DIET, PREY DELIVERY RATES, AND PREY BIOMASS OF NORTHERN GOSHAWKS IN EAST-CENTRAL ARIZONA

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Abstract. Recent concern over persistence of Northern Goshawk (*Accipiter gentilis*) populations in Arizona has stemmed from two long-term demography studies that report substantial yearly fluctuations in productivity and evidence of a declining population. Although many factors could be involved in changes in productivity and population declines, availability of food is one such factor. As part of a demography study on the Sitgreaves portion of the Apache-Sitgreaves National Forest in Arizona, we used remote cameras to assess diets of goshawks. Northern Goshawks preyed upon 22 species during two nesting seasons. Adult pairs tended to specialize on particular species of prey. Prey delivery rates decreased throughout the nesting season with a corresponding increase in biomass in the latter stages of the nestling and fledgling periods. Adults appeared to take larger prey as nestlings increased in age.

Key Words: *Accipiter gentilis,* Arizona, diet, food habits, Northern Goshawk, remote cameras, video surveillance.

DIETA, TASA DE ENTREGA DE PRESA Y BIOMASA DE LA PRESA DEL GAVILÁN AZOR EN ARIZONA DEL ESTE CENTRAL

Resumen. La reciente preocupación acerca de las poblaciones del Gavilán Azor (*Accipiter gentilis*) en Arizona, ha sido estancada en dos estudios demográficos de largo plazo, los cuales reportan substanciales fluctuaciones anuales en la productividad y evidencia en la disminución en la población. A pesar de que muchos factores podrían estar involucrados en los cambios en la productividad y en la disminución de la población, la disponibilidad de alimento es uno de ellos. Como parte del estudio demográfico en la porción Sitgreaves del Bosque Nacional Apache-Sitgreaves en Arizona, utilizamos cámaras remotas para evaluar las dietas de los gavilanes. Gavilanes Azor cazaron 22 especies durante dos temporadas de anidación. Las parejas adultas tendieron a especializarse en particulares especies de presa La tasa de entrega de presa disminuyó durante la temporada de anidación, con un incremento correspondiente a la biomasa en los estados tardíos en los períodos de crecimiento y volanteo. Al parecer los adultos tomaron presas más grandes, conforme los polluelos crecían.

Concern and controversy exist over the persistence of Northern Goshawk (*Accipiter gentilis*) populations in the western US (Reynolds et al. 1982, Crocker-Bedford 1990). A long-term demographic study conducted on the Apache-Sitgreaves National Forest reported substantial yearly fluctuations in productivity of goshawks, and equivocal evidence of a declining local population (Ingraldi 1999). Probable causes of decline have been linked to habitat alterations that include timber harvesting, fire suppression, and grazing, some of which have reduced numbers of large diameter trees and increased the density of smaller diameter trees (Kochert et al. 1987, Lehman and Allendorf 1987, Moir and Deteriech 1988).

In Arizona, Northern Goshawks are found in mature ponderosa pine (*Pinus ponderosa*) and mixed conifer forests in the northern and central parts of the state, with the southernmost edge of the sub-species *Accipiter gentilis atricapillus* range reaching the rim of the Mogollon Plateau. The changing structure of mature forests may decrease habitat for goshawks by limiting nest sites and reducing the availability

of certain prey (Beier and Drennan 1997, DeStefano and McCloskey 1997). Some important prey species in the Southwest include eastern cottontail (*Sylvilagus floridanus*), Steller's Jay (*Cyanocitta stelleri*), Northern Flicker (*Colates auratus*), and Abert's squirrel (*Sciurus aberti*) (Kennedy 1991, Reynolds et al. 1992, Boal and Mannan 1994). To better understand goshawk-prey relationships in central Arizona, we examined prey delivery by adult goshawks to their nests. Studying raptor diets allows a better understanding of raptor niches and may provide information on prey distribution (Marti 1987). In addition, information on raptor diet is important for understanding ecological aspects such as diet overlap between and among species, predation, and prey availability (Hutto 1990, Rosenberg and Cooper 1990, Redpath et. al 2001).

Diet is most commonly measured through indirect methods, such as examination of pellets and prey remains, and direct methods, such as observations from blinds. These methods are not only time intensive, but evidence suggests that they can be subject

to bias (Duffy and Jackson 1986, Beilefeldt et al. 1992, González-Solís et al. 1997). We chose video monitoring as a primary method to quantify goshawk diet. We investigated diet, prey delivery rates, and prey biomass of nesting Northern Goshawks during the breeding seasons of 1999 and 2000 in east-central Arizona. Our objectives were to assess patterns related to prey consumption by breeding goshawks by (1) identifying and quantifying prey items, delivery rates, and biomass of prey brought to nests by adult goshawks, and (2) assessing the effect of nestling age, brood size, and time of day on prey delivery rates and biomass.

METHODS

STUDY AREA

Our study took place on the Sitgreaves portion of the Apache-Sitgreaves National Forest in east-central Arizona. The Sitgreaves Forest encompasses about 330,300 ha and is located on the Mogollon Plateau, a large glacial escarpment stretching east across central Arizona and into New Mexico. The rim of the plateau formed the southern boundary of our study area (Rogers 2001). A wide variety of vegetation communities occur within the study area (Brown 1982). The Mogollon Rim edge has deep drainages with mixed-conifer communities of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), aspen (*Populus tremuloides*), ponderosa pine, New Mexico locust (*Robinia neomexicana*), and Gambel oak (*Quercus gambelii*). Ridgetops are commonly dominated by ponderosa pine forest. Elevations range from 1,800–2,400 m and decrease going north as ponderosa pine and juniper-pinyon forest transitions to a pinyon-juniper woodland dominated by alligator juniper (*Juniper deppeana*), Utah juniper (*Juniper osteosperma*), and Rocky Mountain pinyon pine (*Pinus edulis*). Lowest elevations are comprised of a grassland community with blue grama (*Bouteloua gracilis*), sand dropseed (*Sprobus crytandrus*), and fourwing saltbush (*Atriplex canescens*). Goshawk nest stands were located within or near major drainage systems, dominated by mature ponderosa or mixed conifer vegetation cover, and spread throughout the study area.

OBSERVATIONS

We recorded nest activities at four nests in 1999 and six nests in 2000. No nests were observed for more than one breeding season. When Northern

Goshawk young were between 4–7 d old we climbed nest trees and mounted weatherproof remote cameras (Electro-optics EOD-1000 remote camera, St. Louis, MO; mention of trade names does not imply endorsement by the U.S. Government) (Rogers 2001). Cameras were equipped with 3.6 mm lenses, had a resolution of 380 lines, a 1 lux digital color system, and measured 3.5 x 12 cm in size. Once positioned, we secured cameras on the trunk of the tree or an overhanging branch. To minimize nestling stress we shaded them with towels during camera installation. Cameras were connected to 75 m of telephone power cord and coaxial video cable, which were tacked along the trunk of the tree. Located away from the base of the nest tree was a 12-volt time-lapse video-cassette recorder (VCR) (Panasonic AG-1070 DC, Secaucus, NJ and Sony SVT-DL224, Park Ridge, NJ), which provided 24 hr of recording per videotape. VCRs were housed in military ammunition cans for weatherproofing and powered by one 12-volt, 64 amp-hour lead acid battery. After camera set-up was complete we locked ammunition cans, attached all ground equipment to trees with cables, and covered equipment with forest litter for shade and camouflage.

We collected video 6 d of each week from 22 June–18 July 1999, and 6 June–31 July 2000. We recorded activity at each nest in a 2-d sequence (12 hr/day) with video recorded from 0450–1650 H on day one and 0800–2000 H on day two. Batteries and tapes were changed at the end of day two, usually at night to reduce disturbance. We continued to record until no prey deliveries were seen on video footage for two consecutive days.

Video was viewed by one person (ASR) to minimize observer bias. We quantified total number and type of prey items delivered (class, genus, or species) and portion size of prey items both delivered and consumed. We aged nestlings (Boal 1994) and assigned each nest a single age value by averaging each nestling's estimated age. We recorded brood size and documented nestling and adult mortality.

PREY DELIVERIES

We calculated prey delivery rate as the total number of prey items delivered per hour. Cached or questionable prey items were those that were identified as the same species and portion re-delivered within a half-hour of the initial delivery. Goshawks may consume a portion of a prey item and then cache the remainder to re-deliver to the nest. Therefore, in order to limit inflated prey delivery rates due to caches, we excluded all questionable prey items

delivered to nests (e.g., five items delivered to the nest before dark, followed by the same items delivered within 2–3 hr the next morning were likely cached items). In addition, we could monitor cached prey delivered to nests more accurately with longer hours of taped observation; therefore, we excluded videotapes in which the sampling day was ≤6 hr.

BIOMASS

We estimated biomass of prey in two ways: (1) total biomass delivered to the nest by adults, and (2) total biomass consumed at the nest by adults and nestlings. Biomass rate was estimated as grams/hour. Total biomass was estimated based on portions delivered, whereas values for consumed biomass were calculated by taking the difference of portion delivered and portion not consumed. As we did with prey delivery rate, we excluded videotapes in which the sampling period was ≤6 hr.

Biomass calculations for whole animals

Whole mass of mammals was assigned from Cockrum and Petryszyn (1992), birds from Dunning (1993), and reptile mass (short-horned lizards [*Phrynosoma hernadesi*]) was calculated from specimens (N = 5) from the University of Arizona's herpetology museum. Within the genus *Eutamius* we were unable to distinguish between the grey-collared chipmunk *(Eutamius cinereicollis)* and cliff chipmunk *(Eutamius dorsalis),* which co-occur on the Sitgreaves Forest (Hoffmeister 1986). We assigned mass for *Eutamius* by averaging mass of both species calculated from specimens in the University of Arizona mammal collection (N = 50).

Prey items described to class only were characterized a priori as small (50–200 g), medium (200–600 g), or large (>600 g) for mammals, and small (<40 g), medium (60–150 g), and large (>150 g) for birds (Cockrum and Petryszyn 1992, Dunning 1993). No size category was used for lizards because all individuals were identified to species. Whole prey items not recognizable to genus or species were assigned biomass values of the mean mass for the size class to which they belonged (Table 1). If prey was not recognizable to class, genus, or species, it was usually small in size. These items were categorized as unknown and given the mass value of the smallest overall prey item delivered to nests (10 g). We estimated whole mass for juvenile birds based on Beilefeldt et al. (1992), and juvenile mammal whole mass from minimum mass from ranges found in Wilson and Ruff (1999).

Biomass calculations for partial animals

Prey delivered in pieces were given proportional mass values, with pieces categorized as minus head, three-quarters, half, two legs and thighs, legs only, and one leg. We calculated partial prey mass for items identified to species by collecting and dissecting one individual of each species (hereafter referred to as reference specimens) represented in the diet of Northern Goshawks on the Apache-Sitgreaves National Forest. When we were unable to collect an individual species we substituted an individual from the same genus or an individual of comparable size. We used the reference specimens to estimate proportional mass of prey pieces by dividing the reference piece weight (half, minus head, etc.) by the total massof the reference animal, then multiplying that proportion times the animal's mean mass from the literature (Rogers 2001).

Partial prey items not recognizable to species were given proportional values based on mean prey mass of partial prey pieces across the size class to which it belonged. For example, a half of a medium sciurid would receive a mass value from averaging half a golden-mantled ground squirrel (*Spermophilus lateralis*) and half a red squirrel (*Tamiasciurus hudsonicus*).

ANALYSES

All prey delivery rate and biomass data were truncated at fledgling age (40 d). Forty days is a combined estimate for average fledging dates for male and female goshawk young. We calculated diet composition by class, genus, and species and expressed values as percentages. We summarized total species in goshawk diet, which included videotapes with <6 hr of daily footage, and videos collected after fledging (40 d). To reflect the percentage of total grams consumed, we expressed delivered biomass and consumed biomass as percentages. We also determined the percentage of time that goshawks consumed entire prey portions rather than leaving the nest with an item to be cached. Lastly, we looked at percent representation of most common prey items for each individual nest.

Daily biomass and prey delivery data were pooled for all 10 nests after determining no difference in rates at age increments of 5 d (analysis of variance [ANOVA]). We used multiple linear regression to assess relationships of brood size and nestling age on biomass and prey delivery rates. For multiple regression analysis we used estimates of consumed biomass instead of total biomass. We transformed

TABLE 1. SIZE CLASSES AND WEIGHTS USED TO CALCULATE BIOMASS OF PREY DELIVERED TO 10 NORTHERN GOSHAWK NESTS ON THE APACHE-SITGREAVES NATIONAL FOREST IN EAST-CENTRAL ARIZONA, 1999 AND 2000.

Prey types		Mass (g)[a]
Small mammal (50–200 g)		
Chipmunk[b]	*Eutamius* spp.	63
White-throated wood rat	*Neotoma albigula*	180
Average small mammal		121.5
Medium mammal (200–600 g)		
Golden-mantled ground squirrel	*Spermophilus lateralis*	200
Red squirrel	*Tamiasciurus hudsonicus*	230
Average medium mammal		215
Large mammal (>600 g)		
Abert's squirrel	*Sciurus aberti*	680
Rock squirrel	*Sciurus variegatus*	760
Eastern cottontail	*Sylvilagus floridanus*	1,500
Black-tailed jackrabbit	*Lepus californicus*	2,100
Average large mammal		1,260
Small bird (<40 g)		
Dark-eyed Junco	*Junco hyemalis*	20
White-breasted Nuthatch	*Sitta carolinensis*	21
Western Bluebird	*Sialia mexicana*	28
Townsend's Solitaire	*Myadestes townsendi*	34
Average small bird		25.8
Medium bird (60–150 g)		
Hairy Woodpecker	*Picoides villosus*	66
American Robin	*Turdus migratorius*	77
Northern Flicker	*Colaptes auratus*	111
American Kestrel	*Falco sparverius*	116
Mourning Dove	*Zenaida macroura*	119
Steller's Jay	*Cyanocitta stelleri*	128
Average medium bird		102.8
Large bird (>150 g)		
Band-tailed Pigeon	*Columba fasciata*	342
Rock Dove	*Columbia livia*	354
Cooper's Hawk	*Accipiter cooperii*	439
Average large bird		378.3
Short-horned lizard	*Phrynosoma hernadesi*	40

[a] Mass calculated by averaging adult male and female mean mass for each species; mass across size classes was calculated from all species within the size class, e.g., average small mammal = mass of chipmunk + mass of wood rat/2.
[b] Mass for chipmunks was calculated by averaging mass of *Eutamius dorsalis* and *Eutamius cineriecollis*.

biomass data using a natural log transformation. We used simple linear regression to assess (1) time of day (morning = 0450–1050 H, afternoon = 1050–1550 H, evening = 1550–2000 H) for the number of prey items delivered, and (2) the effect of nestling age on average daily prey mass brought in by adults.

RESULTS

We had no nest abandonment due to camera presence, and eight of ten goshawk nests were successful (i.e., fledged ≥1 young). Of 23 nestlings from 10 nests, 19 survived to fledging, and brood size varied from two (seven nests) to three (three nests) individuals. The two failed nests were due to an adult

female choking on a piece of rabbit (Bloxton et al. 2002) and nestling mortality by a Great Horned Owl (*Bubo virginianus*). We collected 2,458 hr of usable video from videotapes (i.e., ≥6 hr for each tape).

PREY DELIVERIES

We documented 670 prey deliveries and observed a mean delivery rate of 0.30 (SE = 0.01, range = 0.00–0.67) prey items/hour. Goshawk diet was composed of 73% mammals, 18% birds, 2% reptiles, and 7% unknown prey items. We successfully identified 627 (93%) prey items to class and were able to identify, at least to genus, 422 (62%) of all prey items. Goshawk diet was comprised of 22 different

species (Table 2). Five mammal and one bird genera contributed 78% of all prey. Mammals contributing >5% each to goshawk diet were eastern cottontails, chipmunks, golden-mantled ground squirrels, red squirrels, and Abert's squirrels. Steller's Jays were the only bird species that contributed >5% to diet (Table 2). Lastly, these six most common prey items were not taken equally among individual nests, with some nests showing possible specialization for particular prey items (Table 3).

Nestling age and time of day affected daily prey delivery rates, but brood size did not (Rogers 2001). Mean prey delivery rates decreased overall, but with a peak in delivery rate near 18 d of age (Fig. 1).

TABLE 2. TOTAL NUMBER OR PREY SPECIES AND BIOMASS DELIVERED AND CONSUMED AT 10 NORTHERN GOSHAWK NESTS ON THE APACHE-SITGREAVES NATIONAL FOREST IN EAST-CENTRAL ARIZONA, 1999 AND 2000.

Prey species		N	Percent number	Percent biomass
Abert's squirrel	*Sciurus aberti*	62	9.25	18.48
Golden-mantled ground squirrel	*Spermophilus lateralis*	63	9.40	7.06
Eastern cottontail	*Sylvilagus floridanus*	89	13.3	42.31
Red squirrel	*Tamiasciurus hudsonicus*	53	7.92	7.66
Chipmunk	*Eutamius* spp.	67	10.1	2.51
Rock squirrel	*Spermophilus variegatus*	8	1.19	3.25
White-throated wood rat[a]	*Neotoma albigula*	–	–	–
Black-tailed jackrabbit[1]	*Lepus californicus*	–	–	–
Unknown mammals		144	21.5	7.42
Northern Flicker	*Colaptes auratus*	10	1.49	0.65
Steller's Jay	*Cyanocitta stelleri*	34	5.08	2.42
Band-tailed Pigeon	*Columba fasciata*	1	0.15	0.18
Mourning Dove	*Zenaida macroura*	3	0.46	0.16
Rock Dove	*Columba livia*	4	0.61	0.39
Hairy Woodpecker	*Picoides villosus*	1	0.15	0.25
American Robin	*Turdus migratorius*	3	0.46	0.10
Dark eyed Junco	*Junco hyemalis*	1	0.15	0.03
American Kestrel	*Falco sparverius*	1	0.15	0.03
Townsend's Solitaire[a]	*Myadestes townsendi*	–	–	–
Cooper's Hawk[a]	*Accipiter cooperii*	–	–	–
Western Bluebird[1]	*Sialia mexicana*	–	–	–
White-breasted Nuthatch[1]	*Sitta carolinensis*	–	–	–
Unknown birds		61	9.10	2.74
Short-horned lizard	*Phrynosoma hernadesi*	16	2.39	0.77
Unknown prey items		49	7.31	0.54
TOTAL		670	100	100

[a] Prey items delivered after fledging of Northern Goshawks, or delivered but not consumed by birds at the nest. Items are not quantified into total prey item or biomass estimates.

TABLE 3. PERCENT OF SIX COMMON PREY SPECIES BROUGHT TO 10 NORTHERN GOSHAWK NESTS ON THE SITGREAVES FOREST, ARIZONA, 1999 AND 2000.

Nest	Eastern cottontail	Golden-mantled ground squirrel	Abert's squirrel	Red squirrel	Chipmunk spp.	Steller's Jay	Total[a]
1	30	3	15	0	6	14	68
2	4	21	26	4	18	2	75
3	11	0	16	0	0	0	27
4	9	21	7	16	10	12	75
5	0	6	0	32	17	4	59
6	2	21	0	0	9	7	39
7	16	2	9	2	6	43	78
8	6	13	0	14	10	6	49
9	23	4	32	0	0	7	66
10	0	11	9	33	25	6	84

[a] Percentages do not total to 100 because of other prey species, not listed here, that were brought to the nest.
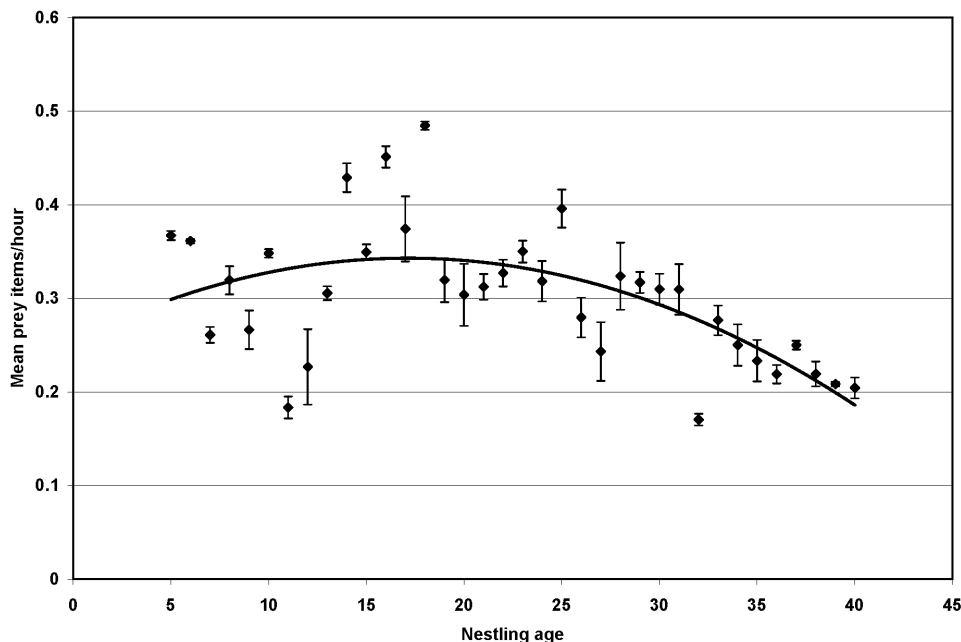
FIGURE 1. Mean prey items per hour plotted against nestling age at 10 Northern Goshawk nests on the Sitgreaves Forest, Arizona, 1999 and 2000.

Daily delivery rates decreased by a factor 0.3% as nestlings aged (t = -2.73, df = 162, P = 0.007). Time of day affected mean prey delivery rates with highest rates during the morning (mean delivery rate = 2.2 items per hr, SE = 1.2, N = 81) and decreasing rates throughout the day (afternoon = 1.4 items per hr, SE = 0.9, N = 151; evening = 1.3, SE = 0.9, N = 76). Prey delivery rates decreased by a factor of 0.46 prey items/interval (t = -5.68, df = 307, P < 0.001) from morning to afternoon to evening.

PREY BIOMASS

Daily mean biomass rate was 42.4 g/hr (SE = 2.75, range 0.00–238.8). Mammals and birds accounted for 92% and 6.9% of the biomass consumed, respectively. Lizards contributed 0.8%, and 0.5% of biomass was attributed to unknown prey items. Four species of mammals (eastern cottontails, red squirrels, golden-mantled squirrels, Abert's squirrels) contributed 75% of the total biomass consumed (Table 2). No bird species contributed >5% biomass consumed.

Of 102,078 total grams of prey delivered, goshawks consumed 79,958 grams (78%) at the nest. Goshawks consumed the entire prey item brought in 73% of the time. Nestling age and time of day affected biomass rates, but brood size did not (P =

0.14). Mean biomass consumed by nestlings at age five was 5.64 g/hr and increased linearly to 51.09 g/hr at 40 d (Fig. 2). Daily biomass rates increased by 1.03 g/hr as nestlings grew older (t = 4.20, df = 158, P < 0.001). Lastly, average prey mass increased by a factor of 46.53 g/d as nestlings aged (t = 4.40, df = 161, P < 0.001). Average prey mass brought to nests with five-day-old chicks was 63.25 g and increased to 792 g by fledging date (Fig. 3).

DISCUSSION

In 1992, the USDA Forest Service (USFS) developed guidelines for Northern Goshawks and forest management that are currently being implemented on some national forests across the southwestern US (Reynolds et al. 1992). These management recommendations recognized 14 consistently abundant and important prey species, out of a total of 66 potential prey species from various goshawk diet studies (Schnell 1958, Meng 1959, Reynolds and Meslow 1984, Kennedy 1991, Boal and Mannan 1994) and suggested managing habitat for all prey species. Among the 14 prey species listed in the guidelines, we observed that six species contributed >5% each to goshawk diet on the Sitgreaves Forest. Our study supports the idea that managing habitat for these consistently hunted prey items is important.
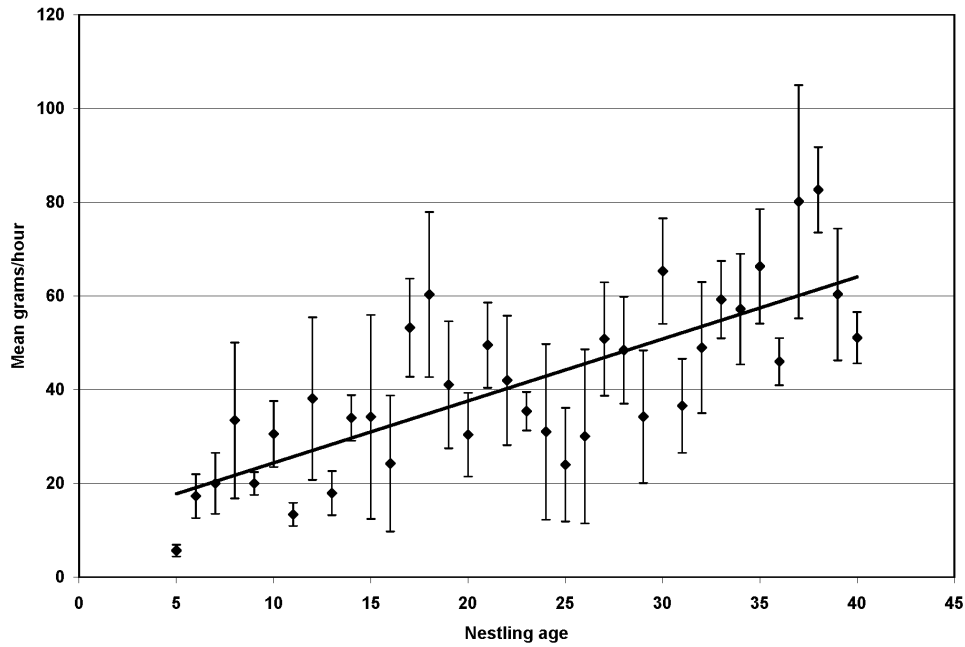
FIGURE 2. Mean biomass of consumed prey plotted against nestling age for 10 Northern Goshawk nests on the Sitgreaves Forest, Arizona, 1999 and 2000.
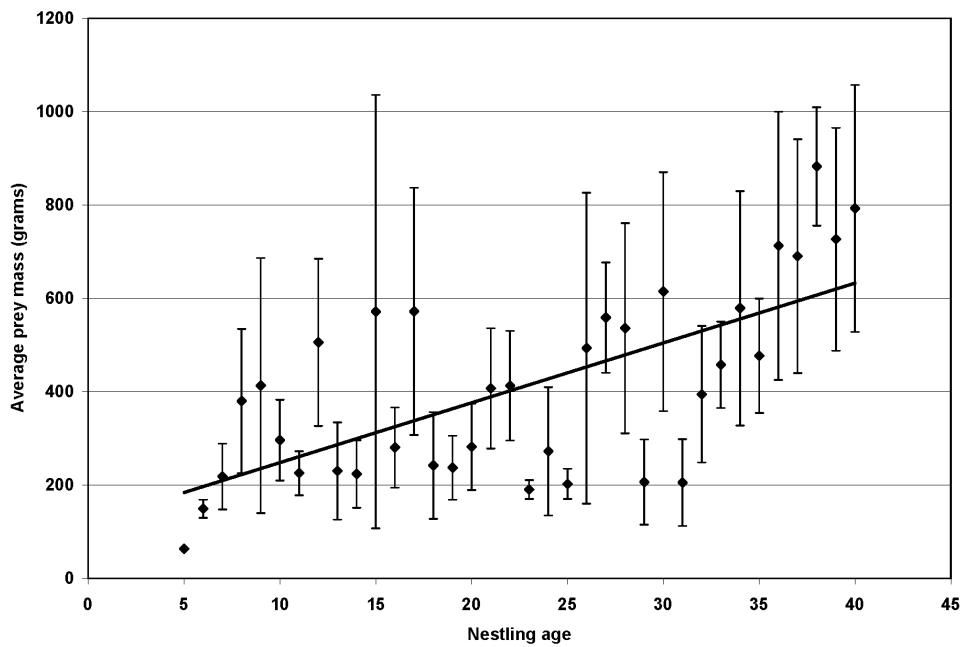

FIGURE 3. Average mass of prey items plotted against nestling age for 10 Northern Goshawk nests on the Sitgreaves Forest, Arizona, 1999 and 2000.

Most goshawk diet studies conclude that goshawks are generalists and opportunistic foragers, with diet reflecting prey availability (Widén 1987, Kennedy 1991). Our study on the Sitgreaves Forest supports the idea that Northern Goshawks as a population are diet generalists, due to the high number of prey species fed upon (22 species). When we looked at diet composition at each nest, however, we saw that one or two prey species often dominated the diet. For example, we reported 21% cottontails by number and 42% by total biomass consumed; however; of the total eastern cottontails consumed, over half (58%) came from only two nests (Table 3). We saw this pattern more dramatically with Steller's Jays: >40% of all Steller's Jays came from one nest. Similarly, goshawks preyed upon red squirrels unequally among nests, with 30% of nests comprising 83% of total red squirrels.

Two reasons may explain why individual goshawks took prey unequally: adult goshawks exhibited preference for particular prey items, or goshawks took the prey within the foraging area that was most available. It is likely that increased proportions of a particular prey species at a nest was due to the habitat requirements of that prey within an individual goshawk foraging area. For example, we only detected red squirrels at nests close to areas of high elevation mixed conifers. Hoffmeister (1986) reported that on the Mogollon Rim, red squirrels are rarely found below 2,400 m in elevation, and rely heavily on Engelmann spruce (*Picea engelmanni*) and Douglas-fir cones. Currently, USFS guidelines in the Southwest recognize three vegetation cover types as important for management of goshawks: ponderosa pine, mixed species, and spruce-fir cover types (Reynolds et al. 1992). Because certain prey appeared frequently in goshawk diet on the Sitgreaves National Forest, it may be important to continue to focus management in these various vegetative cover types where these prey could occur in high numbers.

Seasonal shifts in diet of goshawks may be due to reproductive timing, hibernation, and/or migration of prey species (Squires and Reynolds 1997). Also, initially abundant juvenile prey (e.g., rabbits) become more scarce as they are preyed upon by entire guilds of predators during the year. It is also plausible, however, that a diet shift may occur in order to meet the energetic needs of growing nestlings. One solution for meeting energetic needs of aging nestlings would be to either capture prey more frequently, or increase the size of prey items delivered to nests. Our results provide some evidence of an increase in average mass of prey items delivered to nests as the nestlings increase in age. In addition, prey delivery rates decreased overall as the nesting season progressed. By bringing fewer but larger prey, adult goshawks may meet the increasing energetic needs of nestlings and simultaneously reduce the number of prey items brought to the nest.

Prey delivery rates lend information on hunting efficiency of adults, frequency and timing of feeding bouts, and correlation with food density (Zammuto et al. 1981). The average daily prey delivery rate we observed was 0.30 prey items/hr, with the rate decreasing as nestlings aged (i.e., one less prey item about every 2 wk). When looking at mean delivery rate versus age, we saw a slight increasing trend around the age of 18–20 d. We speculate that this increase could be due to additional items brought to the nest by the adult female. During this time (18–20 d), females begin to spend greater time off the nest and could be hunting more frequently.

Problems associated with using delivery rates as a measure of availability include (1) differences in efficiency of capturing prey in various vegetative cover (Buchanen 1996), (2) the physiological condition of the hawk, and (3) age of the hawk (Bennetts and McClelland 1997). Part of the explanation regarding decreased delivery rates could be due to the increase in average biomass delivered to nests in the latter part of the nestling season, and the ability of nestlings to consume and manipulate prey more efficiently as they get older (Schnell 1958). However, this speculation would require further research.

Sutton (1925) reported that Northern Goshawks are inclined to take avian prey more frequently than mammalian prey. In a review of diet studies from across the US, Squires and Reynolds (1997) reported that southern populations of goshawks may depend less on mammals than northern populations, with the exception of Boal and Mannan's (1994) study in northern Arizona, where they found that mammals and birds comprised 76% and 24% frequency of occurrence, respectively. DeStefano et al. (*this volume*) reported a possible trend in increasing proportions of birds to mammals in prey taken by nesting goshawks as one moves from south to north in eastern Oregon. Reynolds et al. (1994) reported 62% mammals and 38% birds on the Kaibab National Forest, Arizona, and Kennedy (1991) observed similar proportions of mammalian and avian prey items contributed to goshawk diet in the Jemez Mountains, New Mexico. Similarly, in our study on the Sitgreaves Forest in Arizona, mammals, birds, reptiles, and unknowns contributed 73%, 18%, 2%, and 7%, respectively, to goshawk diet. In summary, evidence suggests that goshawks in the Southwest

are taking mammals more frequently than previous studies have suggested. In general, however, it is likely that the goshawk's role as a diet generalist allows them to exploit prey based on prey availability. Prey availability, in turn, is at least partly dictated by forest vegetation type and structure, as well as other local habitat variables.

Past discrepancies among studies with respect to proportions of mammalian and avian prey items might be attributable to the method used to quantify diet. Most studies that reported a higher percent of birds than mammals in goshawk diet used indirect methods such as analysis of pellets or prey remains to assess dietary components. These methods have been scrutinized because they can overestimate bird species due to the relative ease in locating feathers over small pieces of mammal fur and bones (Simmons et al. 1991, Beilefeldt et al. 1992). Goshawks on the Sitgreaves National Forest regularly pluck feathers and discard them outside the nest bowl, whereas bits of mammal fur and bones are usually consumed. Goshawks in our study consumed entire prey items (excluding feathers) most of the time (73%) which meant that entire prey

items were consumed, including the feet, tails, and bones of mammals and birds. Thus, in order to locate mammalian prey items, we would have been restricted mainly to pellet analysis. It seems likely, based on our observations of goshawks consuming entire prey items, that collecting prey remains alone would have overestimated avian prey. We conclude that through the use of remote cameras, we minimized the bias toward avian prey and furthered evidence suggesting indirect methods of diet assessment are skewed toward birds (Rogers 2001).