Age-Related Differential Migration Strategies in Northern Saw-Whet Owls (Aegolius acadicus)

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AGE-RELATED DIFFERENTIAL MIGRATION STRATEGIES IN NORTHERN SAW-WHET OWLS (*AEGOLIUS ACADICUS*)

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Abstract.—We analyzed differences in wing loading and body condition indices (BCI) between hatch-year (HY) and after-hatch-year (AHY) Northern Saw-whet Owls (*Aegolius acadicus*) captured during autumn migration in south-central Indiana. From 2002 to 2012, banders captured 1469 owls at two sites, including 826 HY owls and 641 AHY owls. The mean BCI (mass to wing chord ratio) was 0.665 g/mm and did not vary between HY and AHY owls. BCI was lowest in 2005 (0.658 g/mm) and highest in 2008 (0.679 g/mm). During autumn 2007, the banders photographed 267 owls at the two banding sites to enable comparisons of wing loading (mass to wing surface area ratio) and BCI for different age categories. Mean wing loading was 0.242 g/cm^2 and also did not vary between HY and AHY owls, confirming the BCI results and suggesting that the age classes were not gaining or losing mass differentially. The median arrival date was 3 d earlier and the nightly median capture time was 10 min later for HY owls. In addition, the mass of HY owls correlated positively with the nightly capture time, whereas this was not true for adults. Together these results suggest that HY Northern Saw-whet Owls in south-central Indiana make up for any limitations in migratory/hunting abilities by migrating earlier each night and foraging more frequently while migrating. Migrating earlier, whether by choice or as a result of density-dependent adult competition, likely affords the younger birds greater access to prey in commonly exploited foraging areas. Available data indicate the potential for regional variation in the mass to wing chord correlation for this species, which needs further research. We also suggest that future studies obtain full wingspan measurements and compare the wingtip shape (amount of point and convexity) between juvenile and adult birds.

Key Words: *Northern Saw-whet Owl*; Aegolius acadicus; *age differences*; *body condition index*; *migration strategy*; *wing loading*.

ESTRATEGIAS DE MIGRACIÓN DIFERENCIAL RELACIONADAS CON LA EDAD EN *AEGOLIUS ACADICUS*

Resumen.—Analizamos las diferencias en las cargas alares y los índices de condición corporal (ICC) entre el año de eclosión (AE) y después del año de eclosión (DAE) de individuos de *Aegolius acadicus* capturados durante la migración otoñal en el centro sur de Indiana. Desde el 2002 hasta el 2012 los ornitólogos capturaron 1469 lechuzas en dos sitios, incluyendo 826 lechuzas AE y 641 lechuzas DAE. La ICC media (el radio entre la masa y la cuerda alar) fue de 0.665 g/mm y no varió entre las lechuzas AE y DAE. El ICC más bajo ocurrió en 2005 (0.658 g/mm) y el más alto en 2008 (0.679 g/mm). Durante el otoño del 2007, los ornitólogos fotografiaron 267 lechuzas en los dos sitios de anillado para permitir comparaciones de cargas alares (radio entre la masa y la superficie alar) e ICC para diferentes categorías etarias. La carga alar media fue de 0.242 g/cm^2 y tampoco varió entre las lechuzas AE y DAE, confirmando los resultados de los ICC y sugiriendo que las diferentes clases de edad no estuvieron ganando ni perdiendo masa de forma diferencial. La fecha de arribo mediana fue de 3 días antes y la hora de captura nocturna mediana fue de 10 minutos más tarde para las lechuzas AE. Además, la masa de las lechuzas AE se correlacionó positivamente con la hora de captura nocturna, mientras que esto no fue así para los adultos. Juntos, estos resultados sugieren que los individuos de *A. acadicus* del centro sur de Indiana compensan cualquier limitación en sus habilidades migratorias/de caza al migrar antes cada noche y al forrajear con mayor frecuencia mientras migran. La migración más temprana, por elección o como resultado de la competencia adulta dependiente de la densidad, probablemente le permite a las aves más jóvenes acceso a presas en áreas de forrajeo comúnmente explotadas. Los datos disponibles indican el potencial para una variación regional en la correlación de la masa y la cuerda alar para esta especie, aseveración que necesita de mayor investigación.

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También sugerimos que se obtengan en estudios futuros medidas de envergadura total y se compare la forma de la punta del ala (cantidad de punta y convexidad) entre aves juveniles y adultas.

[Traducción del equipo editorial]

Wing morphology plays an important role in enabling birds to migrate long distances between seasonal ranges (Savile 1957, Andersson and Norberg 1981, Lockwood et al. 1998). Wing length is generally proportionately long in species that migrate longer distances (Savile 1957, Lockwood et al. 1998). Wing morphology also plays an important role in enabling the continuous-flapping flight of some raptors, including Northern Saw-whet Owls (*Aegolius acadicus*; hereafter ''saw-whet owls''), by helping to maximize the efficiency of this energy-intensive flight style (Tobalske et al. 2007, Rasmussen et al. 2008). Longer, narrower wings are more efficient for prolonged powered flight, whereas shorter elliptical wings facilitate maneuverability (Savile 1957). In addition, birds with proportionately greater wing surface area relative to overall body size have lower wing loading. For example, saw-whet owls (0.287 g/cm^2) and Long-eared Owls (*Asio otus*; 0.216 g/cm^2) had lower wing loadings than similarly sized Western Screech-Owls (*Megascops kennicottii*; 0.472 g/cm^2) and Boreal Owls (*Aegolius funereus*; 0.398 g/cm^2; Poole 1938, Hayward and Garton 1988). The more migratory Saw-whet and Long-eared Owls have lower wing loadings than the two more sedentary species, suggesting a relationship between wing loading and migration strategy.

Wing morphometrics often vary among age and sex classes within species, with likely influences on relative maneuverability for capturing prey, and on efficiency of migratory flight. Mueller et al. (1981, 2002) documented age and sex differences in wing loading among Merlins (*Falco columbarius*) and Sharp-shinned Hawks (*Accipiter striatus*), and later (Mueller et al. 2004) hypothesized that the demographic differences in wing loading and other aerodynamic characteristics in these species and, to a lesser degree, Red-tailed Hawks (*Buteo jamaicensis*) were adaptations that reflected different hunting methods. Merlins and Sharp-shinned Hawks, whose diets include more birds, require more maneuverability than Red-tailed Hawks, which are generalists that both scavenge more and feed more on less mobile prey such as reptiles and mammals. The age-related differences of the former two species, with greater wing loadings in adults than juveniles, are larger than the age-related differences observed in Red-tailed Hawks (Mueller et al. 1981, 2002, 2004). The greater wing loading of adult raptors likely reflects increased musculature and decreased flight feather length, with the resulting increase in flight power compensating for the greater wing loading (Mueller et al. 1981, Bortolotti 1984). Alternatively, the greater wing loading of adults may reflect larger fat stores, resulting from their being more capable hunters than their younger counterparts, which is a possibility that Mueller et al. did not address.

Sex-specific differences in wing characteristics (e.g., surface area or wing length) are expected in a sexually dimorphic species such as the saw-whet owl (Brinker et al. 2000); however, age-related differences in wing morphometrics are not well documented in this species. Preliminary research on migratory saw-whet owls in Indiana indicated that after-hatch-year (AHY) owls had significantly longer wing chords than hatch-year (HY) owls (Brittain et al. 2009). Hatch-year saw-whet owls captured on the Delmarva Peninsula also had shorter wing chords than adult owls (Whalen and Watts 2002). The body condition scores of HY and AHY owls did not differ on the Delmarva Peninsula; however, the body condition scores were lower for both age groups during irruption years compared to non-irruption years (Whalen and Watts 2002). Conversely, a similar study near Boise, Idaho, found that HY owls had significantly lower body condition scores than AHY owls in both irruptive and non-irruptive years (Stock et al. 2006), indicating potential regional differences in age-specific body condition or in the effects of migration on immature owls. Although based on very small sample sizes, Johnson (1997) estimated sex-specific wing-loading values for saw-whet owls as 0.186 g/cm^2 for one male and 0.235 g/cm^2 for three females.

Wing measurements alone are likely skewed by the correlation with overall body size, particularly in sexually dimorphic species such as saw-whet owls. Combining wing morphometrics with other indices, to produce metrics such as ratios of mass to wing chord (body condition index [BCI]) or mass to wing surface area (wing loading), has greater potential to illustrate adaptive migratory strategies. Previous researchers calculated wing surface area by photographing live birds or using dead birds (Poole 1938, Mueller et al. 1981, Johnson 1997). Poole (1938)

used a polar planimeter on dead birds. Mueller et al. (1981) photographed wings of live birds against a grid of known cell size, and used a polar planimeter to measure the area of the traced wing. Johnson (1997) employed digital image analysis using a geographic information system (GIS) to measure hand-drawn tracings of wings from freshly deceased specimens.

We measured saw-whet owl wing morphometrics to investigate the potential adaptive significance of age differences. We hypothesized that immature saw-whet owls would have lower BCIs and wing loadings than adults, reflecting reduced foraging and flying efficiency of immature owls. We also evaluated the relative effectiveness of a newer digital image analysis method for determining wing surface area.

METHODS

From 2002 to 2012, banders captured and banded migrating saw-whet owls at three stations in Brown and Greene counties in south-central Indiana. Previous research in this area characterized the magnitude and demographics of fall migration over a 6-yr period (2002–2007) and described the banding locations (Brittain et al. 2009). Banders identified the sex of owls according to mass and wing-chord criteria defined by Brinker et al. (2000). They classified owls as HY or AHY based on remigal molt patterns (Evans and Rosenfield 1987), using long-wave ultraviolet light to help identify the presence (AHY) or absence (HY) of multiple generations of feathers (new feathers show brighter fluorescence of porphyrins; Weidensaul et al. 2011). Other data recorded at the time of capture included mass (g), wing chord (mm), and the capture date and time.

We calculated the BCI of each owl as the ratio of mass to wing chord (g/mm). Because we sexed the owls using mass and wing chord measurements, the sex classifications violate the necessary assumption that there is no correlation between BCI and other structural components (e.g., mass and wing chord) or between BCI and the demographic parameter of interest (e.g., sex; Green 2001). To meet the BCI assumptions, other studies corrected the data by raising the raw BCI value to the power of the slope (0.1818) of the log-log plot of mass versus wing chord (Whalen and Watts 2002, Stock et al. 2006). This slope transformation did not remove the correlation between BCI and wing chord in our data (post-transformation $r = 0.49$, $P < 0.001$). Therefore, because intrinsic differences in the size of the owls would confound analysis of sex-specific differences in BCI, we limited our analyses to age-related differences and used the more interpretable raw BCI scores.

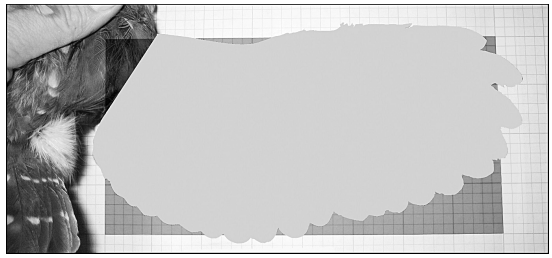

Figure 1. Digital shape areas used to measure the wing surface area of Northern Saw-whet Owls.

In 2007, we digitally photographed the wings of 267 individual saw-whet owls against grid paper (cell sizes of 1.2 cm^2 and 0.6 cm^2). We then measured the surface area of each wing using the image analysis feature in Adobe® Photoshop® CS3 Extended (Adobe Systems Incorporated, San Jose, California, U.S.A.). This method has not been widely used to estimate the surface area of bird wings, but the technique has been used to estimate the surface area of lichen cover (McCarthy and Zaniewski 2001), leaf area (Bradshaw et al. 2007), and the relative area of larval pigmentation in butterflies (Davis et al. 2004). We created a sample shape area (Fig. 1) to match a known area on the grid paper, and the ''record measurement'' function of the software counted the pixels (px) within the selected area. We measured the pixel/cm^2 ratio for each image to account for variability between the two grid sizes, three camera resolutions, and different photographing distances. We created and selected the wing-area shape and recorded the pixel count for each wing area. We then used the following formula to calculate the wing surface area (cm^2):

$$\mathrm{SA_w} = \left(WA_{px} \bullet AS_{cm}\right) / AS_{px}$$

where $\mathrm{SA_w}$ is the surface area of one wing in cm^2, WA_{px} is the surface area of the wing in number of pixels, AS_{cm} is the sample area in cm^2, and AS_{px} is the sample area in number of pixels. We then doubled the $\mathrm{SA_w}$ value to approximate the surface area of both wings, and divided by the owl's mass to arrive at wing loading (g/cm^2). We tested the accuracy of this method by comparing it to a secondary method: visually counting the number of grid cells to the nearest $^1/_{10}$ of a cell. We created one or

Table 1. Number of Northern Saw-whet Owls captured during autumn migration at two banding stations in south-central Indiana by age and year.

	Newark		Yellowwood State Forest		
Year	HY[1]	AHY	HY	AHY	Total
2002	–	–	38	21	59
2003	39	16	39	30	124
2004	9	31	20	34	94
2005	16	9	11	26	62
2006	14	6	42	27	89
2007	164	84	130	63	441
2008	6	57	8	68	139
2009	10	15	4	5	34
2010	22	19	15	8	64
2011	10	29	17	26	82
2012	73	24	139	43	279
Total	**363**	**290**	**463**	**351**	**1467**

[1] HY = hatch-year; AHY = after-hatch-year.

multiple grids for 15 images, using the vanishing point filter in Photoshop® and overlays to match the perspective and grid-cell proportion in the photograph. The estimates of wing surface area based on the grid and image-analysis methods did not differ ($t = -0.43$, df = 25, $P = 0.673$). Therefore, we report only the image-analysis results, because they represented a greater sample size.

We compared the individual metrics used to calculate BCIs (mass and wing chord) and BCI by year and age using general linear models (GLM) with interactions, and Tukey's post-hoc multiple comparisons to evaluate differences among individual years. We compared the wing loadings of HY and AHY owls using a two-tailed *t*-test. Capture dates (Julian) and times were not normally distributed (Kolmogorov-Smirnov tests, $P < 0.01$). Therefore, we compared the captures dates and times of HY and AHY owls using Mann-Whitney rank tests, and we used Spearman's rank correlation to compare the mass of owls to Julian date and capture time. We conducted all statistical tests using Minitab 16.1.1 (State College, Pennsylvania, U.S.A.), considered results significant at $\alpha = 0.05$, and present all data as means ±SE.

RESULTS

Banders at the Newark station in Greene County captured 653 owls, including 363 HY (56%) and 290 AHY (44%) owls. Banders at the Yellowwood State Forest station in Brown County captured 814 owls, including 463 HY (57%) and 351 AHY (43%) owls. Only the Yellowwood State Forest station was open in 2002. The 2007 capture totals were nearly double that of the next highest year (2012; Table 1). Given that the level of effort remained consistent after 2002, the much higher capture totals in 2007 reflected an irruptive year for saw-whet owls in south-central Indiana. Another minor irruption occurred in 2012, with that year's capture totals approximately double that of the next highest year (2008).

The mass of owls varied by age ($F_{1,1464} = 12.17$, $P = 0.001$) and year ($F_{10,1455} = 1.96$, $P = 0.034$), with no age × year interaction ($F_{12,1453} = 1.01$, $P = 0.431$; Table 2). HY owls (90.8 ± 0.3 g) averaged lighter than AHY owls (92.8 ± 0.3 g). The GLM indicated a significant year effect, but post-hoc tests revealed no significant pairwise comparisons ($P > 0.34$). The GLM for wing chord length indicated similar results: significant variation by age ($F_{1,1464} = 56.31$, $P < 0.001$) and year ($F_{10,1455} = 2.79$, $P = 0.002$), and no significant interaction ($F_{12,1453} = 0.59$, $P = 0.826$; Table 2). HY wing chord length averaged 2.1 mm shorter than those of AHY owls. Interannual variation in wing chord length was greater than for mass, with wing chords averaging significantly longer in 2002 and 2003, and significantly shorter in 2009 compared to other years.

BCI did not differ between HY and AHY owls ($F_{1,1464} = 0.68$, $P = 0.408$), but did vary by year ($F_{10,1455} = 1.86$, $P = 0.047$), and there was no age × year interaction ($F_{12,1453} = 0.95$, $P = 0.485$; Table 3). Owls captured in 2005 averaged the lowest BCI and those captured in 2008 averaged the highest BCI; however, post-hoc analysis revealed no significant pairwise differences ($P > 0.25$). Among the 2007 subsample of saw-whet owls, neither wing loading ($t_{159} = 1.32$, $P = 0.188$) nor BCI ($t_{150} = 0.83$, $P = 0.408$) differed between HY owls and AHY owls.

The mass of HY saw-whet owls was positively correlated with nightly capture time ($r_S = 0.087$, $P = 0.012$; Fig. 2), whereas no such correlation was shown for AHY owls ($P = 0.282$). The median capture time for HY owls (21:50 H) was 10 min later than for AHY owls (21:40 H; $W = 632047.0$, $P = 0.001$). The median Julian date of saw-whet owl captures was 3 d earlier for HY owls (307) than for AHY owls (310; Mann-Whitney $W = 519290.5$, $P < 0.001$).

Table 2. Mean (±SE) mass and wing chord of Northern Saw-whet Owls captured during autumn migration in south-central Indiana by age and year.

	Mass (g)			Wing Chord (mm)		
Year	HY[1]	AHY	Pooled[2]	HY	AHY	Pooled[2]
2002	94.1 (1.3)	93.0 (1.7)	93.7 (1.1)[a]	138.3 (0.8)	140.7 (0.8)	139.2 (0.6)[a]
2003	91.5 (0.9)	93.1 (1.6)	92.1 (0.8)[a]	138.2 (0.5)	140.3 (0.7)	139.0 (0.4)[a]
2004	90.7 (0.5)	94.8 (0.9)	93.6 (0.8)[a]	137.0 (0.9)	140.1 (0.5)	139.1 (0.5)[a,b]
2005	90.7 (1.1)	91.2 (1.3)	91.0 (0.8)[a]	138.2 (0.7)	139.5 (0.6)	139.0 (0.5)[a,b]
2006	92.9 (1.0)	92.8 (1.4)	92.9 (0.8)[a]	137.4 (0.7)	139.2 (0.7)	138.1 (0.5)[a,b]
2007	90.2 (0.4)	91.2 (0.6)	90.5 (0.3)[a]	136.8 (0.2)	138.9 (0.3)	137.5 (0.2)[a,b]
2008	93.1 (1.8)	93.8 (0.6)	93.7 (0.6)[a]	136.9 (0.9)	138.1 (0.4)	138.0 (0.3)[a,b]
2009	88.1 (3.3)	92.6 (1.7)	90.8 (1.7)[a]	134.0 (1.3)	138.4 (0.8)	136.6 (0.8)[b]
2010	89.2 (1.0)	93.1 (1.1)	90.9 (0.8)[a]	137.3 (0.7)	139.6 (0.8)	138.3 (0.6)[a,b]
2011	89.7 (1.2)	93.1 (1.1)	90.0 (0.8)[a]	137.4 (0.8)	139.0 (0.5)	138.5 (0.4)[a,b]
2012	90.8 (0.6)	93.2 (0.9)	91.4 (0.5)[a]	136.5 (0.3)	139.2 (0.4)	137.2 (0.3)[a,b]
Average	**90.8 (0.3)**	**92.8 (0.3)**	**91.7 (0.2)**	**137.0 (0.2)**	**139.1 (0.2)**	**137.9 (0.1)**

[1] HY = hatch-year; AHY = after-hatch-year.

[2] General linear modeling revealed heavier mass and longer wing chords among adults, and significant overall variation among years in both measurements. For each measurement, pooled values that do not share superscript letters are significantly different ($\alpha = 0.05$) based on Tukey's post-hoc multiple comparisons.

DISCUSSION

Although lower wing loadings appear to be a general adaptation for migratory owls, such as saw-whet owls and Long-eared Owls (Poole 1938, Hayward and Garton 1988, Johnson 1997), our analysis did not support the hypothesis of lower wing loadings and BCI in HY saw-whet owls. The immature owls migrating through south-central Indiana had shorter wing chords than the adults, but the condition indices of immature and adult owls were similar. The similar BCI of HY and AHY saw-whet owls agrees with results from the Delmarva Peninsula (Whalen and Watts 2002), but contrasts with the results from Idaho (Stock et al. 2006). This suggests there is regional variation in BCI demographics, perhaps reflecting differences among populations from the western mountain and Great Plains regions.

Table 3. Mean (±SE) body condition index (BCI) and wing loading of Northern Saw-whet Owls captured during autumn migration in south-central Indiana by age and year.

	BCI (g/mm)			Wing Loading (g/cm^2)	
Year	HY[1]	AHY	Pooled	HY	AHY
2002	0.680 (0.008)	0.661 (0.011)	0.673 (0.051)		
2003	0.662 (0.005)	0.663 (0.010)	0.662 (0.055)		
2004	0.662 (0.009)	0.677 (0.005)	0.672 (0.045)		
2005	0.657 (0.008)	0.654 (0.008)	0.655 (0.046)		
2006	0.676 (0.006)	0.666 (0.008)	0.672 (0.047)		
2007	0.659 (0.003)	0.657 (0.004)	0.658 (0.049)	0.240 (0.001)	0.244 (0.002)
2008	0.680 (0.013)	0.679 (0.004)	0.679 (0.047)		
2009	0.657 (0.022)	0.669 (0.011)	0.664 (0.064)		
2010	0.650 (0.006)	0.670 (0.006)	0.657 (0.037)		
2011	0.653 (0.008)	0.670 (0.007)	0.664 (0.051)		
2012	0.665 (0.003)	0.670 (0.006)	0.666 (0.049)		
Average	**0.663 (0.002)**	**0.667 (0.002)**	**0.664 (0.001)**		

[1] HY = hatch-year; AHY = after-hatch-year.

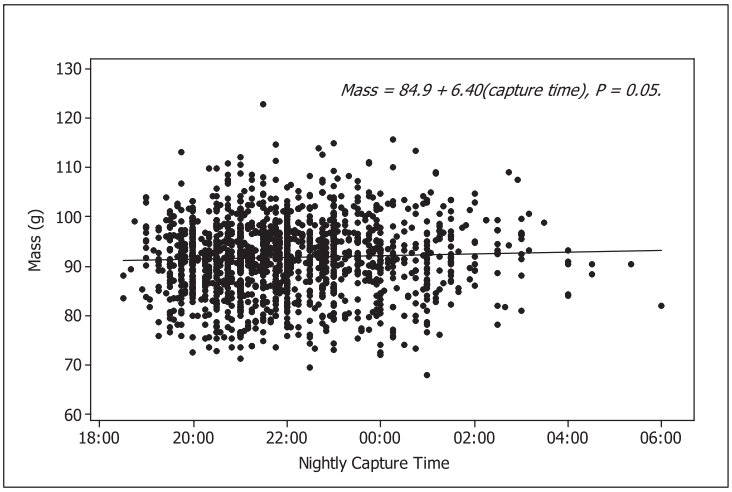

Figure 2. Mass of hatch-year Northern Saw-whet Owls captured during autumn migration in south-central Indiana, plotted against nightly capture time.

BCI and wing loading do not reveal the complete story of age-specific differential migration. Although it appears saw-whet owls may not have evolved differential wing morphologies that afford age-specific advantages during migration, we would still expect HY owls to be less efficient in their first migration due to a lack of experience in both hunting and long-distance movements. What immature saw-whet owls lack in terms of hunting and migration experience, they appear to make up for by adjusting their migration timing. Immature saw-whet owls arrived in south-central Indiana on average 3 d earlier than adult owls. This difference may afford them the first opportunity to exploit prey resources in commonly used stopover and winter locations. It is not known if the immature owls passed through earlier by choice or because density-dependent adult competition forced them to depart earlier from their natal regions.

Juvenile owls also passed through the banding stations an average of 10 min later than the adults on any given night, and appeared to gain mass as the night wore on, whereas the mass of adults did not vary with capture time. The fact that HY owls are gaining mass during the night suggests that they either preferentially feed before they continue migrating or feed en route, like immature Sharp-shinned Hawks (*Accipiter striatus*; Delong and Hoffman 2004). Saw-whet owls primarily prey on small rodents (Swengel and Swengel 1992), however; therefore, aerial hunting en route is unlikely, and the owls likely delay migration to forage or stop and forage in the middle of migratory movements. The adult owls also may forage during migration, because their mass did not decrease with time of capture, but their movements may be less dependent on refueling. Thus, juvenile saw-whet owls in south-central Indiana are apparently able to maintain similar BCIs as adults by migrating earlier and foraging more during migration. This age-dependent strategy of saw-whet owls, coupled with seasonal and annual BCI variability, supports the Stock et al. (2006) hypothesis that this species uses a short-distance migration strategy.

The available data suggest regional variation in age-related migration strategies. Saw-whet owls migrating through Canadian breeding grounds showed no age-related differences in migration timing (De Ruyck et al. 2012), whereas adults moved through earlier than immature owls in New Jersey and Virginia (Duffy and Kerlinger 1992, Iliff 2000). Saw-whet owls migrating south from Saskatchewan frequently moved in a more easterly direction rather than west or south, following the southern boundary of the boreal forest, to reach the east coast of North America while remaining within their preferred forest habitat (Priestley et al. 2010). In contrast, owls migrating into south-central Indiana reach this area by crossing open agricultural fields or prairie habitat. It is possible that age-related migration differences are correlated with habitat differences. Saw-whet owls in Saskatchewan may not exhibit age-related differences in migration timing, because differences in migration strategies may not

yet be manifest so close to the breeding grounds, but as the owls travel over longer distances the inherent differences in strategies may become apparent.

In Flammulated Owls (*Otus flammeolus*), fat scores were better predictors of body mass than pectoral-muscle scores (DeLong 2006), indicating that owls may have larger flight muscles without exhibiting a greater BCI. Adult owls with larger body mass are more likely to carry larger fat stores, similar to adult Cooper's Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks in New Mexico (DeLong and Hoffman 2004). Thus, adult saw-whet owls moving through contiguous forest habitats may be able to migrate more quickly and arrive earlier than immature owls in coastal areas such as New Jersey and Virginia, because of greater muscle development, larger fat stores, and greater foraging efficiency. Conversely, immature owls moving across open prairies and fields of row crops, where the densities of preferred prey are lower, may be forced from stopover sites due to density-dependent adult competition. Further research on regional or habitat-based, age-related stopover behaviors should test the validity of this hypothesis.

Various theories have been offered to explain differential migration. The extent of saw-whet owl migrations has been linked to population fluctuations of small rodents on the owls' summer ranges (Côté et al. 2007, Bowman et al. 2010). Priestley et al. (2010) stated that saw-whet owls are primarily migratory, but portions of their study population remained in breeding locations year-round and others exhibited nomadic behavior, indicating the species is a partial migrant. De Ruyck et al. (2012) claimed that the movements of saw-whet owls correlated with prey abundance and predator-prey density effects on competition and reproduction, but that different age and sex classes still began migrating at similar times. Brinker et al. (1997) suggested that male saw-whet owls do not migrate as far from their breeding grounds to ensure quicker repossession of nest cavities in spring. Sex-specific differential migration has also been observed in the closely related Boreal (Tengmalm's) Owl (*Aegolius funereus*) in western Finland (Korpimäki 1987), where the movements of nomadic females are dependent upon prey availability, while less nomadic, site-tenacious males shift nest cavities only within their own territory. Age and sex differences in the timing of fall migration for other raptors suggests that juveniles and, in most cases, females, migrate earlier, because they are not responsible for defending the territory established on the breeding range, and immature owls may be forced away by competition with adults (Mueller et al. 2000). Brittain et al. (2009) reported no evidence for time-dependent differential migration between the sexes, but our study showed that juvenile saw-whet owls migrated on average 3 d earlier than adults.

Another, more recent, hypothesis for differential migration strategies suggests that saw-whet owls are more nomadic than they are migratory (Bowman et al. 2010). Some evidence for this can be found in irruptive migrations linked to fluctuations in populations of small rodents (Côté et al. 2007, Bowman et al. 2010, Priestley et al. 2010). Cyclical population influxes are more likely to support nomadic predators than are random prey increases (Andersson 1980). Irruptive events have been documented in Indiana (Brittain et al. 2009), eastern Canada (Côté et al. 2007), Idaho (Stock et al. 2006), and Virginia (Whalen and Watts 2002); however, a recent study of more than 80 000 banding records supported true migration in saw-whet owls (Beckett and Proudfoot 2011).

Using wing surface area to evaluate wing loading and wing chord to calculate BCI revealed the same pattern of no age differences in the 2007 subsample, suggesting that neither approach differed in its insight about age-specific migration strategies. It is possible, however, that evaluation of wing loading values across multiple years would reveal differences. The pixel-count method for determining wing surface area was more efficient, because the grid-cell count method required approximately twice the time to measure wing surface area. Uniformity of photographs (distance, focal length, and lighting) would further improve the technique. Digital image analysis has served as an invaluable tool for measuring the surface area of various feathers (McCarthy and Zaniewski 2001, Bradshaw et al. 2007), and our work suggests that it should be a preferred option for researchers studying the surface area of bird wings.

We did not compare BCI and wing loading values between the sexes, because we used mass and wing chord to sex owls, and we were unable to remove the correlations between the original and calculated metrics using standard transformations. Other researchers who studied saw-whet owls were able to remove the correlation between wing chord and BCI by raising the raw BCI to the power of the slope of a log-log mass versus wing chord plot (Whalen and Watts 2002, Stock et al. 2006); why we were not

able to do so was unclear. Perhaps there is regional variation in the mass to wing chord correlation for this species.

Wing chord measurements may be limited in their usefulness for understanding various aspects of wing shape and aerodynamics for many species (Johnson 1997), but they are useful for sexing Saw-whet Owls (Brinker et al. 2000) and were just as useful as surface area for predicting body condition. We suggest that additional research should include measurements of wingspan in the field, and quantification of wingtip shape and convexity (Lockwood et al. 1998). These measurements may provide more insight into the comparative wing morphometrics of juveniles and adults.

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