SEXUAL DIMORPHISM AND FOOD HABITS IN THREE NORTH AMERICAN ACCIPITERS

ROBERT W. STORER

THE three widespread North American bird hawks, the Sharp-shinned Hawk (*Accipiter striatus velox*), Cooper's Hawk (*A. cooperii*), and the Goshawk (*A. gentilis atricapillus*) differ greatly in size. In the course of studies on weight, wing area, and skeletal proportions of these three species (Storer, 1955), it became apparent that although the females of all three species average larger than the males, the sexual difference in size was greatest in the smallest species, the Sharp-shinned Hawk, and least in the largest species, the Goshawk. To determine more precisely the degree of sexual dimorphism in these three species, I measured the wing length (arc) of study skins in the collection of The University of Michigan Museum of Zoology. The series used were large enough to provide both a good estimate of variation within the species and an accurate mean. All birds measured were in adult plumage and were collected in the region between Grafton, in extreme eastern North Dakota, and Point Pelee, Ontario, Canada. The sample of the Sharp-shinned Hawk consisted entirely of birds taken in Michigan; those of the other species included birds from most of the broader area.

Mis-sexed accipiters, especially Goshawks, appear to be not infrequent in collections, and I strongly suspect that a few mis-sexed specimens have led Friedmann (1950: 150–152) and possibly others to describe the variation both in measurements and plumage as overlapping more than actually will be found to be the case. Much of the mis-sexing probably results from the collectors' mistaking the paired ovaries (usual in birds of this genus) for testes. In our collections, four Goshawks sexed as males by the collectors measure 348, 357, 360, and 361 mm in wing length. All were taken in the winter months (December to February) when the gonads are small, and all have the heavy black streaking on the under parts, which is usually found in adult females. A fifth Goshawk, sexed as a female, measures 324 mm in wing length, has the fine barring characteristic of adult males, and lacks heavy black streaking. These five birds were omitted from the samples, and even so the coefficient of variation is over 10 per cent larger for both sex groups of the Goshawk than for those of the other species (Table 1). A Cooper's Hawk sexed as a male but measuring 261 mm in wing length and having the brownish plumage of the upper parts characteristic of adult females was also omitted from the data.

The measurement data are summarized in Tables 1 and 2. Judging from the difference between the means for males and for females and from

TABLE 1
VARIATION IN WING LENGTH IN NORTH AMERICAN ACCIPITERS

Form	*Sex*	*Number*	*Observed range*	*Mean ± standard error*	*Standard deviation*	*Coefficient of variation*
A. striatus velox	♂	25	161–178	170.8 ± 0.7	3.72	2.18
	♀	25	191–209	201.5 ± 0.8	4.14	2.05
A. cooperii	♂	24	226–246	234.9 ± 1.0	4.92	2.09
	♀	20	256–273	264.8 ± 1.1	4.88	1.85
A. gentilis atricapillus	♂	25	309–338	322.8 ± 1.6	7.78	2.42
	♀	42	339–374	354.2 ± 1.3	8.60	2.44

the standard deviations, a small amount of overlap in size between the sexes of the Goshawk is to be expected. No overlap in wing length is to be expected between the sexes of the Sharp-shinned or Cooper's hawks. The data demonstrate that the degree of dimorphism is greatest in the small Sharp-shinned Hawk, intermediate in the medium-sized Cooper's Hawk, and least in the large Goshawk.

The size of a predator is clearly related to the size of its prey. In the first place, the larger the predator, the larger the prey it can subdue; in the second, there is a lower limit to the size of prey which a predator can utilize efficiently (particularly in the cases of predators which must hunt and capture each prey item separately). Granted that there are both upper and lower limits to the size of prey available to a predator of any given size, we can assume that there is also an optimal prey size or range of prey sizes. For similarly adapted species like the three North American accipiters, we can also assume that the optimal prey size (and presumably also the mean prey size) will be greater the larger the predator. Thus we can assume that an increased difference in size between the sexes increases the optimal range of prey sizes for the species.

In order to test these assumptions, it was necessary to determine the extent of difference in size of prey taken by males and females of these three species of hawks. Through the courtesy of Allen J. Duvall, I was

TABLE 2
DIMORPHISM IN WING LENGTH IN NORTH AMERICAN ACCIPITERS

Form	*A*	*B*	*A/B × 100*
	Mean ♀♀ − Mean ♂♂ (in mm)	*Mean ♂♂/2 + Mean ♀♀/2 (in mm)*	*Dimorphism index*
A. striatus velox	30.7	186.2	16.5
A. cooperii	29.9	249.9	12.0
A. gentilis atricapillus	31.4	338.5	9.3

TABLE 3
NUMBER OF SPECIMENS AVAILABLE FOR ANALYSIS OF FOOD HABITS

Month	A. striatus velox		A. cooperii		A. gentilis atricapillus	
	Males	*Females*	*Males*	*Females*	*Males*	*Females*
January	4	4	3	5	4	3
February	0	1	5	5	11	10
March	3	3	6	4	11	10
April	3	7	2	6	2	4
May	12	15	4	9	1	1
June	6	2	1	7	1	0
July	2	0	3	5	0	3
August	12	3	4	6	2	3
September	28	35	13	10	1	0
October	34	29	8	13	5	5
November	8	5	8	9	22	27
December	3	4	5	5	8	10
Totals	76	68	84	62	108	115

able to use the food habits files of the United States Fish and Wildlife Service. In these files, the sex of the predator is usually given (in contrast to almost all of the food habits data reported in the literature); it was thus possible to list prey items for males and females of each of the three species.

As shown in Table 3, most of the birds from which the data were taken were collected in winter or in the season of migration. Fewer represent birds collected in the breeding season. This paucity of breeding birds in my sample accounts, in part, for the marked difference between the data reported here for the American Goshawk and those for the European Goshawks as reported by Uttendörfer (1939) since the high proportion of jays, pigeons, and crows in the diet of the latter reflects the season at which the sample was collected. Steller's Jays (*Cyanocitta stelleri*) were one of the two most important prey species of a pair of nesting Goshawks in California (Schnell, 1958) and Common Crows (*Corvus brachyrhynchos*) have been reported as important prey species of nesting Goshawks in Minnesota (Eng and Gullion, 1962) and in New York and Pennsylvania (Meng, 1959). There is evidence, summarized by Schorger (1955: 209–210), that at least in northern Pennsylvania, Goshawks preyed heavily upon the now extinct Passenger Pigeon (*Ectopistes migratorius*).

Most predators, including accipiters, are to a large extent opportunistic, preying upon the species which are most easily obtained at a given time and place. For this reason, food habits data for individuals and from many populations are needed to provide adequate data on the food habits of a species. At present, there are not sufficient data to give a good over-all picture of the food habits of our accipiters in the nesting season.

TABLE 4

FREQUENCY OF OCCURRENCE OF PREY ITEMS BY GENUS

A. striatus velox		A. cooperii		A. gentilis atricapillus	
Genus (Group)	*Number*	*Genus (Group)*	*Number*	*Genus (Group)*	*Number*
Dendroica (2)	153	*Melospiza* (3)	14	*Sylvilagus* (18, 19)	37
Melospiza (3)	78	*Colinus* (9)	13	*Bonasa* (13, 14)	34
Turdus (6)	54	*Passer* (3)	13	*Lepus* (20)	17
Hylocichla (4)	43	*Pipilo* (4)	9	*Tamiasciurus* (9)	16
Spizella (2, 3)	41	*Junco* (3)	6	*Phasianus* (18)	8
Vireo (2, 3)	39	*Spizella* (2, 3)	5	*Colinus* (9)	7
Pipilo (4)	35	*Eutamias* (5)	5	*Peromyscus* (3)	4
Passer (3)	33	*Sturnella* (7)	4	*Sciurus* (13, 16)	3
Sciurus (3)	27	*Tamias* (7)	4	*Microtus* (4)	3
Iridoprocne (3)	20	*Sigmodon* (7)	4	*Lagopus* (14?)	2
Junco (3)	17	*Turdus* (6)	3	*Colaptes* (8)	2
Dumetella (4)	16	*Hylocichla* (4)	3	*Hylocichla* (4)	2
Geothlypis (2)	15	*Cyanocitta* (6)	3	*Passerculus* (3)	2
Pooecetes (4)	14	*Colaptes* (8)	3	*Clethrionomys* (3)	2
Zonotrichia (4)	13	*Lophortyx* (8)	3	*Citellus* (9, 11)	2
Carpodacus (3)	12	*Tamiasciurus* (9)	3	Duck sp.? (17?)	2
Sialia (4)	12	*Zonotrichia* (4)	3	Misc.	17
Peromyscus (3)	12	*Carpodacus* (3)	3		
Misc.	199	*Quiscalus* (7)	3		
		Misc.	41		
Total items	833	Total items	142	Total items	158
Total genera	81	Total genera	51	Total genera	53

This picture, however, may bear little relation to the problem of sexual differences in food habits, because the male provides most of the food for the female and young and because food is generally most abundant during this period. The data obtained from the United States Fish and Wildlife Service's files, while not as extensive as might be hoped for, are, I think, sufficient to give a fairly representative idea of the food habits of our three accipiters in fall and winter. The frequency of occurrence of prey items by genus is shown in Table 4.

Weight was selected as the best measure of prey size. For each prey species listed a mean weight was calculated, largely from data on specimens in The University of Michigan Museum of Zoology. In the case of icterids and other species in which there is considerable sexual difference in size, the mean weight was calculated for each sex. Next, a series of weight groups was set up. These groups, numbered from 1 to 20, were arranged by cubic functions: the limits of Group 1 were 1.5^3 to 2^3 (or 3.4 to 8) g, those for Group 2 were 2^3 to 2.5^3 (or 8 to 15.6) g, and so on. This grouping, in effect, arranges the prey species of similar form in categories differing by a constant increase in linear measurements. The prey species thus arranged are listed below.

Group 1 (3.4 to 8 g).—Birds: *Psaltriparus minimus, Polioptila* spp., *Regulus* spp., *Parula* spp., *Wilsonia pusilla*.

Group 2 (8 to 15.6 g).—Birds: *Empidonax* spp., *Contopus virens, Riparia riparia, Parus carolinensis, P. atricapillus, Sitta canadensis, Cistothorus platensis, Telmatodytes palustris, Troglodytes aedon, Vireo bellii, V. gilvus, V. philadelphicus, Mniotilta varia, Vermivora celata, Dendroica* spp., *Geothlypis trichas, Oporornis agilis, O. philadelphia, Wilsonia citrina, W. canadensis, Spinus pinus, S. tristis, Acanthis flammea, Passerina amoena, P. cyanea, Passerherbulus caudacutus, Spizella pusilla, S. breweri*; Mammals: *Lasiurus borealis*.

Group 3 (15.6 to 27 g).—Birds: *Erolia minutilla, Chaetura pelagica, Dendrocopos pubescens, Iridoprocne bicolor, Petrochelidon pyrrhonota, Sitta carolinensis, Thryothorus ludovicianus, Anthus spinoletta, Vireo olivaceus, V. flavifrons, V. solitarius*, vireo sp.?, *Seiurus* spp., *Icteria virens, Passer domesticus, Icterus spurius, Carpodacus purpureus, C. cassinii*, finch sp.?, *Passerculus sandwichensis, Ammodramus savannarum, A. bairdii, Ammospiza caudacuta, Amphispiza belli, Junco hyemalis, Spizella arborea, Melospiza* spp., *Calcarius ornatus*, sparrow sp.?; Mammals: *Blarina brevicauda, Clethrionomys gapperi, Peromyscus maniculatus, P. leucopus, Mus musculus*.

Group 4 (27 to 42.9 g).—Birds: *Ereunetes pusillus, Lobipes lobatus, Tyrannus tyrannus, Nuttallornis borealis, Campylorhynchus brunneicapillum, Dumetella carolinensis, Hylocichla minima, H. ustulata, H. guttata, Hylocichla* sp.?, *Sialia sialis, Bombycilla cedrorum, Molothrus ater* (♀), *Icterus galbula, Dolichonyx oryzivorus, Piranga rubra, P. olivacea, Pipilo erythrophthalmus, P. e. maculatus, Pooecetes gramineus, Calamospiza melanocorys, Zonotrichia leucophrys, Z. albicollis, Passerella iliaca*; Mammals: *Microtus pennsylvanicus, M. longicaudus mordax*.

Group 5 (42.9 to 64 g).—Birds: *Coccyzus erythropthalmus, Sphyrapicus varius, Progne subis, Mimus polyglottos, Molothrus ater* (♂), *Euphagus carolinus* (♀), *E. cyanocephalus* (♀), *Agelaius phoeniceus* (♀); Mammals: *Parascalops breweri, Eutamias amoenus*.

Group 6 (64 to 91.1 g).—Birds: *Ixobrychus exilis, Rallus limicola, Porzana carolina, Charadrius vociferus, Coccyzus americanus, Chordeiles minor, Cyanocitta cristata, Toxostoma rufum, Turdus migratorius, Sturnus vulgaris, Euphagus carolinus* (♂), *E. cyanocephalus* (♂), *Agelaius phoeniceus* (♂); Mammals: *Eutamias townsendi*.

Group 7 (91.1 to 125 g).—Birds: *Falco sparverius, Zenaidura macroura* (♀), *Quiscalus quiscula, Sturnella* spp.; Mammals: *Tamias striatus, Sigmodon hispidus*.

Group 8 (125 to 166 g).—Birds: *Lophortyx* spp., *Zenaidura macroura* (♂), *Otus asio, Colaptes auratus*; Mammals: *Citellus townsendi, Glaucomys sabrinus*.

Group 9 (166 to 216 g).—Birds: *Falco columbarius, Oreortyx pictus, Colinus virginianus*; Mammals: *Tamiasciurus* spp., *Citellus lateralis*.

Group 10 (216 to 275 g).—Mammals: *Citellus richardsoni, Rattus norvegicus*.

Group 11 (275 to 343 g).—Birds: *Columba* spp.

Group 12 (343 to 422 g).—Birds: *Perdix perdix, Corvus brachyrhynchos*.

Group 13 (422 to 512 g).—Birds: *Canachites canadensis, Bonasa umbellus umbelloides*; Mammals: *Sciurus carolinensis*.

Group 14 (512 to 614 g).—Birds: *Bonasa u. togata, Lagopus lagopus*?

Group 15 (614 to 729 g).—Mammals: *Citellus columbianus*.

Group 16 (729 to 856 g).—Mammals: *Sciurus niger*.

Group 17 (856 to 1,000 g).—Birds: *Anas acuta, Pedioecetes phasianellus*.

Group 18 (1,000 to 1,158 g).—Birds: *Anas platyrhynchos, Phasianus colchicus*; Mammals: *Sylvilagus floridanus*.

TABLE 5

PREY ITEMS, ARRANGED BY WEIGHT GROUP, OF ACCIPITERS

	A. striatus velox		A. cooperii		A. gentilis atricapillus	
Weight group	*Males*	*Females*	*Males*	*Females*	*Males*	*Females*
1	14	2		1		
2	41	27	2	7		
3	50	47	28	25	9	3
4	14	29	6	15	1	3
5	1	2	3	2	2	
6	4	10	6	5		2
7	1*	6	5	11	3	
8			2	7	4	
9		*	7	12	5	12
10				2		
11		2	*	1		1
12					1	1
13			1	*	8	7
14					8	4
15				1		
16					*	
17					2	1
18				3	9	5*
19					6	14
20					6	6
Total number of prey items	124	125	60	92	64	59
Range of prey weight (in groups)	1–7	1–11	2–13	1–18	3–20	3–20
Mean weight of prey (in groups)	2.7	3.6	4.2	4.9	12.2	13.6
Mean weight of prey (in grams)	17.6	28.4	37.6	50.7	397	522
Mean weight of hawks (in grams)[1]	98.8	171	295	441	818	1137
$\frac{\text{Mean weight of prey}}{\text{Mean weight of hawk}} \times 100$	17.8	16.6	12.8	11.5	48.5	46.0
Per cent of prey items in hawk's group or above	0.9	1.6	1.7	4.3	35.9	42.4

* Group to which hawk belongs.

[1] Data from Storer (1955: table 1).

Group 19 (1,158 to 1,331 g).—Birds: *Larus argentatus*; Mammals: *Sylvilagus transitionalis.*

Group 20 (1,331 to 1,521 g).—Mammals: *Mephitis mephitis, Lepus americanus.*

The grouping of prey species is, of course, only approximate, and certain arbitrary decisions had to be made in the placing of species. In the several species of birds in which the males were placed in one group and the females in another, it was assumed that the hawks took equal numbers of each sex, and the numbers of these species taken were equally divided between the groups. Mammals were assumed to be adults unless otherwise stated in the original data, in which case they were omitted from the calculations of size. Domestic animals were also omitted from these calculations both because they do not constitute prey taken under natural conditions and because they could not be satisfactorily grouped into weight

TABLE 6

SEVEN PREY SPECIES MOST FREQUENTLY TAKEN BY THREE NORTH AMERICAN ACCIPITERS[1]

A. striatus velox (869)[2]			A. cooperii (153)[2]			A. gentilis atricapillus (165)[2]		
Prey	*Number*	*Per cent*	*Prey*	*Number*	*Per cent*	*Prey*	*Number*	*Per cent*
Melospiza melodia	67	7.7	*Passer domesticus*	13	8.5	Hares and rabbits (three species)	54	32.8
Turdus migratorius	54	6.2	*Colinus virginianus*	13	8.5	*Bonasa umbellus*	34	20.6
Pipilo erythrophthalmus	35	4.0	*Melospiza melodia*	10	6.5	*Tamiasciurus hudsonicus*	16	9.7
Passer domesticus	33	3.8	*Pipilo erythrophthalmus*	9	5.9	*Phasianus colchicus*	8	4.9
Iridoprocne bicolor	20	2.3	*Junco hyemalis*	6	3.9	*Colinus virginianus*	7	4.2
Junco hyemalis	17	2.0	*Tamias striatus*	4	2.6			
Dumetella carolinensis	16	1.8	*Sigmodon hispidus*	4	2.6			
Totals	242	27.8		59	38.5		119	72.2

[1] Data from U. S. Fish and Wildlife files.

[2] Total number of prey items.

classes. This reduced the number of data for the Goshawk considerably, for most of the stomachs were from birds wintering outside of the usual breeding range and over 40 per cent of the prey items of these birds consisted of domestic fowl.

The position of the hawks themselves in these weight groups is significant. The male and female Sharp-shinned Hawks belong in Groups 7 and 9, the male and female Cooper's Hawks in Groups 11 and 13, and the male and female Goshawks in Groups 16 and 18, respectively.

The distribution of prey items by weight group is shown in Table 5. While there is considerable overlap between the sexes, and even the species, in the size of prey taken, the larger predators on the average take larger prey. Furthermore, there is an increase from the smallest to the largest predator in the percentage of prey items in or above the predator's weight group. As I have pointed out earlier (1955: 289), the larger the species, the faster it must fly to remain aloft. There may be a similar relationship between size and speed at time of striking prey. If this is true, the force with which a hawk strikes (the product of its weight and its velocity) will be greater by more than the difference in weight in larger hawks than small ones. In the case of the Goshawk, greater striking power may not be the only reason for the high proportion of large prey items. Rabbits and hares, which are among the most important prey, are for their size relatively easy to kill. Similarly, grouse, another important food item, are

TABLE 7

PER CENT OF TOTAL PREY ITEMS ACCOUNTED FOR BY THE FIVE GENERA MOST FREQUENTLY TAKEN

Predator	Genera of prey in order of frequency (with number of species recorded)	Total species	Per cent of prey items
A. gentilis atricapillus	*Sylvilagus* (2), *Bonasa* (1), *Lepus* (1), *Tamiasciurus* (1), *Phasianus* (1)	6	71
A. cooperii	*Melospiza* (3), *Colinus* (1), *Passer* (1), *Pipilo* (1), *Junco* (1)	7	36
A. striatus velox	*Dendroica* (14), *Melospiza* (3), *Turdus* (1), *Hylocichla* (3), *Spizella* (4)	25	44
A. gentilis[1]	*Columba* (3), *Garrulus* (1), *Perdix* (1), *Turdus* (6), *Corvus* (3)	14	71
A. nisus[1]	*Passer* (2), *Turdus* (6), *Parus* (6), *Sylvia* (5), *Fringilla* (2)	20	52

[1] Data for European races based on Uttendörfer, 1939.

relatively easy to kill, especially when compared with ducks and other water birds of comparable size.

While there is a tendency for the larger species to take prey from a greater size range, there is at the same time a tendency for them to "specialize" on fewer prey species. The latter is well expressed by the percentage of the total kills made up by the seven species most frequently taken (Table 6), as well as by the percentage made up by the five genera most frequently taken (Table 7).

A comparison with the data for the two common European species of *Accipiter* shows a similar trend (see Tables 7 and 8). In the European Sparrow Hawk (*Accipiter nisus*), the male is approximately the size of a female Sharp-shinned Hawk and the female is approximately the size of a male Cooper's Hawk. The European race of the Goshawk (*Accipiter g. gentilis*) is slightly smaller than the American subspecies. Uttendörfer, in his important monograph on the food habits of European hawks and owls (1939) lists more than 43,000 prey items for the European Sparrow Hawk and more than 7,000 for the European Goshawk. (Unfortunately, the kills were not broken down by the sex of the predator.) The results show that the bulk of the European Goshawk's diet consists of fewer prey species and genera than that of the smaller species. The fact that the seven species most frequently taken by the European Sparrow Hawk constitute a greater percentage of the total kill than is the case with the Sharp-shinned or Cooper's hawks probably reflects the smaller geographical area covered by Uttendörfer and the relatively poorer fauna from which the prey had to be selected.

This inverse relationship between the size of the predator and the number of species and genera making up a given percentage of its kills

TABLE 8

THE SEVEN PREY SPECIES MOST FREQUENTLY TAKEN BY TWO EUROPEAN ACCIPITERS[1]

A. nisus *(43,211)*[2]			A. g. gentilis *(7,333)*[2]		
Prey	*Number*	*Per cent*	*Prey*	*Number*	*Per cent*
Passer domesticus	4293	9.9	*Garrulus glandarius*	1173	16.0
Fringilla coelebs	3451	8.0	*Columba livia*	1155	15.8
Turdus ericetorum	3051	7.1	*Perdix perdix*	835	11.4
Alauda arvensis	2922	6.8	*Columba palumbus*	578	7.9
Emberiza citrinella	2785	6.4	*Sturnus vulgaris*	335	4.6
Hirundo rustica	2196	5.1	*Corvus corone*	309	4.2
Parus major	2022	4.7	*Sciurus vulgaris*	235	3.2
Totals	20,720	48.0		4,620	63.1

[1] Data from Uttendörfer, 1939; pp. 39 and 56.

[2] Total number of prey items.

is clearly related to the pyramid of numbers (Elton, 1935: 68–70)—there being more species and more individuals of small animals than large ones.

The proportion of mammals to birds in the kills (Table 9) is related in part to the pyramid of numbers, but the relationship is more complex than that between the size of predator and the variety of species taken. Accipiters are diurnal and are adapted for hunting in wooded cover, where small birds are the most abundant and readily available prey. The smallest diurnal mammals in North American woodlands are chipmunks (Groups 5 to 7), followed by tree squirrels (Groups 9 to 16). Rabbits and hares (Groups 18 to 20) are active early and late in the day, as are a few mice (e.g., *Clethrionomys*) and shrews. All of the strictly diurnal mammals are well above the mean prey size of the Sharp-shinned Hawk. The paucity of smaller mammals in the diet of this species may be explained by the greater abundance, and possibly greater ease of capture, of small birds. In any case, the Sharp-shinned Hawk depends almost entirely on birds as prey, and its existence in the northern forests is contingent upon its ability to move south when the bulk of the small birds leave.

Cooper's Hawks take considerable prey within the size range of chipmunks and red squirrels (Group 9) but still feed largely on birds. Birds within the size range most frequently utilized by the Cooper's Hawk are far more numerous than these mammals both in summer, when migratory birds are present, and in winter when chipmunks are in hibernation. According to the A.O.U. Check-List (1957), the winter ranges of the Cooper's and Sharp-shinned hawks are nearly the same. However, as the latter species nests considerably farther north than the Cooper's Hawk, it occupies far less of its breeding range in winter than does the Cooper's Hawk. And while I know of no statistical evidence to prove it, I think

TABLE 9
PROPORTION OF BIRDS TO MAMMALS TAKEN BY ACCIPITERS

Form	*Total*	*Per cent birds*	*Per cent mammals*
A. striatus velox			
Males	130	97.7	2.3
Females	127	96.8	3.2
Sexes combined	869	97.0	3.0
A. cooperii			
Males	63	84.1	15.9
Females	95	81.1	18.9
Sexes combined	158	82.3	17.7
A. gentilis atricapillus			
Males	64	60.9	39.1
Females	61	34.4	65.6
Sexes combined	165	44.8[1]	55.2
A. nisus[2]			
Sexes combined	43,211	97.8	2.2
A. gentilis gentilis[2]			
Sexes combined	7,333	91.2	8.8

[1] If domestic animals (chickens, guinea-fowl, kitten) are included, this figure is 68.1 per cent.
[2] Data from Uttendörfer (1939).

that the majority of Sharp-shinned Hawks winters farther south than the majority of Cooper's Hawks. This I think is correlated with the broad generalization, again unsupported by statistical evidence, that there is an inverse relationship between size and distance migrated among northern birds, more of the Sharp-shinned Hawk's prey species moving farther south than those of the Cooper's Hawk.

In contrast to the two smaller species, the Goshawk is non-migratory, although in some years there are extensive southward movements, presumably corresponding with low points in the cycles of abundance of their prey species. Of the prey animals within the size range most frequently utilized by Goshawks, grouse, tree squirrels, and lagomorphs comprise the majority of those available throughout the year. Thus it is not surprising that mammals should be preyed upon more frequently by Goshawks than by the two smaller accipiters.

Amadon (1959: 534–535), Cade (1960: 241–246), and Selander (1966: 138–140) have reviewed some of the theories concerning the significance and origin of the "reversed" sexual dimorphism in raptors. All agree that this type of dimorphism is correlated with predatory habits, and Amadon appears to prefer the idea that the greater size of the female has been evolved as a protection for the young from possible predation by the male parent. As he puts it (p. 535) "the male of birds of prey, in which the parental instincts are weaker than in the female, may represent a threat to the young especially when they are small. The larger and fiercer female

TABLE 10
SEXUAL DIMORPHISM IN NORTH AMERICAN FALCONS[1]

Form	*A*	*B*	*A/B × 100*
	Mean of ♀♀ − Mean of ♂♂ (in mm)	*Mean ♂♂/2 + Mean ♀♀/2 (in mm)*	*Dimorphism index*
Falco (Hierofalco)[2] *mexicanus*	43.4	321.1	13.5
Falco (Hierofalco) rusticolus obsoletus	38.3	383.5	10.0
Falco (Falco) albigularis albigularis	30.9	204.6	15.1
Falco (Rhynchodon) peregrinus anatum	42.1	335.3	12.6
Falco (Tinnunculus) columbarius columbarius	18.9	198.4	9.5
Falco (Cerchneis) sparverius paulus	7.7	175.2	4.4
Falco (Cerchneis) sparverius sparverioides	8.8	179.0	4.9
Falco (Cerchneis) sparverius sparverius	11.9	189.1	6.3

[1] Data from Friedmann (1950).

[2] Classification to subgenus follows Peters (1931).

stays with the young and prevents cannibalism from becoming prevalent—it already is known to occur from time to time." While I have no alternative theory to offer on the origin of this dimorphism, I think that there are several reasons for questioning the "anti-cannibalism" idea. Parental instincts of such notorious nest-robbers as gulls, crows, jays, and grackles are sufficiently strong to prevent the males of these birds from killing their own young, yet the males of these birds are somewhat larger than the females. In the course of the breeding season of the Canary (*Serinus canarius*), dominance shifts from the male to the female, although the female is smaller than the male (Shoemaker, 1939), and H. B. Tordoff tells me that the same is true of the Red Crossbill (*Loxia curvirostra*). Such dominance, presumably effected through a hormonal control of behavior, might just as well, if not more easily in an evolutionary sense, prevent cannibalism. Obviously, selection against killing one's own young must be strong.

Cade thinks the larger size of the female in hawks is related to the difficulty of forming pair bonds in predatory birds, especially those which feed on birds and react to flying birds as prey. Amadon (*in litt.*) now agrees with Cade in this. Selander, however (1966: 139), thinks "the basic adaptive function of the dimorphism is related to differential niche utilization."

I think that regardless of how this dimorphism arose, the different degrees of dimorphism now found in different accipiters are related to niche utilization. But I think that different selective factors or groups of factors may operate in determining the degree of sexual dimorphism in different groups of predators. For example, in the North American falcons (genus *Falco*), these factors probably differ from one group to another.

Table 10, based on data in Friedmann (1950), shows the dimorphism index of six North American falcons. That the genus *Falco* includes a variety of morphologically different species is indicated by the arrangement of these six species into five (Peters, 1931; American Ornithologists' Union, 1957) or six (Friedmann, 1950) subgenera. In the two most closely related species, the Prairie Falcon (*F. mexicanus*) and the Gyrfalcon (*F. rusticolus*), the larger species has less sexual dimorphism, as is the case in the three accipiters; a similar trend is found in the Bat Falcon (*F. albigularis*) and the Peregrine (*F. peregrinus*), which are probably more closely related to each other than to any other species included in Table 10. On the other hand, among the subspecies of the Sparrow Hawk (*F. sparverius*), the smallest has the least dimorphism. For a group as complex as this, it is not safe to generalize about the relationship between size and sexual dimorphism.

One approach to an analysis of this relationship in the three North American accipiters, which form a more uniform group than the falcons, is to look for ways in which the three species differ in a graded series. The position in the pyramid of numbers provides three such ways: as regards prey, the smallest hawk has available to it the largest number of species and individuals within its optimal size range, and conversely, the largest hawk can take prey from the greatest total size range; as regards enemies, the smallest hawk will have the most species and individuals preying on it. Size is also related to striking power, the largest hawks having the greatest striking power. The degree to which the species are migratory is still another way in which these species differ—most Sharp-shinned Hawks are migratory, fewer individuals of the Cooper's Hawk appear to be migratory, and the Goshawk is largely resident.

I think that the action of at least the following selective factors may be responsible for the high degree of sexual dimorphism in the Sharp-shinned Hawk. During the nesting season, the selective advantage of large females is greatest in this smallest species because there are the most species and individuals of predators which can successfully prey on the female or, by subduing the female, the contents of the nest. On the other hand, the larger numbers of species and individuals of prey within the optimal size range for smaller hawks may be a selective factor favoring small size. The male, which spends little time at the nest, is less vulnerable than the female to predators there; and when he is away from the nest, the advantage of increased maneuverability which small size bestows may overbalance the disadvantage of the increased number of potential predators. Character displacement as a result of partial sympatry with the Cooper's Hawk is probably responsible for maintaining the size difference between the two species and would be a factor tending to reduce the size of both male and female Sharp-shinned Hawks. The selective value of decreased competition between the sexes (and between the species) for food is presumably greatest when the hawks are concentrated, where they share their range with similarly adapted species, or when food is scarce. This might be on migration, although prey species are also migrating at this time. More likely it is on the wintering ground. It would be difficult to prove, especially after the deforestation of so much of North America, but I think it likely that the area in which most of the northern Sharp-shinned Hawks winter is smaller than the breeding range of the same population. If this is true, competition between the sexes and with resident hawks taking similar food would favor increased dimorphism.

In the largest of the three species, the Goshawk, the factors responsible for maintaining and increasing sexual dimorphism appear to be least effective or are counterbalanced at least in part by other factors. During the nesting season, the selective advantage of large females is least in this species because there are the fewest species and individuals of predators which can successfully prey on the female or the contents of the nest. In summer, when a wide variety of prey is available, small males may have a temporary selective advantage over large ones through having more available prey within the optimal size range for them, but in winter the situation is different. Throughout most of the geographical range of the Goshawk in North America, there are then probably no more than five available prey species within the optimal size range for the species in any one area; and the population density of these prey species is considerably lower than that of smaller species. I think that under these conditions, the advantage of being large enough to take any of these species easily (the first encountered) would tend to outweigh any advantage which specialization for smaller prey might confer.

The Cooper's Hawk, being intermediate in size between the Sharp-shinned Hawk and the Goshawk, occupies an intermediate position in the pyramid of numbers. One can then assume that selection for increased dimorphism would be stronger in the Cooper's Hawk than in the Goshawk and weaker than in the Sharp-shinned Hawk. Such appears to have been the case.

SUMMARY

In the Sharp-shinned Hawk, Cooper's Hawk, and Goshawk, the males are smaller than the females and, on the average, take smaller prey.

The degree of sexual dimorphism in size is greatest in the smallest species, the Sharp-shinned Hawk, and least in the largest species, the Goshawk, and thus appears to be directly correlated with the hawk's relative position in the pyramid of numbers. Some factors related to the degree

of sexual dimorphism are thought to be: the greater number of species and individuals of available prey for the smaller hawks, and, conversely, the more species and individuals of potential predators which might subdue a smaller female at the nest; the degree to which the birds are migratory; and possible competition on the wintering grounds with other hawks taking the same kind of prey.

LITERATURE CITED

AMADON, D. 1959. The significance of sexual differences in size among birds. Proc. Amer. Philos. Soc., **103**: 531–536.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-List of North American birds. Fifth edit.

CADE, T. J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. Univ. California Publs. Zoöl., **63**: 151–290.

ELTON, C. 1935. Animal ecology. New York, Macmillan.

ENG, R. L., AND G. W. GULLION. 1962. The predation of Goshawks upon Ruffed Grouse on the Cloquet Forest Research Center, Minnesota. Wilson Bull., **74**: 227–242.

FRIEDMANN, H. 1950. The birds of North and Middle America. U. S. Natl. Mus., Bull. 50, pt. 11.

MENG, H. 1959. Food habits of nesting Cooper's Hawks and Goshawks in New York and Pennsylvania. Wilson Bull., **71**: 169–174.

PETERS, J. L. 1931. Check-list of birds of the world. Vol. 1. Cambridge, Harvard Univ. Press.

SCHNELL, J. H. 1958. Nesting behavior and food habits of Goshawks in the Sierra Nevada of California. Condor, **60**: 377–403.

SCHORGER, A. W. 1955. The Passenger Pigeon; its natural history and extinction. Madison, Univ. Wisconsin Press.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor, **68**: 113–151.

SHOEMAKER, H. H. 1939. Social hierarchy in flocks of the Canary. Auk, **56**: 381–406.

STORER, R. W. 1955. Weight, wing area, and skeletal proportions in three accipiters. Acta XI Congr. Internat. Ornith., 1954: 287–290.

UTTENDÖRFER, O. 1939. Die Ernährung der deutschen Raubvögel und Eulen. Berlin, J. Neumann-Neudamm.

The University of Michigan Museum of Zoology, Ann Arbor, Michigan.