in other regions in the Cascades, regardless of elevation.

Number of Prey Captured Per Year. The estimated mean number of prey captured per year was 271 ± 22 for non-nesting individuals, 543 ± 44 for non-nesting pairs, and 705 ± 57 for nesting pairs with two young (Table 5). Mean estimates for non-nesting individuals ranged from 217–384 prey/yr among regions, or 0.6–1.0 prey items captured/d (Table 5). The only region in which the estimated number of prey captured per year per non-nesting owl was >300, was the Eastern Cascades, which was the only region where the diet included large numbers of insects.

Table 5. Estimated number of prey captured per year by northern Spotted Owls in Oregon, 1970–2003. Numbers under geographic regions indicate the mean number of each prey type captured per individual owl. Numbers in the overall mean columns indicate the mean number of each prey type captured by individuals, non-nesting pairs, and nesting pairs with two young.

	Geographic Regions							Overall Mean		
Prey[a]	North Coast	Central Coast	South Coast	Interior Southwest	Central Cascades	North Cascades	East Cascades	Per Owl	Per Pair	Pair + 2 Young
Shrews	6.4	2.7	3.2	8.0	6.9	12.8	5.9	6.6	13.1	17.2
Moles	0.0	0.4	0.1	6.5	2.7	0.0	4.1	2.0	4.0	5.2
Bats	0.0	0.3	1.1	0.5	1.1	0.0	1.3	0.6	1.2	1.6
Rabbits/hares	1.8	8.4	9.9	4.9	10.7	0.0	10.8	6.7	13.3	17.4
American pika	0.0	0.0	0.0	0.2	2.0	0.0	1.1	0.5	0.9	1.3
Douglas' squirrel	2.2	1.4	0.7	0.4	1.0	0.0	0.4	0.9	1.7	2.3
Chipmunks	5.4	1.7	1.3	2.6	4.0	4.7	5.2	3.5	7.1	9.1
N. flying squirrel	107.7	119.8	79.2	61.7	94.0	153.1	113.4	104.1	208.2	270.6
Gophers	7.1	1.4	0.2	12.0	13.6	0.0	19.9	7.7	15.5	20.0
Deer mouse	46.8	30.5	14.6	11.9	18.1	0.0	10.8	18.9	37.9	49.1
Woodrats	24.3	15.1	34.8	46.1	19.4	4.7	11.5	22.3	44.5	58.0
W. red-backed vole	0.0	5.8	6.6	14.9	31.1	94.8	39.4	27.5	55.0	71.5
Red tree vole	9.8	38.5	43.1	5.4	23.9	0.0	0.0	17.2	34.5	44.7
Microtus spp.	0.0	3.2	4.0	6.8	10.9	0.0	5.3	4.3	8.6	11.2
Other mammals	17.4	9.9	10.1	3.5	7.4	0.0	4.5	7.5	15.1	19.5
Birds	13.4	12.1	8.6	11.0	8.8	33.3	7.5	13.5	27.0	35.1
Insects	1.6	8.0	4.8	20.7	12.7	0.0	143.1	27.3	54.5	71.0
Other	0.9	0.3	0.1	0.1	0.3	0.0	0.2	0.2	0.5	0.5
Total	244.7	259.4	222.4	217.4	268.6	303.4	384.4	271.4	542.9	705.8

[a] See appendix for complete list of common and scientific names of prey.

DISCUSSION

Composition of the Diet. Our results are similar to previous studies of Spotted Owl diets in Oregon, Washington, and northern California, in that diets were dominated by a few species of mammals, especially flying squirrels, woodrats, tree voles, red-backed voles, and juvenile lagomorphs (e.g., Forsman et al. 1984, 2001, Ward 1990, Cutler and Hays 1991, Hamer et al. 2001). The relative frequency of these mammals in the diet varied among regions, at least partly in response to regional differences in their abundance or distribution (Ward et al. 1998, Carey et al. 1999). Flying squirrels tend to be the most common item in the diet in western Washington and northwestern Oregon, whereas woodrats predominate in diets in southwest Oregon and northern California (Barrows 1980, Ward et al. 1998; Tables 2–3).

In contrast to diets of northern Spotted Owls, diets of Spotted Owls in the southwestern U.S.A. and Mexico tend to include fewer arboreal mammals, and more woodrats, terrestrial small mammals, bats, and insects (e.g., Duncan and Sidner 1990, Ganey 1992, Ward and Block 1995, Smith et al. 1999). These differences are probably due primarily to regional differences in prey availability. For example, flying squirrels are uncommon or absent in the mountains of southern California and the southwestern U.S.A.

As in our study, Smith et al. (1999) found that the majority of insects captured by Spotted Owls were large crickets and beetles. Apparently, these types of insects are easier for Spotted Owls to detect and capture or are taken selectively because of their relatively high biomass per unit effort. However, we also suspect that small, soft bodied insects are generally underestimated in analyses of owl pellets because they are more completely digested. It is possible that the apparent specialization on large insects is at least partially due to this bias.

Mean Prey Size. The mean mass of prey captured in this study and in previous studies of northern Spotted Owls (Ward et al. 1998, Forsman et al. 2001, Hamer et al. 2001) indicated that Spotted Owls feed on larger prey, on average, than most other large owls of the northern hemisphere. For example, the much larger Great Horned Owl (*Bubo virginianus*) and Snowy Owl (*B. scandiaca*), while capable of taking large prey, feed primarily on voles and other small prey in many areas where they occur (Watson 1970, Cromich et al. 2002). In an area where they were sympatric, Spotted Owls captured larger prey on average than Barred Owls (*Strix varia*; Hamer et al. 2001).

Regional Variation. All studies that have examined variation in diets of Spotted Owls have found differences among regions, territories, years, and seasons (e.g., Forsman et al. 1984, 2001, Laymon 1988, Ward 1990, Ganey 1992, Verner et al. 1992). As discussed by Forsman et al. (1984, 2001), Bull and Henjum (1990), and Ward and Block (1995), there are numerous factors that probably contribute to this variation, including (1) annual, seasonal or local variation in prey abundance, or availability, (2) individual variation in prey selection, (3) small sample size or unequal sampling effort, and (4) biased delivery of large prey to the female and young by nesting males. All of these factors may be important, but there is compelling evidence that spatial and temporal variation in prey populations and selective foraging by the owls are key factors influencing the diet (Forsman et al. 1984, Ward 1990, Carey et al. 1992, Ward and Block 1995, Ward et al. 1998). For example, a number of studies suggest that densities of dusky-footed woodrats and deer mice vary considerably among years (Linsdale and Tevis 1951, Spevak 1983, Ward and Block 1995, Rosenberg et al. 2003), and among and within owl territories (Ward et al. 1998). Carey et al. (1992) found that densities of northern flying squirrels and woodrats were highly variable in sample plots in different Spotted Owl territories in western Oregon.

Some of the regional differences observed in our study suggest interesting hypotheses regarding differences in abundance of small mammals. For example, regional differences in the abundance of red-backed voles in owl diets (Table 2) suggest that red-backed voles are roughly 5–10 times more abundant in the Oregon Cascades than in the central and northern Coast Ranges. However, data from field studies of red-backed voles suggest that they are actually more common in the Coast Ranges than in the Cascades (Aubry et al. 1991). The higher proportions of red-backed voles in owl diets in the Cascades, especially at higher elevations, may be due to prey switching, perhaps in response to lower numbers of alternate prey such as red tree voles at higher elevations (Corn and Bury 1986). It is also possible that terrestrial species like the red-backed vole are more difficult for Spotted Owls to capture in the Coast Ranges than in the Cas-

cades because of the dense brush that covers the ground in many areas in the Coast Ranges.

Timing of Foraging. In our study, and all previous studies of Spotted Owls, the diet was dominated by nocturnal animals, indicating that Spotted Owls forage primarily at night (e.g., Laymon 1988, Cutler and Hays 1991, Ward 1990, Verner et al. 1992, Ward and Block 1995). However, it has been well documented that Spotted Owls do forage during the day, especially if they are feeding fledged young (Miller 1974, Laymon 1988, Sovern et al. 1994). Laymon (1988) even suggested that Spotted Owls with fledged young traveled considerable distances away from their roost areas to forage during the day. However, Forsman et al. (1984), and Sovern et al. (1994) found that Spotted Owls moved very little during the day and that most diurnal foraging involved opportunistic attempts to capture prey near day roosts. Some diurnal prey were probably also captured when they were discovered at night, or when owls were foraging at dawn or dusk.

Seasonal Variation. Predation by Spotted Owls on large mammals and birds was restricted primarily to the spring and summer when large numbers of small, naive juveniles were available (Forsman et al. 1984, 2001, this study). This suggests that adult snowshoe hare, mountain beaver, and grouse are difficult for Spotted Owls to capture. Seasonal predation on juvenile hare and rabbits has been documented in many other owls, including Tawny Owls (*Strix aluco*; Southern 1970), Northern Hawk Owls (*Surnia ulula*; Rohner et al. 1995), Great Gray Owls (*Strix nebulosa*; Mikkola 1983), Barn Owls (*Tyto alba*; Marti 1988), Long-eared Owls (*Asio otus*; Marti 1976), and Snowy Owls (Watson 1970). Forsman et al. (1984) found that diets of northern Spotted Owls during winter became increasingly dominated by arboreal mammals as insects, birds, and juvenile Lagomorphs became less available, and many terrestrial small mammals either became less active above the snow, or went into hibernation.

Numbers of Prey Captured. Based on an analysis of the number of prey in individual pellets, Forsman (1980) estimated that individual Spotted Owls in the central Cascades of Oregon captured 0.7–1.05 prey/d during the fall, winter, and spring (September–April). These estimates, based on a different method than we used in this study, were nearly identical to our present estimate of 0.6–1.0 prey captured/d. Northern Spotted Owls are able to survive on such a low capture rate because many of the prey they capture are squirrels, woodrats, or lagomorphs that can be stored and eaten in several meals spanning 2 or more d (Forsman et al. 1984).

Prey Selection. Shrews, western red-backed voles, deer mice, and jumping mice are abundant mammals in many forest types in the Pacific Northwest (e.g., Aubry et al. 1991, Corn and Bury 1991, West 1991, Rosenberg et al. 2003, Gomez and Anthony 1998). In most areas they are much more numerous than the flying squirrels, woodrats, lagomorphs, gophers, and tree voles that form the core diet of northern Spotted Owls (Carey et al. 1992, Rosenberg and Anthony 1992, Ward et al. 1998). It is tempting to conclude, therefore, that northern Spotted Owls feed selectively on certain kinds of mammals, especially large mammals that are arboreal or scansorial (Barrows 1980, Forsman et al. 1984, Verner et al. 1992). Ward et al. (1998) presented evidence that Spotted Owls in northern California were preying selectively on large prey, especially woodrats. Ward et al. (1998) further suggested that the energetic reward per unit effort was higher for large prey like woodrats than for smaller prey, and that Spotted Owls were foraging preferentially in areas where woodrats were abundant. However, an alternative hypothesis is that the owls are not selecting for certain kinds of prey, but are simply preying opportunistically on prey that are easiest for them to capture, given the particular morphological attributes of the owl and the structural attributes of the dense forests in which they live. Experimental tests of these hypotheses have not been conducted, but it is obvious that Spotted Owls in the Pacific Northwest rely on a few species of nocturnal mammals for the majority of their food, and that forest management practices that produce healthy populations of these species should benefit Spotted Owls.

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Appendix. Species, common names, mean mass, activity codes, and total number of prey identified in pellets of northern Spotted Owls in Oregon, 1970–2003.

SPECIES	MEAN MASS (G)[a]	ACTIVITY CODE[b]	*N*
MAMMALS			22 421
Soricidae			
Sorex bendirii—Pacific water shrew	18 (1)	N, T	7
Sorex monticolus—dusky shrew	6 (1)	N, T	1
Sorex bairdii (obscurus)—Baird's shrew	9 (1)	N, T	1
Sorex palustris—water shrew	12 (1)	N, T	1
Sorex trowbridgii—Trowbridge's shrew	5 (1)	N, T	39
Sorex vagrans—vagrant shrew	5 (1)	N, T	8
Sorex pacificus (S. yaquinae)—Pacific shrew	7 (1)	N, T	17
Sorex spp.—unidentified shrew	7 (4)	N, T	243
Talpidae			
Neurotrichus gibbsii—shrew-mole	9 (1)	N, T	68
Scapanus latimanus—broad-footed mole	69 (1)	N, T	7
Scapanus orarius—coast mole	56 (1)	N, T	98
Scapanus spp.—unidentified mole	56 (4)	N, T	66
Chiroptera			
Myotis lucifugus—little brown myotis	6 (1)	N, F	2
Myotis yumanensis—Yuma myotis	6 (1)	N, F	1
Myotis spp.—unidentified myotis	6 (4)	N, F	3
Lasionycteris noctivagans—silver-haired bat	11 (1)	N, F	5
Eptesicus fuscus—big brown bat	15 (1)	N, F	7
Unidentified bat	10 (4)	N, F	49
Ochotonidae			
Ochotona princeps —American pika	171 (1)	B, T	85
Leporidae			
Sylvilagus bachmani—brush rabbit	50–750 (3)	B, T	224
Lepus americanus—snowshoe hare	50–1400 (3)	B, T	528
Unidentified rabbit/hare	50–900 (3)	B, T	258
Aplodontidae			
Aplodontia rufa—mountain beaver	100–550 (3)	N, T	56
Sciuridae			
Tamias amoenus—yellow-pine chipmunk	48 (1)	D, S	2
Tamias townsendii—Townsend's chipmunk	83 (1)	D, S	203
Tamias senex—Allen's chipmunk	85 (1)	D, S	21
Tamias spp.—unidentified chipmunk	83 (4)	D, S	26
Spermophilus beecheyi—California ground squirrel	626 (1)	D, T	2
S. lateralis—golden-mantled ground squirrel	169 (1)	D, T	1
Sciurus griseus—western gray squirrel	60–795 (3)	D, A	15
Tamiasciurus douglasii—Douglas' squirrel	221 (1)	D, A	103
Glaucomys sabrinus—northern flying squirrel	130 (1)	N, A	8826
Unidentified Sciurid spp.	130 (4)	U, S	17
Geomyidae			
Thomomys bottae—Botta's pocket gopher	142 (1)	N, T	2
Thomomys mazama—western pocket gopher	95 (1)	N, T	435
Thomomys talpoides—northern pocket gopher	102 (1)	N, T	7
Thomomys spp.—unidentified gopher	95 (4)	N, T	145
Muridae—Sigmodontinae			
Peromyscus maniculatus—deer mouse	22 (1)	N, T	1830
Neotoma cinerea—bushy-tailed woodrat	284 (1)	N, S	512

Appendix. Continued.

SPECIES	MEAN MASS (G)[a]	ACTIVITY CODE[b]	*N*
Neotoma fuscipes—dusky-footed woodrat	286 (1)	N, S	529
Neotoma spp.—unidentified woodrat	285 (4)	N, S	2258
Muridae—Murinae			
Rattus rattus—black rat	250 (3)	N, T	5
Muridae—Arvicolinae			
Clethrionomys californicus—western red-backed vole	23 (1)	N, T	1491
Phenacomys intermedius—heather vole	28 (1)	N, T	10
Arborimus albipes—white-footed vole	23 (1)	N, T	5
Arborimus longicaudus—red tree vole	26 (1)	N, A	2954
Microtus californicus—California vole	43 (1)	N, T	19
Microtus canicaudus—gray-tailed vole	36 (1)	N, T	6
Microtus longicaudus—long-tailed vole	56 (1)	N, T	28
Microtus oregoni—creeping vole	20 (1)	N, T	187
Microtus richardsoni—Richardson's vole	70 (1)	N, T	45
Microtus townsendii—Townsend's vole	54 (1)	N, T	25
Microtus spp.—unidentified vole	30 (4)	N, T	143
Muridae spp.—unidentified vole/mouse	25 (4)	U, U	616
Dipodidae			
Zapus trinotatus—Pacific jumping mouse	24 (1)	N, T	54
Zapus princeps—western jumping mouse	30 (1)	N, T	2
Procyonidae			
Bassariscus astutus—ringtail	200–400 (3)	N, S	5
Mustelidae			
Mustela erminea—ermine	55 (1)	N, T	43
Mustela frenata—long-tailed weasel	110 (3)	N, T	2
Mephitidae			
Spilogale gracilis—spotted skunk	500 (3)	N, T	1
Unidentified mammals	30–400 (3)	U, U	67
BIRDS			1042
Anatidae			
Aix sponsa—Wood Duck	658 (2)	D, F	1
Anatidae spp.—unidentified duck	658 (4)	D, F	3
Phasianidae			
Bonasa umbellus—Ruffed Grouse	100–576 (3)	D, F	11
Dendragapus obscurus—Blue Grouse	500–890 (3)	D, F	2
Grouse spp.	100–600 (3)	D, F	7
Odontophoridae			
Oreortyx pictus—Mountain Quail	224 (2)	D, F	10
Columbidae			
Patagioenas fasciata—Band-tailed Pigeon	392 (2)	D, F	1
Strigidae			
Asio otus—Long-eared Owl	262 (2)	N, F	1
Strix occidentalis—Spotted Owl	610 (2)	N, F	3
Megascops kennicottii—Western Screech Owl	169 (2)	N, F	59
Glaucidium gnoma—Northern Pygmy Owl	68 (2)	N, F	21
Aegolius acadicus—Northern Saw-whet Owl	83 (2)	N, F	44
Strigidae spp.—unidentified small owl	124 (4)	N, F	4

Appendix. Continued.

SPECIES	MEAN MASS (G)[a]	ACTIVITY CODE[b]	*N*
Picidae			
Colaptes auratus—Northern Flicker	142 (2)	D, F	30
Sphyrapicus ruber—Red-breasted Sapsucker	49 (2)	D, F	22
Picoides albolarvatus—White-headed Woodpecker	61 (2)	D, F	1
Picoides arcticus—Black-backed Woodpecker	69 (2)	D, F	1
Picoides pubescens—Downy Woodpecker	50 (2)	D, F	1
Picoides villosus—Hairy Woodpecker	66 (2)	D, F	9
Dryocopus pileatus—Pileated Woodpecker	287 (2)	D, F	6
Picidae spp.—unidentified Woodpecker	106 (4)	D, F	2
Tyrannidae			
Contopus cooperi—Olive-sided Flycatcher	32 (2)	D, F	2
Corvidae			
Cyanocitta stelleri—Steller's Jay	128 (2)	D, F	83
Perisoreus canadensis—Gray Jay	73 (2)	D, F	12
Paridae			
Poecile rufescens—Chestnut-backed Chickadee	10 (2)	D, F	4
Certhiidae			
Certhia americana—Brown Creeper	8 (2)	D, F	4
Sittidae			
Sitta canadensis—Red-breasted Nuthatch	10 (2)	D, F	8
Troglodytidae			
Troglodytes troglodytes—Winter Wren	9 (2)	D, F	5
Regulidae			
Regulus calendula—Ruby-crowned Kinglet	7 (2)	D, F	2
Regulus satrapa—Golden-crowned Kinglet	6 (2)	D, F	3
Turdidae			
Catharus ustulatus Swainson's Thrush	31 (2)	D, F	2
Catharus guttatus—Hermit Thrush	31 (2)	D, F	5
Ixoreus naevius—Varied Thrush	78 (2)	D, F	19
Turdus migratorius—American Robin	77 (2)	D, F	12
Turdus/Ixoreus spp.—thrush/robin spp.	78 (4)	D, F	101
Bombycillidae			
Bombycilla cedrorum—Cedar Waxwing	32 (2)	D, F	1
Parulidae			
Dendroica occidentalis—Hermit Warbler	9 (2)	D, F	4
Dendroica spp.—unidentified warbler	10 (4)	D, F	1
Thraupidae			
Piranga ludoviciana—Western Tanager	28 (2)	D, F	4
Emberizidae			
Pipilo maculatus—Spotted Towhee	40 (2)	D, F	6
Passerella iliaca—Fox Sparrow	32 (2)	D, F	1
Junco hyemalis—Dark-eyed Junco	18 (2)	D, F	8
Cardinalidae			
Pheucticus melanocephalus—Black-headed Grosbeak	42 (2)	D, F	1

Appendix. Continued.

SPECIES	MEAN MASS (G)[a]	ACTIVITY CODE[b]	*N*
Fringillidae			
Carpodacus purpureus—Purple Finch	25 (2)	D, F	1
Carpodacus spp.—unidentified finch	30 (4)	D, F	1
Loxia curvirostra—Red Crossbill	36 (2)	D, F	4
Carduelis tristis—American Goldfinch	13 (2)	D, F	1
Coccothraustes vespertinus—Evening Grosbeak	64 (2)	D, F	13
Unidentified birds			
Large bird	300–1000 (3)	U, F	6
Medium-size bird	60–299 (3)	U, F	185
Small bird	5–59 (3)	D, F	304
AMPHIBIANS			7
Rana spp.—frog spp.	30 (6)	B, T	7
REPTILES			12
Elgaria coerulea—northern alligator lizard	35 (6)	D, T	1
Sceloporus occidentalis—western fence lizard	10 (6)	D, T	2
Thamnophis ordinoides—northwestern garter snake	100 (6)	D, T	1
Thamnophis spp.—garter snake spp.	100 (6)	D, T	2
Unidentified snake	100 (4)	D, T	6
MOLLUSCS—GASTROPODA (Terrestrial snails)			7
Haplotrema vancouverense	7 (6)	B, T	2
Monedenia fidelis	5 (6)	B, T	2
Unidentified snail	5 (4)	B, T	3
INSECTS			1005
Orthoptera—Tettigoniidae (Camel crickets)			
Cyphoderris monstrosa—great grig	2.0 (5)	N, S	412
Orthoptera—Blattidae			
Cryptocercus punctulatus—wood-feeding cockroach	1.0 (5)	U, T	5
Parcoblatta spp. wood roach	1.0 (5)	N, T	1
Orthoptera spp.	1.0 (5)	U, U	2
Hemiptera—Pentatomidae (stink bugs)			
Chlorochroa spp.	0.3 (5)	U, U	1
Homoptera—Cicadidae (cicadas)			
Okanagana spp.	0.4 (5)	U, U	5
Neuroptera—Corydalidae (nerve-winged insects)			
Dysmichohermes disjunctus	2.0 (5)	N, U	4
Neuroptera—Raphidiidae (snakeflies)			
Raphidiidae spp.	0.2 (5)	U, U	3
Coleoptera—Cicindelidae (tiger beetles)			
Omus californicus	0.5 (5)	U, U	1
Omus dejeani	0.5 (5)	U, U	1
Coleoptera—Carabidae (ground beetles)			
Pterostichus amethystinus	0.3 (5)	U, U	1
Pterostichus lama	0.3 (5)	U, U	7
Pterostichus neobrunneus	0.3 (5)	U, U	1
Pterostichus spp.	0.3 (5)	U, U	1
Scaphinotus spp.	0.3 (5)	U, U	1

Appendix. Continued.

SPECIES	MEAN MASS (G)[a]	ACTIVITY CODE[b]	*N*
Coleoptera—Scarabaeidae (dung beetles)			
Bolboceras obesus	0.3 (5)	U, U	1
Pleocoma dubitalis	0.3 (5)	U, U	10
Coleoptera—Lucanidae (stag beetles)			
Ceruchus striatus	0.5 (5)	U, U	1
Sinodendron rugosum	0.5 (5)	U, U	4
Coleoptera—Buprestidae (metallic woodborers)			
Buprestis aurulenta	0.3 (5)	U, U	1
Coleoptera—Elateridae (click beetles)			
Ctenicera spp.	0.3 (5)	U, U	1
Coleoptera—Tenebrionidae (darkling beetles)			
Iphthimus serratus	0.5 (5)	U, U	1
Helops spp.	0.5 (5)	U, U	1
Coleoptera—Cerambycidae (long-horned woodborers)			
Ergates spiculatus—ponderous borer	3.0 (5)	N, U	249
Prionus californicus—giant root borer	2.0 (5)	U, U	5
Acmaeops proteus	0.5 (5)	U, U	1
Centrodera spurca	0.5 (5)	U, U	2
Plectrura spinicauda	0.5 (5)	U, U	1
Coleptera—Curculionidae (weevils)			
Dyslobus lecontei	0.3 (5)	U, U	3
Dyslobus spp.	0.3 (5)	U, U	10
Panscopus spp.	0.3 (5)	U, U	1
Coleoptera spp.—unidentified beetles	0.3 (5)	U, U	11
Lepidoptera—unidentified moths	0.5 (5)	U, U	2
Hymenoptera—Formicidae (ants)			
Camponotus spp.	0.1 (5)	U, U	12
Formica fusca	0.1 (5)	U, U	1
Formicidae spp.	0.1 (5)	U, U	1
Hymenoptera—Vespidae (hornets and yellowjackets)			
Dolichorespula maculata	0.1 (5)	U, U	1
Unidentified large insect	2.0 (5)	U, U	21
Unidentified small insect	0.3 (5)	U, U	218
CRUSTACEANS			
Pacifastacus leniusculus—crayfish	20 (6)	B, T	2
ARACHNIDA			
Uroctonus mordax—scorpion	3 (5)	N, T	1

[a] Source of mass estimate is in parentheses: 1 = Verts and Carraway 1998; 2 = Dunning 1993; 3 = mass of each individual estimated based on comparison with reference specimens of known mass; 4 = mean of all species in group, 5 = means based on estimates from similar species in this genus or group; 6 = estimates from local specimens.

[b] First letter indicates primary period of activity (D = diurnal, N = nocturnal, B = active both day and night, U = unknown). Second letter indicates primary area of activity (T = terrestrial, A = arboreal, S = scansorial, F = flying or aerial animal, U = unknown).

[c] Verts and Carraway (1998) split the "*Tamias townsendii* Complex" into three species, but we treated all *Tamias* species west of the crest of the Cascades as one species, because we could not tell them apart based on bone fragments in pellets.