SIZE DIMORPHISM AND FOOD HABITS OF NORTH AMERICAN OWLS

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Although in most species of birds the male is characteristically larger than the female, the direction of size dimorphism among many birds of prey is reversed; the female is larger than the male. This reversal is present in the orders Falconiformes and Strigiformes and in the families Stercorariidae and Fregatidae (Amadon 1959:534).

Several authors have discussed the possible origin and significance of sexual dimorphism in size in raptorial birds. Brüll (1937), Hagen (1942), Dementiev (1951), Storer (1952, 1966), and Selander (1966) believe that the increased size of the female over the male permits differential niche utilization by the sexes; that is, a difference in sizes of the sexes would allow an increase in the optimal size range of prey species and would reduce intersexual competition. Cade (1960) feels that the larger size of the female in hawks is related to the difficulty of pair bonding in such birds. Hagen (1942) and Amadon (1959) postulate that this dimorphism may have evolved in order to protect the young from possible predation by the male parent. The male birds of prey may have weaker parental instincts but stronger predatory instincts than do the females and thus represent a threat to the young; a larger, dominant female could better protect her young from possible cannibalism.

The paper by Hill (1944) seems to have been overlooked by most recent authors dealing with dimorphism, although he presents data (unsupported by statistics) on sexual differences in size for 49 forms of Falconiformes based on measurements of over 2200 museum specimens. Although he attempts correlations of amount of dimorphism with various aspects of behavior and of breeding biology, no convincing relationships are shown. He concludes that the more primitive members of the Falconiformes show less dimorphism than do the more highly derived forms and that the evolution of the size difference involved a decrease in the size of the male rather than an increase in the size of the female.

For a thorough discussion of the foregoing arguments and of the evolution and ecologic significance of dimorphism in birds in general, see Amadon (1959), Cade (1960), Selander (1966), and Storer (1966).

While these workers agree that reversed size dimorphism is associated with a predatory mode of life, their studies have concentrated on the Falconiformes. To our knowledge there has been no detailed examination of the relative degree of sexual dimorphism among the other birds of prey. Because current generalizations on reversed dimorphism in predatory birds are based in large part on data from hawks, it is of considerable interest to determine to what extent data on other raptors corroborate these findings.

The primary purpose of this paper is to describe the extent and possible function of interspecific and intraspecific size dimorphism in species of North American owls. Secondly, we summarize principal food habits of these species from data in the literature and from unpublished notations on museum specimen labels. We have little to say about the reversed direction the dimorphism has usually taken; of greater ecological relevance is the degree of dimorphism and its possible relationship to competition. Finally, this compilation has demonstrated the lack of basic data on body weights and food habits for certain forms, and we wish to call attention to the need for this information.

METHODS AND MATERIALS

Our analysis of dimorphism is based upon body weights ($n = 1144$) and wing lengths ($n = 1602$) of museum specimens of 32 forms of owls. Stomach contents listed on labels of specimens of known sex, body weight, and wing length are of particular interest because they demonstrate the food habits of individuals of known size and sex.

All wing measurements (the chord of the arc of the unflattened wing) were made by Johnson. Wing measurements were not used if the owl was molting or if the wing feathers were incompletely grown.

Because weight is the best indicator of overall body size, it is unfortunate that body weights are not commonly recorded for museum specimens. Thus, sam-

ples of weights are insufficient for many species for which adequate samples of wing measurements are available. As recommended by Amadon (1943), the cube root of each body weight, rather than the weight itself, was used, thereby reducing the variability of this measurement to a value comparable to the variability of the linear wing dimension. Weights were not included in the computations if the collector's label indicated that the bird was "very fat" or "extremely fat," "emaciated," or "found dead" (= possibly emaciated or mummified to varying degrees).

Sixteen specimens of nine forms of owls were not included because their weights and wing lengths were so far deviant from the respective means that we concluded the bird had been mis-sexed, had been found dead without the information having been recorded on the label, or had been weighed with a faulty balance.

The index of dimorphism devised by Storer (1966: 424) in his examination of sexual dimorphism in size in accipiters was applied to these measurements:

Dimorphism Index

$$= \frac{100 \ (\text{size average female} - \text{size average male})}{\frac{1}{2} \ (\text{size average female} + \text{size average male})}.$$

This index will be positive if the female is larger, that is, if reversed sexual dimorphism is present, and negative if the male is larger.

The sequence of presentation of species follows that of the A.O.U. Check-list (1957:272–290). Computations and statistical analyses were performed at the Computer Center, University of California, Berkeley.

DEGREE OF SEXUAL DIMORPHISM IN SIZE

The mean wing lengths and mean weights, with their corresponding measures of dispersion, for all forms under consideration are shown in tables 1 and 2. The dimorphism indices for wing length and for cube root of body weight were calculated from these means and are presented in table 3. In contrast with Storer's findings (1966) on three species of hawks of the genus *Accipiter*, the various forms of North American owls examined usually do not show the same degree of sexual dimorphism in wing length and in body weight.

Wing length. Indices for wing length show that reversed sexual dimorphism is not present in either *Speotyto cunicularia hypugaea* or *Otus flammeolus*; actually the males have slightly longer wings than do the females in these species. Furthermore, a *t*-test indicates that the means for wing lengths of males and females are not significantly different (*P* > 0.90) in *Otus asio inyoensis, Otus trichopsis aspersus, Glaucidium brasilianum ridgwayi, Micrathene whitneyi sanfordi, Asio flammeus,* and *Asio otus wilsonianus.* For the majority of the forms indicated by the *t*-test to be significantly dimorphic in wing length, index values ranged from 2.13 in *Otus asio cineraceus* to as high as 6.64 in *Bubo virginianus virginianus* (table 3).

Body weight. Dimorphism indices of mean cube root of body weight are larger than the dimorphism indices of wing length for almost every species. Surprisingly, this is true even for those species mentioned in the previous section which are monomorphic in length of wing (for example, the two species of *Asio* and *Glaucidium brasilianum ridgwayi*), all of which have substantial body weight dimorphism indices. *Nyctea scandiaca* and *Speotyto cunicularia* are the only species in which the relative difference between the mean wing lengths of the sexes is greater than the relative difference between the mean cube roots of weight. In addition, *Speotyto cunicularia* is the only species analyzed with a negative body weight index value, indicating that the males average slightly heavier than the females.

Wing-loading. Unless further studies show that the female has evolved a compensation for her shorter wing (e.g., increased the wing area, developed a more efficient wing shape, etc.) to permit her to carry greater weight, the differences in these dimorphism indices suggest that the female owl has greater wing-loading and may be therefore less maneuverable than is the male. Poole (1938) measured the wing areas and calculated the wing-loading of the Screech Owl and the Longeared Owl and found that in these two species the female does have greater wing-loading. In *Otus asio naevius* the male has 2.94 cm² of wing area per gram of body weight, compared with 1.87 for the female; in *Asio otus wilsonianus* the male has 5.13 cm² of wing area per gram of body weight to 4.22 for the female. This increased wing-loading and presumably decreased maneuverability of the female could conceivably be related to modified feeding behavior and, therefore, to differential niche utilization by the sexes.

RELATIONSHIP BETWEEN BODY SIZE AND DEGREE OF DIMORPHISM

The species comprising a genus tend to show increasing dimorphism with increasing size (fig. 1). The correlation coefficient (*r*) of the dimorphism index of the cube root of body weight and the mean cube root of body weight of the females for all the species considered in this report is 0.504 (*P* < 0.005).

When wing length is used as the standard, the same tendency occurs in *Strix, Otus,* and *Aegolius,* but not in *Asio* or *Glaucidium* (fig. 2). The correlation coefficient of the dimorphism index of wing length and mean wing length of females for all species considered in this report is 0.342 (*P* < 0.05).

TABLE 1.   Variation in wing length among certain forms of North American owls.

Species	Sex	x̄ mm	n	SE	V	Range
Tyto alba pratincola	M	311.7	38	1.51	2.99	287–329
	F	316.1	40	1.85	3.70	286–335
Otus asio naevius	M	162.7	53	0.52	2.32	150–171
	F	166.9	61	0.63	2.94	153–176
Otus asio inyoensis	M	163.5	10	1.06	2.04	158–167
	F	165.5	14	1.25	2.82	160–175
Otus asio cineraceus	M	155.7	16	1.38	3.55	145–166
	F	159.1	9	1.18	2.23	153–165
Otus asio suttoni	M	152.2	17	0.92	2.50	144–159
	F	157.6	11	1.27	2.67	150–167
Otus asio kennicottii	M	167.8	34	0.95	3.31	150–176
	F	175.3	19	0.92	2.29	166–183
Otus asio bendirei	M	159.8	64	0.55	2.76	147–170
	F	163.5	43	0.88	3.54	155–176
Otus asio quercinus	M	159.1	45	0.71	2.97	150–168
	F	164.9	32	0.91	3.13	153–174
Otus trichopsis aspersus	M	140.0	11	1.39	3.30	132–146
	F	140.7	4	1.93	2.74	135–143
Otus flammeolus	M	131.9	67	0.50	3.10	119–142
	F	130.4	17	0.65	2.07	124–134
Bubo virginianus wapacuthu	M	345.3	11	2.37	2.28	333–353
	F	361.2	8	2.27	1.78	353–372
Bubo virginianus virginianus	M	339.0	12	4.07	4.15	319–371
	F	362.3	15	2.80	2.99	343–382
Bubo virginianus occidentalis	M	348.1	27	1.77	2.64	331–372
	F	363.9	32	1.45	2.25	349–379
Bubo virginianus pacificus	M	332.5	47	1.30	2.68	316–362
	F	351.4	46	1.36	2.63	335–375
Bubo virginianus pallescens	M	337.2	28	2.08	3.26	318–363
	F	348.9	17	2.90	3.42	332–372
Nyctea scandiaca	M	393.6	22	1.48	1.76	383–408
	F	420.0	18	2.52	2.54	397–446
Surnia ulula caparoch	M	220.9	28	0.90	2.14	211–230
	F	226.0	23	0.97	2.06	216–235
Glaucidium gnoma grinnelli	M	90.3	41	0.30	2.12	86–95
	F	94.6	22	0.48	2.39	91–99
Glaucidium gnoma californicum	M	91.2	71	0.30	2.77	87–95
	F	94.9	34	0.44	2.68	89–100
Glaucidium brasilianum ridgwayi	M	93.5	11	0.79	2.81	90–99
	F	95.1	8	1.20	3.57	91–100
Micrathene whitneyi whitneyi	M	107.6	12	0.87	2.79	102–111
	F	110.2	12	0.57	1.78	107–113
Micrathene whitneyi sanfordi	M	103.6	23	0.57	2.65	100–109
	F	104.3	11	0.79	2.50	100–108
Speotyto cunicularia hypugaea	M	168.7	67	0.57	2.75	156–179
	F	165.8	36	0.78	2.83	158–174
Strix varia varia	M	311.5	6	2.95	2.32	302–322
	F	320.0	15	2.06	2.49	302–330
Strix occidentalis[a]	M	303.9	15	1.17	1.49	295–309
	F	310.7	25	1.03	1.65	295–317
Strix nebulosa nebulosa	M	404.4	7	6.51	4.26	387–429
	F	423.1	14	2.61	2.31	408–438
Asio otus wilsonianus	M	281.0	47	0.83	2.01	269–298
	F	283.5	36	1.24	2.63	268–293
Asio flammeus flammeus	M	295.7	34	1.42	2.80	279–307
	F	297.1	44	1.26	2.81	280–311
Aegolius funereus richardsoni	M	161.5	10	1.21	2.38	155–168
	F	174.4	5	2.48	3.18	165–179
Aegolius acadicus acadicus	M	132.2	37	0.63	2.90	125–141
	F	139.0	20	0.55	1.76	134–144

[a] The races caurina and occidentalis have been combined.

TABLE 2. Variation in body weight (grams) among certain forms of North American owls.

Species	Sex	$\bar{x}$	n	$\sqrt[3]{\bar{x}}$	SE[a]	V	Range
Tyto alba pratincola	M	442.2	16	7.597	0.106	5.60	299–580
	F	490.0	21	7.872	0.068	3.96	382–580
Otus asio naevius	M	159.6	38	5.401	0.059	6.76	99–229
	F	184.0	36	5.674	0.046	4.88	126–252
Otus asio mccallii	M	125.1	12	4.992	0.066	4.58	94–154
	F	131.2	10	5.076	0.054	3.35	115–162
Otus asio inyoensis	M	132.5	10	5.095	0.041	2.55	119–149
	F	154.6	12	5.364	0.040	2.58	135–173
Otus asio cineraceus	M	111.2	35	4.804	0.025	3.14	88–137
	F	122.7	18	4.961	0.050	4.24	92–160
Otus asio suttoni	M	107.6	27	4.752	0.028	3.10	87–129
	F	127.1	18	5.022	0.042	3.53	108–154
Otus asio kennicottii	M	152.5	14	5.338	0.044	3.08	130–178
	F	186.5	11	5.707	0.058	3.37	152–215
Otus asio bendirei	M	141.4	49	5.206	0.021	2.86	100–173
	F	157.3	23	5.380	0.067	6.01	100–223
Otus asio quercinus	M	134.3	26	5.114	0.037	3.68	108–170
	F	152.1	10	5.333	0.053	3.12	130–164
Otus trichopsis trichopsis	M	84.5	23	4.384	0.031	3.37	70–104
	F	92.2	8	4.510	0.073	4.58	79–121
Otus flammeolus	M	53.9	56	3.774	0.014	2.86	45–63
	F	57.2	9	3.852	0.024	1.87	51–63
Bubo virginianus wapacuthu	M	1238.6	10	10.733	0.085	2.50	1035–1389
	F	1556.0	12	11.571	0.132	3.96	1357–2000
Bubo virginianus virginianus	M	1317.8	22	10.941	0.108	4.63	985–1588
	F	1768.5	29	12.072	0.094	4.21	1417–2503
Bubo virginianus occidentalis	M	1154.3	18	10.467	0.118	4.80	865–1460
	F	1555.1	18	11.539	0.178	6.55	1112–2046
Bubo virginianus pacificus	M	991.7	26	9.949	0.096	4.92	680–1272
	F	1312.4	23	10.895	0.164	7.21	825–1668
Bubo virginianus pallescens	M	914.2	18	9.693	0.082	3.58	724–1257
	F	1142.2	12	10.418	0.182	6.06	801–1550
Nyctea scandiaca	M	1642.4	27	11.778	0.096	4.26	1320–2013
	F	1962.9	30	12.491	0.112	4.91	1550–2690
Surnia ulula caparoch	M	299.4	16	6.688	0.024	1.45	273–326
	F	345.0	14	7.010	0.045	2.39	306–392
Glaucidium gnoma californicum	M	61.9	42	3.953	0.018	2.96	54–74
	F	73.0	10	4.175	0.047	3.54	64–87
Glaucidium brasilianum ridgwayi	M	61.4	29	3.940	0.027	3.62	46–74
	F	75.1	16	4.211	0.046	4.36	62–95
Speotyto cunicularia hypugaea	M	158.6	31	5.399	0.050	5.20	120–228
	F	150.6	15	5.312	0.056	4.10	129–185
Strix varia varia	M	631.9	20	8.562	0.093	4.85	468–774
	F	800.9	24	9.258	0.107	5.67	610–1051
Strix occidentalis	M	582.2	10	8.341	0.093	3.53	518–694
	F	637.1	10	8.597	0.087	3.19	548–760
Strix nebulosa nebulosa	M	935.3	7	9.771	0.119	3.23	790–1030
	F	1297.5	6	10.900	0.125	2.81	1144–1454
Asio otus wilsonianus	M	245.3	38	6.247	0.046	4.54	178–314
	F	279.4	28	6.524	0.057	4.65	210–342
Asio flammeus flammeus	M	314.7	20	6.790	0.066	4.35	206–368
	F	378.0	27	7.218	0.058	4.18	284–475
Aegolius funereus richardsoni	M	101.6	5	4.657	0.101	4.86	85–119
	F	139.5	4	5.181	0.099	3.82	121–160
Aegolius acadicus acadicus	M	74.9	27	4.206	0.039	4.80	54–96
	F	90.8	18	4.480	0.061	5.75	65–124

[a] The statistics SE and V refer to the cube root of the mean body weight.

TABLE 3. Dimorphism indices[a] of wing length and of cube root of body weight in certain North American owls.

Species	D. I.$_{wing}$	D. I.$\sqrt[3]{wt.}$
Tyto alba pratincola	1.42	3.56
Otus asio naevius	2.54	4.94
Otus asio mccallii	—	1.68
Otus asio inyoensis	1.22	5.13
Otus asio cineraceus	2.13	3.22
Otus asio suttoni	3.52	5.53
Otus asio kennicottii	4.35	6.68
Otus asio bendirei	2.31	3.28
Otus asio quercinus	3.56	4.19
Otus trichopsis aspersus	0.53	—
Otus trichopsis trichopsis	—	2.84
Otus flammeolus	−1.10	2.06
Bubo virginianus wapacuthu	4.52	7.51
Bubo virginianus virginianus[b]	6.64	9.83
Bubo virginianus occidentalis	4.42	9.74
Bubo virginianus pacificus	5.53	9.07
Bubo virginianus pallescens	3.39	7.21
Nyctea scandiaca[c]	6.49	5.88
Surnia ulula caparoch	2.25	4.69
Glaucidium gnoma californicum	3.98	5.45
Glaucidium gnoma grinnelli	4.62	—
Glaucidium brasilianum ridgwayi	1.77	6.63
Micrathene whitneyi whitneyi	2.45	—
Micrathene whitneyi sanfordi	0.64	—
Speotyto cunicularia hypugaea	−1.71	−1.62
Strix varia varia	2.69	7.81
Strix occidentalis	2.23	3.02
Strix nebulosa nebulosa	4.51	10.92
Asio otus wilsonianus	0.87	4.33
Asio flammeus flammeus	0.48	6.11
Aegolius funereus richardsoni	7.68	10.64
Aegolius acadicus acadicus	5.04	6.31

[a] See text for method of calculation.

[b] McDowell (1940) measured and weighed 895 male and 772 female *Bubo v. virginianus*, all taken in Pennsylvania. The dimorphism index for wingspread was 6.38 and the dimorphism index for cube root of body weight was 9.10, both in close agreement with our sample.

[c] Meade (1948) provided average weights for 15 males (3 lb., 1 oz.) and eight females (3 lb., 11 oz.) of *Nyctea scandiaca*. From these averages we calculated the dimorphism index for cube root of body weight as 6.25, in good agreement with our index value of 5.88. His low weights for both sexes suggest that many of his birds were emaciated, which would be expected in view of the fact that they were part of a winter invasion into New York.
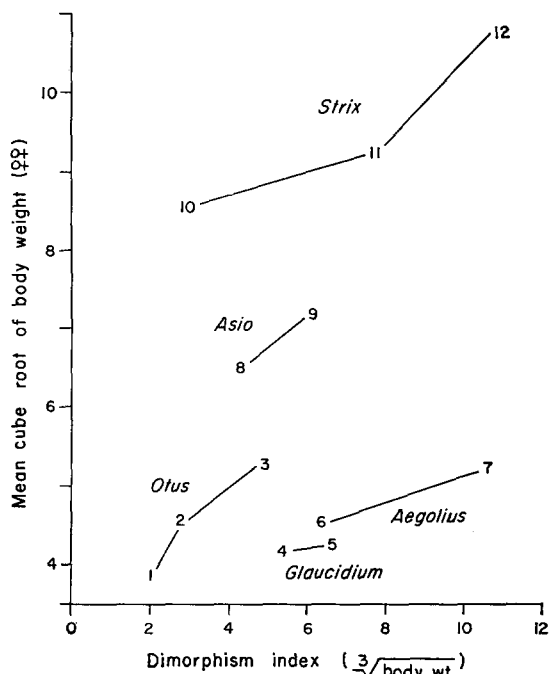

FIGURE 1. Interspecific and intergeneric comparisons of the relationship between degree of dimorphism in body weight and the mean cube roots of body weights of females of 12 forms of North American owls. For *Otus asio*, the mean cube roots of body weight for each sex, and the corresponding dimorphism indices, were calculated using all individuals of all races considered in this report. 1, *Otus flammeolus*; 2, *Otus t. trichopsis*; 3, *Otus asio*; 4, *Glaucidium gnoma californicum*; 5, *Glaucidium brasilianum*; 6, *Aegolius acadicus*; 7, *Aegolius funereus richardsoni*; 8, *Asio otus wilsonianus*; 9, *Asio flammeus*; 10, *Strix occidentalis*; 11, *Strix varia varia*; 12, *Strix nebulosa*.

The races within a species show a similar trend. With the exception of *Bubo virginianus wapacuthu*, dimorphism of the races of the Great Horned Owl increases directly with body weight (fig. 3); there is no apparent relationship between dimorphism and mean wing length among these races. We do not trust the dimorphism index values for *wapacuthu* because our original data include measurements of several smaller birds which are labelled as females but are possibly males. If these individuals were not included, the mean body weight of females would be higher and the dimorphism index value would consequently be greater, bringing this form more in line with the trends seen in other subspecies of the Great Horned Owl. Also, the sample size of *wapacuthu* is not large, so that the misleading

influence of a few incorrectly sexed individuals would be great.

The same trend of increasing dimorphism with increasing body size is seen in lesser degree in the Screech Owl (fig. 4), although *Otus asio suttoni* seems a bit deviant.

This increased dimorphism in the larger species contradicts "Rensch's Rule," which holds that among the birds of prey, the largest degree of dimorphism is found among the smallest species and the smallest degree of dimorphism is found among the largest species (Rensch 1950, 1960). Storer's (1966) work on the North American accipiters indicates that this rule is applicable to that particular group of hawks since the smallest accipiter, the Sharp-shinned Hawk (*Accipiter striatus*), has the greatest degree of dimorphism and the largest accipiter, the Goshawk (*A. gentilis*), has the smallest degree of dimorphism, while the dimorphism index of the intermediate-sized Cooper's Hawk (*A. cooperi*) is between those of the other species. However, according to
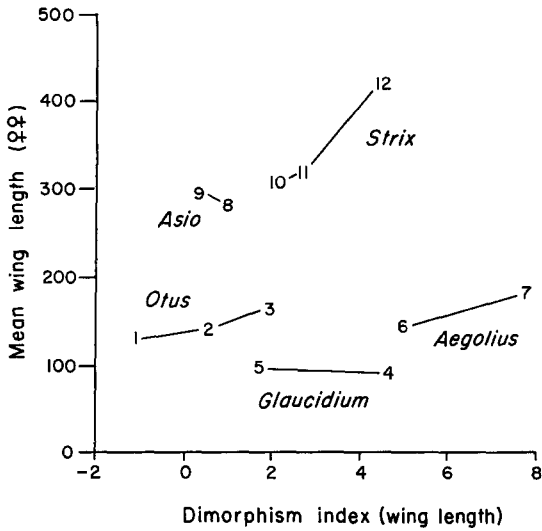
FIGURE 2. Interspecific and intergeneric comparisons of the relationship between degree of dimorphism in wing length and mean wing lengths of females of 12 forms of North American owls. For *Otus asio* the mean wing lengths for each sex, and the corresponding dimorphism indices, were calculated using all individuals of all races considered in this paper. 1, *Otus flammeolus*; 2, *Otus trichopsis aspersus*; 3, *Otus asio*; 4, *Glaucidium gnoma grinnelli*; 5, *Glaucidium brasilianum ridgwayi*; 6, *Aegolius acadicus*; 7, *Aegolius funereus richardsoni*; 8, *Asio otus wilsonianus*; 9, *Asio f. flammeus*; 10, *Strix occidentalis*; 11, *Strix varia varia*; 12, *Strix n. nebulosa*.
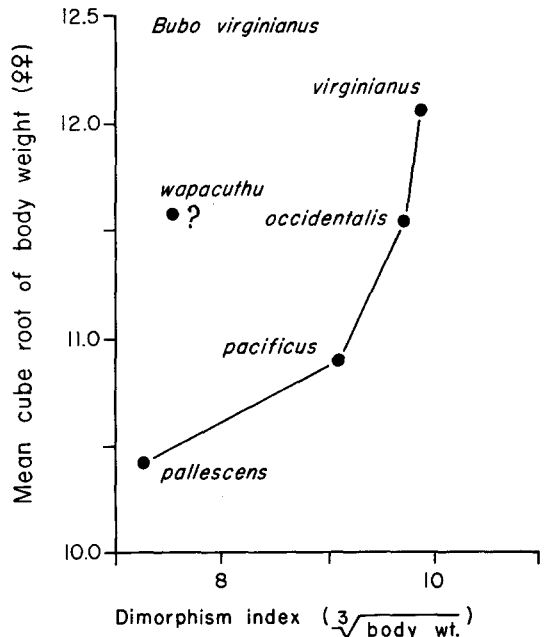

FIGURE 3. Relationship between degree of dimorphism and mean body size of females among five subspecies of *Bubo virginianus*. See text for comments on *B. v. wapacuthu*.

Selander (1966), all other North American Falconiformes, including *Falco* and *Buteo*, do not appear to fit this "rule." From the present study we find also that the owls do not support Rensch's claim; instead, the smallest owls are for the most part insectivorous and show the least degree of dimorphism while the larger, vertebrate-eating species are highly dimorphic. There are so many exceptions that the "rule" appears to have little general applicability among either the Strigiformes or the Falconiformes.

FOOD HABITS

In the following accounts we summarize the findings of published studies of food habits of the owls considered in this paper. Not all references found are cited, but those mentioned will provide the reader with an entree into other pertinent literature. We attempt to provide enough documentation for the various forms to permit generalizations on diets and to enable the grouping of species of broadly similar food habits into categories for subsequent analysis. In view of the nature of the basic data at hand, more detailed treatment would be both improper and unnecessary for our purposes because of the confounding influence on the interpretation of diets of (1) seasonal variation, (2) geographic variation, and (3) small sample size. Indeed, for several subspecies of some forms, and for certain species, we could find in the literature little or no information on food habits. Furthermore, reports on food habits of owls are rou-

tinely the results of pellet analysis and are not separable by sex. Even when the examination of stomach contents formed the basis of the report, authors often unfortunately combine the sexes in the presentation of data for a given species.

Barn Owl. *Tyto alba pratincola.* This species primarily takes small mammals (voles, mice, wood rats, cotton rats, shrews, rabbits, gophers) with occasional birds (rails, doves, passerines). Amphibians, reptiles, and insects are eaten rarely. See Wilson (1938), Cowan (1942), Selleck and Glading (1943), Hawbecker (1945), Fitch (1947), Kirkpatrick and Conaway (1947), Pearson and Pearson (1947), Boyd and Shriner (1954), and Parmalee (1954).
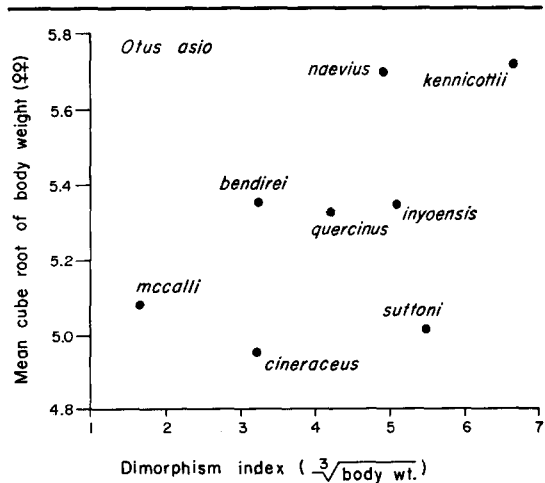

FIGURE 4. Relationship between degree of dimorphism and mean body size of females among eight subspecies of *Otus asio*.

TABLE 4. Stomach contents[a] of the Screech Owl.

	O. a. bendirei and O. a. quercinus combined		O. a. cineraceus	
	22♂♂	11♀♀	22♂♂	8♀♀
Scorpions	1	–	3	–
Spiders	2	–	2	–
Centipedes	2	–	3	2
Insects				
unidentified	3	3	6	1
Orthoptera				
Cockroaches	–	–	1	1
Mantids	–	–	–	1
Walkingsticks	–	–	3	1
Grasshoppers, crickets	10	7	11	6
Coleoptera	2	–	1	–
Lepidoptera				
Moths	1	–	2	1
larvae	5	–	1	–
Reptiles	–	–	1	1
Birds	1	1	1	–
Mammals	1	1	1	1

[a] Total occurrence of the categories of prey in the sample is listed. For example, grasshoppers and/or crickets occurred in 11 of the 22 stomachs (= 50%) of male O. a. cineraceus. The number of items of a category found in a single stomach is not indicated.

Screech Owl. *Otus asio.* This species feeds upon insects (grasshoppers, crickets, beetles, moths, caterpillars) plus other arthropods (scorpions, spiders, centipedes, crayfish) and vertebrates (fishes, amphibians, reptiles, birds, mammals). It is difficult to characterize the food habits of the species as a whole because certain subspecies (*cineraceus, quercinus*) feed almost entirely upon arthropods while more northern forms (*naevius, macfarlanei, kennicottii*) frequently take vertebrates, especially during the winter. At that season vertebrates may form the bulk of the diet, at least for certain individuals of *naevius*. *O. a. asio*: see Stewart 1969. *O. a. cineraceus*: Campbell 1934; Bent 1938; Marshall 1957; table 4. *O. a. bendirei*: Bent 1938; table 4. *O. a. quercinus*: table 4. *O. a. naevius*: Allen 1924; Cahn and Kemp 1930; Errington 1932; Wilson 1938; James and Martin 1950; Craighead and Craighead 1956; Stewart 1969. For *O. a. macfarlanei*, specimen tags possessed the following information on stomach contents: for one male, "insects;" for five females, crayfish, fish ("bullhead?"), amphibians (*Ascaphus truei* and "salamander"), and "mouse." For *O. a. kennicottii*, specimen tags of five males had the following: "insects" for two stomachs; "salamander;" and "Coleoptera and squirrel? hair," two stomachs. For the latter subspecies, see also Bent (1938).

Whiskered Owl. *Otus trichopsis aspersus.* This species takes primarily insects (caterpillars, beetles, moths, crickets, grasshoppers) and other arthropods (scorpions, centipedes). See Jacot (1931), Campbell (1934), van Rossem (1936), and Marshall (1957). According to Jacot (1931:8) caterpillars and black crickets are staples in the year-around diet, and more centipedes are taken during the winter than at other seasons. Marshall (1957:76) found a mouse in a winter specimen.

Flammulated Owl. *Otus flammeolus.* This species feeds entirely upon insects (beetles, moths, caterpillars, crickets) and other arthropods (scorpions, spiders,

centipedes). See Jacot (1931), van Rossem (1936), Marshall (1939, 1957), and Johnson and Russell (1962).

Great Horned Owl. *Bubo virginianus.* All subspecies of this species feed predominately upon mammals (*Neotoma, Sylvilagus, Dipodomys, Thomomys, Peromyscus, Citellus, Microtus, Reithrodontomys, Rattus*), upon several species of birds (pheasants, quail, woodpeckers, passerines), and upon occasional amphibians (*Scaphiopus*) and reptiles (*Pituophis, Coluber,* lizards). Jerusalem crickets, beetles, and scorpions are also eaten. *B. v. pallescens*: see Bailey 1928. *B. v. pacificus*: Fitch 1947; Dixon and Summer 1953; Cunningham 1960. *B. v. occidentalis*: Bond 1940. *B. v. virginianus*: Errington 1932; McDowell 1940; Kirkpatrick and Conaway 1947; Orians and Kuhlman 1956.

Snowy Owl. *Nyctea scandiaca.* This species feeds primarily upon lemmings on the breeding grounds. Other mammals (voles, rats) and a variety of birds (longspurs, ducks, ptarmigan) have also been reported in the diet. See Murie (1929), Gross (1944), Pitelka et al. (1955), Sutton and Parmalee (1956), and Watson (1957).

Hawk-Owl. *Surnia ulula caparoch.* This species feeds primarily upon mammals (mice, lemmings, shrews), but takes occasional birds (ptarmigan) in the winter and insects during the summer (Fisher 1893; Bent 1938; Mendall 1944). We examined 16 specimens with information on stomach contents. Nine males contained mice (*Peromyscus, Microtus, Mus*), and seven females contained mice (*Peromyscus, Microtus*) and other mammals ("chipmunk," "shrew"). One female was "chasing a rabbit" at the time of collection, which suggests that the larger females of this medium-sized owl may prey upon fairly large mammals.

Pygmy Owl. *Glaucidium gnoma.* The races *G. g. californicum, G. g. grinnelli,* and *G. g. swarthi* take small mammals, small birds, lizards, and insects. Table 5 provides information on the contents of 70 stomachs of this species, separated by sex. Also, see Bent (1938) and Brock (1958).

Ferruginous Owl. *Glaucidium brasilianum.* Except for the fanciful accounts in Bent (1938:436–437), we were unable to find information on the food habits of this species. Two males of *G. b. cactorum* examined had the notations "insects" and "Sceloporus" on their specimen tags.

Elf Owl. *Micrathene whitneyi whitneyi.* This species feeds principally upon insects (beetles, grasshoppers, moths, crickets) and other arthropods (scorpions). See Fisher (1893), Campbell (1934), Bent (1938), Marshall (1957), and, especially, Ligon (1968), who discusses seasonal changes in insect prey and provides detailed lists of food items. Ligon also reports the rare occurrence of vertebrate prey items in the diet of the Elf Owl, a lizard (*Sceloporus jarrovi*) and a snake (*Leptotyphlops dulcis*).

Burrowing Owl. *Speotyto cunicularia hypugaea.* This species takes insects (especially Coleoptera and Orthoptera), scorpions, lizards, a few small mammals (*Microtus, Mus, Peromyscus, Reithrodontomys*) and occasional birds. See Fisher (1893), Errington and Bennett (1935), Scott (1940), Bond (1942), Longhurst (1942), Glover (1953), and Hennings (unpub. MS).

Barred Owl. *Strix varia varia.* This species feeds mainly upon mammals (mice, squirrels, hares, shrews), with smaller numbers of fish, amphibians, reptiles, and birds. Insects are eaten only rarely. See Cahn and Kemp (1930), Errington (1932), Errington and

TABLE 5.   Occurrence of prey in stomach contents of the Pygmy Owl.[a]

	Males (n = 41)			Females (n = 29)		
	No.	%	Specific prey[b]	No.	%	Specific prey[b]
Insects	11	27	Jerusalem crickets,	11	38	Jerusalem cricket, black
Apr.–Aug.[c]	4	19.5	cicadas, grasshoppers,	1	33.3	crickets, grasshoppers
Nov.–Mar.[d]	2	20.0	beetles	2	11.1	
Reptiles	6	15	*Sceloporus*, "small	1	3.4	*Sceloporus*
Apr.–Aug.	5	23.7	alligator lizard"	–	–	
Nov.–Mar.	–	–				
Birds	14	34	house wren, winter wren,	6	21	redpoll, "pine finch"
Apr.–Aug.	9	42.8	"kinglet," "chickadee,"	–	–	
Nov.–Mar.	3	30.0	"sparrow," junco	3	16.6	
Mammals	15	37	*Microtus*, "shrew"	15	52	*Microtus*, *Arvicola*,
Apr.–Aug.	5	23.7		1	33.3	*Mus*, "shrew"
Nov.–Mar.	5	50.0		10	55.5	

[a] Combined data: 44 *Glaucidium gnoma californicum* from British Columbia, Oregon, Idaho, California, Arizona, and Coahuila; 17 *G. g. grinnelli* from British Columbia and California; and 9 *G. g. swarthi* from Vancouver Island, British Columbia.
[b] Notations of stomach contents on specimen tags are often very general (e.g., "hair," "birds," "insects"); only those fairly specific prey items recorded are listed here.
[c] For this period 21 males and 3 females are available.
[d] For this period 10 males and 18 females are available.

McDonald (1937), Wilson (1938), Mendall (1944), Taylor (1944), and Rusling (1951).

Spotted Owl. *Strix occidentalis.* This species takes mammals (flying squirrels, deer mice, wood rats, bats, shrews, moles), birds (small owls, passerines), amphibians, and insects (crickets, roaches, beetles). See Marshall (1942, 1957), Johnson and Russell (1962), and Smith (1963). Two additional unreported stomachs of female *S. o. lucida* contained insects.

Great Gray Owl. *Strix nebulosa nebulosa.* This species feeds upon mammals (mice, rats, shrews, moles, gophers) plus occasional small birds (Fisher 1893; Bent 1938; Tryon 1943; Godfrey 1967). We examined seven specimens for which food data were recorded; three males had eaten field mice or voles and four females had eaten mice, one a shrew, and one a rabbit. Blair (1962) provides food data for *S. n. lapponica* in Norway, which seems to have a diet generally similar to that of the North American form.

Long-eared Owl. *Asio otus wilsonianus.* The Long-eared Owl feeds primarily upon small mammals (particularly *Microtus*), plus many species of other mice, shrews, rats, and gophers. Birds are taken uncommonly; amphibians and reptiles rarely (Warthin and Van Tyne 1922; Cahn and Kemp 1930; Errington 1932; Spiker 1933; Kirkpatrick and Conaway 1947; Randle and Austing 1952; Johnson 1954; Armstrong 1958; Graber 1962).

Short-eared Owl. *Asio flammeus flammeus.* This owl feeds chiefly upon small mammals (primarily *Microtus, Lemmus, Peromyscus, Mus, Rattus, Reithrodontomys*) plus occasional birds and few insects (Errington 1932, 1937; Hendrickson and Swan 1938; Pitelka et al. 1955; Johnston 1956; Kirkpatrick and Conaway 1957; Stegeman 1957; Fisler 1960; Graber 1962; Short and Drew 1962; Munyer 1966).

Boreal Owl. *Aegolius funereus richardsoni.* This species primarily takes mammals (mice, shrews), fewer birds, and, uncommonly (?), insects. We have

data from specimen tags as follows: three males, *Blarina*, mouse, and White-winged Crossbill; one female, House Sparrow. See Fisher (1893), Preble (1908), Wolfe (1923), and Bent (1938). Uttendörfer (1952) provides food data for *A. f. tengmalmi* which indicate that this form has the same general diet as mentioned above for the North American subspecies.

Saw-whet Owl. *Aegolius acadicus.* This owl takes small mammals (*Microtus, Peromyscus, Mus, Blarina, Synaptomys*), plus occasional birds (Errington 1932; Santee and Granfield 1939; Mendall 1944; Rusling 1951; Randle and Austing 1952; Graber 1962).

SEXUAL DIFFERENCES IN FOOD HABITS OF THE PYGMY OWL

For the Pygmy Owl we have data on the stomach contents of 70 individuals separated by sex (table 5). In addition to the main analysis where all months are combined, we have subdivided the data into "summer" (April through August) and "winter" (November through March) periods. This breakdown reveals certain seasonal differences in the diets and, in addition, permits us to examine food data for that time of year (winter) when the males are definitely not feeding the females in the nest. In the analysis of the combined data, 35 of 41 (85.3 per cent) stomachs of males and 22 of 29 (75.9 per cent) stomachs of females contained vertebrates. Approximately one-third of the stomachs of each sex contained insects. Thus, in the broadest sense, the sexes seem to take essentially the same
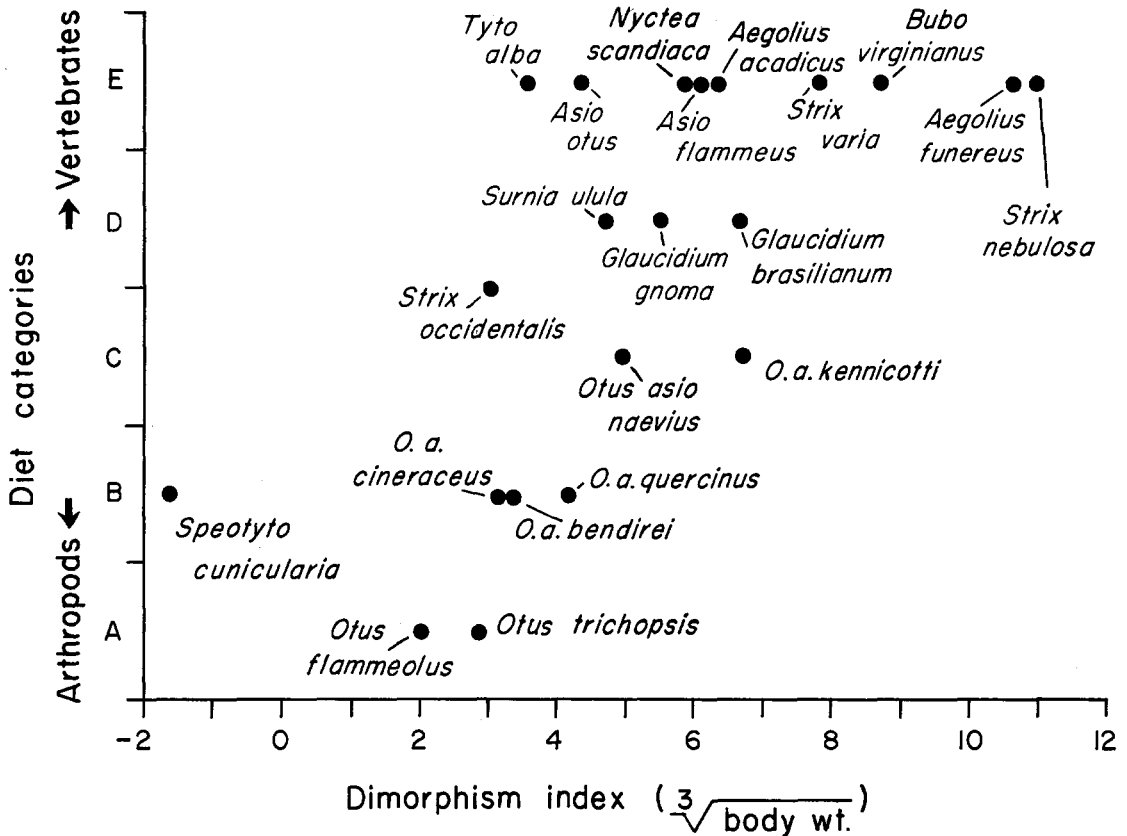
FIGURE 5. The relationship between general food habits and dimorphism in 17 species of North American owls. Diet categories are as follows: A, feeds exclusively on arthropods; B, primarily arthropods, few vertebrates; C, arthropods and vertebrates in equal numbers; D, primarily vertebrates, few arthropods; E, exclusively vertebrates. The dimorphism index value for *Bubo virginianus* is the average of the values for all of the races as given in table 4.

kinds of food. Reptiles are taken in the spring and summer, when they are available; the small number of females analyzed for the summer period precludes the assumption that males take more reptiles than females. Very small samples suggest that females seem to take more insects than do males. Females feed more on mammals (52 vs. 37 per cent) and less on birds (21 vs. 34 per cent) than do the males, on an annual basis. These differences are highly significant; using the data for males as the basis for the theoretical frequencies, $x^2 = 11.05$ (1 df; $P < 0.01$). Again, for these categories of prey, the summer period is difficult to analyze because of the scarcity of stomachs of females in the samples.

It is conceivable that the increased wing-loading of the female has deprived her of the maneuverability necessary to catch small agile birds efficiently. The female Pygmy Owl may, on the average, take as prey larger and more sluggish birds, in contrast to the male, but our present limited data do not verify such a supposition. Furthermore, the increased body weight of the female may have produced more

effective striking power, enabling her more successfully to subdue mammals, but at the same time reduced her capacity for the speed and agility necessary for an aerial chase. Only field observations of the hunting habits of each sex will determine if this is true. On the basis of the present information sexual differences in food habits in the Pygmy Owl seem very likely. Only the three stomachs of summer females may be included improperly in the analysis, for it is during this period that the male may capture prey and feed it to the female at the nest.

DISCUSSION AND CONCLUSIONS

The two aspects of size dimorphism, namely, degree and direction, have not always been distinguished clearly in discussions of the evolution of sexual differences in size. In our view the existence of a difference in size between the sexes is clearly an adaptation to more efficient utilization of environmental resources, which has resulted from both intersexual and interspecific competition. The important factor which selection has favored in response to

competition is a size difference; which sex is larger or smaller is irrelevant in this context. However, the direction of the dimorphism in nearly all hawks and owls, with the female being the larger sex, is not explicable on the general grounds of competition, and as has been proposed by authors previously, it may relate instead to either or to both the nature of the pair bond or to an adaptive dominance relationship.

RELATIONSHIP BETWEEN FOOD HABITS
AND DEGREE OF SIZE DIMORPHISM

Data plotted in figure 5 indicate that the degree of dimorphism in body weight tends to be greatest among species taking a large percentage of vertebrates and smallest in species concentrating upon arthropods. Species which take both arthropods and vertebrates have intermediate dimorphism indices. Variation in diets and dimorphism of several subspecies of the Screech Owl also follows the same trend. *Otus asio naevius* and *Otus asio kennicottii*, races which commonly take numbers of vertebrates, are more dimorphic than the highly insectivorous *Otus asio cineraceus* and *Otus asio bendirei*. However, *Otus asio quercinus*, also an insectivorous subspecies, has a dimorphism index value between that of *bendirei* and *naevius*. The correlations are not perfect, but a general trend is obvious. Species which seem to deviate from the trend more than would be expected on the basis of their diets are *Tyto alba pratincola* and *Asio otus wilsonianus*. As has been stressed by Selander (1966: 132–141), there are several ways by which intersexual competition can be avoided or reduced between mates on a territory. One way is through dimorphism which permits differential niche exploitation. Perhaps *Tyto alba* and *Asio otus* forage partially in microgeographic allopatry or utilize some other means in addition to moderate dimorphism to reduce competition (also, see beyond). Before we attempt to explain the unexpected degrees of dimorphism found in vertebrate eaters such as these, it would be well to have further data on the nature of their food exploitation patterns on an intersexual basis.

Because the small species tend to feed primarily on arthropods and the large species tend to feed on vertebrates, the degree of dimorphism is correlated somewhat with food habits as well as with body size. Smaller owls are often less dimorphic than larger owls. However, it is of interest that three small species which take a large percentage of vertebrates, the Pygmy Owl, the Saw-whet Owl, and the Boreal Owl, all have relatively large dimorphism indices (fig. 5). This may suggest that the evolution of sexual dimorphism in size is more closely related to food habits than to size per se.

Frochot (1967), who has analyzed sexual differences in size in a variety of European hawks and owls on the basis of body weight, presents data for the European forms of four species covered in this paper. Among species of a group with sexes moderately different in size (15–25 per cent), he lists *Asio otus otus* and *Aegolius funereus tengmalmi*. In a category composed of species with a very small or no difference (less than 15 per cent) between the sexes, he places *Asio flammeus* and *Tyto alba*. It is surprising that he found so little dimorphism in *Asio flammeus* and *Aegolius funereus*, species which we found to be moderately and strongly dimorphic, respectively. Because he provides no actual data or statistics on size for the various forms treated, it is difficult to interpret the significance of his findings.

Frochot also attempts correlations of degree of dimorphism with diet and states (translation): "the difference [between the sexes] is very strong in the predators of birds or of birds and mammals which are eclectic [= take diverse prey], moderate among the rodent-eaters capable of eclecticism (in winter, for example), weak or absent among the strict specialists of rodents, fish, reptiles, and insects. The most important differences are found when the species depend on a range of much larger prey, especially if one considers the dimensions of the prey. On the other hand, the size of the predator is not important. . . ." Concerning species of direct interest to us, Frochot (1967: 51) writes (translation): "The taxonomic relationship does not matter either: The Long-eared Owl, regularly eclectic in winter (usually taking birds of diverse sizes) shows a notable variation between weights of males and females, while the Short-eared Owl, closely related but the most monophagous of nocturnals, has sexes of strictly equal weight." Finally, Frochot writes (translation): "One can compare all the species and conclude: —That a species which eats prey of the same size or very small prey has sexes of the same size . . . [and] . . . That a species which eats prey of diverse sizes shows a maximal size difference between the two sexes." Thus Frochot brings consideration both of breadth of diet and of size of prey items into his explanation of sexual dimorphism of hawks and owls in Europe.

Perhaps our unexpectedly low dimorphism index values for the Barn Owl, Long-eared Owl, Short-eared Owl, and Snowy Owl (fig. 5) can be accounted for by Frochot's explanation; they are species which may stress prey of fairly uniform size, although exceptions to this generalization are common for all four forms.

In discussing dimorphism in bill size, Selander (1966) and Selander and Johnston (1967) note that small degrees of sexual dimorphism occur in omnivorous species of birds which exploit food supplies of sufficient abundance to permit extensive sexual overlap in utilization. Marked sexual divergence in bill size, with an accompanying sexual difference in niche utilization functioning to alleviate intersexual competition for food, is characteristic of food specialists. Schoener (1965) has called attention to a similar relationship between food abundance and degree of interspecific difference in bill size among sympatric species of congeneric birds.

If we may extrapolate this explanation of variation in bill dimorphism to that of variation in degree of dimorphism in body size—a reasonable extrapolation because as Schoener (1965:189) notes, "For many birds of prey body size is probably a better indicator of the size of food preferred than bill size"—we find a parallel relationship between food size and amount of sexual difference in size in the owls. The insectivorous owls are less dimorphic than are the species which feed upon vertebrates. Therefore, the owls seem to support the relationship described by Schoener (1965) and by Selander (1966) for other birds. However, the correlation of reduced dimorphism with what is termed an "abundant" food source implies that there is more food biomass on the territory than is required for existence. It occurs to us that the real relevance of the term "abundant" may not be in its implication of an *excess of available food biomass*, but rather in its use in describing the *number of food pieces* that are present. We propose that the lack or reduction of dimorphism in insectivorous owls is related to the fact that they feed on a food source which consists of items of relatively small size which exist as numerous fragments in the environment. If the food resource exploited by a species exists in the form of relatively small items, we hypothesize that the increased time necessary for the removal of these items by any one individual reduces competition between individuals because, at least while these items are numerous, the predators will be pursuing and removing separate items. This hypothesis stresses the temporal aspects of exploitation and does not suggest that there is more food than needed on the territory. Conversely, if the food resource consists of items relatively large in size, the food can be removed more rapidly because it exists in the environment as fewer items, and thus competition for these items would occur more rapidly in a given period of time.

Consider a segment of a territory of a mated pair of Screech Owls with a food resource that consists of one 20-g mouse opposed to a resource that consists of 20 g of insects existing as many individuals. Capture of the single mouse by one owl would quickly eliminate the food supply, but where the same weight of prey is available in numerous pieces and with each owl foraging independently, the two owls can co-exist for a much longer period, at least until the insects become scarce. There would be no adaptive value of size dimorphism in such a system.

Suggested topics for future study. Many questions relating to degree and direction of dimorphism among owls remain to be answered. Obviously we lack properly refined basic data on sexual differences in food habits and on body size (body weight) for many of the forms considered. Of great interest would be information on the size relationship and food habits of known mated pairs. These data could throw light on the problem of differential prey removal by the sexes from a single area as well as clarify what sizes of mates are able to form proper pair bonds. Additionally, the prey of individual owls of various sizes, regardless of sex, needs close examination in order to answer the question of whether owls of the same species and general size feed on the same prey under conditions which are otherwise equal. Such information might also reveal possible behavioral constraints in food preference, as well as indicate the physical capacity for the exploitation of certain size-weight ranges of food by individual predators. Since Elf Owls are known to capture insects with their feet, subtle differences between the sexes in tarsal length and/or foot mass should be studied, even in insectivorous forms. The intersexual food habits and foraging behavior of the insectivorous Flammulated Owl also need further close examination because in this species the female is larger in over-all body size and the male has slightly longer wings; the female may concentrate on ground-dwelling insects while the more agile (?) male may stress aerial captures.

THE FEMALE DOMINANCE HYPOTHESIS

Our data neither support nor refute the hypothesis of female dominance as a protection against cannibalism by the male. The literature occasionally reports cannibalism in owls, but the accounts usually fail to give age or sex data on the individuals involved. It is noteworthy that the species in which cannibalism is most commonly reported, the Burrowing Owl (Bent 1938; Robinson 1954; Hennings, unpubl. MS), is a species in which the male is the larger sex, an exceptional situation among the owls studied. Although this species is primarily insectivorous, it will on occasion take a fair number of rodents; thus we can assume that the male has some inclination to prey upon vertebrates. It has been reported that the male gathers essentially all of the food for the young in this species, but that he transfers the prey items to the female who then takes the food into the burrow to the young (Hennings, unpubl. MS). If we assume that the male's parental instincts are weaker than those of the female, it is conceivable that this behavior has been evolved in order to keep the larger, perhaps dangerous male away from the young. In totally insectivorous species the male probably would have no inclination to feed upon vertebrates, so would not consider the young a possible food; hence the male could be equal to or larger in size than the female without representing a threat to the young. At any rate the absence of reversed sexual dimorphism and the tendency toward vertebrate feeding renders the Burrowing Owl a suitable species to study in order to test the female dominance hypothesis.

SUMMARY

This paper presents the results of an analysis of sexual dimorphism in size in 32 forms of North American owls. Like diurnal birds of prey, owls usually show reversed size dimorphism, with the females being as much as 28 per cent larger than the males in body weight. Several species which are moderately dimorphic in weight are monomorphic in wing length, although these two indices of size difference are usually positively correlated. The Burrowing Owl is exceptional in that the males are both slightly longer winged and heavier than the females; in all other forms examined dimorphism in body weight is reversed. In the Flammulated Owl the males have slightly longer wings but are somewhat lighter than the females.

Within a genus the smaller species are less dimorphic in body weight than are the larger species. When wing length is used as the standard, smaller species within Strix, Otus, and Aegolius are less dimorphic than are their larger congeners. However, species within Asio and Glaucidium do not show this relationship. Based on body weight, subspecies of Bubo virginianus and of Otus asio show a similar trend of increasing dimorphism with increasing size. Therefore, "Rensch's Rule" is not supported by comparisons made at either intraspecific or intrageneric levels.

General food habits for all species are summarized from the literature and from data on stomach contents from specimen labels. Because almost all data on food of owls reported in the literature are not separated by sex, it is usually impossible to determine from this information whether the sexes of dimorphic species are taking different sizes or different types of prey items. For the Pygmy Owl we offer preliminary information on diets which suggests that males feed more on birds and less on mammals than do the females. Differential feeding behavior between the sexes probably occurs in other sexually dimorphic owls as well, although the relevant supporting data are not yet available.

Species of owls which feed predominately on vertebrates show the greatest degree of dimorphism; owls concentrating on arthropods either show low degrees of dimorphism or are essentially monomorphic. Species which feed on both arthropods and vertebrates have intermediate dimorphism indices. The same correlation of dimorphism and diet applies to several subspecies of the Screech Owl. These findings support the theory that sexual dimorphism in size is related to differential niche utilization.

We explain reduced dimorphism in insectivorous owls by postulating that they are subjected to lowered competition because they are adapted to feed upon a narrow size range of small prey items; great sexual divergence in body size would not be selected for under these circumstances. The owls that feed chiefly on vertebrates have a much broader total range of prey sizes but fewer total prey individuals available to them; divergence in body size in response to more intense intersexual competition would be of adaptive value under these conditions, with each sex emphasizing a certain size range or type of prey.

DEDICATION

This paper is respectfully dedicated to the memory of Professor Alden H. Miller, teacher, friend, and authority on New World owls.

ACKNOWLEDGMENTS

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