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SEX-SPECIFIC MIGRATION TRENDS OF NORTHERN SAW-WHET OWLS IN EASTERN NORTH AMERICA

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ABSTRACT.—We used information compiled by the U.S. Geological Survey's Bird Banding Laboratory to identify sex-specific trends in annual Northern Saw-whet Owl (*Aegolius acadicus*) movement during autumn migration across eastern North America. The study included 40 710 individuals with assigned sex, 14% of which were assigned male and 86% were assigned female. Males were disproportionately banded at higher latitudes, and regional differences existed in sex ratios of owls at different banding stations, suggesting sex-specific migration patterns exist in this species. We used DNA analysis of 592 saw-whet owls caught in eastern New York to evaluate the accuracy of the morphometric methods used by banders to sex the majority of saw-whet owls reported in the Bird Banding Laboratory archives. Eighty-five percent of these owls could be sexed morphometrically and 97% of the morphometric assignments were congruent with genetic analysis. However, the current morphometric method disproportionately assigned males to the "unknown" class. We tested measurement reproducibility between banders and morphometric plasticity by comparing measurements of owls banded and subsequently recaptured by different banders. Mass changed 0.66 ± 6.82 g and wing chord changed $0.29 \text{ mm} \pm 3.34$ on average between captures. The low variation in measurements between captures and the high congruence between genetic and morphometric sexing methods support the sex-specific migration hypothesis.

KEY WORDS: *Northern Saw-whet Owl*; *Aegolius acadicus*; migration; morphometrics; sex ratio.

TENDENCIAS MIGRATORIAS ESPECÍFICAS DE LOS SEXOS DE *AEGOLIUS ACADICUS* EN EL ESTE DE AMÉRICA DEL NORTE

RESUMEN.—Empleamos información compilada por el Laboratorio de Anillado de Aves del Observatorio Geológico de EEUU para identificar tendencias específicas de los sexos en los movimientos anuales de *Aegolius acadicus* durante la migración de otoño a través del este de América del Norte. El estudio incluyó 40 710 individuos sexados, 14% de los cuales fueron determinados como machos y 86% como hembras. Los machos fueron anillados con mayor frecuencia a latitudes más altas, y existieron diferencias regionales en el cociente de sexos de las lechuzas en diferentes estaciones de anillado, sugiriendo que existen patrones específicos de migración vinculados al sexo en esta especie. Empleamos análisis de ADN de 592 individuos de *A. acadicus* capturados en el este de Nueva York para evaluar la precisión de los métodos morfométricos usados por los anilladores para determinar el sexo de la mayoría de las lechuzas *A. acadicus* registradas en los archivos del Laboratorio de Anillados de Aves. El 80% de estas lechuzas podrían haber sido sexadas morfométricamente y el 97% de las asignaciones morfométricas fueron congruentes con los análisis genéticos. Sin embargo, el método morfométrico actual asignó de modo desproporcionado a los machos a la clase de "desconocido." Evaluamos la replicabilidad de las medidas entre anilladores y la plasticidad morfométrica comparando las medidas de las lechuzas anilladas y subsecuentemente recapturadas por diferentes anilladores. Entre capturas en promedio el peso varió en $0.66 \text{ g} \pm 6.82$ y la cuerda alar en $0.29 \text{ mm} \pm 3.34$. La baja variación en las medidas entre las capturas y la alta congruencia entre los métodos de sexado genético y morfométrico apoyan la hipótesis de migración específica de los sexos.

[Traducción del equipo editorial]

The Northern Saw-whet Owl (*Aegolius acadicus*; hereafter saw-whet owl) is a common North American raptor that is monitored during autumn migration at banding stations in eastern North America (Davis

et al. 1966, Weir et al. 1980, Brinker et al. 1997, Whalen and Watts 2002, Paxton and Watts 2008, Brittain et al. 2009). Over 125 banding stations are currently allied with Project OwlNet, a network established to monitor saw-whet owl movement and help standardize banding and measurement methodology between

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stations (www.projectowl.net; Huy 2010). Regional banding studies have reported preliminary evidence of sex-specific migration patterns. For example, females typically outnumber males caught in mist nets (Slack 1992, Brinker et al. 1997, Stock et al. 2006, Brittain et al. 2009), and male:female ratios of saw-whet owls caught at banding stations may increase with latitude (Brinker et al. 1997). Such trends may be inconsistent or conflicting among local studies (Weir et al. 1980, Stock et al. 2006), making it difficult to draw large-scale conclusions about differential movement patterns in this species. The extensive banding dataset generated by saw-whet owl banders in the last decade has made it possible to analyze patterns at scales heretofore unexplored in regional studies.

The ability to understand sex-specific patterns in saw-whet owls using the U.S. Geological Survey's Bird Banding Laboratory (BBL) information depends on the accuracy of morphometric estimates and the validity of the discriminant function analysis (DFA) table currently used to sex saw-whet owls (Brinker 2000). Brinker's DFA table was generated from morphometric estimates of 73 known females and 43 known males from Maryland, Tennessee, and Virginia. It was designed to assist a small group of banders associated with Project Owl and was not intended to be used universally (Brinker 2000). However, Brinker's DFA table is an accepted sexing criterion of the Bird Banding Laboratory and, to the best of our knowledge, most banders without access to genetic tools now use the DFA table for sexing saw-whet owls. Although the DFA table is an improvement over previous sexing methods (Sheppard and Klimkiewicz 1976, Buckholtz et al. 1984), there has been some debate regarding its reliability. The DFA table has a 5–10 g range of "unknowns"; individuals within that mass range cannot be reliably sexed. Several authors have observed that the mass of a single prey item may exceed this range, and have noted that the body mass of saw-whet owls may significantly fluctuate spatially and temporally (Mueller and Berger 1967, Swengel and Swengel 1992, Holt and Leroux 1996, Paxton and Watts 2008). Here, we use DNA analysis to further assess the validity of the current saw-whet owl morphometric sex assignment methodology published by Brinker (2000).

Project Owlnet encourages banders to standardize protocols among banding stations, but discrepancies in wing and weight measurement techniques may still exist and natural morphological plasticity may also result in sex miscategorization when parameters

in the DFA table are used to assign sex. Therefore, we evaluated the consistency of wing and mass estimates of saw-whet owls caught multiple times and assessed the effect of measurement reproducibility or morphological plasticity on sex assignments made with the DFA table. We use these comparisons to test the accuracy of the sex category assigned using morphometric methods, and to evaluate the validity of sex-specific migration patterns proposed in this and earlier studies (Brinker et al. 1997, Stock et al. 2006, Brittain et al. 2009).

METHODS

Sex-specific Migration Patterns. We assessed sex-specific patterns using the BBL's database of 170 468 saw-whet owl banding events. We selected from this database owls with assigned sex that were banded between 1 September and 31 December in eastern North America from 1999–2008. Records west of the Mississippi River and south of Virginia were excluded due to low sample size and paucity of banding stations. We assumed the seasonal parsing ensured that most records represented migrating owls. Because we excluded pre-1999 records, we assumed that owls were sexed either genetically or morphologically according to the most recent morphology-based sex-determination system, which uses a combination of wing length and body mass and discriminant function analysis to sex individuals (Brinker et al. 1997, Brinker 2000). These two methods are accepted by the BBL and account for approximately 99% of banded owls with assigned sex. The remaining records represented birds sexed using methods described in Buckholtz et al. (1984), the only other method accepted by the BBL. Excluding pre-1999 records also ensured that most owls were banded using the audiolure mist-netting technique described in Erdman and Brinker (1997). We evaluated the proportions of males versus females banded each year using a χ^2 contingency test, followed by a *post-hoc* analysis of means for proportions to identify which years were significant deviants (JMP 9.0, SAS Institute Inc., Cary, North Carolina, U.S.A.).

We tested whether spatial differences exist between male and female movement patterns by aggregating banding events into 1°-latitude bars and calculating the sex ratios of all saw-whet owls banded within each bar. We assessed the relationship between sex ratio and latitude using linear regression. This was done with pooled data and separately for each year (1999–2008). We compared mean

banding latitude by sex class of all migrating saw-whet owls using Wilcoxon rank-sum tests. This was done with pooled data (1999–2008) and separately for each year.

We examined regional differences in sex-specific migration by performing surface interpolations based on the sex ratio of owls at banding stations with ≥ 50 banding events. This was done for all owls and separately for adults and juveniles. All interpolations used inverse-distance weighting (ArcGIS 9.3, ESRI, Redlands, California, U.S.A.) of sex ratios at all banding stations within a 3° search radius of each predicted raster cell (power = 2). This radius was chosen to restrict the influence of distant banding stations, while being wide enough to provide interpolation of the entire surface. The BBL database reports banding locations as either an exact latitude-longitude or as the corner coordinates of a 10-min or 1-min block that the banding event falls within. The database does not report station or bander names. Thus, we defined a “banding station” as any coordinate where at least one saw-whet owl was banded. Because a 10-min block is < 20 km wide, the variation in coordinate precision was negligible at the scale of this study. We used male-to-female ratios rather than raw totals at banding stations to normalize varying banding effort among stations.

Genetic Analysis. Whole blood or tissue was collected from 592 saw-whet owls captured during fall migration 2006–10 in Ulster County, NY. DNA was extracted using tissue lysing buffers, Proteinase K digestion, and spin column purification according to DNeasy Blood and Tissue Kit (Qiagen®, Valencia, California, U.S.A.) protocol. Polymerase chain reactions (PCR) were performed in 12- μ l volumes and included 0.5 μ l of 10 mM solution of each primer, 2.25 μ l of $10\times$ reaction buffer with 20 mM MgCl, 1.25 μ l dNTP mix (0.2 mM each), 0.1 μ l Taq polymerase, and 0.8 μ l of DNA template. Primers 2550F and 2718R (Fridolfsson and Ellegren 1999) designed to amplify two conserved chromohelicase-DNA-binding (CHD) genes that are located on the sex chromosomes of most birds were used in each reaction. The thermal profile used in all PCRs was described in Fridolfsson and Ellegren (1999). PCR products were run on 2% agarose gels in a standard TBE buffer and stained with ethidium bromide for visualization. No samples with weak signals or secondary bands were accepted when interpreting the gels. Samples with unclear signals after two PCRs were removed from analysis. Signals were interpreted using an ultraviolet table and inverse-grayscale

UV photography. The proportions of male and female owls as determined by genetic analysis were compared to those obtained using the Brinker (2000) DFA table.

Measurement Reproducibility. To test measurement reproducibility among stations, the weight, wing chord, and morphometric sex assignments according to the Brinker (2000) DFA table were collected and compared for 181 saw-whet owls at banding and recapture. Of these, 66 were recaptured in the same year as banding, and 115 were recaptured in different years. Banding-site morphometric data were the products of 47 banding stations in nine states in the U.S. and two provinces of Canada. Recapture-site morphometric data was the product of 39 banding stations in 12 states in the U.S. and two provinces of Canada. Banding sites were located in Maryland, Massachusetts, Michigan, New Hampshire, New York, Pennsylvania, Vermont, Virginia, and Wisconsin in the U.S., and Ontario and Quebec, Canada. Recapture sites were in Alabama, New Hampshire, New York, Maine, Maryland, Massachusetts, Michigan, Pennsylvania, Vermont, Virginia, West Virginia, and Wisconsin in the U.S., and Ontario and Quebec, Canada.

RESULTS

Sex-specific Migration Patterns. We reviewed information on 40 710 saw-whet owls with assigned sex banded in eastern North America during autumn migration (1 September to 31 December) 1999–2008. Fourteen percent of these owls were assigned male and 86% were female. Banding information originated from 252 unique banding locations, 96 of which contributed ≥ 50 banding events. Ten banding stations produced 44% of the selected records. The proportion of males versus females banded differed significantly among years ($\chi^2_9 = 331.32$, $P < 0.001$, Fig. 1). The proportion of males banded was significantly higher than expected in 1999 and 2007, and lower than expected in 2000, 2006, and 2008 ($P < 0.05$).

Male:female ratios within each 1° -latitude bar increased significantly with latitude across all years 1999–2008 ($n = 40\,710$, $r^2 = 0.59$, $P = 0.004$, Fig. 2). By-year analysis indicated that male:female ratios increased significantly with latitude in 5 of 10 yr, but the trend was in a consistent direction in all 10 yr (Table 1). There were no significant correlations for any analyses when using 1° -longitude bands instead of latitude bands to group banding events.

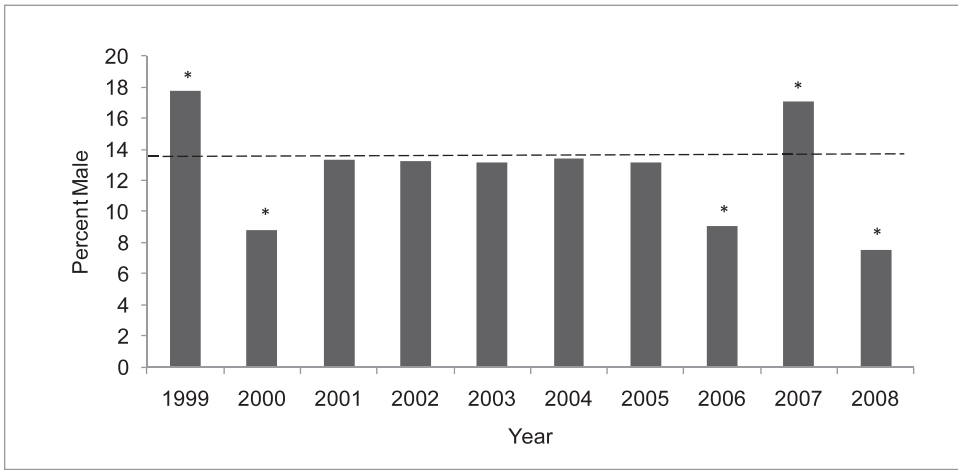


Figure 1. Percentage of male Northern Saw-whet Owls banded during fall migration in eastern North America, based on 40 710 banding events 1999–2008. Asterisks indicate years that differed significantly ($\alpha = 0.05$) from the overall percentage of males (13.5%) indicated by the dashed line.

Males were caught significantly farther north than females in every year, 1999–2008, and in all years combined (Wilcoxon rank-sums $P < 0.001$, Table 2).

Surface interpolation predicted high male:female ratios around the western Great Lakes and in the tri-state area of eastern Massachusetts, Rhode Island, and coastal New York. Lower male:female ratios were predicted in eastern Ontario, south of the Great Lakes, and along the Atlantic seaboard. The

lowest male:female ratios were predicted in the Appalachian Mountains between New York and Virginia, and in western Wisconsin (Fig. 3a). For adult saw-whet owls, the highest male:female ratios were predicted for the western Great Lakes, and the lowest were predicted along the Appalachian Mountains and in southern Indiana (Fig. 3b). Male:female ratios of juvenile saw-whet owls were predicted higher overall, but followed similar regional

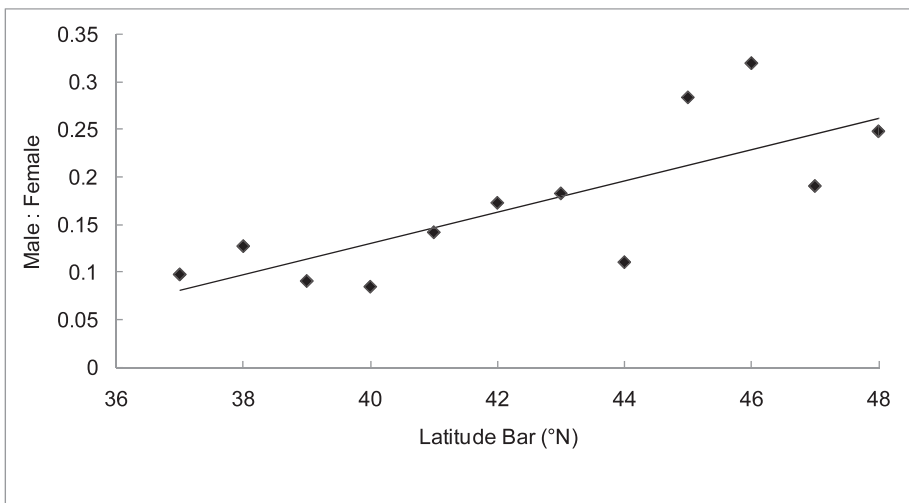


Figure 2. Sex-specific distribution by latitude of migrating Northern Saw-whet Owl banding events during fall migration across eastern North America, based on 40710 banding events 1999–2008 grouped into 1°-latitude bars ($y = -0.016x + 0.278$, $r^2 = 0.586$, $F_{11} = 14.15$, $P = 0.004$).

Table 1. Linear relationship between male-to-female ratio (y) and latitude bar (x) of Northern Saw-whet Owls in eastern North America 1999–2008.

YEAR	$y =$	R^2	F	df	P	n
1999	$0.040x - 1.402$	0.245	2.26	8	0.176	3119
2000	$0.009x - 0.309$	0.191	2.13	10	0.179	1843
2001	$0.021x - 0.676$	0.172	1.87	10	0.2	3219
2002	$0.016x - 0.511$	0.376	5.41	10	0.045	3001
2003	$0.035x - 1.322$	0.646	16.44	10	0.003	4688
2004	$0.026x - 0.924$	0.669	18.22	10	0.002	4965
2005	$0.014x - 0.433$	0.293	3.74	10	0.085	4662
2006	$0.024x - 0.920$	0.565	11.7	10	0.008	4027
2007	$0.020x - 0.602$	0.193	2.15	10	0.17	8928
2008	$0.030x - 1.134$	0.098	8.59	10	0.017	2257

trends as adult owls and for all owls combined (Fig. 3c).

Genetic Analysis. Five-hundred-ninety-two saw-whet owls were assigned sex using genetic analysis, 82 (14%) of which were assigned male and 510 (86%) were assigned female. Using the morphometric methods described in Brinker et al. (1997) and the DFA table provided in Brinker (2000), 33 (5.6%) of these owls were assigned male, 92 (15.5%) were classified as unknown, and 467 (78.9%) were assigned female. This equated to a 2.3-fold difference in male:female ratio between genetic and morphometric sexing methods. Of the 84.5% of owls that could be sexed morphometrically, however, 97% were congruent with the sex assigned using genetic analysis. Of the 92 morphometrically unknown owls, 56 were genetically female and 36 were genetically male. Considering all 592 genetically sexed owls, 16% of males were miscategorized as females, and

an additional 44% were indeterminate using morphometric sexing methods. One female was miscategorized as male, and only 11% were indeterminate.

Measurement Reproducibility. Mass and wing-chord estimates differed between banding and recapture of saw-whet owls (Table 3). These data appeared normally distributed around the mean. Mass and wing chord estimates for 27 (15%) owls were sufficiently different to cause reassignment of records between male and unknown (3) or between female and unknown (23). Only one individual was recategorized from female to male.

DISCUSSION

Sex-specific Migration Patterns. The highest percentages of male saw-whet owls were banded in irruption years 1999 and 2007, and the lowest percentages were banded in the years immediately after these irruptions (Fig. 1). This trend may be related

Table 2. By-year one-way analysis of mean male banding latitude versus mean female banding latitude of Northern Saw-whet Owls in eastern North America 1999–2008 (Wilcoxon rank-sum tests).

YEAR	FEMALE n	MALE n	BANDING LATITUDE ($^{\circ}$ N) (MEAN \pm SE)		WILCOXON Z	P
			FEMALE	MALE		
1999	2566	553	40.72 ± 0.04	41.52 ± 0.10	7.86	<.001
2000	1681	162	42.62 ± 0.06	43.45 ± 0.19	4.01	<.001
2001	2789	430	41.67 ± 0.05	42.47 ± 0.13	6.30	<.001
2002	2604	397	43.39 ± 0.06	44.11 ± 0.13	5.77	<.001
2003	4071	617	42.92 ± 0.04	44.23 ± 0.11	11.37	<.001
2004	4298	667	42.71 ± 0.04	43.85 ± 0.10	9.85	<.001
2005	4049	613	43.23 ± 0.04	43.92 ± 0.11	5.80	<.001
2006	3661	366	43.99 ± 0.04	45.24 ± 0.14	8.52	<.001
2007	7403	1526	42.96 ± 0.03	43.23 ± 0.08	3.27	<.001
2008	2087	170	42.58 ± 0.06	43.43 ± 0.27	2.96	<.001
Totals	35 209	5501	42.79 ± 0.02	43.47 ± 0.04	15.9	<.001

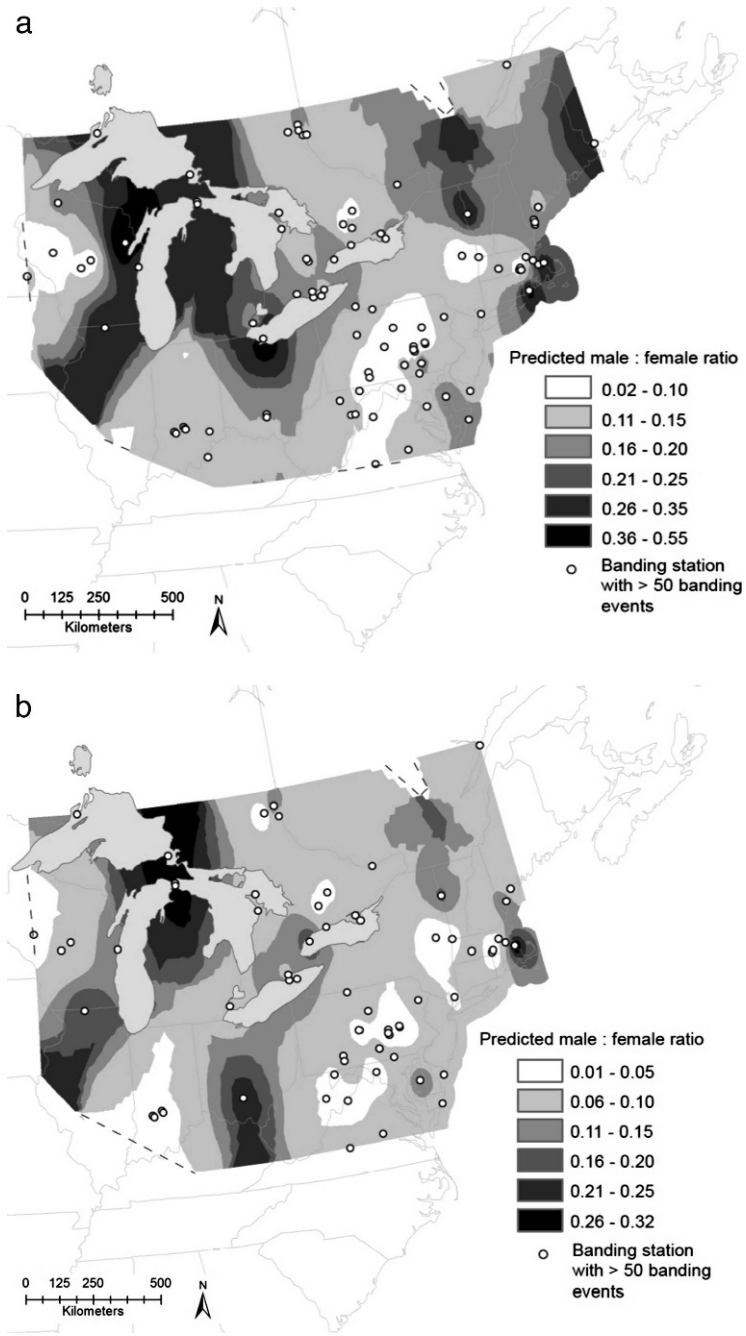


Figure 3. (a) Predicted sex distribution of migrating Northern Saw-whet Owls across eastern North America 1999–2008, based on sex ratios at 96 banding stations with ≥ 50 banding events. (b) Predicted sex distribution of adult owls at 66 banding stations.

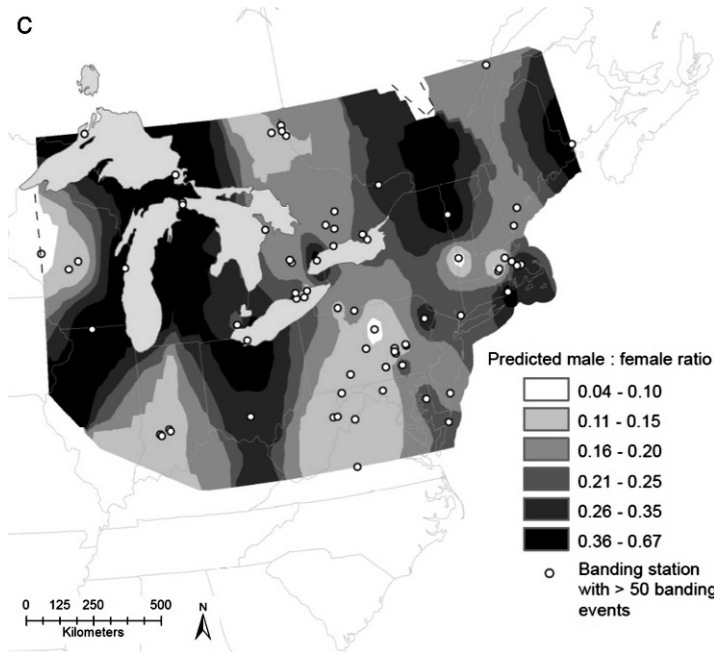


Figure 3. Continued. (c) Predicted sex distribution of juvenile owls at 72 banding stations. Interpolations use inverse-distance-weighting of male:female ratios of owls at banding stations within a 3°-radius of each predicted raster cell. Dashed lines represent interpolation boundary.

to resource availability. For example, fluctuating rodent populations may fail to support saw-whet owl population booms in the summer range and increased competition may drive males farther south that would otherwise remain closer to breeding territories (Weir et al. 1980, Marks and Doremus 2000, Whalen and Watts 2002). The highest proportions of juvenile owls were banded in these irruption years across eastern North America, and the lowest

proportions were caught in the years immediately after (Beckett and Proudfoot 2011). This correlation in capture proportions between males and juveniles suggested that immature male saw-whet owls may be more migratory than adult males in irruption years, possibly due to age-dependent abilities (i.e., hunting experience or site familiarity) to survive in regions where food is scarcer. Alternatively, increased competition during irruption years may

Table 3. Differences in mass and wing chord estimates of 181 Northern Saw-whet Owls banded and recaptured at different banding stations in eastern North America (1999–2008). Sixty-six owls were banded and recovered in the same year and 115 were banded and recovered in different years.

VARIABLE AND STATISTIC	ALL OWLS	BANDED/RECAPTURED IN SAME YEAR	BANDED/RECAPTURED IN DIFFERENT YEARS
Mass change			
Mean ± SD (g)	0.66 ± 6.82	0.96 ± 6.86	0.49 ± 6.83
Range (g)	−16–17.7	−16–13	−16–17.7
IQR (g)	−4–5.4	−4.08–5.83	−3.95–5.35
Wing chord change			
Mean ± SD (mm)	0.29 ± 3.34	0.71 ± 3.76	0.05 ± 3.06
Range (mm)	−9–9	−9–9	−8–7
IQR (mm)	−2–2	−1–2	−2–2

reduce owl mass overall, causing an artificial increase in male assignment according to the DFA table.

Our results differed from earlier studies that reported no difference in sex ratios among years (Whalen and Watts 2002), or no increase in male capture rate in irruption years (Brinker et al. 1997, Stock et al. 2006, Brittain 2008). We suspect this study shows a population-level trend that does not exist at smaller scales of previous research, where too few males are banded to reveal significant differences.

No study has determined the sex ratio for the entire saw-whet owl population, but deviation from 1:1 is rare (Fisher 1930). Here, females often greatly outnumber males at banding stations during fall migration (Slack 1992, Brinker et al. 1997, Stock et al. 2006, Brittain 2008) and multiple analyses in this study revealed that males are caught in greater proportion at northern latitudes (Fig. 2, Table 1, 2). These findings are congruent with earlier research that was conducted at a considerably smaller scale (Brinker et al. 1997). If this species does not have an exceptional overall sex ratio, then males and females exhibit different migratory tendencies in the fall. Our analyses suggest that males may be less migratory and remain farther north than females. Such sex-specific migration trends have been documented in other small forest owls including Boreal (Tengmalm's) Owls (*Aegolius funereus*; Hipkiss 2002), Long-eared Owls, (*Asio otus*; Erritzoe and Fulle 1999), and Eurasian Pygmy-Owls (*Glaucidium passerinum*; Polakowski et al. 2008). Sex-specific migration patterns may be related to different resource demands between males and females. Weir et al. (1990) suggested that because female saw-whet owls are larger than males, they may be more vulnerable to winter's diminishing food supply. Alternatively, females may be more migratory because egg development demands additional resources not required of males. Males caught at stations in Idaho had lower body condition and a later molt pattern than females (Stock et al. 2006), possibly indicating that migrating males are less fit than those remaining on breeding territories, and are driven south to avoid starvation. Males may also winter closer to northern breeding areas in order to facilitate quicker access to territories in the spring.

The interpolation maps (Fig. 3a–c) revealed regional differences in sex ratio of banded saw-whet owls. The power and accuracy of any surface interpolation depends on the density and accuracy of

sampling points. Many unaccountable situations at individual banding stations may affect the sex ratio implied by the BBL database, including bander error, data entry error, inconsistent sexing practices between years, or uncommon banding practices during the fall migration. These potentially erroneous influences are heightened in areas with low sample size and low station density. We therefore forego interpretation on areas of the interpolation maps that have low station density (i.e., southern Quebec) or are heavily influenced by a single banding station (i.e., southern Ohio and eastern Maine). However, for the large-scale trend analysis of this study, the interpolation maps clearly revealed broad regional patterns that are indicative of sex-specific migration tendencies. The western Great Lakes had among the highest male:female ratios of banded owls, and the Appalachian Mountains had among the lowest ratios (Fig. 3a), suggesting that fewer males winter in the Appalachians. This was consistent in both adult (Fig. 3b) and juvenile (Fig. 3c) saw-whet owls, suggesting that movement patterns in males may be less influenced by juvenile dispersal than by sex-specific migration pressures. This also was supported by the higher predicted juvenile male:female ratios across most of the study compared to adults. We recognize that local breeding populations of saw-whet owls at high elevations in the Appalachian Mountains (Rasmussen et al. 2008) may influence the predicted sex ratios of migrating owls in this area. However, if we assume that breeding populations are close to a 1:1 sex ratio (Fisher 1930), then the low predicted male:female ratios throughout the Appalachians indicates that resident saw-whet owls are not obscuring the trend in this region.

The regional variation in sex ratio of banded saw-whet owls showed that the sex-specific migration tendencies of this species are more complicated than a simple latitudinal gradient. Forest cover and structure vary across eastern North America, as does prey population density. Suitable wintering grounds may therefore be different for males and females due to different resource or reproduction pressure. Analysis of the underlying causes of the regional variation was beyond the scope of this study, but the interpolation maps demonstrated that regional patterns do exist.

Duffy and Matheny (1997) found that the proportion of females compared to all owls (male, female, and unknown) caught using audiolures in New Jersey was significantly higher than with passive netting. This inconsistency between capture methods

suggests the extensive banding data, now available largely due to the increased capture rates afforded by audiolures, may not represent the true male:female ratio during migration. Testing of these two methods, however, was carried out in different locations during different years. This lack of uniform sampling may have influenced their results and generated erroneous inferences. Furthermore, there was no difference in the proportion of males caught compared to all owls. Clearly, the ubiquitous use of audiolures may bias the sex ratio of banded owls. However, females greatly outnumbered males in both methods (Duffy and Matheny 1997). Any bias associated with the sampling method is more likely to disguise real differences than lead researchers to false conclusions.

Genetic and Morphometric Analysis. When evaluating the mass change of individuals captured more than once during the same migration season, temporal mass variability resulted in 7.4% ($n = 873$; Brittain et al. 2009) to 51% ($n = 376$; Paxton and Watts 2008) change in sex assignment of individual saw-whet owls according to Brinker's (2000) DFA categories (female, male, or unknown). Most of these changes were male to unknown, female to unknown, or vice-versa. The percentage of individuals that actually changed sex assignment from male to female, or vice-versa, was 0% in Brittain et al.'s (2009) study and 3% in Paxton and Watts (2008), well within the 95% confidence limits established by Brinker (2000). Sex assignments in Paxton and Watts (2008) and Brittain et al. (2009) were not validated with DNA analysis, or by any other means. However, the level of assumed error (individuals assigned to the opposite sex due to temporal mass variability) was congruent with results of a study in Idaho that reported 4% ($n = 249$) error (96% agreement) between DNA and morphometric sex assignment using the DFA table (Stock et al. 2006). From the same study, Paxton and Watts (2008) noted that temporal mass variability may significantly change the perceived male:female ratio, from 1:13 to 1:6 in their study. However, because Paxton and Watts (2008) grouped saw-whet owls according to the upper and lower limits of their data, i.e., the high and low mass values, the disparity in the male:female ratio they presented represented unlikely extremes and not the actual ratio estimates of banding and recapture. The discrepancy in the percentage of individuals that changed assignment categories in Brittain et al. (2009) and Paxton and Watts (2008) is noteworthy and, because the two

study sites were separated geographically by approximately 1000 km, may support the hypothesis of geographic and seasonal influences on temporal mass variability. For instance, owls captured in south-central Indiana (Brittain et al. 2009) were likely midway through their migration and maintaining a more uniform condition among captures compared to those captured at potential migrant traps like the Lower Delmarva Peninsula in Virginia (Paxton and Watts 2008), where recaptures include recent migrants, wintering birds, and individuals gaining mass in preparation for overwater crossing of the Chesapeake Bay. The mass of saw-whet owls recaptured in Indiana may therefore be less variable than those in the Lower Delmarva Peninsula that are no longer maintaining an optimal mass for migrating. Thus, these studies suggest the morphometric table generated with DFA may be somewhat geographically or temporally limited, but they do not prove it to be inaccurate.

Our results showed that the DFA table disproportionately underrepresented male saw-whet owls. Of genetic males, the majority were either morphometrically unknown or miscategorized as females, resulting in a 2.3-fold difference in perceived sex ratio between morphometric and genetic sex assignment. Previous research (Stock et al. 2006) comparing morphometric sex to genetic sex assignment of saw-whet owls failed to find this bias because the makeup of owls falling within the unknown region of the DFA table was not analyzed.

The DFA table is problematic in the number and quality of individuals of unknown assignment. However, it accurately assigned sex to >95% of owls in this and earlier studies from geographically disparate areas of Idaho, Maryland, New York, Tennessee, and Virginia (Brinker et al. 1997, Stock et al. 2006). In Alberta, Canada, genetic sex assignment of migrating saw-whet owls was 93% ($n = 363$) congruent with the DFA table (Priestley 2008), showing that Brinker's table remained rather accurate even at great geographic distances. In addition, our morphological plasticity assessment showed that most banding-station measurements are relatively consistent and that average individual variations were minimal, supporting the current morphometric method and the sex-specific trends described in our analyses. Furthermore, the widespread use of the DFA table makes the post-1997 banding database internally consistent. Thus, the conclusions drawn in this study represent real trends rather than nonuniformity in DFA accuracy. The proportion of banded

males is underrepresented by the DFA table, so the ratios returned by our analyses are not the actual sex ratios of migrating owls. However, a strong female bias would still exist even if all miscategorized males were correctly assigned. Errors associated with the DFA are therefore more likely to disguise real differences than lead researchers to false conclusions. Because of this, we used the sex ratios generated in our analyses to identify broad trends rather than differences dependent on specific values.

The spatial variation in the accuracy of the DFA table could be better understood if all banded owls (male, female, and unknown) were included in the analysis. However, the BBL database does not reliably discriminate between owls that were never sexed and owls that were assigned unknown by the DFA table. If researchers continue to use Brinker's (2000) DFA table to analyze sex-related trends in saw-whet owls, banders should clarify how each owl was assigned as unknown.

A more broadly applicable morphometric sexing system, or a combination of morphometric and genetic sexing, will allow researchers to resolve finer sex-specific differences in migration behavior and population demographics in this species. Considering the time and cost associated with genetic analyses, genetically sexing all banded owls is unfeasible. However, our results indicated that conducting genetic analysis on only morphometrically unknown individuals would have improved the accuracy of male representation from 40.2% to 84.1%. Therefore, genetically sexing a small subset of banded owls would greatly improve accuracy at a reasonable cost. Thus, researchers should consider the tradeoff between the high cost and increased accuracy of genetically sexing saw-whet owls.

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