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Source: Journal of Raptor Research, 50(1) : 60-69

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/rapt-50-01-60-69.1

J. Raptor Res. 50(1):60–69

SEX DIFFERENCES IN LONG-EARED OWL PLUMAGE COLORATION

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ABSTRACT.—Most species of owls lack distinctive sexual color dimorphism, and plumage is not considered reliable for distinguishing sex. In North America, Long-eared Owls (*Asio otus*) are generally considered monomorphic in color, although there are subtle color differences between the sexes. From 1987 to 2015, we investigated differences in plumage coloration of male and female Long-eared Owls in western Montana. We initially used an observational method (1987–1993), followed by a quantitative method (1994–1999), and then a simplified method (2000–2015). When we used the observational method, we correctly sexed all 22 Long-eared Owls. For the quantitative method, we used a Munsell Soil Color Chart to score underwing coverts, tarsometatarsus, and facial disc of breeding males and females and museum specimens purportedly sexed correctly. We found significant sex-specific color differences: underwing coverts ($G = 136.77$, df = 5, $P < 0.01$), tarsometatarsus ($G = 44.50$, df = 4, $P < 0.01$), and facial disc ($G = 50.62$, df = 7, $P < 0.01$). Underwing coverts differed the most between sexes. Based on these plumage color differences, we then correctly sexed all 19 owls captured during fall and winter and later recaptured as breeding birds. Using the simplified method, we correctly predicted the sex of 55 of 58 (93%) owls captured during fall and winter and later recaptured as breeders. Overall, we correctly predicted sex of 96 of 99 (96.9%) Long-eared Owls in Montana. We suggest that plumage coloration differences should be investigated in other study areas outside of Montana.

KEY WORDS: *Long-eared Owl*; Asio otus; *Munsell Soil Color Chart*; *plumage color*; *sex determination*; *sex prediction*.

DIFERENCIAS SEXUALES EN LA COLORACIÓN DEL PLUMAJE DE *ASIO OTUS*

RESUMEN.—La mayoría de las especies de búhos no presenta dimorfismo sexual distintivo en cuanto a su coloración, y su plumaje no se considera confiable para distinguir entre sexos. En América del Norte, *Asio otus* es considerada generalmente como monomórfica en cuanto a la coloración del plumaje, aunque existen diferencias sutiles de color entre los sexos. Desde 1987 hasta 2015, investigamos las diferencias en la coloración del plumaje de individuos machos y hembras de *A. otus* en el oeste de Montana. Inicialmente utilizamos un método observacional (1987–1993), seguido de un método cuantitativo (1994–1999) y luego un método simplificado (2000–2015). Cuando utilizamos el método observacional, determinamos correctamente el sexo de los 22 individuos de *A. otus* estudiados. Para el método cuantitativo utilizamos una cartilla de color del suelo de Munsell para calificar las plumas coberteras subalares, tarso-metatarso y disco facial de machos y hembras reproductivos y de especímenes de museo cuyo sexo fue supuestamente determinado de manera correcta. Encontramos diferencias significativas de color específicas del sexo para las plumas coberteras subalares ($G = 136.77$, gl = 5, $P < 0.01$), tarso-metatarso ($G = 44.50$, gl = 4, $P < 0.01$) y disco facial ($G = 50.62$, gl = 7, $P < 0.01$). Las plumas coberteras subalares fueron las plumas que más difirieron entre los sexos. Basados en estas diferencias de color del plumaje, determinamos correctamente el sexo de los 19 búhos capturados durante el otoño e invierno y luego recapturados como aves reproductivas. Utilizando el método simplificado, predijimos correctamente el sexo de 55 individuos de un total de 58 (93%) individuos de *A. otus* en Montana. Sugerimos que las diferencias en el color del plumaje deben ser investigadas en otras áreas de estudio además de Montana.

[Traducción del equipo editorial]

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Researchers distinguish sex of individual animals for a variety of reasons (e.g., demographic or behavioral studies) and reliable methods to assign sex are important to such studies. Numerous methods to determine sex in owls have been reported (Harris 1980). Morphometric comparisons (Earhart and Johnson 1970, Snyder and Wiley 1976, McGillivray 1987), coupled with multivariate models (Duncan 1996, Hayward and Hayward 1991, Brinker et al. 1997, Delgado and Penteriani 2004, Paxton and Watts 2008, Brittain et al. 2009) are commonly used. Yet, reliability of some morphological methods has been questioned (Mueller 1990, Slack 1992, Stock et al. 2006, Paxton and Watts 2008, Brittain et al. 2009).

Other methods have included cloacal inspection (Hamerstrom and Skinner 1971), cytology (Mengden and Stack 1975), analysis of plasma steroid hormones (Dieter 1973), tail-bar patterns (Barrows et al. 1982, Carpenter 1992) and DNA analysis (Fleming et al. 1996, Arroyo et al. 2000, Brommer et al. 2003, Leppert et al. 2006, Gebhardt and Waits 2008, Smith et al. 2012). DNA techniques show the most promise for correctly identifying sex of owls, although limitations exist for some methods (Leppert et al. 2006, Gebhardt and Waits 2008).

Natural selection appears to have favored monomorphic plumage coloration for most owl species (Bruce 1999, Holt et al. 1999). Consequently, sex differences in owl plumage are rarely studied. The Long-eared Owl is a medium-sized open country species whose distribution includes North America and Europe (Marks et al. 1994, Holt 1997, Holt et al. 1999). North American Long-eared Owl plumage includes a mix of colors ranging from black, brown, buff, gray, white, and yellow. These colors and their patterning result in a mottled look on the back, and barring and streaking pattern on the breast and belly (Marks et al. 1994, Holt et al. 1999). However, plumage color of the facial disc, underwing coverts, and tarsometatarsus are rather uniforms. Apparently, Long-eared Owls exhibit little sexual size dimorphism (McGillivray 1987).

Several authors have mentioned plumage differences possibly related to sex for Long-eared Owls (Bent 1938, Evans and Rosenfield 1987, Marks et al. 1994). Bent (1938) reported male Long-eared Owls averaged paler with white underparts, and females were more ochreous. Evans and Rosenfield (1987) suggested that males were paler and less buff than females. However, they concluded the sex of Long-eared Owls could not be reliably identified by plumage color.

Herein, we provide new information on plumage color differences between the sexes for Long-eared Owls from Montana. Our objectives were: (1) develop a field technique to reliably quantify plumage color differences between males and females; and (2) predict sex of individuals using plumage coloration during the nonbreeding season, and confirm or dispel our predictions by determining the sex of the same individuals during the breeding season. We also discuss the applicability of this information outside of our study area.

Study Area and Methods

Our study was conducted in Mission and Missoula valleys of western Montana. Here, DWH has led year-round studies of Long-eared Owls for 29 consecutive years, 1987–2015. The valleys are characterized by farm and rangelands, with several wildlife management and conservation areas. Both valleys are divided by small creeks, major rivers, and in the Mission Valley, portions are dotted with glacial ponds.

Observations of Plumage Color Differences Between the Sexes. Between 1987 and 1993, DWH conducted pilot studies and used an observational method to predict sex of nonbreeding Long-eared Owls. During autumn and winter, sex was tentatively assigned based upon experience with the species, and general impression of overall plumage color differences of the facial disc, underwing coverts, tarsometatarsus, breast, back, and wing bar patterning (Figs. 1–3). Purportedly, males were lighter colored than females. In particular, there appeared to be distinct color differences on the underwing coverts. Most owls were captured during daylight and this allowed us to keep track of individuals, and assess plumage color in natural light conditions. During the breeding seasons, we confirmed or rejected our predictions after recapturing previously banded Long-eared Owls, and sexing these individuals based upon brood patch presence/absence and behavioral observations. This pilot study led to the development of a replicable quantitative method to score color differences between male and female Long-eared Owls.

Quantification of Plumage Color Differences Between the Sexes. Between 1994 and 1999, we devised a method to quantify plumage coloration. Because only female Long-eared Owls develop a brood patch, incubate eggs, and brood nestlings, they were positively identified to sex after being captured flushing from their nests or when roosting next

Figure 1. Munsell Color Chart used to score (a) overall plumage coloration of the facial disc and (b) overall plumage coloration of the underwing coverts of Long-eared Owls in western Montana, U.S.A.

Figure 2. (a) Male and female Long-eared Owls' underwings. Male on left (low) and female on right (high). Female's underwing covert feathers contrast more with flight feathers than do male's. (b) Male and female tarsometatarsus and lower belly. Female on left and male on right. Female is buffy in color.

Figure 3. (a) Frontal view of Long-eared Owls, showing facial disc, breast, and overall color. Male on left and female on right. The female has noticeably darker overall color. (b) Dorsal view showing wing-patch, primary (P) feather barring, and overall color. Male on left and female on right. The male has fewer bars that are spaced more widely on P6–P9, creating a more distinctive wing patch pattern.

Table 1. Munsell color chart score of underwing, based upon owls captured in the field and museum specimens. See Methods for more details.

	MALES					FEMALES				
AREA SCORED	COLOR HUE	COLOR SCORE	COLOR	*n*	%	COLOR HUE	COLOR SCORE	COLOR	*n*	%
Underwing	10YR	8/1, 8/2	White	32	56	10YR	6/6, 6/8	Brownish yellow	21	43
		8/3, 8/4	Very pale brown	21	37		7/6, 7/8	Yellow	15	31
		7/1, 7/2	Light gray	1	2		7/3, 7/4	Very pale brown	10	20
		7/3, 7/4	Very pale brown	1	2		6/3	Pale brown	1	2
		8/6, 8/8	Yellow	2	2		6/4	Light yellowish brown	1	2
							8/6, 8/8	Yellow	1	2
TOTAL				57	99				49	100

to the nest, by confirmation of a brood patch, or by the re-growth of feathers from a brood patch. Female brood patch feathers are not completely regrown until young are about 5 wk old. Males roosted individually within 10–20 m of their nests. They were captured in mist nets, and positively identified as the owl roosting near the nest, or engaged in nest defense. Although breeding males have been reported to roost together, and engage in communal nest defense (Marks 1985), we never observed this behavior, and are confident of our sexing and pair assignments. All owls were captured during daylight.

We used a Munsell Soil Color Chart (1985; Fig. 1a, b) to assign color hues to the facial disc, underwing coverts, and tarsometatarsus. We chose this chart because it is widely used, easily accessible, and provides a variety of earth tone colors, which are typical of owl plumage coloration. The Munsell chart assigns one to several color hues to color definition. For example, even though a score is designated 8/1 or 8/2, either choice gives the same color: "white." Similarly, scores 8/3 and 8/4, and 7/3 and 7/4 designates the color "very pale brown," whereas, 6/4 only designates "light yellowish brown" (see Table 1). We scored the overall color of the facial disc, underwing coverts, and tarsometatarsus, not individual feathers.

The scoring of plumage colors was standardized to the best of our ability. Scorers were trained prior to data collection. Color hues were scored once each from two independent observers. Scores were registered silently, using a double-blind technique so scorers could not influence one another. We then compared the scores from these independent observers. In all cases, independent double-blind scores were nearly identical, and thus, scores were pooled. For example, if scorers A and B ranked color hues differently, these hues were always consistent within a sex, and the differences were considered negligible (i.e., 10 YR 8/1–2 and 10 YR 8/6–8; see Fig. 1a, b). We recognized variation in color interpretation exists among people, but did not experimentally test that as a confounding factor. Scoring and measuring took about 10 min per owl.

In addition to scoring live owls in the field, we also scored color from photographs of known-sex breeding owls from our study area. However, for these birds, we could not score the tarsometatarsus because researchers were holding the owls' legs.

We then scored museum specimens from the P.L. Wright Zoological Museum (PLWZM), University of Montana, Missoula ($n = 6$) and the Vertebrate Museum of Zoology (VMZ), University of California, Berkeley ($n = 32$). We scored these specimens before checking the information on the specimen tags, and then checked the tags for data on sex. Eight of the 38 specimens that were labeled to sex provided no data on follicle, gonad, or mass; thus, they were excluded from our analysis. The remaining 30 specimens provided evidence of sex. We disagreed with two of these, but included them in our color score analysis (but see Pyle [1997] for cautionary notes regarding museum specimens).

We then combined all color score results and arranged the data into an R × C contingency table and used the G-statistic to test whether the number of birds scoring in each color category differed between the sexes. We collapsed cells where values were under five to meet assumptions of the G-statistic, according to Fowler and Cohen (1990). Alpha levels were significant at $P < 0.05$.

To test our color score results in the field, we captured unknown-sex nonbreeding Long-eared Owls at autumn and winter communal roosts within our study area, and scored their plumage colors using the techniques we developed with the known-sex breeding birds and museum specimens. Based on the color differences of the known-sex birds, we predicted the sex of the nonbreeding owls.

Simplification of Plumage Color Assessment Between the Sexes. Between 2000 and 2015, we performed a quicker, simplified assessment of plumage color. We did not record scores of color hue for each individual or anatomical region. For each owl captured, we visually examined the facial disc, underwing coverts, tarsometatarsus, and overall plumage color to predict sex. When we recaptured these owls in subsequent years, we took all measurements and predicted sex prior to checking data books. We did this to eliminate bias in our predictions. Sex was confirmed during the breeding season using the criteria described above.

In all years, we followed U.S.G.S. Bird Banding Laboratory Manual for age (year class) codes (i.e., AHY, after-hatch-year; SY, second-year; ASY, after-second-year; TY, third-year; 5Y, fifth year). All owls were banded with a U.S.G.S. aluminum leg band (U.S.G.S. master permit no. 22151 and all Montana State FWP permits and FWP IACUC 2012).

RESULTS

Observations of Plumage Color Differences Between Sexes. During the pilot study between 1987 and 1993, we recaptured 22 breeding owls. We correctly predicted the sex of all owls: SY (three male, six female); ASY (one male, one female); TY (two male); and AHY (three male, six female).

Quantification of Plumage Color Differences Between the Sexes. Between 1994 and 1999, we captured 77 owls during the breeding season and we confirmed their sexes according to our criteria. Fifty-one were captured and their plumage color scored in the field, and 26 were captured in the field and scored from color photographs. An additional 30 owls whose sex was presumably correct on the specimen label were scored from museum specimens. In sum, 107 were scored for facial disc, 106 for underwing coverts, and 86 for tarsometatarsus.

Coloration of the underwing coverts differed most between the sexes. Ninety-three percent of males scored in two color categories, with 56% white, and 37% very pale brown, whereas 94% of females scored in three color categories: 43% brownish yellow; 31% yellow; and 20% very pale brown (Table 1). The color difference between males and females (Fig. 2a) was significant ($G = 136.77$, df = 5, $P < 0.01$).

Coloration of the tarsometatarsus also differed between the sexes. Eighty-seven percent of males scored in three color categories, with 37% very pale brown, 35% a variant of very pale brown, and 15% yellow, whereas 83% of females scored in three color categories: 33% brownish yellow, 30% yellow, and 20% very pale brown (Table 2). The color difference between males and females (Fig. 2b) was significant ($G = 44.50$, df = 4, $P < 0.01$).

Coloration of the facial disc also differed significantly between the sexes ($G = 50.62$, df = 7, $P < 0.01$; Fig. 3a). Seventy-four percent of males scored in three color categories, with 44% very pale brown, 16% yellow, and 14% a variation of very pale brown (Table 3). In contrast, 38% of females scored in one color category, brownish yellow, whereas 52% scored in four categories: 16% yellow, 14% very pale brown, 12% yellowish brown, and 10% light yellowish brown.

Based on the coloration differences we noted, we predicted the sex of 19 owls that were first captured during the nonbreeding season and then recaptured and sexed by nesting activity or brood patch presence/absence during the breeding season. We correctly predicted the sex of all 19; 11 males and 8 females. They were originally aged and their sex predicted as: HY (two male, two female); SY (three male, two female); ASY (one male, two female); AHY (four male, two female) and 5Y (one male), and confirmed as breeders at various ages.

Simplification of Plumage Color Assessment Between the Sexes. Between 2000 and 2015, we evaluated facial disc, underwing coverts, tarsometatarsus, wing patch (Fig. 3b), and overall plumage color during the nonbreeding seasons and predicted owl sex. We recaptured 58 breeding owls that had been previously evaluated and then determined their sexes using nesting activity, nest defense, behavior, and brood patch criteria (above). We correctly predicted sex of 55 of 58 (93.1%) owls (20 females and 35 of 38 males). They were originally aged and their sex predicted across multiple age classes as: HY (eight male, two female); SY (14 male, 10 female); ASY (15 male, four female); and AHY (one male, four female). There were three discrepancies. In one case, two experienced researchers independently scored different sexes. In two cases, an experienced researcher and trainee scored different sexes. In all cases, the same experienced researcher correctly

Table 2. Munsell color chart score of tarsometatarsus, based upon owls captured in the field and museum specimens. See Methods for more details.

	MALES					FEMALES				
AREA SCORED	COLOR HUE	COLOR SCORE	COLOR	*n*	%	COLOR HUE	COLOR SCORE	COLOR	*n*	%
Tarsus	10YR	7/3, 7/4	Very pale brown	17	37	10YR	6/6/8	Brownish yellow	13	33
		8/3, 8/4	Very pale brown	16	35		7/6, 7/8	Yellow	12	30
		7/6, 7/8	Yellow	7	15		7/3, 7/4	Very pale brown	8	20
		8/1, 8/2	White	4	9		5/4, 5/6, 5/8	Yellowish brown	1	2
		8/6, 8/8	Yellow	2	4		6/3	Pale brown	2	5
							6/4	Light yellowish brown	3	8
							8/6, 8/8	Yellow	1	2
TOTAL				46	100				40	100

predicted the owls' sex. In all three cases, the incorrectly sexed birds were males (one HY, one SY, one ASY).

DISCUSSION

Plumage differences between male and female Long-eared Owls have been suggested for North America (Bent 1938, Evans and Rosenfield 1987, Marks et al. 1994). Our data present the only quantification of these differences, and our successful predictions of sex highlight the potential for an objective method for sexing this species based on color. Our low recapture and high turnover rates, and the species' migratory and nomadic habits, as well as North American banding records, indicate we likely sampled individuals from a wide geographic area. Our data may also call into question the current recognition of two subspecies of Long-eared Owls in North America; we suggest it is possible that sexual color dimorphism may have been mistaken for subspecific differentiation.

Interestingly, our data were consistent with those from other North American owl species that reside in open-country habitats. These species also exhibit subtle sexual color dimorphism: Barn Owl (*Tyto alba*; Marti 1992), Burrowing Owl (*Athene cunicularia*; Haug et al. 1993), and Short-eared Owl (*A. flammeus*; Holt and Leasure 1993). The Snowy Owl (*Bubo scandiacus*) is the only distinctly sexually color-dimorphic

Table 3. Munsell color chart score of facial disc, based upon owls captured in the field and museum specimens. See Methods for more details.

	MALES					FEMALES				
AREA SCORED	COLOR HUE	COLOR SCORE	COLOR	*n*	%	COLOR HUE	COLOR SCORE	COLOR	*n*	%
Face	10YR	8/3, 8/4	Very pale brown	25	44	10YR	6/6, 6/8	Brownish yellow	19	38
		7/6, 7/8	Yellow	9	16		7/6, 7/8	Yellow	8	16
		7/3, 7/4	Very pale brown	8	14		7/3, 7/4	Very pale brown	7	14
		8/1, 8/2	White	5	9		5/4, 5/8	Yellowish brown	6	12
		8/6, 8/8	Yellow	3	5		6/4	Light yellowish brown	5	10
		5/4, 5/8	Yellowish brown	1	2		6/3	Pale brown	2	4
		6/2	Light brownish gray	1	2		8/1, 8/2	White	1	2
		6/4	Light yellowish brown	1	2		8/3, 8/4	Very pale brown	2	4
		6/6, 6/8	Brownish yellow	2	3					
		7/1, 7/2	Light gray	2	3					
TOTAL				57	100				50	100

owl species (Parmelee 1992, Holt et al. 2015). In all these species, females are darker than males.

The ultimate mechanism driving sexual color dimorphism in Long-eared Owls and these other species is unknown. We hypothesize that natural selection favors darker colors and cryptic plumage patterns for females, and this may enhance their camouflage while nesting, and reduce detection from predators of adults, eggs, and young. Darker colors may also be less susceptible to fading or bleaching from ultraviolet light, thus maintaining cryptic coloration. The reason for light coloration in males is unknown, but may involve sexual selection, male-male competition, or relaxed selective pressure due to limited incubation/brooding responsibilities. In this study, both Long-eared Owl sexes bred as yearlings (i.e., <1 yr old), and all were correctly sexed. If females are darker for camouflage or sexual-selection reasons, then it is reasonable to assume that sexual color dimorphism is favored during the first year of life. Our data support this hypothesis. One male owl was banded as a nestling in 2001, retrapped annually until 2008, and consistently predicted as a male based on plumage coloration.

Our investigation should be replicated outside Montana. We encourage this based upon suggestions of sexual color dimorphism of Long-eared Owls from other areas of North America (Bent 1938, Evans and Rosenfield 1987), and the fact that the European Long-eared Owl has been successfully sexed by plumage color (Wijnandts 1984, Cramp 1985).

Our results also suggested that age, plumage variation, slight color overlap, and observer color interpretation does not significantly affect the results. By autumn of their first year, and perhaps throughout their lives, Long-eared Owls can be reliably sexed by plumage color.

By using a Munsell Soil Color Chart, our field scores of males and females (Table 1), and Figures 1–3, a fully quantified sexing technique could easily be developed. Scoring color in the field is fast, inexpensive, and reproducible.

ACKNOWLEDGMENTS

We are grateful to many field researchers over the years. We are indebted to Julie Petersen-Parrett who helped design the project in its earlier years. We thank Dave Ellis, David Evans, Jeff Marks, Glenn Proudfoot, Peter Pyle, an anonymous reviewer, and the JRR editors for many helpful comments.

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Received 30 May 2013; accepted 8 December 2014
Associate Editor: Joseph B. Buchanan