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# MORPHOMETRIC VARIATION IN FLAMMULATED OWLS CAPTURED DURING AUTUMN MIGRATION IN THE WESTERN UNITED STATES

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**ABSTRACT.**—Knowledge of the migration geography of Flammulated Owls (*Otus flammeolus*) is limited. We combined data from multiple studies in the western United States to evaluate patterns of variation in Flammulated Owl morphometrics. Measurements from autumn migration study sites in New Mexico, Nevada, and Idaho followed a geographic cline from southeast to northwest across the species' range. Our objectives were to: (1) describe age- and sex-specific variation in the morphometrics of Flammulated Owls captured at the three sites, and (2) discuss the implications of this variation for understanding the species' migration geography. Based on a hierarchical series of factorial two-way ANOVAs, we discovered significant overall sex-specific differences in wing chord, exposed culmen length, and hallux length, and a consistent pattern of site-specific differences for most measurements. Most measurements increased from southeast to northwest, consistent with previous data on clinal variation in the species. Evidence of significant variation in the morphometrics of owls captured at the three migration sites suggests little longitudinal mixing of migrants in the region.

**KEY WORDS:** *Flammulated Owl*; *Otus flammeolus*; *Bergmann's rule*; *DNA-based sexing*; *migration geography*; *morphometrics*; *sexing*; *sexual size dimorphism*; *western United States*.

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## VARIACIÓN MORFOMÉTRICA EN INDIVIDUOS DE *OTUS FLAMMEOLUS* CAPTURADOS DURANTE LA MIGRACIÓN DE OTOÑO EN EL OESTE DE ESTADOS UNIDOS

**RESUMEN.**—El conocimiento sobre la geografía de la migración de *Otus flammeolus* es escaso. Combinamos datos de varios estudios del oeste de Estados Unidos para evaluar los patrones de variación en la morfometría de *O. flammeolus*. Las medidas registradas en los sitios de estudio de la migración otoñal en Nuevo México, Nevada, e Idaho presentaron un gradiente geográfico desde el sudeste hacia el noroeste del rango de la especie. Nuestros objetivos fueron: (1) describir la variación específica ligada a la edad y al sexo en la morfometría de individuos de *O. flammeolus* capturados en los tres sitios, y (2) analizar las implicancias de esta variación para entender la geografía migratoria de esta especie. Basados en una serie jerárquica de ANOVAs factoriales de dos vías, descubrimos diferencias significativas generales vinculadas al sexo en la cuerda del ala, largo expuesto del culmen y largo del hálux, y un patrón consistente de diferencias vinculadas al sitio para la mayoría de las medidas. La mayoría de las medidas aumentaron desde el sudeste hacia el noroeste, de modo consistente con datos anteriores del gradiente de variación en esta especie. La evidencia sobre la variación significativa en la morfometría de los individuos de *O. flammeolus* capturados en los tres sitios de migración sugiere poca mezcla longitudinal de migrantes en la región.

[Traducción del equipo editorial]

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Little is known about the biogeography and migration ecology of the Flammulated Owl (*Otus flammeolus*). As a small nocturnal insectivore restricted to montane forest habitats (McCallum 1994), the Flammulated Owl has been difficult to study, especially during migration. Although the species appears to be more common than once believed, Partners in Flight placed the Flammulated Owl on its Species of Continental Importance Watch List because of concerns about its restricted distribution and low population size (Rich et al. 2004). Flammulated Owls were once thought to be nonmigratory (Phillips 1942), but the species is now commonly considered an obligate, medium- to long-distance, north-south migrant (Banks 1964, Ligon 1968, Winter 1974, Balda et al. 1975, McCallum 1994).

Flammulated Owls breed in montane forests of western North America and Mexico (McCallum 1994). Overall, the species appears to increase in size from the southeastern to the northwestern parts of its range (Bergmann's rule; Marshall 1967; Blackburn et al. 1999). This size cline may be intertwined with subspecific differences across the range. Marshall (1967, 1978) recognized no subspecies, but Hekstra (1982) suggested there might be as many as six subspecies of Flammulated Owl in North America (also see McCallum 1994). More recently, Pyle (1997) described two subspecies: *O. f. idahoensis* and *O. f. frontalis*. Under *idahoensis*, Pyle suggested that a "borealis" subtype in the northern parts of the range might average larger than its southern counterparts (Pyle 1997).

Flammulated Owls are one of the least sexually size-dimorphic North American owls (Earhart and Johnson 1970). It is unknown whether sexual size dimorphism varies in magnitude across the subspecies or latitudinal size cline, or if it is approximately constant across the species' range, as it is in some other owl species (McGillivray 1989). The difficulty in discriminating females from males also has obscured the detection of other common patterns in migration geography, such as differential migration in timing or distance by sex (DeLong and Hoffman 1999). Although a discriminant function developed to sex owls captured during migration based on external measurements was approximately 73% effective (J. DeLong unpubl. data), variation in size across the range suggests that this function may not accurately identify sex in other populations.

Recent efforts to study the migration ecology of Flammulated Owls yielded an opportunity to study

the biogeography of size in this species across a southeast-to-northwest gradient in the western United States (DeLong 2004, 2006, DeLong et al. 2005, Stock et al. 2006, Linkhart and Reynolds 2007). Using the combined data from mostly contemporary autumn banding efforts in New Mexico, Nevada, and Idaho, we present an assessment of sex-, age-, and site-specific morphometric variation in this species. We use these results to assess differences in size and sexual size dimorphism across the sites, and we consider the implications for understanding the species' migration geography.

#### METHODS

From 1998–2010, annual capture totals for Flammulated Owls banded during autumn migration on Boise Ridge in west-central Idaho ranged from 2–66 owls (Stock et al. 2006, Idaho Bird Observatory unpubl. data: technical reports at <http://www.idahobirdobservatory.org>). From 1993–2003, autumn capture totals in the Manzano Mountains of central New Mexico ranged from 20–156 owls (DeLong 2004, 2006, DeLong et al. 2005; Hawk-Watch International [HWI] unpubl. data: technical reports at <http://www.hawkwatch.org>). From 2001–08, autumn capture totals in the Goshute Mountains of northeastern Nevada ranged from 19–72 owls (HWI unpubl. data: technical reports at <http://www.hawkwatch.org>). All three study sites are on mountain ridgetops where long-term studies of both diurnal and nocturnal raptors occur (Fig. 1).

The Idaho study was in the same area as the long-term Boise Ridge Raptor Migration Project (43°36.32'N, 116°03.62'W; elevation ca. 1799 m; Smith et al. 2008); Stock et al. (2006) and Leppert et al. (2006) previously described the study site and relevant owl capture and banding methods. Measurements collected at this site included mass and unflattened wing chord, with standard tail length, exposed culmen length, and tarsus length collected less regularly. The New Mexico study was in the same area as the long-term Manzano Mountains Raptor Migration Project (34°42.25'N, 106°24.67'W; elevation ca. 2805 m; DeLong and Hoffman 1999, Hoffman et al. 2002, Smith et al. 2008); DeLong et al. (2005) previously described the owl study site and relevant methods.

The Nevada study site was in the same area as the long-term Goshute Mountains Raptor Migration Project (43°25.42'N, 114°16.28'W; elevation ca. 2740 m; Hoffman 1985, Hoffman et al. 2002,

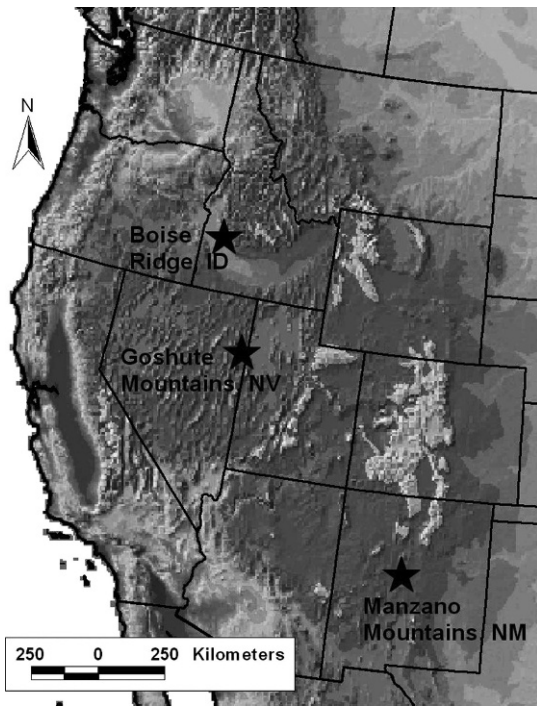


Figure 1. Locations of Flammulated Owl migration study sites in the western United States.

Smith et al. 2008). The owl capture arena was in a mixed conifer forest and sagebrush meadow area approximately 150 m below and 150–200 m east of the main ridgetop area where most of the diurnal count and banding operations occurred. The methods used to capture owls were similar to those used in Idaho and New Mexico. During 2008, when samples for DNA sexing were collected, banders lured owls into a capture arena consisting of 17 stationary mist nets (60-mm mesh, 9–12 m in length) using Flammulated Owl calls broadcasted via a recorded audiolure through an amplified stereo unit (Reynolds and Linkhart 1984). Weather permitting (absence of precipitation and winds <24 kph), netting occurred nightly from 23 August through 28 October from approximately 30 min after sundown to 30 min before sunrise. Measurements collected included mass, unflattened wing chord, standard tail length, and exposed culmen length, with hallux length and tarsus length collected less regularly. When possible, banders determined the age of Flammulated Owls in the field based on flight feather molt and fault bars (Pyle 1997, DeLong 2004). Hatch-year (HY) owls

had retained juvenile plumage or uniform fault bars. After-hatch-year (AHY) owls showed flight-feather molt or multiple generations of flight feathers.

Sexing Flammulated Owls based on external characteristics is problematic (McCallum 1994). In each of the studies considered here, researchers collected samples to enable DNA-based sexing of selected owls. Leppert et al. (2006) used DNA to sex 55 owls captured in Idaho, including 16 HY owls (10 female, 6 male), 9 AHY owls (4 females, 5 males), and 30 owls of unknown age (9 females, 21 males). The New Mexico sample of DNA-sexed owls (DeLong et al. 2005) included 13 female and 20 male HY owls, plus another 20 females and 33 males of unknown age. The Nevada sample of DNA-sexed owls included 21 female and 37 male HY owls. Wildlife Genetics International (Nelson, British Columbia, Canada) processed all of the New Mexico and Nevada samples, and all three sets of samples were processed following methods developed by Griffiths et al. (1998).

Given availability of DNA sexing data from all three sites, we initially focused on analyzing site and sex differences in individual measurements among known-sex HY owls. Guided by the results of these analyses, we conducted additional analyses that included other owls of unknown age, sex, or both. Because not all measurements were taken on all owls, we took a progressive, hierarchical approach to these additional analyses to maximize consideration of as many individual owls as possible while investigating sex-, age-, and site-specific variation in individual measurements. Our analyses included various two-way (site \* sex, site \* age, sex \* age) factorial ANOVAs and, when appropriate, Bonferroni *post-hoc* comparisons to further discern differences among the three sites (Systat v. 10; SPSS, Inc. 2000). We did not take a multivariate approach with aggregate measurement indices, such as principle components analysis, because there were too few owls from each site with full suites of measurements suited to multivariate analysis. In addition, our interest extended beyond examining variation in overall size and shape; we were specifically interested in determining which measurements differed among sites, sexes, and age classes. Diagnostic plots confirmed reasonable conformity to assumptions of normally distributed residuals and heteroscedastic variances. We considered results significant if  $P \leq 0.05$ , but we also highlight marginally significant results with  $0.05 < P \leq 0.10$ .

Table 1. Comparisons (2-way factorial ANOVA, least-squares means) of the sex-specific morphometrics of DNA-sexed, hatch-year Flammulated Owls captured during autumn migration on Boise Ridge, Idaho, in the Goshute Mountains, Nevada, and in the Manzano Mountains, New Mexico.

MEASURE	SITE	FEMALE			MALE			MODEL $R^2$	SITE $P$	SEX $P$	INT. $P$
		$n$	MEAN	SE	$n$	MEAN	SE				
Mass (g)	Idaho	9	64.4	1.90	6	63.2	2.32	0.273	<0.001 <sup>a</sup>	0.432	0.407
	Nevada	20	60.2	1.27	37	60.9	0.94				
Wing chord (mm)	New Mexico	13	56.3	1.58	20	53.6	1.27	0.291	<0.001 <sup>b</sup>	<0.001	0.839
	Idaho	10	134.3	1.06	6	132.2	1.37				
	Nevada	21	133.4	0.73	37	130.5	0.55				
	New Mexico	13	131.1	0.93	20	127.7	0.75				
Exposed culmen length (mm)	Idaho	8	8.7	0.17	6	8.7	0.20	0.098	0.066	0.096	0.733
	Nevada	21	9.1	0.11	37	8.8	0.08				
Hallux length (mm)	New Mexico	13	8.9	0.14	20	8.7	0.11	0.095 <sup>c</sup>	0.067	0.028	0.613
	Nevada	13	6.4	0.08	31	6.2	0.07				
Tarsus length (mm)	New Mexico	13	6.4	0.11	20	6.0	0.11	0.132	0.486	0.002	0.440
	Idaho	8	25.0	0.43	6	24.3	0.50				
Standard tail length (mm)	Nevada	7	22.6	0.46	25	22.2	0.24	0.349	<0.001	0.160	0.837
	New Mexico	13	23.0	0.34	20	22.8	0.27				
	Idaho	10	63.0	1.34	6	62.0	1.73				
	Nevada	21	62.0	0.93	36	61.0	0.50				
	New Mexico	13	61.0	1.18	20	60.6	0.95	0.059	0.187	0.246	0.903

<sup>a</sup> Bonferroni pairwise comparisons, model  $P \leq 0.05$ ; Idaho = Nevada > New Mexico.

<sup>b</sup> Bonferroni pairwise comparisons, model  $P \leq 0.05$ ; Idaho = Nevada > New Mexico.

<sup>c</sup> Analysis rerun excluding Idaho data.

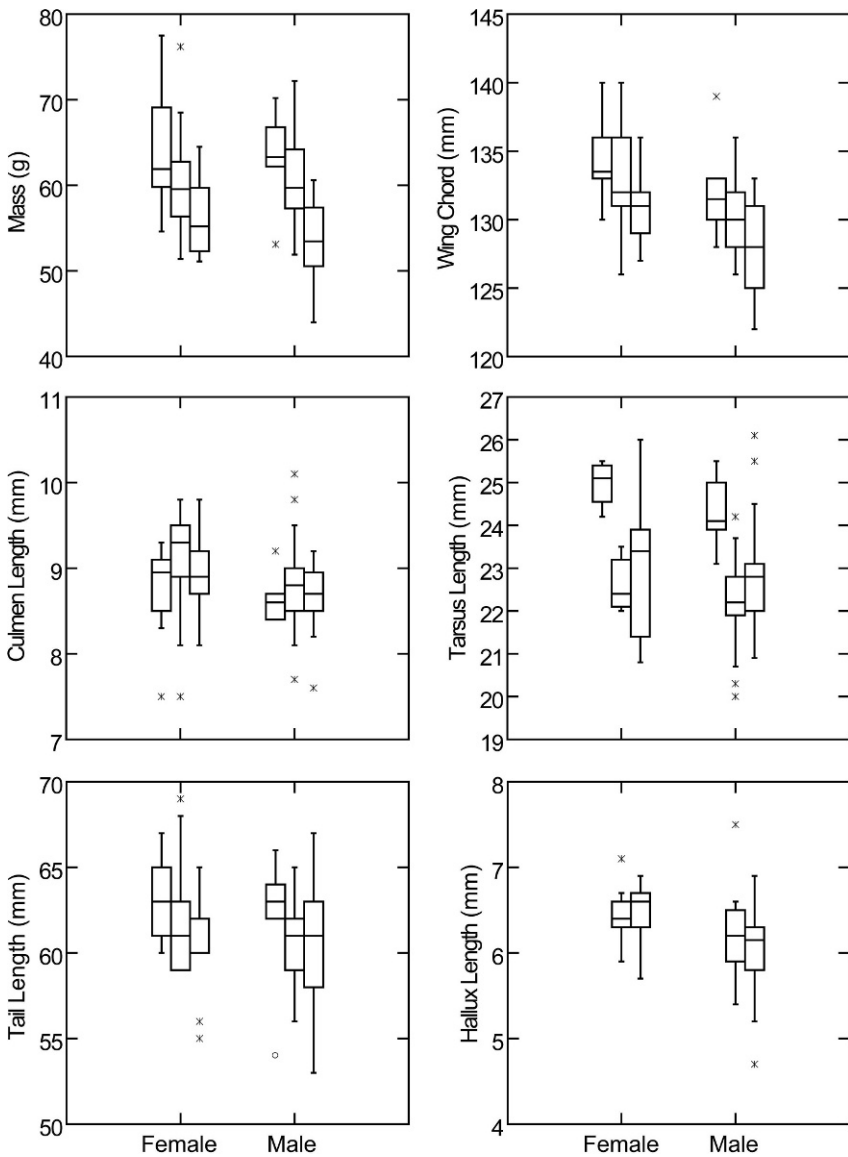


Figure 2. Box and whisker plots (Systat 10.0, SPSS Inc. 2000) illustrating variation by sex (DNA-based) and site (from left to right within sexes: Boise Ridge, ID, Goshute Mountains, NV, and Manzano Mountains, NM) in measurements of hatch-year Flammulated Owls captured during autumn migration in the western United States.

RESULTS

Analyses for HY birds of known sex indicated no significant site \* sex interactions; overall sex differences (females > males) for wing chord and hallux length; and overall site differences for mass, wing chord, and tarsus length (Table 1, Fig. 2). A similar sex difference was indicated for culmen length, but the difference was only marginally significant ( $P = 0.066$ ); closer inspection revealed

inconsistency across sites, with no difference in sex-specific means for culmen in Idaho. Site-specific means revealed a clinal pattern of declining mass, wing chord, tail length, and hallux length (NV to NM only) from northwest to southeast, with post-hoc comparisons confirming significant differences between Idaho and New Mexico for mass and wing chord. A marginally significant ( $P = 0.096$ ) site difference also was indicated for culmen length;

Table 2. Comparisons (2-way factorial ANOVA, least-squares means) of the age-specific morphometrics of Flammulated Owls (female, male, and unknown-sex combined) captured during autumn migration on Boise Ridge, Idaho, in the Goshute Mountains, Nevada, and in the Manzano Mountains, New Mexico.

MEASURE	SITE	HATCH-YEAR			AFTER-HATCH-YEAR			MODEL $R^2$	SITE $P$	AGE $P$	INT. $P$
		$n$	MEAN	SE	$n$	MEAN	SE				
Mass (g)	Idaho	15	63.9	1.32	9	63.6	1.70	0.321	<0.001 <sup>a</sup>	0.043	0.062
	Nevada	151	59.2	0.42	39	60.6	0.82				
	New Mexico	168	53.1	0.39	23	57.4	1.06				
Wing chord (mm) <sup>b</sup>	Idaho	16	133.5	0.93	9	134.1	1.24	0.214	<0.001 <sup>c</sup>	0.004	0.546
	Nevada	152	131.8	0.30	39	134.2	0.59				
	New Mexico	168	128.8	0.29	23	131.2	0.77				
Exposed culmen length (mm) <sup>b</sup>	Idaho	14	8.7	0.17	9	8.5	0.21	0.105	<0.001	0.190	0.107
	Nevada	140	9.1	0.05	37	9.4	0.10	0.081 <sup>d</sup>	0.020	<0.001	0.477
	New Mexico	166	8.9	0.05	23	9.3	0.13				
Hallux length (mm) <sup>b</sup>	Nevada	104	6.2	0.05	32	6.5	0.08	0.052	0.190	0.006	0.473
	New Mexico	110	6.2	0.05	13	6.3	0.14				
	Idaho	14	24.7	0.38	9	24.7	0.47	0.143	<0.001	0.436	0.762
Tarsus length (mm)	Nevada	64	22.8	0.18	18	23.3	0.33	0.008 <sup>d</sup>	0.801	0.304	0.550
	New Mexico	112	22.9	0.13	13	23.1	0.39				
	Idaho	16	62.6	0.82	9	62.1	1.09	0.024	0.131	0.843	0.712
Standard tail length (mm)	Nevada	150	61.5	0.23	38	61.4	0.53				
	New Mexico	167	60.8	0.25	23	61.2	0.68				

<sup>a</sup> Bonferroni pairwise comparisons, model  $P \leq 0.05$ ; Idaho > Nevada > New Mexico.

<sup>b</sup> Note that these analyses may be confounded by significant sex-specific variation (see Table 1), but were conducted to enable tentative investigations of age- and site-specific variation based on larger non-sex-specific sample sizes.

<sup>c</sup> Bonferroni pairwise comparisons, model  $P \leq 0.05$ ; Idaho and Nevada > New Mexico.

<sup>d</sup> Analysis rerun excluding Idaho data.

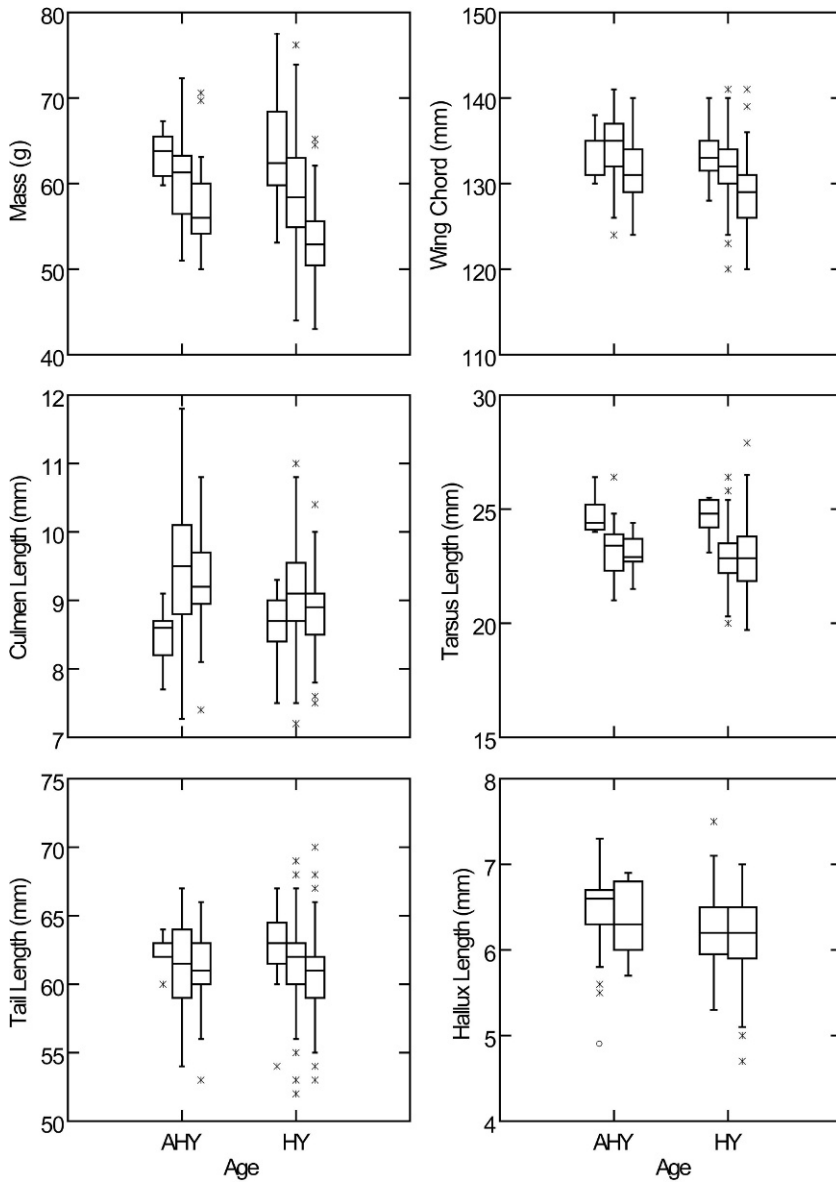


Figure 3. Box and whisker plots (Systat 10.0, SPSS Inc. 2000) illustrating variation by age (AHY = after-hatch-year, HY = hatch-year) and site (from left to right within sexes: Boise Ridge, ID, Goshute Mountains, NV, and Manzano Mountains, NM) in measurements of Flammulated Owls (sexes combined) captured during autumn migration in the western United States.

however, although the pattern of increasing measurements held between New Mexico and Nevada, unlike all other measurements, culmen lengths averaged shortest in Idaho. Tarsi averaged significantly longer in Idaho than in Nevada and New Mexico; however, unlike for any other measurement, both

sexes averaged nonsignificantly shorter tarsi in Nevada than in New Mexico (Table 1). Noting these results for Idaho as potentially anomalous (see Discussion), we ran the analyses for culmen and tarsus length again excluding Idaho data. This yielded no site or sex differences for tarsus length, but a significant sex



Table 3. Comparisons (2-way factorial ANOVA, least-square means) of the sex-specific morphometrics of Flammulated Owls (HY, AHY, and unknown-age combined) captured during autumn migration on Boise Ridge, Idaho, in the Goshute Mountains, Nevada, and in the Manzano Mountains, New Mexico.

MEASURE	SITE	FEMALE			MALE			MODEL R <sup>2</sup>	SITE P	SEX P	INT. P
		n	MEAN	SE	n	MEAN	SE				
Mass (g) <sup>a</sup>	Idaho	22	62.8	1.07	32	63.6	0.89	0.354	<0.001 <sup>b</sup>	0.770	0.524
	Nevada	20	60.2	1.13	37	60.9	0.83				
Wing chord (mm) <sup>a</sup>	New Mexico	32	55.3	0.89	42	54.4	0.78	0.304	<0.001 <sup>b</sup>	<0.001	0.210
	Idaho	23	134.3	0.69	32	133.7	0.59				
	Nevada	21	133.4	0.72	37	130.5	0.54				
	New Mexico	33	130.3	0.58	42	128.5	0.51				
Exposed culmen length (mm)	Idaho	18	8.6	0.12	18	8.6	0.12	0.104	0.003	0.024	0.439
	Nevada	21	9.1	0.11	37	8.8	0.08				
Hallux length (mm) <sup>a</sup>	New Mexico	33	8.8	0.09	42	8.6	0.08	0.100 <sup>c</sup>	0.009	0.005	0.720
	Nevada	13	6.4	0.11	31	6.2	0.07				
Tarsus length (mm)	New Mexico	32	6.2	0.07	42	6.1	0.06	0.058	0.112	0.020	0.538
	Idaho	18	24.8	0.28	18	24.8	0.28				
Standard tail length (mm)	Nevada	7	22.6	0.45	25	22.2	0.24	0.396	<0.001 <sup>d</sup>	0.328	0.865
	New Mexico	33	22.9	0.21	42	22.7	0.19				
Standard tail length (mm)	Idaho	23	62.4	0.60	20	62.7	0.65	0.075	0.005	0.358	0.575
	Nevada	21	62.0	0.63	36	61.0	0.48				
	New Mexico	33	61.0	0.50	33	60.5	0.45				

<sup>a</sup> These analyses may be confounded by significant age-specific variation (see Table 2), but were conducted to enable tentative investigations of sex- and site-specific variation based on larger non-age-specific sample sizes.

<sup>b</sup> Bonferroni pairwise comparisons, model  $P \leq 0.05$ : Idaho > Nevada > New Mexico.

<sup>c</sup> Analysis rerun excluding Idaho data.

<sup>d</sup> Bonferroni pairwise comparisons, model  $P \geq 0.05$ : Idaho > Nevada and New Mexico.

difference (female > male) and marginally significant site difference (Nevada > New Mexico;  $P = 0.067$ ) for culmen length (Table 1).

With no DNA-based sexing data for known AHY Nevada or New Mexico owls, we were restricted to examining the Idaho data for possible age-related variation in wing chord and culmen lengths, while simultaneously accounting for apparent sex effects. This analysis revealed only marginally ( $P = 0.094$ ) longer wing chords for females (least-squares mean  $\pm$  SE:  $134.9 \pm 0.92$ ) compared with males ( $132.6 \pm 0.94$ ); however, small sample sizes ( $n = 6$  HY male, 5 AHY male, 10 HY female, and 4 AHY female) compromised the statistical power of this analysis. Also note that, in Idaho, AHY owls averaged nonsignificantly lighter ( $63.5 \pm 2.00$  vs.  $63.8 \pm 1.58$  g), longer wing chords ( $134.3 \pm 1.05$  vs.  $133.2 \pm 0.81$  mm) and tarsi ( $24.7 \pm 0.26$  vs.  $24.6 \pm 0.21$  mm), and shorter culmens ( $8.5 \pm 0.16$  vs.  $8.7 \pm 0.13$  mm) and tails ( $62.1 \pm 0.91$  vs.  $62.5 \pm 0.70$  mm) than HY owls.

Because there was no evidence of sex-specific differences, we expanded the analyses of mass, tail length, and tarsus length to include owls of known age but unknown sex from Nevada and Idaho (Table 2, Fig. 3). Analysis of mass revealed significant site and age main effects and a marginally significant sex \* age interaction. *Post-hoc* comparisons confirmed Idaho > Nevada > New Mexico. AHY owls tended to average greater mass than HY owls. The marginally significant interaction reflected this tendency diminishing from southeast to northwest, with no age-related mass difference apparent in Idaho. Analysis of tarsus length, excluding Idaho data, revealed no site or age effects and no consistent pattern of difference between Nevada and New Mexico within age groups. Analysis of tail lengths revealed no significant effects, but again suggested at least a slight declining trend from northwest to southeast.

To enable larger-sample site comparisons we expanded analyses of wing chord, culmen length, and hallux length to include owls of known age but unknown sex (Table 2, Fig. 3), keeping in mind that sex-specific differences may confound these comparisons. AHY owls averaged longer wing chords and halluxes than HY owls, and wing chords averaged shorter in New Mexico than in Nevada and Idaho. Culmen lengths averaged longer among AHY birds in both Nevada and New Mexico, but not in Idaho. With Idaho data excluded, culmens averaged longer in Nevada than in New Mexico; a similar but nonsignificant ( $P > 0.10$ ) difference was shown for hallux length.

Because there was no evidence of age-specific differences in either tarsus or tail length, we expanded analyses of these measurements to include owls of known sex but unknown age from Idaho and New Mexico (Table 3). Similar to the HY-only analyses, the expanded analyses indicated no significant sex differences for either measurement and no significant difference in tarsus length between Nevada and New Mexico. Unlike the HY-only analysis, however, the new analysis indicated longer tails in Idaho than in New Mexico, with Nevada not significantly different from either. Given no evidence of sex or age differences, final site-only analyses incorporating all available data (including additional owls of unknown age and sex from all sites, but primarily Nevada and Idaho) again confirmed no difference in tarsus lengths between Nevada (least-squares mean  $\pm$  SE:  $22.9 \pm 0.145$  mm) and New Mexico ( $22.8 \pm 0.07$  mm;  $r^2 = 0.003$ ,  $F_{1,457} = 1.17$ ,  $P = 0.280$ ), and a distinct clinal pattern of increase in tail length from southeast to northwest (NM:  $61.1 \pm 0.13$ ,  $n = 453$ ; NV:  $61.3 \pm 0.17$ ,  $n = 249$ ; ID:  $62.6 \pm 0.40$ ,  $n = 47$ ). In this case, however, the tails of Idaho owls emerged as significantly longer than those of Nevada and New Mexico owls ( $r^2 = 0.017$ ,  $F_{2,749} = 6.35$ ,  $P = 0.002$ ).

To produce more robust sex and site comparisons, we expanded analyses of mass, wing chord, culmen length, and hallux length to include owls of known sex but unknown age (Table 3), keeping in mind that age differences may confound these comparisons. These expanded analyses again confirmed overall sex differences (female > male) for wing chord, culmen length, and hallux length, and site differences for mass, wing chord, and culmen length (NV > NM; ID excluded). *Post-hoc* comparisons confirmed Idaho > Nevada > New Mexico for mass and wing chord.

#### DISCUSSION

Geographic variation in size is of broad interest to ecologists and evolutionary biologists (Brown and Lomolino 1998). For some species, including the Flammulated Owl, biogeographic patterns have been difficult to document due to the difficulty of obtaining geographically distributed samples. We contribute to overcoming this historical limitation by combining data from three studies distributed across the western United States to identify patterns of size variation among sites, ages, and sexes.

Most measurements, especially mass and wing chord, showed evidence of an increase along a southeast-to-northwest gradient. These results confirm the

latitudinal cline suggested by Marshall (1967) and are consistent with Pyle's (1997) subspecies classification. Interestingly, two anomalies arose: (a) culmens averaged longest in Nevada and shortest in Idaho; and (b) tarsi averaged longer in Idaho, but no significant or consistent (within sexes or age groups) differences were apparent in comparing owls from Nevada and New Mexico. Thus, the cline may not be consistent across all measurements; however, whether these anomalies reflect ecological factors that differ among sites, sampling errors, or perhaps the influence of relatively small sample sizes in Idaho, remains unknown. For example, longer wings and tails may correlate with northern birds migrating longer distances, and longer culmens may correlate with northern birds taking larger insect prey. Skeletal measurements such as tarsus length often are the most reliable for detecting changes in overall size (Smith 1988), but this measurement was not taken at the Idaho site.

Within sites, females averaged longer wing chords and, to a lesser degree, longer culmens (except in Idaho) and halluxes than males, with similar but nonsignificant differences usually shown for other measurements. Thus, a very slight reversed sexual size-dimorphism was evident, which remained roughly constant across sites (Table 3). Therefore, it is unlikely that a discriminant function to identify sex in these owls would function well from one site to the next, although it remains technically plausible that further research focused on a geographically restricted breeding population could enable reliable discrimination of sex from external morphometrics. Although statistically significant, the magnitude of many differences was small; i.e., a few grams/millimeters or <5% difference. Nevertheless, some site-specific differences may reflect important elements of sex-specific ecology. For example, similar mass but longer wings suggests lighter wing loading in females. Though difficult to investigate in a nearly monomorphic species, this characteristic may suggest that females migrate longer distances to more southerly winter ranges than males. However, the consistent degree of sexual size dimorphism suggests the possibility that northern birds do not necessarily travel farther than southern birds. In addition, longer culmen and hallux measurements in females may suggest the selection of larger prey compared with males, possibly resulting in a broader combined food niche for these insectivorous owls.

Within sites, AHY owls usually averaged heavier and longer wing chords, culmens, and halluxes than HY

owls (Table 2). The difference in mass and culmen length diminished from southeast to northwest, however, with no age difference evident in Idaho for these measurements. This mass result suggests differences in body condition and migratory activity among the sites. In New Mexico, HY birds had lower fat and muscle content than adults, but HY birds gradually got heavier as the migration season progressed (DeLong et al. 2005). The presence of some owls at the site throughout the season suggested that many HY owls at the New Mexico site were in a premigratory phase, departing on migration only after their body condition was adequate (DeLong et al. 2005). The fact that HY and AHY owls in Nevada and Idaho showed little difference in mass suggested that either HY owls had already attained adult mass and were actively migrating or AHY owls were in poor condition relative to HY owls. Because energy reserves are a crucial aspect of the migratory ecology of most birds (Bairlein and Gwinner 1994), such differences may signify geographic variation in migratory strategy within this species.

It appeared anomalous that culmen length averaged shortest in Idaho rather than extending the more typical pattern of an increasing cline in size from southeast to northwest. Similarly, it appeared anomalous that tarsus lengths averaged substantially longer in Idaho than in both Nevada and New Mexico, but no significant or consistent differences were evident between the latter two sites. This contrasted with the clinal patterns shown for most other measurements where Idaho > Nevada > New Mexico or Idaho/Nevada > New Mexico. These two anomalies suggested possible biases due to either different measuring protocols, with the Nevada and New Mexico data collected by one organization and the Idaho data by another, or the influence of lower sample sizes in Idaho. Eliminating this concern from further consideration by reducing the comparison to Nevada and New Mexico led to more robust final conclusions: (1) no significant variation in tarsus length due to sex, age, or site; and (2) significant variation in culmen length due to sex (longer in females), age (longer in AHY owls), and site (longer in NV than in NM).

Unless migrating birds travel well east of their summer ranges in Idaho and the Pacific Northwest to fly down through the Rocky Mountains of New Mexico, larger birds should be more common among the Idaho-Nevada as opposed to New Mexico migrants, because the Boise Ridge and Goshute Mountains sites both lie several hundred kilometers farther north and likely draw migrants from a broader range of northern geography. Put another way, significant differences in

the average size of Idaho-Nevada and New Mexico migrants clearly suggested that larger northern birds are an uncommon component of the New Mexico migrant population. This notion also was consistent with evidence from analysis of hydrogen stable-isotope ratios in feathers of New Mexico owls, which suggested that most owls captured at this site originated relatively nearby in Colorado and northern New Mexico (DeLong et al. 2005). In addition, although less frequently significant, evidence of detectable differences in the size ranges of Nevada and Idaho owls further suggested relatively limited mixing of the populations that migrate through these two sites.

Variable sample sizes and incomplete representation across the three study sites of accurately sexed and aged owls complicated this investigation. Nevertheless, a careful series of hierarchical analyses, gradually incorporating data for additional owls of unknown age, sex, or both, yielded valuable new insights into both sex- and age-specific variation, as well as regional variation in the morphometrics of Flammulated Owls.

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