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THE EVOLUTION OF REVERSED SEXUAL DIMORPHISM IN OWLS: AN EMPIRICAL ANALYSIS OF POSSIBLE SELECTIVE FACTORS

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ABSTRACT.—No less than 20 hypotheses have been proposed to explain reversed sexual dimorphism (RSD) in raptorial birds. I have generated a prediction from each of these hypotheses and tested the prediction using the available information and nonparametric statistics. RSD correlates significantly only with female dominance in intraspecies interactions and with prey type. Unfortunately, the data on dominance interactions are limited, but the best working hypothesis appears to be that RSD has evolved primarily as a result of epigamic selection, with female dominance facilitating pair formation and maintenance. Prey specialization appears merely to influence the degree of, and does not cause, RSD. Most species of owls are specialists on either invertebrates or small mammals. Specialists on invertebrates show little RSD and specialists on small mammals show moderate to high RSD. *Received 22 Feb. 1985, accepted 31 Jan. 1986.*

Much has been published on reversed sexual dimorphism (RSD) in Falconiformes in the past two decades (e.g., Newton 1979, Andersson and Norberg 1981, Cade 1982, Mueller and Meyer 1985). In contrast, only two major works have dealt with RSD in Strigiformes: the pioneering work of Earhart and Johnson (1970) and the monograph of Snyder and Wiley (1976), which concentrated on Falconiformes and gave owls only perfunctory treatment. Both of these studies deal mainly with the correlation between RSD and prey type. It appears timely to reexamine the possible adaptive functions of RSD in owls with new data and in the light of recent analyses of Falconiformes. The primary premise in my analysis is that if a given trait was important in the evolution of RSD it should be exhibited to a greater degree in highly dimorphic species than in less dimorphic ones. My approach is empirical, using the most rigorous statistical test permitted by the data available.

No fewer than 20 hypotheses have been proposed to explain RSD in raptorial birds. Most of the recent attempts to explain RSD in raptors have involved combining several of the many hypotheses. Each hypothesis, however, must be tested separately and I thus provide a list, along with predictions formulated from each hypothesis. All but one of these hypotheses can be grouped into three categories: (1) ecological hypotheses, (2) sex-role differentiation hypotheses, and (3) behavioral hypotheses.

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ECOLOGICAL HYPOTHESES

There are several of these, but all share the premise that RSD has evolved to permit the sexes to capture different sizes of prey, thus reducing competition between the sexes and allowing a pair to exploit a wider range of sizes of prey (Brüll 1937, Hagen 1942, Storer 1966, Reynolds 1972, Snyder and Wiley 1976, Newton 1979, Andersson and Norberg 1981). A prerequisite (but not proof) for these hypotheses is that the sexes take different sizes of prey. Selander (1972) has stated: "Only when trophic structures alone are modified can we conclude that the dimorphism results primarily or wholly from selection for differential niche utilization." This can be tested by comparing RSD in trophic structures with RSD in body size and nontrophic structures.

SEX-ROLE DIFFERENTIATION HYPOTHESES

The difference in size permits the sexes to perform better various activities associated with reproduction than if the sexes were monomorphic and shared breeding duties equally.

Egg size.—Large females can lay larger eggs than smaller individuals (Reynolds 1972, Selander 1972, Schantz and Nilsson 1981, Cade 1982). This leads to the prediction that species with high RSD should lay relatively large eggs.

Follicle protection.—Large females provide a better cushion for developing eggs than smaller ones (Walter 1979). A relationship between RSD and egg size or clutch size might be considered as evidence for this hypothesis.

Breeding increment in weight.—Females of many species increase in weight prior to egg laying. Wheeler and Greenwood (1983) have suggested that large females are better able to carry this increment and continue to hunt elusive prey. I will test this hypothesis using their method: a linear regression of female weight plus egg weight on dimorphism in wing length in those species with similar predatory habits.

Incubation.—Large females incubate more efficiently than smaller individuals (Snyder and Wiley 1976, Cade 1982). Females should perform a greater share of incubation in species showing high RSD than in those that are less dimorphic.

Nest protection.—Large females are more effective in deterring predators than smaller individuals (Storer 1966, Reynolds 1972, Snyder and Wiley 1976, Andersson and Norberg 1981, Cade 1982). Females of highly dimorphic species should perform a greater proportion of nest defense than those of less dimorphic species.

Territorial defense.—Small, agile males are better in the aerial defense of territory against conspecifics than larger, less agile individuals (Schmidt-

Bey 1913, Nelson 1977, Widen 1984). As it is unlikely that more than a few species of owls engage in aerial defense of territory (Amadon 1959), this hypothesis appears to be invalid for owls (Widen 1984).

Feeding efficiency.—Large females are more efficient at dismembering prey and feeding bits to small young (Andersson and Norberg 1981). Females in species with high RSD should perform a higher proportion of direct feeding of young than those in species with low RSD.

Foraging interference.—It is more efficient for only one member of the pair to hunt alert and agile prey than to have two birds moving about alerting prey and thus interfering with each other (Andersson and Norberg 1981). This hypothesis leads to the prediction that the male, who is the primary provisioner, should do proportionally more of the hunting in highly dimorphic than in less dimorphic species.

Energy conservation.—Energy consumption is a function of body size and small males thus might forage, and provide food for the young, more efficiently than large females (Reynolds 1972, Mosher and Matray 1974, Balgooyen 1976). However, in-flight metabolism of Common House-Martins (*Delichon urbica*) does not vary with body size (Bryant and Westerterp 1982), and the use of differences in resting metabolism (Mosher and Matray 1974) as a basis for this hypothesis is questionable. However, if smaller individuals require less energy in flight than larger ones, then males should forage more in highly dimorphic species than in less dimorphic ones.

Pyramid of numbers of prey sizes.—Small prey are more abundant than large prey, and small males should do most of the hunting until the food demands of the young become sufficiently great, and the supply of small prey sufficiently depleted, at which time the female must join in hunting, capturing, and delivering larger prey (Storer 1966, Reynolds 1972, Schantz and Nilsson 1981). Thus, provisioning by males should be greater in species with high RSD than in those with low RSD.

BEHAVIORAL HYPOTHESES

Sociability.—Coloniality may inhibit the evolution of RSD (Walter 1979). Another possibility is that colonial species may be less dimorphic than noncolonial species because communal defense against predators reduces the need for larger females (Snyder and Wiley 1976). Either hypothesis predicts lower RSD in colonial species than in noncolonial ones.

The remaining behavioral hypotheses hold that RSD has evolved to facilitate female dominance of the male.

Anticannibalism.—Large females prevent small males, who are presumed to have less of a "parental instinct," from eating their young (Hagen 1942, Amadon 1959). This leads to the prediction that males should

perform less brooding of young in highly dimorphic than in less dimorphic species.

Pair-bonding.—Formation and maintenance of pairbonds is facilitated by female dominance and large size facilitates dominance (Perdeck 1960, Amadon 1975, Ratcliffe 1980, Cade 1982, Smith 1982, Mueller and Meyer 1985). This hypothesis predicts that females should be more dominant in species with high RSD than in those with low RSD.

Role-partitioning.—Female dominance excludes the male from incubation, brooding, etc. and forces him into the role of provider of food (Cade 1960, 1982; Monneret 1974).

Female selection of males who are good provisioners.—Male raptors begin to provision females well in advance of egg laying (Safina 1984). This could allow the female to assess the male's quality as a provider. Safina proposes that females select males that are frequent providers. He argues that small males can provide food to females more frequently than large males because (1) size of prey is correlated with size of raptor, particularly in species that pursue agile prey, and (2) small prey is more abundant and thus captured more frequently. This hypothesis predicts that smaller owls should take smaller prey than large owls.

There is one remaining hypothesis that does not fit into the above categories. It is also unique in that it limits, rather than promotes, RSD. Nesting in cavities inhibits the development of RSD (Walter 1979). Cavities, particularly those produced by woodpeckers, are available only in a limited variety of sizes. Cavities in general are scarce in comparison to other nest sites. This scarcity of sizes of cavities might inhibit evolution of large females.

MATERIALS AND METHODS

Wing measurements (chord) of North American owls are taken from Earhart and Johnson (1970) and weights are from Dunning (1984), except for the Boreal Owl, where I have chosen to use the rather small sample of North American weights given in Earhart and Johnson rather than the European weights given by Dunning. Data on food habits of North American owls were taken from Snyder and Wiley (1976). Information on clutch size, behavior, and other aspects of the life histories of North American owls were taken from Bent (1938). Weights, wing measurements, and data on food habits of European owls were taken from Mikkola (1983). Other information on European owls was obtained from Glutz and Bauer (1980). Egg weights were taken from Schönwetter (1967). I have chosen the best available secondary sources of data in a deliberate effort to avoid biases that might result from my own summarization of primary sources. The data are presented in Tables 1 and 2.

This paper attempts to test as many hypotheses on RSD as possible, using, primarily, nonparametric statistics (Siegel 1956). Unless otherwise indicated, probability values given are one-tailed. I have chosen to treat the North American and European owls separately in part because the quality of the data available is quite different for the two continents, and

also because there are considerable regional variations in the biology of at least several species of owls.

In Tables 1 and 2, RSD is expressed simply as the mean for males divided by the mean for females. For weights, I have used the cube root in calculating the dimorphism ratio, following time-honored convention and thus permitting some comparison with the ratio derived from wing chord.

RESULTS

Ecological Hypotheses

Data permitting a comparison of the sizes of prey taken by the sexes in owls are available for only 3 species (Mikkola 1983: table 55). Mikkola's data are from Finland, where all three species show great overlap in geographic range, habitat preference, and are known to breed in the vicinity of each other. Mikkola's prey sizes are estimates based on the average weights of the prey species and the most appropriate way to deal with such estimates is to place them in size classes (Storer 1966). The female Boreal Owl takes significantly larger prey than the male, ($\chi^2 = 4.09$, $P < 0.05$), but there are no significant differences between the sexes in size of prey in the Great Gray ($\chi^2 = 3.84$, $P > 0.05$) or Ural Owls ($\chi^2 = 3.42$, $P > 0.06$). The differences in the last two species are close to significance, but in the Ural Owl it is the male that takes larger prey than the female. The Boreal Owl exhibits high RSD, particularly in weight, but less so than the Great Gray Owl (Table 2). Both sexes of both species of *Strix* are considerably larger than female Boreal Owls, with average weights ranging from 4.3× greater for male Ural owls to 7.4× for female Great Gray Owls. A comparison of the size of prey taken by the female Boreal Owl with both sexes of the other two species shows that only the male Ural Owl captures significantly larger prey ($\chi^2 = 7.27$, $P < 0.01$). A similar comparison for the male Boreal Owl shows that only the female Great Gray Owl captures significantly larger prey ($\chi^2 = 4.08$, $P < 0.05$). The apparent inconsistencies in the above are largely the result of small sample sizes for the Boreal Owl and the way cells must be combined to yield a minimum expected value of 5 for a chi-square test. Overall, the evidence strongly suggests that there are no real differences in the size of prey taken within or between these three species of owls. It is remarkable that the very large female Great Gray Owl not only captures prey of the same size as the small female Boreal Owl, but there also is no difference in the composition of the species taken (Spearman rank correlation coefficient, $r_s = 0.6192$, $P < 0.04$).

Earhart and Johnson (1970) report a significant difference in the proportions of mammals and birds taken by male and female Northern

TABLE 1

SEXUAL DIMORPHISM IN SIZE AND ASPECTS OF THE BIOLOGY OF NORTH AMERICAN OWLS

	Dimorphism[a]				Food[d]				
	$\sqrt[3]{\text{Weight}}$	Wing	Wing loading[b]	Mean species weight[c]	% Mammals	% Birds	% Invert.	Clutch size	Egg weight
Common Barn-Owl (*Tyto alba*)	0.966	0.986	0.928	466.1	91.4	6.9	1.6	6	25.5
Flammulated Owl (*Otus flammeolus*)	0.980	1.012	0.920	55.6	0	0	100	3.5	10.3
Eastern Screech-Owl (*O. asio*)	0.951	0.975	0.906	180.5	65.5	3.3	30.7	3.6	17.4
Western Screech-Owl (*O. kennicotti*)	0.951	0.967	0.921	143.0	65.5	3.3	30.7	3.7	18.0
Whiskered Screech-Owl (*O. trichopis*)	0.971	0.995	0.925	88.4	1.8	0.4	97.4	3.2	14.1
Great Horned Owl[e] (*Bubo virginianus*)	0.912	0.952	0.845	1308.7	77.6	6.1	14.7	2.7	66.5
Snowy Owl[e] (*Nyctea scandiaca*)	0.942	0.937	0.953	1802.7	78.0	21.3	0.1	6	63.5
Northern Hawk-Owl (*Surnia ulula*)	0.954	0.977	0.909	322.2	93.7	3.8	0	5	21.6
Northern Pygmy-Owl (*Glaucidium gnoma*)	0.947	0.958	0.924	67.5	23.3	12.8	61.4	3.5	9.5
Ferruginous Pygmy-Owl (*G. brasilianum*)	0.935	0.983	0.847	68.3	—	—	—	3.5	8.3
Elf Owl (*Micrathene whitneyi*)	—	0.985	—	41.0	1.9	0	98.1	3.2	7.3
Burrowing Owl (*Athene cunicularia*)	1.017	1.017	1.018	154.6	6.9	0.3	90.9	6.8	11.1
Spotted Owl (*Strix occidentalis*)	0.970	0.978	0.956	609.7	37.5	4.5	57.4	2.3	47.0
Barred Owl (*S. varia*)	0.924	0.973	0.833	716.4	76.0	5.8	15.8	2.3	47.2
Great Gray Owl[e] (*S. nebulosa*)	0.897	0.956	0.789	1116.4	93.3	6.7	0	2.6	52.0
Long-eared Owl[e] (*Asio otus*)	0.958	0.991	0.894	262.4	97.1	2.3	0.6	4.5	23.3
Short-eared Owl[e] (*A. flammeus*)	0.941	0.995	0.841	346.4	94.5	4.0	1.5	6	21.3
Boreal Owl (*Aegolius funereus*)	0.900	0.926	0.849	120.6	93.6	6.4	0	5	12.7
Northern Saw-Whet Owl (*A. acadicus*)	0.938	0.951	0.912	82.9	96.8	1.6	1.4	5.5	10.2

[a] Dimorphism = ♂♂/♀♀.
[b] Wing loading. An index of (♂♂ weight/♂♂ wing^2)/(♀♀ weight/♀♀ wing^2).
[c] Mean species weight (g) = $\bar{x}$ ♂♂ weight + $\bar{x}$ ♀♀ weight/2.
[d] Food. Percent of total food items. The percent of lower vertebrates is not presented. It can be obtained by adding the percentages given and subtracting from 100.
[e] Breeds in open nests.

TABLE 2

SEXUAL DIMORPHISM IN SIZE AND ASPECTS OF THE BIOLOGY OF EUROPEAN OWLS[a]

	Dimorphism				Food				
	$\sqrt[3]{\text{Weight}}$	Wing	Wing loading	Mean species weight	% Mammals	% Birds	% Invert.	Clutch size	Egg weight
Common Barn-Owl	0.952	0.997	0.868	337.0	95.0	2.7	0.8	4.6	21.0
European Scops-Owl (*Otus scops*)	0.950	0.977	0.898	104	—	—	—	3.5	12.4
European Eagle-Owl[b] (*Bubo bubo*)	0.960	0.932	0.856	2665.5	59.7	35.8	0.4	2.7	77.5
Snowy Owl[b]	0.917	0.926	0.899	1982.5	97.8	1.6	0.1	8	63.5
Northern Hawk-Owl	0.955	0.992	0.885	303.0	96.2	2.7	<1.1	7	21.8
European Pygmy-Owl (*Glaucidium passerinum*)	0.948	0.942	0.960	62.0	62.3	36.8	<0.9	5	9.0
Little Owl (*Athene noctua*)	0.994	0.988	1.006	173.5	14.9	0.7	83.7	4.1	15.8
Tawny Owl (*Strix aluco*)	0.933	0.956	0.888	528.5	80.3	9.2	6.0	3.24	39.5
Ural Owl (*S. uralensis*)	0.939	0.966	0.887	795.5	78.6	14.2	2.2	3.65	50.0
Great Gray Owl[b]	0.888	0.931	0.888	1056.5	98.5	1.0	0.1	4.05	53.0
Long-eared Owl[b]	0.959	0.987	0.882	307.5	92.0	7.7	0.2	4.5	23.0
Short-eared Owl	0.948	0.992	0.866	380.5	97.6	1.1	1.1	6.85	21.3
Boreal Owl	0.901	0.933	0.840	145.5	94.5	5.4	0.1	5.0	12.5

[a] Conventions as in Table 1.
[b] Breeds in open nests.

Pygmy-Owls; however, all of my attempts to replicate their calculations show no significant difference.

Although too few data are available for a conclusive answer to the question as to whether trophic appendages are more dimorphic than body size or nontrophic appendages in owls, a preliminary analysis is possible, Mlikovsky and Piechocki (1983) present 7 measurements for 6 species of European owls: (1) body weight, which I express as the cube root to permit comparison with linear measurements; (2) wing arc (flattened wing); (3) tail length; (4) tarsus length; (5) foot size, the distance between the tips of the claws of the middle and hind toe, with the foot outstretched; (6) beak length, including cere; (7) beak depth, the vertical thickness of the beak measured in a straight line at the edge of the feathers. RSD values for these seven measurements are presented in Table 3.

To compare the relative dimorphism of the various structures and of body size, I looked at the number of species in which RSD in one structure exceeds RSD in another structure (Table 4). No clear picture emerges; only one structure appears to be more dimorphic than any other; beak depth is significantly more dimorphic than tail length in all six species (sign test, $P = 0.016$). Foot size, the measure of the most probable trophic appendage (Mueller and Meyer 1985) exhibits greater dimorphism in only half of the comparisons with other measurements.

A starting point for most ecological hypotheses is to show that RSD is correlated with the type of prey taken, and such evidence does exist for owls (Tables 1 and 2). RSD is correlated with the proportion of vertebrates in the diet: weight, North America, $r_s = 0.6519$, N = 16, $P < 0.004$; Europe, $r_s = 0.5785$, N = 12, $P < 0.03$; wing, North America, $r_s = 0.5785$, N = 17, $P < 0.02$; Europe, $r_s = 0.5901$, N = 12, $P < 0.03$. There is no consistent correlation between RSD and birds or mammals in the diet. RSD is correlated with percent birds in the diet for North American owls: weight, $r_s = 0.5676$, $P < 0.02$; wing, $r_s = 0.6233$, $P < 0.005$; but there is no correlation between birds consumed and RSD in European owls: weight, $r_s = 0.1926$, $P > 0.26$; wing, $r_s = 0.1807$, $P > 0.24$. RSD is correlated with mammals taken only with weight for North American owls, $r_s = 0.5676$, $P < 0.02$, and not with wing, $r_s = 0.3789$, $P > 0.06$; and neither with weight, $r_s = 0.2867$, $P > 0.16$, nor wing, $r_s = 0.0385$, $P > 0.45$, for European owls. The correlation between birds in the diet and RSD in North American owls is of dubious importance. Half of the species consume less than 4% birds and only 11.8% take more than 10% birds (Table 1). In contrast half the species consume more than 77% mammals and 41.2% take more than 90% mammals. The situation is similar with European owls, where half the species consume less than 3% birds and only 25% take more than 10% birds (Table 2). Mammals constitute more than

TABLE 3

REVERSED SEXUAL DIMORPHISM OF BODY SIZE AND VARIOUS STRUCTURES IN SOME EUROPEAN OWLS[a]

Species	$\sqrt[3]{\text{weight}}$	Wing	Tail	Tarsus	Foot	Beak	
						Length	Depth
Common Barn-Owl	0.982	0.999	0.992	1.009	0.996	0.975	0.973
European Eagle-Owl	0.893	0.946	0.938	0.987	0.909	0.861	0.932
Little Owl	1.015	0.978	0.985	0.927	1.027	1.012	0.984
Tawny Owl	0.916	0.957	0.969	0.981	0.942	0.924	0.939
Long-eared Owl	0.946	0.984	0.984	0.946	0.934	0.995	0.965
Short-eared Owl	0.990	1.030	1.007	0.986	0.890	0.892	0.938

[a] Data from Mlikovsky and Piechocki (1983). Measurements of the structures are described in the text.

90% of the diet of 58.3% of the European species of owls. It is enigmatic that European owls consume significantly more birds than North American owls (Mann-Whitney *U*-test, $P < 0.05$) but show no correlation between RSD and birds in the diet.

Snyder and Wiley (1976) found that birds yielded the highest correlation between diet and a composite index of RSD for a combined sample of North American Falconiformes and owls. Johnson (1978), in a review of Snyder and Wiley's monograph, notes that if Falconiformes are divided into two approximately equal subsamples, one containing species with low RSD and the other those with high RSD, then there is a correlation between birds consumed and RSD only in the subsample with high RSD. As Johnson notes, there appears to be an abrupt threshold below which birds in the diet have no influence on RSD. Johnson's method is even more revealing for owls.

Only 4 species of North American owls consume more than 90% invertebrates: the Flammulated, Whiskered Screech-, Elf, and Burrowing Owls. There is no correlation between RSD in wing and diet in these 4 species: vertebrates, $r_s = -0.4000$; birds, $r_s = -0.2108$; mammals, $r_s = -0.2000$ (with N = 4, r_s must be 1.0 for $P = 0.05$). No weights are available to calculate RSD for the Elf Owl, and a sample size of 3 is inadequate to calculate r_s. However, there would be no correlation between RSD and weight for these 4 species, regardless of what might be the RSD for the Elf Owl, because the Burrowing Owl has the lowest rank for RSD and the highest rank for vertebrates, birds, and mammals in the diet. There is also no correlation between RSD and diet in the remaining 13 species: vertebrates, weight, $r_s = 0.3646$, $P > 0.10$; wing, $r_s = 0.2707$, $P > 0.18$; birds, weight, $r_s = 0.1978$, $P > 0.25$; wing, $r_s = 0.3407$, $P > 0.13$; mammals, weight, $r_s = 0.1813$, $P > 0.27$; wing, $r_s = -0.1374$, $P > 0.35$.

TABLE 4

COMPARISONS OF REVERSED SEXUAL DIMORPHISM OF TROPHIC AND OTHER STRUCTURES IN 6 SPECIES OF EUROPEAN OWLS

	Beak length	Foot	$\sqrt[3]{\text{Weight}}$	Tarsus	Tail	Wing
Beak depth	3[a]	3	3	4	6	5
Beak length		4	4	4	4	4
Foot			2	5	4	5
Weight				3[b]	5	5
Tarsus					3	3
Tail						4[b]

[a] The number of species showing greater dimorphism in the measurement listed on the left than in the measurement listed above.
[b] One tie, reducing maximum possible N = 5.

The species of North American owls that consume more than 90% invertebrates show low RSD in both wing and weight. The remaining species, which consume a mean of 85.8% vertebrates (range = 38.1–100%), 6.6% birds (range = 1.6–21.3%), and 78.3% mammals (range = 23.3–97.1%), are at least moderately dimorphic.

A similar analysis of European owls produces basically similar, but slightly less distinct results. The Little Owl is the only European Owl with a large proportion of invertebrates in its diet (83.7%). It is also the least dimorphic in weight, and its removal from the sample leaves no significant correlation between vertebrates consumed and RSD in weight in the remaining 11 species ($r_s = 0.4506$, $P > 0.06$). These 11 species consume a mean of 86.6% (range = 59.7–98.5) mammals, 10.7% (range = 1.0–36.8) birds, and 1.3% (range = 0.1–6.0) invertebrates.

The correlation between RSD in wing and vertebrates in the diet persists in this sample of 11 species ($r_s = 0.5853$, $P < 0.03$). Indeed, it is necessary to divide the sample into the 5 species ranked lowest and the 7 ranked highest in consumption of vertebrates to eliminate correlations with RSD in wing in both subsamples ($r_s = -0.6842$, $P > 0.05$; $r_s = 0.4818$, $P > 0.05$; respectively). The 7 species in the subsample with a high consumption of vertebrates are not significantly more dimorphic in RSD in wing than the 5 species in the low subsample (Mann-Whitney $U = 7$, $P > 0.10$, two-tailed). The correlation between RSD in wing and vertebrates consumed thus appears to be the result of combining a tendency to a negative correlation in the low subsample with a tendency to a positive correlation in the high subsample. The division into subsamples leaves us with no consistent difference in the type of prey taken: invertebrates, low sample mean 18.8% (range = 1.1–83.7), high sample mean 0.4% (range = 0.1–

<0.9); mammals, low sample mean 73.5% (range = 14.9–97.6), high sample mean 73.0% (range = 59.7–98.5); birds, low sample mean 5.6% (range = 0.7–14.2), high sample mean 13.0% (range = 1.0–36.8).

Andersson and Norberg (1981) have noted that size affects flight performance of birds, particularly in such aspects as pursuit of prey, and have suggested that this might be an important factor in the evolution of RSD. Schantz and Nilsson (1981) believe that an important factor in the evolution of RSD is the relative ability to transport large prey. These aspects of flight performance are greatly influenced by wing loading. There is virtually no information available on sex differences in wing loading in owls. A crude index of wing loading can be obtained by dividing weight by the square of wing length, and this index is probably adequate for ranking species in respect to RSD in wing loading (Tables 1 and 2). This index of RSD in wing loading is correlated with vertebrates in the diet of both European and North American owls ($r_s = 0.5750$, $P < 0.03$; $r_s = 0.4897$, $P < 0.03$; respectively). The index is also correlated with mammals consumed for North American owls ($r_s = 0.5118$, $P < 0.02$), but not for European owls ($r_s = 0.4196$, $P > 0.08$). There is no correlation with birds in the diet (Europe, $r_s = -0.0911$, $P > 0.40$; North America, $r_s = 0.1132$, $P > 0.32$). Deletion of the Little Owl, the only specialist on invertebrates in the European owls, results in no significant correlation between vertebrates in the diet and RSD in the wing-loading index in the remaining sample ($r_s = 0.4510$, $P > 0.08$). Removal of the 3 species of specialists on invetebrates from the North American sample results in no correlation between RSD in wing-loading index and vertebrates ($r_s = 0.3591$, $P > 0.10$) or mammals ($r_s = 0.3681$, $P < 0.10$) in the diet of the remaining 13 species.

Sex-role Differentiation Hypotheses

Egg size.—Although it is true that larger owls lay larger eggs than smaller owls, it is also true that the eggs of large owls are smaller, relative to body weight, than the eggs of smaller owls (Tables 1 and 2). This makes it extremely difficult to test the hypothesis that RSD has evolved to permit females to lay larger eggs. I propose the following solution to the problem. A regression of egg weight (y) on mean body weight (x) of females yields a "predicted" egg weight for each species. These regressions are excellent fits to the data: North American owls, $y = 0.033x + 10.67$, $r = 0.9479$, $P < 0.0001$; European owls, $y = 0.023x + 14.87$, $r = 0.9426$, $P < 0.0001$. The observed values for egg weight can be greater or less than the weight "predicted" by the regression line. The difference between observed and expected values, expressed as a percentage of mean body weight for the species, should be correlated with RSD if highly dimorphic species lay

relatively larger eggs than less dimorphic species. There is no such correlation (North American owls, weight, $r_s = -0.0176$, $P > 0.45$; wing, $r_s = 0.0062$, $P > 0.45$; European owls, weight, $r_s = 0.3242$, $P > 0.10$; wing, $r_s = 0.1871$, $P > 0.25$).

Clutch size.—There is no correlation between RSD and clutch size in owls. In the North American species: $r_s = 0.2729$ for weight, $P > 0.12$; $r_s = -0.0960$ for wing, $P > 0.35$. In the European owls: $r_s = 0.1678$ for weight, $P > 0.28$; $r_s = -0.0165$ for wing, $P > 0.47$.

Breeding increment in weight.—Wheeler and Greenwood (1983) divide the Falconiformes into four categories of flight performance in pursuit of prey. All of the North American owls except the Flammulated, Whiskered Screech-, Elf, and Burrowing owls fit into their "high" category: "aerial hunters of fast moving prey on the ground (mainly birds and mammals) which is usually taken on the ground or in the early stages of flight." A linear regression of the inverse of RSD of wing (y) on female weight plus egg weight divided by female weight (x) yields: $y = -0.060x + 1.10$, $r_s = -0.0834$, $P > 0.60$; two-tailed. All of the European owls except the Little Owl fit into the "high" category of Wheeler and Greenwood. A linear regression of the inverse of RSD on breeding increment on these 11 species yields $y = -0.556x + 1.63$, $r = -0.5562$, $P > 0.11$, two-tailed. Breeding increment thus shows a slight tendency to be negatively correlated with RSD.

Incubation.—In all European owls, all incubation is performed by the female. The same is almost certainly true of North American species, although it is easy to find accounts of males sharing in incubation (Bent 1938). Males may briefly cover eggs while the female leaves to defecate, preen, etc. (Glutz and Bauer 1980 list this behavior for *Otus scops, Surnia ulula,* and *Aegolius funereus*) and this may have led to the conclusion that males participate in incubation in some species. As females do all of the incubating in all species, there obviously is no correlation between RSD and the roles of the sexes in incubation behavior.

Nest protection.—There appears to be no relationship between RSD and which sex performs most of the defense of the nest against predators. Information on the relative role of the sexes in nest defense is available for 8 European species; in 4 the female performs more defense than the male (Eagle-, Tawny, Ural, Long-eared owls) and in 4, the male is the primary defender (Scops-, Snowy, Great Gray, Short-eared owls). A Mann-Whitney U-test on these data yields $U = 5$, $P = 0.243$, for RSD in weight and $U = 7$, $P = 0.443$ for wing. The evidence thus indicates no difference between the sexes in nest defense and no relationship with RSD.

Feeding efficiency.—Statements on which sex feeds the young are given for 10 species of European owls, including the least dimorphic, the Little

Owl, and the most dimorphic, the Great Gray Owl. There is no evidence that males tear apart prey and feed their young the pieces in any of the 10 species. There is thus no correlation between RSD and the direct feeding of young by the female.

Foraging interference, energy conservation, and pyramid of numbers of prey sizes.—These three hypotheses predict that the male should do most of the hunting and provision the female and brood at least until the young are quite large. Again, the information for North American owls is too limited to be useful. Provisioning of the female by the male begins in courtship and the male is the exclusive, or nearly exclusive, provider of food for the female and young through the end of the brooding phase in all European owls. Exceptions to this rule occur only when the male fails to deliver sufficient food, usually in times of prey scarcity, which occur primarily during the cyclic population "lows" of Microtine rodents. There is no evidence of a correlation between RSD and the provisioning efforts of the male.

Behavioral Hypotheses

Sociability.—Only one species of North American or European owl exhibits breeding behavior that can be interpreted as colonial: the Burrowing Owl. This species' lack of RSD supports the hypothesis that coloniality inhibits the development of dimorphism. The Burrowing Owl is also known to engage in group defense against predators thus supporting the hypothesis that this reduces the "need" for dimorphism.

Anticannibalism.—Clear statements that the female performs all of the brooding of nestlings are given for 9 species of European owls. All brooding also appears to be done by the female in *Tyto alba, Glaucidium passerinum,* and *Athene noctua* although there is no explicit statement on the role of the sexes in these species. Possible brooding by the male is described only for *Aegolius funereus*; in this species the male has been recorded to spend much time in the nest cavity with the female during the first week after hatching and the male *may* help with brooding of the nestlings during this time. The absence of brooding by the male in the remaining 12 species suggests that there is no correlation between RSD and the participation in brooding by the male.

Pair-bonding. Information on dominance relationships between the sexes is available for 6 species of European owls. These are, listed in descending order of female dominance: *Glaucidium passerinum, Bubo bubo, Surnia ulula, Athene noctua, Otus scops,* and *Tyto alba.* This ranking of female dominance is significantly correlated with RSD in weight, $r_s = 0.943$; but not with RSD in wing, $r_s = 0.714$. ($P = 0.05$, at $r_s = 0.829$, and $P = 0.01$, at $r_s = 0.943$.)

Mueller and Meyer (1985) were unable to rank female dominance in species of Falconiformes and simply compared the RSD of species for which female dominance was recorded with the RSD of those for which there was no record of dominance. This method of analysis is unsuitable for the data available for owls because almost all the information is from observations of birds breeding in captivity and would thus show the relationship between captive breeding and RSD. A Mann-Whitney U-test on presence or absence of recorded dominance and RSD for European owls yields $U = 6$, $P = 0.017$, one-tailed for weight; and $U = 15$, $P = 0.223$, for wing; showing that dominance has been recorded significantly more often in species with low RSD in weight than in species with high RSD in weight, and suggesting that more species with low RSD have been bred in captivity than species with high RSD.

Nest-site preference.—Fourteen of the 19 species of North American owls prefer to nest in cavities; the remaining 5 nest in old stick nests of other birds, on cliff ledges or in open nests on the ground. A Mann-Whitney U-test reveals no significant relationship between RSD and nest-site preference for the 19 species (weight, $U = 17$ [for $P = 0.05$, $U = 15$]; wing, $U = 26$ [for $P = 0.05$, $U = 16$]). Seven of the 13 species of European owls prefer to nest in cavities, and the remainder breed in open nests. This sample also shows no relationship between RSD and nest-site preference (weight, $U = 13$, $P = 0.177$; wing, $U = 14$, $P = 0.217$).

DISCUSSION

The most widely accepted hypotheses on RSD in raptorial birds all include differential use of sizes of prey by the sexes. Although most species of birds of prey show a statistically significant difference in size of the sexes, there is remarkably little evidence that the sexes take significantly different sizes of prey. The available evidence for owls indicates that female Boreal Owls take larger prey than males. However, the sample is small, the difference barely significant, and female Boreal Owls take prey that is of the same size and species composition as the much heavier (7.4×), female Great Gray Owl. The data on the Great Gray, Ural, and Boreal owls are not unique in showing great interspecific difference in size of owl but little difference in species of prey taken. Mikkola (1983) has shown that 10 species of Fenno-Scandian owls have an average similarity in diet of 0.80, using the index of community similarity of MacNaughton and Wolf (1973). This index ranges from 0 to 1, with 1 indicating complete overlap. Six of the 10 species (Snowy, Northern Hawk-, Great Gray, Long-eared, Short-eared, and Boreal owls) show a similarity index of 0.97–1.00, indicating virtual total overlap in diet. In 4 of the 6 species (Snowy, Northern Hawk-, Great Gray, Short-eared owls) the diet consists of 91.3–

97.4% Microtine rodents. The mean weights for these four species of owls range from 303 to 1983 g, a 6.5-fold difference. There is thus considerable evidence that the differences in body size of owls, either within or between species, generally result in small differences in the size of prey taken.

Although data are available from only 6 species, there is not even a suggestion of support for the prediction that trophic structures should be more dimorphic than nontrophic structures. Overall, the balance of evidence from owls is quite strongly against the ecological hypotheses of RSD.

My analyses have revealed some differences between correlations of RSD in wing measurement and weight and various other factors. I agree with Johnson (1978) that a composite index of several measures of body size and appendages acts to obscure important differences. I also agree with Earhart and Johnson (1970), Amadon (1977), and Cade (1982) in their suggestion that weight is the best measure of body size. A number of species of owls do show differences between RSD in wing and weight. Dimorphism in the cube root of weight is greater than dimorphism in wing in 21 of the 25 species. Earhart and Johnson (1970) present statistics separately for each subspecies of owl and the variance presented for weight is for the cube root. This presentation makes it difficult to establish, unequivocally, which species show statistically significant dimorphism. It appears that male Burrowing Owls have a significantly longer wing chord than females. The Flammulated, Whiskered Screech-, Ferruginous Pygmy-, Long-eared, and Short-eared owls appear to be sexually monomorphic in wing. Only the Whiskered Screech- and Burrowing owls appear to be monomorphic in weight. North American species not mentioned above appear to show significant RSD in wing or weight. Insufficient information for most European owls precludes a determination of the statistical significance of RSD; however, it appears likely that most species of owls show significant RSD in weight.

The only advantage of wing chord as a measure of body size is that it easily can be obtained from museum specimens. It is difficult to envisage any other type of animal where the most commonly used estimator of body size would be epidermal outgrowths of digits of the forelimb. The fact that the length of the longest primary does influence flight capability is not an adequate justification for widespread reliance on wing chord as the standard measure of body size. I suggest that weight is by far the best measure of body size and also that RSD in weight is of greater biological significance than RSD in wing.

Newton (1979) and Andersson and Norberg (1981) show that RSD is correlated with speed and agility of prey. Many of the invertebrates captured by owls are insects that fly at night, and owls do capture insects

in flight (e.g., Glutz and Bauer 1980). Capture of a nocturnal flying insect probably requires greater agility than capturing a nocturnal, running small mammal. If "flycatching" is important in the foraging of insectivorous owls, then agility in flight may be more important for them than for owls that specialize on small mammals. Flight performance is size-related and a bird that pursues and captures prey in flight ideally should be not much larger than its prey (Andersson and Norberg 1981). The small size, and relatively small range of sizes of insects available for capture by owls leads to the prediction that insectivorous owls should be small and show limited RSD. The range of sizes of most of the prey exploited by owls that specialize on mammals is also limited. Perhaps the limited agility required for capture not only permits a great range of sizes of species specializing on small mammals but also the evolution of considerable RSD within species. In both of the hypotheses presented above, diet permits, or limits, but does not cause RSD.

Temeles (1985) found a correlation between RSD and prey vulnerability (relative ease of capture by the predator) in the Falconiformes. Temeles' hypothesis also predicts prey-size partitioning between the sexes and species, based on body size, and thus appears to be an inadequate explanation for RSD in owls.

It is surprising to find no correlation between RSD and any of the predictions generated from the hypotheses concerning sex-role differentiation. Owls are a remarkably uniform group in the relative roles of the sexes in parental care. Females perform all incubation, brooding, and apparently all the tearing apart of prey and the direct feeding of bits of food to the young. Males perform all of the hunting and provisioning of the female and young from before the beginning of egg laying through at least the end of brooding with the exception that females will hunt if prey is so scarce that the male is unable to deliver sufficient food.

Differentiation of sexual roles in incubation, brooding, provisioning, and rearing of young occurs in a great variety of birds with "normal" dimorphism (Mueller and Meyer 1985), and it is inconsistent to argue a special case for hawks or owls except, possibly, for nest defense. There is no relationship between RSD in owls and which sex is the primary defender of the nest and young against predators. Mueller and Meyer (1985) found the same to be true for European Falconiformes. Several authors have given great importance to more efficient nest defense by large females as the deciding factor as to which sex is the larger one in raptorial birds. Snyder and Wiley (1976) emphasize that in the Burrowing Owl the male is larger than the female and is the primary nest defender. (But note that the species is monomorphic in weight.) Glutz and Bauer (1980) show that the male is the primary defender in half of the European species for which

information is available, and all of these species show RSD. More recently, Wiklund and Stigh (1983) have shown that male Snowy Owls perform almost all nest defense, and this species shows high RSD.

I have found no reasonable evidence for any of the ecological or sex-role partitioning hypotheses concerning the evolution of RSD. This leaves only the behavioral hypotheses as a possibility. Absolutely conclusive proof will be very difficult to obtain for the hypothesis that RSD facilitates the formation and maintenance of the pairbond. However, it is very important to note that female dominance is shown in species of owls with relatively low RSD, yet the degree of dominance appears to be correlated with RSD. There is no such evidence for any other hypothesis. The facilitation of female dominance is thus the most viable hypothesis on the evolution of RSD, in spite of the scarcity of data on dominance relationships. The lack of information on the breeding behavior of the more dimorphic species is also interesting. Almost all the information available on interpair relationships is from owls breeding in aviaries. Perhaps high RSD inhibits pair formation and breeding in a situation where a male cannot keep his distance and escape from an aggressive female when she is not receptive to sexual advances.

Smith (1980) lists more than 40 species of more than 20 families of birds in which the female is dominant during the breeding season. All these species are monogamous. Data are lacking for other species, but it appears likely that female dominance during the breeding season occurs in most monogamous species. All North American and European owls are monogamous, with only occasional occurrences of polygyny.

We know relatively little about the initial courtship behavior of owls. What little information we do have suggests that the female is socially dominant over the male even before the inception of courtship. Courtship behavior has been studied in detail in a variety of other monogamous birds, and the early phases almost invariably involve at least some aggression on the part of the male (Armstrong 1947, Hinde 1973). In many species the male is fully as hostile to an arriving female as to an intruding male. Smith (1982) notes that raptors possess potentially lethal weapons and suggests that RSD has evolved to facilitate female dominance. In most other species of birds, males are dominant outside of the breeding season and some aggression occurs before dominance is reversed during pair formation. Prior female dominance eliminates this potentially dangerous transition in raptorial birds.

There appears to be great reluctance to accept the idea that RSD in birds without reversal of sexual roles might be the result of sexual selection. The reluctance to accept sexual selection for RSD in raptors is apparently due to the recent concentration of work on intrasexual selec-

tion, with so little thought given to epigamic selection that it appears to be virtually forgotten. Selander (1972) has shown that it is extremely difficult to differentiate between the two types of selection. It is obvious that the female does the mate selecting in most species of birds, but it is rarely clear what influences her selection. I suggest that female raptors tend to select less dominant and aggressive males and this selection has led to the evolution of RSD.

The observed relationships between diet may be the result of prey type permitting or restricting the degree of RSD, as I have suggested. Alternatively (or also, since the hypotheses are not mutually exclusive), the rapacity of the species may be an important determinant of RSD. Species that prey upon vertebrates are certainly more rapacious than those that capture invertebrates. Perhaps the formation and maintenance of the pairbond are more difficult in formidable predators than in less rapacious species and this may be mitigated by increased RSD. Amadon (1975) has pointed out that dimorphism in size in animals, regardless of which sex is the larger, is nearly always related to mating behavior.

Cautionary note.—This entire paper is based on correlations, which cannot distinguish cause from effect. It is further based on the assumption that a trait important in the evolution of RSD should be expressed to a greater extent in species with high RSD than in those with low RSD. These premises are arguable, but I can see no better alternative. More work is needed on the functions and evolution of RSD in owls. We appear to have a sufficient number of hypotheses and remarkably little in the way of useful data. Further studies of RSD should concentrate on obtaining data that offer a reasonable possibility of proving or falsifying hypotheses. We particularly need observations of pair formation and other aspects of interaction between males and females, both in nature and in captivity. Further information on the diet of the sexes might be informative. Any field study on raptors should record information separately for the sexes wherever this is possible. For the present, the most viable working hypothesis appears to be that RSD evolved to facilitate female dominance which in turn facilitates formation and maintenance of the pairbond.

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