

A comparison of 3 methods for assessing raptor diet during the breeding season

Stephen B. Lewis, Mark R. Fuller, and Kimberly Titus

Abstract Video recording of prey deliveries to nests is a new technique for collecting data on raptor diet, but no thorough comparison of results from traditional methods based on collections of prey remains and pellets has been undertaken. We compared data from these 3 methods to determine relative merits of different methods for assessing raptor diet as part of a study of the breeding-season diet of northern goshawks (*Accipiter gentilis*) in Southeast Alaska. We applied these methods to 5 nests during each of the northern goshawk breeding seasons of 1998 and 1999 and identified 1,540 prey from deliveries, 209 prey from remains, and 209 prey from pellets. The proportions of birds and mammals varied among techniques, as did relative proportions of prey groups and age groups. Prey remains and pellets gave the least-similar diet descriptions. Over 2-day intervals during which data were collected using all 3 methods, prey-delivery data gave more individual prey and prey categories than the 2 other sources of information. We found that prey were not directly tracked in either prey remains or pellets compared with prey delivery videography. Analysis of prey-delivery videography provided the most complete description of diet, and we recommend that studies attempting to describe diet use this technique, at least as part of their methodology.

Key words *Accipiter gentilis*, diet, food habits, methods, northern goshawk, pellets, prey remains, raptors, remote videography

Knowledge of an animal's diet is important to understanding its biology, and for some species there has been extensive study. Historically, persons investigated raptor diets to determine effects of raptor predation on domestic and game animals (e.g., Fisher 1893, McAtee 1935) and in relation to raptor ecology (e.g., Craighead and Craighead 1956). More recently, researchers have examined diets in relation to raptor niche in a community (e.g., Green and Jaksic 1983, Reynolds and Meslow 1984). Diet studies are important for management and conservation, and some management strategies now focus on prey as a key element for maintaining

populations of predator species of concern, such as the northern goshawk (*Accipiter gentilis*; e.g., Reynolds et al. 1992).

Some behaviors common to most raptor species (Falconiformes and Strigiformes) are conducive to studying food habits: 1) parts of large prey items (i.e., those that cannot be swallowed whole) usually are discarded; 2) some parts (e.g., hair, feathers) of consumed prey are not digested, but subsequently regurgitated, frequently in a well-formed pellet; and 3) food is delivered to the nest to feed the attendant adult or nestlings. Direct techniques, those in which the diet is described from observa-

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tions, and indirect techniques, where diet is inferred from evidence (e.g., prey remains) found at nest sites or perching or feeding areas, have been used to quantify raptor diets (Rosenfield et al. 1995). The majority of raptor diet studies focus on the breeding season because bird activity is concentrated around and at the nest, where dietary data are relatively easy to collect.

Each method has advantages and disadvantages (Marti 1987, Rosenberg and Cooper 1990). Pellets and prey remains can be collected at or beneath nests, roosts, and kill sites, and therefore large samples can be obtained with little disturbance to the birds. Prey parts from pellets and remains can be preserved and carefully identified later (Marti 1987). Pellets and prey remains left by many different birds distributed over space and time can be gathered for information about diet diversity and spatial and temporal shifts in food habits (Barrows 1989, Nielsen and Cade 1990). Prey parts can be a basis for determining qualitative and quantitative information about raptor diets, but they can result in incomplete or biased data (Marti 1987, Rosenberg and Cooper 1990).

Interpretation of dietary information gained from indirect methods warrants caution because of biases associated with these methods. The effectiveness of pellet analysis in determining diet varies among raptor species because of physiological and behavioral differences. Falconiformes usually tear prey apart as they feed, thereby consuming fewer diagnostic prey parts, such as bones. Once ingested, most bone is digested readily in their gastrointestinal tracts by highly acidic gastric juice (Duke et al. 1975, Cummings et al. 1976). Thus larger, undigested bone material and undigested fur and feathers in pellets can lead to overestimation of prey species from which this material originated (Marti 1987, Rosenberg and Cooper 1990). The most complete diet description based on indirect methods depends on finding plucking posts and perches early in the season of interest. Collection of prey remains can be biased toward larger or more conspicuous prey (Widén 1987, Bielefeldt et al. 1992, Real 1996) that can persist in the environment longer (Marti 1987) relative to smaller prey items that either are consumed whole or leave few remains (Sherrod 1978). In addition, remains of juvenile prey often are difficult to identify because they can lack some of the identifying characteristics of adults (Bednarz 1988). Finally, the source of the remains or pellets can be uncertain because the

raptor plucking the prey item or egesting the pellet is not seen (Mañosa 1994).

Direct observation is advantageous because the researcher sees the prey delivered to the nest. Small, inconspicuous prey items, often overlooked with indirect methods, and conspicuous prey items that often are overestimated, can be accurately counted (Bielefeldt et al. 1992, Boal and Mannan 1994, Doyle and Smith 1994). Prey biomass can be estimated more accurately than with indirect methods because the researcher usually has more information about prey age and size (Collopy 1983, Joy et al. 1994). In addition to diet information, food-habits behavior such as delivery rates and schedules, prey handling, and consumption rates can be recorded (Younk and Bechard 1994, Real 1996, Warnke et al. 2002). However, direct observation is labor-intensive, resulting in high project costs or a smaller sample of nests (Marti 1987), and can disturb nesting raptors (Rosenberg and Cooper 1990). Misidentification of prey species or inaccurate estimation of size or age of prey also is possible (Rosenberg and Cooper 1990, Carss and Godfrey 1996).

Remote videography of nests (e.g., monitoring using time-lapse video) offers most of the benefits of direct observations and some additional advantages. Maintaining video cameras is not as labor-intensive as constant nest observation, and cameras can be placed so as to avoid disturbing the nesting raptor (McQuillen and Brewer 2000). A permanent record of nest activity is created, which can be viewed repeatedly to inspect the tape frame-by-frame for clues to the identity, age, and size of the prey (Lewis et al. 2004). A limitation to filming prey deliveries is the cost of the equipment, which can be thousands of dollars (Cutler and Swann 1999). Moreover, items eaten away from the nest area, or not in the camera's view, remain undetected (Bull et al. 1989, Sonerud 1992).

Video recording of prey deliveries (i.e., prey-delivery videography) at nests is a relatively new technique for determining diet and food habits (Cutler and Swann 1999) that has not been compared with results from prey remains and pellet analyses. Such a comparison was warranted to determine relative merits of different methods for assessing diet because some methods have changed little over time and are still used today. As part of broad research of northern goshawk ecology in Southeast Alaska (Iverson et al. 1996), we used 3 techniques to describe and quantify the breeding-

season diet of this species. We needed to understand how data from 2 indirect methods, analysis of prey remains and analysis of pellets, compared with the direct technique of analysis of prey deliveries recorded on videotape. Our goal was to supplement the data from the video with that from prey remains and pellets to obtain the most complete nesting-season diet description possible for goshawks in our study area. In this paper we compare results from 3 sources used to collect diet data during the goshawk nesting season in Southeast Alaska: videography of prey delivered to the nest, prey remains, and pellets of undigested food.

Study area

We studied northern goshawk food habits in Southeast Alaska at nests on islands of the Alexander Archipelago and the narrow strip of mainland west of the Coast Mountains (Figure 1). Southeast Alaska comprises thousands of islands and is characterized by steep, rugged topography and coastal fjords. It is a naturally fragmented landscape caused by mountainous terrain, wetlands, and various forest patches. A cool and wet maritime climate characterized the region. Precipitation was

distributed evenly throughout the year but varied from north to south, ranging from 130–600 cm, respectively (Harris et al. 1974, Farr and Hard 1987). The temperate rainforest of Southeast Alaska was dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), and occurred at low elevations as a mosaic with muskegs and other wetlands (Neiland 1971). See Alaback (1982) and Schoen et al. (1988) for a more complete description of Southeast Alaska. Differing prey-species diversity and occurrence in various island groups in this region resulted in a spatially variable prey base available to northern goshawks (Armstrong 1995, MacDonald and Cook 1996).

Methods

Study design

We sampled nests in 2 geographically separate locations of Southeast Alaska: the Juneau area in the north and Prince of Wales Island (POW) and Heceta Island area in the south (Figure 1). We concentrated remote videography around Juneau (4 nests/year), where there was a number of previously documented, accessible nest sites. Furthermore, an established road system facilitated frequent site visits to gather prey remains and pellets and to service the video system (Lewis 2001). We established study sites in the POW area (1 nest/year) to document prey delivered to nests in a landscape of relatively low diversity of potential prey species (Armstrong 1995, MacDonald and Cook 1996). Our sample of 10 nesting areas (2 were repeats of the same nesting area in consecutive years) included 2 found originally by members of the public, 3 found by agency field crews, and 3 found by locating radiotagged adult females that moved between nesting areas. Subsequently, field

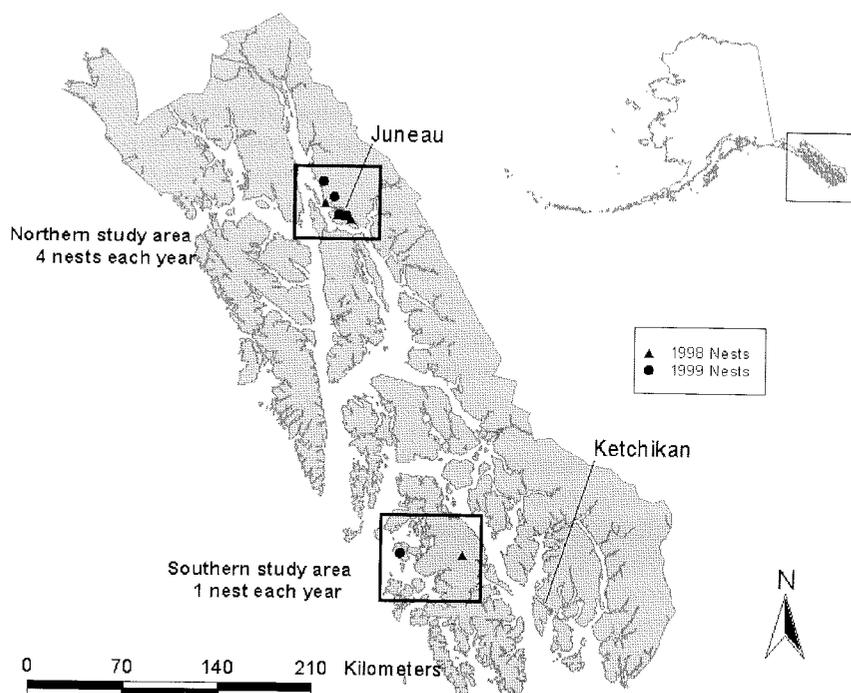


Figure 1. Locations of northern goshawk nests studied in 2 areas of Southeast Alaska during 1998 and 1999. The northern study area was located near the city of Juneau; the southern area was located on Prince of Wales and Heceta Islands near Ketchikan.

research staff found all sample nests for this study.

We collected data during the goshawk breeding season (i.e., May through August) of 1998 and 1999. We compared data from prey-delivery videography with data from prey remains and pellets. We had data from 10 nests at which prey-delivery videography and prey remains were collected. The pellet analysis was based on data from 9 nests because crews maintaining the video systems at the 10th nest did not collect pellets.

Prey collection and identification

Prey-delivery videography. We used a video surveillance system to record prey deliveries to goshawk nests during the breeding season (Lewis et al. 2004). We began recording in the early nestling stage and continued past the fledging date, when the young no longer received deliveries at the nest. Recording began 15–30 minutes before sunrise and continued until 15–30 minutes after sunset.

We identified each delivery species when possible, using a reference collection of study skins of locally breeding birds and mammals and several published sources with drawings or photographs (Armstrong 1995, Terres 1996, Baicich and Harrison 1997, National Geographic Society 1999). When we were unable to identify an item to species, we used any diagnostic part to categorize the item into a more general category (e.g., genus or family). We used still more general categories for items that shared some diagnostic part but could not be categorized more specifically. For example, “unknown passerines” were those birds we could not identify to species or genus but that had an anisodactylous (i.e., perching-type) foot. Most birds in this category were nestlings that had not developed identifiable feathers but did have identifiable feet. We also used an “unknown bird” category divided into large (greater than jay [*Cyanocitta* spp.] sized), medium (sparrow [Emberizidae]- to jay-sized), and small (less than sparrow-sized) birds. This category contained items we could identify only as birds. We used “unknown small mammals” for unidentified mammals smaller than squirrels (*Tamiasciurus* spp.); they likely included mice (*Peromyscus keeni*) and voles (*Clethrionomys* spp. and *Microtus* spp.). We also used the categories “unknown mammals” for squirrel-sized or larger mammals and “unknown” for anything we could not identify. Prior to removal of one system, we recorded representative samples from each prey size-class on the

nest to act as size and color reference.

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 did not recount them.

We aged identified avian prey based on plumage as follows: avian prey with unsheathed feathers (i.e., completely grown feathers) were considered adults; an item with feathers partially in sheath was considered a fledgling; birds with completely sheathed feathers or down were considered nestlings (Reynolds and Meslow 1984). We aged precocial, ground-nesting species of grouse (blue grouse, *Dendragapus obscurus*; spruce grouse, *Falci pennis canadensis*) and ptarmigan (*Lagopus* spp.) based on feather development and timing of the nestling season when the delivery occurred. We were unable to reliably age mammals.

Prey remains. Every 2 days, until the young no longer received deliveries at nests, we collected prey remains from beneath nests, plucking posts, and perches located around nesting areas. We searched the entire nest stand within 100 m of the nest tree for plucking posts during the video setup. Additional plucking posts were located opportunistically throughout the nesting season. We revisited known plucking posts on each visit to collect prey remains. Prey remains included feathers, bills, feet, and other skeletal parts of birds, and tails, fur, skin, and skeletal parts of mammals. We bagged and labeled remains of each prey separately from each location within the nesting area (e.g., plucking post). Later, we dried remains in an exhaust hood and stored them for identification.

We reconstructed prey remains following Reynolds and Meslow (1984) and combined all remains collected during a visit, regardless of location in the nest stand, as one daily collection. We identified and classified prey remains using the criteria we used for prey-delivery items. We used prey remains to indicate only the minimum number of each prey category found. We tallied 1 of each prey category from a collection unless evidence showed that >1 individual was present (e.g., >10 but <21 Steller's jay (*Cyanocitta stelleri*) rectrices = 2 Steller's jays). We were unable to reliably age mammal remains.

Pellets. During each visit to a nest area, we collected egested pellets from on or beneath nests,

plucking posts, and perches located around nests. We found that pellets were intact, broken into large pieces (i.e., 2 or 3 pieces that could be fit back together), or broken into smaller fragments. To avoid double-sampling from the same pellet, we sorted pellets into 2 categories: 1) whole pellets and partial pellets for which the other part was not in the bag; or 2) partial pellets and small pieces for which we could not rule out that the other part was in the bag. We sent whole and partial pellets (i.e., first category) to F Doyle (Wildlife Dynamics Consulting, Telkwa, British Columbia, Canada) for identification.

F Doyle removed and identified fur, feathers, and vegetation stuck to the surface of pellets and then teased apart each pellet and separated them into piles of similar items (e.g., nails or claws of similar size and shape, feathers, teeth). He compared teeth and jaws to reference keys and material, and he compared fur with keys (e.g., Mayer 1952, Stains 1958, Adorjan and Kolenosky 1969, Moore et al. 1974) and his reference collection. When identification of fur was confirmed by identification of other items (e.g., nails, whiskers, teeth) in the pellet, no further analysis took place. If identification was not confirmed, he examined additional fur samples from the pellet to attempt to identify the prey. He compared feathers to his reference collection. If identification to species was not made, he assigned the prey to a size class (i.e., small, medium, or large) by comparison to known reference feathers. F Doyle counted, measured, and compared nails and claws to reference materials, and determined whether >1 individual of that species was present in a pellet. He used bird foot parts to augment identification (e.g., distinctive shape of woodpecker claws aided in identification of medium-sized black and white birds). Presence of carapace fragments in the pellets indicated insects, but he did not identify them further. Based on video observation of goshawk feeding behavior, we assumed that insects found in pellets were consumed incidentally.

We pooled all pellets collected around a nest on a given day. We tallied the minimum amount of each prey category found in those pellets, so 1 of each prey category was tallied from a collection unless evidence in the pellet (e.g., >18 squirrel claws) suggested >1 individual was present.

Quantification

We reported bird and mammal prey in the diet

by frequency by number of prey (Marti 1987). Prey frequency by number of prey quantifies the diet to show which prey categories most commonly occur in relation to all prey in a sample (e.g., sample of videotaped prey deliveries to a nest). We calculated frequency by number of prey by summing the number of individuals in deliveries, remains, or pellets in each prey age category in the sample and calculated the proportion of each prey category (all methods), prey category-age class (deliveries and remains), and age class (deliveries and remains) in the total sample.

Comparison of techniques

We used a generalized linear mixed model (Poisson error, log link; Littell et al. 1996) to compare frequencies by number of prey of taxa (bird and mammal) and of groups of similar prey among data from deliveries, prey remains, and pellets. For groups of similar prey, we separated prey categories with many occurrences and lumped categories of like species with few occurrences. Groups included: 1) Grouse=blue grouse and spruce grouse; 2) Jay=Steller's jay; 3) Thrush=*Catbarus* 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 (*L. leucurus*), and rock ptarmigan (*L. mutus*); 6) Other birds=all other avian prey categories; 7) Squirrels=red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel (*Glaucomys sabrinus*); and 7) Other mammals=all other mammalian prey categories. These groups were based on results from analysis of prey deliveries and represented prey groups that constituted >5% of all deliveries. We calculated confidence intervals on percent bird and mammal following a technique for estimating variation for binomial variables (Zar 1999), and for the prey groups following Bailey (1980) and Cherry (1996). We compared frequency of age classes (adult, fledgling, nestling; and adult, subadult) from deliveries and remains using the same model. We tested the null hypothesis of no difference among results of the 3 methods (i.e., no interaction between results of methods and taxa, group, or age) and evaluated all analyses at the $\alpha=0.05$ significance level.

From each diet classification method, we obtained a list of species that occurred in the diet. We measured the similarity between each prey species list to determine how much the separate

methods differed in prey species identified in the diet (Krebs 1998). 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 = Morisita's index of similarity between technique j and k ;

p_{ij} = Proportion prey category i is of total in technique j ;

p_{ik} = Proportion prey category i is of total in technique k ;

n_{ij} = Number of nests in technique j that used prey category i ;

n_{ik} = Number of nests in technique k that used prey category i ;

N_j, N_k = Total number of individuals of each prey category in sample;

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

We examined variation of results among methods by comparing the number of individual prey among nests detected by each technique over the entire sampling period using the same mixed model (Littell et al. 1996). In addition, we compared results from collections of remains and pellets made at 2-day intervals with results from the videotapes for periods that coincided with those periods during which $\geq 90\%$ of the time was recorded on video. We compared numbers of individual prey, number of birds, number of mammals, and number of prey categories detected using the same model (Littell et al. 1996).

Additionally, we looked at whether evidence of specific prey deliveries was found using the indirect techniques. We examined instances when we documented delivery of easily identified prey and then determined whether that item was subsequently detected in prey remains and pellet collections made within 4 days (2 collections) after the delivery. In this manner we attempted to track prey identified in the deliveries through the 2 indirect methods.

We constructed a saturation curve to determine whether we had a sample of nests that would cap-

ture the heterogeneity within goshawk diet in this region (Sherry 1984). We used a modified form of Simpson's index (Levins 1968), calculated using the following equation (Krebs 1998):

$$B = \frac{1}{\sum_i^n p_i^2};$$

where

p_i = proportion of individuals in prey genus i , and
 n = number of prey genera.

Simpson's index ranges from 1 to the number of genera, in this case 25 (Krebs 1998). To create the saturation curve, we calculated Simpson's index by randomly choosing 1 nest (of the 10 monitored) and calculating the index, a second nest was randomly chosen (from the 9 remaining) and the pooled (i.e., nest 1 plus nest 2) numbers of prey genera were used to calculate the index and so on until all 10 nests were incorporated (following Sherry 1984). We used 15 trials to generate the mean B .

Results

Diet assessment

Prey-delivery videography. We monitored 10 nests with video cameras during 1998 ($n=5$) and 1999 ($n=5$) and documented 1,663 prey deliveries (Table 1). Some items (7.3%) were previously cached and delivered more than once, resulting in 1,542 new prey deliveries. We identified 35 prey categories, including 18 avian genera and 7 mammalian genera, and classified 1,450 (94.0%) to class and 1,208 (78.3%) to genus. Thrushes (25.7%), grouse (20.2%), and squirrels (17.0%) were the 3 most commonly identified prey groups (Table 2). We aged 1,382 (89.6%) of the avian prey items that were video recorded at the nest, and the majority were subadults (fledgling = 14.4%, nestlings 53.5%; Table 2).

Prey remains. In 2 years we collected 182 bags of prey remains during 88 daily collections at the 10 nests where we maintained video systems (Table 1). Twenty-three prey categories were represented in prey remains, including 13 avian and 3 mammalian genera. We identified 209 prey (100%) individuals from these collections to class, of which 181 (86.6%) were identified to genus. The 3 prey groups we most commonly identified from remains

Table 1. Prey deliveries recorded, prey remains and pellets collections made, and the number of prey identified at northern goshawk nests in southeast Alaska, 1998–1999.

Year	Nest	Prey deliveries			Prey remains			Pellets			
		Deliveries ^a	Identified ^b	Categories	Collection ^c	Identified	Categories	Collection ^d	Pellets ^e	Identified	Categories
1998	1	231	208	17	11	28	6	10	30	30	11
	2	127	118	15	6	13	9	6	17	11	6
	3	42	34	12	2	5	4	1	1	2	2
	4	207	198	17	10	20	6	6	26	25	13
	5	148	137	16	10	30	10	6	19	17	8
1999	1	200	197	18	17	42	12	11	28	35	15
	2	88	84	8	3	5	4	4	30	16	5
	3	164	155	20	9	22	6	9	32	33	14
	4	159	145	15	5	9	6	0	0	0	0
	5	176	174	15	15	35	10	11	47	40	13
Total		1542	1450	35 ^f	88	209	23 ^f	64	230	209	29 ^f

^a Number of new deliveries.

^b Prey identified to at least Class (bird or mammal).

^c Number of days on which prey remains were found and collected.

^d Number of days on which pellets were found and collected.

^e Number of whole or partial pellets dissected.

^f Number of categories of all deliveries, remains, and pellets, respectively.

were jays (21.1%), other birds (18.2%), and ptarmigan (16.3%; Table 2). We aged 190 (99.5%) of the avian remains, and the majority of these were adults (60.5%; Table 2).

Pellets. We collected 86 bags of pellets during 64

daily collections from 9 nests at which we maintained video systems. After drying and sorting, we identified 29 prey categories from pellets, including 11 avian and 7 mammalian genera (Table 1). From 230 whole or partial pellets, we identified 209 prey

Table 2. Prey taxa, prey group, and avian prey age-class in northern goshawk diets, based on 3 techniques of data collection in southeast Alaska, 1998–1999.

	Prey deliveries			Prey remains			Pellets		
	% ^a	CI ^b	Nests ^c	% ^a	CI ^b	Nests ^c	% ^a	CI ^b	Nests ^c
Prey taxa									
Birds	77.8	75.9–79.6	10	91.4	87.5–94.3	10	59.3	53.4–65.0	9
Mammals	22.2	20.4–24.1	10	8.6	5.6–12.5	8	40.7	35.0–46.6	9
Prey groups									
Thrushes	25.7	22.6–28.9	10	9.6	4.7–16.2	6	27.3	19.1–36.4	8
Grouse	20.2	17.4–23.2	9	15.3	9.0–23.0	7	3.4	0.8–8.1	4
Squirrels	17.0	14.3–19.8	9	6.2	2.4–12.0	7	27.3	19.1–36.6	8
Jays	13.3	10.9–15.9	10	21.1	13.7–29.5	8	9.6	4.7–16.3	7
Crows	6.7	5.0–8.6	6	11.0	5.7–17.9	4	6.7	2.7–12.7	5
Other birds	6.1	4.5–8.0	10	18.2	11.3–26.3	10	10.5	5.0–16.9	9
Ptarmigan	5.8	4.2–7.6	8	16.3	9.8–24.1	7	1.9	0.2–6.0	3
Other mammals	5.4	3.7–7.0	9	2.4	0.3–6.7	3	13.4	7.6–20.9	9
Avian age class									
Adult	32.1	28.2–36.0	10	60.5	50.0–69.8	10			
Fledgling	14.4	11.7–17.6	9	22.6	14.7–31.6	8			
Nestling	53.5	49.2–57.5	10	16.8	9.9–25.2	8			

^a Percent of total occurrences.

^b 95% confidence intervals on percent in diet.

^c Number of nests out of maximum (deliveries = 10, remains = 10, pellets = 9).

(100%) to class, of which 160 (76.6%) we identified to genus. Thrushes and squirrels (27.3% each) and other mammals (13.4%) were the most commonly identified prey groups in pellets (Table 2). We aged no prey from pellets.

Comparison of techniques. We identified birds more commonly than mammals with each technique (Prey taxa: $F_{2, 29} = 4.99$, $P = 0.014$), but proportions of birds and mammals varied among techniques (Table 2). The relative proportions in prey groups also varied with technique (Prey groups: $F_{14, 182} = 4.25$, $P \leq 0.001$; Table 2). The difference between deliveries and remains in relative proportions of different-aged birds (adults, fledglings, and nestlings) was less strongly supported (Prey age-class: $F_{2, 54} = 2.94$, $P = 0.061$). However, when we combined fledglings and nestlings into a subadult category, analysis of prey deliveries showed more subadult birds than analysis of prey remains ($F_{1, 36} = 6.19$, $P = 0.018$; Table 2). Similarity values between deliveries and remains (0.86) and between deliveries and pellets (0.80) were relatively comparable, whereas remains and pellets provided the least-similar diet descriptions (0.55).

We identified more prey individuals from prey deliveries than from prey remains or pellets ($F_{2, 22} = 7.24$, $P = 0.004$) over the entire time we monitored goshawk nests. Additionally, we identified more prey categories from prey deliveries than from prey remains and pellets (Table 1). Over 2-day periods during which deliveries were recorded and prey remains and pellets were collected, analysis of deliveries gave higher numbers of individual prey ($F_{2, 39} = 24.45$, $P \leq 0.001$), birds ($F_{2, 39} = 16.53$, $P \leq 0.001$), mammals ($F_{2, 39} = 6.53$, $P = 0.004$), and different prey categories ($F_{2, 39} = 7.49$, $P = 0.002$; Figure 2). We detected no difference in number of individual prey items, number of birds, or numbers of prey categories between prey remains and pellets.

In general, we could not track most prey items with prey remains or pellets when compared with the detailed videography. For example, 10 sharp-shinned hawks (*Accipiter striatus*) were delivered to nests, but none were detected in remains or in pellets within 4 days of each delivery. More commonly delivered species were tracked better than uncommon ones, but the specific number of each item seen in deliveries was not registered in the other techniques. For example, at 1 nest we saw 15 Steller's jays delivered over 11 days, during which we collected prey remains and pellets 5 times. Steller's jay remains were found in each collection

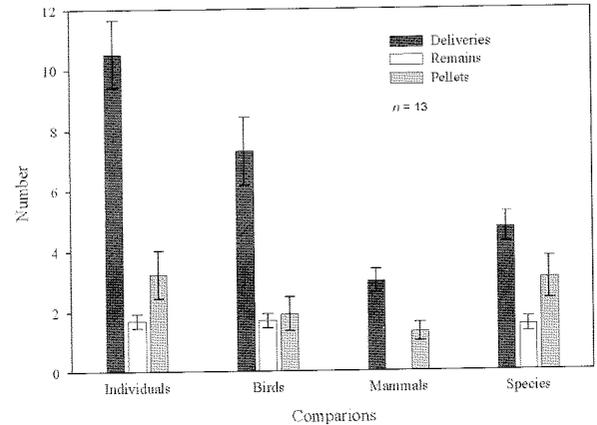


Figure 2. Mean number of individuals, number of birds, number of mammals, and number of species detected in data from 3 techniques of diet collection during 13 2-day periods at northern goshawk nests in Southeast Alaska, 1998 and 1999. Error bars represent SE.

of remains and in 4 of the pellet collections, and totaled 5 and 4 Steller's jays, respectively, compared to 15 individuals delivered.

Simmons et al. (1991) concluded that combining data from indirect methods would generate a reasonably accurate (within 10%) description of diets of bird- and mammal-eating raptors. We combined counts from prey remains and pellets to assess this conclusion. Proportions of birds and mammals in the diet based on a combination of prey remains and pellet data were similar to those from prey deliveries (birds = 75.4% of the combined diet versus 77.8% from prey deliveries). There was no difference in the proportions of prey-group frequencies ($F_{2, 144} = 0.98$, $P = 0.447$) when we compared prey-delivery data with the combined data from remains and pellets.

Discussion

Analysis of prey deliveries recorded by remote videography provided a more complete description of the breeding season diet of northern goshawks than analysis of prey remains or analysis of pellet contents. Over the 2 years of our study and during 2-day intervals when data from all 3 methods were available, we videographed more prey individuals for enumerating and categorizing prey items in the diet than we found in prey remains or pellets (Table 1; Figure 2). Videography not only showed the range of different prey genera used, but also revealed which prey genera goshawks fed most

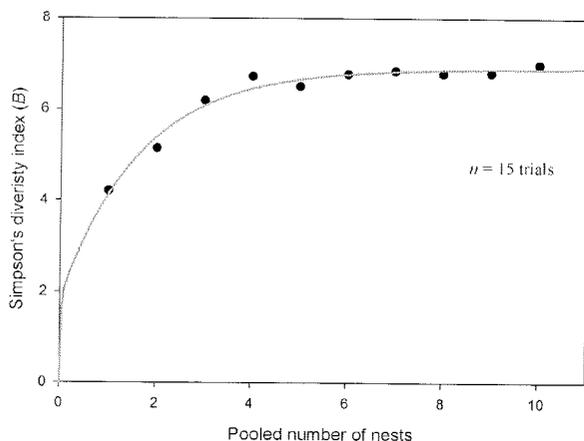


Figure 3. Saturation curve of mean Simpson's diversity index (B), calculated from prey genera delivered to northern goshawk nests in Southeast Alaska during 1998 and 1999, as a function of sample size (number of nests at which prey deliveries were recorded). Prey delivered frequently (i.e., important prey in the diet) were accounted for by the first few nests monitored, and only rare (i.e., uncommonly delivered) prey were added to the diet description after 7 nests.

often to young at the nest. The sample of nests we videographed was adequate to describe the breeding-season diet of goshawks because it revealed commonly eaten (i.e., important) prey, as well as many rare prey in the diet (Figure 3; Sherry 1984, Krebs 1998). Video data obtained on age structure of the prey in the diet were more complete and accurate because they were based on several characteristics of the prey (e.g., plumage development and color, size) compared to the other methods with which age was based solely on feather development or could not be determined. In addition, accurate estimation of the biomass of each item was possible from the videography, providing another indication of which prey are most important in the diet (Lewis 2001). Changes in prey composition during the time of monitoring, in this case the breeding season, can be documented with the videography as well (Lewis 2001). For these reasons we agree with others who have used videography and concluded that identifications of prey and estimates of number of prey are best obtained from videography of prey delivery (Grønnesby and Nygard 2000, Booms and Fuller 2003).

We believe the ability to see each prey item delivered to the nest and manipulated while it is fed to the young, and the ability to review those deliveries, make videography of prey deliveries the most accurate technique for determining food habits at raptor nests. This is at least partly because of the

larger sampling intensity of the video method compared with indirect methods that sample a smaller population of prey items. Overall, both indirect methods resulted in a list of prey in the diet similar to that from analysis of deliveries. However, the video provided more fine detail to the description. Six prey species were found in video analysis only. Some of these species were seen only once and presumably were classified into an unknown category or missed entirely using an indirect technique. Nearly continuous video provided evidence of species that are rare in the diet. For example, we identified 2 spotted sandpipers (*Actitis macularia*) on the video but were able to identify individuals in prey remains and pellets only as "unknown wading birds." However, 2 categories were found solely in prey remains and 1 in pellets. These results suggest that all 3 sources of data can be useful for developing the list of prey species or categories.

While the diet described from prey deliveries was relatively thorough (i.e., almost a complete record of prey deliveries), technical problems and maintenance requirements of the video systems can limit use of this technique (Lewis et al. 2004). In Southeast Alaska goshawks nest in low density and at nests that are relatively inaccessible (Iverson et al. 1996); thus, we could use video at only a subset of known goshawk nests. Technical difficulties (e.g., power loss) associated with operating an electronic system in a cool rainforest climate resulted in recording failure and presumably missed prey deliveries (Lewis et al. 2004). Our ability to identify an item depended on its condition upon delivery and the image quality. Small items (e.g., nestling birds, mice, and voles) were difficult to identify to species or genus and often had to be lumped into categories that were more general. Despite these limitations, we concluded that videography of prey deliveries was the best technique for obtaining relatively complete coverage of prey brought to a sample of raptor nests, and therefore considered it as the standard to which we compared the other techniques.

Collection of prey remains in our study resulted in a bias favoring birds, which confirms conclusions made by other authors (Simmons et al. 1991, Mersmann et al. 1992, Boal 1993). Remains from birds with brightly colored feathers (e.g., ptarmigan, Steller's jay) that are highly visible in nest stands were identified most frequently from remains (Table 2). Mammals, on the contrary, were identified infrequently (squirrels 6.2%, others 2.4%)

from remains. Birds delivered to nests were plucked more often and more completely than mammals, and feathers remained visible longer than hair in the rainforest environment (personal observation). Only birds could be aged using prey remains, and predominantly we found adults. We believe this was because nestlings were rarely plucked. In addition, some bird remains might be incorrectly aged because adults in molt can have feathers in the sheath and subadults can have completely grown feathers.

In contrast, diet based on prey identification from pellets was biased toward mammals. Feathers often were plucked from avian prey prior to delivery and were harder to identify in pellets (F Doyle, WDC, personal communication), resulting in overestimation of mammals. Quantifying prey found in pellets is difficult because more than 1 prey item can contribute to 1 pellet (Marti 1974). Conversely, more than 1 pellet can contain evidence of a single prey item because large prey items can appear in more than 1 pellet (Lowe 1980, Mersmann et al. 1992) or, as we observed, several raptors (e.g., young in a nest) can each generate a pellet from 1 large prey item. It was more difficult to find pellets than many types of remains because pellets become obscured in the ground vegetation beneath nests, and wet rainforest conditions cause them to disintegrate or decompose rapidly. Prey age could not be determined reliably using parts from pellets (F Doyle, WDC, personnel communication).

The diet descriptions based on prey remains and pellets were least similar of the 3 combinations. Intuitively, this is because results from prey remains overestimated birds while results from pellets underestimated birds. By combining counts from prey remains and pellets, we found no difference in the proportions of prey-group frequencies when we compared prey-delivery data with the combined data from remains and pellets. While combining results from prey-remains analysis and pellet analysis does not address the bias toward adult prey in these indirect techniques, it does reflect the taxa in the goshawks' diet relatively well.

Another factor to consider when interpreting the comparisons of results from different techniques is that pellets and prey remains from our collections were made at roosts and plucking perches and thus reflect the diet of adults as well as food delivered to the nest. Therefore, we conclude that a thorough sample of remains and pellets from nests provided

a reasonable basis for the list of species eaten by goshawks during the nesting season in our study area in Southeast Alaska. However, we required data from videography to quantify the diet, which is especially important for agencies that want to emphasize habitat management prescriptions for species commonly found in the diet.

Recommendations

Several investigators have compared raptor diet based on prey deliveries recorded by direct observation with analysis of prey remains and pellets (Collopy 1983, Simmons et al. 1991, Bielefeldt et al. 1992, Mersmann et al. 1992). All concluded that for their objectives, results from pellets and prey-remains collections were more biased than those based on direct observations. While the inherent biases of prey remains and pellets data are well known (Marti 1987), these sources have been (e.g. Reynolds and Meslow 1984) and continue to be (e.g., Watson et al. 1998) used to describe raptor diets because of the advantages we noted previously.

We agree with the general conclusion that direct methods are the least biased of the diet collection techniques (Marti 1987, Rosenberg and Cooper 1990). We recommend that studies attempting to describe diet use some direct technique. Recent technology makes remote videography feasible for direct recording of prey deliveries (Lewis 2001). Furthermore, videography equipment and maintenance are cost-effective compared to labor costs for prolonged observation from a blind (Lewis et al. 2004), and therefore we recommend using videography of prey deliveries. Additional research into diet techniques should involve a comparison of videography with that of persons watching nests from a blind (hide).

In general, no single technique provides a complete dietary description, but by using several techniques, a more complete description and rigorous quantification can be obtained (Collopy 1983, Simmons et al. 1991, Rosenfield et al. 1995). Prey deliveries provide detailed information about prey species and ages. While the nests we videographed were not a random sample of goshawk nests, the diet description from these nests showed the variability in the diet (i.e., the extent of prey eaten) while also quantifying which species are most preyed upon by goshawks during this time of year (Figure 3). However, Southeast Alaska has a vast heterogeneous landscape, and it would be neces-

sary to monitor more nests to detect differences in the diet among areas of the region. This is not unlike circumstances commonly encountered with raptors that have wide distributions. We suggest that videography be used to subsample a larger set of nests throughout the study areas of interest. This subsample should encompass differences in prey abundance within this area because videography of prey deliveries is especially suited to capture the fine-scale nuances of the diet that result from these differences. Using a subsample with videography will limit the costs of video equipment and maintenance while providing data with which to "calibrate" collections of large numbers of prey remains and pellets that can be made relatively inexpensively at many nests over time and space. This combination of techniques provides a practical method for monitoring the diet of birds during the nesting season.

The most complete estimates of the diet can be generated by combining results from direct and indirect methods, with videotaping of prey deliveries being used to ensure that the extent and quantity of the diet described by the indirect techniques is realistic. In addition, specific questions regarding age structure of prey in the diet can be addressed best with the video—information that is becoming increasingly important in management strategies focusing on prey population dynamics.

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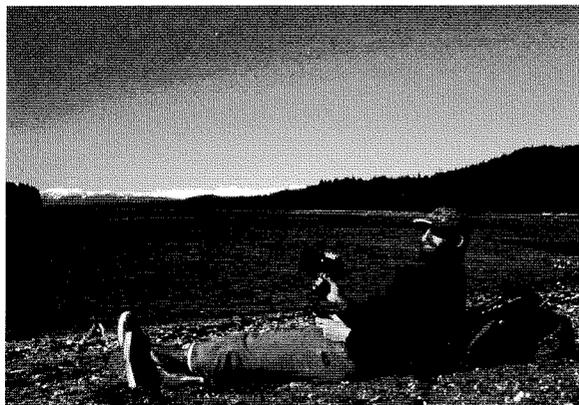
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