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FEEDING ECOLOGY OF SHARP-SHINNED HAWKS NESTING IN DECIDUOUS AND CONIFEROUS FORESTS IN COLORADO[1]

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Abstract. Feeding ecology of 11 Sharp-skinned Hawk (*Accipiter striatus*) pairs nesting in aspen (*Populus tremuloides*), conifer (*Abies, Picea* spp.), and mixed aspen-conifer habitats in southwest Colorado was investigated during 1988–1989. Small birds ($\bar{x}$= 20.9 g, SE = 0.8 g) and mammals ($\bar{x}$ = 41.1 g, SE = 3.3 g) comprised 91 and 9% of 513 prey identified at nests that fledged at least one young, respectively. Sixty percent of the birds eaten during the hawks' nestling and fledgling stages were nestlings or fledglings. Accordingly, median mass of birds eaten decreased from 17.4 g during incubation to 12.1 g during the nestling stage. Although more birds were consumed than mammals during all nesting stages (birds = 91.1%; mammals = 8.9%), the proportion of birds relative to mammals in diets progressively decreased from incubation through fledging. Taxa of birds in the diet were consumed in proportion to their occurrence in the most abundant of three different habitats surrounding nests, whereas some mammalian taxa were consumed in greater proportion than their relative "availability" in these habitats. This suggested that Sharp-shinned Hawks foraged opportunistically for birds, but may have selectively foraged for mammals. Differences in the habits of mammals (e.g., fossorial vs. terrestrial behavior), and hence their relative availability, may explain the apparent selection for certain species of mammals by Sharp-shinned Hawks.

Key Words: Accipiter striatus; *Sharp-shinned Hawk; diet; food habits; feeding ecology; aspen forest; conifer forest; Colorado.*

INTRODUCTION

Sharp-shinned Hawks (*Accipiter striatus*) are small, forest-dwelling raptors that feed primarily on small birds (10–30 g) associated with forest canopies (Craighead and Craighead 1956, Storer 1966, Reynolds and Meslow 1984). In Colorado, Sharp-shinned Hawks breed in quaking aspen (*Populus tremuloides*) and conifer (*Abies, Picea, Pseudotsuga*) forests. Forests in which hunting Sharp-shinned Hawks have been observed include mature aspen, conifer, and mixed aspen-conifer. Within mature aspen forests, however, these hawks nest only in patches of conifers (S. M. Joy and R. T. Reynolds, pers. observ.).

Smith and MacMahon (1981) demonstrated that avian species diversity and community composition differed among aspen, spruce, and fir forests in Utah and Idaho. If bird and mammal numbers differ among these forests in Colorado and if Sharp-shinned Hawks forage opportunistically, then diets of the hawks might reflect the relative abundance or availability of prey in forest types surrounding nests. Foraging opportunism would allow Sharp-shinned Hawks to use a variety of forest types in spite of different faunal communities, provided that sufficient food and nest sites were available.

We examined the diets of nesting Sharp-shinned Hawks in mature forests of aspen, conifer, and mixed aspen-conifer in Colorado during 1988–1989. We tested for differences in prey

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sizes and prey numbers among nesting pairs, among nesting stages, and between avian and mammalian prey. To evaluate the hypothesis that Sharp-shinned Hawks are opportunistic foragers, taxonomic composition and the size-frequency distribution of birds and mammals in Sharp-shinned Hawk diets were compared with estimates of relative abundances of birds and mammals in each of the three forest types.

STUDY AREA

The study was conducted on 28,750 ha of the Gunnison and Grand Mesa National Forests in west-central Colorado and included portions of Gunnison, Delta, and Mesa counties. Elevations ranged from 2,750–3,200 m. In western Colorado, aspen forests comprise as much as 25% of forested lands (Green and Van Hooser 1983). Within our study area, aspen existed as both seral and stable (contained no conifers) communities in small (<10 ha) patches and extensive (>500 ha) forests. In the study area, seral aspen patches and forests (often with emergent conifers in the aspen canopies) are successional to Englemann spruce (*P. engelmannii*) and subalpine fir (*A. lasiocarpa*), and at lower elevations blue spruce (*P. pungens*) (Langenheim 1962, Morgan 1969). Situated within these aspen forests were small to large areas of pure, or nearly pure, conifer forests. As a result, forests on the study area were composed of a mosaic of large (>500 ha), medium (200–500 ha), and small (<200 ha) patches of aspen, conifer, and mixed aspen-conifer forests. Throughout the study area, the majority (>70%) of aspen forests were in mature (70–120 year) and old-growth (120+ year) age classes (Shepperd 1990).

Vegetative composition of the understory in these forests varied with elevation, slope, aspect, and type of forest. Aspen and, to a lesser extent, mixed aspen-conifer had tall (>1 m), well-developed, herbaceous understories with a minor shrub component. Dominant forbs included butterweed groundsel (*Senecio serra*), white geranium (*Geranium richardsonii*), Barbey larkspur (*Delphinium barbeyi*), white-flowered peavine (*Lathyrus leucanthus*), and monkshood (*Aconitum columbianum*). Prominent low-growing plants included elk sedge (*Carex geyeri*), wild strawberry (*Fragaria ovalis*), yellow prairie violet (*Viola nuttallii*), and fringed brome (*Bromus ciliatus*). The shrub component consisted of snowberry (*Symphoricarpos* spp.), chokecherry (*Prunus virginiana*), and mountain-mahogany (*Cercocarpus montanus*).

Conifer understories were sparsely vegetated and dominated by low-growing (<1 m) herbs and shrubs including heart-leafed arnica (*Arnica cordifolia*), field horsetail (*Equisetum arvense*), elk sedge, myrtle blueberry (*Vaccinium myrtillus*) and kinnikinnik (*Arctostaphylos uva-ursi*). Plant names follow Weber (1976). Sheep and cattle foraged freely in the study area during July and August.

METHODS

DIET DETERMINATION

Areas intensively searched for nests within the study area were identified from aerial photographs (1:24,000) and topographic maps (7.5-min series) following Joy (1990) and included patches, as well as extensive areas, of aspen, conifer, and mixed aspen-conifer. Nest searches began in May in both 1988 and 1989 and were conducted throughout the nesting season. Prey remains (feathers, bills, feet, fur, skull fragments, and regurgitated pellets) were collected from nest sites as least once every seven days, and as often as every two days. Four days prior to changes in nesting stage (incubation to nestling, nestling to fledgling), prey remains were collected every two days. Activities of pairs (food exchanges between males and females, prey handling, feeding at nests, and roosting behavior) were recorded from blinds near all nests. Areas of approximately 5 ha, centered on nest trees, that contained prey-handling sites were thoroughly searched for prey remains during each visit to nests. Searches for prey remains often required 1–3 hr/visit. Prey remains were collected from nest sites until fledged young dispersed or nests failed.

Prey remains were sorted by nest and collection date. Avian remains (remiges, contour feathers, rectrices, feet, bills, and bones) were reconstructed and compared with National Museum of Natural History (Washington, D.C.) specimens for identification and a minimum count of individuals was determined as described by Reynolds and Meslow (1984). Single feathers of a species were excluded. Mammalian remains (fur, feet, tails, skull fragments, and teeth) were identified in a similar manner at the U.S. Fish and Wildlife Service museum in Fort Collins, Colorado.

Diet determinations based on the collection of prey remains may not include all prey consumed by Sharp-shinned Hawks. Potential biases are the omission of prey plucked away from nest sites, an over-representation of more colorful and conspicuous avian prey remains, under-representation of less conspicuous mammalian prey remains, and the underestimation (because of limited remains) of taxa such as reptiles, amphibians, and arthropods (Reynolds and Meslow 1984, Bielefeldt et al. 1992). Although the extent of these biases in our study is unknown, we minimized them by conducting exhaustive searches for prey remains and examining pellets for herptofauna. Furthermore, mammals and reptiles typically contribute less than 10% and 5% (by number) to Sharp-shinned Hawk diets, respectively (Craighead and Craighead 1956, Storer 1966, Snyder and Wiley 1976, Clarke 1984, Reynolds and Meslow 1984).

Adult body mass for each species was obtained from Hall (1946), Armstrong (1972), Dunning (1984), and museum specimens. Mass of prey identifiable only to genus was estimated as the mean mass of all local species in the genus. Mass of "unknown" birds was estimated as the mean mass of birds consumed in the study area.

Avian prey were classified as "adult" and "young" (nestlings and fledglings) by plumage and amount of epitrichium sheathing on flight and tail feathers. We assigned fledglings three-quarters of their adult mass and nestlings one-half adult mass. These estimates may have overestimated the mass of altricial nestlings and fledglings and underestimated the masses of young precocial birds (Reynolds and Meslow 1984). We assumed that our estimates approximated the mean mass of young birds. We were unable to distinguish the age classes of mammalian prey and thus assigned adult masses (Armstrong 1972, 1975) to all mammalian prey. The effect of this potential bias on total-diet analyses of prey mass should be small because mammals comprise less than 10% of Sharp-shinned Hawk diets (Craighead and Craighead 1956, Storer 1966, Clarke 1984, Reynolds and Meslow 1984).

DIET COMPOSITION

Frequency of total prey (birds and mammals combined) in diets was compared among nesting pairs, among nesting stages, and between avian and mammalian classes using a maximum likelihood log-linear model (MLLM) (CATMOD, SAS Inst. Inc. 1987). The same analysis (MLLM) was used to compare, for avian prey only, diets among nesting pairs, among nesting stages, and between adult and young age classes. Differences in mean mass of total-prey (birds and mammals) among hawk pairs, among nesting stages, and between avian and mammalian prey were determined with general linear models (GLM) (GLM, SAS Inst. Inc. 1987). The same analysis (GLM) was used to examine differences in mean mass, for avian prey only, among pairs, among nesting stages, and between adult and young age-classes. Diets of pairs whose nests failed to produce fledglings (n = 5) were excluded from the log-linear and general linear analyses to eliminate unbalanced cells from the tests. We tested the null hypotheses of no difference in (1) frequency of prey and (2) mass of prey among independent effects (pairs, nesting stages, prey classes, and ages of birds in diets).

Differences in the frequency distribution of prey masses for (1) avian and (2) mammalian prey at all nests (n = 11) were tested among nesting stages using multi-response permutation procedure (MRPP; Mielke and Berry 1982, Biondini et al. 1988). When differences among frequency distributions occurred, nonparametric pairwise test for equal variances (Moses' rank-like procedure) (Hollander and Wolfe 1973) and tests of equal means and medians (Wilcoxon rank-sum test) (NPAR1WAY, SAS Inst. Inc. 1987) were used to identify the source of the differences. All analyses (MLLM, GLM, MRPP) were evaluated at the $\alpha = 0.05$ significance level and pairwise comparisons at the $\alpha = 0.05/3 = 0.017$ (Bonferroni inequality) level.

PREY ABUNDANCE, FOREST TYPE, AND DIETS

Estimates of relative abundances of birds and small mammals during the period that we sampled Sharp-shinned Hawk diets (1988 and 1989) were available from 1987–1989 censuses on 15 plots (nine in aspen, three in conifer, three in mixed aspen-conifer forests) (R. T. Reynolds and D. M. Finch, unpubl. data). All of these census plots were within the Sharp-shinned Hawk study area: one Sharp-shinned Hawk nest occurred inside a census plot, nine occurred within 620 m of plots, and one occurred within 3.1 km of a plot.

For our purposes we used estimates of the relative abundances of bird species in the three forest types that derived from raw counts of individuals in 8-min circular variable plot censuses (Reynolds et al. 1980) at 15 stations (100-m spacing) in each plot. Stations in each of the 15 census plots were censused five times during June of each year (1988–1989). All censuses occurred between 05:30–12:30 MDT (D. M. Finch and R. T. Reynolds, pers. comm.).

Relative abundances of small mammals in each forest type were estimated by totaling the number of individuals per species captured once (excluding recaptures) during late-July to mid-September, 1988–1989, in the 15 plots (R. T. Reynolds and D. M. Finch, pers. comm.). Mammal trapping grids (10 × 10 at 15-m spacing) were nested within the larger bird census grids and had one Sherman trap (7.6 cm × 8.9 cm × 23.0 cm) at each of 100-grid points per plot (100 Sherman traps/plot) and one circular pit-fall trap (160 cm depth, 130 cm dia.) at every-other grid point (25 pitfall traps/plot). Small mammal plots were live-trapped for one session of six consecutive nights per year (750 trap nights/plot^{-1} year^{-1} × 2 year = 22,500 total trap nights) (R. T. Reynolds and D. M. Finch, unpubl. data). We assumed that these abundance estimates approximated the relative "availability" of birds and mammals to Sharp-shinned Hawks in the three forest types within our study area.

Forests within 2-km radii of each Sharp-shinned Hawk nest were classified as aspen ($\geq$90% aspen trees in overstory), conifer ($\geq$90% conifer trees in overstory), or mixed aspen-conifer (mixed stands with <90% aspen and <90% conifer trees in overstory) from aerial photographs (1:24,000) taken in October 1978 when the color contrast between aspen and conifers was at a maximum. The 2-km radius was selected because 2 km is about half the nearest-neighbor distance between nests of this hawk (Reynolds and Wight 1978, Clarke 1984) and circles with this radius encompass all estimates of home-range size in this species (see review in Reynolds 1983). Around each nest, the three forest types were assigned to one of three habitat-dominance categories (dominant, secondary, or limited) based on the proportion of the 2-km radius circle each forest type occupied. Forest types comprising $\geq$50% of the area around nests were considered "dominant". "Secondary" habitats were defined as forest types occupying >5% and <50% of the area. Forest types comprising $\leq$5% of the area were termed "limited".

Program PREFER (Johnson 1980) was used to examine whether birds or mammals in diets (n = 11 nests) reflected the relative abundance—by taxa (bird and mammal families) and size-class categories (after Storer 1966)—in the (1) dominant, (2) secondary, and (3) limited habitat-dominance categories surrounding nests. Null-hypotheses tested were that: 1) avian and 2) mammalian taxa were eaten in proportion to their abundance in each of the three habitat-dominance categories (dominant, secondary, and limited); and that 3) avian and 4) mammalian size-classes were eaten in proportion to their abundance in each of the three habitat-dominance categories. PREFER requires that the number of "preference components" (i.e., taxa and size-class categories) not exceed the number of "individuals" (i.e., nests) in tests (Johnson 1980). Thus, taxonomic categories of prey containing fewer than 2 individuals at all nests combined (families Scolopacidae, Trochilidae, Mimidae, and Mustelidae) were omitted from analyses. Mammalian prey in size-class categories nine (166–216 g), eight (125–166 g), six (64–91.1 g), and two (8–15.6 g) (Storer 1966) were also omitted because they were not tallied in prey remains or during census counts. Diet and relative-abundance data were paired by year to eliminate differences in prey abundance between years. Waller and Duncan's (1969) multiple comparison procedure was used in PREFER to assess relative "preferences".

Finally, we examined the overall pattern of food-resource use of nesting Sharp-shinned Hawks by comparing the hawks' diets to the entire range of bird and mammal sizes that occurred in the study area.

RESULTS

Diets of 11 Sharp-shinned Hawk nesting pairs were determined, four nests during 1988 and seven nests during 1989. Ten (91%) nests were in small (1–14 ha), insular conifer patches surrounded primarily by aspen (n = 8) or mixed aspen-conifer (n = 2) forests, and one nest was within a large, contiguous conifer forest. Prey were collected from all nest sites during all nesting stages in 1988. In 1989, five of seven nests failed prior to fledging. Prey remains were collected from all seven nest sites during incubation, from four nest sites during the nestling stage, and two nest sites during the fledgling stage. A total of 686 prey items was identified (Appendix 1), including 53 species (39 genera, 14 families) of

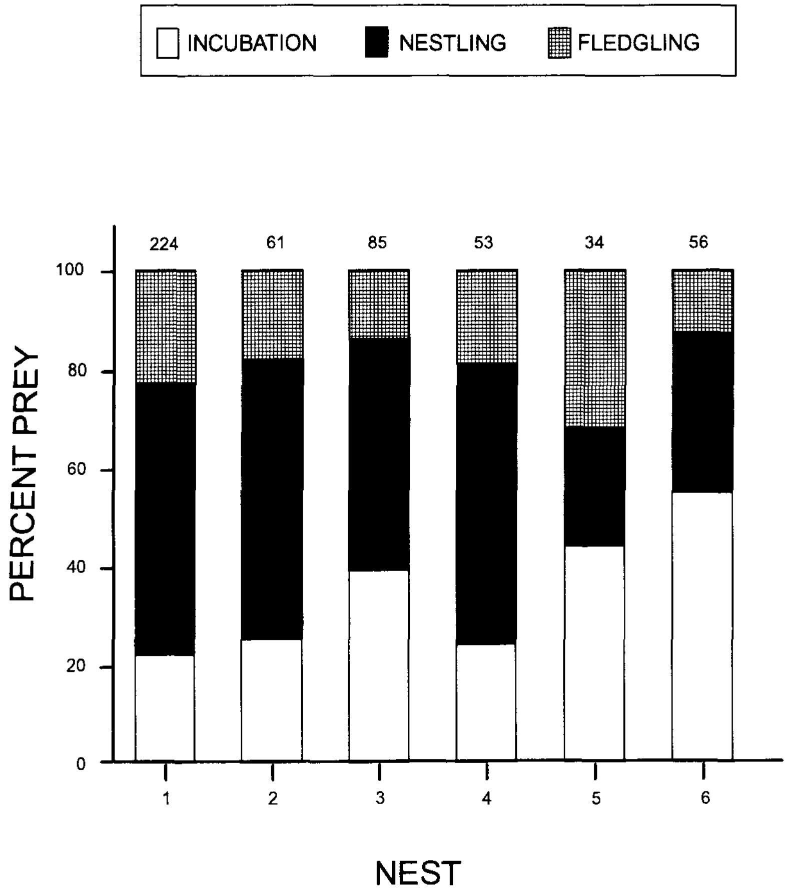

FIGURE 1. Proportion of total prey consumed during incubation, nestling and fledgling stages at six successful nests of Sharp-shinned Hawks in Colorado, 1988–1989. Numbers above columns are prey counted/nest.

birds and 10 species (nine genera, six families) of mammals.

DIET COMPOSITION

Prey Frequency. Mammals were consumed at 10 of 11 nests and birds were consumed at all nests. Of 686 total prey items, 513 were from the six successful nests. Birds comprised the largest (91.1%) portion of prey consumed at successful nests. The proportion of mammals consumed (overall = 8.9%) ranged from 1.8 to 11.8% for the five successful nests surrounded by aspen forests to 28.3% for the one successful nest surrounded by conifers. Although neither of the two nests surrounded by mixed aspen-conifer fledged young, the proportions of mammals consumed prior to nest failure were 4.3 and 6.7%. Yellow-rumped Warblers (*Dendroica coronata*) appeared most often in the avian diet, followed by American Robins (*Turdus migratorius*), White-crowned Sparrows (*Zonotrichia leucophrys*), and Dark-eyed Juncos (*Junco hyemalis*) (12.5, 8.3, 7.0, and 6.5% of 626 items consumed, respectively). Voles (*Clethrionomys, Microtus, Phenacomys*) comprised over 60% (37 of 60) of the mammals eaten.

Numbers of total prey (birds and mammals) varied by nesting × and nesting stage interactively (Table 1); that is, more prey were collected during the nestling period at four of six nests (67%) than during other nesting stages (Fig. 1). Prey numbers also varied by prey class (birds vs. mammals) × nesting stage interactively (Table 1) that is, the proportion of mammals in the diet increased from 7.7 to 16.5% from incubation to fledging (Table 1, Fig. 2).

TABLE 1. Maximum likelihood log-linear model for numbers of total prey (birds and mammals) and birds alone in diets of six pairs of nesting Sharp-shinned Hawks in Colorado, 1988–1989.

Source of variation	df	χ^2	P
Total prey			
Pair	5	74.07	<0.001
Nesting stage[a]	2	4.50	0.105
Pair × Nesting stage	10	37.07	<0.001
Class (birds, mammals)	1	89.83	<0.001
Pair × Class	5	25.02	<0.001
Nesting stage × Class	2	7.39	0.025
Goodness of fit	10	8.41	0.589
Avian prey			
Pair	5	183.14	<0.001
Nesting stage	2	49.59	<0.001
Pair × Nesting stage	10	23.93	0.008
Age (adult, young[b])	1	32.81	<0.001
Pair × Age	5	0.31	0.379
Nesting stage × Age	2	54.96	<0.001
Goodness of fit	10	8.41	0.838

[a] Incubation, nestling, and fledgling stages.
[b] Fledglings and nestlings.

For avian prey alone, numbers of prey also varied interactively by nesting pair × nesting stage (as for total prey), and by nesting stage × age class (Table 1). That is, adult birds comprised a larger proportion (61%) of the avian diet than nestlings and fledglings (39%), but the number of adults collected declined seasonally, whereas that of nestlings and fledglings increased (Fig. 2).

Prey Mass. Mean mass of mammals consumed by the hawks was almost twice the mean mass of birds (mammals: $n = 47$, $\bar{x} \pm \text{SE} = 41.1 \pm 3.3$ g vs. birds: $n = 466$, $\bar{x} \pm \text{SE} = 20.9 \pm 0.8$ g) (Table 2); in part due to assigning less than adult masses to young birds, but not to mammals. Over 54% of the total mammal biomass consumed was contributed by voles. Fifty percent of the total avian biomass consumed was comprised of Yellow-rumped Warblers, American Robins, White-crowned Sparrows, and Dark-eyed Juncos. At individual nests, mean masses of birds and mammals eaten differed with nesting stage (Table 2, Fig. 3). This interaction demonstrated that, although the mean mass of mammals consumed was greater than birds, the difference varied with hawk nesting stage (mammals were not consumed in all nesting stages) and individual pairs (some pairs ate larger birds and/or mammals). No difference was detected in mean avian-prey mass among hawk pairs, nesting stages, avian age-classes, or among interactions (nest × nesting stage, nest × age, nesting stage × age, or nest × nesting stage × age) (Table 2).

Prey-mass Distribution. The null hypothesis that the distribution of avian prey masses by nesting stage did not vary was rejected ($P = 0.051$). Pairwise tests revealed significant ($P = 0.011$) variation in the distribution of avian prey-sizes between incubation and nestling stages. There were no differences in measures of dispersion (distributional variance), or mean mass between

TABLE 2. General linear model analysis of variance for total prey (avian and mammalian) mass and avian mass alone in diets of six pairs of nesting Sharp-shinned Hawks in Colorado, 1988–1989.

Source of variation	df	SS	F	P
Total prey				
Pair	5	1,342.00	0.87	0.500
Nesting stage[a]	2	1,169.25	1.90	0.151
Pair × Nesting stage	10	4,199.25	1.36	0.195
Class (birds, mammals)	1	4,343.62	14.09	<0.001
Pair × Class	5	1,328.34	0.86	0.506
Nesting stage × Class	2	1,054.51	1.71	0.182
Pair × Class × Nesting stage	8	3,993.77	2.59	0.025
Avian prey				
Pair	5	3,033.24	2.12	0.062
Nesting stage	2	151.46	0.26	0.768
Pair × Nesting stage	10	4,828.30	1.69	0.082
Age (adult, young[b])	1	171.18	0.60	0.440
Pair × Age	5	1,022.71	0.71	0.613
Nesting stage × Age	2	341.03	0.60	0.552
Pair × Nesting stage × Age	8	4,356.00	1.90	0.158

[a] Incubation, nestling, and fledgling stages.
[b] Fledglings and nestlings.

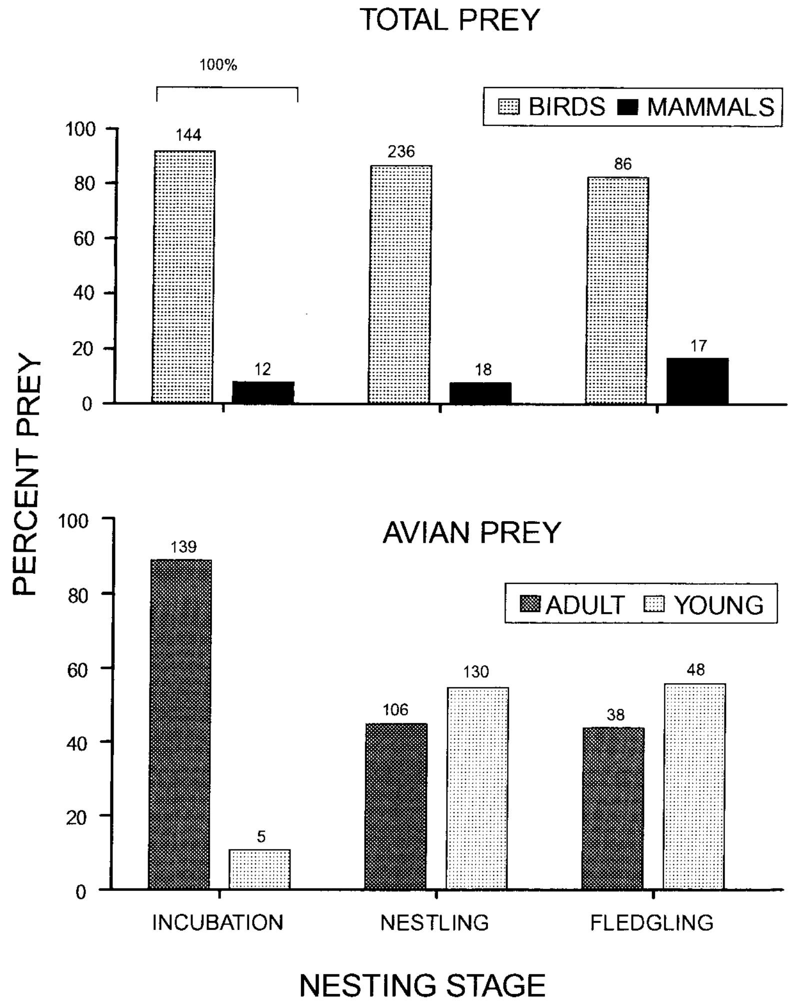

FIGURE 2. Proportion of total (birds and mammals) prey consumed, and total adult and young avian prey consumed during incubation, nestling, and fledgling stages at six successful nests of Sharp-shinned Hawks in Colorado, 1988–1989. Numbers above columns are prey counted/nest.

the two stages ($P \geq 0.017$ [Bonferroni inequality] for all tests). Median avian-prey mass, however, decreased ($P < 0.001$) between incubation (17.4 g) and nestling (12.1 g) stages. Between nestling and fledgling (14.7 g) stages, median avian masses did not differ ($P = 0.224$). Distributions of mammalian prey masses did not differ ($P = 0.323$) among hawk nesting stages.

PREY ABUNDANCE, FOREST TYPE, AND DIETS

Mature aspen was the most common "dominant" habitat (eight of 11 nests), while mixed aspen-conifer was the most common "secondary" habitat (nine of 11 nests). Around nine of the 11 nests, conifer forest was a "limited" habitat type (Fig. 4). Conifer forest was the dominant habitat around one nest.

All of the vertebrates found in the Sharp-shinned Hawk diets were represented in the census data. In all forest types combined, Warbling Vireos (*Vireo solitarius*) (n = 3,403), Yellow-rumped Warblers (n = 3,346), House Wrens (*Troglodytes aedon*) (n = 2,481), Dark-eyed Juncos (n = 2,016), and American robins (n = 1,902) were the most abundant bird species (total = 28,085) in the censuses. Voles were the most abundant (n = 1,082) of the small mammals (*So-*

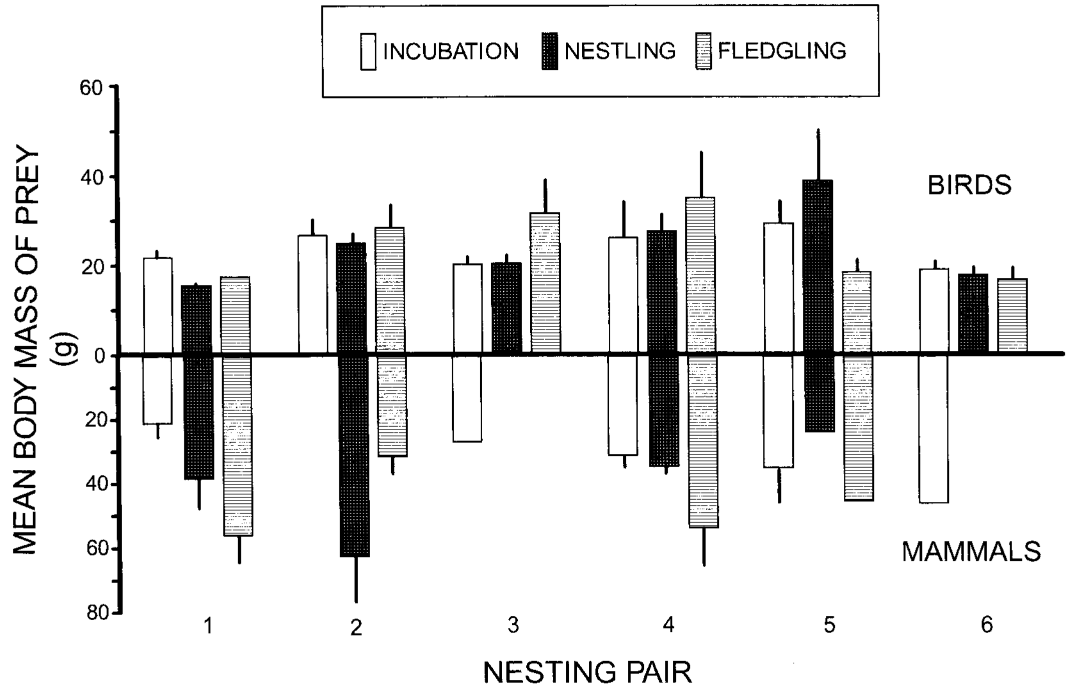

FIGURE 3. Mean body mass (vertical bar) and SE (vertical line) of birds and mammals consumed during incubation, nestling, and fledgling stages by six pairs of Sharp-shinned Hawks in Colorado, 1988–1989.

rex, $n = 692$; *Tamias*, $n = 327$; *Thomomys*, $n = 29$; *Zapus*, $n = 37$) tallied during the counts.

Birds were eaten in proportion to their relative size-frequency in dominant ($P \geq 0.25$) and secondary ($P = 0.172$) habitat types, but proportions eaten differed ($P = 0.037$) from relative abundance in limited habitats. Bird taxa were consumed in proportion to their abundance in all habitats ($0.15 \leq P \leq 0.25$).

Sharp-shinned Hawks demonstrated "preference" among available prey-size classes and taxa of mammals ($P \leq 0.01$ for all habitat categories). Dipodidae and Geomyidae were eaten more often relative to their abundance, and Sciuridae and Soricidae were eaten less often in all habitat categories. Muridae occurred in diets in about the same proportion as its abundance in all habitat categories. Mammals in size-classes 4 (27.0–42.9 g) and 7 (91.1–125 g) were consumed in greater proportion than their relative abundance; whereas mammals in size-class 1 (3.6–8.0 g) contributed a smaller proportion to the hawks' diet than their relative abundance (Table 3).

Overall Sharp-shinned Hawks captured prey from only the smaller size classes (1–7) that were "available" in the forests of the study area (Fig. 5). Within the prey-size classes utilized, the hawks consumed prey—especially avian species—in approximate proportion to their overall relative abundance.

DISCUSSION

Patterns in prey-size use by Sharp-shinned Hawks in Colorado are similar to those reported for the species elsewhere; although a few mammals were captured, the hawks primarily consumed small birds (Craighead and Craighead 1956, Storer 1966, Clarke 1984, Reynolds and Meslow 1984). More prey were found at nests during the nestling period than during the incubation or fledgling stages. Changes in the number of prey consumed by nesting stage may reflect changing energetic demands of developing young or seasonal changes in abundance or availability of different prey species. Although birds were consumed more often than mammals during all nesting stages, the proportion of mammals in diets increased between incubation and fledgling stages. A reduction in the numbers of birds eaten during the fledgling stage, rather than an increase in the number of mammals eaten, was responsible for the increased proportion of mammals in the diet.

Although Sharp-shinned Hawks fed primarily on adult birds through the breeding season, the proportion of adult, fledgling, and nestling birds consumed changed with nesting stage. During incubation, diets consisted almost entirely of adult birds. During the hawks' nestling stage, the proportion of nestling and fledgling birds in the diet increased fivefold, and remained high through the hawks' fledgling period. This shift resulted in a decrease of median prey size from incubation (17.4 g) to the nestling (12.1 g) stage. Furthermore, the shift to small (young) prey was countered by the increased number of prey captured during the nestling stage. The congruence of maximum energy requirements during the hawks' nestling stage and the early summer flush of young nestling and fledgling birds has been noted elsewhere for Sharp-shinned Hawks and other accipiters (Newton 1979, Geer 1982, Newton and Marquiss 1982, Clarke 1984).

Sharp-shinned Hawks appeared to forage opportunistically for sizes and taxa of birds in dominant and secondary habitats. In limited (mostly conifer) habitats, diets differed from "availability" of bird sizes but not bird taxa, suggesting that the hawks foraged selectively for bird sizes in this habitat category or that bird "availability" among size classes differed between limited (conifer) and other habitats.

In each of the three habitat-dominance classes, some taxa and size classes of mammals were "preferentially" eaten. However, differences in capture probabilities among species of mammals during the census period may have biased the results of our preference analysis (e.g., *Thomomys* spp. were probably undersampled by the type of traps used). Differences between the use by Sharp-shinned Hawks and relative abundance of mammals (Fig. 5) suggested that the hawks either foraged for a limited range of mammalian sizes (hence species) or that there were differences in "availability" of mammals (e.g., the contrast-

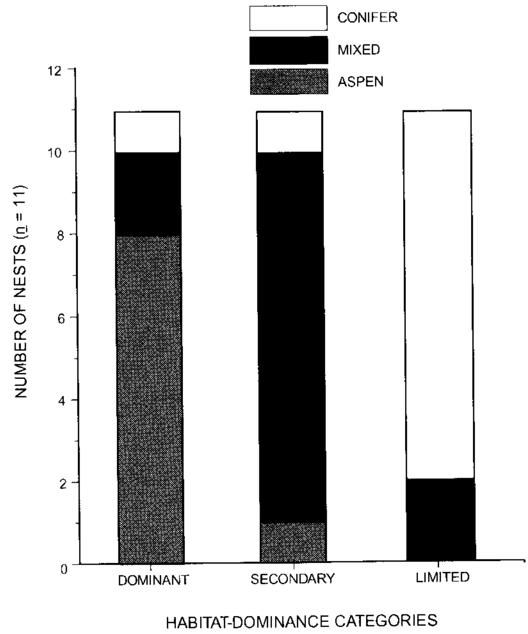

FIGURE 4. Number of nests and composition of forest types surrounding 11 Sharp-shinned Hawk nests in the dominant, secondary, and limited habitat-dominance categories in Colorado, 1988–1989. Dominant habitat types comprise ≥50%, secondary habitat types >5% and <50%, and limited habitat types ≤5% of 2.0-km radius circles centered on nests (see text).

TABLE 3. Ranking of size categories of mammalian prey consumed by Sharp-shinned Hawks in dominant, secondary, and limited habitats surrounding nests in Colorado, 1988–1989. Sizes and average difference between ranks (MRD) of use and relative abundance are listed from most to least used. Dominant forest types comprised ≥50% of foraging areas; secondary forest types comprised >5% to <50% of foraging areas; and limited forest types comprised ≤5% of foraging areas (see text). Size-class usage differed ($P \leq 0.01$) from relative abundance in all habitats.

Dominant		Secondary		Limited	
Mass (g) (size class[a])	MRD[b]	Mass (g) (size class)	MRD	Mass (g) (size class)	MRD
91.1–125.0 (7)	−1.05	27.0–42.9 (4)	−1.00	91.1–125.0 (7)	−1.00
27.0–42.9 (4)	−0.85	91.1–125.0 (7)	−0.90	27.0–42.9 (4)	−0.90
42.9–64.0 (5)	−0.65	42.9–64.0 (5)	−0.65	42.9–64.0 (5)	−0.65
15.6–27.0 (3)	0.70	15.6–27.0 (3)	1.00	15.6–27.0 (3)	1.00
3.4–8.0 (1)	1.85	3.4–8.0 (1)	1.55	3.4–8.0 (1)	1.55

[a] Following Storer (1966). Sizes classes not counted during surveys were excluded.

[b] Mean rank difference. Negative values indicate proportional use was greater than abundance; positive values indicate proportional use was less than abundance.

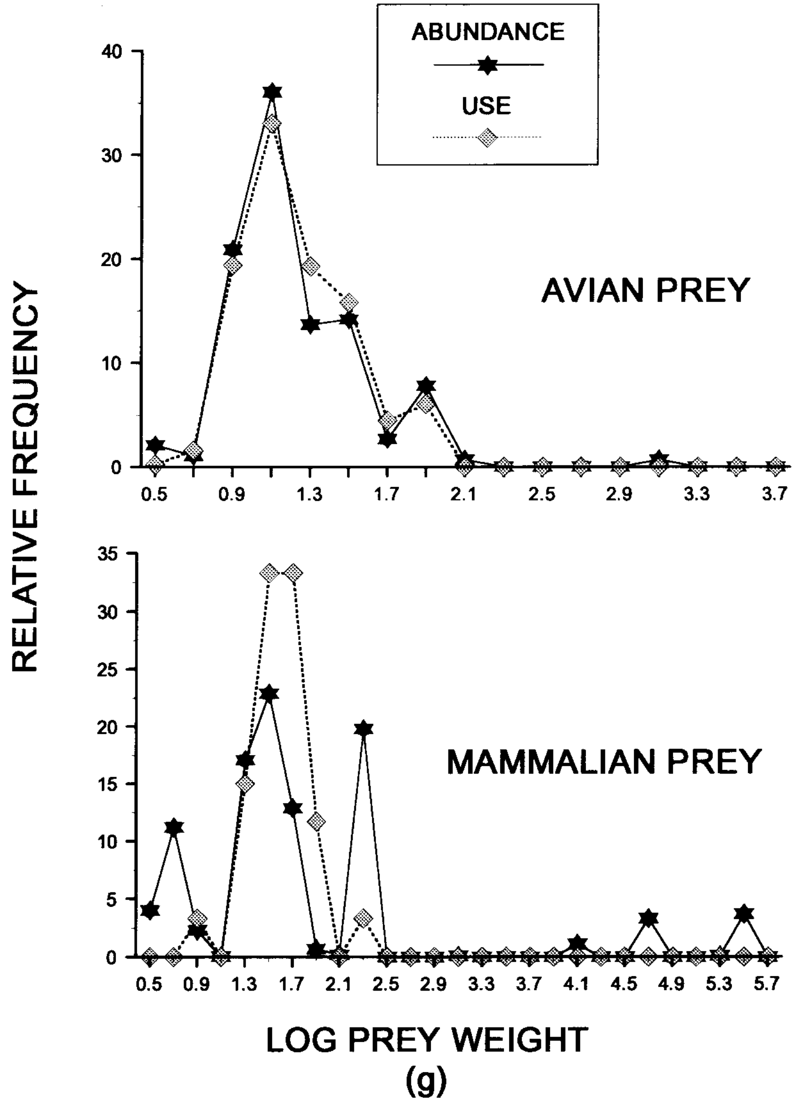

FIGURE 5. Relative abundance of birds and mammals by size class and their relative frequency in diets of Sharp-shinned Hawks in aspen and conifer forests in Colorado, 1988–1989.

ing fossorial vs. terrestrial behavior of Geomyidae and Muridae).

Although aspen and mixed aspen-conifer habitats comprised the majority of dominant and secondary habitats surrounding nests, all Sharp-shinned Hawks nested in conifer trees. The singular use of conifers, which have long and dense crowns, for nesting is probably related to a need for this small hawk to hide its nest from predators (Reynolds 1989).

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APPENDIX 1. Prey species at 11 Sharp-shinned Hawk nests in Colorado during 1988–1989.

		Prey age		
Prey	Adult mass[a,b] (g)	Adult (*n*)	Fledgling[c] (*n*)	Nestling[d] (*n*)
Birds				
Actitis macularia	40.4	2		
Selasphorus platycercus	3.6	1		
Sphyrapicus nuchalis	50.3	3		
Picoides pubescens	27.0	6		
P. villosus	66.3	2		
Picoides spp.	46.7	1		
Contopus sordidulus	12.8	13	3	
Empidonax hammondii	10.1	10		
E. oberholseri	10.4	6		
E. difficilis	10.9	4	2	
Empidonax spp.	10.3[e]	2	1	
Progne subis	49.4	1		
Tachycineta bicolor	20.1	16	1	
T. thalassina	14.2	8	(1)[f]	
Parus atricapillus	10.8	5	9 (3)	
P. gambeli	10.8	9	18 (2)	
Parus spp.	10.8	2	1	
Sitta canadensis	9.8	1		
Certhia americana	8.4	3		
Salpinctes obsoletus	16.5	1		
Troglodytes aedon	10.9	23	5	
Regulus satrapa	6.2	3		
R. calendula	6.7	11	6 (1)	
Regulus spp.	6.4	2	1	
Siala mexicana	28.1	2		
S. curroides	29.6	1		
Myadestes townsendii	34.0	1		
Catharus ustulatus	30.8	1	2	
C. guttatus	31.0	10	4 (8)	
Catharus spp.	30.9	5	2	
Turdus migratorius	77.3	27	15 (9)	1
Dumatella carolinensis	36.9	1		
Vireo solitarius	16.6	6	14 (3)	
V. gilvus	12.0	14	1	
V. olivaceus	16.7		2 (1)	
Vireo spp.	15.1	1		
Vermivora celata	9.0	2	4	
Dendroica petechia	9.8 ♂♂	7		
	9.2 ♀♀	3	1	
D. coronata	12.1	39	38 (1)	
Dendroica spp.	10.8	1		
Oporornis tolmiei	10.4	5		
Wilsonia pusilla	6.9	8		
Piranga ludoviciana	28.1	6	5	
Pipilo chlorurus	29.4	5	1	
Aimophila spp.	19.7	1		
Spizella arborea	20.1		(1)	
S. passerina	12.3	1	1	
Pooecetes gramineus	25.7		1 (1)	
Passerculus sandwichensis	20.1	6		
Melospiza melodia	20.8	5		
M. lincolnii	17.4	26	1	
Zonotrichia leucophrys	25.5	35	6 (3)	
Junco hyemalis	19.6	25	12 (4)	
Unknown juvenile sparrow	21.1		2	
Agelaius phoeniceus	41.5		(1)	

APPENDIX. Continued.

Prey	Adult mass[a,b] (g)	Prey age Adult (n)	Fledgling[c] (n)	Nestling[d] (n)
Molothrus ater	49.0 ♂♂	1	1	
	38.8 ♀♀	8	1 (2)	
Pinicola enucleator	56.4	1	1	
Carpodacus cassinii	26.5	2		
C. mexicanus	21.4	2		
Carduelis pinus	14.6	10	10	
Coccothraustes vespertinus	59.4	1		
Unknown juvenile bird	22.1		2	4
Mammals				
Sorex monticolus	6.8[g]	2		
Tamias minimus	46.1	3		
Tamiasciurus hudsonicus	225.3	2		
Thomomys talpoides	94.6[h]	7		
Peromyscus maniculatus	24.6	1		
Clethrionomys gapperi	26.8	17		
Phenacomys intermedius	36.8	3		
Microtus montanus	45.3	2		
M. longicaudus	46.8	5		
Microtus spp.	46.1	10		
Zapus princeps	23.8	7		
Unknown mouse	24.2	1		

[a] Bird masses are from Dunning (1984) and mammal masses are from Armstrong (1972) unless specified.

[b] Fledglings with unsheathed remiges and partly sheathed rectrices were assigned an adult mass; fledglings with partly sheathed remiges and rectrices were assigned 3/4 (adult mass); nestlings received 1/2 (adult mass).

[c] Birds with partially sheathed feathers.

[d] Birds with fully sheathed rectrices and remiges.

[e] Mass = (*E. hammondii* mass + *E. oberholseri* mass)/2.

[f] Numbers in parentheses are fledglings with unsheathed remiges (adult mass).

[g] Hall (1946).

[h] U.S. Fish and Wildlife Service museum specimen labels, Fort Collins, CO.