

SEX AND AGE DIMORPHISM IN THE BARN OWL AND A TEST OF MATE CHOICE

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ABSTRACT.—I investigated sex and age dimorphism and the possible effect of body size on mate choice in a northern Utah population of the Barn Owl (*Tyto alba*). In all characters measured (body mass; length of body, tarsus, foot, tail, and wing; and wing area), females averaged larger than males, but the ranges of these values overlapped considerably. Females were significantly larger than males in all characters except wing chord and tail length. Males had significantly lower wing loading than females. Lower wing loading could contribute to more efficient foraging by males and thus support hypotheses that partitioning of reproductive duties between the sexes may play an important role in reversed sexual dimorphism. Adults and immatures did not differ in size. I found no evidence to support the hypothesis that females choose small males as mates. Received 21 February 1989, accepted 21 September 1989.

FEMALES are larger than males in the majority of animals (Shine 1988), but males are often larger than females in vertebrates (Andersson and Norberg 1981). In most raptors (Strigiformes and Falconiformes), females exceed males in size (Amadon 1975). Because this condition is counter to the normal avian pattern, it is *reversed sexual dimorphism* (RSD). More than 20 hypotheses to account for RSD have been developed. Mueller and Meyer (1985) and Mueller (1986) evaluated these hypotheses, which fall into three major groups: food partitioning between sexes, sexual selection, and division of roles in reproduction. Plausible genetic models exist for all three groups of hypotheses (Hedrick and Temeles 1989).

Two mechanisms have been proposed by which female choice of smaller males could have produced and maintained RSD in raptors. One mechanism proposes that large females may dominate smaller males, thus facilitating pair formation and maintenance of pair bonds (Cade 1960, Amadon 1975, Smith 1982). An alternative mechanism hypothesizes that females may indirectly select small mates if smaller males hunt more efficiently and deliver prey faster than larger males during courtship (Safina 1984).

The Barn Owl (*Tyto alba*) reportedly exhibits less sexual dimorphism than most raptors (Earhart and Johnson 1970, Mlikovský and Piechocki 1983, Lundberg 1986), but few investigators have examined sexual dimorphism intensively within one Barn Owl population. Indeed, within-species variation in sexual size dimorphism is poorly known for most birds

(Rising 1987). Adults and immatures also differ in size in some raptors (Mueller et al. 1976; Amadon 1980; Mueller et al. 1981a, b). No one, apparently, has critically examined age dimorphism in the Barn Owl, and no one has examined mate choice in the species.

I describe size dimorphism for a population of the North American Barn Owl (*T. a. pratincola*) and test the hypothesis that the maintenance of RSD results from female choice of small mates. I also discuss how results from the Barn Owl may contribute to an understanding of RSD in general.

METHODS

Dimorphism.—Specimens examined were from Box Elder, Davis, Salt Lake, Utah, and Weber counties in northern Utah. I measured both live and dead owls. Owls caught at nest and roost sites were subjected only to weighing and measurement of wing chord. I minimized disturbance because reproduction was also being studied in this population. I measured body mass to the nearest 5 g with a spring scale. Mass was measured only on live healthy owls because most of the dead birds examined had died of starvation (see below). The cube root of mass was calculated to allow comparison with linear measurements (Schmidt-Nielsen 1984). I measured wing chord to the nearest 1 mm by placing the end of the folded, unflattened wing against the right-angle stop on one end of a ruler. Length was taken to the end of the longest primary.

Sex of live owls was determined by a combination of morphological and behavioral traits: (1) males average smaller in mass than females (see below); (2) females are darker in color on the ventral surfaces

and on the facial disk than males, and have more and larger breast spots (pers. obs., Colvin 1984, Looman 1985); (3) females alone have an incubation patch (Howell 1964) and incubate and brood exclusively (Cramp 1985). None of these criteria alone is adequate to determine the sex of all Barn Owls throughout the year; coloration and body size both overlap between the sexes, and incubation patches are present only during breeding. When used together, however, they identify correctly the sex of most owls. I tested the validity of color and markings alone as sex differences by using them to predict the sex of all dead owls before necropsy; sex was predicted correctly in 91% of 170 individuals. With the addition of data on mass, presence or absence of incubation patch, and differences in incubation and brooding behavior, sex of nearly all Barn Owls in this population could be determined correctly. I eliminated from analysis the few individuals for which sex was uncertain. Live owls were measured in all months of the year from 1977 through 1987. Many owls were caught and measured several times, but only the first mass and wing-chord measurements from each owl were used to calculate means and compare sexes.

Some dead owls were collected after collisions with vehicles or stationary objects, but the majority died of starvation in winter (Marti and Wagner 1985). Dead specimens were subjected to a more comprehensive analysis than live ones. Sex was verified by internal examination of the gonads, and the following measurements were taken:

Length of bill—taken to the nearest 0.1 mm with calipers as the straight line from the tip of the upper mandible to the proximal end of the culmen.

Length of tail—taken to the nearest 1 mm with a thin plastic ruler from the skin between the middle rectrices to the tip of the longest rectrix with the tail folded.

Length of tarsus—taken to the nearest 0.1 mm with calipers from the joint between the tibia and metatarsus to the joint at the base of the middle toe.

Total length—taken to the nearest 1 mm from the tip of the bill to the tip of the longest rectrix with the specimen on its back and gently stretched.

Length and width of foot—taken to the nearest 1 mm by placing the foot flat on a diagram representing the angle of the toes in prey-capture position (Payne 1962, see also Johnsgard 1988: 59). Measurements were made between the points where the tips of the claws touched the diagram. Length was taken between the claws of toes I and III, and width between toes II and IV.

Wing area—measured by placing the specimen on its back and tracing the outline of the wing on paper (not including the portion of the body between the wings). The wing was held in a natural,

fully extended position while tracing. Wing tracings were cut out and weighed. Surface area was then calculated proportionately to the ratio of the weight of a 100 cm² sample of the same kind of paper. The square root of the wing area was also calculated for comparison with linear measurements (Schmidt-Nielsen 1984).

Wing loading—estimated by dividing mass by the wing surface area. Because most of the dead specimens were emaciated, normal mass could not be obtained; wing loading was thus estimated by dividing the mean mass of live healthy owls (adult or first-year male, or adult or first-year female, as appropriate) by the wing area (obtained as above) of individual dead owls.

I classified the owls into two age categories: first year and older-than-first year. This rationale is derived from the facts that Barn Owls reach sexual maturity and begin breeding at approximately one year of age, the lifespan of most Barn Owls is short, and these age categories are easily separable by the pattern of wing molt. North American and European races of the Barn Owl undergo their first wing molt at ca. 13 months of age (pers. obs., P. Bloom pers. comm., Piechocki 1974). Once begun, this molt is continuous; individuals older than 13 months always have primaries and secondaries of different generations that are easily detected by differences in color and wear.

To measure sexual dimorphism I used Storer's (1966) index: $DI = 100 (\text{mean size of female} - \text{mean size of male}) / 0.5 (\text{mean size of female} + \text{mean size of male})$. This index is widely used and permits comparisons among species, populations, and characters within species.

Mate choice.—Mueller (1986) concluded that RSD most likely evolved under the selective advantage of female dominance over males in pair formation. This hypothesis predicts that females should choose small males as mates. I tested this using body mass of mated pairs. Mass is considered by many to be the best measure of body size in birds (Cade 1960, Earhart and Johnson 1970, Amadon 1977, Mueller 1986). For this analysis I used two data sets that consisted of weights of paired Barn Owls. In each set both members of pairs were banded, positively identified as mates, and sexed with certainty using the above criteria. I obtained one set from the Utah study area and the second set from a French population (*T. a. alba* and *T. a. guttata*; H. Baudvin, J-L. Dessolin, and A. Fooimbi unpubl. data). I analyzed these data in two ways. The body mass of owls in both samples was standardized ($z = (X - \bar{x})/SD$) to create a distribution with a mean of 0 and a standard deviation of 1. Standardized masses of each bird were then categorized as either small ($z < -0.43$), medium ($-0.43 < z < 0.43$), or large ($z > 0.43$). These cutoff points were determined by probabilities of the normal distribution (1/3 of the population should be greater than $z = 0.43$, and 1/3 less than

TABLE 1. Summary statistics for morphological variables in adult and yearling Barn Owls from Utah, and statistical comparisons between age categories.^a

Variable ^b	Yearling		Adult		<i>t</i>	<i>P</i>
	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$		
Male						
Wing chord (mm)	72	326.2 ± 8.6	31	329.3 ± 7.9	1.83	0.07
Wing area (cm ²)	48	1,589.9 ± 154.5	17	1,538.6 ± 131.8	1.22	0.23
Wing area ^b	48	39.8 ± 1.9	17	38.9 ± 1.6	1.79	0.08
Wing loading	48	0.30 ± 0.03	17	0.32 ± 0.03	1.93 ^c	0.06
Tail length (mm)	66	138.7 ± 6.7	19	141.7 ± 4.5	1.86	0.07
Body mass (g)	79	471.1 ± 30.8	33	479.2 ± 34.8	1.22	0.23
Body mass ^b	79	7.8 ± 0.17	33	7.8 ± 0.19	1.20	0.23
Total length (mm)	65	363.0 ± 19.0	19	369.8 ± 17.4	1.40	0.16
Beak length (mm)	66	21.4 ± 0.8	19	21.4 ± 1.0	0.17	0.86
Tarsus (mm)	66	71.4 ± 3.3	19	70.3 ± 3.5	1.16	0.25
Foot length (mm)	48	87.2 ± 5.2	15	87.3 ± 5.5	0.07	0.94
Foot width (mm)	48	88.6 ± 5.8	15	90.7 ± 5.0	1.24	0.22
Female						
Wing chord (mm)	114	328.5 ± 8.9	41	328.0 ± 7.6	0.39	0.70
Wing area (cm ²)	42	1,656.5 ± 156.2	22	1,678.1 ± 124.9	0.53	0.60
Wing area ^b	42	40.7 ± 1.9	22	40.9 ± 1.5	0.58	0.56
Wing loading	42	0.35 ± 0.03	22	0.34 ± 0.03	0.94 ^c	0.35
Tail length (mm)	57	141.3 ± 6.8	24	139.5 ± 8.1	1.13	0.26
Body mass (g)	125	569.3 ± 58.8	41	568.4 ± 58.4	0.17	0.86
Body mass ^b	125	8.3 ± 0.29	41	8.3 ± 0.28	0.03	0.98
Total length (mm)	55	373.7 ± 19.9	24	377.7 ± 17.3	0.78	0.58
Beak length (mm)	56	22.1 ± 1.0	22	22.8 ± 1.0	2.34	0.02
Tarsus (mm)	56	72.4 ± 3.5	24	72.3 ± 2.9	0.03	0.98
Foot length (mm)	43	90.7 ± 4.8	22	91.8 ± 3.8	0.98	0.33
Foot width (mm)	43	90.6 ± 4.2	22	92.5 ± 4.2	1.72	0.09

^a Wing chord and body mass from live owls; all others from dead specimens (see text).

^b See text for methods of measurement. The square root of wing area and the cube root of mass are given for comparison with linear measurements.

^c *t*-value calculated from Mann-Whitney *U*-statistic (Sokal and Rohlf 1981: 435).

$z = -0.43$). Weights of members of pairs were entered into regression analysis with males as the dependent variable. Secondly, pairs of owls were classified in one of nine possible pairings (e.g. small male-small female, small male-medium female). These pairings were subjected to a 3×3 contingency table analysis.

RESULTS

Dimorphism.—I examined and measured 166 dead owls (85 males and 81 females) and 278 live owls (112 males and 166 females). Adults and yearlings did not differ significantly within sexes in any of the traits measured except beak length in females (Table 1).

Females were significantly larger than males in all characters except wing chord and tail length (Table 2). The ranges of all traits, however, overlapped considerably between males and females. Wing loading was significantly less in males than females. Wing shape was also different between sexes; wing length did not

differ significantly but females' wings were significantly wider than those of males ($t = 7.71$, $df = 123$, $P < 0.0001$).

The characters that I measured do not all scale proportionately between sexes. Body mass in particular is disproportionately greater in females (or disproportionately less in males) (Table 3). Prey capture and handling structures (foot, leg, beak) are not appreciably larger in female Barn Owls. Foot size (especially important among these structures in evaluating whether the size of males' prey is different from that of females' prey) averaged only ca. 4% longer and 2% wider in females.

Mate choice.—Body size did not appear to be a factor in mate choice among 66 pairs from Utah and 93 pairs from France. No correlation was found between standardized weights in 159 pairs (Utah and French data combined; $r_s = 0.09$, $P = 0.25$). In fact, pairing by size was not significantly different from random ($\chi^2 = 3.17$, $P = 0.53$). Of 59 small females, 19 mated with

TABLE 2. Summary statistics for morphological variables in Barn Owls from Utah, and statistical comparisons between sexes.^a

Variable ^b	n		$\bar{x} \pm SD$		Range		Comparison	
	Male	Female	Male	Female	Male	Female	t	P
Wing chord (mm)	103	155	327.2 ± 8.5	328.4 ± 8.5	310-353	310-360	1.15	0.25
Wing area (cm ²)	65	64	1,576.5 ± 149.6	1,663.9 ± 145.5	1,286-1,944	1,340-1,898	3.59	0.0005
Wing area ^c	65	64	39.6 ± 1.9	40.7 ± 1.8	35.9-44.1	36.6-43.6	3.60	0.0005
Wing loading	65	64	0.30 ± 0.03	0.34 ± 0.03	0.24-0.37	0.28-0.42	6.32 ^c	<0.0001
Tail length (mm)	85	81	139.3 ± 6.4	140.7 ± 7.2	120-155	120-157	1.41	0.16
Body mass (g)	112	166	473.5 ± 32.3	566.4 ± 66.2	400-560	420-700	15.75	<0.0001
Body mass ^c	112	166	7.8 ± 0.2	8.3 ± 0.2	7.4-8.2	7.5-8.9	16.01	<0.0001
Total length (mm)	84	79	364.5 ± 18.8	374.9 ± 18.9	320-395	335-403	3.53	0.0005
Beak length (mm)	85	78	21.4 ± 0.8	22.3 ± 1.0	19.4-23.3	18.8-25.5	6.22	<0.0001
Tarsus length (mm)	85	80	71.1 ± 3.4	72.3 ± 3.3	60.5-78.9	61.5-79.5	2.34	0.02
Foot length (mm)	63	65	87.2 ± 5.3	91.1 ± 4.5	73-98	78-103	4.40	<0.0001
Foot width (mm)	63	65	89.1 ± 5.6	91.2 ± 4.3	74-102	80-100	2.46	0.01

^a Data sources as in Table 1.
^b See text for methods of measurement. The square root of wing area and the cube root of mass are given for comparison with linear measurements.
^c t-value calculated from Mann-Whitney statistic (Sokal and Rohlf 1981: 435).

TABLE 3. Indices of sexual dimorphism for a Utah population of the Barn Owl.

Variable ^a	Dimorphism index ^b
Wing chord	0.37
Wing area	5.39
Wing area ^b	2.74
Wing loading	12.50
Linearized wing loading ^c	3.15
Tail length	1.00
Body mass	17.87
Body mass ^b	6.20
Total length	2.81
Beak length	4.12
Tarsus length	1.67
Foot length	4.37
Foot width	2.33

^a See text for methods of measurement. The square root of wing area and the cube root of body mass are given for comparison with linear measurements.

^b Storer (1966).

^c Linearized wing loading = cube root of body mass divided by square root of wing area (Jaksić and Carothers 1985).

large males, 18 with medium-sized males, and 22 with small males. Of all females, only 30% paired with males in smaller size categories. Only 8.8% of large females paired with males in the small category. Thirty-five percent of the males paired with females in size categories smaller than their own.

I also performed these analyses on the Utah and French sets separately. Despite a large difference in mean mass between the two populations (males: Utah = 473.5 g, France = 310.4 g; females: Utah = 566.4 g, France = 367.1 g), mate pairings followed essentially the same pattern in both populations. In Utah pairs, females averaged 81.8 ± 60.0 g (16.8%) greater in mass and ranged from 40 g lighter to 275 g heavier than their mates. In the French sample, females averaged 55.1 ± 47.1 g (17.7%) heavier than their mates, ranging from 50 g lighter to 160 g heavier.

Males in Utah breeding pairs were significantly heavier than nonpaired males (486.7 g vs. 465.6 g; *t* = 3.71, *df* = 112, *P* = 0.0003). Nonpaired individuals included birds weighed outside the breeding season as well as unmated ones during the breeding season. Wing lengths of breeding males and nonpaired males were not significantly different (327.4 m vs. 326.9 m; *t* = 0.23, *df* = 100, *P* = 0.82). The greater mass of breeding males might be an indication of good body condition because body mass and

TABLE 4. Seasonal body mass of the Barn Owl from Utah.^a

Season	Male			Female		
	<i>n</i>	\bar{x} (g)	SD	<i>n</i>	\bar{x} (g)	SD
Nov.–Feb.	74	474.6	32.1	109	548.1	52.8
March–June	29	473.1	34.1	63	609.3	53.1
July–Oct.	28	467.1	28.3	37	530.9	55.2

^a See text for statistical comparisons.

wing length were significantly correlated in the year-round sample of all males ($r_s = 0.21$, $P = 0.03$). Males may be heavier because they occupy good hunting areas which may also enhance their chances of obtaining mates. Paired females, however, were not significantly heavier than nonpaired females (574.3 g vs. 566.2 g; $t = 0.89$, $df = 166$, $P = 0.37$). Mean wing lengths of the two groups were not different either (329.8 mm vs. 327.6 mm; $t = 1.24$, $df = 153$, $P = 0.22$). In the year-round sample of all females, I found that body mass and wing length did not correlate significantly ($r_s = -0.05$, $P = 0.54$). Female mass varied considerably through the year (see below). A large part of this fluctuation may be due to the success of food provisioning by their mates during breeding (H. Mueller pers. comm.). Weights of nonpaired individuals of both sexes were taken throughout the year, and the sample probably contained individuals that paired and bred later.

Mass change among seasons is an important consideration in testing whether mate choice is affected by body size. To assess this effect, I divided the year into three segments to reflect the reproductive cycle: March through June (egg laying and brood rearing), November through February (mate and nest-site choice), and July through October (nonbreeding). Male mass did not differ significantly among these seasons (Table 4; ANOVA, $F = 0.56$, $df = 130$, $P = 0.57$). Male Utah Barn Owls weighed on two or more occasions ($n = 14$) had a mean change of 42.9 g with a range of 0–120 g difference between weighings. The sample was too small to be conclusive, but it showed the same pattern as in Table 4—lowest mass occurred in the nonbreeding season.

Body mass of females differed among seasons (Table 4; ANOVA, $F = 34.9$, $df = 197$, $P < 0.0001$). Significant differences occurred between the seasons of mate choice and breeding ($t = 7.3$, $df = 170$, $P < 0.0001$) and between breeding

TABLE 5. Summary of statistical conclusions about sexual dimorphism in the Barn Owl.

Character	Study location			
	Utah ^a	Utah ^b	New Jersey ^c	Germany ^d
Wing chord	NS	NS	NS	NS
Body mass	<0.0001	<0.001	<0.001	NS
Tail length	NS	NS	<0.001	NS
Beak length	<0.0001	<0.05	—	<0.05
Tarsus length	0.02	NS	<0.001	NS
Foot length	<0.0001	—	<0.001	—
Total length	0.0005	NS	<0.001	—

^a This study.

^b Looman (1985).

^c Colvin (1984).

^d Mlikovský and Piechocki (1983).

and nonbreeding seasons ($t = 7.02$, $df = 98$, $P < 0.0001$). Mean female mass was not significantly different between nonbreeding and mate-choice seasons ($t = 1.69$, $df = 144$, $P = 0.09$). Females were heaviest in March, the month in which most egg laying commences. Females weighed more than once ($n = 25$) showed greater individual variance in weight change than males: 0–250, with a mean of 66.6 g. Thus, the time of year strongly influences female mass and must be considered when attempting to evaluate mate choice by size. However, the time of year that male mass is taken does not appear to be particularly critical in judging whether mate choice by size occurs.

The 66 Utah pairs included 46 owls weighed during November–January, the season during which most pair bonds are formed. Mean mass of males ($n = 27$) in this subsample was greater than that of any other subsample from the Utah population (499.2 ± 38.3 g). These data further support the idea that males successful in pairing are those that occupy good hunting areas. Mean mass of females ($n = 19$) in this group, however, was much less than other subsamples of the Utah population (533.2 ± 40.2 g). These data are too few to be conclusive, but they cast further doubt that female Barn Owls chose mates on the basis of small size.

DISCUSSION

Sexual dimorphism.—Sexual dimorphism has also been studied in breeding Barn Owls in New Jersey (Colvin 1984) and in juvenile Barn Owls in Utah (Looman 1985). My results are con-

TABLE 6. Sexual dimorphism indices^a compared from several Barn Owl populations.

	California (Earhart and Johnson 1970)	Utah (this study)	New Jersey (Colvin 1984)	East Germany (Mlikovský and Piechocki 1983)	France (Baudvin et al. pers. comm.)
Wing chord	1.40	0.37	1.19	0.14	—
Body mass ^b	3.35	6.20	6.09	1.81	5.60

^a Storer 1966.

sistent with these studies. Differences in individual characters are minor among the three studies, and may be the result of measuring techniques (Table 5). Two studies of European birds concluded that the Barn Owl (*T. a. alba* and *T. a. guttata*) is the least dimorphic of owls in the western Palearctic (Mlikovský and Piechocki 1983, Lundberg 1986). Measurements of RSD in three subspecies of Barn Owls reveal high consistency in wing chord but less so in mass (Table 6). Some Barn Owl races may not exhibit any sexual dimorphism (Amadon 1942, De Groot 1983).

Earhart and Johnson (1970) determined that the Barn Owl is less sexually dimorphic than most other North American owls, but this conclusion was based on a small sample (males = 16, females = 21) of museum specimens. The mean mass that Earhart and Johnson (1970) calculated was only 86% of what I found for females and 93% for males. I discovered considerably higher dimorphism in mass than they did (Table 6).

Age dimorphism.—Few investigators have studied size dimorphism by age in raptors, and the results are inconsistent. Adults of North American accipiters are significantly larger and heavier than immatures (Mueller et al. 1976, 1981a, b). Wings of adult Northern Harriers (*Circus cyaneus*; Bildstein and Hamerstrom 1980) and adult Northern Saw-whet Owls (*Aegolius acadicus*; Mueller and Berger 1967) are significantly longer than yearlings. Conversely, immatures of heavy-bodied short-tailed falconiforms have longer wing and tail feathers than adults have (Amadon 1980). No differences in size are apparent in Merlins (*Falco columbarius*; Temple 1972) or Snowy Owls (*Nyctea scandiaca*; Josephson 1980) between adults and immatures.

Differences in morphology between adults and juveniles of some raptors have been attributed to difficulties in refining the techniques of prey capture (Amadon 1980, Mueller et al. 1981b). Immature Barn Owls may not require a

set of morphological traits different from adults to perfect their hunting prowess. Barn Owls hunt in slow quartering flight, and attack by closing their wings and dropping on their prey. Their nocturnal hunting and nearly silent flight make it difficult for prey to detect them. Thus, even though Barn Owls prey upon agile species, the prey must seldom have the opportunity to escape.

Mate choice.—There are many potentially important reasons for animals to choose mates rather than to mate indiscriminantly (Halliday 1983). Apparent mate choice in the field, though, may not be choice if there is little or no opportunity to discriminate between potential mates (Parker 1983). Theoretical arguments strongly favor active female choice of a mate (Mayr 1972, Trivers 1972) and, if it occurs, female choice of a mate by size could be a powerful force in shaping some male characteristics. In fact, sexual selection has been invoked as an explanation of RSD in raptors (Smith 1982, Safina 1984, Mueller 1986).

Trivers (1972) hypothesized that sexual selection is governed by the relative parental investment in the offspring. Triver's hypothesis has been neglected by those seeking to implicate sexual selection as a cause of RSD. Among owls, both sexes exhibit extensive, though largely different, parental investment. Females produce eggs, incubate, and brood; and males hunt for and provision their mates and young. Asynchrony of incubation and hatching in owls lengthens the dependency period compared with birds that hatch synchronously. Large clutches, common in the Barn Owl, further extend the time to raise young. Thus, one might expect both sexes to exhibit mate choice because of the relatively long time when sex-role partitioning is important. Based on my results, the basis for that choice in Barn Owls is some trait other than body size.

Population density is another seemingly overlooked factor in relation to both mate choice

and its possible influence upon RSD. Owls are top predators and exist at lower population densities than many bird species. As a result there may be little opportunity for either sex to compare and choose among potential mates. If owls have only limited opportunity for choice among potential mates, the origin and maintenance of RSD probably has little to do with mate choice. The Barn Owl population I studied occupied a restricted area on the fringe of the species' distribution. The population was small and probably offered less mate choice than denser populations. My sample represents a large percentage of the population, and I am confident that the conclusions on mate choice are valid for this population. My data, in failing to support the notion of females choosing small mates, are consistent with Bowman's (1987) conclusion about the American Kestrel (*Falco sparverius*).

Other considerations about RSD.—Earhart and Johnson (1970) concluded that sexual size dimorphism is an adaptation for efficient use of environmental resources. They found that greater size dimorphism correlated with a high percent of vertebrates in the diet among North American owls. However, the intersexual differences in diet among owls that they proposed are not supported by available evidence (Lundberg 1986), nor does the Barn Owl correspond with Earhart and Johnson's trend. Barn Owls on my study area consumed nearly 100% vertebrate prey (Marti 1988a) as they do in most other populations (Marti 1988b), but they rank low in size dimorphism compared with other owls. Interspecific comparisons of diet cast further doubt that RSD is important in diet partitioning between sexes. Of 8 western Palearctic owl species with a wide range in degree of RSD and body size, all feed on prey of very similar size, primarily microtine rodents (Mikkola 1983).

Mate choice (females choosing small males) and diet separation appear to be weak explanations for RSD in the Barn Owl. Several investigators have proposed that a division of labor in reproduction may be what originated and maintained RSD (Andersson and Norberg 1981, Korpimäki 1986, Lundberg 1986, Mendelsohn 1986). My results support the suggestion that smaller body size in males would be more efficient for finding and transporting prey to the mates and young (Mosher and Matray 1974, Wijnandts 1984). Mosher and Matray (1974) predicted that RSD in the Broad-winged Hawk (*Bu-*

teo platypterus) could save 23% of the pair's daily energy requirements compared with a pair of the same body size. Wijnandts (1984) documented a seasonal mass change in female Long-eared Owls (*Asio otus*) similar to what I report in the Barn Owl. He estimated that at peak mass (time of hatching), the female's flight cost is twice that of the male. Male Long-eared Owls double their flight expenditure during the breeding season making smaller body size especially important for energy conservation. The advantages of RSD in wing loading may be greater for Barn Owls than for most other owls because Barn Owls produce larger broods, occasionally have two or more broods per year, and are sometimes polygynous (pers. obs., B. Colvin and P. Hegdal, pers. comm.). Thus, smaller males with lower wing loading may be able to raise more young than males less efficient in flight.

I suggest that the following sequence of events may be responsible for the evolution of RSD in Barn Owls and other raptors. During egg development, females that quit hunting and are fed by their mates produce more offspring than those that risk egg damage in hunting. Females are predisposed to stay at the nest because of their investment in the eggs. Increased size could result in the ability to accumulate energy reserves for egg laying (Perrins 1970), production of larger eggs (Reynolds 1972, Selander 1972), more effective incubation (Snyder and Wiley 1976), ability to withstand lower temperatures without increasing heat production (Peters 1983), protection of the nest (Storer 1966, Reynolds 1972), and the ability to withstand periods of food shortage (Lundberg 1986). In fact, McGillivray (1987) found that the body core of female owls is larger than that of males, whereas other skeletal parts are not. On the other hand, males required to provision their mates and young would have been affected by a different array of selective pressures that emphasize efficiency of hunting. These factors predict, in accord with Pleasants and Pleasants' (1988) conclusion about falconiforms, that females increased in size from the ancestral type, whereas males did not change in size.

It seems likely that any prey-size differences between sexes in raptors are the result of—and not the cause of—RSD. The diversity of niches and behavior (i.e. prey type, hunting mode, hunting habitat) could be responsible for the degrees of RSD among raptor species. A correct

understanding of the origin and maintenance of RSD will most likely come through comparative studies of many species (Mueller and Meyer 1985, Mueller 1986, Pleasants and Pleasants 1988). Before this question can move from theoretical considerations and be tested adequately, detailed information on the morphology, behavior, and ecology (including precise sex-specific time and energy budgets) of many species is needed.

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