KEMPTON, R. M.
1927. Notes on the Home Life of the Turkey Vulture. Wilson Bull., 38: 142–145.
MASLOWSKI, K. H.
1934. An Aerial Nest of the Turkey Vulture. Auk, 51: 229–230.

Teachers College
University of Cincinnati
Cincinnati, Ohio

SEXUAL DIMORPHISM IN THE FALCONIFORMES

BY NORMAN P. HILL

IT has been known for a long time that the males of certain species of Falconiformes are smaller, sometimes much smaller, than the females. This fact has been common knowledge but apparently there has never been any careful work to determine in which species and to what degree this dimorphism is exhibited. The present work is intended to fill this gap in ornithological information.

Sexual dimorphism is exhibited in a majority of orders of birds, and in most cases the male sex is the larger. This is the case in all groups for which data are available, except the Falconiformes, the Strigiformes, and the Superfamily Charadrioidea (Shore-birds) of the Charadriiformes, where the opposite is true. The similarity of the Strigiformes to the Falconiformes in this respect might have been developed because of the similarity of habits, but this theory cannot be carried too far because the equally predacious Laniidae (Shrikes) of the Passeriformes show the opposite dimorphism. The presence of the Charadrioidea here is harder to explain; perhaps they are following the pattern of the rest of the Charadriiformes in which the sex most concerned with incubating and brooding is the smaller, for in this superfamily, the males take on most of the nest duties,[1] a habit most highly developed in the Phalaropodidae.

The amount of size difference between the sexes in birds can be demonstrated most easily by the ratio of the size of one sex to that of the other. This gives a series of percentages showing the size differential. From the percentages, more information may be deduced.

The most accurate measurement of the 'size' of a bird is, most naturally, that of weight. However, there are practically no data on weights of hawks. What exist are taken largely from birds which have been in captivity for considerable lengths of time for the purpose

[1] This statement is open to question. There is much evidence that in most of the shorebirds, both sexes incubate. *Cf.* Ticehurst, Ibis, (13) 1: 582–583, 1931.—ED.

of falconry. It can not be assumed that these birds were in their natural physical condition. Such data on wild birds as are available check fairly closely with the information deduced from the measurements of skins. Unfortunately, few collectors have been in the habit of recording the weights of their freshly killed specimens.

Since insufficient material on weights is at hand, it has been necessary to devise some suitable substitute with measurements that could be taken from the large number of study skins that have been available. Four measurements were found to be suitable. These were, of necessity, linear measurements, so, since weight varies as the cube of linear dimensions, the average of each measurement for each sex was cubed and a percentage was taken of the relation of the male to the female. Thus, a value of 100% means that, for that measurement, the male is the same size as the female, whereas one of 50% means that the male is half the size of the female. Since these percentages have no relation to each other, they can not be averaged to get a single value for that species. The separate parts must be considered separately.

The measurements found to be most practical were the folded wing, the tail, the tarsus, and the bill. Certain other measurements, such as the total length and maximum circumference, were found to depend in study specimens entirely on the preparation of the skin. Therefore, no confidence could be placed in such figures and they were neither taken nor used in this study. All measurements were taken with a straight edge or dividers so that the chord, rather than the arc, of any curved structure was recorded.

A total of over 2,300 specimens of North American hawks was measured in the collections of the Museum of Comparative Zoölogy, Cambridge, Mass.; the Boston Society of Natural History, Boston, Mass.; and the American Museum of Natural History, New York, N. Y. A small number of these measurements were discarded for reasons shortly to be mentioned and the rest (2,259) were used to determine the averages from which following percentages were derived.

The measurements of certain specimens were disregarded for one or other of the following reasons: (1) that the sex was not indicated on the original label; (2) that the bird was molting so that true figures on the lengths of wing and tail could not be obtained; and (3) that the measurements did not fit into the normal range for that sex of that species—*i.e.*, that a mistake had been made in the determination of the sex of that bird.

Here follows a table of the ratio of the measurements of the male

TABLE 1

PERCENTAGES OF MALE TO FEMALE MEASUREMENTS

Species	*Wing*	*Tail*	*Tarsus*	*Bill*
Cathartes aura septentrionalis	96.0%	102.0%	99.4%	103.5%
Coragyps atratus atratus	95.7	87.5	91.5	87.2
Gymnogyps californianus	108.0	91.5	121.0	104.0
Elanus leucurus majusculus	101.0	100.5	111.0	113.5
Elanoides f. forficatus	96.7	94.0	94.5	98.5
Ictinia mississippiensis	94.0	100.2	97.5	93.0
Rostrhamus sociabilis plumbeus	92.5	94.0	90.0	113.0
Astur a. atricapillus	77.5	66.0	89.5	73.5
Astur a. striatulus	80.0	63.0	75.5	79.5
Accipiter v. velox	60.2	68.8	71.4	56.2
Accipiter cooperi	66.8	66.8	71.0	55.5
Buteo b. borealis	83.0	80.7	85.5	81.2
Buteo b. umbrinus	76.2	74.5	84.8	63.5
Buteo b. krideri	85.0	83.5	80.5	77.0
Buteo b. calurus	84.7	90.5	96.0	78.5
Buteo b. harlani	78.5	79.0	87.0	75.0
Buteo l. lineatus	86.0	83.0	92.8	81.0
Buteo l. alleni	86.3	84.5	95.0	76.2
Buteo l. extimus	81.2	80.8	90.0	79.4
Buteo l. texanus	83.5	90.0	93.5	80.5
Buteo l. elegans	83.3	77.5	80.0	84.2
Buteo p. platypterus	91.0	85.8	97.5	83.8
Buteo swainsoni	82.5	86.7	79.2	76.2
Buteo albonotatus	78.0	86.5	87.0	69.0
Buteo albicaudatus hypospodius	91.2	90.0	93.5	82.5
Buteo brachyurus	83.0	85.5	98.5	71.2
Buteo lagopus s.johannis	86.5	87.0	97.5	75.5
Buteo regalis	84.3	90.2	85.4	70.0
Parabuteo unicinctus harrisi	72.5	82.5	82.5	76.5
Asturina plagiata plagiata	74.5	72.5	87.2	79.0
Urubitinga a. anthracina	85.0	82.0	95.0	87.5
Aquila chrysaëtos canadensis	94.5	85.0	92.0	90.0
Haliaeetus leucocephalus alascanus	85.0	84.0	91.5	83.3
Haliaeetus l. leucocephalus	76.0	74.0	131.5	71.5
Circus hudsonius	73.5	70.0	73.5	65.0
Pandion haliaëtus carolinensis	86.5	77.5	92.0	81.5
Polyborus cheriway auduboni	87.0	81.8	93.0	85.5
Falco rusticolus ssp.	76.4	67.6	80.8	74.5
Falco mexicanus	77.8	74.9	77.0	71.5
Falco peregrinus anatum	66.2	57.0	72.0	61.0
Falco p. pealei	68.0	63.5	69.5	50.0
Falco fusco-coerulescens septentrionalis	71.0	74.8	97.5	61.0
Falco c. columbarius	76.5	79.0	81.5	63.5
Falco c. suckleyi	73.2	72.0	71.0	70.0
Falco c. richardsoni	76.2	73.2	77.8	62.2
Falco c. bendirei	72.0	70.8	79.0	66.8
Falco s. sparverius	85.5	66.0	107.5	88.0
Falco s. phalaena	88.0	91.0	102.0	95.5
Falco s. paulus	84.6	84.5	89.6	82.0

to those of the female in each of the four characters chosen. The classification and sequence of the fourth edition (1931) of the A. O. U. Check-List is used throughout, and all subspecies, with the exception of those of the Gyrfalcons (*Falco rusticolus*), are treated individually.

On the basis of these percentages, the birds involved can be divided into three general groups: (1) those in which the male is practically as large as the female; (2) those in which there is only a moderate size difference; and (3) those in which the male is much smaller than the female.

The first group, rather arbitrarily chosen, includes:

Cathartes a. septentrionalis
Coragyps a. atratus
Gymnogyps californianus
Elanus l. majusculus
Elanoides f. forficatus
Ictinia mississippiensis
Rostrhamus s. plumbeus
Aquila c. canadensis
Falco s. phalaena

The third group contains:

Astur a. atricapillus
Astur a. striatulus
Accipiter v. velox
Accipiter cooperi
Buteo b. umbrinus
Buteo b. harlani
Asturina p. plagiata
Haliaeetus l. leucocephalus
Circus hudsonius
Falco rusticolus subsp.
Falco mexicanus
Falco p. anatum
Falco p. pealei
Falco f-c. septentrionalis
Falco c. columbarius and subspecies

All other species fall into the second group.

On superficial examination of these lists, it would seem that the birds which inhabit a climate with more severe seasonal variations show a more marked sexual dimorphism. A closer inspection shows that this is not true; the Golden Eagle of Group I is distinctly northern in distribution, the Aplomado Falcon of Group III is unquestionably subtropical, and certain tropical *Accipiters,* namely *A. fringilloides, chionogaster,* and *salvini* show fully as great or even greater size difference than does their temperate representative, *A. v. velox.* Thus, climate alone may be ruled out as the factor causing this dimorphism in size.

Various differences in habits, activities, and the like seem to be correlated with the amount of size difference. It would seem, from data included in life histories, that those species in which the male is much smaller than the female show: (1) the female somewhat more active than the male; (2) a larger average set of eggs; (3) a somewhat shorter incubation period; and (4) a somewhat shorter period between the hatching and the fledging of the young. There are no data giving

any indication whether these characteristics are the cause of the sexual dimorphism or the result of it. Nevertheless, they may bear investigation.

Throughout the species of Group I, both sexes apparently share nearly equally the tasks of nest building, incubating, guarding, and feeding the young. The Golden Eagle is the only possible exception; here the male does slightly less incubating and more hunting, and in this respect approaches the habits of the species of Group III.

In Group III, on the other hand, the female, in many cases, takes on much of this activity herself. After building most of the nest, the female often does most of the incubation while the male guards the nest and brings food for her and for the young after they are hatched; the male may feed the young directly or may surrender the food to the female who then feeds them. This general arrangement is found in the Goshawk, the Marsh Hawk, the Gyrfalcons, the Prairie Falcon, the Duck Hawk, and the Pigeon Hawk and its subspecies. The other species of this group do not show this increase of activity of the female to so great an extent, though nowhere is there such equality as in Group I.

The number of eggs found in a set in Group I averages two. The exceptions to this are the California Condor which lays only one egg about every other year and the White-tailed and Everglade Kites which lay three or four eggs yearly. The birds of Group III never lay less than two eggs in a clutch (and that only in the case of *Haliaeetus l. leucocephalus*) and may lay as many as five or six; the average is four or five. The Duck Hawk lays four or five eggs, whereas in Group I, the Mississippi Kite, a bird only slightly smaller than the Duck Hawk, lays only one or two.

The number of eggs laid by any species is supposed to be an indication of the degree of difficulty to be anticipated in the rearing of a brood. It is hard to see why birds nesting in similar situations in the same area should have to meet apparently drastically different conditions. Yet, this seems to be the case very often; Cooper's and Sharp-shinned Hawks, which lay four or five eggs, breed throughout the southern states, whereas the Mississippi and Swallow-tailed Kites, which breed, or formerly bred, in the same areas, lay only two. It would almost seem that the number of eggs in a set is more characteristic of the general group with which the bird is classified than of the ecological conditions of the breeding area.

As regards the incubation and fledging periods, again the birds of Group III hold the advantage. The bird is immobilized and ex-

posed to danger for a shorter time during the incubation period and the young are able to get out and shift for themselves earlier, so that there is a scattering of the resources and a greater chance for survival of any one nestling. Here again, equally successful birds that are found together have entirely different reproductive time schedules. For instance, the Marsh Hawk incubates for twenty-five days and broods for five weeks, whereas the Black Vulture sits for thirty days and the young remain in the nest from ten to fourteen weeks.

To be sure, there is some correlation between the length of time of incubation and of brooding and the size of the egg, and hence the size of the bird involved. In Group III, however, the size of the egg in proportion to the size of the bird is clearly and definitely related to the taxonomic group rather than to any possible size difference between the sexes. The correlation between the size of the egg and the time of incubation may be pertinent to some extent, but it does not explain the difference in the case of birds that are more or less of the same size, such as the medium-sized falcons and the kites. Here there is something more than just the size of the bird.

One further striking feature will be noticed on comparative examination of the percentages of size in each species; as a general rule, the tarsus of the male is nearer equal in size to that of the female than are most of the other measurements. This fact could be predicted because both the male and the female capture and eat the same food, and in the hawks, the talons are the principal weapons of offence. Thus, for the birds to hunt together for the same prey, the apparatus for the capture of that prey must be more or less equal, even though they, themselves, are of considerably different bulk.

This proposition may be carried on still further and it may be said that the size difference came about by a decrease on the part of the male rather than an increase in the size of the female. The more primitive members of the Falconiformes show less size difference between the sexes so it is probably logical to assume that the ancestral forms of the higher groups likewise showed little or none. Now if the male should, for some reason, begin to decrease in bulk, the legs must stay large in proportion to the rest of the bird if, to put it teleologically, the two sexes are to continue to eat the same food. The other possibility is that the female happened to grow larger and the male, in order to eat the same food, had to grow also, but he accomplished his purpose by merely getting larger feet! It must be assumed throughout that the two sexes eat the same food, because if they live on separate diets, the food supplies can vary independently and it might be that one region could not support both sexes.

CONCLUSIONS

(1) The amount of sexual dimorphism in the Falconiformes varies from the Cathartidae, in which the male is practically of the same size as the female, to the Falconinae and the Accipitriinae, in which the male may be only two-thirds the size of the female.

(2) There is no apparent reason for this difference in the life histories of the birds concerned. The extent of this dimorphism is more characteristic of the taxonomic position than of the environment of the individual species.

(3) There are indications (tarsal measurements) that this dimorphism has come about by a decrease in the size of the male, and, therefore, that the sexes of the ancestors of the Falconiformes were equal in size. This conclusion is further suggested by the fact that the more primitive members of the order show less dimorphism than do the more advanced forms.

SELECTED BIBLIOGRAPHY

ALLEN, G. M.
1925. Birds and Their Attributes.

AMERICAN ORNITHOLOGISTS' UNION
1931. Check-List of North American Birds (4th ed.).

BENDIRE, C.
1892. Life Histories of North American Birds. U. S. Nat. Museum, Special Bull., 1.

BENT, A. C.
1937. Life Histories of North American Birds of Prey, Pt. 1. U. S. Nat. Museum, Bull. 167.
1938. Idem. Pt. 2. U. S. Nat. Museum, Bull. 170.

FISHER, A. K.
1893. Hawks and Owls of the United States. U. S. Dept. Agriculture, Biol. Survey, Bull. 3.

FORBUSH, E. H.
1925–1929. Birds of Massachusetts and Other New England States.

HEINROTH, O.
1922. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht und Brutdauer. Journal für Ornithologie, 70: 172–285.

MAY, J. B.
1935. The Hawks of North America.

PETERS, J. L.
1931. Checklist of Birds of the World, Vol. 1.

SWANN, H. K.
1924–1936. A Monograph of the Birds of Prey.

WITHERBY, H. F., JOURDAIN, F. C. R., TICEHURST, N. F., AND TUCKER, B. W.
1939. The Handbook of British Birds, Vol. 3.

[Also numerous papers on the Falconiformes, etc., published in The Auk, The Condor, The Wilson Bulletin and Bird Banding.]

Arlington
Massachusetts