Research Note

Northern Goshawk Diet During the Nesting Season in Southeast Alaska

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(JOURNAL OF WILDLIFE MANAGEMENT 70(4):1151–1160; 2006)

Key words

Accipiter gentilis, *breeding season, diet, food habits, northern goshawk, pellets, prey remains, remote videography, southeast Alaska, video camera.*

Northern goshawks (*Accipiter gentilis*; hereafter, goshawks) occur throughout forests of North America and have received much attention as a target species for management (Reynolds et al. 1992, Iverson et al. 1996, Andersen et al. 2003). Goshawks nest in forest stands with high timber volumes and dense overstory canopies above relatively open understories (Reynolds et al. 1982, Squires and Reynolds 1997, Daw and DeStefano 2001), and goshawk foraging is often associated with similar high-volume forest stands (Widén 1989, Beier and Drennan 1997). This association with high-volume forests has caused concern about the effects of forest management on goshawk populations (Crocker-Bedford 1990, Kennedy 1997, Andersen et al. 2003). Initially, management for goshawks concentrated on nesting habitat (Reynolds et al. 1982, Reynolds 1983), but recently the focus has been on managing for abundant and available prey populations (Reynolds et al. 1992, Graham et al. 1999). Thus, understanding the goshawks' diet is a practical step in any attempt to manage this species.

Across their range, goshawks consume a wide variety of small- to medium-sized birds and mammals associated with forested habitats, including grouse, tree squirrels, corvids, large passerines, woodpeckers, and hares (Cramp and Simmons 1980, Squires and Reynolds 1997). However, goshawks can also be local specialists, so diet patterns might be different across geographic scales.

In 1991, the Alaska Department of Fish and Game (ADF&G) and the United States Forest Service (USFS) began cooperative studies of goshawks in southeast Alaska, USA. Roughly 80% of southeast Alaska is managed by the USFS as part of the 6.8 million ha Tongass National Forest (hereafter, Tongass). This region contains some of the largest remaining tracts of pristine temperate rainforest in the world and has supported industrial-scale logging of old growth forests for $\sim$50 years (Iverson et al. 1996, USFS 1997). Concern for the effects of this logging led to the filing of a petition to list the goshawk as endangered in this region (Federal Register 1995); this petition continued to be litigated in federal court through 2004 (P. Schempf, U.S. Fish and Wildlife Service, personal communication). The most contentious issues for the Tongass relate to management of medium- to high-volume forests, which are critical to wildlife and valuable to the timber industry (Schoen et al. 1988).

A better understanding of goshawk diet during the nesting season in southeast Alaska can provide insight into the importance of different habitats for nesting goshawks. The USFS recognizes that the link among goshawk prey species, prey habitats, and habitat management practices are key elements for conservation of the goshawk and the biotic communities in which it occurs (Reynolds et al. 1992, Iverson et al. 1996). Our objectives were to describe and quantify the nesting season diet of northern goshawks in southeast Alaska, USA, and to examine spatial and temporal variability in goshawk diet within this region.

Study Area

We studied northern goshawk food habits in the Alexander Archipelago of southeast Alaska, USA (Fig. 1), which comprises thousands of islands and is characterized by steep, rugged topography, and coastal fjords. This landscape is naturally fragmented by mountainous terrain, wetlands, and forest patches of various sizes. A cool and wet maritime climate characterizes the region. Precipitation was distributed evenly throughout the year but varied throughout the region, ranging from 130–600 cm (Harris et al. 1974, Farr and Hard 1987).

The forests of southeast Alaska, USA, are coastal, temperate rainforests dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), and they occur at low elevations as a mosaic with muskegs and other wetlands (Neiland 1971). The forest floor is a complex terrain of decaying logs and tipped-up root wads cloaked in shrubs, herbs, ferns, and mosses (Alaback 1982, Schoen et al. 1988). Industrial-scale timber harvesting in this region significantly added to the already fragmented landscape in some portions of the archipelago, and approximately 15% of the original forest containing commercial timber was harvested (Iverson et al. 1996, USFS 1997).

The natural fragmentation in this landscape, combined with anthropogenic changes (e.g., logging, species introductions to islands), created a mosaic of goshawk prey occurrence. Based on this, we qualitatively delineated 2 areas in southeast Alaska, USA. We defined a prey-rich area as all of southeast Alaska, except for Prince of Wales Island (POW) and its associated islands (Fig. 1).

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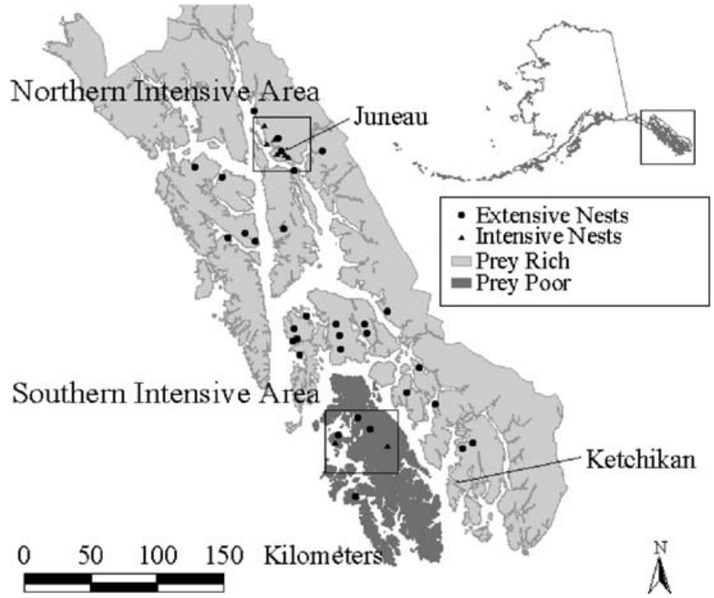

Figure. 1. Nesting and intensive study areas included in northern goshawk breeding-season diet study in southeast Alaska, USA, 1991–1999.

The prey-rich area was characteristic of the majority of southeast Alaska in prey species diversity and abundance. We defined the POW area as prey-poor because it lacked 2 prey species (blue grouse and red squirrel; Armstrong 1995, MacDonald and Cook 1996, Smith et al. 2001) present in the prey-rich area and important to goshawks in other regions (Squires and Reynolds 1997).

Methods

We quantified the diet of nesting goshawk in southeast Alaska, USA, using videography of prey deliveries and by examining prey remains and pellets. We used remote videography to record prey deliveries to 10 nests in 2 spatially distinct locations, one in each prey area, during 1998 and 1999 to describe the diet in detail (Fig. 1). We could not randomly select nests at which to video-record deliveries because the logistics of remote videography combined with difficult and costly access to most nests (Lewis et al. 2004*a*). Instead, we concentrated remote videography around Juneau (i.e., the northern intensive area), Alaska, where there were a number of previously documented, accessible nest sites. In addition, we used remote videography in the POW area (i.e., the southern intensive area) to document prey delivered to nests in a landscape with a relatively low diversity of potential prey species. We examined spatial variation in the diet between the 2 locations and temporal variation in the diet seasonally and during 2 consecutive years.

We used prey identified from prey remains and pellets collected at 36 nests throughout southeast Alaska, USA, over 9 years to describe the diet of the goshawk across broader spatial and temporal scales (Fig. 1). Since 1991, biologists visiting goshawk nesting areas during the breeding season have routinely collected prey remains and pellets. Although some of these remains had undergone preliminary analysis, the composition of the diet had not been quantified (Titus et al. 1994). We used all these data sources to describe the diet over the area in which we knew that goshawks nest in southeast Alaska. Our study was approved by the Boise State University Institutional Animal Care and Use Committee (Protocol No. 692-98-007).

We used a video-surveillance system to record prey deliveries to goshawk nests during the goshawk-breeding season (Lewis et al. 2004*a*). We began recording in the early nestling stage in late May and continued past the fledgling date in early August, when the young no longer received food at the nest. We attempted to record during all daylight hours (range = 16.5–18.3 hr; Lewis et al. 2004*a*). We identified each delivery to species, if possible, using a reference collection of study skins from locally breeding birds and mammals and published sources with drawings or photographs (Armstrong 1995, Terres 1996, Baicich and Harrison 1997, National Geographic Society 1999). We evaluated the age of birds as described in Lewis et al. (2004*b*), and we evaluated the age of mammals based on pelage and relative size. A detailed description of our identification methods is available in Lewis (2001) and Lewis et al. (2004*b*). Northern goshawks cache prey items and consume them later (Schnell 1958, Zachel 1985). When a partially consumed item was delivered, we compared the size, shape, and appearance of it with that of items recently delivered but only partially consumed. We assumed that items recognized in this way had been cached, and we did not recount them.

During each visit, we collected prey remains from beneath nests, plucking posts, and perches located around the nesting area. Prey remains included feathers, bills, feet and skeletal parts of birds, and tails, fur, skin, and skeletal parts of mammals. We bagged each prey remains separately and labeled it with nest name, date of collection, and location within nest area (e.g., plucking post). Later, we dried the remains and stored them for identification. Prey remains identification followed the methods of Reynolds and Meslow (1984) and are detailed in Lewis (2001) and Lewis et al. (2004*b*).

During each visit to a nest, we collected egested pellets (i.e., undigested prey remains regurgitated by the goshawks) from on or beneath nests, plucking posts, and perches located around the nest area. We sent pellets to F. Doyle (Wildlife Dynamics Consulting [WDC], Telkwa, Canada) for identification using methods described in Lewis (2001) and Lewis et al. (2004*b*).

We quantified prey from each technique, resulting in a sum of individuals in each prey category from each technique. We reported prey in the diet as frequency by number of prey (FNP; Marti 1987), quantifying the occurrence of each prey category in relation to all prey categories in the combined sample (i.e., combined sample of videotaped prey deliveries to a nest). We calculated FNP by summing the number of individuals in each prey category in the sample, and we calculated the proportion of the total sample from each prey category. We ranked items for comparisons between areas of southeast Alaska, years, and habitats.

We also reported prey by frequency of biomass. We define biomass as an estimate of the average live mass of an item (Bielefeldt et al. 1992), and we calculated biomass using the average mass of an item in each prey category (e.g., Steller's jay adult) multiplied by the number of occurrences in that prey category. We took the mass of adult birds from Zwickel (1992), Dunning (1993), Russell (1999), or from museum specimens. We used the mean of the mass of both sexes because it was not possible to determine the sex of individual items in most instances.

We estimated the mass of prey identified to the genus level by averaging the mass of all species within that genus that occurred in southeast Alaska, USA (Reynolds and Meslow 1984). We computed estimates of mass for the age class of nestlings, fledglings, and unknown ages following the methods of Bielefeldt et al. (1992). We assigned unidentified avian prey the average mass of identified birds occurring in the size class: small (3.4–42.9 g), medium (43.0–166 g), and large (166.1–1,158 g), following the methods of Storer (1966) and Boal (1993). Quantities that resulted from the use of biomass are given as a percentage of the total biomass in birds and mammals and of each prey category.

We performed a full analysis of FNP and the biomass of prey in the diet. However, because we collected information on the diet based on a count of different prey delivered to nests and because our biomass information provided similar findings, we present the analysis based on the FNP data.

We tested for differences in the number of birds and mammals between 3 factors (and levels): years (all nests in 1998 and 1999; nests sampled in both years), habitat types (hemlock- and spruce-dominated stands), and regions (prey-rich and prey-poor areas). We used general linear mixed models (GLMMs; Poisson error, log link; Littell et al. 1996), which are appropriate for count data analysis based on assumed overdispersed Poisson distributions (McCullagh and Nalder 1989, Bennetts et al. 1999). We used separate models because of low sample size. We considered differences significant at the 95% level ($P \leq 0.05$). If there were significant differences for any of the factors, we further examined dietary variation by comparing diet niche breadth, and the degree of nest similarities, among factor levels.

We calculated dietary niche breadth based on prey identified to genus at each nest using a modified form of Simpson's index (Levins 1968). We standardized that value to account for unequal numbers of prey categories among nests (Hurlbert 1978, Reynolds and Meslow 1984). We calculated the standardized niche breadth (B_{st}) values with the equation: $B_{st} = (B - 1)/(n - 1)$, where $B = 1/\sum p_j^2$, p_j is the proportion of individuals in prey genus j, and n is number of prey genera.

Standardized niche-breadth values ranged from 0–1; a value close to zero reflects specialization on a few prey categories and a less-diverse diet, whereas a B_{st} closer to one reflects more diversity in the diet (Hurlbert 1978, Reynolds and Meslow 1984).

We calculated Morisita's index of similarity (Morisita 1959, cited in Krebs 1998) with the equation:

$$C = \frac{2\sum_i^n p_{ij}p_{ik}}{\sum_i^n p_{ij}[(n_{ij}-1)/(N_j-1)] + \sum_i^n p_{ik}[(n_{ik}-1)/(N_k-1)]},$$

where C is Morisita's index of similarity between variables j and k, p_{ij} is the prey category i proportion of the total in variable j, p_{ik} is the prey category i proportion of the total in variable k, n_{ij} is the number of nests in variable j that used prey category i, n_{ik} is the number of nests in variable k that used prey category i, and N_j, N_k is the total number of individuals of each prey category in sample

$$\sum_{i=1}^n n_{ij} = N_j, \qquad \sum_{i=1}^n n_{ik} = N_k.$$

We qualitatively compared this value among the independent factors to examine the overlap in the diet. We selected Morisita's index because it gives the least biased result given small sample sizes (Smith and Zaret 1982) and is useful with counts (Krebs 1998).

We examined seasonal variation in the diet in 2 ways. First, we compared the numbers of prey within groups of similar prey categories delivered to nests as the nesting season progressed. Groups included 1) Grouse = blue grouse and spruce grouse, 2) Jay = Steller's jay, 3) Thrush = *Catharus* spp., varied thrush (*Ixoreus naevius*), American robin (*Turdus migratorius*), and unknown passerines, 4) Crow = northwestern crow (*Corvus caurinus*), 5) Ptarmigan = willow ptarmigan (*Lagopus lagopus*), white-tailed ptarmigan (*Lagopus leucurus*), and rock ptarmigan (*Lagopus mutus*), 6) Other birds = all other avian prey categories, 7) Squirrels = red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel (*Glaucomys sabrinus*), and 8) Other mammals = all other mammalian prey categories. We could not compare these groups in one model because our small sample of video-monitored nests and the large number of prey groups lacked sufficient degrees of freedom. Therefore, we examined proportions of these groups in the diet separately for patterns of use during the season. Second, we tested for differences in age of prey delivered across the nestling season by comparing the number of adults and young delivered to nests across 5- and 10-day periods of the nestling season using a GLMM (Littell et al. 1996).

We combined prey counts from prey remains and pellet collections made at all nests in southeast Alaska, following the methods of Simmons et al. (1991) and Lewis et al. (2004*b*). Although we collected prey remains and pellets from a greater number of nests than we monitored with video cameras, few nests had enough individual prey items identified at them to use for an overall analysis. After comparing results from 2 years where we had prey delivery, prey remains, and pellet data from the same nests (Lewis et al. 2004*b*), we chose to combine the prey remains and pellet data. A statistical analysis of the prey remains and pellet data would not have improved our understanding of the goshawks diet. We report all prey as FNP and calculated the modified form of Simpson's index (Levins 1968), standardized to account for unequal numbers of prey categories among nests (Hurlbert 1978, Reynolds and Meslow 1984).

Results

We videotaped 10 nests during 1998 ($n = 5$) and 1999 ($n = 5$), documenting 1,663 prey deliveries. Some items (7.3%) had been cached and delivered more than once. Thus, we documented 1,542 new prey deliveries. We identified 1,450 (94.0%) of the new items to at least class and 1,208 (78.3%) to at least genus. Items from 35 prey categories were delivered, including 18 avian and 7 mammalian genera (Appendix). We estimated the age of 1,382 (89.6%) of the video-recorded prey items.

Taxa were a significant source of variation in 3 of the 4 GLMMs (Table 1). More birds than mammals were delivered 1) to nests that were monitored during both study years, 2) to all nests during both years, and 3) to nests monitored in both regions of southeast Alaska, USA (Table 1). Region was a significant source of variation (Table 1) because of the difference in the number of nests monitored ($n_{north} = 8$ nests, $n_{south} = 2$ nests) and, therefore, the numbers of prey deliveries used in this model ($n_{north} = 1{,}272$

Table 1. Generalized linear-mixed model results for comparisons of numbers of bird and mammal prey delivered to nests of breeding northern goshawks in Southeast Alaska, USA, 1998–1999.

Source of variation[a]	F	P
Year[b]	0.87	0.440
Taxa	27.84	0.040
Year × Taxa	1.21	0.394
Year[c]	1.52	0.236
Taxa	18.28	≤0.001
Year × Taxa	2.81	0.113
Habitat[d]	0.42	0.551
Taxa	0.97	0.381
Habitat × Taxa	3.73	0.126
Region[e]	6.19	0.024
Taxa	53.06	≤0.001
Region × Taxa	11.68	0.004

[a] " × " denotes the interaction between factors.
[b] Nest common to both years, 1998 ($n = 2$) and 1999 ($n = 2$); df: numerator = 1, denominator = 2.
[c] All nests, 1998 ($n = 5$) and 1999 ($n = 5$); df: numerator = 1, denominator = 16.
[d] Hemlock-dominated forests ($n = 2$) and spruce-dominated forests ($n = 2$); df: numerator = 1, denominator = 4.
[e] Prey-rich area ($n = 8$) and prey-poor area ($n = 2$); df: numerator = 1, denominator = 16.

deliveries, $n_{south} = 179$ deliveries). Goshawks delivered fewer birds to nests in the north (72.8%) than nests in the south (90.6%; Table 2), as indicated by the significant effect of the interaction between region and taxa (Table 1).

In the northern area, blue grouse was most frequently identified in prey deliveries (Fig. 2). Steller's jay, varied thrush, northwestern crow, and unknown passerine birds, composed of varied thrushes, *Catharus* thrushes, American robins, and some smaller passerines, were other birds accounting for a considerable proportion (≥5%) of deliveries (Fig. 2). Red squirrel was the only mammal that accounted for ≥5% of identified prey deliveries (Fig. 2), and all other prey categories accounted for <5%. Blue grouse and red squirrels contributed the most biomass to the diet. Other categories that provided ≥5% of biomass in the diet included northwestern crows, ptarmigan, and Steller's jays. All other categories contributed <5% of the biomass in the diet.

In the southern area, goshawks delivered spruce grouse to the nest most frequently (Fig. 2). Steller's jays and ptarmigan were delivered nearly as frequently, and unknown passerines and varied thrushes were important prey categories. The only mammals delivered with any frequency to southern nests were unknown small mammals (i.e., voles and mice; 6% of deliveries); prey that contributed little (<1%) to the overall biomass brought to these nests. Ptarmigan and spruce grouse contributed the most biomass to the diet, and only these categories and Steller's jays contributed ≥5% of the biomass delivered to these nests in the prey-poor region.

The food niche breadth value of goshawks nesting in the north was lower ($\bar{X} = 0.25$, range = 0.08–0.38) than that of birds nesting in the south ($\bar{X} = 0.53$, range = 0.48–0.59; Table 2). Morisita's overlap value showed that diets of goshawks nesting in the northern area were not very similar to those in the southern area ($\bar{X} = 0.37$, $n = 16$ combinations of nests; Table 2), and comparisons among all nests showed considerable variability (range = 0.07–0.70) in this overlap index depending on the diet at each nest (Table 2).

We found no significant difference in numbers within prey groups delivered throughout the nesting season. We examined this seasonal variation in diet among 5-day ($F_{70,496} = 0.99$, $P = 0.507$) and 10-day intervals ($F_{36,199} = 1.15$, $P = 0.267$). Grouse, jays, thrushes, and squirrels were abundant in the diet throughout the nesting season, whereas crows, ptarmigan, other birds, and other mammals made only small contributions. However, qualitative analysis showed that relative proportions of some prey groups differed through the nestling season (Fig. 3; Lewis 2001). The proportion of grouse in the diet increased throughout the nestling period from a low-average FNP of 7.5% (in early Jun) to a high-average FNP of 45.6% (in early Jul; Fig. 3); the proportion of thrushes in the diet decreased from 36.5% (in early Jun) through the nesting season to a low of 6.8% (in mid-Jul; Fig. 3).

We evaluated the age of all types of prey delivered to goshawk nests except small mammals (i.e., voles, mice, and shrews), which accounted for 4% of deliveries. Young prey (i.e., fledgling and nestling birds, juvenile mammals) accounted for the greatest frequency (58.6%) of delivered items for which we were able to

Table 2. Percentage of birds (remaining prey was mammalian), based on frequency (freq.) of occurrence and biomass (biom.), standardized niche breadth, and Morisita's index of overlap, based on videography of prey delivered to northern goshawk nests within regions of southeast Alaska, USA, during 1998 and 1999.

			% birds		Standardized niche breadth		Overlap index[a]	
Year	Region	Nest area	Freq.	Biom.	B_{st}	No. genera	98–3	99–4
1998	North	98–1	87.6	87.6	0.25	12	0.49	0.44
		98–2	89.0	92.5	0.10	11	0.12	0.07
		98–4	81.8	85.1	0.30	12	0.48	0.40
		98–5	91.2	92.4	0.26	13	0.70	0.52
	South	98–3	85.3	94.6	0.59	8		0.77
1999	North	99–1	82.2	84.0	0.28	13	0.52	0.32
		99–2	27.4	11.9	0.08	6	0.11	0.07
		99–3	66.5	61.6	0.38	14	0.56	0.43
		99–5	56.3	52.4	0.33	12	0.34	0.36
	South	99–4	95.9	99.6	0.48	11	0.77	
Combined[b]	North		72.8	70.9	0.25			
	South		90.6	97.1	0.53			

[a] Morisita's index of overlap between each northern nest and each southern nest (98–3 and 99–4).
[b] Mean value of percent birds and standardized niche breadth.

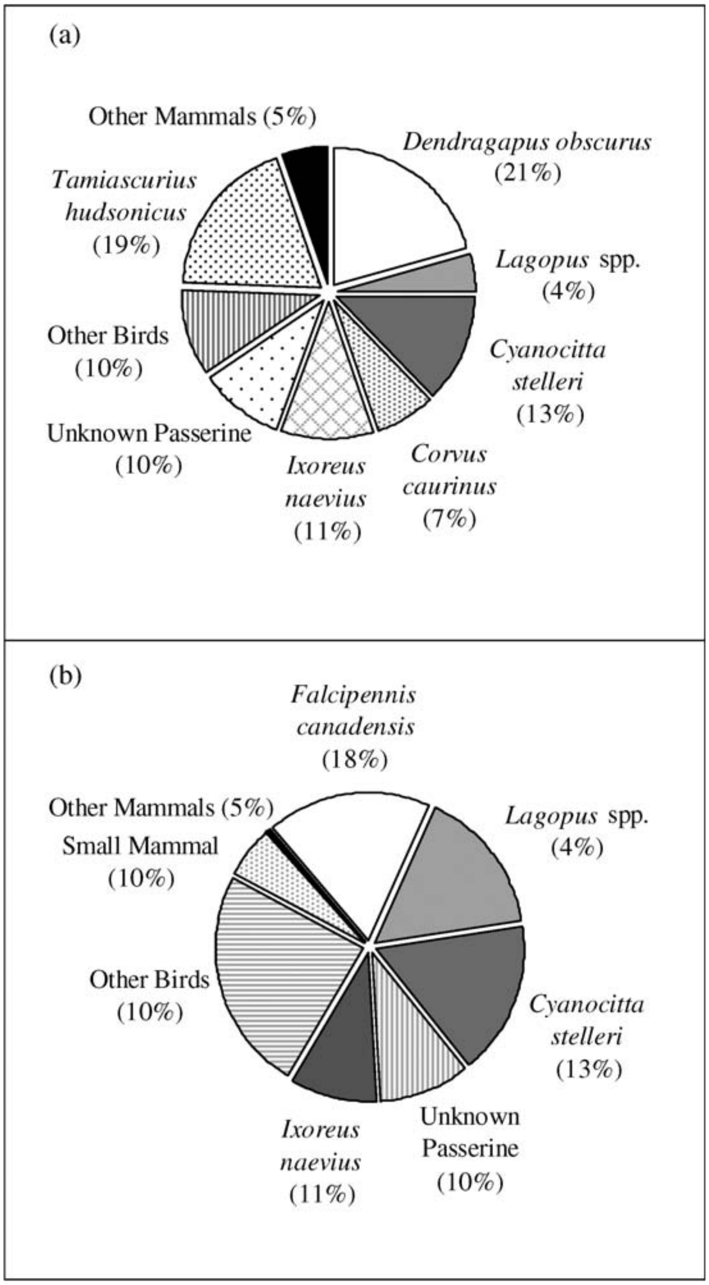

Figure. 2. Proportions of important prey (i.e., prey that accounted for ≥5% of deliveries) to northern goshawk nests in the southeast Alaska, USA, during 1998 and 1999. (a) Frequency by number in the prey-rich northern area. (b) Frequency by numbers of prey-poor southern area.

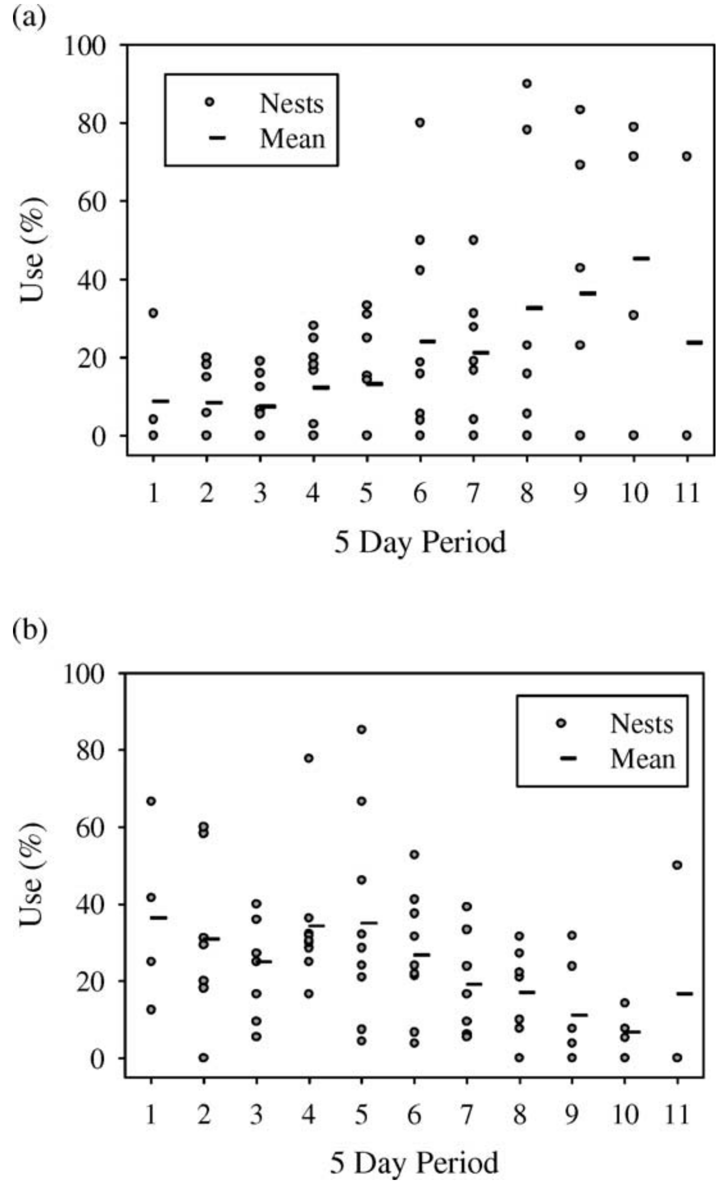

Figure. 3. Prey group percentage (individual nests and weighted mean) delivered over 5-day intervals through the nesting season, beginning at the start of the first surveillance system (28 May), to northern goshawk nests in southeast Alaska, USA, during 1998 and 1999. (a) Grouse. (b) Thrushes.

determine an age. However, by biomass, adult prey (57.0%) contributed more to the diet than young prey (43.0%). Nestlings were most frequently delivered, followed by adults, and fledglings. Adult birds contributed the most biomass to the diet, followed by nestlings, and fledglings. Adult mammals were delivered much more often than juveniles, and they contributed the most biomass. We detected no significant difference in the numbers of various-aged prey among 5-day intervals ($F_{11,40} = 0.86$, $P = 0.581$). However, an increase in juvenile prey in the diet over 10-day intervals was marginally significant ($F_{4,66} = 2.14$, $P = 0.086$).

Agency personnel collected prey remains from 77 nests in 37 nesting areas in southeast Alaska, USA. We identified 681 (100%) prey individuals from these collections to at least class and 557 (81.8%) to at least genus. We assigned prey remains to 38 prey categories, including 21 avian and 5 mammalian genera. We did not attempt to determine the age of prey remains.

Agency personnel collected pellets from 75 nests in 40 nesting areas in southeast Alaska, USA. After drying and sorting, WDC analyzed 753 whole or partial pellets, identifying 686 (100%) prey individuals to class and 527 (76.8%) to at least genus. We identified 31 prey categories from pellets, including 12 avian and 9 mammalian genera. We did not attempt to determine the age of prey from pellets.

In the prey-rich area, birds accounted for 75.1% and mammals for 24.9% of individuals identified from the combined prey remains and pellets collected at 65 nests from 36 nesting areas. Red squirrel was the most commonly identified prey category.

Steller's jay was the most commonly identified bird category, followed by blue grouse and ptarmigan species. We also found unidentified passerines and varied thrushes in >5% of remains.

In the prey-poor area, birds accounted for 92.2% and mammals for 7.8% of the combined prey remains and pellets collected at 8 nests from 5 nesting areas. Unidentified large birds (composed of spruce grouse and ptarmigan species) was the most commonly identified category, followed by Steller's jay and spruce grouse. We also found unidentified passerines, alcid species, and red-breasted sapsuckers in >5% of the identified prey.

Discussion

Videography of prey deliveries provided an essentially complete and unbiased list of prey brought to the nest in 2 areas of southeast Alaska, USA (Lewis et al. 2004*b*). Combining this sample with the data based on collection of prey remains and pellets from nests distributed throughout southeast Alaska, we obtained a sample representative of the breeding season diet of the northern goshawk throughout southeast Alaska during the 9 years of our study (Lewis et al. 2004*b*). One limitation to our work was our inability to collect data on prey abundance, and thus to examine how differing prey populations affect the vital rates of this goshawk population.

We speculated that, because of the mosaic of habitats (e.g., forest, wetlands, shoreline) available to potential prey species in southeast Alaska, USA, species uncommon elsewhere in the diet throughout the goshawks' range would be more common prey in southeast Alaska. Although some of these species occasionally occurred in the diet (e.g., Lewis 2003), they did not contribute substantially to the diet during the nesting season. Overall, the species and types of prey important to goshawks in southeast Alaska were similar to those in other parts of the goshawks' range (Squires and Reynolds 1997) and were predominately avian.

This predominance of birds in the goshawks' diet in southeast Alaska, USA, probably reflects the relatively limited mammalian prey base throughout this region. Red squirrels are absent from some islands (MacDonald and Cook 1996). Snowshoe hares occur only near Juneau, Alaska, USA, and in isolated locations of the northern mainland (MacDonald and Cook 1996); even where they occur, hares are uncommon to rare. Northern flying squirrels are distributed sparsely in the area, occurring on the mainland and some islands in the southern part of southeast Alaska (MacDonald and Cook 1996, Smith and Nichols 2003). Other comparably sized mammals (e.g., ground squirrels and rabbits) are absent from southeast Alaska (MacDonald and Cook 1996).

Goshawks in southeast Alaska, USA, nest among and adapt to different prey assemblages throughout this area. Although many factors can cause diet variation in raptors (Newton 1979), this heterogeneity in prey occurrence within the Alexander Archipelago (Iverson et al. 1996, MacDonald and Cook 1996) is an important factor for goshawks in southeast Alaska. Goshawks nesting in the northern part of southeast Alaska, specifically around Juneau, had more mammals in their diet than those goshawks nesting on POW and associated southern islands. Neither red squirrels nor snowshoe hares occurred in the POW area (MacDonald and Cook 1996). Red squirrels are an important prey where they occur, but elsewhere, goshawks use other species (e.g., ptarmigan at nest 99–4) relatively more. Similarly, in coastal Norway, where no red squirrels or woodland grouse occur, goshawks preyed on ptarmigan (Myrberget 1989).

A few species consistently appeared in the goshawks' diet, but the relative numbers of prey species in the diet varied among nests. At one nest, located in a large alluvial spruce stand, red squirrels accounted for nearly 73% of deliveries. Red squirrels feed preferentially on spruce seeds (Brink and Dean 1966, Smith 1968) and are more abundant in alluvial Sitka spruce forests (Willson et al. 2003). At a nest located near the beach, northwestern crows accounted for the greatest proportion of biomass delivered to the nest. Northwestern crows are strongly associated with intertidal areas and beach-fringe forests located along this interface (Verbeek and Butler 1999), and thus were preyed upon more heavily by this pair of goshawks.

Goshawks nesting in the north specialized on a few important prey species, based on food niche breadth, whereas those nesting in the south exhibited more equitable use of prey species. Interestingly, there were more prey species available to goshawks in the north, yet their diet was more specialized on a few important prey species. In the south, with fewer prey from which to select, goshawks exhibited a more even use of their prey. The diet of goshawks nesting in the north did not overlap greatly with those in the south, but this varied among nest combinations. The lowest overlap values resulted from the goshawks in the north feeding on species not available in the south and vice versa.

Seasonal use of certain prey appeared to change as the season progressed. Grouse eggs begin to hatch by late May, but the majority hatch between mid-June and mid-July (Zwickel 1992, Russell 1999). Grouse broods leave the nest soon after hatching and travel in family flocks with the adult female, making them vulnerable to predation (Zwickel 1992). Therefore, increased abundance and higher vulnerability results in the availability of young grouse to foraging goshawks (Tornberg 1997), and likely, the increase in the proportion of grouse in the diet as goshawk nestlings grew.

The proportion of young prey increased in the diet as the nesting season progressed, reflecting their appearance in the environment and, probably, their vulnerability to predation (Tornberg 1997). In the coastal lowlands of northern Finland, goshawks' selected juvenile grouse increasingly through the nestling season until August when young grouse were the most common prey item (Tornberg 1997). In Wales, the occurrence of juvenile prey in the goshawks' diet coincided with the abundance of these prey in the environment and with peak food demands of goshawk nestlings (Toyne 1998). Age was evaluated for the most commonly delivered mammal, red squirrel, by the relative size of the item. This method of evaluating age became less reliable as the goshawk-nestling season progressed because juvenile squirrels approach the size of adults. Thus, juvenile red squirrels might be more important seasonally than was evident.

Goshawks exhibited flexible hunting in response to different prey occurrence and availability, including different species and age classes. However, there is an apparent limit to this adaptation. Prince of Wales Island has the least-diverse potential goshawk prey base in southeast Alaska. Unlike nearby Heceta Island, where ptarmigan occur in the forest to sea level, ptarmigan only occur in higher elevations on POW (C. Flatten, ADF&G, personal

Table 3. Northern goshawk diet information from coastal and boreal nesting populations of North America and Europe.

Region	Location	Years monitored	Nests	% bird	Standardized niche breadth[a] B_{st}	No. genera	Source
Coastal N. A.	Southeast Alaska[b]	1998–1999	10	74.3	0.26	24	This study
	Southeast Alaska[c]	1991–1999	75	76.6	0.35	39	This study
	Queen Charlotte Islands[d]	1996–1998	11	51.5	nd	nd	Roberts 1997, Chytyk and Dhanwant 1998
	Vancouver Island[c]	1996–1997	37	56.7	0.21	14	E. McClaren, unpublished data
	Western Washington[d]	1986–1996	38	53.4	0.44	18	Watson et al. 1998
Boreal N. A.	Interior Alaska[d]	1979–1980	18	16.9	0.11	21	Zachel 1985
	Southwest Yukon[b]	1989–1991	15	22.7	nd	nd	Doyle and Smith 1994
Coastal and boreal Europe	Northern Norway[d]	1964–1978	6	91.3	0.06	20	Myrberget 1989
	Northern Finland[c]	1988–1994	12	79.7	nd	nd	Tornberg 1997
	Central Norway[b]	1996	2	99.3	nd	nd	Grønnesby and Nygård 2000
	Southwestern Finland[c]	1969–1977	33	85.0	0.19	45	Wikman and Tarsa 1980

[a] nd denotes no data available to calculate standardized niche breadth.
[b] Data from prey deliveries, either observed from a blind or with video camera.
[c] Data from combination of prey remains and pellets.
[d] Data from collection of prey remains.

communication). Only one occupied goshawk nest has been located on POW in recent years despite considerable effort (ADF&G, unpublished data), and that nest failed early in the nestling period. Although the ultimate cause of the nest failure was not determined, siblicide, cannibalism, and possibly infanticide were evidence that finding food for nestlings could be a limiting factor on that island (Estes et al. 1999; S. Lewis, Boise State University, unpublished data). Use-areas (≈home ranges) of birds monitored on POW are nearly an order of magnitude larger than any other recorded in North America (ADF&G, unpublished data). Kenward (1982) found that goshawk use-areas are directly related to availability of prey. All this suggests that finding sufficient food is difficult for goshawks attempting to breed on Prince of Wales Island.

Patterns in prey use seen in southeast Alaska, USA, are reflected at broader scales within their range. In coastal British Columbia, Canada, where the specific prey base is very similar to southeast Alaska, goshawks prey on the appropriately-sized birds (e.g., varied thrush and Steller's jay; Beebe 1974). More recent studies show a larger proportion of mammals in the diet in coastal British Columbia (Roberts 1997, Chytyk and Dhanwant 1998, Ethier 1999; Table 3), but these reports were based mostly on pellet data. We believe that the proportion of mammals in the diet was actually less, and use of a direct technique would clarify the diet in coastal British Columbia (Lewis et al. 2004*b*). In western Washington and Oregon, USA, avian prey was more prevalent than mammalian prey in the goshawks' diet (Reynolds and Meslow 1984, Watson et al. 1998, Thrailkill et al. 2000; Table 3). However, in those locations, a more diverse mammalian community was available, and the relative proportion of birds was only slightly greater than that of mammals. Again, use of a direct technique to document the diet would clarify whether the proportions seen in those locations actually reflect use of the diverse potential prey base or were due to biases in the techniques used to collect evidence of the diet. Birds were large portions of the goshawks' diet in coastal areas of Europe (Myrberget 1989, Tornberg 1997; Table 3).

Boreal goshawks from interior Alaska and southwest Yukon, Canada, fed primarily on mammalian prey, specifically snowshoe hare (McGowan 1975, Zachel 1985, Doyle and Smith 1994; Table 3). During years of low hare numbers, avian prey became more important, but small samples limit the interpretation of those data. In boreal locations of Europe, grouse species make up the majority of the goshawks' diet (Wikman and Tarsa 1980, Grønnesby and Nygård 2000; Table 3).

We studied goshawk diet during the breeding season only, but prey occurrence and availability change throughout the year. During the winter, many species that goshawks prey on migrate from the area (e.g., varied thrush; Armstrong 1995), switch habitats (e.g., blue grouse; Zwickel 1992), or become less abundant (e.g., Steller's jay; Dellasala et al. 1996). Thus, based on the breeding-season diet, a few resident prey (i.e., those that occur year-round), such as grouse and red squirrels, probably become more important during winter. In fact, those species could be critical to goshawk overwinter survival if goshawks must specialize on the few remaining prey available to them (Drennan and Beier 2003).

Management Implications

Our results indicate that northern goshawks in southeast Alaska, USA, rely on a few important prey species (i.e., grouse and red squirrels). Several of those prey species occur at reduced abundance in association with the even-aged silvicultural practices (e.g., clearcut logging) commonly used by the timber industry in southeast Alaska (Doerr et al. 1984, Carey 1995, Russell 1999). We recommend that studies of these prey species in southeast Alaska should focus on how alteration of forest structure and landscape patterns specifically affect their abundance and availability to northern goshawks. For goshawks, management should focus on their habitat and accompanying prey base for long-term viability and sustainability in this region.

Acknowledgments

The Alaska Department of Fish and Game and United States Forest Service–Alaska Regional office, Tongass National Forest, and Juneau Forestry Sciences Laboratory funded and facilitated our research. The United States Fish and Wildlife Service provided additional funding for our study. R. E. Lowell and C. J. Flatten provided assistance throughout all aspects of this project, and their insights regarding goshawks were fundamental in the success of the project. G. C. Iverson was instrumental in initiation of our research. G. Pendleton assisted with statistical analyses. We thank D. C. Crocker-Bedford, E. J. DeGayner, G. C. Iverson, M. L. Kissling, P. F. Schempf, T. Shaw, W. P. Smith, and T. Woods for their support and provocative comments. P. DeSimone and R. Chandos constructed the video-surveillance systems. We thank F. Doyle for identifying prey in pellets. Many other individuals associated with these agencies provided field assistance, collected prey remain and pellets, or facilitated this work in some other way. M. D. Kirchhoff, M. L. Kissling, R. E. Reynolds, and 2 anonymous reviewers provided thoughtful comments on an earlier draft of this manuscript.

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Associate Editor: Bechard.

Appendix. Northern goshawk prey identified from prey deliveries recorded by remote videography during 1998–1999 and collections of prey remains and pellets made during 1991–1999 at nesting areas in southeast Alaska, USA.

			Diet analysis method[a]			
			Prey deliveries		Combined indirect[b]	
Prey category	**Common name**	**Biomass (g)**	**No.**	**Nests**	**No.**	**Nests**
Birds						
Ardea herodias	Great blue heron[c]	71.7	2	1	0	0
Anas platyrhynchos	Mallard	902.0	0	0	6	4
Anas crecca	Green-winged teal	—	0	0	1	1
Unknown duck[d]	Unknown duck	531.7	8	3	14	8
Accipiter striatus	Sharp-shinned hawk	138.5	10	6	8	6

Appendix. continued.

Prey category	Common name	Biomass (g)	Diet analysis method[a]			
			Prey deliveries		Combined indirect[b]	
			No.	Nests	No.	Nests
Accipiter gentilis	Northern goshawk	120.0	2	1	2	2
Falcipennis canadensis	Spruce grouse	548.3	32	2	9	5
Dendragapus obscurus	Blue grouse	1,056.0	261	7	133	32
Lagopus spp.[e]	Ptarmigan species	445.2	84	8	105	26
Actitis macularia	Spotted sandpiper	40.4	2	2	0	0
Unknown charadiform[f]	Unknown wader	95.2	0	0	12	10
Gallinago gallinago	Common snipe	122.0	0	0	2	2
Larus glaucescens	Glaucous-winged gull	—	0	0	1	1
Cepphus columba	Pigeon guillemot	487.0	1	1	0	0
Brachyramphus marmoratus	Marbled murrelet	222.0	11	6	31	21
Unknown alcid[g]	Unknown alcid	288.3	0	0	25	20
Glaucidium gnoma	Northern pygmy owl	67.5	1	1	1	1
Aegolius acadicus	Northern saw-whet owl	82.9	0	0	1	1
Ceryle alcyon	Belted kingfisher	146.5	1	1	2	2
Sphyrapicus ruber	Red-breasted sapsucker	48.9	1	1	26	17
Picoides pubescens	Downy woodpecker	27.0	2	1	1	1
Picoides villosus	Hairy woodpecker	66.3	2	2	8	4
Picoides spp.[h]	Woodpecker species	53.0	2	1	12	10
Cyanocitta stelleri	Steller's jay	128.0	193	10	187	51
Corvus caurinus	Northwestern crow	392.0	97	6	56	20
Corvus corax	Common raven	659.5	0	0	2	2
Cinclus mexicanus	American dipper	57.8	1	1	0	0
Catharus spp.[i]	Thrush species	30.9	25	8	44	29
Ixoreus naevius	Varied thrush	79.3	152	10	65	30
Turdus migratorius	American robin	77.3	50	10	40	25
Junco hyemalis	Dark-eyed junco	—	0	0	2	2
Carduelis pinus	Pine siskin	14.6	0	0	3	3
Unknown sparrow[j]	Unknown sparrow	—	0	0	3	3
Unknown passerine[k]	Unknown perching bird	37.4	146	10	82	50
Unknown small bird	Bird, sparrow-sized or smaller	33.0	2	2	11	9
Unknown medium bird	Bird, sparrow- to jay-sized	78.8	26	8	40	24
Unknown large bird	Bird, jay-sized or larger	484.4	14	7	62	27
Unknown bird	Unknown bird	237.2	0	0	21	16
Subtotal			1,128	10	1,019	64
Mammals						
Unknown *Sorex* spp.[l]	Unknown shrew		0	0	6	6
Mustela erminea	Ermine	54.0	1	1	4	3
Marmota caligata	Hoary marmot	1,894.2	6	2	7	5
Tamiasciurus hudsonicus	Red squirrel	229.1	244	8	208	49
Glaucomys sabrinus	Northern flying squirrel	141.8	2	2	19	13
Peromyscus keeni	Keen's mouse	19.5	4	1	6	4
Clethrionomys rutilus	Northern red-backed vole	19.0	14	7	6	6
Microtus spp.	Unknown *Microtus*	19.3	0	0	2	2
Unknown vole/mouse[m]	Unknown vole or mouse	19.4	42	9	35	25
Lepus americanus	Snowshoe hare	1,118.0	5	3	13	6
Unknown mammal	Squirrel-sized or larger	385.5	4	3	1	1
Subtotal			322	10	307	58
Total			1,450	10	1,326	65

[a] Number of occurrences of each prey category and number of nests at which each category was found.
[b] Prey found in combined indirect techniques: prey remains and pellets.
[c] Prey item likely scavenged; only parts delivered.
[d] *Anas crecca, Anas platyrhynchos, Anas acuta, Anas discors, Anas clypeata, Anas strepera, Anas americana*, or *Histrionicus histrionicus*.
[e] *Lagopus lagopus, Lagopus mutus*, or *Lagopus leucurus*.
[f] *Tringa melanoleuca*, *Tringa flavipes*, *Tringa solitaria*, *Heteroscelus incanus*, *Actitis macularia*, or *Gallinago gallinago*.
[g] *Cepphus columba, Brachyramphus marmoratus*, or *Brachyramphus brevirostris*.
[h] *Picoides pubescens, Picoides villosus*, or *Picoides tridactylus.*
[i] *Catharus minimus, Catharus ustulatus*, or *Catharus guttatus*.
[j] *Spizella arborea*, *Passerella iliaca*, *Melospiza melodia*, or *Junco hyemalis*.
[k] *Catharus minimus, Catharus ustulatus*, *Catharus guttatus*, *Cinclus mexicanus*, *Cyanocitta stelleri*, *Ixoreus naevius*, or *Turdus migratorius*.
[l] *Sorex monticolus* and *Sorex cinereus*.
[m] *Peromyscus keeni, Clethrionomys gapperi*, *Clethrionomys rutilus*, *Microtus longicaudus*, or *Microtus pennsylvanicus*.