Size, Dimorphism, and Related Characteristics of *Ciccaba* Owls From Guatemala

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Abstract.—Tropical owls, being poorly studied, have been excluded from discussions of reversed size dimorphism. As part of a breeding and food habits study, we weighed and measured 20 Mottled Owls (*Ciccaba virgata*) and a mated pair of Black-and-white Owls (*C. nigrolineata*) in northern Guatemala. Mottled Owls exhibited pronounced dimorphism with respect to body mass, wing chord, and tail length. A mated pair of Black-and-white Owls was also quite dimorphic with respect to body mass. Mate choice in six pairs of Mottled Owls was not correlated with size (mass or wing chord). Since both species are highly insectivorous, they do not fit an alleged trend among owls toward increasing dimorphism with increased reliance on vertebrate prey. Indeed, our results are at odds with important assumptions or predictions of numerous hypotheses regarding the evolution of reversed size dimorphism in owls.

Whereas in most bird species, males are larger than females, in owls (Strigiformes) and other raptors (Falconiformes) females are generally the larger sex. More than 20 hypotheses have been advanced to explain the evolution of this reversed size dimorphism, or RSD (for a summary, see Andersson and Norberg 1981, Mueller and Meyer 1985, and Mueller 1986). To date, owl data used for advancing and testing these hypotheses and associated assumptions and predictions have come from studies of those species living in northern temperate zones. Such studies have almost exclusively dealt with 18 North American owl species and 13 owl species that breed in Europe (a total of 24 species, since 7 are found on both continents). This temperate bias is natural enough, since little information on owls outside these areas is available. None-the-less, this bias may have important implications on the validity and generality of the resulting hypotheses.

Most researchers and theorists agree that the most valid field measurement for discussions of dimorphism is body mass (Amadon 1977, Cade 1960, Earhart and Johnson 1970, McGillivray 1987, Mueller 1986), and McGillivray (1987)

suggested that these be taken during the breeding season, since most hypotheses link the role of RSD to this critical period of the annual life cycle. Other measurements that have been analyzed for degree of dimorphism include wing length, tail length, bill length, tarsal length, and foot span (Earhart and Johnson 1970, Marti 1990, McGillivray 1987, Mueller 1986).

Between 1989 and 1992, we conducted research on two sympatric species, the Mottled Owl (*Ciccaba virgata*) and the Black-and-white Owl (*C. nigrolineata*), in Tikal National Park in Guatemala (Gerhardt 1991; Gerhardt *et al.* 1994a, 1994b). We studied the breeding biology, home range (Gerhardt *et al.* 1994b), and food habits (Gerhardt *et al.* 1994a) of these tropical owls, and recorded body mass and other measurements as we captured them. In this paper, we analyze those measurements with respect to dimorphism, and then discuss the implications of our findings upon various hypotheses regarding the causes and roles of RSD in owls.

METHODS

Trapping methods are described in Gerhardt *et al.* (1994b). All measurements were taken from breeding adult owls captured during the period beginning 1 month prior to egg-laying and ending at fledging of the young. Female body masses used in this analysis include only those

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taken during the nestling period. Owls were weighed to the nearest gram using a Pesola spring scale. Flattened wing chord and tail length (from insertion to tip) were measured to the nearest mm. Measurements are reported as means ± standard deviation. We applied to these measurements the dimorphism index (D.I.) devised by Storer (1966), D.I. = 100 (mean size of female - mean size of male) / 0.5 (mean size of female + mean size of male); we used the cube root of body mass to make the resulting index comparable to the indices of the linear measurements (Amadon 1943, Earhart and Johnson 1970). We also compared measurements between sexes using the Mann-Whitney "U" test (Siegel 1956), and applied Spearman rank correlations (Zar 1984) to size data from mated pairs to test for a linear relationship.

We weighed eggs (to the nearest 0.5 g) within the first week after they were laid, and checked clutch sizes periodically (Gerhardt *et al*. 1994b). We assessed diet through analyzing pellets collected from under roosts and near nests, and from direct observation and prey remains in nests (Gerhardt *et al*. 1994a). The percentage of pellets containing parts of prey taxa are reported.

Data on North American owls used for comparison were taken from Earhart and Johnson (1970).

RESULTS

Female Mottled Owls (334.9 ± 22.0 g, N = 11) weighed significantly more than males (239.7 ± 13.3 g, N = 7; U = 77; $p < 0.001$). D.I. for (the cube root of) body mass was 12.05. Females also had significantly longer wing chords (24.6 ± 0.6 cm, N = 12 vs. 23.3 ± 0.6 cm, N = 8; U = 96, $p < 0.001$) and tails (15.0 ± 1.0 cm, N = 11 vs. 14.1 ± 0.6 cm, N = 7; U = 71, $p = 0.002$). Dimorphism indices for wing chord and tail length were 5.43 and 6.19, respectively.

The female Black-and-white Owl had a body mass of 535 g, a wing chord of 29.3 cm, and a tail length of 18.7 cm. Her mate had a body mass of 436 g, a wing chord of 28.6 cm, and a tail length of 16.5 cm. These data yield dimorphism indices of 6.81 (cube root of body mass), 2.42 (wing chord), and 3.13 (tail).

The dimorphism of body mass of these two species is compared graphically with those of North American owls in figure 1.
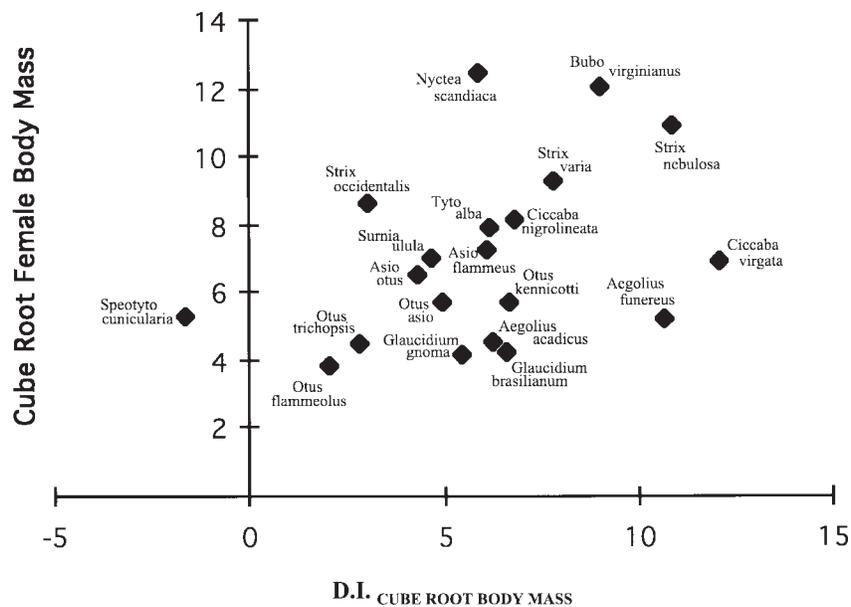

Figure 1.—*Cube root of female body mass vs. D.I.* CUBE ROOT OF BODY MASS *for North American owls and two* Ciccaba *owls.*

Mate choice in six pairs of Mottled Owls was not correlated with body mass (r_s = -0.147, p > 0.5) or wing chord (r_s = -0.135, p > 0.5), as no linear relationship existed for these measurements between mated birds.

Mean mass of Mottled Owl eggs was 28.2 ± 1.8 g (N = 16), and that of Black-and-white Owl eggs was 33.8 ± 2.3 g (N = 4). Mean clutch size for Mottled Owls was 2.2 ± 0.14 eggs (N = 13); each Black-and-white Owl clutch consisted of just one egg (N = 4) (Gerhardt *et al*. 1994b). Mottled Owl eggs and clutches weighed 8.4 percent and 18.5 percent of mean female body mass, respectively. Black-and-white Owl eggs (and, therefore clutches) weighed 6.3 percent of female body mass.

These two *Ciccaba* species differed in the mammalian component of their diets (Gerhardt *et al*. 1994a). Mottled Owls ate rodents, whereas Black-and-white Owls captured bats. Both species were highly insectivorous, however, and elytra and other hard beetle parts appeared in most pellets. Indeed, we observed other, more soft-bodied insects being eaten that were absent from pellets (and thus under-represented). Nonetheless, 98 percent of Mottled Owl pellets contained insect matter, and 44 percent contained only insect parts. Similarly, all Black-and-white Owl pellets contained insect parts, although 74 percent also contained some vertebrate remains (Gerhardt *et al*. 1994a). Figure 2 compares these two species, with respect to dimorphism and diet, with North American owls.

DISCUSSION

With respect to body mass, these Mottled Owls exhibited the most pronounced dimorphism yet documented among owls (fig. 1; Andersson and
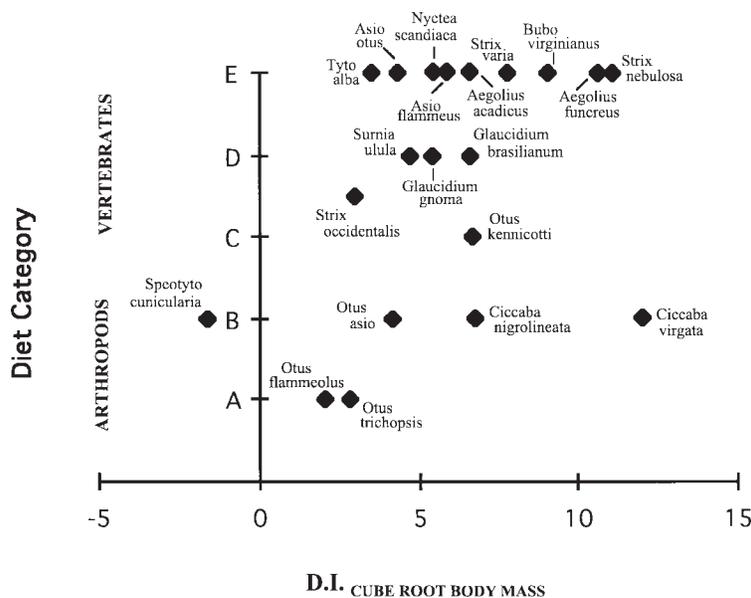

Figure 2.—*Relationship between food habits and dimorphism of North American owls (adapted from Earhart and Johnson 1970) with* Ciccaba virgata *and* C. nigrolineata *added. Diet categories are as follows: (A) feeds exclusively on arthropods; (B) primarily arthropods, few vertebrates; (C) arthropods and vertebrates in equal numbers; (D) primarily vertebrates, few arthropods; (E) exclusively vertebrates.*

Norberg 1981, Earhart and Johnson 1970, Mueller 1986), with the possible exception of the European form of *Aegolius funereus*, Tengmalm's Owl (Lundberg 1986, Korpimäki 1986). Extent of weight dimorphism might have been less if body mass had been measured during the non-breeding season. Most hypotheses concerning the role and evolution of RSD are associated with aspects of breeding biology, however, and we agree with McGillivray (1987) that this is the most appropriate time for measuring body mass. Given that weights were taken during the breeding season, our results were conservative; we used female body masses only from the nestling period (higher values would likely have been obtained pre-laying and during incubation) and male masses from throughout the breeding season (male weights would likely have been lower had we used only nestling period values). Moreover, Mottled Owls ranked third among new-world owls in dimorphism of wing chords, behind only *Nyctea scandiaca* and *Aegolius funereus* (Earhart and Johnson 1970).

The mated pair of Black-and-white Owls was relatively dimorphic with respect to body mass (fig. 1) and tail length, but less so with respect to wing chord. In other pairs that we observed, but did not capture, a similar size difference was quite visible. We suspect that Black-and-white Owls probably exhibit significant size dimorphism, and that the extreme dimorphism exhibited by these Mottled Owls is not an anomaly among tropical owl species.

Although no body masses are given, Wetmore (1968) reports wing and tail measurements suggesting substantial RSD in *C. virgata*, *C. nigrolineata*, and the Pulsatrix Owls, but not in Lophostrix. Among African owls, RSD is clearly indicated by body masses reported for the African Wood Owl (*C. woodfordii*) and the eagle owl species *Bubo africanus*, *B. capensis*, *B. lacteus*, and *B. poensis* (Kemp 1987, Fry *et al*. 1988), whereas fishing owls of the genus Scotopelia are apparently monomorphic with respect to body mass (Fry *et al*. 1988).

Walter (1979) suggested that nesting in cavities inhibits the development of RSD. Our findings refute this idea, since Mottled Owls invariably nested in cavities (Gerhardt *et al*. 1994b). Similarly, an important prediction of the nest defense hypothesis (Andersson and Norberg 1981, Cade 1982, Reynolds 1972, Snyder and Wiley 1976, Storer 1966) is that, since cavity

nests generally experience lower predation rates than open nests, cavity-nesting species should exhibit little dimorphism. Again, Mottled Owls bely this notion.

Proponents of the starvation hypothesis (Korpimäki 1986, Lundberg 1986) have used data primarily from European owl species to support their arguments. Simply stated, this hypothesis holds that larger females are better able to withstand harsh breeding season conditions, particularly in the early stages and at higher latitudes, and can incubate and brood longer during periods of poor or inconsistent prey deliveries by males. During 4 years of research in Guatemala, the harshest breeding season conditions were two consecutive nights of rain, with temperatures near 17° C. Moreover, during such conditions, prey remained abundant and active. If the starvation hypothesis accurately explains the role of RSD in European owls, it clearly does not do so for dimorphic tropical owls such as these *Ciccaba* species.

Researchers have tested whether mate choice is size-related in Barn Owls *Tyto alba* (Marti 1990) and Burrowing Owls *Speotyto cunicularia* (Plumpton and Lutz 1994), the latter being the only North American owl species in which males have larger body masses than females (Earhart and Johnson 1970). As in the Mottled Owls we examined, these studies concluded that mate choice was not influenced by size. It has been suggested (Marti 1990) that such findings refute the hypothesis that RSD evolved to facilitate female dominance in formation and maintenance of pair bonds (Amadon 1975, Cade 1982, Mueller 1986, Ratcliffe 1980, Smith 1982). We do not believe this to be the case. The evolution of RSD may be largely an accomplished process, in which case nearly all present-day individuals may fall within optimal size limits, and size may now be a less important factor in mate choice than other factors. The pair bond hypothesis remains an attractive one to us in that it would be equally applicable to tropical and temperate owls.

Three related hypotheses link RSD with relatively larger eggs (Cade 1982, Reynolds 1972, Selander 1972, von Schantz and Nilsson 1981), larger clutches (Mueller 1986), and more efficient incubation (Cade 1982, Snyder and Wiley 1976). That is, selection acts upon females, and favors larger size for reasons associated with egg-laying and incubation.

Mueller (1986) showed that a regression of egg mass upon female body mass had excellent predictive value, and found no correlation between RSD and the difference between observed and expected egg mass. Both Mottled Owls and Black-and-white Owls had egg masses much larger than those expected from the regression of data from North American owls (Mueller 1986), but it would be pointless to attempt to draw any conclusions from this fact. Rather, the point here is that, as with any hypothesis for the role of RSD, supporting arguments should be viewed as tentative and speculative until data on dimorphism and the associated trait, in this case egg mass, are available from the majority of owl species, most of which occur outside of the northern temperate zone.

The reproductive behavior of both *Ciccaba* species is in keeping with the trend among birds in general, in that tropical species have smaller clutches than ecologically similar or closely related temperate species (Lack 1966, Moreau 1944, Ricklefs 1969). That these *Ciccaba* owls also exhibit pronounced dimorphism is further evidence that facilitating larger clutches or more efficient incubation of clutches were not important causes of the evolution of RSD in owls.

Several hypotheses share the idea that RSD has evolved to allow members of a pair to capture different prey types or sizes (Andersson and Norberg 1981, Newton 1979, Reynolds 1972, Snyder and Wiley 1976, Storer 1966). These ideas enjoyed early popularity and, although more recent theorists (Korpimäki 1981, Lundberg 1986, Mikkola 1983, Mueller 1986, Mueller and Meyer 1985) have argued convincingly against prey-partitioning as a cause of RSD, these hypotheses remain in the conciousness when the subject of RSD arises. That the notion persists is exemplified by the following quote from Voous (1989): "Probably due to a rich supply of prey of different size, the Mottled Owl has apparently not needed to develop a noteworthy sexual dimorphism in size..." Taken as a whole, this statement appears to assume the validity of the prey-partitioning hypotheses. We have documented that the latter part of this statement is not true for the population that we studied. This is in spite of the fact that the first clause, that a rich supply of prey is available, is likely accurate.

Data on the diets of temperate owls generally fail to show that the sexes within a species are in fact utilizing different prey types or sizes (Korpimäki 1981, Lundberg 1986, Mikkola 1983, Mueller 1986, Mueller and Meyer 1985). Rather, proponents of prey-partitioning hypotheses have argued that there is a positive correlation between RSD and percentage of vertebrate prey in the diet (Andersson and Norberg 1981, Earhart and Johnson 1970, Snyder and Wiley 1976) and that highly insectivorous owls exhibit relatively little dimorphism. The diet of these *Ciccaba* owls is at odds with this assumption, since both species are quite insectivorous and exhibit pronounced dimorphism (fig. 2). Whereas the positive correlation between RSD and percentage of vertebrate prey is the strongest, albeit indirect, argument for the prey-partitioning hypotheses, even this correlation is not supported with the inclusion of these tropical species.

Most discussions of the role and evolution of reversed size dimorphism in owls have had, naturally enough, a temperate zone bias. In some, there seems to be an underlying assumption that unstudied tropical owls neither exhibit pronounced dimorphism nor confound our favorite hypotheses. We have documented pronounced dimorphism in *Ciccaba virgata*, and have evidence for dimorphism in *C. nigrolineata* as well. This finding is at odds with basic assumptions or predictions of numerous hypotheses regarding the evolution of RSD. A gap clearly remains in our understanding of tropical owls; we believe that, as a corollary, a large gap remains in our understanding of the role and evolution of RSD in owls.

ACKNOWLEDGMENTS

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