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UNFOUNDED ASSUMPTIONS ABOUT DIET OF THE COOPER'S HAWK[1]

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Abstract. Prior analyses and reviews of diet in the Cooper's Hawk (*Accipiter cooperii*) have suggested that avian prey usually provides a majority of items and biomass, but this interpretation may be compromised by methodological problems. In Wisconsin, we found that indirect collection of prey remains near nests (92% birds) overestimated the proportion of avian items in comparison to direct observation of prey deliveries to nestlings (51–68% birds). Previous studies using indirect methods may have overstated the frequency of birds in the diet. Also, most avian items brought to nestlings in Wisconsin, as elsewhere, were young birds. Some prior studies relying on indirect methods and using prey species' adult mass to calculate avian biomass have probably accentuated the methodological bias toward birds among prey remains. In Wisconsin, birds provided a minority of prey biomass (40–46%) in two of our three sampling pools. Proportions of avian items and biomass are highly variable in the small set of other direct dietary studies of the Cooper's Hawk, all from the breeding season. Because of methodological, seasonal, geographic, and other limitations, existing data do not warrant an assumption that birds prevail in the diet. Because vulnerable ground foraging animals (as well as young birds) appear to constitute most of the breeding season diet, we also question the assumption—based mainly on breeding season studies—that Cooper's Hawks feed principally on prey of high "agility," as proposed in some theories of reversed sexual size dimorphism.

Key words: Cooper's Hawk; Accipiter cooperii; *nestling diet; dietary methods.*

INTRODUCTION

Many investigators have enumerated prey species or prey items taken by Cooper's Hawks (*Accipiter cooperii*). Although reptiles or mammals have been numerically preponderant among prey in some individual hawks and some areas (e.g., Fitch et al. 1946, Reynolds and Meslow 1984), reviews have typically reported (Sherrod 1978, Jones 1979, Rosenfield 1988) that birds are the most frequent prey in proportions ranging from 55% (Duncan 1966, as recalculated by Jones 1979) to 91% (Craighead and Craighead 1956). Only four studies, all in the breeding season, have estimated prey biomass. Avian prey reportedly accounted for the majority of biomass in three instances (Kennedy 1980, Millsap 1981, Toland 1985) but a minority in the remaining case (Reynolds and Meslow 1984).

Methodological differences, however, may cloud the comparability or reliability of previous dietary studies. Stomach analyses (Fisher 1893 [see also Sherrod 1978], Duncan 1966, Storer 1966) have employed data from hawks of all ages collected over wide geographic areas at every time of year. Seasonal, regional, or age-related biases might exist in such data. Specimens from poultry or gamebird farms may also give an unrepresentative sample of hawks' ages and stomach contents (Meng 1959). Other dietary work on Cooper's Hawks has been done almost exclusively in the breeding season. Methods include analyses of the crop contents of nestlings (e.g., Errington 1933), direct observations of food deliveries to nestlings (e.g., Snyder and Wiley 1976), collation of prey remains in pellets, nests, or plucking areas near nests (e.g., Meng 1959), or combinations of these techniques (e.g., Craighead and Craighead 1956). The potential biases of these methods in analyzing falconiform diets are well recognized (Marti 1987) but remain unevaluated in Coo-

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per's Hawks. Here we contrast direct observations and collection of prey remains as methods of assessing the prey of breeding Cooper's Hawks in Wisconsin. We use the former method to compare biomass of avian and non-avian prey, and we also estimate biomass for prey items tabulated by Hamerstrom and Hamerstrom (1951) in analyses of the crop contents of young Cooper's Hawks in Michigan.

We suggest that dietary studies based on prey remains may be biased toward avian items. We also show that most prey items delivered to nestling Cooper's Hawks are sub-adult individuals and ground-foraging species. Review of previous dietary studies indicates that generalizations about a predominant class of prey or the "agility" of prey are not warranted by available data.

METHODS

All original data were collected in Wisconsin, almost entirely in central or southeastern counties within 85 km of the sites where nest deliveries were observed. We did not attempt to evaluate prey availability.

NEST DELIVERIES

We recorded prey deliveries to nestlings aged 5–28 days from blinds erected within 10 m of four nests in two study areas: two nests in the semi-urban Amherst area in Portage County in June–July 1986 and 1987, and two nests about 185 km farther south in the Kettle Moraine State Forest in Waukesha County in June 1986. The same marked male but different females bred at the Amherst area in both years.

During 44 all-day and eight part-day watches (734 hours), we noted species, age, and condition (intact, headless, eviscerated) of prey when possible. We initially categorized items into three *a priori* size classes (SC) following Kennedy and Johnson (1986) and Storer (1966), using known mass and bulk of familiar species as reference points: SC1 $\leq$ 27 g, SC2 = 28–91 g, and SC3 = 92–216 g. Because we encountered only one prey item $>$ 132 g among nest deliveries, we here truncate SC3 at 92–132 g. We also recorded 40 prey deliveries and five items retrieved from adult or nestling crops during late incubation (10 items) and nestling (35) stages, respectively, at 35 additional Wisconsin nests, 1981–1989. We combine these observations as a fifth sample of deliveries to "other" nests.

Snyder and Wiley (1976) and Kennedy and Johnson (1986) assumed that prey items delivered to nests by female Cooper's Hawks were also captured by females if the vocalizations characteristically accompanying male-female prey transfers did not precede the delivery. We do not separate deliveries into captures by sex under this criterion because both sexes cache and retrieve uneaten or untransferred prey during the breeding season (pers. observ.). Although we have not seen one sex retrieve items cached by the other, we assume that females retrieve prey cached by males at regularly used transfer sites. It nevertheless seems likely that most delivered items were captured by males, as indicated by other nesting season studies (e.g., Reynolds and Meslow 1984), because females rarely leave the nest site until nestlings reach $\geq$14 days of age (pers. observ.). After excluding five items (1.5%) that could not be identified as either avian or non-avian prey, we estimated biomass for nest deliveries as follows. Biomass here refers to the live mass of an item, not the mass delivered to the nest or consumed by nestlings.

Nearly all mammals (95%) were identifiable to genus or species; most were eastern chipmunks (*Tamias striatus*). We calculated mass of "adult" (SC3) chipmunks from an independent sample (n = 26, 88–126 g, $\bar{x}$ = 107 g) collected in late May to mid-July in both study areas; we also weighed sub-sets of headless and eviscerated specimens. Juvenal chipmunks may be two-thirds grown in Wisconsin in the latter half of June (Jackson 1961); the median date of our blind observations was 27 June, and we often had problems in gauging the age and size of delivered chipmunks at the margin between SC2 and 3. Among 25 reliably aged deliveries, seven (28%) were juveniles in SC2. We extrapolated this proportion to all deliveries, and calculated a mean mass of 74 g for SC2 chipmunks from condition and mass of five deliveries, assuming that head and visceral masses were proportionally similar to those of adults. A mean mass of 98 g for all chipmunks was derived from these estimates. Local specimens of similar age were also used to estimate mass of thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*)—all juveniles—at 55 g. We assumed mice (*Peromyscus* spp.) and voles (*Microtus* spp.) to be adults, and a single gray squirrel (*Sciurus carolinensis*) to be a three-fourths grown juvenile; in these cases mass was estimated from Craighead and Craighead (1956:429) and Jackson (1961). Six mammals of unknown identity were assigned a mean mass of 60 g on the basis of relative size and preceding estimates.

All of 202 avian items delivered to nests were assignable to size class but only one-third were identifiable to genus or species. Adult mass of identifiable bird species was taken from regionally and seasonally appropriate samples in Clench and Lieberman (1978) and Dunning (1984). When possible, age of avian prey was determined by feather sheathing in nestlings and recent fledglings, or distinctive juvenal plumages in independent young. From the literature on growth rates, we estimated mass of identifiable birds by size and age classes as follows. Most species in SC1 fledge at ≥90% of adult mass, so we ignored age in these cases. For ground foraging birds, the usual category of avian prey of Cooper's Hawks in our samples (see Results), we calculated mass of altricial, open-nesting species at nestling/fledgling, independent juvenal, and unknown ages as 70, 90, and 95% of adult mass, respectively, for smaller species (28–59 g) in SC2; 65, 85, and 90% for larger species (60–91 g) in SC2; and 55, 80, and 85% for species in SC3 as truncated. Woodpeckers and most hole-nesting passerines also fledge at near-adult size, so we estimated both juveniles and birds of unknown age at 95% of adult mass in such species. Mean mass of 32 avian prey deliveries in SC2, weighed or identified and aged in hand, was 65 g. We use this figure in estimating biomass of unidentified birds in SC2. Unidentified birds in SC1 and SC3 were assumed to average 25 and 115 g, respectively.

We applied the same procedures in estimating biomass for prey species and ages listed by Hamerstrom and Hamerstrom (1951), except that unidentified birds (10.3% of total items) were excluded, tentatively identified birds (6.5%) were assigned a mean mass (as above) by size class, unidentified *Sciurus* were assumed to be juvenal gray squirrels, and "immature" Ring-necked Pheasants (*Phasianus colchicus*) were assumed to be 4–5 week old poults with a mass of 150 g.

PREY REMAINS

We tabulated remains of 132 prey items found in or <100 m from 69 active nests in 39 geographically separate nesting areas, 1980–1989, during incubation through fledgling stages of breeding. These items were mainly pluckings (>80%), occasionally skeletal remains or uneaten prey; we did not collect pellets. Although these items include remains from the same reoccupied nesting areas over as many as four years (in some cases the same marked adult[s] over 2–3 years), we treat the data as independent because no one nesting area provided >9 items across 10 years of collecting remains, and because nests yielding remains involved ≥96 different, individually marked adult hawks. Because of small annual sample sizes at each stage of breeding, we combined years. Because proportions of avian prey were very similar (91–93%), we also combined incubation (35 items), nestling (59), and fledgling (38) stages.

Although we often searched for regularly-used plucking sites near the nest at the incubation stage, we did not revisit these sites on a systematic basis to collect prey remains. Most remains were thus found incidentally during other work.

PREY FORAGING HEIGHTS

In all data sets, we used personal observations to partition identifiable prey items (excluding nestlings) into two categories: taxa that primarily (e.g., American Robin, *Turdus migratorius*) or frequently (e.g., Blue Jay, *Cyanocitta cristata*) forage on the ground, and those that do not (e.g., Northern Oriole, *Icterus galbula*).

RESULTS

We did not detect prey items other than birds and mammals.

NEST DELIVERIES

Avian prey formed half or more of delivered items at all four Wisconsin nests but proportions of avian items were greater at the two Amherst nests than the two Kettle Moraine nests (Table 1). Differences among nests are significant ($\chi^2 = 9.37$, df = 3, $P < 0.05$) and remain significant if the Amherst nests, where the same male bred in both years, are considered non-independent ($\chi^2 = 7.08$, df = 2, $P < 0.05$). Inter-year differences at Amherst were not significant ($P > 0.10$). We thus pool Amherst nests (68% avian items, $n = 194$) and Kettle Moraine nests (51% avian items, $n = 90$), respectively, in subsequent analyses. The composite sample from 35 "other" Wisconsin nests (56% avian items, $n = 45$) is treated as a separate pool.

Avian biomass accounted for 58% of total prey biomass among nest deliveries at Amherst, 40% in the Kettle Moraine, and 46% at "other" Wisconsin nests (Table 2). Eastern chipmunks were

TABLE 1. Numbers and frequency (%) of mammalian and avian prey items among Wisconsin nest deliveries.

	Kettle Moraine		Amherst		
	1	2	1	2	Other nests
Mammalian					
E. chipmunk	19	24	23	28	18
Other	0	1	7	5	2
Total	19 (50)	25 (48)	30 (28)	33 (38)	20 (44)
Avian					
SC1	1	6	17	11	0
SC2	18	19	56	37	24
SC3	0	2	5	5	1
Total	19 (50)	27 (52)	78 (72)	53 (62)	25 (56)
Total	38	52	108	86	45

strongly predominant among mammalian items in all Wisconsin nest delivery samples (Table 1), accounting for 36–59% of total prey biomass (Table 2).

PREY REMAINS

Avian items provided 92% of total items among Wisconsin prey remains at incubation through fledgling stages of breeding (Table 3). This proportion—virtually identical (93%, $n = 59$) if the nestling stage is considered alone—is much larger than any obtained in our direct observations of prey deliveries to nestlings. As in nest deliveries, chipmunks were the leading item among mammalian prey remains.

CROP CONTENT ANALYSES

Hamerstrom and Hamerstrom (1951) reported that birds provided 221 (84%) of 262 prey items retrieved from crops of nestlings and tethered fledglings at four nests in Michigan, 1941–1946. Proportions of avian items were not significantly different among nests ($P > 0.25$). Our further analyses of their data exclude 27 unidentified birds of unknown size.

We used their lists of prey species and prey ages to calculate that avian prey accounted for 71% of total prey biomass (Table 2). Chipmunks constituted 59% of mammalian items ($n = 41$) but only 11% of total prey biomass in Michigan (Table 2). These proportions, while relatively large, are all substantially less than comparable figures for chipmunks in Wisconsin nest deliveries.

PREY AGES

Data on the ages of mammalian prey are scant because of problems in ageing chipmunks in both Wisconsin (see Methods) and Michigan (Hamerstrom and Hamerstrom 1951) but it appears that

TABLE 2. Biomass (g) and relative biomass (%) of mammalian and avian prey among Wisconsin nest deliveries and Michigan crop content analyses.

	Wisconsin			
	Kettle Moraine	Amherst	Other nests	Michigan
Mammalian				
E. chipmunk	4,214	4,998	1,764	2,352
Other	60	846	64	3,624
Total	4,274 (60)	5,844 (42)	1,828 (54)	5,976 (29)
Avian				
SC1	175	739	0	1,050
SC2	2,413	6,031	1,419	6,407
SC3	230	1,157	125	3,055
>SC3	0	0	0	4,235
Total	2,818 (40)	7,927 (58)	1,544 (46)	14,747 (71)
Total	7,092	13,771	3,372	20,723

TABLE 3. Numbers and frequency (%) of mammalian and avian items among Wisconsin prey remains (n = 132).

Mammalian			Avian				
E. chipmunk	Other	Total	SC1	SC2	SC3	>SC3	Total
9	1	10 (8)	1	82	31	8	122 (92)

up to 43% of mid-sized mammals (chipmunks and ground squirrels, n = 37) and 100% of larger mammals (sciurids and lepids, n = 7) were subadults among *ageable* mammals in the combined nest delivery and crop content data of these studies.

Among avian prey in Michigan, 108 (74%) of 145 ageable items were young of the year, and 11 (10%) of these 108 young birds were nestlings. Among avian items both ageable and identifiable (n = 136), young birds (73% of items) accounted for 62% of avian biomass.

A bias against adults might exist among *ageable* birds, however, for species in which feather sheathing (rather than distinctive juvenal plumage) is the only available criterion of age; many adults might be consigned to an "age unknown" category in such cases. More conservatively, young of the year accounted for ≥56% of total avian items (n = 194) and ≥53% of avian biomass among identifiable items (n = 177) when birds of unknown age are included in the Michigan data. A similarly conservative estimate for Wisconsin comes from 42 reasonably intact avian items examined in hand as nest deliveries or found in nests as prey remains; at least 24 (≥57%) of these were young of the year and approximately half of the young birds were nestlings or recent fledglings. Identifiable sub-adult birds averaged 86% of adult mass in Michigan (n = 74) and 82% in Wisconsin (n = 25) for species in which adult mass falls within SC2 and 3 (28–132 g). All species in this calculation were altricial; median adult mass of these items was 79 g in both states.

PREY FORAGING HEIGHTS

Most small to mid-sized mammals in Wisconsin and Michigan are at least partly terrestrial in foraging habits. It is not surprising that mammals foraging primarily or frequently on the ground accounted for all but one of the 171 identifiable mammalian prey items (chiefly chipmunks) in the combined two-state tally for nest deliveries, prey remains, and crop retrievals. The exception was a flying squirrel (*Glaucomys volans*) in Michigan.

The proportion of identifiable avian prey items that primarily or frequently forage on the ground was uniformly high among nest deliveries (94%, n = 53) and prey remains (93%, n = 107) in Wisconsin as well as crop retrievals (82%, n = 169) in Michigan.

DISCUSSION

PREY FREQUENCY AND BIOMASS

Errington (1932) proposed that indirect methods are less accurate than direct techniques in evaluating the diets of nestling falconiforms, and other researchers have concurred (Snyder and Wiley 1976, Marti 1987, Rosenberg and Cooper 1990). Our results for Cooper's Hawks also agree: an indirect sample of prey remains (92% avian items) from Wisconsin nest sites apparently overestimated the frequency of birds in nestling diets in comparison to direct observations of nest deliveries (51–68% avian items). This result is unsurprising. It presumably occurs because avian pluckings are larger, often more colorful, and hence more conspicuous than mammalian or other non-avian remains. The colorful Blue Jay, for example, accounted for 39 items (36%) among identifiable avian remains (n = 108) but only nine items (15%) among identifiable birds (n = 60) delivered to nests.

Certain biases may exist in our own samples, but we contend that none of them is likely to obviate our methodological results. Most prey remains were collected incidentally during other work. More intensive searches would perhaps have discovered larger numbers of inconspicuous mammalian items, yet it is also possible that persistent searching would have found more small or drably-colored birds. Also, our nest delivery data might be skewed toward certain types of prey if some items (e.g., small birds) were selectively consumed by adult hawks rather than delivered to nestlings. A similar bias would arise among prey remains to the extent that such items are consumed where captured, which is nearly always beyond the immediate vicinity of the nest (Rosenfield et al. 1991, pers. observ.). Moreover, a very large number of selectively consumed birds (12 per day per adult at the nests watched from blinds) would be required to eliminate the proportional disparity of avian items in nest deliveries vs. prey remains.

Finally, our samples of nest deliveries and prey remains were drawn from different sets of nests and in part from different years. Results might stem from annual or local contrasts in prey availability, or differing predilections for prey types among individual hawks, instead of a bias toward avian items among prey remains. Both samples, however, come from the same parts of Wisconsin. We collected small numbers of prey remains at each of many nests over 10 years, while nest deliveries, aside from blind observations, include a sub-sample from 35 "other" nests over nine years (see Methods). It remains possible that mammals (i.e., chipmunks) were unusually prominent in the regional prey base during blindwork on nest deliveries in 1986–1987. If so, more mammals might also appear among prey remains in those years, but this sub-sample of remains (n = 23 items at 16 nests) was exclusively birds.

We conclude that the methodological bias indicated by our results is real. Previous studies relying partly or mainly on prey remains (Craighead and Craighead 1956, Meng 1959, Millsap 1981, Reynolds and Meslow 1984, Toland 1985) may have overestimated the relative frequency of avian prey in the diet of Cooper's Hawks. Although careful pellet analyses (Reynolds and Meslow 1984) might alleviate the bias of relying on prey remains, only Janik and Mosher (1982) have presented results separately or specified the numbers of items identified by pelletal remains vs. other techniques. They found avian items to be more frequent in pellets (54%) than in nest deliveries (30%, see Table 4) but the sample of pelletal items was very small (n = 13).

Even though birds formed the majority of prey items among Wisconsin nest deliveries, mammals outranked birds in terms of prey biomass in two of our three delivery pools. Precise proportions of biomass (Table 2) depend heavily on our estimates of mass for chipmunks and unidentified SC2 birds, but the conclusion that avian biomass was in the minority is robust to simultaneous overestimates of mass (for chipmunks) and underestimates of mass (for birds) of 10% at "other" nests and 20% at Kettle Moraine nests, respectively.

Among previous studies, only Reynolds and Meslow (1984: Table 1) had reported a majority of mammalian biomass. However, a bias toward avian items among prey remains could obviously be compounded in studies that have used remains, in part, to estimate prey biomass (Millsap 1981, Toland 1985). Both Millsap and Toland also assumed that all identifiable birds (88% of total avian items in both instances) were adults, and calculated avian biomass on that basis while assigning sub-adult mass to most mammals. As discussed later, our results and other studies show that a large fraction of birds taken by nesting Cooper's Hawks are sub-adults. Inappropriate assignment of adult mass to birds when calculating biomass will accentuate the bias toward avian items among prey remains.

It thus seems probable that Toland's (1985) report of 65% avian biomass in the prey of breeding Cooper's Hawks is an overestimate. Millsap (1981) inadvertently mis-calculated the mass of Gambel's Quail (*Callipepla gambelii*) at 287 rather than 187 g per adult (B. Millsap, pers. comm.), and his sum for mammalian biomass omitted one black-tailed jackrabbit (*Lepus californicus*) (Millsap 1981: Table 14). Recalculated avian biomass would thus be 50% (34,020/67,862 g), not 54% as given in Millsap (1981). Because of biases toward birds, discussed above, even this revised figure seems likely to overestimate avian biomass in his breeding season prey sample.

Our results for Wisconsin nest deliveries as well as our methodological critique thus indicate that the diet of breeding Cooper's Hawks is more variable with respect to class of prey than prior studies and reviews have suggested. The degree to which studies using indirect means have overstated the importance of avian prey is unknown. Eight studies using direct observation of crop contents or nest deliveries (Table 4) have shown that birds may indeed be strongly predominant in diets in some cases. The same studies have nonetheless reported a wide range in the shares of avian, mammalian, and reptilian prey provided to nestling hawks, both among studies (26–90% avian) and within study areas (see especially Snyder et al. 1973). Four of these eight studies found that birds accounted for ≤50% of prey items (Fitch et al. 1946, Janik and Mosher 1982, Snyder et al. 1973) or prey biomass (this study) at most observed nests.

Potential sources of dietary variation include individual, age-related, or sexual propensities for certain sizes and/or classes of prey as well as regional, local, annual, or seasonal differences in the availability or vulnerability of prey types. Although Cooper's Hawks breed or winter throughout the conterminous U.S. and southern

TABLE 4. Proportions of avian prey in studies using direct observations of nest deliveries or crop contents.

	State	No. nests	No. items	% Avian (range)
Fitch et al. 1946	CA	1	38	26[a]
Janik and Mosher 1982	MD	(a)	57	30[a]
Snyder et al. 1973	AZ-NM	11	473	56 (8–93)
This study	WI	5	329	61 (50–72)
Peterson and Murphy in press	ND	2	74	70[a]
Errington 1933	WI	3	24	71[a]
Hamerstrom and Hamerstrom 1951	MI	4	262	84 (80–90)
Kennedy 1980	WA	6	240	90 (76–95[b])

[a] Not available or not applicable.
[b] Five successful nests.

Canada, direct observations of diet—all for the breeding season—have come mainly from a few states in southwestern and midwestern regions (Table 4). Using unstated methods presumably involving prey remains, Millsap (1981) reported that birds provided 51% of prey items in two southwestern states in winter. Except for stomach analyses pooling regions, ages, seasons, and sometimes sexes, other data for non-breeding seasons are lacking.

In view of the methodological, geographic, seasonal, and other limitations of existing dietary data for the Cooper's Hawk, generalizations about a predominant class of prey are unwarranted. Indeed, further research may show that variations in its diet hold more ecological interest than an attempt to describe a "typical" diet (Wiens 1989).

PREY AGES AND FORAGING HEIGHTS

Although they gave no systematic data on prey ages, Craighead and Craighead (1956) and Meng (1959) remarked that young birds formed a large share of the avian prey provided to nestling Cooper's Hawks. Our results and other quantitative studies support their comments. In both Wisconsin nest deliveries and Michigan crop content analyses, a conservatively estimated 56–57% of avian items were young of the year. About half of these young birds were nestlings or newly-fledged individuals in Wisconsin, and 10% were nestlings in Michigan.

In addition, Reynolds and Meslow (1984:766, Appendix) reported that "nestlings and fledglings" accounted for 33% of avian items (n = 267) among prey remains, while P. Kennedy (pers. comm.) has judged that 35% of ageable avian prey items in New Mexico were nestlings or fledglings. It seems that incidental observations of nestling birds as prey (Linduska 1943, Meng 1959, Nelson 1968) can be regarded as unexceptional. Young of the year have also provided the majority of avian prey items in direct observations of nest deliveries among various other falconiforms: the congeneric Sharp-shinned Hawk (*A. striatus*) in Alberta (Quinn 1991), Broad-winged Hawks (*Buteo platypterus*) in several U.S. states (Fitch 1974, Mosher and Matray 1974, Rosenfield et al. 1984), and the Peregrine Falcon (*Falco peregrinus*) in Greenland (pers. observ., RNR).

Among identifiable avian prey with an adult mass of 28–132 g, sub-adult items averaged 82–86% of adult mass in our Wisconsin and Michigan analyses. This figure is somewhat less than the 90% assigned to juvenile birds of all adult size classes by Kennedy (1980) but substantially greater than the 50% assumed by Reynolds and Meslow (1984). These differences do not seem wholly attributable to the varying taxa, ages, or adult sizes encountered or considered in these respective analyses. Future studies probably need to consider such variables when calculating biomass for sub-adult birds, rather than relying on an arbitrary estimate. For example, proportional mass of sub-adult prey items may be relatively low in larger or precocial species such as quail (*Colinus virginianus, Callipepla* spp.). Quail are frequent prey elsewhere (e.g., Kennedy 1980, Millsap 1981, Toland 1985) but were lacking in our Wisconsin and Michigan samples.

Data on the age and corresponding mass of mammalian prey are less satisfactory. Juveniles are common prey—ca. 50% of ageable mammalian items in Wisconsin nest deliveries and Michigan crop content analyses—but better methods of determining age and mass are desirable, especially for lepids and larger sciurids where undocumented assumptions about age can have strong effects on calculations of prey biomass.

This effect was not a problem in Wisconsin nest deliveries, which included only one larger mammal. There appear to be no reports of the ages of reptilian prey.

Wisconsin and Michigan results furthermore suggest that nearly all mammalian prey and large majorities of avian items (≥82% excluding nestlings) can be classed as species that forage primarily or frequently on the ground. Among prior studies, only Reynolds and Meslow (1984: Appendix) attempted to quantify the distribution of foraging heights in prey species taken by Cooper's Hawks. Their five-part classification identified only 23% of Oregon prey items as "ground-shrub" foragers. However, of the 33 prey taxa they treated as "shrub-canopy" or "generalist" foragers, we would class 24 as primary or frequent ground foragers; the latter would include such "shrub-canopy" species as Rufous-sided Towhee (*Pipilo erythrophthalmus*) and Fox Sparrow (*Passerella iliaca*) and such "generalists" as American Robin, Dark-eyed Junco (*Junco hyemalis*), and chipmunks (*Eutamias* spp.). Under our classification, 73% of Oregon prey items would qualify as primary or frequent ground foragers.

Also, a list of the 25 genera providing ≥5.0% of identifiable prey items in one or more of 12 dietary studies (Table 5) includes 24 genera, excepting only *Melanerpes*, that we would class as primary or frequent ground foragers. Although many of these data may be subject to the methodological problems discussed earlier, the lack of such widespread bark, shrub, or canopy foraging genera as *Picoides, Pheuticus, Piranga,* or *Icterus* seems notable. In the absence of unbiased observations of actual prey captures, interpretations of prey foraging heights are obviously subjective. Nevertheless, available evidence suggests that many or most prey items may be taken from the ground.

As Meng (1959) suggests, Cooper's Hawks probably take whatever prey is easiest to catch. Sub-adult and ground foraging animals may be particularly vulnerable to the hunting tactics of Cooper's Hawks, which typically employ a series of brief perch-and-scan episodes to locate potential prey (Fischer 1986, Kennedy 1991) and probably take most prey by surprise attack rather than active aerial pursuit (Meng 1951). Such tactics should be most effective and economical against nestling birds, inagile fledglings, and other inexperienced juvenile animals as well as ground foraging individuals (especially mammals) whose avenues of predator detection and escape are more limited than those of arboreal species and individuals (Reynolds and Meslow 1984).

TABLE 5. Genera (no. studies) providing ≥5.0% of identifiable prey items in one or more of 12 dietary studies.

Birds
- *Turdus* (8)
- *Cyanocitta* (5)
- *Sturnus* (4)
- *Colaptes* (3)
- *Melanerpes* (3)
- *Callipepla* (3)
- *Colinus* (2)
- *Phasianus* (2)
- *Zenaida* (2)
- *Pipilo* (2)
- *Passer* (2)
- *Dolichonyx* (1)
- *Agelaius* (1)
- *Quiscalus* (1)
- *Sturnella* (1)
- *Junco* (1)
- *Melospiza* (1)
- *Bonasa* (1)

Mammals
- *Sylvilagus* (3)
- *Tamias* (3)
- *Eutamias* (2)
- *Spermophilus* (2)
- *Microtus* (1)

Reptiles
- *Cnemidophorus* (1)
- *Sceloporus* (1)

Sources (no. genera, cumulative % of items): Errington 1933 (6, 93); Fitch et al. 1946 (5, 91); Hamerstrom and Hamerstrom 1951 (8, 64); Craighead and Craighead 1956 (4, 51); Meng 1959 (5, 80); Storer 1966 (4, 34); Kennedy 1980 (4, 56); Millsap 1981 (4, 46); Janik and Mosher 1982 (3, 92); Reynolds and Meslow 1984 (6, 59); Toland 1985 (6, 55); this study (4, 72).

In Michigan crop content analyses and Wisconsin nest deliveries, the aggregate numbers of mammals, sub-adult birds, and ground foraging avian taxa suggest that prey of relatively low agility and relatively high vulnerability is strongly predominant in the diet of nestling Cooper's Hawks. Highly agile prey (i.e., adult birds) of other foraging strata provided ≤10% of identifiable items in both states.

Some theories of reversed sexual size dimorphism (RSSD) in the genus *Accipiter* (Reynolds 1972) and other raptors (Earhart and Johnson 1970, Snyder and Wiley 1976) have noted a positive correlation between the degree of a species' RSSD and the agility of its principal class of prey; birds are assumed to be the most agile prey category. For the Cooper's Hawk, one of the most strongly dimorphic falconiforms, this correlation rests upon an assumed predominance of birds in the diet (as inferred from studies conducted almost entirely in the breeding season) as well as the presumed agility of avian prey. We have shown, however, that birds are not necessarily the dominant class of prey in the breeding season in terms of frequency (Table 4 and earlier discussion) or biomass (this study). We have also shown that most birds taken by Cooper's Hawks at this season are inagile or inexperienced young of the year. We have furthermore suggested that most breeding season prey items, avian or otherwise, are vulnerable ground foraging species and individuals captured by tactics that allow them little chance to exercise whatever agility they may possess.

The assumptions underlying a correlation between prey agility and the pronounced RSSD of the Cooper's Hawk might indeed be valid in nonbreeding seasons but adequate dietary data are not available for those seasons, and we doubt that studies from the breeding season provide sufficient support for such assumptions. The predominance of young birds in the avian component of breeding season diets of some other falconiforms, as noted earlier, suggests that assumptions about prey agility may also need reevaluation in other cases, to the extent that dietary data are derived from studies of breeding hawks.

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