

Wilson Bull., 101(3), 1989, pp. 486–491

The evolution of reversed sexual dimorphism in owls: corrections and further analyses.—

My paper on reversed sexual dimorphism (RSD) in owls (Mueller 1986) contains three errors in transcription and one serious computational error. In Table 1, the dimorphism ratio for wing loading for the Great Horned Owl (*Bubo virginianus*) is 0.836, not 0.845. In Table 2, the dimorphism ratio for the cube root of weight for the European Eagle-Owl (*Bubo bubo*) is 0.906 not 0.960, and the ratio for dimorphism in wing loading for the Great Gray Owl (*Strix nebulosa*) is 0.808, not 0.888. In computing the Spearman Rank correlation coefficient between female dominance and RSD in weight, I inadvertently used a sample of weights taken from Glutz and Bauer (1980), which I had used in a preliminary version of the manuscript. The weights used in all other calculations were taken from Mikkola (1983), which I chose because it provided much more data on diet and slightly more data on weights and wing measurements. The correlation between the weights from Mikkola and female dominance is only $r_s = 0.486$, far from statistically significant and far from the $r_s = 0.943$, $P = 0.01$ obtained using the weights from Glutz and Bauer. I discovered this computational error in comparing my paper with that of Lundberg (1986).

The considerable differences between the samples of Lundberg, Mikkola, and Glutz and Bauer led me to extract yet another sample from Cramp (1985). This sample was selected with the following guidelines: (1) that an adequate sample be obtained, (2) where possible, weights from the breeding season were avoided because of the great changes that occur in the weights of females at this time, and (3) where possible, weights and wing measurements were from the same locality or region because RSD in wing and weight appear to vary geographically. The sample I extracted from Glutz and Bauer (1980) followed guidelines (1) and (3) but used weights from the entire year. Lundberg (1986) attempted to calculate an average weight for the entire year and generally used the largest sample or samples available for both weight and wing. Mikkola (1983) simply lists the sources from which he compiled his sample. The four samples of RSD in wing and weight are given in Table 1. Rankings for female dominance as given in Mueller (1986) are correlated with RSD in weight in two of the four samples: Glutz and Bauer (as indicated above), Cramp ($r_s = 0.943$, $P = 0.01$) and nearly so for Lundberg ($r_s = 0.771$, the critical value for $P = 0.05$ is 0.829). Female dominance is correlated with RSD in wing for the samples from Lundberg, Glutz and Bauer, and Cramp, and nearly so for the sample from Mikkola ($r_s = 0.829, 0.886, 0.829$, and 0.714, respectively).

Cramp (1985) provides further information on female dominance in intra-pair interactions, allowing the ranking of two additional species. Description of the essentials of behaviors suggesting female dominance as extracted from Glutz and Bauer (1980) and Cramp (1985) are summarized below, with the species listed in descending order of estimated relative female dominance. All of these owls have been well studied in the field and in captivity except where noted. Scientific names are given in Table 1.

(1) *Eurasian Pygmy-Owl*.—Males and females appear to be shy of contact with each other, even during the breeding season. Pairbonding includes alternation of fear and aggression to the mate. Pursuits and attacks occur and females chase males for 20–30 m. If the male loiters in the vicinity of the nest without food when the young are hungry, the female will drive him away. In small cages, females will kill males.

(2) *Boreal Owl*.—Captives have not been observed. Territorial males drive off all intruders including females that fail to give the appropriate vocalization. A male will break-off courtship if a female ceases vocalizing or switches to aggressive vocalizations. Pair formation may take days when behavioral interactions are not balanced and the male is strongly

TABLE 1
REVERSED SEXUAL DIMORPHISM (MALE/FEMALE) IN WING AND THE CUBE ROOT OF
WEIGHT^a OF EUROPEAN OWLS

	Mikkola	Lundberg	Glutz	Cramp
Common Barn-Owl (<i>Tyto alba</i>)	0.997 (0.952)	1.000 (0.956)	1.002 (0.980)	0.997 (0.991)
Eurasian Scops-Owl (<i>Otus scops</i>)	0.977 (0.950)	0.978 (0.950)	0.972 (0.950)	0.994 (0.975)
Northern Eagle-Owl (<i>Bubo bubo</i>)	0.932 (0.906)	0.943 (0.920)	0.945 (0.935)	0.921 (0.927)
Snowy Owl (<i>Nyctea scandiaca</i>)	0.926 (0.917)	0.931 (0.930)	0.926 (0.934)	0.913 (0.847)
Northern Hawk-Owl (<i>Surnia ulula</i>)	0.992 (0.955)	0.985 (0.945)	0.993 (0.945)	0.983 (0.945)
Eurasian Pygmy-Owl (<i>Glaucidium passerinum</i>)	0.942 (0.948)	0.919 (0.936)	0.924 (0.926)	0.926 (0.926)
Little Owl (<i>Athene noctua</i>)	0.988 (0.994)	0.973 (0.977)	0.968 (0.968)	0.982 (0.978)
Eurasian Tawny Owl (<i>Strix aluco</i>)	0.956 (0.933)	0.953 (0.927)	0.965 (0.935)	0.960 (0.947)
Ural Owl (<i>S. uralensis</i>)	0.966 (0.939)	0.979 (0.913)	0.978 (0.919)	0.986 (0.879)
Great Gray Owl (<i>S. nebulosa</i>)	0.931 (0.888)	0.981 (0.898)	— (0.905)	0.987 (0.899)
Long-eared Owl (<i>Asio otus</i>)	0.987 (0.959)	0.983 (0.946)	0.985 (0.932)	0.983 (0.950)
Short-eared Owl (<i>A. flammeus</i>)	0.992 (0.948)	0.989 (0.949)	0.995 (0.948)	0.988 (0.991)
Boreal Owl (<i>Aegolius funereus</i>)	0.933 (0.901)	0.961 (0.861)	0.947 (0.847)	0.977 (0.857)

^a In parentheses.

intimidated by the female. When food deliveries are insufficient, the female will leave the nest cavity and chase the male for minutes at a time.

(3) *Northern Eagle-Owl*.—No intersexual aggression has been recorded in the wild. Seldom show aggressive tendencies in captivity if kept at high densities. If only one female and one male are placed in an aviary, the female will kill the male if pair formation does not occur.

(4) *Ural Owl*.—No observations of intrapair aggression in the field, but considerable aggression seen in captivity (Scherzinger 1980). Although each sex will threaten and attack the other, most frequently females are the aggressor, particularly in intrapair interactions. High intensity aggressive behavior includes an owl flying rapidly at and over another and grazing it with outstretched talons. Birds displace partners from a roosting perch by bumping them or pulling them by the beak. A female will show a threat display to her mate if he is slow to deliver food or will even tug strongly on his beak.

(5) *Northern Hawk-Owl*.—All observations of pair formation and other interpair interactions are from captives in aviaries. Females react to courting males with aggressive vocalizations and with high intensity threat displays. In one case a female attacked her suitor and rammed him with her breast.

(6) *Little Owl*.—Little information from field studies and not much more from captives. In small cages, a female strikes strangers of both sexes and will even strike her own mate at the end of the period of the dependency of the young.

(7) *Eurasian Scops-Owl*.—Essentially no information from the field. Females will strike strangers of both sexes; males will not attack strange females. A male entering the nest cavity is repelled by vocalizations of his mate.

(8) *Common Barn-Owl*.—Although usually very sociable in captivity a female will chase a courting male if she is not in a mood for pairing.

These rankings for female dominance are significantly correlated with both RSD in weight and wing in all four samples: Lundberg, wing $r_s = 0.826$, weight $r_s = 0.762$; Mikkola, wing $r_s = 0.810$, weight $r_s = 0.667$; Cramp, wing $r_s = 0.833$, weight $r_s = 0.857$; Glutz and Bauer, wing $r_s = 0.786$, weight $r_s = 0.857$ ($P = 0.05$ at $r_s = 0.643$, $P = 0.01$ at $r_s = 0.833$). An evaluation of the limited amount of information available relevant to female dominance in owls by another investigator might yield rankings that differ from mine. I found indications of intersexual dominance from field studies for only two species and for seven species from studies of captives. Species (1), (3), (4), and (8) have been well studied in both field and captivity; in three species intrapair aggression was noted only in captivity, in species (1) females were more aggressive in captivity than in the field. Pair formation and intrapair interactions are certainly much easier to observe in captives, but it appears that confinement escalates levels of aggression. It also appears likely that the size of the cage and presence or absence of con- or even heterospecifics in the same, adjacent or nearby aviaries may influence the levels of aggression. This is obvious for the European Eagle-Owl and at least some of Scherzinger's (1980) observations of Ural Owls could be interpreted as aggression redirected to the mate because of the presence of mated pairs of conspecifics in nearby aviaries. In my rankings I gave priority to field observations. A more conservative approach would be to consider only the information from captive studies thus deleting species (2). Further conservative steps would be to assign tied ranks to species (1) and (3) because females of both species will kill potential mates, consider species (4), (5), and (6) as ties because all three females actually strike suitors or mates, and assign tied ranks to (7) and (8) because females both threaten suitors or mates but do not make aggressive physical contact. This approach eliminates the correlation between female dominance and RSD in weight: Lundberg, $r_s = 0.567$; Mikkola, $r_s = 0.472$; Cramp, $r_s = 0.661$; Glutz and Bauer, $r_s = 0.661$ ($P = 0.05$ at $r_s = 0.714$; $P = 0.01$ at $r_s = 0.893$). However, the correlation remains between female dominance and RSD in wing: Lundberg, $r_s = 0.810$; Mikkola, $r_s = 0.756$; Cramp, $r_s = 0.945$; Glutz and Bauer, $r_s = 0.756$. This quite conservative method of examining the information available yields a strong suggestion that there is a relationship between RSD and female dominance. However, we need considerably more, and better, data on behaviors associated with the formation and maintenance of pairbonds before we can really evaluate the possibility that RSD evolved to facilitate pairing in owls.

Jehl and Murray (1986) have proposed that reversed sexual dimorphism (RSD) evolved as a result of selection for small size in males for agility in aerial displays, and they predicted that aerial displays would be found in owls. This hypothesis was not considered in my 1986 paper. The 13 species of European owls have been sufficiently well-studied to permit a comparison of the degree of RSD in a species with the agility of aerial displays.

I present below condensed accounts of behaviors that appear to be aerial displays taken from each of the 13 species, with the species ranked in order of the complexity, variety and frequency of aerial displays (Glutz and Bauer 1980, Cramp 1985).

(1) *Short-eared Owl*.—Overall, this owl is primarily crepuscular, but during territory establishment it is inactive only for about 3–4 h during mid-day and for a longer period at night. It clearly has the most varied, elaborate and acrobatic flight displays of any species of European owl. Individual display flights may last for more than an hour, with the bird climbing quite rapidly to heights as great as 350 m with rhythmic wing-beats, with the wings appearing to pause momentarily at the peak of the upstroke and then bouncing back rapidly from the horizontal at the end of the downstroke. At the end of the circular climb, further climbing is interspersed with multiple wing-clapping in which the bird claps its wings together beneath the body usually 3–10, and sometimes as many as 20, times between wing-beats, producing sounds audible at some distance and losing altitude rapidly with each such display. The display flight culminates in a nearly vertical dive with wings held in a deep V and the bird rolling from side to side. Territorial encounters between males include aerial pursuit, rearing up in flight, attempting to get above the rival and grappling with each other, occasionally resulting in both males spiraling downward. The most spectacular and ritualized territorial display is the underwing-display in which a male flies with slow, deep wing-beats, bringing the wings high over the back to expose the undersides to rivals.

(2) *Long-eared Owl*.—This owl is crepuscular and nocturnal. The male regularly performs display flight, zig-zagging between trees, sometimes rising above them, flying with deep, slow wing-beats interspersed with glides and wing-claps. Maximum rate of wing-clapping is once per three wing-beats. Females also wing-clap occasionally, and the dominant of the two females paired with a bigamous male wing-clapped more often than the male.

(3) *Snowy Owl*.—This species primarily is diurnal and crepuscular. Displays are frequent; when the female is present (even as much as 1 km away) the male flies with wings held in a very deep V at the top of the stroke, causing it to drop ca 0.5 m; the height is regained with the subsequent downstroke. This undulating flight may cover as much as 1.5 km, and at the end the male rises 1.5 to 3 m and drops to the ground vertically with wings held in a V, sometimes flapping, sometimes not.

(4) *Common Barn-Owl*.—This species is nocturnal. The male often flies steadily over the territory, repeatedly changing direction and calling frequently. Males have been observed to ascend to a height of 50 m and descend in a spiral with exaggerated wing-clapping. In courtship, a male pursues a female in a twisting and turning flight with occasional wing-clapping, but the sound produced is variable in volume and the display does not appear to be as ritualized as in either species of *Asio*. In “moth flight,” the male hovers over the female for up to 5 sec, with occasional wing-clapping. The male flies with rapid wing-beats repeatedly in and out of the prospective nest site in the presence of a female.

(5) *Great Gray Owl*.—It is primarily crepuscular but is also active in daylight and at night. In courtship display, the male, usually carrying food in his beak, approaches the female in slow undulating flight, alternately flapping and then gliding with wings held in a V, although not as high as in the Short-eared Owl. Males will also pursue females in flight and there is one observation of a pair spiraling upwards in a circle of 6–10 m diameter, touching each others wings and later performing circular undulating flight, audibly beating wings against branches.

(6) *Eurasian Pygmy-Owl*.—This owl is crepuscular and diurnal. A highly aggressive species both in territorial defense and in early courtship, and most observations are of chases and attacks. When highly aroused by a rival, an individual may leave its perch in a flight that appears stiff and clumsy, moving to another perch or spinning upward in the air in tight circles.

(7) *Northern Hawk-Owl*.—This species is diurnal and crepuscular. The male performs territorial display-flights among trees, vocalizing frequently. Wing-clapping has been observed.

(8) *Northern Eagle-Owl*.—This owl is primarily crepuscular and nocturnal. Individuals of both sexes will chase others of their sex, but no contact has been recorded. The only apparent aerial display is driving flight in which the male follows the female in apparently normal flight behavior. Wing-clapping has been recorded once.

(9) *Boreal Owl*.—This species is nocturnal. Territorial defense appears to be almost entirely vocal. Males will approach playbacks and, exceptionally, swoop low over the observer. In one such case, the male bill-snapped and wing-clapped. Extensive observations of courtship have revealed no aerial courtship displays.

(10) *Tawny Owl*.—This species is crepuscular and nocturnal. Possible flight displays have been recorded only rarely. In one instance, a male left his roost 30 min after sunset and flew silently in broad spirals to a height of 200 to 250 m. In four other cases, a male descended to the female on stiff quivering wings. Reports of wing-clapping given in older handbooks have not been confirmed by modern observations.

(11) *Little Owl*.—This owl is active both nocturnally and diurnally. The only described behavior that might be an aerial display is that the male occasionally hovers over a perched female.

(12.5) *Eurasian Scops-Owl*.—This owl is nocturnal. No aerial displays have been noted, but the dominant pair will perform diving attacks on other individuals attempting courtship in an aviary.

(12.5) *Ural Owl*.—This owl is crepuscular and nocturnal. No aerial displays have been noted. Other courtship and territorial behaviors are similar to those of the Tawny Owl, and it is likely that aerial displays are absent or rare.

Spearman rank correlations between the ranks for aerial displays and RSD are: weight, Mikkola, $r_s = -0.022$; Lundberg, $r_s = -0.143$; Glutz and Bauer, $r_s = -0.019$; Cramp, $r_s = -0.146$; wing, Mikkola, $r_s = -0.078$; Lundberg, $r_s = -0.311$; Glutz and Bauer, $r_s = -0.396$; Cramp, $r_s = -0.017$. None of these approach statistical significance and all are negative. One might argue with some of my rankings of aerial displays, but no remotely reasonable reordering of ranks will begin to provide a significant positive correlation between RSD and the complexity, variety, and frequency of aerial displays in the species of European owls. This strongly suggests that the hypothesis of Jehl and Murray (1986) is not a viable explanation for the evolution of RSD in owls.

I have noted the inadequacies in the available data on pairbond formation and maintenance. There are also deficiencies in the data on weights and wing measurements. Some samples merely give means and not the sample size; few present standard deviations. Some samples are very small, e.g., the total number of individuals in all four samples of weights of the European Scops-Owl is six males and seven females; three of the samples are identical, consisting of average annual weights of four captives of each sex. A few of the samples of wing measurements are also of fewer than 10 individuals. The weights for some species (e.g., the Boreal Owl) appear to be entirely from the breeding season, for others the weights appear to be from all times of year. In some cases, weights are from one locality and wing measurements from another. There are more samples of weights and wing measurements available for the Little Owl than for any other species in Table 1. The range of the means of individual samples of RSD in wing for the Little Owl is 45% to 54% of that shown between the 13 species within the four compiled samples in Table 1. RSD in wing tends to increase with increasing geographic latitude in the Little Owl ($r_s = 0.725$, $N = 6$, $P > 0.05$). The range of the means of RSD in the cube root of weight for individual samples of the Little Owl is 77%–116% of that shown between the 13 species within the four compiled samples in Table 1. RSD in weight tends to decrease with increasing geographic latitude ($r_s = 1.000$, $N = 4$, $P = 0.05$). The range of the monthly means for a sample from a restricted geographic area (Westphalia) (Glutz and Bauer 1980) is 50% to 63% of the range between

the 13 species within the 4 compiled samples in Table 1. At the beginning of the breeding season, the weight of male Little Owls decreases 5.8% between March and April ($P < 0.07$), and that of females increases 11.4% ($P < 0.001$), producing a change in RSD from 0.977 to 0.924. The considerable differences in RSD between geographic regions, plus the seasonal differences in weights, can easily result in biased estimates of RSD.

Weights are subject to greater bias than wing measurements because they can vary with the season as well as tending to show greater geographical variation. Many of the samples in Table 1 are compilations from several sources; these sources often are used in more than one sample. All of the four samples in Table 1 for some species may be biased. We need more data on all aspects of the biology of owls before we can attempt to resolve the question of the evolution of RSD.

Acknowledgments.—I thank N. S. Mueller for independent rankings of flight displays and C. Marti, M. Green, and N. S. Mueller for comments on previous drafts of the manuscript.

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Wilson Bull., 101(3), 1989, pp. 491–493

Incidental “egg dumping” by the House Wren in a Yellow Warbler nest.—Incidental deposition of eggs in the nests of other species has been recorded occasionally in several species of birds (e.g., Bailey 1887; Wiens 1965, 1971; Holcomb 1967; Gustafson 1975; Carter 1987). Here I describe an instance of “egg dumping” by the House Wren (*Troglodytes aedon*) in a nest of the Yellow Warbler (*Dendroica petechia*). In addition, I introduced House Wren eggs into active Yellow Warbler nests to reveal the extent to which these eggs are tolerated and the likelihood that wrens will hatch and be reared by warblers.

On 31 May 1982, while studying the nesting biology of the Yellow Warbler in the dune-ridge forest, Delta Marsh, Manitoba (study area described in MacKenzie 1982), I discovered a lined, empty warbler nest about 1.5 m high in a sand-bar willow (*Salix interior*). Single Yellow Warbler eggs were laid in the nest each day from 1 through 3 June; three eggs were present on 4 June, but on 5 and 6 June the nest was empty. Single Yellow Warbler eggs