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PREY OF BREEDING NORTHERN GOSHAWKS IN WASHINGTON

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ABSTRACT.—We identified 936 prey from food remains and pellets collected at 82 Northern Goshawk (*Accipiter gentilis*) nest sites in Washington from 1986–96. Mammals and birds constituted half of the prey by frequency and biomass throughout Washington, although birds were more prevalent ($P = 0.050$) in the diet of goshawks nesting in the Olympic and Cascade mountains of western Washington (53%), than in the Cascades of eastern Washington (47%). Douglas' squirrels (*Tamiasciurus douglasii*), grouse (*Dendragapus obscurus* and *Bonasa umbellus*), and snowshoe hares (*Lepus americanus*) were jointly the most frequently represented prey on the west side (41%) and east side (54%). Grouse and snowshoe hares accounted for the overwhelming majority of prey biomass in these respective areas (76% and 80%). Relative to other Northern Goshawk populations, goshawks in Washington appeared to prey on species from a similar number of genera, but they had a smaller food-niche breadth and they took larger-sized birds primarily due to their high consumption of grouse. Northern Goshawks in western Washington took prey in more equal numbers than those on the east side. Potential bias from examination of prey remains when compared to pellets reinforced the need for inclusion of observations on prey deliveries at nests when determining the diet of nesting Northern Goshawks.

KEY WORDS: *Northern Goshawk;* Accipiter gentilis; *diet; food habits; grouse; hare; Washington.*

Presas del azor en reproducción en Washington

RESUMEN.—Identificamos 936 presas de restos de comida y egagrópilas recolectadas en 82 nidos de *Accipiter gentilis* en Washington desde 1986–96. Los mamíferos y las aves constituyeron la mitad de las presas por frecuencia y biomasa en Washington, aunque las aves prevalecieron ($P = 0.050$) en la dieta de las montañas Olympic y Cascade del oeste de Washington (53%), al contrario de las Cascade del este Washington (47%). *Tamiasciurus douglasii, Dendragapus obscurus, Bonasa umbellus* y *Lepus americanus* fueron en conjunto las presas mas representadas en el oeste (41%) y este (54%). *Dendragapus obscurus* y *Lepus americanus* representaron la mayoría de la biomasa de presas en estas areas respectivas (76% y 80%). Con relación a otras poblaciones de azores del norte, los azores de Washington aparentemente depredaron a especies de un número similar de géneros, pero tuvieron nichos de alimentación de menor tamaño y una media mayor en el peso de las aves, lo cual es el resultado del alto consumo de *Dendragrapus obscurus* y *Bonasa umbellus.* Sin embargo, los azores del norte en el oeste de Washington tuvieron un uso mas equitativo de presas que los del este. El sesgo potencial del exámen de los restos de presas comparado con las egagrópilas refuerza la necesidad de incluir observaciones para la determinación de la dieta de los azores del norte en anidación.

[Traducción de César Márquez]

In the Pacific Northwest, the association of Northern Goshawks (*Accipiter gentilis*) with mature forests (Bull and Hohmann 1994, Hargis et al. 1994, Woodbridge and Detrich 1994) may be related to the structural characteristics of stands that optimize the availability of goshawk prey (Reynolds et al. 1992). Even where preferred prey are abundant, structural characteristics of habitat such as tree density and understory may reduce prey availability thereby affecting habitat selection and distribution of nests (Beier and Drennan 1997, DeStefano and McCloskey 1997).

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In Washington, nesting Northern Goshawks are distributed east and west of the Cascade Mountains, where there are different climates, forest communities and potentially different prey species and prey abundance. In western Washington, maritime influences at nest sites in the Olympic Mountains may further influence prey and diets of nesting Northern Goshawks. Diets in this area could be very different from that of goshawks nesting inland in the west Cascade Mountains. In the Coast Range of Oregon, for example, dense understory vegetation and high rainfall are believed to contribute to low populations of nesting goshawks due to their negative effects on prey availability (Reynolds and Wight 1978, DeStefano and McCloskey 1997). There is also the potential for dietary differences in Northern Goshawks nesting in managed stands in national forests and private timberland, where timber harvest may influence prey availability, and in national parks, where there is no timber harvest (Crocker-Bedford 1990).

Prey frequency, prey biomass, and food-niche breadth are commonly used to quantify raptor diets (Marti 1987). Methods of identifying raptor prey, including direct observation, examination of prey remains, and pellet examination provide data on diet, but each is subject to potential biases (Marti 1987). Here, we examine prey species identified in prey remains and pellets of nesting Northern Goshawks throughout Washington, with specific objectives to contrast prey frequency, biomass and food-niche breadth for populations of Northern Goshawks east and west of the Cascade Mountain crest; contrast major prey groups among subregions of these populations, and in areas potentially subject to timber harvest and those without harvest; identify differences in prey species or food-niche breadth peculiar to Washington Northern Goshawks relative to other areas in North America; and identify biases associated with identification of prey from remains or pellets.

STUDY AREA AND METHODS

Prey remains and pellets were collected at 38 Northern Goshawk nest sites in western Washington (16 in the Olympic Mountains, 22 in the Cascade Mountains) from 1986–96, and at 44 nest sites in the Cascades of eastern Washington (17 in the central Cascades, 27 in northern Cascades) from 1992–96 (Fig. 1). Prey and pellets were collected from nests, under nest trees, and at plucking posts. Most remains were collected incidentally during breeding surveys from the nestling stage through post-fledging, and nests were not sampled equally among years (65% sampled 1 yr, 24% sampled 2 yr, and 11% sampled >2 yr). Most nest trees were in late successional forests and were located in national forests (N = 58), national parks (N = 11), private timberland (N = 9), and state land (N = 4). In ownerships other than national parks, landscapes surrounding nests and within nesting territories were potentially subject to forest management. The actual degree of timber harvest within these territories was unknown.

The climate in western Washington is characterized by mild, wet winters and warm, dry summers. Forests are predominantly Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Sitka spruce (*Picea sitchensis*) is present at a few lower elevation nest sites on the west side of the Olympic Peninsula. Forests in the Cascades of eastern Washington, a region with cool winters and hot, dry summers, are dominated by stands of Douglas-fir, ponderosa pine (*Pinus ponderosa*), and western hemlock.

For each collection of prey remains, we attempted to identify the minimum number of individuals represented to species level from pooled occurrences in food remains and pellets. Matched hair and feather samples from prey and pellets were considered to represent the same individual, whereas counts of pooled bones and flight feathers allowed for identification of >1 individual. When we found skeletal remains of snowshoe hares (*Lepus americanus*) and grouse (*Dendragapus obscurus* and *Bonasa umbellus*), we estimated the age of individuals through size comparisons with museum specimens and the degree of bone fusion at joints. Ages of these species were used to estimate their respective contributions to prey biomass. Solid remains (e.g., skeletal remains, beaks) were identified from museum specimens (University of Washington, Seattle, or University of Wisconsin, Madison) or identification keys (Olsen 1964, 1972). Fur and feathers were matched to museum specimens or descriptions in field guides (Peterson 1947, Burt and Grossenheider 1976). Arthropods were excluded from data analyses. Our suspicion was that many insects found in prey remains, particularly beetles and ants, were consumed indirectly when small mammals and grouse were eaten. Presence of ants was correlated (r^2 = 0.18, P = 0.001) with the occurrence of Douglas' squirrels (*Tamiasciurus douglasii*) and chipmunks (*Tamias* spp.) in prey remains, and stomach contents of three whole carcasses of Douglas' squirrels and chipmunks contained numerous beetle shell fragments. Several pellets contained insect fragments mixed with fir needles, seeds, and grouse remains.

We reported mammalian and avian prey by frequency and biomass. Biomass estimates were derived from average weights of species from Reynolds and Meslow (1984) and other published sources (Table 1). Weights were derived for juvenile and adult age classes of snowshoe hares and grouse. For prey for which we could estimate biomass (i.e., not including unidentified birds or mammals), we calculated the mean weight of avian prey (MWAP), mean weight of mammalian prey (MWMP) and mean weight of total prey (MWTP). Food-niche breadth was calculated for prey genera using the following equation (Levins 1968):

$$B = \frac{1}{\Sigma P_i^2}$$

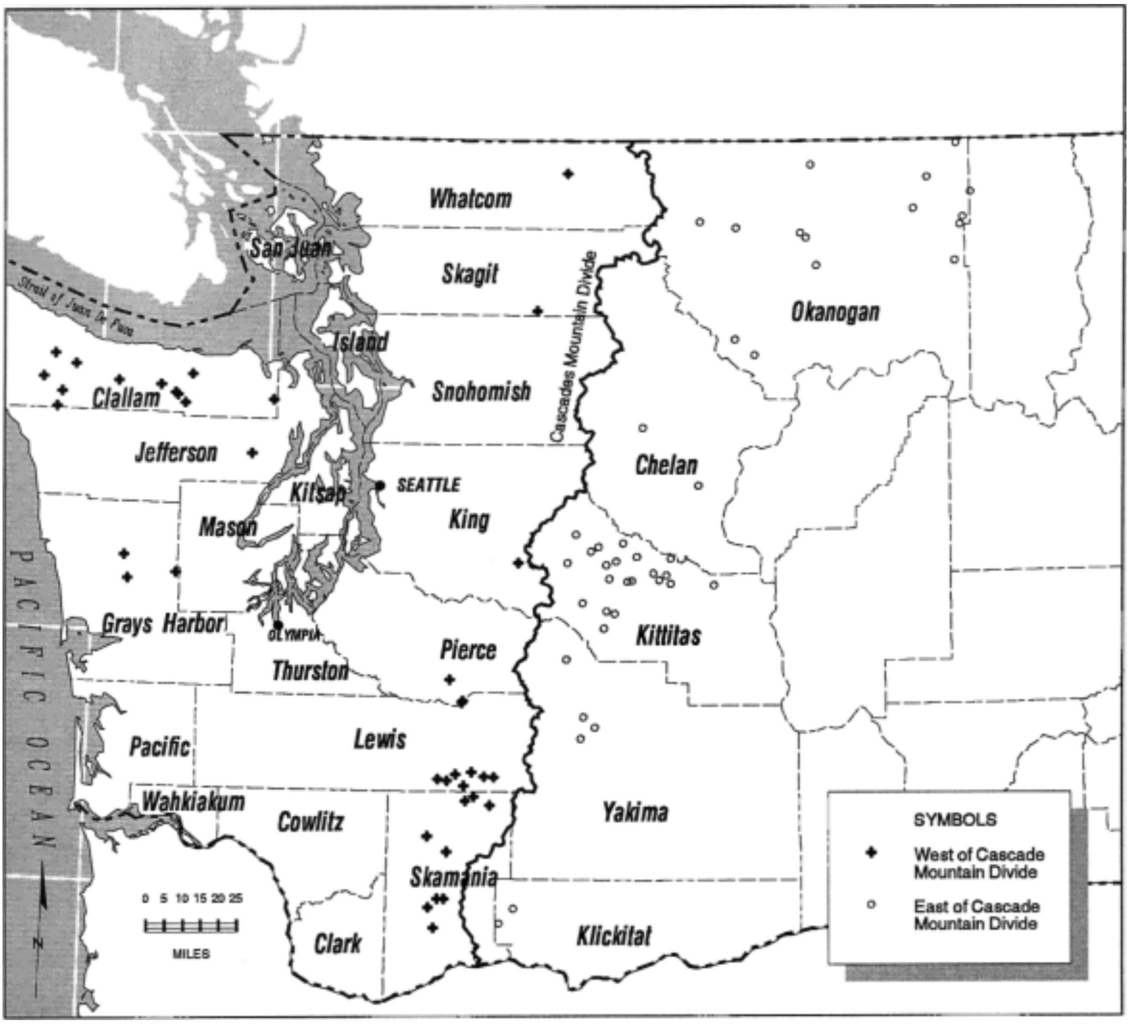

Figure 1. Locations of Northern Goshawk nest sites in Washington State where prey were collected from 1986–96.

where P_i was the proportion of prey in each taxon. In order to compare food-niche breadth with other northern goshawk research, breadth was standardized (Reynolds and Meslow 1984) using:

$$B_s = (B - 1)/(n - 1)$$

where n = the total number of taxons. Values approaching 1 were indicative of relatively more equitable use of prey, with lower values indicative of narrower diet breadth.

We used chi-square contingency tests at the $P = 0.05$ significance level for frequency comparisons of prey species and classes by region (east side and west side, and four study areas) and collection type (prey remains or pellet), ages of major prey species (adult or juvenile) by region, and major prey species by forest management status (managed or unmanaged). Unidentified mammalian and avian prey were excluded from analyses involving prey species, and prey with combined frequencies ≤ 1 were pooled into a miscellaneous species category.

RESULTS

We identified 936 prey at 82 Northern Goshawk nest sites. West side prey collections ($N = 38$ sites) accounted for 57% of identified prey, and east side collections ($N = 44$ sites) accounted for 43% of prey. An average of 11.0 (SD = 10.5, range = 1–53) individual prey items were identified per nest site. Prey remains were not identified beyond class for 11% of 465 mammalian remains and 17% of 471 avian remains. These remains typically consist-

Table 1. Northern Goshawk prey assessed from prey remains and pellets at 44 nest sites in the Olympic and Cascade mountains of western Washington, and at 38 nest sites in the Cascade mountains of eastern Washington from 1986–96.

			Western Washington			Eastern Washington		
Species	Common Name	Weight (g)[a]	No.	%[b]	% Biomass[c]	No.	%[b]	% Biomass[c]
Mammals								
Tamiasciurus douglasii	Douglas' squirrel	201.2	80	15.1	9.6	78	19.2	10.0
Lepus americanus	snowshoe hare	[d]	47	8.9	32.6	57	14.1	40.6
Tamias spp.	Unidentified chipmunk	80.5	31	5.8	1.5	26	6.4	1.3
Unidentified mammal	n/a		27	5.1	n/a	19	4.7	n/a
Glaucomys sabrinus	northern flying squirrel	167.0	28	5.3	2.8	12	3.0	1.3
Clethrionomys gapperi	red-backed vole	27.0[e]	7	1.3	0.1	9	2.2	0.2
Unidentified vole		25.0	13	2.5	0.2	1	0.3	<0.1
Peromyscus spp.	Unidentified mouse	19.5[f]	6	1.1	<0.1	6	1.5	<0.1
Thomomys mazama	Mazama pocket gopher	103.0[e]	5	0.9	0.3	0	0.0	0.0
Unidentified small mammal		n/a	2	0.4	n/a	3	0.7	n/a
Scapanus townsendii	Townsend's mole	140.0[e]	1	0.2	<0.1	1	0.3	<0.1
Thomomys talpoides	northern pocket gopher	104.0[e]	0	0.0	0.0	2	0.5	0.1
Ochotona princeps	pika	146.5[e]	1	0.2	<0.1	0	0.0	0.0
Sorex cinereus	masked shrew	4.5[e]	1	0.2	<0.1	0	0.0	0.0
Neotoma cinerea	bushytail woodrat	396.0[e]	0	0.0	0.0	1	0.3	0.3
Martes americana	marten	[g]	0	0.0	n/a	1	0.3	n/a
Subtotal			249	47.0	47.1	216	53.5	53.8
Birds								
Unidentified grouse		[h]	73	13.8	35.1	74	18.3	35.8
Unidentified bird		n/a	49	9.2	n/a	32	7.9	n/a
Cyanocitta stelleri	Steller's Jay	106.6	46	8.7	2.9	16	4.0	1.1
Colaptes auratus	Northern Flicker	148.8	26	4.9	2.3	23	5.7	2.2
Ixoreus naevius	Varied Thrush	79.3	25	4.7	1.2	4	1.0	0.2
Turdus migratorius	American Robin	81.2	18	3.4	0.9	1	0.3	<0.1
Dendragapus obscurus	Blue grouse	[i]	11	2.1	7.1	5	1.2	2.7
Picoides villosus	Hairy Woodpecker	48.3	3	0.6	<0.1	8	2.0	0.2
Unidentified woodpecker		165.2[j]	7	1.3	0.7	3	0.7	0.3
Perisoreus canadensis	Gray Jay	89.4[k]	9	1.7	0.5	0	0.0	0.0
Unidentified passerine		168.7[l]	3	0.6	0.3	6	1.5	0.6
Bonasa umbellus	Ruffed Grouse	550.0[m]	3	0.6	1.0	3	0.7	1.1
Varied Thrush or American Robin		80.0	1	0.2	<0.1	3	0.7	0.2
Spinus pinus	Pine Siskin	13.0	1	0.2	<0.1	3	0.7	<0.1
Corvus spp.	Northwestern or American Crow	460.0[f]	2	0.4	0.6	1	0.3	0.3
Unidentified owl		259.0[n]	0	0.0	0.0	3	0.7	0.5
Bombycilla cedrorum	Cedar Waxwing	33.5	1	0.2	<0.1	1	0.3	<0.1
Glaucidium gnoma	Northern Pygmy Owl	42.8[o]	1	0.2	<0.1	0	0.0	0.0
Junco hyemalis	Dark-eyed Junco	17.6	1	0.2	<0.1	0	0.0	0.0
Loxia leucoptera	White-winged Crossbill	24.1[p]	1	0.2	<0.1	0	0.0	0.0
Sturnus vulgaris	European Starling	74.5	1	0.2	<0.1	0	0.0	0.0
Dryocopus pileatus	Pileated Woodpecker	282.0	0	0.0	0.0	1	0.3	0.2
Sphyrapicus varius	Red-breasted Sapsucker	48.3[q]	0	0.0	0.0	1	0.3	<0.1
Anas platyrhynchos	Mallard	1185.0[f]	0	0.0	0.0	1	0.3	0.8
Subtotal			282	53.4	52.6	189	46.9	46.2

ed of hair samples and feather shafts, but no skeletal remains.

At least 13 species of mammals and 18 species of birds were identified in prey remains (Table 1). Douglas' squirrels, grouse (unidentified grouse, Blue Grouse [*Dendragapus obscurus*] and Ruffed Grouse [*Bonasa umbellus*]), and snowshoe hares were the most common prey species, and together accounted for 54% of all prey in eastern Washington and 41% in western Washington. They were also the most widely distributed prey, with Douglas' squirrels identified at 69% of the 82 nest sites statewide, grouse identified at 57% of nest sites, and snowshoe hares identified at 61% of all nest sites. Other species that accounted for ≥3% of prey by frequency in both eastern and western Washington included chipmunks (*Tamias* spp.), northern flying squirrels (*Glaucomys sabrinus*), Steller's Jays (*Cyanocitta stelleri*) and Northern Flickers (*Colaptes auratus*). Passerines accounted for 28% of west side prey and 18% of east side prey.

Mammals and birds composed equal proportions (50%) of goshawk prey throughout Washington by frequency. However, proportions of mammals and birds in prey remains differed between western and eastern Washington ($\chi^2 = 3.81$, df = 1, $P = 0.050$). Birds were more prevalent than mammals in prey remains of west side goshawks (53% vs. 47%), while mammals more prevalent than birds on the east side (53% vs. 47%). Relative to other birds, proportions of grouse, Steller's Jays, Varied Thrush (*Ixoreus naevius*), American Robins (*Turdus migratorius*), and Gray Jays (*Perisoreus canadensis*) were greater in west side than east side avian remains ($\chi^2 = 38.89$, df = 5, $P = 0.001$). Conversely, relative to other mammals combined, proportions of Douglas' squirrels and snowshoe hares in east side remains were greater than in western Washington ($\chi^2 = 6.96$, df = 2, $P = 0.031$).

Mammals and birds accounted for similar proportions of prey biomass throughout Washington (51% and 49%, respectively). While Douglas' squirrels were the most prevalent species in prey remains, they accounted for only 10% of prey biomass on both east and west sides (Table 1). Snowshoe hares and combined grouse species were the most important to overall biomass. These taxons accounted for 80% of all prey biomass in eastern Washington, and 76% of all biomass in western Washington. Adult specimens accounted for much of the biomass; adult snowshoe hares composed 87% of 67 hares that were aged, and adult grouse composed 75% of 113 grouse remains that were aged. There was no difference in age of captured snowshoe hares ($P = 0.458$) or grouse ($P = 0.410$) between eastern and western Washington. Other prey species contributed <3% of overall biomass throughout Washington (Table 1).

Mean weight of mammalian ($N = 399$), avian ($N = 390$) and total prey was 411, 415, and 413 g,

←

[a] Weight of individual prey item used in biomass estimation. From Reynolds and Meslow (1984) unless noted otherwise.

[b] Percent of prey in overall diet.

[c] Percent of prey biomass to overall biomass.

[d] Weight of juvenile (150 g) and adult *L. americanus* (1500 g) from Forsman et al. (1984); mean weight of adult and juvenile used to estimate weight of unaged specimens. Remains included 27 adults, 3 juveniles and 16 unaged specimens.

[e] Burt and Grossenheider (1976).

[f] Steenhof (1983).

[g] Mass for this prey not used in estimate of biomass due to the inherent bias; guard hairs found in pellets likely from a scavenged carcass.

[h] Average weight of adult (1053 g) and juvenile (909 g) *D. obscurus* (Zwickel et al. 1966) and adult (575 g) and juvenile (550 g) *B. umbellus* (Bump et al. 1947); mean weight of adults and juveniles used to estimate weight of unaged specimens. Remains included 37 adults, 9 juveniles and 30 unaged specimens.

[i] Average weight of adult and juvenile *D. obscurus* (Zwickel et al. 1966); mean weight of adult and juvenile used to estimate weight of unaged specimens. Remains included 4 adults, 1 juvenile and 7 unaged specimens.

[j] Average weight of *P. villosus* and *D. pileatus.*

[k] Average weight of unidentified jay from Reynolds and Meslow (1984).

[l] Average weight of passerines identified to species.

[m] Average weight of juvenile *B. umbellus* (Bump et al. 1947). Remains were of 1 juvenile.

[n] Used weight of medium-sized owl (*Asio otus*) from Karalus and Eckert (1974).

[o] Karalus and Eckert (1974).

[p] Average weight of White-crowned Sparrow (*Zonotrichia leucophrys*) from Reynolds and Meslow (1984).

[q] Used weight of *P. villosus* from Reynolds and Meslow (1984).

respectively. The standardized food-niche breadth (FNB) was 0.27, based on frequencies of prey among 20 genera. However, goshawks in western Washington had a more equitable use of prey (FNB = 0.44, 18 genera) than those in eastern Washington (FNB = 0.31, 16 genera).

Proportions of mammals and birds in the diet were different (χ^2 = 17.67, df = 3, P = 0.001) among prey of goshawks nesting in the Olympic Range, western Cascade Range, the central/southern east Cascades, and northern Cascades in eastern Washington (N = 16, 22, 27, and 17 territories, respectively). Goshawks in the central and southern Cascades of eastern Washington ate the highest proportion of mammals (57%), with fewer mammals eaten in the Olympic Range (54%), northern Cascades in eastern Washington (44%), and west Cascade Range (41%). Proportions of Douglas' squirrels in prey remains differed (χ^2 = 14.79, df = 3, P = 0.002) among goshawks in the central and southern region of the east Cascades (22%), Olympic Range (20%), northern Cascades in eastern Washington (15%), and west Cascades (11%). Proportions of snowshoe hares also differed (χ^2 = 11.73, df = 3, P = 0.008) in the central and southern region of the east Cascades (16%), Olympic Range (10%), northern Cascades in eastern Washington (10%), and west Cascades (7%). Proportions of grouse were different (χ^2 = 22.43, df = 3, P = 0.001) in the northern Cascades in eastern Washington (32%), west Cascades (20%), central and southern region of the east Cascades (17%), and Olympic Range (12%).

We found no difference (P = 0.853) among frequencies of Douglas' squirrels, snowshoe hares and grouse relative to each other on land ownerships with potential timber harvest (i.e., national forest, state, and private land) and without harvest (i.e., national park).

We collected pellets 17% less often (χ^2 = 5.34, df = 1, P = 0.021) when sampling nests on the west side (N = 47 visits) compared to the east side (N = 76 visits). We suspected that some skeletal remains on the west side were misclassified as coming from prey remains rather than pellets due to the rapid breakdown of pellets in the moist climate. Twenty-eight percent more birds than mammals were identified in prey remains when compared to pellets (χ^2 = 81.59, df = 1, P = 0.001). Remains of snowshoe hares were 24% more prevalent among prey than pellets when compared to all mammals of smaller size (χ^2 = 19.81, df = 1, P = 0.001). Remains of grouse were 15% more prevalent among prey than pellets when compared to other birds (χ^2 = 15.82, df = 1, P = 0.001).

DISCUSSION

Raptor diets are most accurately described through the combination of observations of prey deliveries at nests and prey collections (Marti 1987). We identified biases associated with the identification of only Northern Goshawk prey remains that overemphasized snowshoe hares and grouse, and believe that by including pellets in the analysis a more complete representation of the actual diet results, particularly in regard to the importance of small mammals. In western Washington, the predominance of collected prey remains compared to pellets may have partly accounted for the greater occurrence of avian prey, particularly grouse, on the west side. We were unable to identify biases that may have resulted from a lack of observations at nests. This may have underestimated the consumption of arthropods and reptiles as was found for *Accipiters* in Oregon (Reynolds and Meslow 1984), and overemphasized avian prey in the diet as determined in several studies (Ziesemer 1981, Reynolds and Meslow 1984, Boal and Mannan 1994). We concluded that most arthropods were eaten by goshawks incidental to the consumption of other prey. Although we identified no reptiles as prey, reptiles, notably garter snakes (*Thamnophis* spp.), were common in all forests we studied throughout Washington (K. McCallister pers. comm.). Other studies have not identified these same biases from prey sampling methodologies. For example, prey and pellet analysis of nesting Northern Goshawks in northeast Spain over-represented *Leporids,* and under-represented thrushes and small birds (Mañosa 1994). The rank of prey taxons assessed from prey remains, pellets and observations did not differ for breeding goshawks in New Mexico (Kennedy 1991). These differences reemphasize the importance of observations of prey deliveries for determining diets of specific populations of nesting goshawks.

Variation in the seasonal and annual timing of prey collections among nest sites introduced other potential biases in diet assessment. Seasonal changes in diet composition of Northern Goshawks may include a shift to fledgling passerines and increased diet diversity as nesting progresses (Squires and Reynolds 1997). Thus, prey constitution may change from the nestling to fledgling periods of the nesting phenology. Our geographical comparisons of Northern Goshawk prey in Washington were based on irregular prey collections over the 10-yr period and at different times of the nesting period; westside prey were collected throughout the entire 10-yr period, whereas eastside prey were collected over a 5-yr period. These collections were a composite of several studies, and each nest site was not sampled equally. It was not known how, or if, cyclic changes of major prey species throughout the state may have biased our analyses because we did not monitor their spatial or temporal variability. In the northern boreal forest, snowshoe hare and Ruffed Grouse undergo region-wide cyclic population fluctuations approximately every 10 yr (Keith and Rusch 1986, Doyle and Smith 1994, Hik 1994). Populations of other potential prey, particularly Douglas' squirrels, may also be subject to periodic cycles depending on the annual production of cones by conifer forests (Buchanan et al. 1990). However, Douglas' squirrels accounted for little biomass relative to other frequently eaten prey of goshawks in Washington suggesting a lesser importance of this species in the diet overall. Reduced hare numbers in southwest Yukon resulted in dietary shifts to smaller mammalian prey and increased avian consumption (Doyle and Smith 1994). A sudden decline in European hare (*Oryctolagus cuniculus*) in northeastern Spain resulted in a reduction in rabbit consumption by nesting goshawks and increased predation on Red-legged Partridge (*Alectoris rufa*) (Mañosa 1994). Consequently, if cyclic population phenomena are similar for hare and grouse in Washington, our regional comparison of prey could, at best, be interpreted to reflect actual differences in statewide prey selection; or, at worst, to be merely the identification of prey species eaten by breeding goshawks in eastern and western Washington.

The same prey species eaten by goshawks in eastern and western Washington accounted for the greatest biomass and frequency of prey in these areas (i.e., snowshoe hares, grouse, and to a lesser degree, Douglas' squirrels, chipmunks, Steller's Jays, and Northern Flickers). These same species have been found to be important prey throughout the goshawk's North American range (Reynolds et al. 1992, Squires and Reynolds 1997). Compared to goshawk diets in other Pacific Coast states, the most pronounced latitudinal differences appear to be the prominence of grouse in diets of Northern Goshawks in Washington relative to southern populations in California (Bloom et al. 1986, Woodbridge et al. 1988) and a greater consumption of snowshoe hares relative to northern populations in southeast Alaska where hares are evidently uncommon (Titus et al. 1994). In California, primary prey species were Douglas' squirrels, Steller's Jays, and Northern Flickers; lagomorphs and sciurids comprise 66% of the total biomass (Bloom et al. 1986). In the southern Cascades of northern California, Steller's Jays and four species of woodpeckers are the principal birds taken and sciurids account for over half of the total biomass (Woodbridge et al. 1988). In Washington, we found grouse accounted for 42% of total biomass and lagomorphs and sciurids composed an additional 46% of total biomass. Even assuming unidentified grouse were the smallest juvenile grouse and unaged hares were all smaller juveniles, these taxons still accounted for 42% and 44% of total biomass, respectively. In southeast Alaska, goshawks eat high numbers of Blue Grouse which were identified at 73% of 25 nest sites, but snowshoe hare were found at only one nest (Titus et al. 1994). Additionally, Steller's Jays, Varied Thrush, and red squirrels (*Tamiasciurus hudsonicus*) have been found at >47% of the southeast Alaskan territories. Comparatively few small mammals are available as prey, which may limit populations (Titus et al. 1994). Queen Charlotte Goshawks on Vancouver Island eat species similar to those eaten by goshawks in Washington including Steller's Jays, Varied Thrush, and Northwestern Crows (*Corvus caurinus*) (Beebe 1974). Shorebirds and seabirds are also common prey, but we did not record them as prey in Washington, most likely because no nests in our study were located near seacoasts.

Even though regional and study area prey class proportions in Washington were statistically different (e.g., regional variation of 46–54%, study area variation of 41–59%), dietary class proportions were more similar to goshawk diets in New Mexico, Arizona and Oregon than to diets in New Jersey and California (Table 2). Goshawks in New Jersey and California eat 10–15% fewer mammals and 10–15% more birds compared to goshawks in Washington. More recent prey collections at goshawk nests in three different areas of eastern Oregon found frequencies of mammalian prey varied from 38–66% (Bull and Hohmann 1994, DeStefano et al. 1994). These results indicate that there can be as much variation in proportions of major prey species and classes of prey between

Table 2. Comparative food-niche breadths (standardized) and prey class ratios of Northern Goshawks in North America. Diet parameters are based on prey remains and pellets collected at nests unless indicated otherwise.

Location	Nests	Mammal : Bird Ratio	Food-Niche Breadth (Number Genera)	Source
New Jersey	16	30:70	0.26 (22)	Bosakowski et al. (1992)
Arizona	20	53:47	0.29 (18)	Boal and Mannan (1994)[a]
Eastern Washington	44	53:47	0.31 (16)	this study
New Mexico	8	49:51	0.36 (22)	Kennedy (1991)[b,c]
California	114	32:68	0.41 (21)	Bloom et al. (1986)[a,c]
Western Washington	38	47:53	0.44 (18)	this study
Oregon	59	45:55	0.45 (30)	Reynolds and Meslow (1984)[c]

[a] Analysis of prey remains.
[b] Pellet analysis.
[c] Standardized food-niche breadth calculated by Boal and Mannan (1994).

study areas separated by <100 km, as there can be in nests separated by several hundred kilometers. Dietary proportions of mammals and birds are reflective of the abundance and availability of potential prey species throughout the range of the Northern Goshawk (Reynolds et al. 1992), suggesting there was considerable variation in local abundance or availability of key prey in Washington. We did not find a relationship in the occurrence of major prey types among managed and unmanaged forests, which we hypothesized might be a factor influencing local prey abundance or availability.

Relative to five other breeding populations throughout the U.S., goshawks nesting in eastern Washington had a low food-niche breadth while those in western Washington had a high food-niche breadth. While similar species were eaten, east side goshawks tended to eat large, cyclic prey such as hares and grouse more frequently. The high consumption of grouse throughout the state resulted in a mean avian prey weight (415 g) that was higher than that reported in New Jersey (332 g) and Connecticut (337 g) (Bosakowski et al. 1992), and Oregon (195 g) (Reynolds and Meslow 1984). The mean weight of mammalian prey (411 g) in Washington was more similar to the range of the average mammalian prey in these same studies (423–445 g). The variety of species we identified as prey suggested that nest occupancy and productivity of goshawks in Washington is not dependent on cyclic fluctuations in the populations of grouse and hare alone, although east side goshawks were more specialized feeders during this study.

While the species is an opportunistic feeder (Doyle and Smith 1994), without a variety of prey species to buffer the effects of specialized feeding, goshawk productivity may mirror the changes in cyclic prey populations (Reynolds et al. 1992, Doyle and Smith 1994). Monitoring temporal changes in hare and grouse populations to assess their cyclic tendencies, and simultaneous collection of prey at the same goshawk nest sites over several years, both in eastern and western Washington, would provide an informative contrast as to the importance of cyclic prey to nest site occupancy and productivity.

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LITERATURE CITED

BEEBE, F.L. 1974. Field studies of the Falconiformes of British Columbia. Occasional papers of the B.C. Provincial Mus. No. 17. Victoria, B.C. Canada.

BEIER, P. AND J.E. DRENNAN. 1997. Forest structure and prey abundance in foraging areas of Northern Goshawks. *Ecol. Appl.* 7:564–571.

BLOOM, P.H., G.R. STEWART AND B.J. WALTON. 1986. The status of the Northern Goshawk in California, 1981–1983. Wildl. Manage. Branch Ad. Rep. 85-1. Calif. Dept. Fish and Game, Sacramento, CA U.S.A.

BOAL, C.W. AND R.W. MANNAN. 1994. Northern Goshawk diets in ponderosa pine forests on the Kaibab plateau. *Stud. Avian Biol.* 16:97–102.

BOSAKOWSKI, T., D.G. SMITH AND R. SPEISER. 1992. Niche overlap of two sympatric-nesting hawks *Accipiter* spp. in the New Jersey-New York Highlands. *Ecography* 15: 358–372.

BUCHANAN, J.B., R.W. LUNDQUIST AND K.B. AUBRY. 1990. Winter populations of Douglas squirrels in different-aged Douglas-fir forests. *J. Wildl. Manage.* 54:577–581.

BULL, E.L. AND J.H. HOHMANN. 1994. Breeding biology of Northern Goshawks in northeastern Oregon. *Stud. Avian Biol.* 16:103–105.

BUMP, G.R., R.W. DARROW, F.C. EDMINSTER AND W.F. CRISSEY. 1947. The Ruffed Grouse/life history/propagation/management. New York State Conserv. Dept., Albany, NY U.S.A.

BURT, W.H. AND R.P. GROSSENHEIDER. 1976. A field guide to the mammals. Houghton Mifflin Co., Boston, MA U.S.A.

CROCKER-BEDFORD, D.C. 1990. Goshawk reproduction and forest management. *Wildl. Soc. Bull.* 18:262–269.

DESTEFANO, S., S.K. DAW, S.M. DESIMONE AND E.C. MESLOW. 1994. Density and productivity of Northern Goshawks: implications for monitoring and management. *Stud. Avian Biol.* 16:88–91.

——— AND J. MCCLOSKEY. 1997. Does vegetation structure limit the distribution of Northern Goshawks in the Oregon Coast Ranges? *J. Raptor Res.* 31:34–39.

DOYLE, F.I. AND J.M.N. SMITH. 1994. Population responses of Northern Goshawks to the 10-year cycle in numbers of snowshoe hares. *Stud. Avian Biol.* 16:122–129.

HIK, D. 1994. Predation risk and the 10-year snowshoe hare cycle. Ph.D. dissertation, Univ. British Columbia, Vancouver, B.C. Canada.

HARGIS, C.D., C. MCCARTHY AND R.D. PERLOFF. 1994. Home ranges and habitats of Northern Goshawks in eastern California. *Stud. Avian Biol.* 16:66–74.

KARALUS, K.E. AND A.W. ECKERT. 1974. The owls of North America. Doubleday and Company, Inc., Garden City, NY U.S.A.

KEITH, L.B. AND D.H. RUSCH. 1986. Predation's role in the cyclic fluctuations of Ruffed Grouse. *Proc. Intl. Congr. Ornith.* 19:699–732.

KENNEDY, P.L. 1991. Reproductive strategies of Northern Goshawks and Cooper's Hawks during brood-rearing in north-central New Mexico. Ph.D. dissertation, Utah State Univ., Logan, UT U.S.A.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ U.S.A.

MAÑOSA, S. 1994. Goshawk diet in a Mediterranean area of northeastern Spain. *J. Raptor Res.* 28:84–92.

MARTI, C.D. 1987. Raptor food habits studies. Pages 67–80 *in* B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.

OLSEN, S.J. 1964. Mammal remains from archaeological sites. Peabody Museum, Cambridge, MA U.S.A.

———. 1972. Osteology for the archaeologist. Peabody Museum, Cambridge, MA U.S.A.

PETERSON, R.T. 1947. A field guide to the birds. Houghton Mifflin Co., Boston, MA U.S.A.

REYNOLDS, R.T. AND H.M. WIGHT. 1978. Distribution, density, and productivity of accipiter hawks breeding in Oregon. *Wilson Bull.* 90:182–196.

——— AND E.C. MESLOW. 1984. Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. *Auk* 101:761–779.

———, R.T. GRAHAM, M.H. REISER, R.L. BASSETT, P.L KENNEDY, D.A. BOYCE, JR., G. GOODWIN, R. SMITH AND E.L. FISHER. 1992. Management recommendations for the Northern Goshawk in the southwestern United States. USDA Forest Service, Gen. Tech. Rep. RM-217, Ft. Collins, CO U.S.A.

SQUIRES, J.R. AND R.T. REYNOLDS. 1997. Northern Goshawk (*Accipiter gentilis*). *In* A. Poole and F. Gill, [EDS.], The Birds of North America, No. 298. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.

STEENHOF, K. 1983. Prey weights for computing percent biomass in raptor diets. *Raptor Res.* 17:15–27.

TITUS, K., C.J. FLATTEN AND R.E. LOWELL. 1994. Northern Goshawk ecology and habitat relationships on the Tongass National Forest. First Ann. Prog. Rpt. USDA Forest Service, Alaska Region, Tongass National Forest, Juneau, AK U.S.A.

WOODBRIDGE, B. AND P.J. DETRICH. 1994. Territory occupancy and habitat patch size of Northern Goshawks in the southern Cascades of California. *Stud. Avian Biol.* 16:83–87.

———, P.J. DETRICH AND P.H. BLOOM. 1988. Territory fidelity and habitat use by nesting Northern Goshawks: implications for management. Unpubl. Rep. Klamath Natl. For., Macdoel, CA U.S.A.

ZIESEMER, F. 1981. Methods of assessing goshawk predation. Pages 144–151 *in* R.E. Kenward and I.M. Lindsay [EDS.], Understanding the goshawk. Int. Assoc. Falconry Conserv. Birds Prey, Fleury en Biere, France.

ZWICKEL, F.C., J.H. BRIGHAN AND I.O. BUSS. 1966. Autumn weights of Blue Grouse in northcentral-Washington, 1954–1963. *Condor* 68:488–496.

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