

DIFFERENTIAL MIGRATION BY SEX IN NORTH AMERICAN SHORT-EARED OWLS

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ABSTRACT: Differential migration of the sexes is known in over 60 bird species and may be the predominant pattern in migratory birds. Identifying the causes of differential migration has been difficult, in part because sex-specific migratory patterns have yet to be described for a majority of species. We used the Internet specimen-data portal Ornis to compile sex-specific data on the seasonal distribution of the Short-eared Owl (*Asio flammeus*), a species that cannot be reliably sexed by external characteristics. We found 1188 specimen records from North America with data on sex, locality, and date of collection. Although the winter distributions of males and females overlapped almost entirely, the mean latitude of females was significantly lower than that of males for the months of November to March. The magnitude of the difference averaged 3.1° between December and February but increased to a peak of 6.0° in March, reflecting earlier onset of spring migration in males. The pattern of differential migration in the Short-eared Owl is compatible with the widely accepted hypothesis that males winter closer to breeding areas because they gain a reproductive advantage from early arrival and establishment of breeding territories (arrival-time hypothesis). Female specimens predominate during late fall and winter and male specimens predominate during the nesting season, suggesting differential seasonal mortality by sex. The skewed sex ratio suggests that differential migration may be caused in part by intrinsic sex differences in foraging efficiency, cold tolerance, or dominance. Comparisons with other raptors reveal that patterns of differential migration are highly species-specific. We conclude, conservatively, that the longer distance female Short-eared Owls migrate is the result of each sex optimizing its migration strategy in light of the higher likelihood of fall and winter mortality of females and the reproductive benefits to males of early arrival on breeding territories.

Differential migration expresses the situation of different demographic classes within a species migrating different distances, by different routes, or on different schedules. As reviewed by Cristol et al. (1999), differential migration by sex has been well documented in over 60 species of mostly North American and European birds, and additional cases are steadily being described (e.g., Olson and Arsenault 2000, Jenkins and Cristol 2002, Stouffer and Dwyer 2003, Catry et al. 2004, Komar et al. 2005, Palacin et al. 2009, Bai and Schmidt 2012). In 85% of the 48 cases described by Cristol et al. (1999), females migrate farther and correspondingly winter at a lower latitude than do males. Three major hypotheses have been recurrently proposed to explain differential migration of the sexes: (1) the body-size hypothesis holds that different latitudes of wintering are driven by different degrees of cold tolerance as mediated by body size (Ketterson and Nolan 1976), (2) the dominance hypothesis proposes that the socially subordinate sex is forced to migrate farther as a way of escaping competitive pressure (Gauthreaux 1978), and (3) the arrival-time hypothesis proposes that the sex whose reproductive fitness will be most enhanced by early arrival on the breeding grounds will make a shorter migration (King et al. 1965, Myers 1981). Each of these three hypotheses is compatible with approximately

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

three-quarters of described cases (Cristol et al. 1999), suggesting that there is no univariate, universal explanation. For example, the hypothesis that a difference in distance of migration is due to greater tolerance of the larger-bodied sex to cold is easily refuted by the fact that in many species in which females migrate to lower latitudes the female tends to be larger than the male (e.g., in the families Accipitridae, Falconidae, Strigidae, and Scolopacidae). The early-arrival hypothesis is a viable alternative explanation for most species with such reverse sexual size dimorphism, but it fails to explain, for example, the Rough-legged Hawk (*Buteo lagopus*) and the Snowy Owl (*Bubo scandiacus*), in which males migrate longer distances but are still thought to establish breeding territories before the arrival of females. In those two species, it has been hypothesized that dominant females may drive males farther south by territorial defense of winter foraging areas (Russell 1981, Kerlinger and Lein 1986), but the direct evidence for that mechanism is weak (Olson and Arsenault 2000). While it is clear that migration strategies are commonly sex-specific, identifying the sex differences that cause divergent migratory behavior will require more detailed descriptions of sex-specific patterns of seasonal distribution than are currently available for most species.

One of the key limitations to our understanding of differential migration has been the inability to distinguish males from females of some species through field observation or banding. This leads to bias because the available data on differential migration are skewed to species that are dimorphic. In the cases of species that are difficult to sex without direct examination of gonads, museum specimens provide a unique record of sex-specific distribution (Kerlinger and Lein 1986, Jenkins and Cristol 2002, Stouffer and Dwyer 2003). For example, the Short-eared Owl (*Asio flammeus*) has no plumage markers that distinguish males from females, and although females average ~20% larger in body mass, the vast majority of individuals cannot be sexed by measurements (Earhart and Johnson 1970, Wiggins et al. 2006). Fortunately, specimen databases are becoming increasingly accessible as a result of digitization projects at individual museums and informatics initiatives such as Ornis (ornisnet.org) and GBIF (gbif.org) that are aimed at facilitating multi-collection searches through convenient Internet portals.

While evaluating the 29 Short-eared Owls in the collection of the Museum of Southwestern Biology, Dickerman noticed that the sex ratio of New Mexico, Arizona, and Texas specimens was heavily skewed toward females (68% female). The preponderance of females in the southern portion of the species' winter range led us to hypothesize that the migration of the Short-eared Owl may differ by sex. In this paper we test this hypothesis and describe the seasonal latitudinal distributions of male and female Short-eared Owls, using the compilation of 170 years worth of specimen data for this species newly available through Ornis.

METHODS

During December 2011, we searched all specimen repositories available through Ornis for *Asio flammeus*, making multiple searches as not all institutional servers returned data on every search. We recovered a total of 2584 specimen records from 35 museum collections. We eliminated specimen

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

records that likely represented subspecies other than *A. f. flammeus* (e.g., all records from Caribbean or Hawaiian islands), all records outside of North or Central America, and all records that did not have sex, month, and locality data. After applying these filters we were left with 1188 specimens—619 females and 569 males. The record was substantial in all parts of the year, with monthly totals varying from a low of 52 in April to a high of 180 in November. Approximately 60% of the records were associated with latitude and longitude coordinates. We georeferenced the remainder of records from the locality named or described, using Biogeomancer Workbench software (version 1.2.4).

We analyzed the latitude of the specimens after categorizing the records by sex and calendar month, with all years (1841–2009) combined. Within each subset, the latitudes were approximately normally distributed, allowing for the application of parametric statistics. We applied independent-samples Student's *t* tests to compare the latitude of each sex in each month. A nonparametric Mann–Whitney *U* test yielded qualitatively identical results. We evaluated the total number of specimens in each month as an indicator of seasonal variation in mortality rate. We recognize that the number of specimens is an imperfect indicator of mortality, but obtaining accurate mortality estimates is a major challenge in population biology (Newton 1979). Although the museum record comprises a mix of birds shot and salvaged, in other raptors specimens from these two sources of mortality produce highly similar age and sex ratios (Haukioja and Haukioja 1970). To examine sex-differential mortality by season, we tested the sex ratio for departure from 50:50 with a binomial sign test. Finally, to evaluate whether females' vulnerability to seasonally challenging environmental conditions differs from that of males we compared the sex ratio in each month to the total number of specimens with a nonparametric Spearman's rank correlation.

RESULTS

Latitudes of males during the winter months (December–February) overlapped almost entirely with those of females during the same period but averaged 3.1° higher, the equivalent of ~344 km farther north (Figure 1). Latitudes of male specimens were significantly farther north than those of female specimens for each month from November through March and nearly significantly farther north in October and April. There was no significant variation with longitude (Table 1, Figure 2). The statistical results were nearly identical for the Student's *t* test and the Mann–Whitney *U* (Table 1). The difference in latitude peaked in March, at which time males shifted northward to 6° of separation from females, on average (~666 km). Although males initiate spring migration before females, our data revealed no apparent difference in the timing of fall migration (Figure 2), though the coarse scale of the data when grouped by month may limit our power to resolve such differences. The total number of specimens was highest during the colder months (October–January), with a secondary peak during June (Figure 3). The sex ratio of the specimens was heavily skewed toward females during the fall and winter, corresponding to the period from September to January (396 females, 308 males; binomial test, two-tailed uncorrected $P = 0.001$),

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

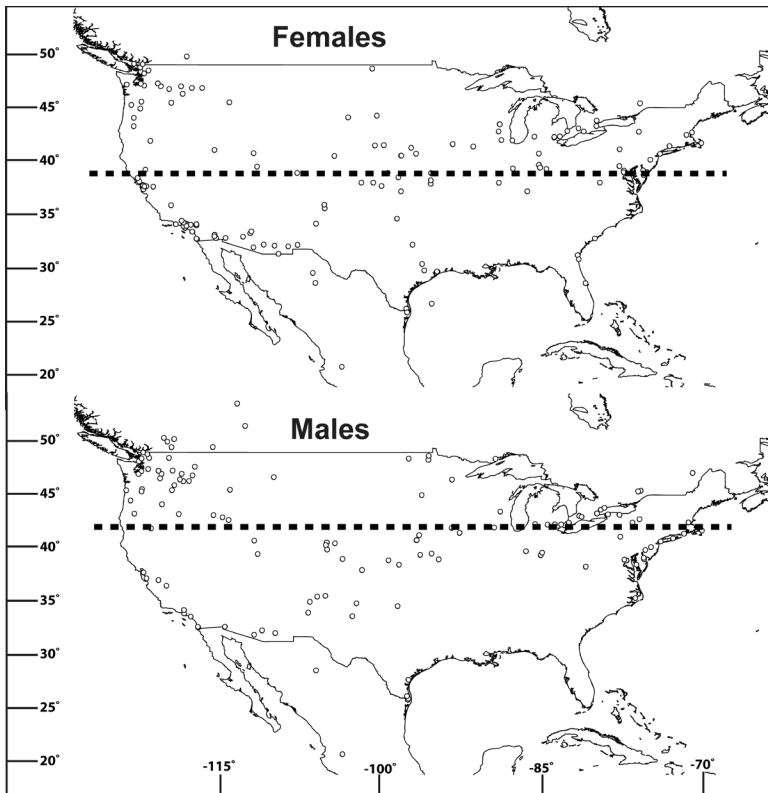


Figure 1. Localities of 1188 North American specimens of the Short-eared Owl collected during December, January, and February, by sex. The dashed lines represent the specimens' mean latitude, 38.9° N for females, 41.9° N for males.

although the only month that was significantly biased toward females by the binomial test was October (86 females, 61 males; binomial test, two-tailed uncorrected $P = 0.048$). The sex ratio was skewed toward males during the spring and early summer, the proportion of males increasing from April to June (82 females, 116 males; binomial test, two-tailed uncorrected $P = 0.019$; Figure 3). The single month that was significantly biased toward males was June (30 females, 51 males; binomial test, two-tailed uncorrected $P = 0.026$). It should be noted that when we applied a Bonferroni correction to these binomial tests, the only difference that remained significant at the 5% level was the excess of females from September to January; however, the Bonferroni correction is likely to be overly conservative, especially when the seasonal trends in sex ratio visible in Figure 3 are considered. The number of total specimens per month was correlated with the proportion of females (Spearman's $\rho = 0.587$; two-tailed $P = 0.045$).

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

Table 1 Sources of Data on Specimens of *Asio flammeus* Including Sex and Locality^a

Institution	No. of specimens
National Museum of Natural History, Smithsonian Institution (USNM)	194
Royal Ontario Museum (ROM)	149
University of Michigan Museum of Zoology (UMMZ)	89
American Museum of Natural History (AMNH)	87
Museum of Comparative Zoology, Harvard Univ. (MCZ)	82
Canadian Museum of Nature (CMN)	77
California Academy of Sciences (CAS)	55
Charles R. Conner Museum, Washington State University (CRCM)	55
University of Washington Burke Museum (UWBM)	54
James R. Slater Museum, University of Puget Sound (PSM)	53
University of Kansas Biodiversity Institute (KU)	41
Los Angeles County Museum of Natural History (LACM)	30
Museum of Southwestern Biology, University of New Mexico (MSB)	29
Dickey Collection, University of California, Los Angeles (UCLA)	29
Western Foundation of Vertebrate Zoology (WVZ)	23
University of Nebraska State Museum (UNSM)	21
Delaware Museum of Natural History (DMNH)	18
Oklahoma Museum of Natural History (OMNH)	15
Utah Museum of Natural History (UMNH)	15
San Diego Natural History Museum (SDNHM)	14
University of Arizona Museum of Natural History (UAZ)	12
University of Colorado Museum of Natural History (CUMNH)	11
Texas Cooperative Wildlife Collection (TCWC)	11
Louisiana State University Museum of Natural Science (LSUMZ)	8
Michigan State University (MSU)	6
Sternberg Museum of Natural History, Fort Hays State University (MHP)	4
Western New Mexico University (WNMU)	4
Illinois State University (ISU)	2

^aThrough www.ornisnet.org, December 2011.

DISCUSSION

The specimen record for the Short-eared Owl in North America shows strong evidence of differential migration of the sexes, with females migrating farther than males by ~344 km, on average (Figure 1). This pattern was previously unrecognized because of the difficulty of distinguishing the sexes without direct examination of the gonads (Wiggins et al. 2006). The fact that females are slightly larger and migrate to lower latitudes directly contradicts the body-size hypothesis. The dominance hypothesis is a potential explanation for the longer migration of females because Short-eared Owls are territorial during both the breeding season and winter and males tend to be more aggressive than females (Clark 1975). If the presence of dominant males directly limits the latitude at which females winter, however, then we might predict that females shift northward during March in response

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

Table 2 Comparison of Latitudes of Specimens of the Short-eared Owl by Sex and Month

Month	<i>t</i>	df	<i>P</i> (2-tailed <i>t</i> test) ^a	Mean difference ^b	95% Confidence interval		<i>P</i> (2-tailed Mann-Whitney <i>U</i>) ^c
					Lower bound	Upper bound	
Jan	-2.64	129	0.009	-3.03	-5.31	-0.76	0.009
Feb	-2.74	96	0.007	-3.15	-5.44	-0.87	0.032
Mar	-4.09	66	<0.001	-5.98	-8.91	-3.06	<0.001
Apr	-1.52	50	0.135	-2.14	-4.98	0.69	0.152
May	-0.12	63	0.904	-0.31	-5.45	4.82	0.878
Jun	-0.09	79	0.930	-0.21	-5.01	4.58	0.710
Jul	-0.79	60	0.430	-1.47	-5.18	2.24	0.507
Aug	-0.40	56	0.687	-0.86	-5.12	3.40	0.607
Sep	-0.60	67	0.550	-1.46	-6.29	3.38	0.567
Oct	-1.82	145	0.071	-1.60	-3.35	0.14	0.114
Nov	-2.33	178	0.021	-1.89	-3.49	-0.29	0.009
Dec	-3.90	175	<0.001	-3.22	-4.85	-1.59	<0.001

^aEqual variance assumed. Variances were equal for all months except November by Levene's test, but relaxing the assumption of equal variance made no substantial difference to the November result.

^bNegative values indicate that females are at lower latitudes than males.

^cThe nonparametric independent-samples Mann-Whitney *U* test produced results qualitatively identical to those of the *t* test.

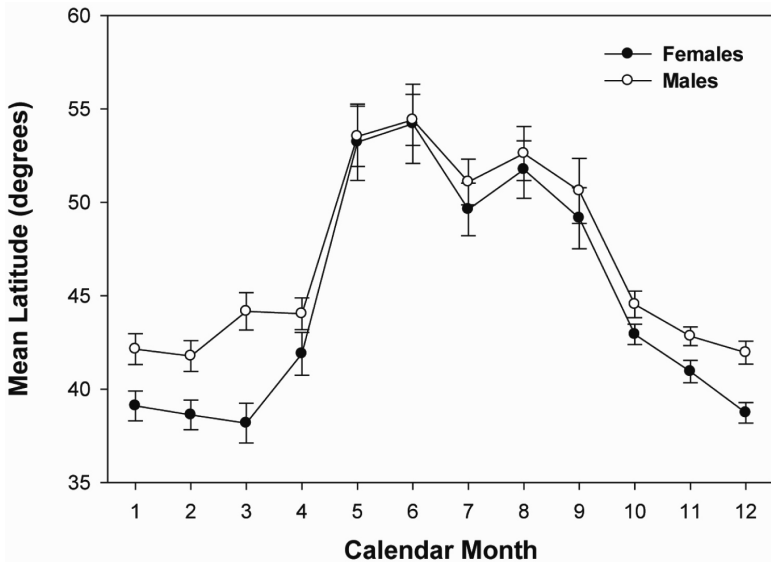


Figure 2. Mean latitude of North American specimens of the Short-eared Owl by sex and month. Vertical bars represent one standard error.

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

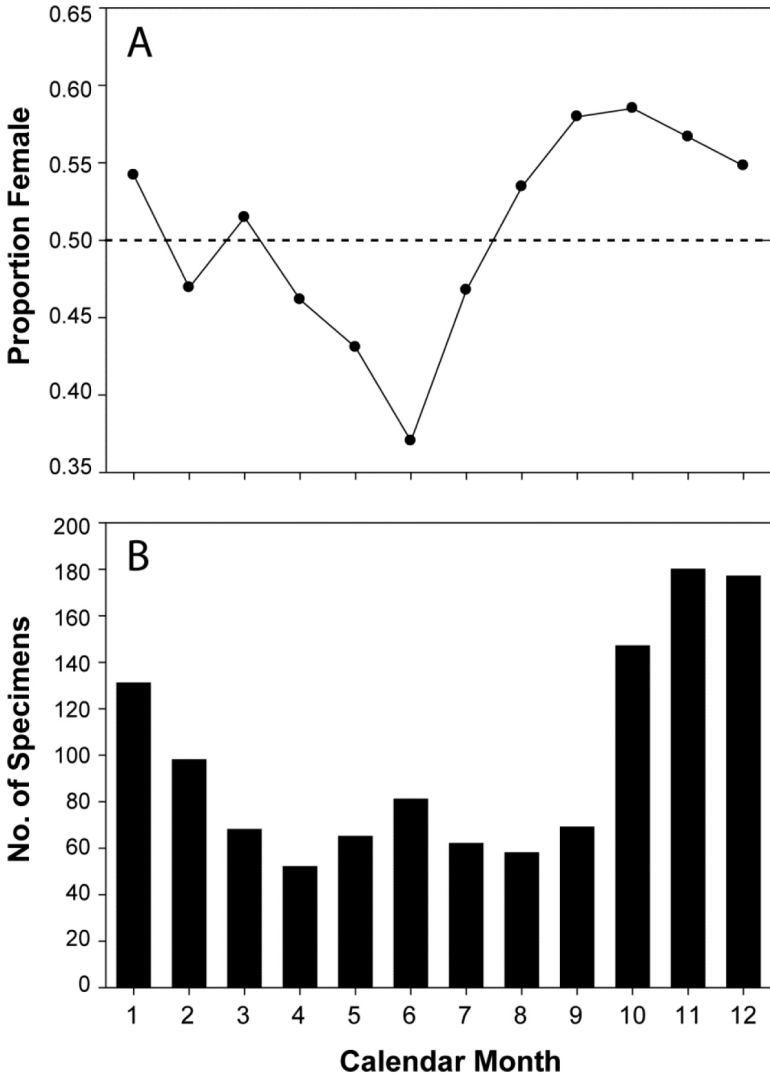


Figure 3. (A) Proportion of North American specimens of the Short-eared Owl that are female by month. The dashed line represents an even 50:50 sex ratio. The seasonal trend emerges although June and October were the only months that deviated significantly from 50:50 by a binomial sign test. (B) Total number of Short-eared Owl specimens by month from searches of www.ornisnet.org in December 2011.

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

to males' departure in spring migration, but this is not the case (Figure 2). Therefore, if dominance is driving differential migration, it is not mediated by a decline in winter territory quality at lower latitudes but by the higher cost of longer migration, as has been suspected previously (Cristol et al. 1999). The arrival-time hypothesis is consistent with the specimen record because males winter closer to the breeding range. This hypothesis is also consistent with the earlier spring migration of males (Figure 2) and with previous observations that males compete intensely for high-quality breeding territories (Clark 1975). Interestingly, the specimen data indicate a slowdown in the northward migration of males in March and April (Figure 2), suggesting that males return to their breeding grounds in stages. The latter pattern needs to be investigated with higher-resolution data.

Although the arrival-time hypothesis fits well with the observed pattern, comparisons with similar species reveal that it is not likely to be the only mechanism causing differential migration of the sexes in the Short-eared Owl. Cristol et al. (1999) reported four species of owls—the Snowy, Northern Hawk (*Surnia ulula*), Boreal (*Aegolius funereus*), and Long-eared Owl (*Asio otus*)—to be differential migrants and another, the Great Gray (*Strix nebulosa*), possibly to be one. In each of these species except the Snowy Owl females migrate farther south than males. In the Snowy Owl, males migrate farther than females, a pattern that may be related to the dominance of females over males on winter feeding territories (Kerlinger and Lein 1986). After controlling for latitude, Kerlinger and Lein (1986) showed that winter temperature could not explain the relative proportions of male and female Snowy Owls, effectively ruling out the body-mass hypothesis. In the Rough-legged Hawk, another boreal raptor, males also migrate farther (Russell 1981, Olson and Arsenault 2000). Female Rough-legged Hawks appear to be socially dominant and are thought to force males to lower latitudes during winter (Russell 1981), although a body-mass effect cannot be ruled out (Olson and Arsenault 2000). The Northern Harrier (*Circus cyaneus*) should be an ideal species to compare to the Short-eared Owl because of its similarity in habitat, distribution, and foraging style. In Europe, male Northern Harriers migrate farther than females (Watson 1977) and females are socially dominant, but in North America data are insufficient to establish the direction of differential migration of the sexes, if it exists (Smith et al. 2011). Furthermore, there are some species, such as the Green-winged Teal (*Anas crecca*), for which none of the major hypotheses adequately explains differential migration of the sexes, and the underlying mechanisms remain a mystery (Guillemain et al. 2009).

The latitudes of Short-eared Owl specimens in each month reveal sex-specific timing of migration. The fall migration appears to be slightly more protracted than spring migration, with the largest southward shift occurring in September and October; however, the timing of fall migration does not differ by sex at this level of resolution. There is no evidence that males remain on the breeding grounds longer than females, potentially to increase their breeding success, as male Ospreys (*Pandion haliaetus*) are known to do (Bai and Schmidt 2012). The difference in mean latitude of the sexes becomes evident between October and December (Figure 2). The mean latitude of each sex holds steady from December through February. The timing of the

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

sexes' spring migration clearly differs, as in many other bird species (Mills 2005). The sexes diverge sharply in latitude during March, at which time males' latitude shifts northward (Figure 2). Females catch up to males by May, with the single largest shifts in latitude for each sex constituting the northward movement between April and May (Figure 2).

The total number of specimens in each month was highly variable and likely reflects different seasonal levels of mortality (natural and anthropogenic), especially because a large proportion of the specimens represents birds that were salvaged rather than actively collected. Although mortality is notoriously difficult to estimate (Newton 1979), Haukioja and Haukioja (1970) found that the age structure of Northern Goshawks (*Accipiter gentilis*) shot or salvaged was closely similar, suggesting that different sources of mortality are correlated. It should be noted, however, that the exact proportion of salvaged specimens remains unknown because collectors and curators did not systematically preserve data on the method of collection until very recently, and some information on specimen labels has not been recorded in databases. Numbers of specimens averaged twice as many from October to February as from March to September (Figure 3). This peak in the specimen record might indicate differential seasonal mortality during fall migration and winter, but it is likely also affected by the disproportionate numbers of young birds at these seasons and the possible higher probability of salvage at lower latitudes, where the human population density is higher. Although we could find no published data on seasonal patterns of mortality in the Short-eared Owl (Wiggins et al. 2006), the observed pattern is compatible with existing data on seasonal mortality in other species of migratory raptors (Newton 1979, Bildstein 2006).

Interestingly, sex ratios of the specimens are also nonrandomly distributed through the year. The specimen record overall is 52.1% female, and the period from September through January is strongly biased toward females (Figure 3). In contrast, the period from April to June is strongly biased toward males (Figure 3). The latter could be explained by the increased demand on males to provision the female and nestlings during the breeding season (Clark 1975) and the correspondingly higher likelihood of their dying or being collected. It is difficult to explain the vastly higher number of female specimens during the fall and winter, the seasons of highest apparent mortality for the species as a whole. We offer six possible explanations that are not mutually exclusive: (1) the specimen record is biased toward females during late fall and winter because, at lower latitudes, they are more likely to be found and/or collected; (2) the sex ratio of offspring produced is skewed toward females; (3) females' longer migration increases their mortality; (4) reduced flight and foraging efficiency increases female's mortality; (5) dominance by males reduces females' access to high-quality habitats, thus increasing females' mortality; or (6) reduced thermogenic capacity independent of body mass increases females' mortality. We find the first explanation to be unlikely because the relatively small 3.1° difference in mean winter latitude is not sufficient to explain the radically skewed sex ratios even if there were a negative correlation between latitude and the probability of an individual bird's being collected or salvaged; furthermore, the months closest to parity in sex ratio are January to March, when the collection bias should be strongest.

DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

The second explanation is feasible, considering that it has been shown that female Tawny Owls (*Strix aluco*) facultatively produce female-biased clutches in response to abundant prey (Appleby et al. 1997). The third explanation implies that differential mortality may be a direct consequence of differential migration, a mechanism that fits with the peak proportion of females occurring during September and October, and that is compatible with both the arrival-time and dominance hypotheses. The fourth, fifth, and sixth explanations imply that differential migration and differential mortality are both caused by intrinsic behavioral or physiological differences between the sexes. These explanations are compatible with the dominance hypothesis, but not with the arrival-time hypothesis. One important intrinsic sex difference may be wing loading. Clark (1975) measured the surface area of the wings of two male and two female Short-eared Owls and found that the females had wing loading 37% higher than that of males. Although based on a small sample, the magnitude of the difference suggests that females fly and forage with lower energetic efficiency. Differences in foraging efficiency have been proposed to explain differential migration among age classes of *Accipiter* hawks, immatures migrating farther because of their greater vulnerability to deteriorating conditions (DeLong and Hoffman 1999). The stark division of labor between the sexes of the Short-eared Owl during breeding, with males performing all of the provisioning at the nest, predicts correspondingly stronger selection on males for foraging efficiency. This type of sex-based specialization in ecology or breeding roles has been proposed as a driver of spatial segregation of the sexes in other bird species (Catry et al. 2005).

The specimen record for the Short-eared Owl is consistent with the arrival-time hypothesis, but it also implicates intrinsic differences between males and females or possible differences in the sex ratio of offspring as potential causes of differential migration. Sex differences in breeding roles and territoriality can lead to dimorphism in morphology, physiology, and foraging behavior that should be expected to engender different tradeoffs associated with migration. To understand these tradeoffs, more data are needed on sex differences in flight energetics, thermogenesis, and social dominance in the Short-eared Owl and other species with differential migration. Detailed studies of seasonal mortality rates and sex ratios of offspring would also be invaluable to the interpretation of patterns in the specimen record. Finally, the specimen record itself needs to be improved through continued collecting, salvaging, and systematic digitization of data to provide a higher-resolution picture of large-scale ecological phenomena such as differential migration.

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DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

Natural History; Museum of Southwestern Biology, University of New Mexico; Dickey Collection, University of California, Los Angeles; Western Foundation of Vertebrate Zoology; University of Nebraska State Museum; Delaware Museum of Natural History; Oklahoma Museum of Natural History; Utah Museum of Natural History; San Diego Natural History Museum; University of Arizona Museum of Natural History; University of Colorado Museum of Natural History; Texas Cooperative Wildlife Collection; Louisiana State University Museum of Natural Science; Michigan State University; Sternberg Museum of Natural History, Fort Hays State University; Western New Mexico University; Illinois State University.

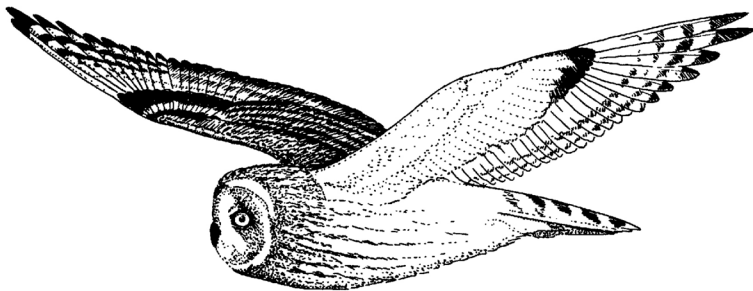
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DIFFERENTIAL MIGRATION BY SEX IN THE SHORT-EARED OWL

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Short-eared Owl

Sketch by George C. West