Sexual Size Dimorphism, Mate Choice, and Productivity of Burrowing Owls

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In most avian species, the male is larger than the female, but birds in the orders Falconiformes and Strigiformes, among several others, exhibit reversed sexual size dimorphism (RSD), with the female characteristically larger than the male (Earhart and Johnson 1970, Amadon 1975, Smith 1982, Pleasants and Pleasants 1988). The Burrowing Owl (*Speotyto cunicularia*) is the only North American strigiform that does not exhibit RSD (Earhart and Johnson 1970).

Many authors have attempted to explain the evolution of female size and RSD in raptors. Mueller (1986) categorized possible causes of RSD as being related to (1) ecology, (2) sex-role differentiation, and (3) behavior. Using empirical analysis, he argued convincingly against theories related to ecology or sex role differentiation. Many remaining behavioral theories of RSD assumed female dominance, which results from greater size. Data on food habits, intersexual differences in diet, and mechanisms of pair formation from individuals for which masses and morphological dimensions were known could help explain the evolution of RSD (Earhart and Johnson 1970, Mueller 1986, Marti 1990).

The possible relationship of body size to mate choice by Burrowing Owls has not been studied previously. Female selection for males based on some phenotypic expression of desirable genotypes has been speculated (O'Donald 1983), but little empirical data exist supporting selection of males with "good genes" by females (Parker 1983). Attributes such as size possess a genetic component, making these traits highly heritable. Although nonrandom mating based on body size is known, no evidence exists to support the view that mate choice is made on the basis of size (Cooke and Davies 1983). Marti (1990) found no evidence that female Common Barn-Owls (*Tyto alba*) selected smaller males as mates.

Our objectives were (1) to determine the degree of RSD exhibited by Burrowing Owls, and (2) to investigate the influence of individual size on mate choice and productivity. We examined the lack of RSD in Burrowing Owls, and illustrated its use in evaluating existing hypotheses of RSD in other raptors.

Methods.—The study was conducted at the U.S. Army Rocky Mountain Arsenal National Wildlife Area (RMA). The RMA is located in Adams County, Colorado and covers 6,900 ha. Elevation ranges from 1,564 to 1,625 m. Five major vegetation communities occur on the area: weedy forbs, cheatgrass (*Bromus* spp.)/weedy forbs, cheatgrass/perennial grassland, native perennial grassland, and crested wheatgrass (*Agropyron cristatum*; Environmental Science and Engineering unpubl. 1989 report).

Burrowing Owls were captured using single-door Tomahawk live traps (Martin 1971, Ferguson and Jorgensen 1981) and modified 7.6 × 8.9 × 22.8 cm Sherman traps (Plumpton and Lutz 1992). Trapping occurred from 11 May to 31 July 1990, and 20 April to 29 July 1991.

Captured owls were banded with U.S. Fish and Wildlife Service leg bands and visual-identification aluminum leg bands (Acraft Sign and Nameplate Co., Edmonton, Alberta, Canada). These bands were color anodized and engraved with an individual alphanumeric code that could be read through a spotting scope. Owls were weighed to the nearest 0.5 g using a spring scale. Wing chord was measured from the notch between the carpal and carpometacarpus bones of the folded wing to the tip of the 10th primary, with the wing unflattened. The tarsometatarsus was measured from the posterior of the hypotarsus to the notch formed between the distal end of the tarsometatarsus and the proximal phalanx of the third toe. The central rectrix was measured from the point of insertion to the distal end along the dorsal surface. Sex was determined by the presence of a brood patch (Martin 1973, Haug and Oliphant 1990) and plumage characteristics (Thomsen 1971, Martin 1973). When these characteristics alone were insufficient, banded owls were sexed later by observing sex-specific behaviors.

Because no differences in sexual dimorphism ($P > 0.05$) were found between years, data were pooled for analysis. Normality was determined using the Shapiro/Wilk test (Shapiro and Wilk 1965), and sexual dimorphism was analyzed using t-tests (SAS Institute 1988). A dimorphism index (DI; Storer 1966) was applied to mass, rectrix length, wing chord, and tarsometatarsus length.

Pearson product-moment correlations (SAS Institute 1988) were used to determine the extent to which mate choice was influenced by relative size. A given female body measurement was regressed against the same measurement from the male to which she was mated. Only those pairs in which both mates were trapped and measured were included in this analysis.

To determine the relationship between adult size

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TABLE 1.   Morphological measurements ($\bar{x} \pm$ SE with n in parentheses) and dimorphism indices (DI) of adult Burrowing Owls.

Measurement	Male	Female	DI[a]
Mass (g)*	146 ± 1.9 (38)	156 ± 3.6 (31)	6.62
Rectrix length (mm)*	80 ± 0.7 (38)	77 ± 0.7 (39)	−3.41
Wing chord (mm)*	163 ± 1.1 (38)	159 ± 1.1 (39)	−2.54
Tarsometatarsus length (mm)**	54 ± 0.4 (38)	51 ± 0.3 (38)	−4.90

*, $P < 0.05$; **, $P < 0.0001$.

[a] DI = $100(\bar{x}_, - \bar{x}_,)/[0.5(\bar{x}_, + \bar{x}_,)]$.

and productivity, Pearson product-moment correlations were used to evaluate the relationship of adult owl measurements to the number of young produced. Correlation matrices were computed separately for male and female adults. Nesting terminology used herein follows Steenhof (1987). Brood-size estimates were based on the maximum number of young observed at the burrow between brood emergence and fledging. These data were collected from captures, incidental observations, and during time-budgeting sessions.

Results.—In 1990 and 1991, 33 adult males (41 times), and 37 adult females (49 times) were captured. Using dimensions from only the first capture of an individual in a given year provided a total of 38 male and 39 female adults in analyses.

Male and female Burrowing Owls were significantly ($P < 0.05$) dimorphic (Table 1). Females were heavier, while males were significantly larger for all linear dimensions.

Mate choice in 27 pairs studied was not influenced by size, as no linear relationship ($P > 0.05$) existed for body measurements between mated birds. As with measurements of the entire adult population captured at RMA, males were larger ($P < 0.05$) than their mates, with the exception of mass (Table 2).

For both years combined, productivity was 4.38 chicks per nesting territory (range 2–10). With the exception of female wing chord ($P = 0.03$), no correlation ($P > 0.05$) existed between any body measurement and productivity for either males or females (Table 3). Female size showed higher, but nonsignificant, correlations to productivity than did male size in the other three measurements.

Discussion.—Wing-length dimorphism indices from the literature ranged from −1.10 for the Flammulated Owl (*Otus flammeolus*) to 6.64 for the Great Horned Owl (*Bubo virginianus virginianus*). The Burrowing Owl

had the largest negative index for wing length for any species presented (−1.71; Earhart and Johnson 1970). For all four body measurements we evaluated, Burrowing Owls exhibited sexual dimorphism that was statistically significant, but mass was the only measurement that showed reversed dimorphism. Female mass in our study fluctuated greatly before and after egg laying. For this reason, masses of females known to be carrying eggs ($n = 8$, range 197–238 g) were excluded from the analysis. However, we believe that female masses still were inflated due to the large number of females trapped shortly before egg laying. Based on wing chord and mass, Burrowing Owls were previously said to be monomorphic (Earhart and Johnson 1970, Mueller 1986). Since females were smaller in all linear dimensions, we believe nonnesting masses would be lower than found for males.

Mueller (1986) refuted ecological and sex-role differentiation hypotheses for RSD, leaving only the behavioral hypotheses as possible explanations of RSD. The behavioral hypotheses include those involving sociability, anticannibalism, pair bonding, role partitioning, and male provisioning. The sociability hypothesis maintains that colonial species are less dimorphic than solitary species, since colonial species engage in group defense against predators, eliminating the need for larger females (Snyder and Wiley 1976, Walter 1979). The Burrowing Owl is one of only a few colonially nesting raptors, and it does not exhibit RSD, which is in support of this theory (Mueller 1986). The Burrowing Owl also is the only burrow-nesting North American raptor.

Male Burrowing Owls were significantly larger than females in all linear measurements. Burrowing Owls, therefore, provide evidence contrary to anticannibalism, pair-bonding, and role-partitioning hypotheses, since the size-induced female dominance on which these theories are based is not found in Bur-

TABLE 2.   Mean morphological measurements (±SE) and correlation coefficients for mated pairs ($n = 27$) of Burrowing Owls.

Measurement	Male	Female	r	P
Mass (g)	148 ± 2.08	172 ± 6.30	0.32	0.12
Rectrix length (mm)	80 ± 0.73	78 ± 0.89	0.05	0.81
Wing chord (mm)	164 ± 1.41	161 ± 1.28	0.15	0.46
Tarsometatarsus length (mm)	55 ± 0.36	52 ± 0.35	−0.02	0.94

TABLE 3. Correlation coefficients (r) of adult morphological variables with productivity (reproductive success) of paired Burrowing Owls.

Adult variable	Male			Female		
	r	P	n	r	P	n
Mass	0.15	0.40	33	−0.26	0.18	28
Rectrix length	0.05	0.56	33	0.37	0.05	36
Wing chord	−0.11	0.79	33	0.33	0.03	36
Tarsometatarsus length	0.09	0.63	33	0.15	0.40	35

rowing Owls. One could argue that Burrowing Owls deviate sufficiently from the "typical" raptor by exhibiting both coloniality and burrow nesting that they can be considered as an exception to these theories. However, all owl species are highly uniform in sex roles during reproduction (Mueller 1986), regardless of nesting substrate. Selection for RSD should therefore have acted similarly on all owls.

Marti (1990) found no evidence to support the hypothesis that female Common Barn-Owls chose small males as mates. Similarly, we found that Burrowing Owls failed to display obvious mate choice based on physical size alone. Processes involved in maintenance of RSD, and selective pressures in mate choice are seemingly independent.

Size and mass of parent birds have been hypothesized to account for different sex roles in reproduction (Mueller 1986). Predatory ability (Andersson and Norberg 1981), nest defense (Storer 1966, Reynolds 1972), and egg-laying and incubating capacity (Reynolds 1972, Cade 1982) may be affected by size. However, we found physical attributes of parent Burrowing Owls were poor predictors of productivity.

We contend that any hypothesis for RSD that is intended to gain acceptance should apply universally to all raptors, and should explain exceptions. Our study has illustrated a largely neglected fact: that Burrowing Owls may represent the extreme opposite of the trend toward RSD in raptors, and may provide clues useful in discerning the true causes of RSD.

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Male Yellow Warblers Vary Use of Song Types Depending on Pairing Status and Distance from Nest

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Male birds use their songs in interactions with females and other males (for review, see McGregor 1991). Males normally use the same songs for both functions, but certain paruline warblers (and some species from other taxa) seem to divide their repertoire according to function (for review, see Spector 1992). For example, male Yellow Warblers (*Dendroica petechia*) sometimes sing one song type repeatedly (type I song), but at other times use a repertoire of several song types with little immediate repetition of each (type II song). Results from Spector (1991) and earlier studies (Ficken and Ficken 1965, Morse 1966) indicate that males use type I songs more in intersexual interactions, and type II songs more in intrasexual ones. Evidence that males direct type I songs toward females comes from the association between the use of this song type and both the male's proximity to his mate and his mating status.

Spector (1991) removed females from the territories of four pairs of Yellow Warblers and monitored the singing behavior of the male. All four females were incubating, a stage of the breeding season when type II singing normally predominates. Each of the four males increased the amount of type I song used after the removal of the female, but showed no corresponding increase in type II songs. Males that re-mated showed a rapid decline in type I singing.

In an attempt to replicate these findings, we performed a similar female-removal experiment using five pairs of Yellow Warblers. This is a small sample, but adequate when considered with four pairs studied by Spector (1991). Removal experiments are disrup-

tive to the birds, so we wished to keep the sample at a minimum.

We also investigated the relationship between song type use and distance from the nest. Spector found that male Yellow Warblers varied their song type use depending on the sex of the individual with which they were interacting; males were more likely to use type I songs when interacting with females, and type II songs when interacting with males. We were not able to identify with certainty the sex of the individual a male was interacting with. However, it is likely that distance from the nest, at least during incubation, was related to whether the male was interacting with his mate or with another male. Females rarely leave the nest at this stage, so when a male was close to his nest he was likely to be close to the female. For the same reason, males were less likely to be directing song toward their own mate when far from the nest (although they may have been directing it toward other females). It is at these greater distances from the nests that the most interactions with other males occurred.

Methods.—Subjects were six male Yellow Warblers from a population at Indian Point, St. Andrews, New Brunswick, Canada. The birds were color banded and their territories mapped during early June 1991. We found nests by following the female during nest building or following the male while the female was incubating (males feed females at the nest during incubation).

Once a nest was discovered and the female was incubating her clutch, we began tape recording the male. We visited each male's territory and recorded for a 10-min period, two to four times a day between 0700 and 1900 EST. Territories were visited in a similar order and, therefore, at similar times during each day of recording. We recorded two of the males (Figs.

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