Wing Loading in 15 Species of North American Owls

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Abstract.—*Information on wing morphology is important in understanding the mechanics and energetics of flight and in aspects related to reversed sexual size dimorphism in owls. I summarized wing span, wing area, wing loading, root box, and aspect ratio calculations from the available literature and from 113 owls examined in this study. Wing loading estimates for 15 species ranged from 0.211 to 0.545 g/cm^2. Measurements were available for both male and female owls in 12 species; males of all species had a lower wing loading. In five species with sufficient sample sizes, males had significantly lower wing loading (18 percent on average) than females of the same species. Root box area (the area between the wings) averaged 15.4 percent of the combined wing and root box areas. Aspect ratio, the ratio of the wing span to mean wing width, ranged from 4.84 to 8.90. Information is presented for the following species: Barn (Tyto alba), Short-eared (Asio flammeus), Long-eared (A. otus), Great Horned (Bubo virginianus), Barred (Strix varia), Great Gray (S. nebulosa), Northern Spotted (S. occidentalis caurina), Snowy (Nyctea scandiaca), Eastern Screech- (Otus asio), Western Screech- (O. kennicottii), Flammulated (O. flammeolus), Northern Pygmy- (Glaucidium gnoma), Northern Saw-whet (Aegolius acadicus), Boreal (A. funereus), and Burrowing (Speotyto cunicularia) Owls.*

The type of habitat a flying or gliding animal chooses to live in, as well as its way of exploiting the habitat, are closely related to its body size, wing form, flight style, flight speed, and flight energetics. Natural selection is likely to act towards a wing structure that minimizes the power required to fly at the speed and style optimal for the animal, and is assumed to result in some near-optimal combination of these variables. The optimal flight speed varies with the flight goal and the type and abundance of food. To understand how flying animals work, their physiology, morphology, ecology, and wing function must be known.

Although there are many styles of wings, ornithologists generally recognize four basic wing types (Savile 1957). Woodpeckers, gallinaceous species, and most passerines have short, broad elliptical wings, designed for maneuvering through dense vegetation. Swifts, swallows, falcons, and plovers have long, narrow, slim, unslotted high-speed wings, designed for fast flight in open habitats. Shearwaters, albatrosses, and other seabirds have long, narrow, flat, high-aspect-ratio wings, designed for long-distance gliding. Last, storks, eagles, and vultures have high-lift or slotted soaring wings, which in large birds produces a very efficient soaring wing (Feduccia 1996). Most owls have relatively large, rounded, and slotted wings. Savile (1957) characterized the Eastern Screech-owl (Otus asio) as having a slotted high-lift wing. The "slotting" is a result of the abrupt narrowing (termed attenuation or emargination) in the distal end of up to five or six of the longest primaries. While this attenuation is limited in some owls, it is quite pronounced in others (see Averill 1927). Withers (1981) suggests that wing-tip slots have evolved because of biomechanical limitations to the bending strength of large, low-aspect ratio bird wings that could have detrimental aerodynamic consequences.

Wing loading is a metric used in determining the speed, dynamics of lift, and turning radius of birds (also bats and aircraft). It is expressed as the relationship between body mass and

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total wing area, calculated by dividing the weight of a bird by the surface area of both wings. Wing loading is expressed by grams per square centimeter (g/cm^2) (Clark 1971). Owls' wings are broad, with a large area in comparison to the weight of the bird, giving them a low wing-loading relative to other birds.

Another expression of wing morphology is called aspect ratio—the ratio of wing span to mean wing width. Thus, long and narrow wings designed for high speed, have a high aspect ratio, while short, broad wings designed for low speed and maneuverability, have a low aspect ratio. In general, wing length is somewhat shorter in those bird species which hunt in cover, and longer in those which hunt in open country or are highly migratory.

The objective of this paper is to summarize the relevant literature and to provide more specific information on wing span, wing loading, root box, aspect ratio, and male/female comparisons for the owls of North America.

METHODS AND MATERIALS

Wing data for eight species was extracted from the limited literature on this topic. Data for this study was obtained from the following locations: Great Gray Owls (Strix nebulosa) from southern Manitoba, Boreal Owls (Aegolius funereus) from Idaho, a Flammulated Owl (Otus flammeolus) from Colorado, and nine species of owls from Oregon. With the exception of eight Great Horned Owls (Bubo virginianus), the owls from Oregon came from the west side of the Cascade Mountains. Except for the Northern Spotted Owls (Strix occidentalis caurina), Boreal Owls, and one Barred Owl (S. varia), all owls examined were dead. Between 1988 and 1997, over 250 owl carcasses were examined. The owls were trauma-killed, the vast majority resulting from vehicle collisions. Only fresh specimens in excellent condition were used; owls with broken wing bones, torn skin tissue, a pronounced keel suggesting cause of death by starvation, other damage, or broken or molted wing feathers were discarded. The sex of dead owls was determined through internal sexing (e.g., by looking for testes or ovaries). The sex of live Northern Spotted Owls and the Barred Owl was determined by their vocalizations and by examination for the presence/absence of a brood patch (if during the nesting season). Northern Spotted Owl wing measurements were acquired during 1988-1989 in association with other activities during a demographic study on this species. Boreal Owls were sexed by their behavior during radio-telemetry studies during the nesting season (e.g., males delivering prey to nest site; females incubating and brooding) (G. Hayward, pers. comm.). Greg Hayward (unpubl. data) submitted wing areas, weights, and capture dates for all of the Boreal Owls examined in this study. Data on a large sample of Barn Owls (Tyto alba) was drawn from Marti (1990); differences in his methodology should be noted. Summary wing loading and aspect ratio calculations were determined using a weighted mean, that is: (mean of males plus mean of females)/2.

Wing span—Wing span is defined as the distance (mm) from one wing tip to the other, with the wings spread horizontally as far out as they will go (fig. 1). Wing span measurements were taken with the owls placed on their backs atop a tape measure.

Wing area—Owls were held with their body facing downward and a single wing spread over a paper on a board or table (see Pennycuick 1989, p. 11). Wing area was measured by tracing around each fully extended and flattened wing. Starting where the front of the

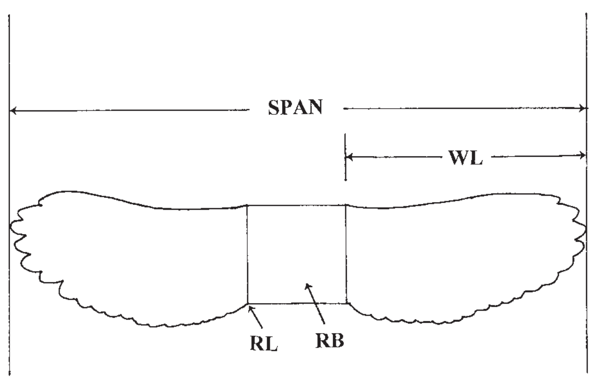

Figure 1.—Wing span is the wingtip-to-wingtip distance (in mm), with wings spread out to the sides to their fullest extent. WL = wing length, as measured (in mm) from the wing root line to tip of the longest primary. RL = root line, a straight line depicting the interface between the wing and the owl's body. RB = root box, (in cm^2). This (reduced) tracing is from a male Western Screech-owl (Otus kennicottii).

wing meets the body, a line was drawn following the outline of the individual feathers. After tracing the wing to where it again met the body (at the inside edge of the secondaries), the bird was lifted off the paper and a wing root line was drawn to the starting point, thus closing the wing polygon. Both wings from each owl were measured (except in Boreal Owls, where only one wing was measured). Wing tracings were digitized into a geographical information system (e.g., ArcInfo software) and the total area (cm^2) calculated. Areas of paired wings were generally within 0-3 percent of each other; the larger wing area was doubled and used in subsequent analysis. Tracing wings requires two people and some practice; the slight differences in paired wing areas were assumed to reflect differences in observer skills rather than real differences in wing areas of individual owls.

Pennycuick (1989) defines wing area differently: "...the projected area of both wings, fully spread out, including the area of that part of the body that is included between the wing roots." The literature on wing loading in owls does not generally reflect Pennycuick's methodology, as the area between the wings (called the "root box") is not typically included. For this paper, I have calculated the wing area and the root box area separately. Readers wishing to follow Pennycuick's methodology will need to sum the wing area and root box area for the owls. The study by Marti (1974) was the only one I could find which included the area between the wings in wing loading calculations. Because of differences in methodology, I was not able to include data from Marti (1974) in the tables or in the analysis.

Owl weights were determined in the field with a spring scale (e.g., Pesola brand) or in the laboratory with a digital scale and recorded to the nearest gram. For dead birds, prey remains and forming pellets were removed from the stomach before weighing.

A two-tailed rank sum test was used to examine statistical differences in wing span, wing area, and wing loading between male and female owls.

Wing loading—The ratio of bird weight to the area of both wings, expressed as g/cm^2. The calculations of wing loading in this paper do not include the area of the root box.

Wing length—Wing length was determined by measuring the perpendicular distance (mm) from the wing root line to the tip of the longest primary feather (fig. 1).

Root box—The area (cm^2) between the wings (fig. 1).

Aspect ratio—The aspect ratio is a simple measure of the shape of the wing. It is the ratio of the wing span to mean wing width. Wing width is the distance from the leading edge to the trailing edge, measured along the direction of flight. The mean wing width was determined by first summing the area of both wings with the area of the root box. This summed area was then divided by the wing span. The resulting number, multiplied by 100, was the mean wing width (in mm). The wing span was then divided by the mean wing width to derive the aspect ratio.

RESULTS AND DISCUSSION

The details of wing loading calculations and related wing measurements for 15 species of owls examined in this study and/or derived from other North American studies is shown in table 1.

Table 2 reflects a simplified, composite summary of wing loading data from table 1 to allow easy comparisons with information published for owls from other countries (e.g., Mikkola 1983, p. 350). Wing loading calculations for some owls from Europe (Mikkola 1983, p. 350) and North America have strikingly similar wing loading: Great Gray Owl (0.35/0.37), Short-eared Owl (0.34/0.33), Barn Owl (0.29/0.32), and Boreal (Tengmalm's) Owl (0.29/0.28), for Europe/North America, respectively. A larger difference was seen for the Long-eared Owl (0.31/0.21) and Northern Pygmy-owl (0.26/0.35), although this difference is likely an artifact of the limited North American sample sizes.

Poole (1938) offered weight, wing area, and wing area per gram (cm^2/g—the inverse of g/cm^2) for 143 species of North American birds. After excluding the owl species, and averaging the data for species with two entries (e.g., making a single entry for males and females of the same species) from Poole's data, 132 species of birds remain. In table 3, I summarize these 132 species by range of wing loading (g/cm^2) and offer an example of a species for each

Table 1.—Details of wing loading calculations for 15 species of North American owls. Weight, wing span, area of both wings, and wing loading data reflect mean ± one standard deviation (SD).

Species	Sex	N	Weight (g ± SD)	Wing span (mm ± SD)	Root box (mean cm^2)	Area of both wings (cm^2 ± SD)	Wing-loading (g/cm^2)	Source
Barn Owl	male	65	473.5 ± 32.3	-	-	1576.5 ± 149.6	0.300 ± 0.030	Marti 1990
(*Tyto alba*)	female	64	566.4 ± 66.2	-	-	1663.9 ± 145.5	0.340 ± 0.030	Marti 1990
	male	1	380	1085	304.3	1394	0.273	This study
	female	6	529 ± 26.9	1133 ± 51	288.2	1691 ± 139.7	0.315 ± 0.030	This study
	unk.	2	505	-	-	1683	0.300[1]	Poole 1938
Short-eared Owl	male	2	304	-	-	1082	0.281	Clark 1975
(*Asio flammeus*)	female	2	392.5	-	-	1016	0.385	Clark 1975
Long-eared Owl	male	1	230	-	-	1182	0.195[1]	Poole 1938
(*Asio otus*)	female	2	288	-	-	1198	0.240[1]	Poole 1938
	female	2	263.7	959	241.8	1293	0.204	This study
Great Horned Owl	male	2	1106	1238	357	2264.4	0.489	This study
(*Bubo virginianus*)	female	16	1345 ± 162	1336 ± 70	412.8	2748 ± 284	0.491 ± 0.046	This study
	female	2	1446.5	-	-	2534	0.571[1]	Poole 1938
(*B. v. pacificus*)	unk.	1	1480	-	-	2426	0.610[1]	Poole 1938
Barred Owl	male	2	655	1140.5	465.3	2128	0.307	This study
(*Strix varia*)	female	2	881	1121.5	343.7	2371	0.372	This study
	unk.	1	510	-	-	1830	0.279[1]	Poole 1938
Great Gray Owl	male	5	1015 ± 178	1348 ± 40	590.0	2822 ± 140	0.349 ± 0.069	This study
(*S. nebulosa*)	female	2	1275	1413	520.7	3275 ± 28	0.390 ± 0.100	This study
Northern Spotted Owl	male[2]	12	576.5 ± 44.9	1040 ± 29	233.2	1879 ± 81	0.275 ± 0.020	This study
(*S. occidentalis caurina*)	female[2]	11	667.2 ± 47.6	1046 ± 20	228.5	1953 ± 82	0.309 ± 0.026	This study
Snowy Owl (*Nyctea scandiaca*)	male	1	1404	-	-	2576	0.545[1]	Poole 1938
Eastern Screech-owl	male	2	178	-	-	523	0.340[1]	Poole 1938
(*Otus asio*)	female	1	254	-	-	476	0.534[1]	Poole 1938
	male[3]	8	152.3 ± 11.5[4]	-	-	406.8 ± 11.0	0.326 ± 0.008	Gehlbach 1994
	female[3]	8	173.9 ± 11.6[4]	-	-	463.3 ± 13.5	0.410 ± 0.012	Gehlbach 1994
Western Screech-owl	male	6	153.9 ± 20.9	581 ± 28	103.8	574.6 ± 55.4	0.269 ± 0.040	This study
(*Otus kennicottii*)	female	9	201.7 ± 27.5	618 ± 26	128.7	613.6 ± 64.9	0.331 ± 0.052	This study
Flammulated Owl (*Otus flammeolus*)	unk.	1	60.2[5]	418	49.8	288.6	0.208	This study
Northern Pygmy-owl	male	1	56.4	341	49.6	163.7	0.345	This study
(*Glaucidium gnoma*)	female	4	61.5 ± 8.3	322 ± 16	36.6	171.6 ± 7.7	0.361 ± 0.063	This study
Northern Saw-whet Owl	male	1	75.0	476	63.8	404.0	0.186	This study
(*Aegolius acadicus*)	female	3	91.2 ± 3.9	502 ± 5	85.4	387.9 ± 10.9	0.235 ± 0.016	This study
	unk.	1	108	-	-	420	0.257[1]	Poole 1938
Boreal Owl	male	13	115.5 ± 6.7	-	-	485.2 ± 21.3	0.239 ± 0.017	This study
(*Aegolius funereus*)	female	12	164.8 ± 11.1	-	-	545.2 ± 36.8	0.329 ± 0.022	This study
Burrowing Owl (*Speotyto cunicularia*)	male	2	145.6	595	102.4	543.9	0.266	This study

[1] Calculated from Poole's data.
[2] Of the Northern Spotted Owls in this sample, nine males and females were mated pairs: mean weight, area of both wings, and wing loading was 576.4, 1891.0, 0.274 for males and 676.1, 1966.2, 0.314 for females, respectively.
[3] These eight male and female Eastern Screech-owls were mated pairs. Except for weight, measurements are from these eight pairs.
[4] Weights from 13 males and 25 females during spring (March-June) (Gehlbach 1994, p. 66), as the specific weights for the 8 males and 8 females used in the wing loading calculations was not reported by Dr. Gehlbach.
[5] Reflects the weighted mean of 27 male and 25 female owls (Reynolds and Linkhart 1987, table 1).

Table 2.—Summary of wing loading calculations for 15 species of North American owls.

Species	Wing-loading (g/cm^2)[1]	Source
Snowy Owl (*Nyctea scandiaca*)	0.55	Poole 1938
Great Horned Owl (*Bubo virginianus*)	0.49	Poole 1938, This study
Eastern Screech-owl (*Otus asio*)	0.38	Poole 1938, Gehlbach 1994
Great Gray Owl (*Strix nebulosa*)	0.37	This study
Northern Pygmy-owl (*Glaucidium gnoma*)	0.35	This study
Barred Owl (*Strix varia*)	0.34	This study
Short-eared Owl (*Asio flammeus*)	0.33	Clark 1975
Barn Owl (*Tyto alba*)	0.32	Marti 1990, This study
Western Screech-owl (*Otus kennicottii*)	0.30	This study
Northern Spotted Owl (*S. occidentalis caurina*)	0.29	This study
Boreal Owl (*Aegolius funereus*)	0.28	This study
Burrowing Owl (*Speotyto cunicularia*)	0.27	This study
Long-eared Owl (*Asio otus*)	0.21	Poole 1938, This study
Flammulated Owl (*Otus flammeolus*)	0.21[2]	This study
Northern Saw-whet Owl (*Aegolius acadicus*)	0.21	This study

[1] Reflects the weighted mean ((mean males + mean females)/2) only for owls where sex was known.
[2] Flammulated Owl data is based on a single individual of unknown sex.

Table 3.—Wing loading data for 132 bird species calculated from Poole (1938). Owl species are excluded from this summary and species for which Poole had entries for both sexes have been averaged.

Range of wing loading (g/cm^2)	Number of species	Example Bird Species (g/cm^2)
0.71 - 0.80	3	American Coot (*Fulica americana*) (0.73)
0.61 - 0.70	4	Dovekie (*Alle alle*) (0.66)
0.51 - 0.60	6	Turkey Vulture (*Cathartes aura*) (0.55)
0.41 - 0.50	16	Common Snipe (*Gallinago gallinago*) (0.45)
0.31 - 0.40	14	Green-backed Heron (*Butorides striatus*) (0.35)
0.21 - 0.30	34	Gray Catbird (*Dumetella carolinensis*) (0.26)
0.11 - 0.20	31	Barn Swallow (*Hirundo rustica*) (0.14)

general range. Small passerines constitute the majority of species with wing loading less than 0.31 (table 3). Many factors (e.g., flight speed, body size, diet, migration, commuting, wing shape) collectively affect wing morphology, ultimately affecting wing loading characteristics.

Data to develop aspect ratio calculations was available for 13 species of owls. The aspect ratio for the owls examined in this study ranged from 4.84 to 8.90 (table 4). Species having the highest aspect ratio (long wing span relative to wing width) were the Short-eared, Barn, and Long-eared owls. This is not surprising as these owls hunt in the open while flying and regularly move over great distances. Those with the lowest aspect ratio (short wing span relative to wing width) were the Barred, Spotted, Northern Saw-whet, and Western Screech-owl. These species are sit-and-pounce hunters that spend their time in closed-canopy forests, often with very dense vegetation.

Root box areas were determined for 11 species (table 1) and averaged 15.4 percent of the combined wing and root box areas. For the

Table 4.—Aspect ratio calculations for 13 species of North American owls.

Species	Sample	Aspect ratio
Short-eared Owl (*Asio flammeus*)	2 males/2 females	8.90[1]
Barn Owl (*Tyto alba*)	1 male/6 females	6.72
Long-eared Owl (*Asio otus*)	2 females	6.00
Great Horned Owl (*Bubo virginianus*)	2 males /16 females	5.77
Eastern Screech-owl (*Otus asio naevius*)	1 unk.	5.50[2]
Burrowing Owl (*Speotyto cunicularia*)	2 males	5.50
Great Gray Owl (*Strix nebulosa*)	5 males/2 females	5.31
Northern Pygmy-owl (*Glaucidium gnoma*)	1male /4 females	5.22
Flammulated Owl (*Otus flammeolus*)	1 unk.	5.16
Northern Spotted Owl (*Strix occidentalis caurina*)	12 males /13 females	5.10
Northern Saw-whet Owl (*Aegolius acadicus*)	1 male /3 females	5.09
Western Screech-owl (*Otus kennicottii*)	6 males /9 females	5.08
Barred Owl (*Strix varia*)	2 males/2 females	4.84

[1] Clark 1975.
[2] Savile 1957.

most part, this percentage was relatively consistent among the owls (root box area was between 14.5 - 16.0 percent in eight species). The percentage of combined area in the root box was the smallest in Northern Spotted Owls (10.5 percent) followed by Great Horned Owls (13.3 percent), and largest in the Northern Pygmy-owl (20.5 percent).

An important aspect in flight is that of drag, some of which is generated from the body and some from its wings. The body diameter for two owl species was recorded by comfortably (feathers not compressed) wrapping a string around the owls, just behind the wings, and the length of the string measured to acquire the circumference. The diameter was then calculated. The diameter for one female Northern Saw-whet Owl was 64.7 mm; average for two male Great Horned Owls was 123 mm; average for four female Great Horned Owls was 133 mm.

Comparisons Between Males and Females

Wing span data was available for males and females of eight species (table 1). Barred Owl and Northern Pygmy-owl males had longer wing spans than females of these species. Female Barn, Great Horned, Great Gray, Spotted, Western Screech-owl, and Northern Saw-whet Owls had longer wing spans than males of these species. Sample sizes allowed statistical examination for two species. Female Western Screech-owls had significantly longer wing spans than males ($P = 0.01$). Northern Spotted Owl females had only slightly longer wing spans (6 mm on average) than males, and the difference was not significant ($P = 0.41$).

Wing area data was available for males and females of 12 species (table 1). While wing areas for male Short-eared and Northern Saw-whet Owls were larger than for females of these species, wing areas of female Barn, Long-eared, Great Horned, Barred, Great Gray, Northern Spotted, Eastern Screech-, Western Screech-, Northern Pygmy-, and Boreal Owls were larger than the males of these species. Sample sizes allowed statistical examination for five species (Barn, Spotted, Eastern Screech-, Western Screech-, and Boreal Owls). Wing areas were significantly larger in female Barn ($P = 0.0005$, Marti 1990), Northern Spotted ($P = 0.04$), Eastern Screech- ($P < 0.001$, Gehlbach 1994, p. 257), and Boreal owls ($P < 0.001$) than in males of the same species. While wing areas in female Western Screech-owls were larger than in males, the difference was not significant ($P = 0.22$). Great Gray Owls had the largest wing area of any of the owl species, and it was interesting that female Great Grays had wing areas 14 percent larger than males of this species.

Wing loading data was available for males and females of 12 species. Males of all species had lighter wing loading than females (table 1).

Sample sizes allowed statistical examination for five species (Barn, Northern Spotted, Eastern Screech-, Western Screech-, and Boreal Owls). For all five species, males had significantly lower wing loading than females of the same species; Barn ($P < 0.0001$, Marti 1990), Northern Spotted ($P = 0.002$), Eastern Screech- ($P = 0.01$, Gehlbach 1994, p. 71), Western Screech- ($P = 0.027$), and Boreal ($P < 0.001$) Owls. On average, wing loading was 18 percent (range 11.0-27.4 percent) lower in males for these five species.

Depending on the season, owl weights can change substantially, thus affecting wing loading calculations (McGillivray 1987). Seasonal weight changes in the Eastern Screech-owl reflected a total weight loss of 19 percent (Gehlbach 1994, p. 257), and 24 percent in Great Gray Owls (J. Duncan, unpubl. data). One nesting Great Gray Owl female went from 1,600 g in March to 1,000 g in July, a 37.5 percent decrease in weight (J. Duncan, pers. comm.). These changes are similar to the 15.2 ± 4.1 percent reported by Korpimäki (1990) for five species of breeding raptors including the Boreal, Little (Athene noctua), and Tawny (Strix aluco) Owls, and the 25 percent change in female Long-eared Owls (Wijnandts 1984). Seasonal weight differences of male and female owls is clearly an important aspect in wing loading and flight mechanics in owls. Sample sizes for some owls in this study were very small, and in general, are difficult to acquire. Additional owl weight information was summarized by Dunning (1985) and readers are referred to that work.

One particular Northern Spotted Owl (a female) examined in this study, had been captured and weighed seven times over a 12-year period. When first captured in 1976, she was 12 months old, and had just become established on a territory. Weights were acquired during the months of May, June, and August (the breeding season; she nested in only 2 of the years in which she was weighed). Her average weight was 683 g (range 605-733 g; a variation of ±13 percent from the mean). Assuming that her wing area remained relatively constant at 1,993 cm^2, her "average" wing loading was 0.343 g/cm^2 (range 0.304-0.368). Whether the change in weight was significant is debatable: (1) at 14 years, she was one of the oldest known Northern Spotted Owls living in the wild, (2) she seldom nested, possibly suggesting that she was in poor physical condition. Deteriorating habitat conditions within her consistently-held territory may have been a factor in her poor condition.

Andersson and Norberg (1981) noted that size affects the flight performance of birds, particularly in pursuit of prey, and suggested that this might be an important factor in the evolution of reversed sexual size dimorphism (RSD). Schantz and Nilsson (1981) believed that an important factor in the evolution of RSD is the relative ability to transport large prey. These aspects of flight are greatly influenced by wing loading. Mueller (1986) developed an index for wing loading, obtained by dividing weight by the square of "wing length" (actually the wrist-to-tip measurement). While a reasonable attempt, the index underestimated the differences in wing loading between male and female owls; differences found in this study were about twice that as determined by Mueller's index.

The aspect ratio for the owls examined in this study ranged from 4.84 to 8.90. In a review of 141 bird species, Norberg (1990, p. 239) noted that the aspect ratio ranged from 4.4 to 17.2. For comparison, the Gray Catbird's (Dumetella carolinensis) aspect ratio is 4.7 (Savile 1957), and that of Archaeopteryx is 7.0 (Norberg 1990, p. 243). In two species of albatross, where wing span greatly exceeds wing width, aspect ratios of 15 and 18 have been calculated.

Since flight is expensive, there should be strong selection to minimize the mechanical power required to fly. Low total power is attainable with a high aspect ratio, particularly when this is combined with a low body mass and low wing loading. Migratory species should have wings of high aspect ratio for enduring flight (Pennycuick 1975). Flying within vegetation puts demands on slow flight and short wings that have to be broad to compensate for their shortness and give enough area to allow slow flight. Slow flight and tight turning radius are achieved by a low wing loading (Norberg 1990). Species taking heavy prey should have a large wing area (low wing loading) so that they can carry the extra weight. The combination of aspect ratio and wing loading can reveal patterns which aid in understanding the relationship between wing shape, flight behavior, and foraging strategies in the owls (as well as in other birds and bats).

In this paper, "wing width" is the same measurement as "wing chord" (see Norberg 1987, Pennycuick 1989, p. 13). Some ornithologists use the term "chord" to refer to the distance from wrist to wing tip of the folded wing. As noted by Pennycuick (1989), the wrist-to-tip measurement is not the chord, and should be given a different name, such as "wrist-to-tip distance" or "folded wing length". The "wrist-to-tip distance" or "folded wing length" does not have any straightforward significance for flight mechanics. Mass, along with wing span, are measurements necessary for calculations of powered flight. Biologists are encouraged to record and report wing span, weights, and wing area information in conjunction with other efforts involving the handling of owls.

Cautionary note.—Sample sizes for many owl species in this study are quite small. As additional sample sizes are obtained, general and statistical comparisons of wing loading and other aspects of wing measurements will be substantially improved. In this study, sample sizes of 10 or more appeared sufficient to capture the majority of the variability in owl wing measurements.

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LITERATURE CITED

Andersson, M.; Norberg, R.A. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biological Journal of the Linnean Society. 15: 105-130.

Averill, C.K. 1927. Emargination of the long primaries in relation to power of flight and migration. Condor. 29: 17-18.

Clark, R.J. 1971. Wing loading—a plea for consistency in usage. Auk. 88: 927-928.

Clark, R.J. 1975. A field study of the Short-eared Owl Asio flammeus (Pontoppidan) in North America. Wildlife Society Monograph. 47. 67 p.

Dunning, J.B., Jr. 1985. Owl weights in the literature: a review. Raptor Research. 19(4): 113-121.

Feduccia, A. 1996. The origin and evolution of birds. Yale University Press. 420 p.

Gehlbach, F.R. 1994. The Eastern Screech-owl: life history, ecology, and behavior in the suburbs and countryside. Texas A&M University Press. 302 p.

Korpimäki, E. 1990. Body mass of breeding Tengmalm's Owl (Aegolius funereus): seasonal, between-year, site, and age-related variation. Ornis Scandinavica. 21: 169-178.

Marti, C.D. 1974. Feeding ecology of four sympatric owls. Condor. 76: 45-61.

Marti, C.D. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. Auk. 107: 246-254.

McGillivray, W.B. 1987. Reversed size dimorphism in 10 species of northern owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM- 142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 56-66.

Mikkola, H. 1983. Owls of Europe. Buteo Books. 397 p.

Mueller, H.C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bulletin. 98(3): 387-406.

Norberg, R.A. 1987. Evolution, structure, and ecology of northern forest owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 9-43.

Norberg, U.M. 1990. Vertebrate flight. New York, NY: Springer-Verlag. 291 p.

Pennycuick, C.J. 1975. Mechanics of flight. In: Farner, D.S.; King, J.R., eds. Avian biology, vol 5. New York, NY: Academic Press: 1-75.

Pennycuick, C.J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press. 153 p.

Poole, E.L. 1938. Weights and wing areas in North American birds. Auk. 55: 511-517.

Reynolds, R.T.; Linkhart, B.D. 1987. The nesting biology of Flammulated Owls in Colorado. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 239-248.

Savile, D.B.O. 1957. Adaptive radiation of the avian wing. Evolution. 11: 212-224.

Schantz, T. Von; Nilsson, I.N. 1981. The reversed size dimorphism in birds of prey: a new hypothesis. Oikos. 36: 129-132.

Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (Asio otus). Ardea. 72: 1-92.

Withers, P.C. 1981. The aerodynamic performance of the wing in Red-shouldered Hawk (Buteo linearis) and a possible aeroelastic role of wing-tip slots. Ibis. 123: 239-247.