SEXUAL DIMORPHISM IN ACCIPITER HAWKS: A NEW HYPOTHESIS

RICHARD T. REYNOLDS
Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331

For several decades the question of the adaptive significance of reversed sexual dimorphism (male smaller than female) in the Orders Falconiformes and Strigiformes has received considerable attention. Numerous theories relating to this problem have been proposed (for review see Amadon 1959; Cade 1960; Selander 1966), yet the issue remains unresolved. A significant point stressed by proponents of several of these theories is that reversed sexual dimorphism is directly correlated with an active predatory existence. This supposition is based on the observed increase in dimorphism from vulturine species, through the intermediate mammalian and insect-feeding predators, to the extreme found in the highly active bird-capturing hawks (e.g., certain accipiters and falcons).

Most of the theories offered in explanation of reversed sexual dimorphism can be categorized into two groups: (1) those which propose that the condition arose as an adaptation reducing intraspecific competition by creating differential feeding habits of the sexes (Brüll 1937; Hagen 1942; Dementiev 1951; Storer 1955, 1966; Selander 1966); and (2) those that cite the need of female dominance to prevent the occurrence of filicidal behavior by the male (Hagen 1942; Amadon 1959). Another aspect of female dominance, proposed by Cade (1960), and presently accepted by Brown and Amadon (1968), is that dimorphism arose in response to the need of female dominance of the male in order to maintain him in his role as food provider during incubation and raising of the young. "A reproductively successful pair bond can result only when the female falcon is clearly dominant to the male, and the male makes a biologically adequate adjustment to his subordinate role in the pairing situation. If this interpretation is correct, then the difference in food habits of the sexes must be considered an obligatory result of their difference in size and not the evolutionary cause of size dimorphism" (Cade 1960).

There is, however, no evidence, except perhaps with the Burrowing Owl, *Speotyto cunicularia* (see Earhart and Johnson 1970), that the male, given the opportunity, would kill and eat the young. Indeed, in several species of accipiter hawks, the male actually broods the young at the nest (Brown and Amadon 1968; Liversedge 1962). In response to Cade's argument, I believe the apparent dominance of the female is a consequence of, and not the cause of, sexual dimorphism. In the genus *Accipiter*, where reversed size dimorphism reaches an extreme, the female could easily overpower and kill the male. The apparent subordination of the male, then, has probably evolved concomitantly with the development of dimorphism, as a means of maintaining the stability of the pair bond. I also question the necessity of female dominance (due to her relatively larger size) in maintaining the male in his hunting role. In some species, e.g., the Sparrow Hawk (*Falco sparverius*) and the Red-tailed Hawk (*Buteo jamaicensis*), the male does most of the foraging during incubation and brooding even though there is little difference in size between the male and female (Willoughby and Cade 1964; Austing 1964).

Selander (1966) and others (see above) have argued that sexual dimorphism has evolved as an adaptation enabling each sex to exploit different prey species. This would have selective advantage in that it would decrease intraspecific competition thereby allowing denser populations and wider distributions of the predators. That size dimorphism gives rise to differential prey selection is evidenced by Storer's (1966) work with the three North American accipiters; Hoglund's (1946) study of the Swedish Goshawk (*Accipiter gentilis*); and Earhart and Johnson's (1970) work with the North American owls. I agree with the hypothesis inasmuch as there is an advantage to the predator through differential niche utilization; however, it reveals nothing as to the origin or cause of reversed dimorphism (although Selander suggests that the reversed condition might be explicable in terms of the advantages of female dominance).

Dementiev (1951), Earhart and Johnson (1970), and Storer (1966) briefly consider the important point that the agility of a predator must at least match that of the prey, and that the physical adaptations which produce this agility—body weight and wing area—are held within progressively stricter bounds as the

TABLE 1. Prey items, arranged by weight group, of accipiters (from Storer 1966).

Weight group	Range (g)	*A. striatus velox*		*A. cooperii*		*A. gentilis atricapillus*	
		♂	♀	♂	♀	♂	♀
1	3.4–8.0	14	2		1		
2	8.0–15.6	41	27	2	7		
3	15.6–27.0	50	47	28	25	9	3
4	27.0–42.9	14	29	6	15	1	3
5	42.9–64.0	1	2	3	2	2	
6	64.0–91.1	4	10	6	5		2
7	91.1–125	1[a]	6	5	11	3	
8	125–166			2	7	4	
9	166–216		[a]	7	12	5	12
10	216–275				2		
11	275–343		2	[a]	1		1
12	343–422					1	1
13	422–512			1	[a]	8	7
14	512–614					8	4
15	614–729				1		
16	729–856					[a]	
17	856–1000					2	1
18	1000–1158				3	9	5[a]
19	1158–1331					6	14
20	1331–1521					6	6
Total number of prey items		125	125	60	92	64	59
Range of prey weight (in groups)		1–7	1–11	2–13	1–18	3–20	3–20
x̄ wt of prey (in groups)		2.7	3.6	4.2	4.9	12.2	13.6
x̄ wt of prey (g)		17.6	28.4	37.6	50.7	397	522
x̄ wt of hawks (g)[b]		98.8	171	295	441	818	1137
$\frac{\bar{x}\text{ wt of prey}}{\text{Mean weight of hawk}} \times 100$		17.8	16.6	12.8	11.5	48.5	46.0
% of prey items in hawk's group or above		0.9	1.6	1.7	4.3	35.9	42.4

[a] Group to which the hawk belongs.
[b] Data from Storer (1955: table 1).

principal prey species become more agile or maneuverable. Thus, one would expect the size of a predator feeding on very agile species (birds) to approach that of the prey. Indeed, Storer (1966) (see Table 1) found that the largest prey species captured by the Sharp-shinned Hawk (*Accipiter striatus*) and the Cooper's Hawk (*A. cooperii*) approximated the weight of their respective captor. The larger Goshawk, however, consistently captured prey of weights exceeding its own. His data also suggest a definite segregation of optimal prey (those size groups most frequently taken) among the three hawk species, which indicates that the energy spent per capture of prey species smaller than optimal size may exceed the energy received from subsequent ingestion. The relationship between agility of prey and the size of predator is further illustrated by numerous food studies of the genera *Buteo* and *Falco* and several species of Strigiformes (Lack 1946; Craighead and Craighead 1956; Earhart and Johnson 1970). As an example, Craighead and Craighead (1956) found that four considerably different-sized predators feed primarily on members of the genera *Microtus* and *Sorex*; the Sparrow Hawk, 87.2% of the diet; the Marsh Hawk (*Circus cyaneus*), 98.4%; the Red-shouldered Hawk (*Buteo lineatus*), 94%; and the Red-tailed Hawk, 92%. These data indicate that small mammalian prey, which may be less agile than birds, can support avian predators of considerably different sizes (less agile prey requiring less agile predators). If, then, reversed sexual dimorphism is correlated with the agility of the principal prey species, it is not surprising to observe little or no sexual size difference in the vulturine species, whose prey are immobile, intermediate sexual dimorphism in mammalian-feeding hawks, and extreme dimorphism in the agile bird-capturing hawks and falcons.

It is in the genus *Accipiter* that reversed sexual dimorphism reaches its greatest development among raptors, and here, then, that investigations of possible adaptive correlates of this reversed dimorphism should be most enlightening. Several years of field work with the three Oregon accipiters have impressed me with the importance of certain behavioral aspects of their ecology and how these might be affected by, or are effecting, reversed sexual dimorphism. These same behaviorisms have been recorded for the accipiters by many workers, but their significance seems to have been overlooked.

SIZE OF THE MALE

Pair formation in the North American accipiters begins in late winter (mid-March for Oregon Cooper's Hawks and Goshawks), when both male and female birds, due to poor over-winter food conditions, may have reduced energy reserves. The female, especially, is in critical need of replenishing these reserves as she must ultimately produce a clutch of eggs (see Perrins 1970, for a discussion of the significance of energy in the formation of eggs). If sufficient energy were unavailable, small clutches or a total cessation of egg production would occur (see Southern 1959; Lack 1966). In storing a sufficient amount of energy for egg formation, the female could pursue three strategies: (1) increase her foraging time and food uptake; (2) rely on the male to supply her with the necessary energy while she remained at the nest site; or (3) combine both of the above. Case 1 would have little selective advantage as the energy gained would not greatly exceed the energy spent per capture of an elusive prey. Case 2 would be advantageous over Case 3, as a complete lack of foraging would result in less energy expenditure, particularly important just prior to egg-laying. Two additional advantages of Case 2 are: 1) storing of excess energy which might be channeled into the production of a second clutch should the first be destroyed and, 2) at least in Oregon where the Sharp-shinned, Cooper's, and Goshawk breed sympatrically, a reduction in interspecific competition for food (for example between a female Sharp-shinned and a male Cooper's) by the elimination of foraging females. Thus, Case 2 would have the greatest selective value *if* the male were efficient enough to allow its operation. Furthermore, if he could continue to feed the female during incubation and brooding of the young, she could devote more time and energy to these duties, and on the average, fledge a greater number of young (see von Haartman 1958, for a similar situation in the Pied Flycatcher, *Ficedula hypoleuca*).

That the male accipiter functions as the major food provider for himself, the female, and, after hatching, the young; and that the female rarely hunts from pair formation to approximately the mid-nestling stage, a period of 50 to 90 days depending on species, has been shown for the Cooper's Hawk by Meng (1951) and Reynolds (in prep.), for the European Sparrow Hawk (*A. nisus*) (in Brown and Amadon, 1968:480). Little is known of early pair formation in raptorial birds. However, it is well documented for most of the world accipiters, and many of the falcons and buteo hawks, that the male is the major provider of food throughout incubation and at least the first half of the nestling period (Brown and Amadon 1968; Cade 1960; Dementiev 1951; Schnell 1958).

Since the fitness of the pair is dependent on the ability of the male to supply the necessary energy, the most efficient and experienced male—and a female that selects such a male—would raise the greatest number of young. A lack of this efficiency, resulting from inexperience, may be why immature accipiter males have not been found nesting, whereas immature females have (Meng 1951; Snyder pers. comm.). To maximize his foraging efficiency, the male must capture the most common prey available, thereby reducing the time spent in search of prey. Storer (1966) points out (see also Schoener 1968) that according to the Eltonian pyramid of numbers, there are more species and individuals of smaller animals than large, so that the smaller the predator the greater the number of prey species and individuals within its optimal prey size. The foraging efficiency of the male, therefore, would increase with a reduction in his size. It has been hypothesized that for predators which locate, pursue, and capture each prey item independently, the number of encounters with optimal, acceptable prey, rather than prey biomass, is the critical factor limiting efficiency. Increasing the number of encounters with optimal prey reduces the time and energy spent in search of food and allows more captures to be made per unit time. The relationship of prey size to numbers is not clear, particularly for forested habitat. However, if this relation should hold, and if it is correct that larger birds require absolutely more food (see Nice 1938) and expend more energy in pursuing each item over a given distance than do smaller ones (Schoener 1969), then the advantages of increased encounters of optimal prey due to size reduction of the male are obvious. Thus, if a smaller male encounters more optimal, accessible prey, and has reduced metabolic needs, then his efficiency at procurring *excess* food more frequently and at more regular intervals is enhanced. Both of these factors lend predictability to the food resource

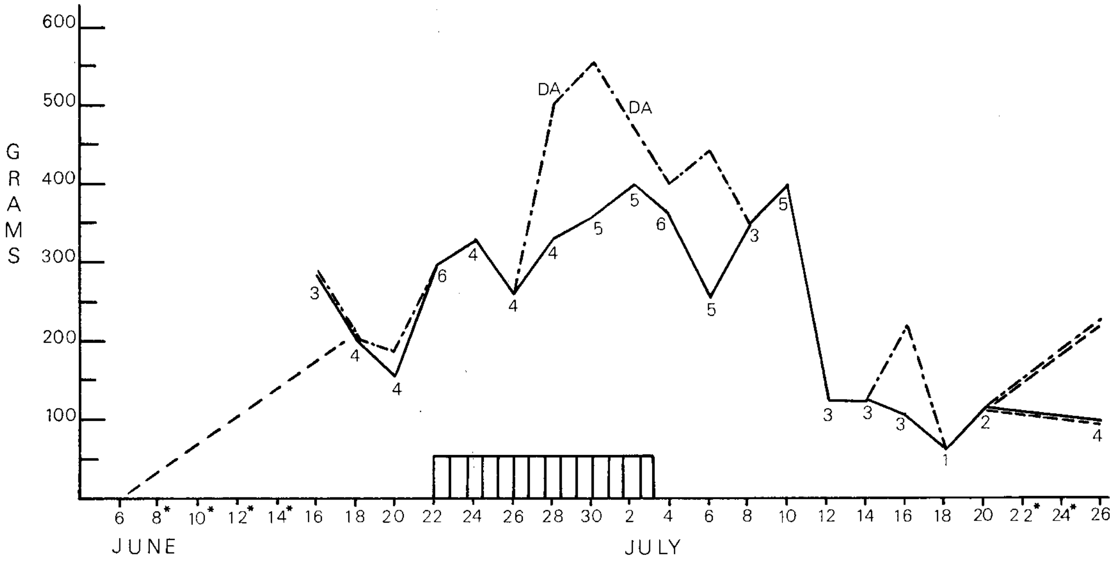

FIGURE I. Food consumption of young Goshawks. Solid lines connect prey weight delivered by the male, dot-dash lines, the prey weight totals when food was delivered by the female. Delivery frequencies of the male are shown by numbers. Period of maximum growth of the young is indicated by vertical hatching. Asterisks indicate data were not taken; on these days, the curve was completed by extrapolation (dashed line). Days of abundance (DA above) indicate times when food brought to the young hawks was in excess of their needs. After Schnell 1958.

and increase the potential for greater reproductive output.

The efficiency of the male (at least in the accipiters) is reflected in the degree of his participation in the incubation duties. Essentially, he incubates only when the female leaves the nest to consume food brought to her. Apparently the male is the more efficient forager of the pair and increased sharing of the incubation and foraging roles has no selective value (this may also reflect the inability of the smaller male to sufficiently cover the eggs for an extended period).

Size reduction of male accipiters may be somewhat limited by interspecific competition for food during the nonbreeding season. Too great a reduction in size of the male Goshawk and Cooper's Hawk may be prevented by direct competition with the female of the next smaller species, while further size reduction of the male Sharp-shinned Hawk is prevented by the paucity of avian prey smaller than its present optimum.

SIZE OF THE FEMALE

At approximately the mid-nestling stage, the female becomes active and begins to assist the male in his foraging efforts, as the increased consumption of food by the rapidly growing young surpasses his efforts (see Schnell 1958). Beginning to forage requires that she abandon, at least temporarily, her role of protecting the nestlings from predation and elements of the environment (sunlight, heat, and cold). That nest predation is an important factor is indicated by the work of Craighead and Craighead (1956). Of 161 active nests of hawks and owls studied, 65 (34%) were destroyed by various predators. If nest predation is this prevalent among the accipiter hawks, then it would be beneficial for the female to be absent from the nestlings as little as possible. These periods of absence could be reduced if she were to maintain a relatively large body size, which, as indicated by Storer's (1966) data (discussed further below), would enable her to capture from a broader prey-size range, and on the average to bring larger bundles of energy to the young, resulting in a reduction of the time she needs forage per day. The maintenance of large size could occur only if large prey presented themselves with some frequency. The presence of a source great enough to allow economic utilization is evidenced by the number of fledgling or young prey brought to the nest at this time (Reynolds, in prep.); that is, selective pressure for female size is greatest when she begins foraging and is concurrent with the doubling or trebling of prey numbers due to their reproduction. Thus, her efficiency at utilizing a higher level of the pyramid of numbers is enhanced not only by increased encounters of optimal prey but by the vulnerability of this inexperienced source. Without question, the fledging of the prey species is an important factor in the timing of the breeding of the accipiters.

The importance of the female's ability to capture from a broader prey-size range and her reluctance to leave the nest area are shown for the Goshawk by Schnell (1958). He found, after plotting separate curves for prey weights contributed by each of the adults, that ". . . it is evident that the foraging efforts of the female are responsible for the peaking of the food consumption curve, whereas the male but slightly increases the daily ration at the time of maximum consumption" (see fig. 1). Schnell (op. cit.) found that two factors influenced the foraging activity of the female: (1) the abundance of prey in the nest area ". . . these captures were completely fortuitous and were affected by prey abundance. If the animals had not entered the nest area they would not have been captured;" and (2) the female foraged when the nestlings were most in need of food. Her greater prey-size range, inherent with her larger size, would better enable her to capture whatever passed through the nest area. Other factors, for example, larger eggs with greater amounts of yolk and greater efficiency at brooding and protecting the nestlings, would also select for larger females.

VARIATIONS OF DIMORPHISM WITHIN THE GENUS *ACCIPITER*

Sexual dimorphism as seen in the North American accipiters is greatest in the Sharp-shinned Hawk, intermediate in the Cooper's, and least in the Goshawk. Several factors may account for this gradation. Storer (1966) suggests that differing degrees of migratory behavior may have selected for it. The Goshawk, essentially nonmigratory, must capture whatever presents itself during winter when food species are often rare. A large male at this time would have an advantage over a smaller individual in that he could capture from a broader prey-size range and would not need to wait for small prey to avail themselves. On the other hand, the migratory Sharp-shinned Hawk follows avian prey southward, and is not confronted with the same situation. The Cooper's Hawk, intermediate in sexual dimorphism, is only partially migratory. While these factors are certainly influential, the principal cause may be due to a decrease in both individuals and numbers of avian prey within the optimal size-range of the accipiter as the size of the hawk increases. As indicated by Storer's (1966) data, the larger the accipiter the disproportionately greater is its prey-size range. The male of the larger species, utilizing the upper portion of the pyramid of numbers, has fewer encounters of optimal prey per unit time. If this deficit in number of encounters could be counteracted by maintaining a broad prey-size range, then there must be selective pressure against too great a size decrease. The smaller species of accipiters, however, have available to them greater numbers of optimal prey within any one size group, neutralizing the need of a wide prey-size range. Also, larger accipiters have lower relative metabolic needs and, therefore, are able to withstand longer periods of food deprivation. This has the same effect as reducing the variation in numbers of encounters of optimal prey. In addition to the increase in both prey-size range and utilization of mammalian prey (see below), the larger accipiters further increase their encounters of optimal prey by foraging over a larger area (Schoener 1968).

Broadening of the prey-size range with increasing size can best be accounted for, at the upper extreme, by the greater weights, relative to avian prey, of mammalian species captured. Storer's data (1966) show that there is an increasing dependence on mammalian prey as accipiter size increases (mammals contributed 3.0% to the diet of the Sharp-shinned, 17.7% to the Cooper's, and 45.2% to the Goshawk). These mammals, mostly Sciurids and Lagomorphs, may also require a larger predator to subdue them. Expansion at the lower end of the size-range is made possible by exploiting the element of surprise. Small avian prey, normally not available to the larger accipiters, can be captured, if surprised, by eliminating an opportunity to elude the predator.

DIFFERENTIAL FORAGING EFFICIENCY AND SEX RATIO

If small prey are more numerous than large, the smaller accipiter male, being even slightly more efficient in terms of numbers of encounters of optimal prey, would suffer less over-winter mortality than would females. If such were the case, the resultant unbalanced sex ratio might be corrected by either increased mortality of males during some other period or by an unbalanced sex ratio of nestlings in favor of the females. Because of the secretive habits of nesting accipiters and the difficulty of sexing nesting hawks on a size basis, little data relating to sex ratios of young have been collected. However, Craighead and Craighead (1956), working with both hawks and owls (including species with little dimorphism relative to the accipiters, and therefore, with less differential foraging efficiency between male and female), found of 225 young, 125 were females and 104 were males. They noted (op. cit.) that the smaller size of the male nestling is a decided disadvantage as they must compete directly with their larger sisters. They also noted that this higher mortality of male nestlings may be counteracted by the mortality of nesting adult females that appears to occur later, thereby leaving the original unbalanced ratio. My data on the Oregon accipiters also indicate, particularly with the Sharp-shinned Hawk, an unbalanced nestling ratio in favor of the female (see also Mayr 1938; Hickey 1942; Beebe 1960). Others, notably Meng (1951), Enderson (1964), and Heintzelman and Nagy (1968), found little or no divergence from a 1:1 sex ratio among nestlings. It is interesting to note, however, that while several of these researchers report only a slight or no difference in favor of females, none, except Meng (1951) who found six females and ten males in five nests of Sharp-shinned Hawks, reports an opposite trend. It is apparent that further evidence pertaining to adult mortality and the sex ratio of nestlings surviving the nestling period needs to be collected.

CONCLUDING REMARKS

This hypothesis is presented in hopes of alerting students of raptorial birds to the possibility that behavioral and ecological factors similar to those proposed to have initiated and maintained sexual dimorphism in the accipiter hawks may be operating in other members of the Falconiformes and Strigiformes, though to a lesser degree. It is my purpose to present a new approach in hopes of stimulating research that may increase our understanding of sexual dimorphism by integrating the behavior and ecology of these predators. The hypothesis presented is, however, based on several factors that need further clarification. The most important of these is the relation of prey size to prey numbers (pyramid of numbers), particularly for forested habitat.

Further data are also desirable pertaining to: (1) early pair formation (exactly when, and to what degree, the female depends upon the male for food); (2) differential food habits of nesting males and females; and (3) when, and how much, does the female contribute to the diet of the nestlings. Factors that point to differences in the foraging efficiencies between the sexes, and morphological characters that may indicate a reduction in body-size on the males' behalf, should also be examined (see Hill 1944).

SUMMARY

Several of the proposed theories of sexual dimorphism in Falconiformes are reviewed and discussed. A new hypothesis is suggested which is based on selection for increasing the hunting efficiency of the male accipiter hawk to better feed himself, the female, and the young through a large portion of the breeding season. Since there are greater numbers of species and individuals of smaller avian prey (Eltonian pyramid of numbers), a decrease in size would result in an increase of encounters of optimal, accessible prey. If a smaller male encounters more optimal, accessible prey, and has reduced metabolic needs, then his efficiency at procuring excess food more frequently and at more regular intervals is enhanced.

The larger size of the female has been maintained as she must supplement the male's foraging when the young are in greatest need of food (just prior to fledging) and greater size allows her to capture from a broader prey-size spectrum. That large prey are sufficiently numerous and vulnerable to maintain or select for greater female size is indicated by the number of young or fledgling prey brought to the nest during the latter portion of the nesting period. Thus, the total number of prey individuals within the females' prey-size range may double or even triple as prey fledge. Fledging of the prey may be an important ultimate factor in timing of accipiter breeding, as it approximates the time of the greatest demand of food by the young hawks.

Several factors point indirectly to the differential foraging efficiency between the male and female: (1) an unbalanced sex ratio of nestling accipiters in favor of the females to balance higher overwinter female mortality; and (2) the lack of a substantial contribution to the incubation duties by the male. The fact that immature accipiter males do not breed, whereas immature females do, may indicate the importance of experience in increasing the foraging efficiency of the male.

In addition to varying degrees of migratory behavior, the decrease in size differential between the male and the female as accipiter size increases can best be accounted for by considering the necessity of increasing the number of encounters of optimal prey per unit of time. Storer's (1966) data indicate that larger predators feed over a disproportionately wider range of food size than do smaller species. The males of the larger species, utilizing less dense prey populations, have increased

their encounters of optimal, accessible prey by maintaining a larger size relative to the female than those of the smaller species. Several other factors apparently function in maintaining the number of encounters of optimal prey as accipiter size increases: (1) an increase in the number of mammals taken; and (2) an increase in the size of the foraging area.

ACKNOWLEDGMENTS

I wish to thank the many individuals who have acted as sounding boards throughout the formulation of this hypothesis, especially Eric Forsman, John W. Pike, Ronald A. Nussbaum, David J. Broderick, Gordon S. Lind, and James E. Tabor. Special appreciation to John A. Wiens who first stimulated me to begin writing on the subject and for reviewing the first and final draft. Howard M. Wight, Kenneth L. Gordon, Noel F. R. Snyder, and Charles E. Warren are thanked for critically reviewing different stages of the manuscript. This is Oregon Agricultural Experiment Station, Technical Paper No. 3110.

LITERATURE CITED

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

AUSTING, R. 1964. The world of the Red-tailed Hawk. J. P. Lippincott Co., Philadelphia.

BEEBE, F. L. 1960. The marine Peregrines of the northwest Pacific coast. Condor 62:145–189.

BROWN, L., AND D. AMADON. 1968. Eagles, hawks and falcons of the world. McGraw-Hill, New York.

BRÜLL, H. 1937. Das Leben deutscher Greifvögel. Gustav Fischer, Jene, Deutscher Demokratische Republik.

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

CRAIGHEAD, J. J., AND F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania.

DEMENTIEV, G. P. 1951. [The order of hunting birds.] *In* G. P. Dementiev et al. [eds.]. Birds of the Soviet Union. Vol. 1. Soviet Science, Moscow.

EARHART, C. M., AND N. K. JOHNSON. 1970. Size dimorphism and food habits of North American owls. Condor 72:251–264.

ENDERSON, J. H. 1964. A study of the Prairie Falcon in the central Rocky Mountain region. Auk 81:332–352.

HAGEN, Y. 1942. Totalgewichts-Studien bei norwegischen Vogelarten. Arch. Naturgesch. 11:1–173.

HEINTZELMAN, D. S., AND A. C. NAGY. 1968. Clutch sizes, hatchability rates, and sex ratios of Sparrow Hawks in eastern Pennsylvania. Wilson Bull. 80: 306–311.

HICKEY, J. J. 1942. Eastern populations of the Duck Hawk. Auk 59:176–204.

HILL, N. P. 1944. Sexual dimorphism in the Falconiformes. Auk 61:228–234.

HOGLUND, N. H. 1946. Uber die Ernahrung des Habicts (*Accipiter gentilis* Lin.) in Schweden. Viltrevy 2:271–328.

LACK, D. 1946. Competition for food by birds of prey. J. Anim. Ecol. 15:123–129.

LACK, D. 1966. Population studies of birds. Oxford University Press, New York.

LIVERSEDGE, R. 1962. The breeding biology of the Little Sparrow Hawk *Accipiter minullus*. Ibis 104:399–406.

MAYR, E. 1938. The proportion of sexes in hawks. Auk 55:522–523.

MENG, H. K. 1951. The Cooper's Hawk *Accipiter cooperii* (Bonaparte). Unpublished Ph.D. thesis, Cornell Univ. 202 p.

NICE, M. M. 1938. The biological significance of bird weights. Bird Banding 9:1–11.

PERRINS, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

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

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123–141.

SCHOENER, T W. 1969. Models of optimal size for solitary predators. Amer. Nat. 103:277–313.

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

SOUTHERN, N. H. 1959. Mortality and population control. Ibis 101:429–436.

STORER, R. W. 1955. Weight, wing area, and skeletal proportions in three accipiters. Acta XI Congr. Int. Ornithol., Basel, p. 287–290.

STORER, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83:423–436.

VON HAARTMAN, L. 1958. The incubation rhythm of the female Pied Flycatcher (*Ficedule hypoleuca*) in the presence and absence of the male. Ornis Fennica 35:71–76.

WILLAUGHBY, E. J., AND T. J. CADE. 1964. Breeding behavior of the American Kestrel (Sparrow Hawk). Living Bird. Third Annual:75–96.

Accepted for publication 20 Sept. 1971.