INVESTIGATING RAPTOR MIGRATION BEHAVIOR USING ORIENTATION CAGES AND WING MEASUREMENTS: A COMPARISON OF THE FLAMMULATED OWL AND NORTHERN SAW-WHET OWL IN SOUTHWESTERN IDAHO

by

Rhonda F. Smith

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Rhonda Finch Smith

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The following individuals read and discussed the thesis submitted by student Rhonda Finch Smith, and they also evaluated her presentation and response to questions during the final oral examination. They found that the student passed the final oral examination, and that the thesis was satisfactory for a Master's degree and ready for any final modifications that they explicitly required.

Marc J. Bechard, Ph.D.	Chair, Supervisory Committee
Mark R. Fuller, Ph.D.	Member, Supervisory Committee
Carl Marti, Ph.D.	Member, Supervisory Committee

The final reading approval of the thesis was granted by Marc J. Bechard, Ph.D., Chair of the Supervisory Committee. The thesis was approved for the Graduate College by John R. Pelton, Ph.D., Dean of the Graduate College.

DEDICATIONS

For Lucas, you bring wildlife and sunshine into every single day.

To Adam, my best friend and lifelong partner in exploration of all God’s wondrous creation; I look forward to many more adventures together. You’re the only person with whom I would ever want to share them.

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CHAPTER ONE:

INTER-SPECIFIC DIFFERENCES IN MIGRATORY RESTLESSNESS AND ORIENTATION IN FLAMMULATED AND NORTHERN SAW-WHET OWLS

Abstract

Flammulated Owls (*Otus flammeolus*) are long-distance migrants, while Northern Saw-whet Owls (*Aegolius acadicus*) exhibit more variable migration tendencies. I investigated the migratory behavior of these species using orientation cages and tested hypotheses concerning (1) the presence of migratory restlessness and orientation, (2) inter-specific differences in migratory restlessness and orientation, and (3) correlates of migratory restlessness and orientation. Only four of 16 Flammulated Owls displayed activity consistent with migratory restlessness although all four owls exhibited significant directionality in their movements. Alternatively, 59 of 97 Northern Saw-whet Owls exhibited activity consistent with migratory restlessness with most of these 59 owls showing preferred directions of orientation. Neither species oriented consistently as a group and, contrary to expectation, Northern Saw-whet Owls exhibited more restlessness in orientation cages. The relative lack of migratory restlessness in Flammulated Owls might be a function of small sample sizes or simply this particular species' reaction to an unfamiliar situation. In Flammulated Owls, migratory restlessness increased with decreasing natural cloud cover, and was more pronounced in birds with larger flight muscles. Contrary to predictions, Flammulated Owls also showed a marginal increase in restlessness in response to decreasing furcular fat stores which could be a function of small samples sizes. Restlessness in Flammulated Owls did not vary with wind speed, moon disk illumination, nor did restlessness change throughout the migration season. Northern Saw-whet Owls tested under a bright moon (>66% moon disk illuminated) oriented consistently to the northeast, but exhibited variable orientation when the moon was <66% illuminated. These results suggest that, in the presence of a bright moon, owls may chose to seek cover in forested habitat rather than migrate over open areas. Restlessness and orientation in Northern Saw-whet Owls did not relate to age or body condition, wind speed or direction, or simulated or natural cloud cover, nor did orientation vary throughout the migration season. However, under the influence of 100% simulated cloud cover, Northern Saw-whet Owls demonstrated significantly lower migratory restlessness compared with simulated partial cloud cover and clear skies. Furthermore, Northern Saw-whet Owls tested late in the night (2 h before sunrise) showed more restlessness than birds tested earlier in the night and immature saw-whets were more active than adults.

Introduction

Migration is a regular, seasonal movement from one area to a different area (Clark 1990). Furthermore, migration is an undistracted movement, characterized by suspended or suppressed responses to resources or home range (Dingle 1996). One of the main pressures that drive birds to migrate is a dependence upon fluctuating food resources which is the case with most insectivorous passerine migrants. The seasonal variability of insect populations results in an obligatory annual migration of many passerine species that breed in northern forests including thrushes, flycatchers, and wood-warblers (Baker 1978). Soms previous studies have focused on how migrant songbirds are able to travel thousands of miles yet precisely locate the same breeding site year after year. Methods such as radar, ceilometry, and direct visual observation have helped to describe movement patterns of migrating birds; however experimental methods that allow researchers to manipulate variables that may affect migratory behavior have provided insight into the cues birds use to navigate during migration (Kerlinger 1995). These methods provide convincing evidence that migrating birds derive navigational cues from multiple environmental sources; the sun, polarized light patterns, stars, visual landmarks, and the earth's geomagnetic field have been implicated as important for migratory navigation (Emlen 1967, Emlen 1975, Dingle 1996, Sandberg et al. 2002, Wiltschko and Wiltschko 2003). The usefulness of specific cues and their effect on orientation varies greatly within and among species depending upon age, experience, and environmental conditions (Able and Bingman 1987, Dingle 1996, Sandberg and Gudmundsson 1996, Sandberg et al. 2000).

During migration, many passerines display a marked increase in activity levels corresponding to their daily migration schedule. This phenomenon, known as migratory restlessness or Zugenrühe, often correlates with the distance a migrant must travel (Dingle 1996, Munro and Munro 1998). Individuals known to cover greater distances often possess a more intense or longer period of restlessness (Munro and Munro 1998). This increase in activity is used as a means of studying the orientation mechanisms of various species. Numerous experiments involving nocturnal and diurnal passerine migrants have utilized circular orientation cages to document the navigation and Zugenrühe of birds (Emlen and Emlen 1966, Åkesson 1993, Berthold 1996, Munro and Munro 1998, Nievergelt et al. 1999, Sandberg et al. 2000). Birds in orientation cages commonly move, often persistently, in the direction corresponding to their migratory route (Emlen and Emlen 1966, Emlen 1967, Akesson 1993, Akesson 1994, Nievergelt et al. 1999). Therefore, orientation cages provide a more controlled, experimental method of studying avian migration relative to field observations or band recoveries (Sandberg and Gudmundsson 1996). Orientation cages have also proven effective in studying migratory restlessness and orientation in several species of shorebirds (Sandberg and Gudmundsson 1996, Munro and Munro 1998). To date no information exists concerning the usefulness of orientation cages in studying nocturnally migrating raptors.

Raptor migration may take one of many forms including long-distance movements, local movements covering short distances, periodic irruptions in response to a cyclic prey source, or nomadic wanderings in response to unpredictable food sources (Clark 1990). The migration strategy of a particular species of raptor may correlate with the species' diet. The insectivorous Swainson's Hawk (*Buteo swainsonii*) is a complete migrant (Berthold 1996), while the Red-tailed Hawk (*Buteo jamaicensis*), a dietary generalist, is a partial migrant (Kerlinger 1995). North American owls demonstrate a wide variety of migratory strategies. For example, Snowy Owls (*Bubo scandiacus*) are differential migrants according to age and sex (Berthold 1996, Newton 2006), Great Gray Owls (*Strix nebulosa*) are unpredictable irruptive migrants in response to prey populations (Bull and Duncan 1993), Great Horned Owls (*Bubo virginianus*) are considered non-migratory (Houston et al. 1998), and Burrowing Owls (*Athene cunicularius*) typically are complete migrants (Haug et al. 1993). Newton (1979) states that the distance a raptor migrates relates to its diet, with birds that feed mainly on cold-blooded prey wintering farther south than birds consuming warm-blooded prey, due to prey availability during the winter months. Migrating owls are thought to move mainly during the first 2 – 3 h after sunset, similar to the strategy of night-migrating passerines (Kerlinger and Moore 1989) with the last four hours of the night spent hunting and searching for a roosting area (Wier et al. 1980, Russell et al. 1991, Duffy and Kerlinger 1992).

Flammulated Owls (*Otus flammeolus*) are small inhabitants of western montane forests. Their breeding range extends from southern British Colombia to central Mexico and from the Cascades and Sierra Nevada , east to Montana and Texas (McCallum 1994a). The species' wintering ecology is poorly understood, but wintering range appears to occur in lowlands adjacent to breeding areas, and from New Mexico and Arizona south through Mexico and Guatemala. Its diet consists primarily of nocturnal arthropods, especially moths, beetles, crickets, and grasshoppers. Although females are slightly larger than males, a large degree of overlap exists between the sexes and no difference is noticeable in the plumage of males and females. It is possible to determine the age of some individuals using molt patterns and fault bars (Pyle et al. 1997, DeLong 2003). Flammulated Owls are strictly nocturnal, with activity peaks generally occurring one hour after sunset and one hour before sunrise (McCallum 1994a).

Few data exist concerning the migratory habits of Flammulated Owls. The currently held view is that the species is a long-distance, north-south migrant. The Flammulated Owl's migratory status is not well documented because no band recoveries exist for Flammulated Owls outside of the vicinity of the original capture site (McCallum 1994b). Current evidence supports the idea that Flammulated Owls migrate southward through breeding habitat beginning sometime in early fall (Aug –Sept; McCallum 1994a, DeLong 2003); and long-term capture data from the study site indicate that movements and body condition observations of Flammulated Owls are consistent with the strategies of a long-distance migrant (Stock et al. 2006).

The Northern Saw-whet Owl (*Aegolius acadicus*) is a forest-dwelling owl whose breeding range extends from southeastern Alaska, east throughout southern Canada to Maine (Rasmussen et al. 2008). Birds winter throughout their breeding range, but rarely at the northern limits. Some individuals migrate southward to the east-central United States, but the southern limits of its wintering range are variable from year to year. Birds that breed in mountainous areas will move into lowlands during winter. In the Mountain West, Northern Saw-whet Owl breeding range completely overlaps that of the Flammulated Owl (Rasmussen et al. 2008).

Northern Saw-whet Owls feed primarily on mice with deer mice (*Peromyscus* spp.) being the dominant prey item (Catling 1972, Cannings 1987, Holt et al. 1991). Other mammalian prey includes voles (*Microtus* spp.), shrews (*Sorex* spp., *Blarina* spp., *Cryptotis* spp.), and house mice (*Mus musculus*). Small birds also make up a small portion of the diet (Graber 1962, Catling 1972, Cannings 1987), and insects such as beetles (Coleoptera) and grasshoppers (Orthoptera) are taken as well (Boula 1982, Swengel and Swengel 1992). The species exhibits reverse sexual size dimorphism with some degree of overlap between the sexes. Northern Saw-whet Owls hunt almost entirely at night, beginning about a half-hour after sunset and ending about a half-hour before sunrise (Forbes and Warner 1974, Hayward and Garton 1988).

Northern Saw-whet Owls are found in their breeding range year-round, but in eastern North America large numbers of birds move south in the fall (Mueller and Berger 1967, Holroyd and Woods 1975, Weir et al. 1980, Duffy and Kerlinger 1992). Annual differences in the number of migrants are likely a result of the number of offspring produced each year. In raptors, the proportion of birds that migrate often depends largely upon environmental circumstances (winter prey availability; Newton 1979, Lundberg 1988), or differences among individuals (age, sex, dominance, body condition), making partial migration a conditional strategy (Lundberg 1988). Since they have the ability to use a variety of habitat types and prey sources, Northern Saw-whet Owls likely follow this strategy of partial migration. Migration routes and timing in the western mountains are poorly understood, but probably involve a combination of altitudinal and latitudinal migration (Rasmussen et al. 2008). Northern Saw-whet Owls migrate throughout the night, but fall banding studies have found fewer birds were captured early in the night, and more in the last four hours before sunrise (Weir et al. 1980, Duffy and Kerlinger 1992).

I address three objectives in this study: (1) to determine whether Flammulated Owls or Northern Saw-whet Owls exhibit migratory restlessness and orientation; (2) to determine if migratory restlessness or orientation correlated with the two different migratory strategies employed by the two species; and (3) to explore possible correlations between the intensity of migratory restlessness or the direction of migratory orientation with a suite of weather, lunar, and body condition variables.

Study Area

I conducted the study at the Idaho Bird Observatory on Lucky Peak in southwestern Idaho. Lucky Peak is the southernmost forested peak in the Boise Ridge, a series of north-south oriented peaks in the Boise Mountains just north of Boise, Idaho. The ridge begins at the town of Horseshoe Bend, Idaho, and continues south to Mountain Home, Idaho, and forms the northern boundary of the Snake River Plain. Lucky Peak is publicly owned and administered by the Idaho Department of Fish and Game. Annual fall monitoring of migrant forest owls is conducted on the peak at an elevation of 1,845 m; Northern Saw-whet Owls and Flammulated Owls are the two most common species of owls captured during migration monitoring.

The upper slopes of Boise Ridge contain a mixed conifer forest consisting of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) with an under story composed predominately of nine bark (*Physocarpus malvaceus*). Forest openings and slopes immediately below tree-line consist of mountain shrub communities of buck brush (*Ceanothus velutinus*) and chokecherry (*Prunus virginiana*). These shrub communities grade into mid-elevation shrubsteppe comprised of mountain big sagebrush (*Artemisia tridentata ssp. vaseyana*) and bitter brush (*Pershia tridentata*) and an under story of native bunchgrasses, primarily blue bunch wheat grass (*Pseudoroegnaira spicata*), threeawn (*Aristida longiseta*), and Sandberg's bluegrass (*Poa secunda*). Fire and overgrazing have converted some areas into monocultures of exotic annual grasses, mostly cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum asperum*).

Methods

Capture and Measurement of Owls

Owls were captured from 25 August to 31 October 2002 and 2003 using standard mist-netting techniques (Bloom 1987) supplemented with audio lures (Duffy and Matheny 1997, Evans 1997). The trap configuration consisted of 11 nets measuring 2.5 x 12 m divided between two trapping stations (comprising six nets and five nets) located approximately 200 m apart placed in mixed conifer forest. Nets were operated from 30 min after sunset to 30 min before sunrise and owls were removed from the nets every hour to hour and a half throughout the night depending upon weather conditions. Each trapping station included one audio lure comprising a compact disc player attached through an amplifier to two external speakers placed in the center of the mist net arrangement. Large speakers were placed on the ground with smaller speakers mounted on nearby trees. This technique has been used successfully at Lucky Peak resulting in an average of over 200 owl captures/year with essentially no mortality (Kaltenecker et al. 2006). All captured owls were banded with USGS aluminum leg bands, sexed and aged when possible, measured using standard techniques (Kemp and Crowe 1990, Pyle et al. 1997), and assessed for body and feather condition. I measured wing chord as the distance from the wrist joint of the folded, unflattened wing to the tip of the longest primary feather. I measured tail length as the distance from the point of insertion to the tip of the longest tail feather. I estimated body fat visually on a scale from 0-5, with 0 representing an owl with no fat in the furcular hollow and 5 representing an owl with fat bulging from the furculum (Helms and Drury 1960). I visually estimated flight musculature relative to the sternal keel on a scale from 0 to 5, with 0 representing an owl with a sharp sternum devoid of musculature and 5 representing an owl with muscles bulging above the sternum (modified from Bairlein 1995).

If an owl selected for testing was captured more than 60 min before the beginning of the next trial, it was placed in a temporary holding cage. The temporary holding cage comprised a ventilated clear plastic cage (30.5 cm x 20.3 cm x 17.8 cm) with a wooden perch secured lengthwise across the cage bottom. In 2003, I constructed larger holding cages (45.7 cm x 45.7 cm x 45.7 cm) to house up to four owls throughout the day, thus making more owls available for trials just after sunset. These larger holding cages comprised a plywood top, bottom, and two sides; the remaining two sides possessed columns of PVC pipe (3.2 cm) spaced 3.2 cm apart with an exterior layer of hardware cloth (0.6 cm) to prevent depredation and allow the owls exposure to the natural light cycle. Each cage contained several branches for perches and were located outdoors in a secluded, forested area of the study site to minimize disturbance. Owls in holding cages could not see one another. Orientation trials were conducted at the study site approximately 1.75km from the capture site in an open area. I offered each Northern Saw-whet Owl a mouse (*Mus musculus*) approximately one hour before sunset. After the completion of the orientation trial, I offered Flammulated Owls live moths (Noctuidae) captured at the study site by hand since the size of the holding cage mesh permitted moths to escape.

Orientation Cage Construction

I constructed four orientation cages using large plastic refuse containers (159 l) with an approximately 400 mm tall transparent Plexiglas® funnel attached to the rim of the cage with brackets and screws (Figure 1.1). Each funnel comprised eight 45°-sectors, one of which was aligned with magnetic north. Moving clockwise around the funnel, the remaining seven sectors corresponded to northeast, east, southeast, south, southwest, west, and northwest, respectively. I placed a Styrofoam® hemisphere in the center of each funnel as a perch for owls. The use of a funnel allowed owls to move in any direction, but required them to return to the center of the cage between movements, thus ensuring that sequential movements were independent. An infrared video camera recorded owl movements through the funnel from below. I covered each cage with a fine (1 mm) nylon mesh material to prevent birds from escaping. When in the orientation cage, owls were able to view approximately 120° of the night sky limited by the artificial horizon of the orientation cage. The orientation cages were placed in an array with individual cages placed a minimum of 1.5 m apart and owl activity in orientation cages was out of sight from other owls in orientation cages. All electronic equipment derived power from rechargeable automobile battery jump starters, thus preventing noise disturbance above ambient conditions.

Quantifying Migratory Restlessness and Orientation

To quantify migratory restlessness and orientation in Flammulated Owls and Northern Saw-whet Owls, I recorded the behavior of individual owls undisturbed in an orientation cage for 70 min. I allowed the owls to acclimate to the orientation cage for 10 min. During the subsequent 60 min, I assigned each owl movement (defined as an attempt at flight or a distinct jump in which both feet left the perch) to the sector in which it occurred; movements occurring at the intersection of two sectors were divided equally between the two sectors. In some instances, owls jumped directly upward from the perch in the middle of the funnel. I included these non-directional movements in the assessment of an owl's restlessness, which thus comprised the total number of movements (directional and non-directional). However, I excluded non-directional movements from tests for directionality or orientation. After each trial, I released owls near the capture site.

Baseline Activity of Breeding Flammulated and Northern Saw-whet Owls

Studies of passerine and shorebird orientation often required at least 40 movements or registrations per test period to consider a bird an active migrant (Sandberg et al. 1988, Åkesson 1993, 1994, Åkesson and Bäckman 1999, Nievergelt et al. 1999, Sandberg et al. 2000). Since orientation experiments have never been performed on owls, and because the number of movements indicative of an actively migrating owl was unknown and may differ from passerines or shorebirds, I designed a method for establishing a baseline level of activity for non-migratory owls in the orientation cage by testing breeding female Flammulated Owls (N = 4) and Northern Saw-whet Owls (N = 4) in the orientation cages. Breeding Northern Saw-whet Owls were sampled on a 6,900 ha hybrid poplar plantation owned by Potlatch Corporation near Boardman, OR, during March 2003. Breeding Flammulated Owls were sampled in May 2003 at two sites in the Wasatch Mountains of Utah: Snow Basin, located in the Wasatch National Forest just east of Ogden; and Mantua, located 32 km north of Snow Basin (Oleyar 2000). Breeding females of both species were captured in nest boxes and were tested at varying times of night between 0.5 and 5 h after sunset. I located orientation cages as near as possible to the nest tree in an attempt to minimize the effects of separating a breeding female from its nest. I noted the azimuth and distance of the orientation cage from each nest. I used the mean number of movements as a guideline level of activity for owls placed in orientation cages outside of the migration season.

Correlates of Migratory Restlessness and Orientation in Migrating Owls

Because the star patterns that an owl sees are easily manipulated in an outdoor setting, I assigned Northern Saw-whet Owls randomly to one of three visual manipulations: (1) unobstructed view of the night sky (CLEAR), (2) partially obstructed view of the night sky (simulated 50% cloud cover; PARTIAL), or (3) completely obstructed view of the night sky (simulated overcast; OVERCAST). PARTIAL and OVERCAST treatments entailed placing opaque, black Plexiglas® lids over the top of orientation cages; for the PARTIAL treatment, I cut 10.2 cm circles from the lid, located at random, until 50% of the lid area was removed. Due to small sample sizes of Flammulated Owls, I assigned all Flammulated Owls to the CLEAR treatment.

To determine whether migratory restlessness and orientation vary throughout the night, I conducted orientation trials at three different times of the night: approximately 1 h after sunset, during the first part of the night (Trial 1; 2003); approximately 5 h after sunset, during the second portion of the night (Trial 2; 2002); and approximately 2 h before sunrise, nearer the end of the night (Trial 3; 2002 and 2003). When more than four owls were available for orientation cage experiments, I selected individuals randomly for inclusion; otherwise, I used owls opportunistically. Again, due to infrequent Flammulated Owl captures, I assigned all Flammulated Owls to Trial 1.

In Northern Saw-whet Owls, I explored correlations among several environmental and body condition variables and migratory restlessness and orientation, while adjusting for simulated cloud cover and time of night. In Flammulated Owls, I explored these correlations only in regards to migratory restlessness since small sample sizes prevented the analysis of birds with significant directionality in this species. Due to the difference in migratory strategies employed by Flammulated Owls and Northern Saw-whet Owls, I explored correlates of migratory restlessness separately for the two species. Additionally, I explored potential changes in migratory restlessness and orientation throughout the autumn migratory season. In Northern Saw-whet Owls only, I examined potential differences in migratory orientation and restlessness as they pertain to an individual’s age. In this case, I distinguished between immature (hatching-year) and adult owls (after hatching-year).

Due to small sample sizes, I categorized three otherwise continuously varying natural variables into ordinal form. Specifically, I classified wind speed at the beginning of the orientation trial using the Beaufort scale. I categorized the percentage of moon disk illuminated (whether waxing or waning) at the beginning of the orientation trial as follows: 0 – less than 33% of the moon disk illuminated; 1 – 33 to 66% of the moon disk illuminated; and 2 – more than 66% of the moon disk illuminated. Similarly, I categorized the percentage of natural cloud cover as follows: 0 – less than 33% cloud cover; 1 – 33 to 66% cloud cover; and 2 – more than 66% cloud cover. All natural variables were measured from the center of the array of orientation cages immediately preceding the owls’ 10 min acclimation period.

Statistical Analysis

I analyzed orientation data using circular statistical procedures that can account for the unique characteristics of circular data. I conducted all statistical analyses involving circular data using Oriana 2.0 (Kovach Computing Services, Wales, U.K.). The analysis of migratory restlessness is possible using linear methods, although I adjusted for the special character of count data by basing the analyses of migratory restlessness on the negative binomial distribution (White and Bennetts 1996). Due to the exploratory nature of this study, I considered explanatory variables significant at $P \leq 0.10$. Unless indicated otherwise, I present means ± SD. I conducted all linear analyses using the GENMOD procedure of SAS/STAT Version 8.2 (SAS Institute 1999). Due to small sample sizes in 2002, I combined data from 2002 and 2003.

For those owls considered to be actively migrating, I calculated the direction of movement of individual owls using vector addition. I then used a Raleigh test (Batschelet 1981) to determine if the pattern of movement exhibited significant directionality ($P \leq 0.05$), and thus orientation. For groups of individuals, the mean direction (α) and length of the mean vector (r) were calculated from the sample of individual directions using vector addition. I excluded owls not meeting the criteria of active migration and significant directionality for analyses of migratory orientation.

To compare directional preferences between the two species, I compared 95% confidence intervals around the mean vector (α); overlapping confidence intervals indicate no difference in direction of migratory orientation between the species. I compared migratory restlessness between species using a negative binomial generalized linear model (NB-GLM). To eliminate the effects of as many potentially confounding variables as possible, I compared migratory restlessness and orientation between Flammulated Owls and Northern Saw-whet Owls exposed to similar test conditions. Specifically, because I tested Flammulated Owls only during Trial 1 and with the CLEAR cloud cover treatment, I compared Flammulated Owls with Northern Saw-whet Owls tested during Trial 1 with the CLEAR treatment. Unfortunately, I was unable to control for other potentially confounding variables (e.g., natural cloud cover, wind direction, and body condition).

I conducted multiple univariate analyses exploring the potential effects of two controlled manipulations (i.e., simulated cloud cover and time of night) and a suite of environmental and body condition variables on migratory orientation in Northern Saw-whet Owls and Flammulated Owls. The necessity of multiple univariate analyses stemmed from the inability of Oriana to analyze the effects of multiple predictive variables on circular data simultaneously. The type of univariate analyses used depended upon the type of explanatory variables being considered. I analyzed the effects of categorical variables on migratory orientation using the nonparametric Mardia-Watson-Wheeler test (Table 1; Batschelet 1981). I explored the effects of linear interval and continuous variables on migratory orientation using circular-linear correlations (CLC; Fisher 1993). Similarly, I explored the effects of circular variables on migratory orientation using circular-circular correlations (CCC; Fisher 1993). I acknowledge the increased possibility of Type I errors (i.e. false positives) resulting from conducting multiple statistical tests. Nonetheless, I elected not to adjust alpha levels in individual tests (e.g., sequential Bonferroni; Rice 1989), but instead to interpret the results of the multiple statistical tests carefully and logically (Moran 2003), so as not to miss potential avenues for more detailed future work in owl orientation.

I evaluated the correlation between environmental and body condition variables and migratory restlessness (counted number of movements) using linear models. Linear models offered more flexibility to accommodate multivariate analyses; however, they were not without their limitations. Specifically, linear models could not accommodate circular predictive variables; thus, I was able only to examine the effects of non-circular environmental and body condition variables (Table 1.1) on migratory restlessness using a multivariate NB-GLM. In the separate analyses for Flammulated Owls and Northern Saw-whet Owls, I constructed a model comprised only of main effects. I did not explore interaction effects for several reasons. First, I was unable to examine interactive effects in the analysis of migratory orientation (see above). Second, the small ratio of owls sampled to explanatory variables made evaluating a large number of interaction terms impossible. Lastly, the exploratory nature of this study lends itself to suggesting future research directions, instead of explicitly addressing the effects of complex interactions between environmental variables on owl orientation. To evaluate the effects of natural cloud cover in saw-whets, I conducted a separate NB-GLM including only those individuals in the CLEAR treatment (N = 30). I included all sampled owls, regardless of the number of movements, when examining migratory restlessness.

Results

Baseline Activity of Breeding Flammulated and Northern Saw-whet Owls

Flammulated Owls (N = 4) averaged 107 ± 54 (mean, SD) movements in 60 min orientation trials during the breeding season. Northern Saw-whet Owls (N = 4) averaged 150 ± 50 (mean, SD) movements in similar trials. In both species, 75% of owls exhibited significant directionality (Raleigh tests, $P < 0.05$). Of these six owls, 50% oriented within one standard deviation of their nest boxes. Although subjective, I believe that the activity levels in these owls were artificially elevated due to anxiety associated with separation from their nests. Consequently, I defined owls moving at least once per minute (60 movements/h) as active in fall migration orientation trials. This criterion is more conservative than similar studies with passerines, which typically define migratory restlessness as 40 movements/h.

Inter-specific Differences in Migratory Restlessness and Orientation

I conducted orientation cage experiments on 16 Flammulated Owls and 97 Northern Saw-whet Owls during the fall migrations of 2002 and 2003. Of the Flammulated Owls, only four met the criterion of migratory restlessness (130 ± 87 movements; range = 60 – 234), all of which also exhibited significant directionality according to Raleigh tests. A total of 59 Northern Saw-whet Owls met the criterion of migratory restlessness (247 ± 227 movements, range = 60 – 1182). Of these owls, 97% exhibited significant directionality according to Raleigh tests. However, mean vectors and their associated confidence intervals clearly indicated that no difference in orientation direction existed between the species, nor did either species orient consistently as a group (Figure 1.2). However, of birds tested in the CLEAR treatment, Northern Saw-whet Owls (145 ± 163 movements, $N = 21$) moved more often than did Flammulated Owls (41 ± 68 movements, $N = 16$; NB-GLM: $\chi^2_1 = 5.7$, $P = 0.02$).

Correlates of Migratory Restlessness and Orientation in Migrating Owls

Directional preferences did not differ between Northern Saw-whet Owls exposed to CLEAR and PARTIAL simulated cloud cover treatments (Mardia-Watson-Wheeler test: W = 1.61, $P = 0.45$; Figure 1.3); small sample sizes precluded comparisons involving the OVERCAST treatment. Likewise, directional preferences in Northern Saw-whet Owls did not differ between the beginning (Trial 1) and end (Trial 3) of the night (Mardia-Watson-Wheeler test: W = 2.39, P = 0.30; Figure 1.4). Furthermore, although it was not possible to assess age-related differences in directional preferences statistically (small adult *N*), mean vectors and their associated confidence intervals clearly indicate that no difference in orientation direction existed between saw-whet age classes (Figure 1.5).

The direction of migratory orientation correlated with the amount of moon disk illuminated at the beginning of the orientation trial (CLC: $r = 0.33$, $P < 0.01$; Figure 1.6). Specifically, Northern Saw-whet Owls tested when >66% of the moon disk was illuminated consistently oriented to the northeast, while owls tested during periods with <66% moon disk illumination exhibited more variable orientation behavior (Figure 1.6). Northern Saw-whet Owl orientation behavior did not correlate with time of year (CLC: $r = 0.19$, $P = 0.15$), furcular fat stores (CLC: $r = 0.16$, $P = 0.26$), keel musculature (CLC: $r = 0.05$, $P = 0.27$), wind speed (CLC: $r = 0.15$, $P = 0.29$) or direction (CCC: $r = 0.04$, $P > 0.90$), or migratory restlessness (CLC: $r = 0.17$, $P = 0.21$). Additionally, natural cloud cover did not correlate with migratory orientation in Northern Saw-whet Owls subjected to the CLEAR treatment ($N = 30$; CLC: $r = 0.11$, $P = 0.75$).

Migratory restlessness in Northern Saw-whet Owls varied among different simulated cloud cover treatments. Specifically, owls in the OVERCAST treatment moved distinctly less frequently than did owls in the PARTIAL and CLEAR treatments; owls exposed to the PARTIAL and CLEAR treatments exhibited a similar degree of restlessness (Table 1.2). Similarly, migratory restlessness in Northern Saw-whet Owls varied throughout the night, with individuals tested just before sunrise (Trial 3) moving more frequently than owls just after sunset (Trial 1) and during the middle of the night (Trial 2); owls exhibited a similar degree of restlessness during Trials 1 and 2 (Table 1.2).

Additionally, immature Northern Saw-whet Owls moved more frequently than did adult Northern Saw-whet Owls (Table 1.2). Migratory restlessness in Northern Saw-whet Owls did not relate, however, to furcular fat deposits, keel musculature, wind speed, or moon disk illumination, and did not vary throughout the migration season (Table 1.2). Finally, for only those Northern Saw-whet Owls in the CLEAR treatment, natural cloud cover did not influence migratory restlessness (NB-GLM: $\chi^2_1 = 0.40$, $P = 0.53$), nor did this lack of influence vary between Northern Saw-whet Owl age classes (NB-GLM: $\chi^2_1 = 1.26$, $P = 0.26$).

In Flammulated Owls, migratory restlessness increased with increasing keel musculature (Table 1.3). Additionally, migratory restlessness in Flammulated Owls decreased slightly as natural cloud cover increased (Table 1.3). Furthermore, migratory restlessness in Flammulated Owls decreased marginally as furcular fat stores increased, although the relationship is tenuous (Table 1.3). Migratory restlessness did not relate to either wind speed or moon disk illumination, and did not vary throughout the migration season (Table 1.3).

Discussion

Baseline Activity of Breeding Flammulated and Northern Saw-whet Owls

I found that non-migratory Flammulated Owls and Northern Saw-whet Owls were very active in orientation cages, averaging 1.8 and 2.5 movements/minute, respectively, nearly three times the typical average of 0.67 movements/minute required to consider birds as active migrants in studies of migratory restlessness in songbirds. The majority of owls exhibiting significant restlessness were also found to orient significantly, suggesting that owls perceive some cue(s) allowing them to identify a particular direction for orientation. Additionally, that partial migrants like Northern Saw-whet Owls demonstrate directional preferences suggests a tendency of individuals to select a specific course although the final destination may be a relatively short distance from the test site. That most breeding owls exhibited significant directionality in the general direction of the nest box, paired with the assumed instinct of brooding females to return to their young, suggest positive bias in the degree of restlessness of breeding owls in orientation cages. Additionally, conspecific individuals could be heard calling from the testing site during many of the breeding bird trials; the effect of these calls on test results is unpredictable at best. I believe that the presence of other vocal individuals whether they be a mate, neighbor, or nestling resulted in an increase in the activity of breeding birds tested. Although it is difficult to capture owls outside of their breeding or migration season, other studies considering establishing a baseline level of activity for owls in orientation cages should consider using birds captured during the non-breeding season or, if restricted to breeding owls, capture owls prior to nest initiation as well as test breeding males to circumvent the potential effects of separating females from the nest.

Inter-specific Differences in Migratory Restlessness and Orientation

The obligatory, long distance annual migration of insectivorous Flammulated Owls, or complete migrant strategy, is a migratory strategy similar to many long-distance, nocturnally migrating passerines. Conversely, while Northern Saw-whet Owls can make long-distance movements in response to changes in food availability and unfavorable environmental conditions, many birds remain within their breeding range throughout the year, making them a partial migrant. Furthermore, Northern Saw-whet Owl migration is complicated in the West where mountains make altitudinal migration an alternative strategy. Due to these differences in the migration pressures and strategies of Flammulated Owls and Northern Saw-whet Owls, I expected Flammulated Owls to exhibit more restlessness and more frequent and consistent directional preferences than Northern Saw-whet Owls. I expected Flammulated Owls exhibiting significant directional preferences to orient approximately southeast toward their wintering area. Conversely, I expected Northern Saw-whet Owls to exhibit more individual variability in orientation cages with some exhibiting increased restlessness and significant directional preferences. However, I did not anticipate a consistent direction of orientation because potentially suitable winter habitat occurs in more than one direction, although at varying distances, from the study site.

In general, and contrary to expectation, this study suggests that migratory restlessness and orientation are not characteristic behaviors of Flammulated Owls in orientation cages. However, the lack of a consistent preference in the direction of intended migration may have resulted from inadequate sample sizes, because all individuals oriented within an approximately 100° interval in a roughly southwestern direction (Figure 1.2). Perhaps individual Flammulated Owls utilize different migration paths, choosing to travel south, southeast, or southwest from Lucky Peak. Birds departing south from Lucky Peak might not encounter forested habitat until flying approximately 200 km (Figure 1.7), which is certainly within the capabilities of the species (McCallum 1994a). Due to the existence of relatively few western migration banding sites and a lack of band recoveries, no concrete data exist concerning the migratory pathways of Flammulated Owls in the northwest. A study involving stable isotope analysis of Flammulated Owls captured during fall migration in New Mexico stated that birds at this site were a combination of local, regional, and a few northern migrants with two owls originating from at least 200 km away (DeLong et al. 2005). Certainly, additional study is warranted.

The behavior of Northern Saw-whet Owls in orientation cages relative to expectations was mixed. As was expected for this partially migratory species, the tendency to exhibit migratory restlessness in orientation cages was not pervasive among individuals (61% of tested owls). Previous studies of migratory songbirds report variable proportions of significantly active birds tested in orientation cages (between 52-100%) although the minimum level of activity required in these studies was 40 movements/h (Akesson 1993, Akesson and Backman 1999, Sandberg et al. 2000), compared to 60 movements/h in this study. Considering their partial migrant strategy, I did not expect the majority of Northern Saw-whet Owls to orient, the vast majority of active owls showed directional preferences, although the lack of a common preferred direction among individuals may be indicative of the varying migration strategies, such as dispersal, altitudinal migration, and latitudinal migration, used by individuals classified as a partially migratory species. Northern Saw-whet Owls are rarely recaptured on Lucky

Peak, suggesting that owls leave the capture site in all directions, likely to different extents depending upon habitat availability.

Since Flammulated Owls completely leave the US during the non-breeding season, I assumed a higher level of migratory restlessness in alignment with the longer distance these birds have to travel. For Northern Saw-whet Owls, I expected a lower level of activity corresponding to their partial migration strategy in the western US. The lower and higher than expected levels of migratory restlessness observed in Flammulated Owls and Northern Saw-whet Owls, respectively, are puzzling. There is a marked difference in the behavioral response to human handling of Flammulated Owls and Northern Saw-whet Owls. Flammulated Owls behaved in a more docile manner during handling, often entering a trance-like state in which birds closed their eyes and appeared to fall asleep, although this behavior varies to some degree among individuals, with a few birds remaining quite active (pers. obs.). This response to handling may have carried over into orientation cage trials and suppressed Flammulated Owl activity levels. In contrast, Northern Saw-whet Owls typically remained very active during capture and handling (pers. obs.). Interestingly, the increased activity in Northern Saw-whet Owls was present in breeding birds as well, with Northern Saw-whet Owls moving, on average, 43 times/h more than Flammulated Owls; however, the behavior of breeding birds was overall more uniform for all individuals tested and comparable between the two species whereas the migrating birds showed a much higher degree of variation. Some may theorize that high levels of activity by caged owls represent escape rather than migratory behavior. However, from the remote video surveillance I noted what I believe to represent escape behavior in which the owls fluttered against the top of the cage and at times grabbed and held the mesh on the cage lid with their feet. Movements such as these were infrequent and documented as restlessness but were not counted in orientation calculations.

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Migrating passerines tested under simulated overcast sky conditions did not demonstrate a significant directional preference and activity of the birds was dramatically reduced under overcast conditions (Akesson 1993, Akesson and Backman 1999). Consequently, under simulated overcast conditions (OVERCAST), I expected Northern Saw-whet Owls to show less restlessness and directional preferences on average relative to simulated partial overcast (PARTIAL) and unobstructed (CLEAR) treatments. Furthermore, I expected less restlessness and less directional preference in the PARTIAL treatment relative to the CLEAR treatment. I also expected natural sky conditions to relate similarly to owl migratory restlessness and orientation.

Northern Saw-whet Owls in the OVERCAST treatment moved significantly less than birds in the PARTIAL and the CLEAR treatments, suggesting two possible explanations. First, a completely overcast sky may suppress the migratory restlessness of owls, presumably due to a lack of celestial cues, while owls under a partially cloudy sky are capable of gathering enough visual information to orient and migrate normally. If this were the case, however, I would have expected a similar pattern in Northern Saw-whet Owls in the CLEAR treatment tested under natural overcast conditions; no such relationship existed. Alternatively, some flaw exists in the nature of the testing arrangement. For example, perhaps the opaque Plexiglas® did not accurately simulate partial or complete cloud cover. The OVERCAST treatment blocked not only lunar and stellar cues, but also any other visual landmarks that a bird might have used to orient itself such as nearby mountain peaks, forested habitat and bodies of water, while the PARTIAL treatment probably left enough area to view major landmarks. This design was adopted from previous studies exploring the importance of visual cues to songbird migration; however, some studies have documented migrating birds that orient accurately under a completely overcast sky (Berthold 1996). Certainly owls could employ different navigation techniques than songbirds, but the fact that the OVERCAST treatment almost completely suppressed migratory restlessness in all birds tested suggests that the treatment affected more than just navigation.

Unlike Northern Saw-whet Owls, natural cloud cover may relate negatively to migratory restlessness in Flammulated Owls. The different response to natural cloud cover between the two species might reflect a difference in the cues the two species rely on for navigation since the use of specific navigation methods can vary even within a species (Akesson 1993); more study is warranted.

Evans (1980) found that a full moon tends to suppress migration, probably due to the higher visibility of a small owl to predators during a bright moon. However, the moon may affect caged birds differently than free-flying birds. Emlen and Emlen (1966) state that birds in orientation cages may be attracted towards a bright moon or disrupted by the shadows created by moonlight. When exposed to a bright moon, many biologists hypothesize that free-flying owls may elect either not to migrate, or to move through forested areas only. Consequently, I expected that both species would display less migratory restlessness and a less pronounced orientation preference under the influence of a bright moon (>66% illuminated) relative to migratory restlessness and orientation under a less illuminated moon. The present study supports such an influence of moon illumination upon Northern Saw-whet Owl orientation, but does not suggest an influence of moon illumination on migratory restlessness in either species. Under the influence of a very bright moon (>66% illuminated), Northern Saw-whet Owls oriented significantly towards northeast, the opposite of direction of expected movement and the direction of nearest forested cover, located approximately 1km away from the test site. During orientation trials in which less of the moon disk was illuminated, owls oriented in a more variable fashion, suggesting that moderate to low ambient light conditions have little influence on Northern Saw-whet Owl movements. Furthermore, the behavior of caged birds may simply be different at times, especially when conditions for migration are less than optimal (Nievergelt et al. 1999). Other studies using orientation cages with passerines and released waterfowl have documented an unexplained “non-sense orientation” phenomenon in which birds orient toward the northwest (Kramer 1951, Matthews 1961, Wiltschko 1980, Sandberg et al. 1988, Sandberg et al. 1991, Akesson 1993).

Previous work comparing numbers of owls observed throughout the night relative to the number of owls captured documented that more owls were observed during the first two to three hours after sunset, while more owls were captured during the last four hours of the night (Russell et al. 1991). Higher capture rates during the last four hours before sunrise are often characteristic of owl migration banding studies (Rasmussen et al. 2008, Kerlinger 1995), including the owls captured at Lucky Peak (pers. obs.); and may be due, in part, to the fact that high flying, migrating owls are less likely to be captured compared to hunting owls flying nearer the ground (Duffy and Matheny 1997). I expected owls tested earlier in the night to exhibit a higher degree of restlessness and more directionality than birds tested later in the night.

The present study suggests that migratory restlessness in Northern Saw-whet Owls increases in the last few hours prior to sunrise. This contrasts with other owl migration studies and the commonly held notion that owls migrate early in the night and spend the last few hours of the night hunting and roosting (Russell et al. 1991, Duffy and Kerlinger 1992). If the marked increase in Northern Saw-whet Owl restlessness just before sunrise indicated selection of a roost site, rather than migratory behavior, I would have also expected a shift in directional preference towards the nearest available roosting habitat (northeast; Figure 1.7); Northern Saw-whet Owls did not exhibit such a shift in orientation. Nievergelt et al. (1999) found that caged birds demonstrated less directional preference early in the migration season and when tested late at night, when free-flying birds simultaneously shifted their flight direction to the west to avoid crossing ecological barriers, and that only 41% of caged birds were active during late-night experiments. For owls, the increase in activity may be a result of increased pressure to capture prey prior to roosting and the increase in activity could demonstrate an important difference in migration behavior of owls versus songbirds. In any case, I cannot exclude the possibility that Northern Saw-whet Owls captured at Lucky Peak migrate primarily during the latter part of the night. All birds tested in Trial 1 were held throughout the previous day in order to have birds available for testing one hour after sunset and, while I made every effort to minimize stress and disturbance, the process of holding birds prior to testing might have influenced activity in orientation cages. However, numerous orientation cage studies have held birds anywhere from a few hours to months at a time with no reported adverse affects (Akesson 1993, Akesson and Backman 1999, Nievergelt et al. 1999, Sandberg et al. 2000, Deutschlander and Muheim 2009). A study in which a group of owls are held in orientation cages continuously throughout the majority of the night may reveal more about changes in restlessness level.

Banding studies involving migratory birds often show a change in the makeup of subpopulations of a species captured throughout the banding season. This trend is a logical one considering the birds migrating through a given area likely originate from multiple breeding areas of varying distances from the migration station. However, given their obligatory migratory status and Lucky Peak's proximity to the northern extent of their range, I did not expect migratory restlessness to change throughout the season in Flammulated Owls since I expected that birds originating from the same area will use similar migration strategies. Conversely, the characterization of Northern Saw-whet Owls as partial migrants suggests that individuals may elect to make either short-distance or long-distance migratory movements. Furthermore, groups of individuals sharing similar migratory strategies may migrate through the study site at similar times. Consequently, in Northern Saw-whet Owls, I expected that the extent of migratory restlessness, and perhaps migratory orientation, may change (in either direction) throughout the fall migration.

I documented no difference in the migratory behavior of either Flammulated or Northern Saw-whet Owls as a function of migration timing. Lucky Peak is located in the northern one-third of the Flammulated Owl's range and all birds moving through our migration site may originate from the same general geographic range and thus behave similarly. Future studies, especially during years of high (40 or more individuals) capture rates of Flammulated Owls, could help to confirm or disprove this hypothesis. A thorough examination of the timing of Northern Saw-whet Owls is complicated by the fact that individuals captured at Lucky Peak likely consist of a combination of regional individuals breeding in southern Idaho and individuals from more northern locations (Adam Smith, unpub. stable isotope data). Incorporating stable isotopes into a future orientation study of owls captured on Lucky Peak could prove informative.

Immature birds may be more prone to migrate than adult birds for a variety of reasons, including the social dominance of adult birds (Mueller et al. 1977; Gauthreaux 1978, 1982; Newton 1979), or the decreased efficiency of foraging in young birds (Rosenfield and Evans 1980, Duncan 1982). The social dominance hypothesis states that young birds should move earlier than their adult counterparts due in part to less acquired experience and an inability to maintain territories (Kerlinger 1989). Consequently, I expected immature Northern Saw-whet Owls to demonstrate increased migratory restlessness and directional preferences relative to adults.

As expected, immature Northern Saw-whet Owls exhibited increased migratory restlessness relative to adult owls. This pattern perhaps relates to the occurrence of differential migration in Northern Saw-whet Owls. For example, dominant adult birds may obtain preferred wintering sites, thus forcing more subordinate immature birds to relocate and seek out alternative wintering sites (Gauthreaux 1985). I suggest that migration strategies used by Northern Saw-whet Owls in the western US may differ among juveniles and adults. Migratory restlessness results suggest that immature Northern Saw-whet Owls captured at Lucky Peak likely show a greater propensity to migrate than adult owls. Differential migration related to the age of Northern Saw-whet Owls is variable. Adults migrate earlier than juveniles in some populations but juveniles can migrate earlier in other populations, although differences in timing often vary from year to year (Rasmussen et al. 2008). Furthermore, the timing of adult and juvenile movements may overlap completely throughout the migration season (Rasmussen et al. 2008). I found no difference in the directionality of adult and juvenile Northern Saw-whet Owl movements.

Many migrants store subcutaneous fat deposits for use as fuel during flights over poor habitat (Blem 1980, Clark 1990, Dingle 1996, Deutschlander and Muheim 2009). Furthermore, flight musculature may be increased in preparation for long migratory flights (Marsh 1984, Lindstrom et al. 2000). Body condition (particularly subcutaneous fat stores) can profoundly influence migratory orientation (Sandberg et al. 1988, Yong and Moore 1993, Sandberg et al. 2002, Deutschlander and Muheim 2009). The accumulation of excess fat stores has also been correlated with increased migratory restlessness (Yong and Moore 1993). Therefore, an owl’s body condition (as indexed by fat stores and keel musculature) may be indicative of migratory condition. I expected owls with more substantial subcutaneous fat stores or keel musculature to exhibit more migratory restlessness and stronger directional preferences than owls possessing less stored fat or less developed keel musculature.

Migratory restlessness increased in Flammulated Owls possessing larger flight muscles (i.e., keel musculature) suggesting that protein stores may be important to successfully completing their migratory journey. The lack of such a relationship in Northern Saw-whet Owls is not surprising, however, as they likely engage less frequently in strenuous long distance movements. Additionally, the present study suggests a potentially interesting relationship between fuel stores (i.e., furcular fat deposits) and migratory restlessness in Flammulated Owls. Specifically, Flammulated Owls possessing more furcular fat stores demonstrated marginally lower restlessness. Some birds respond to decreases in body fat and lack of food resources by increasing their migratory restlessness as if crossing an ecological barrier (Gwinner et al. 1988). If birds with low body fat are active and moving southward, this could indicate a lack of good migration stopover habitat around Lucky Peak, which seems reasonable given the low within-season band recapture rate of owls at IBO (Sarah Stock, Greg Kaltenecker, pers. comm.); Recaptures typically indicate the use of an area as stopover habitat.

There existed no relationship between restlessness or orientation and fat deposits in Northern Saw-whet Owls. Akesson (1993) likewise reported no relationship between orientation and fat stores, while Deutschlander and Muheim (2009) found that fat scores affected orientation but not migratory restlessness as lean birds exhibited movement, but not in the expected direction. Since migratory restlessness and orientation are hard-wired, innate characteristics, I would expect that a bird without sufficient fat stores to fuel its next step in the migratory journey would not physiologically be "ready" to exhibit migratory orientation. One might expect an evolutionary mechanism to suspend migratory movements in individuals not yet physically fit to undertake the next migratory flight. My results, however, do not support this hypothesis for Flammulated Owls. Furthermore, Akesson (1993) suggests that some species may exhibit flexible migration behavior and alter their migratory strategy when necessary. For example, some owls may accumulate large fat reserves and make long-distance flights while other owls keep small fat reserves and use a series of short successive "hops" to complete the migratory journey. Perhaps the Flammulated Owl varies its migratory strategy from year to year or throughout the migration journey depending upon food availability and their interaction with ecological barriers.

The speed and direction of wind is known to influence the decision to migrate as well as the heading chosen for a migratory course (Richardson 1978, Berthold 1996, Åkesson and Hedenström 2000). Headwinds can dramatically increase the amount of energy necessary to cover a given distance, whereas tailwinds often improve the energy efficiency of migration (Åkesson and Hedenström 2000). Assuming that owls in orientation cages can sense wind direction and velocity, I expected increased migratory restlessness and more specific directional preferences associated with tailwinds (some northerly component) than with headwinds (some southerly component). I expected no influence of crosswinds on migratory restlessness, but that crosswinds may influence the heading chosen by migratory owls to accommodate for wind drift.

That Northern Saw-whet Owl restlessness and orientation did not correlate with wind speed or direction suggests that these factors are not important or that birds were not able to sense them while in orientation cages. A study comparing birds in Emlen funnels with free-flying birds found that unlike free-flying birds, birds in the funnels did not react to the wind direction (Nievergelt et al. 1999). However, some night migrating species adjust their flight paths to compensate for wind drift, while others do not exhibit any obvious pattern (Richardson 1991). Either situation may apply to the species in this study and a concurrent examination of the behavior of free-flying migrating owls would address this question.

Conclusions and Recommendations

This study is the first to demonstrate that the migratory behavior of owls may be studied with orientation cages, and that environmental and body condition variables can influence owl directional preferences and migratory restlessness. Future studies involving owls and orientation cages should address any of several interesting findings revealed in the present study. Of particular importance is the establishment of a more accurate baseline level of activity of non-migratory owls in orientation cages. Furthermore, larger Flammulated Owl samples will help to clarify the response of this species to a study implementing orientation cages and will be necessary to examine the influence of environmental and body condition variables on migratory restlessness and orientation behavior. Further study of the effects of these variables on Flammulated Owl migratory behavior may indeed reveal differences in the orientation mechanisms of the two species.

Future studies of owl orientation and restlessness would benefit from modifications to the experimental setup used herein. Specifically, using black Plexiglas® lids to simulate cloud cover (particularly overcast conditions) may have blocked so much natural light that birds were unwilling to move at all. I suggest the use of an elevated cover or canopy in order to allow more natural light into the cages while still blocking visual cues such as the stars and moon from a bird's view. Doing so will assist in separating the influence of factors such as sky conditions and body condition on Zugenrühe and orientation. Since data extraction from video taped orientation trials is a tedious and potentially subjective method of data collection, recording owl movements in orientation cages with an electronic registration devise would greatly improve the efficiency of documenting migratory restlessness and orientation. Additionally, until a larger body of information is accumulated, I caution that the results presented here remain exploratory and should be interpreted carefully.

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Table 1.1. Summary of environmental and body condition variables explored as they relate to migratory orientation and restlessness in Flammulated Owls and Northern Saw-whet Owls.

Variable	Variable type	Assessment method
Migratory Orientation		
Simulated cloud cover	Categorical	Mardia-Watson-Wheeler test
Time of night	Categorical	Mardia-Watson-Wheeler test
Age	Categorical	Mardia-Watson-Wheeler test
Fat score	Ordinal/Interval	Circular-linear correlation
Keel musculature	Ordinal/Interval	Circular-linear correlation
Wind direction	Circular	Circular-circular correlation
Wind speed	Interval	Circular-linear correlation
Moon disk illumination	Interval	Circular-linear correlation
Time of year	Interval	Circular-linear correlation
Natural cloud cover	Interval	Circular-linear correlation
Migratory restlessness	Ordinal	Circular-linear correlation
Migratory restlessness		
Simulated cloud cover	Categorical	Negative binomial linear model

Table 1.1. Continued.

Variable	Variable type	Assessment method
Migratory restlessness		
Time of night	Categorical	Negative binomial linear model
Age	Categorical	Negative binomial linear model
Fat score	Ordinal/Interval	Negative binomial linear model
Keel musculature	Ordinal/Interval	Negative binomial linear model
Wind speed	Interval	Negative binomial linear model
Moon disk illumination	Interval	Negative binomial linear model
Time of year	Interval	Negative binomial linear model
Natural cloud cover	Interval	Negative binomial linear model

Table 1.2. Results of a negative binomial generalized linear model describing the relationship between migratory restlessness in Northern Saw-whet Owls (*N* = 97; 20 adult and 77 immature owls) and a variety of environmental and body condition variables. Global tests are reported for all classification variables. Effect estimates are omitted for non-significant (*P* > 0.10) explanatory variables. Least-squares means are reported for simulated cloud cover and time of night treatments and the different owl age classes, as they are more readily interpretable.

Parameter	df	Estimate	SE	$\chi 2$	P
Simulated cloud cover	2			15.41	< 0.01
OVERCAST		2.80	0.36		
PARTIAL		4.56	0.29		
CLEAR		4.70	0.27		
Time of night	2			9.72	< 0.01
Trial 1		3.88	0.24		
Trial 2		3.39	0.48		
Trial 3		4.80	0.24		
Age	1			4.92	0.03
Adult		3.57	0.34		
Immature		4.47	0.20		
Fat	1			2.48	0.12

Table 1.2. Continued.

Parameter	df	Estimate	SE	$\chi 2$	P
Keel	1			0.15	0.70
Wind speed	1			0.35	0.56
Moon disk illumination	1			0.24	0.62
Time of year	1			0.82	0.37

Table 1.3. Results of a negative binomial generalized linear model describing the relationship between migratory restlessness in Flammulated Owls (*N* = 16) and environmental and body condition variables. Effect estimates are omitted for non-significant (*P* > 0.10) explanatory variables.

Parameter	df	Estimate	SE	$\chi 2$	P
Keel	1	2.49	1.11	5.05	0.02
Natural cloud cover	1	-1.51	0.71	4.26	0.04
Fat	1	-2.07	1.49	2.83	0.09
Wind speed	1			2.43	0.12
Moon disk illumination	1			0.42	0.52
Time of year	1			0.75	0.39

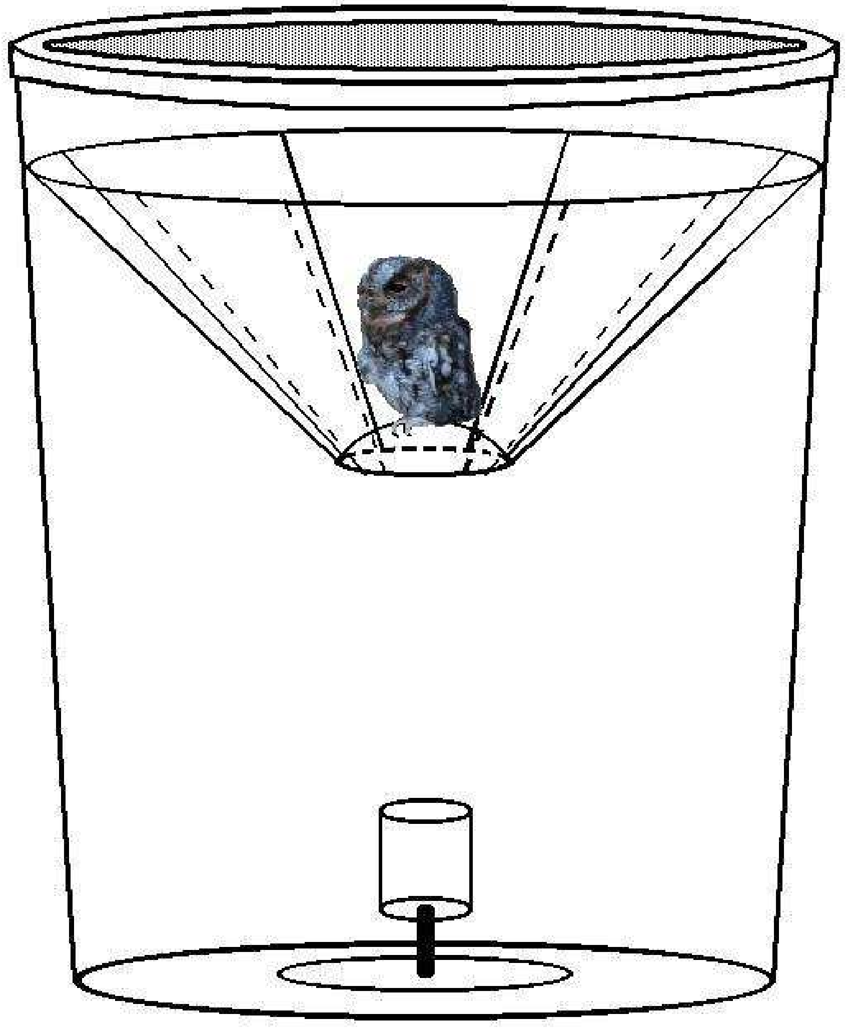


Figure 1.1. Diagram of the orientation cages constructed to assess migratory orientation and restlessness in Flammulated Owls and Northern Saw-whet Owls. The owl may move in any direction within the clear Plexiglas® funnel while a fine mesh cover prevents escape. After each movement, the owl returns to the center of the funnel, thus ensuring that sequential movements are independent. The diagrammed construction allows owls to view approximately 120^o of the night sky. An infrared camera records movements through the funnel from below.

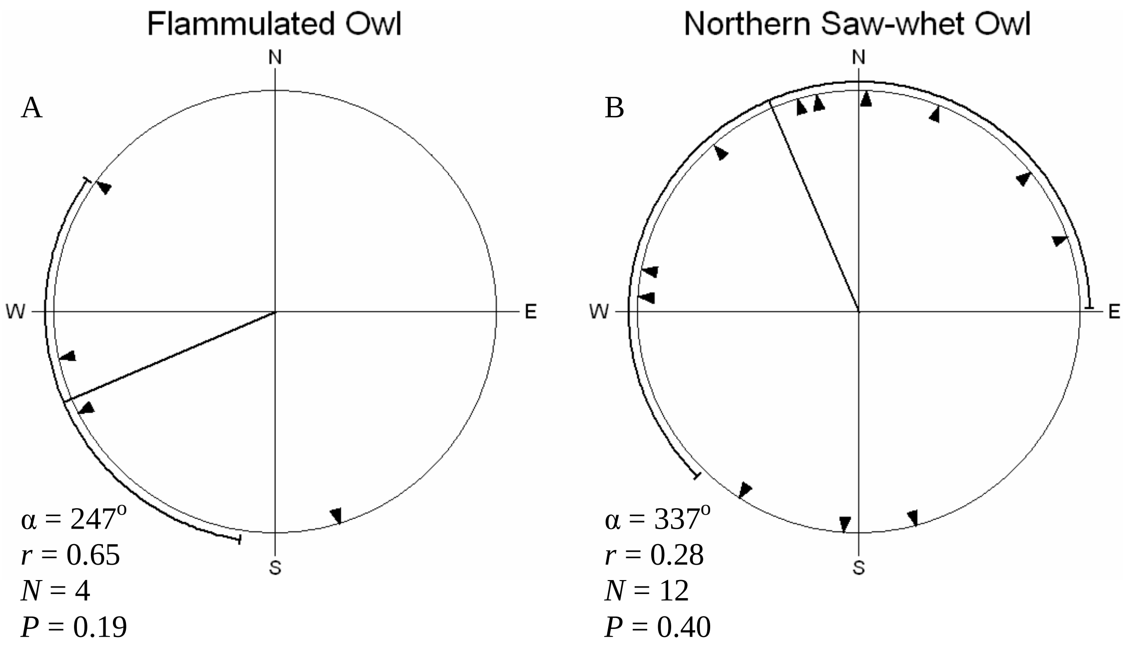


Figure 1.2. Orientation behavior of Flammulated (A) and Northern Saw-whet Owls (B) during autumn migration in southwestern Idaho. Individuals of both species were tested in orientation cages approximately one hour after sunset with unobstructed views of the night sky. Each triangle at the periphery of both diagrams represents the mean heading of one individual. The mean vector (α) of each sample is illustrated by a straight line from the center of the diagram and is surrounded by the 95% confidence intervals, represented by curved lines along the periphery of the diagram. *P* values determined using a Raleigh test (Batschelet 1981).

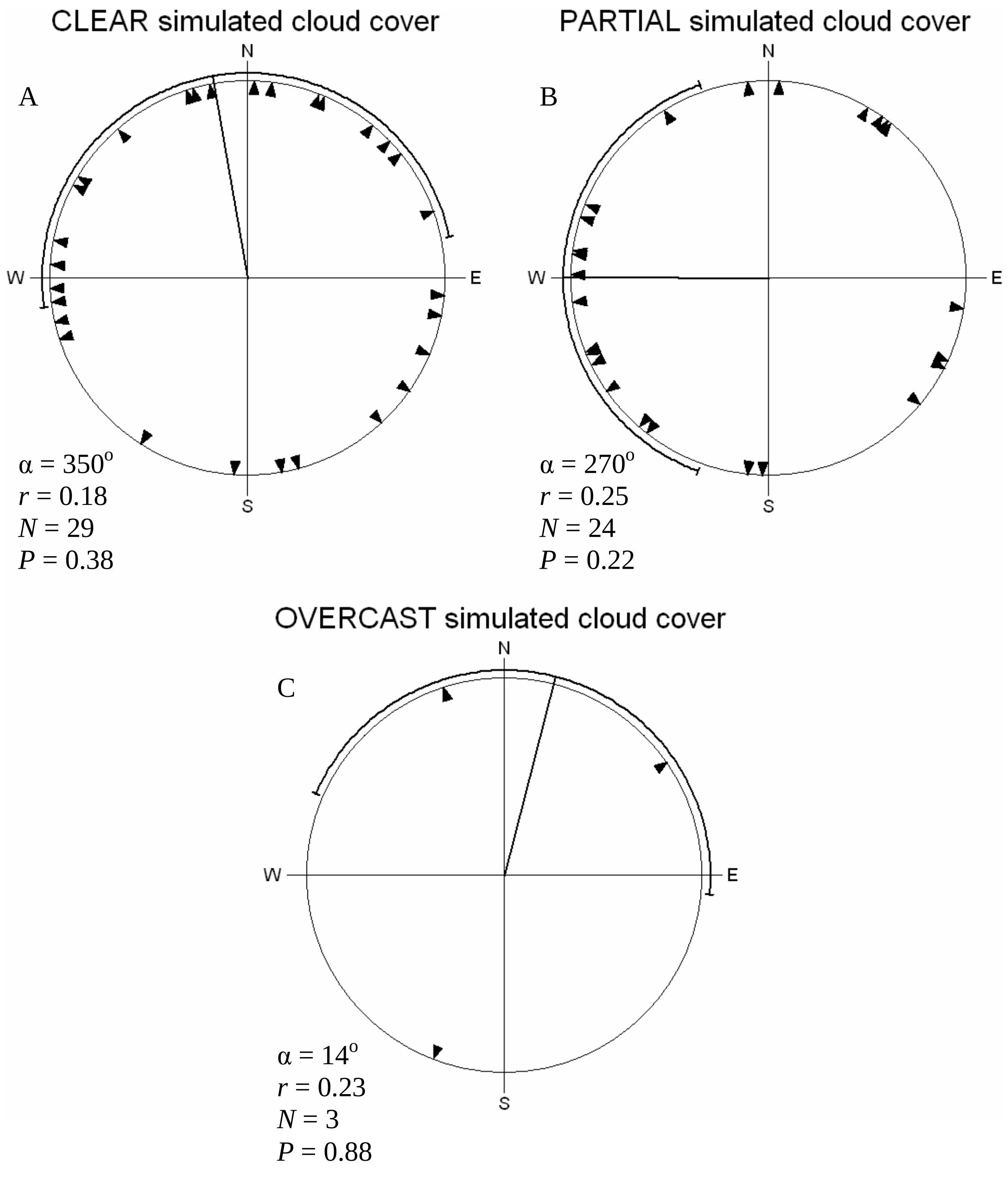
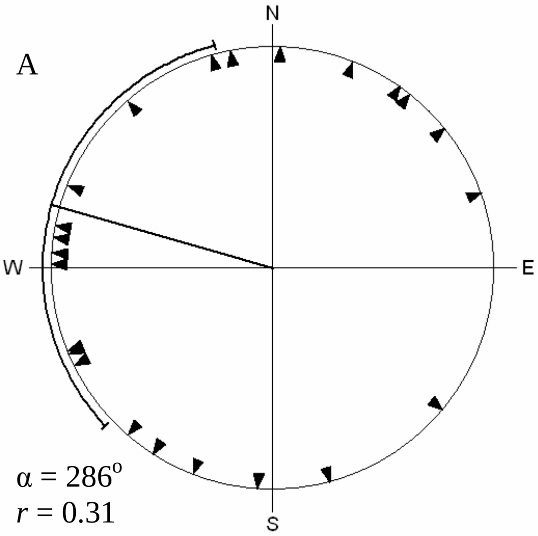

CLEAR simulated cloud cover
PARTIAL simulated cloud cover
A
B
N
W
E
S
α = 350°
r = 0.18
N = 29
P = 0.38
α = 270°
r = 0.25
N = 24
P = 0.22
OVERCAST simulated cloud cover
C
α = 14°
r = 0.23
N = 3
P = 0.88

Figure 1.3. Orientation behavior of Northern Saw-whet Owls under three treatments of simulated cloud cover during autumn migration in southwestern Idaho: (A) CLEAR, unobstructed view of the night sky, (B) PARTIAL, partially obstructed view (simulated 50% cloud cover), and (C) OVERCAST, completely obstructed view. Each triangle at the periphery of the three diagrams represents the mean heading of one individual. The mean vector (α) of each sample is illustrated by a straight line from the center of the diagram and is surrounded by the 95% confidence intervals, represented by curved lines along the periphery of the diagram. *P* values determined using a Raleigh test (Batschelet 1981).

Trial 1

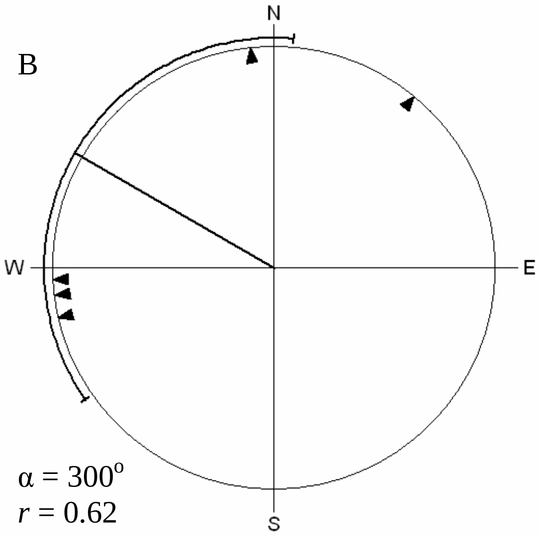
A



$\alpha = 286^{o}$
$r = 0.31$
$N = 22$
$P = 0.12$

Trial 2

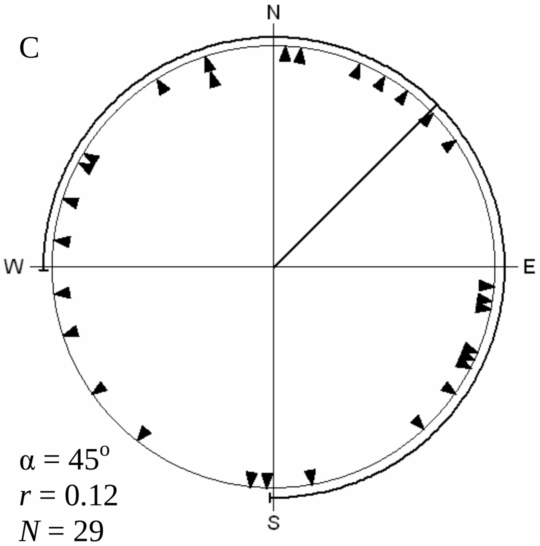
B



$\alpha = 300^{o}$
$r = 0.62$
$N = 5$
$P = 0.14$

Trial 3

C



$\alpha = 45^{o}$
$r = 0.12$
$N = 29$
$P = 0.66$

Figure 1.4. Orientation behavior of Northern Saw-whet Owls during three time trials throughout the night during autumn migration in southwestern Idaho: (A) beginning approximately 1 h after sunset (Trial 1); (B) beginning approximately 5 h after sunset, during the middle of the night (Trial 2); and (C) beginning approximately 2 h before sunrise (Trial 3). Each triangle at the periphery of the three diagrams represents the mean heading of one individual. The mean vector (α) of each sample is illustrated by a straight line from the center of the diagram and is surrounded by the 95% confidence intervals, represented by curved lines along the periphery of the diagram. *P* values determined using a Raleigh test (Batschelet 1981).

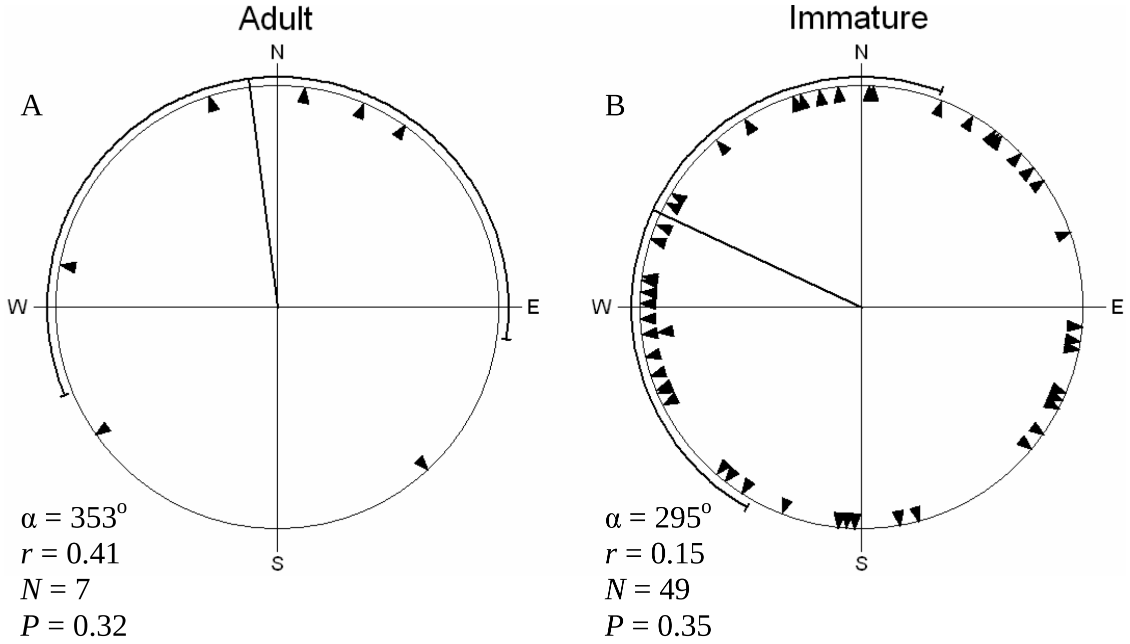


Figure 1.5. Orientation behavior of adult (A) and immature (B) Northern Saw-whet Owls during autumn migration in southwestern Idaho. Each triangle at the periphery of both diagrams represents the mean heading of one individual. The mean vector (α) of each sample is illustrated by a straight line from the center of the diagram and is surrounded by the 95% confidence intervals, represented by curved lines along the periphery of the diagram. *P* values determined using a Raleigh test (Batschelet 1981).

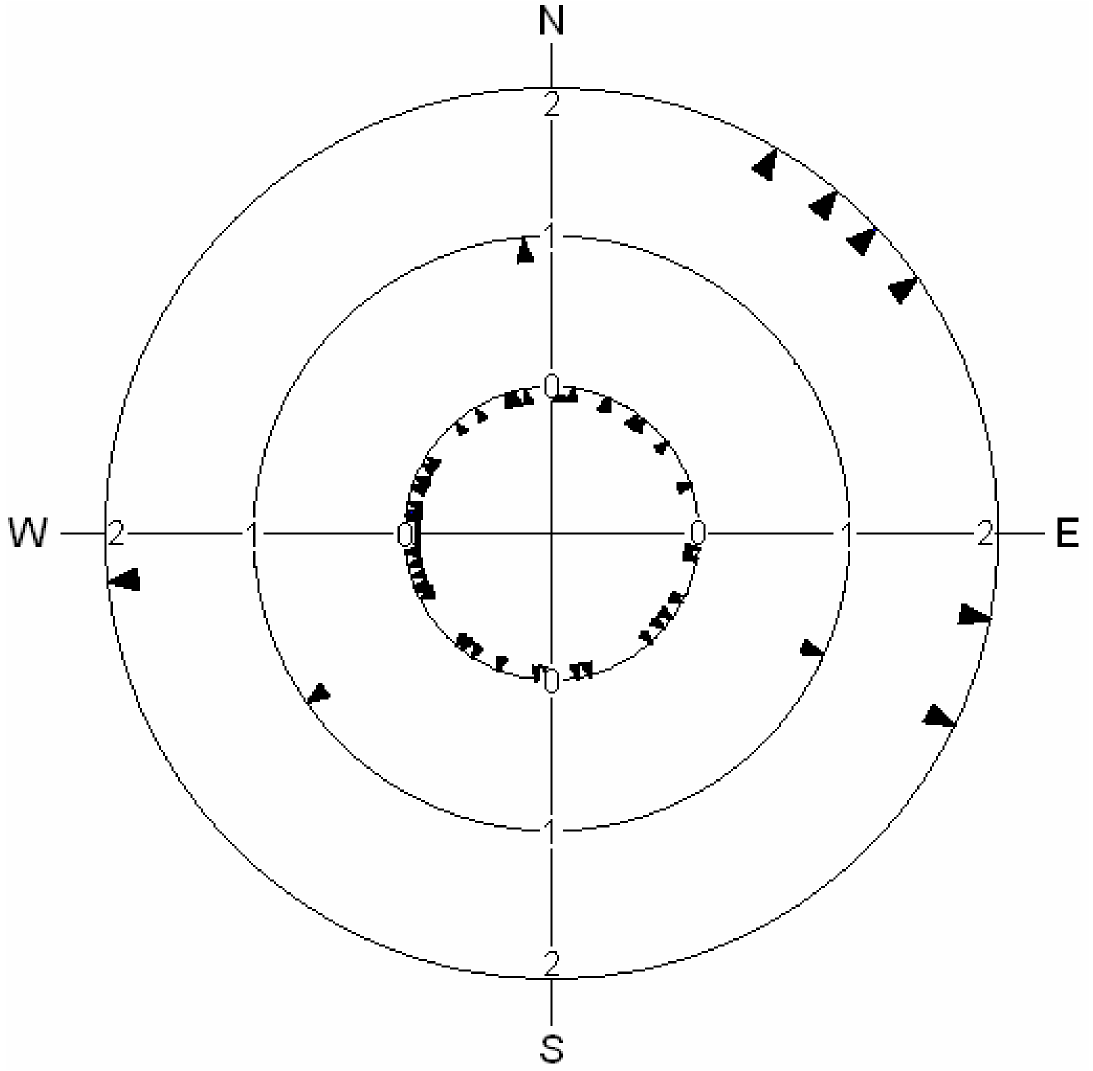


Figure 1.6. Orientation behavior of Northern Saw-whet Owls (*N* = 57) during autumn migration in southwestern Idaho related to the percentage of moon disk illuminated at the initiation of the orientation trial. The three rings in the diagram represent one of three categories of moon disk illumination: (0) less than 33% illuminated; (1) 34 to 66% illuminated; and (2) greater than 66% illuminated. Each triangle around the periphery of a ring represents the mean heading of one individual tested under the corresponding lunar illumination.

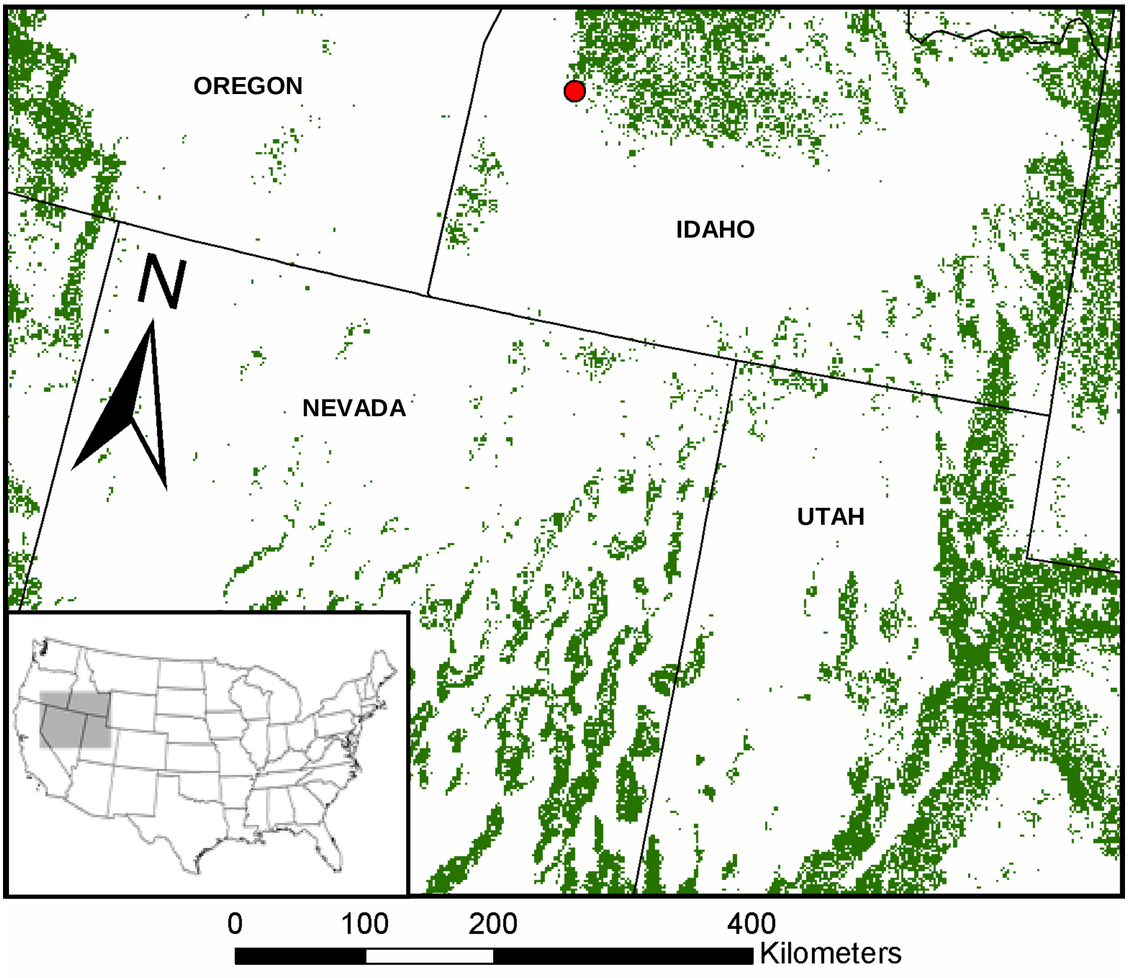


Figure 1.7. Distribution of forested habitat (shown in green) available to migrating Flammulated and Northern Saw-whet Owls leaving Lucky Peak (red circle). Forested habitat includes evergreen, mixed, and deciduous forest from the 2001 National Land Cover Data (NLCD; Homer et al. 2004).

CHAPTER TWO:

WING SHAPE IN RELATION TO MIGRATORY HABIT IN THE FLAMMULATED OWL (*OTUS FLAMMEOLUS*) AND NORTHERN SAW-WHET OWL (*AEGOLEUS ACADICUS*)

Abstract

Migration places strong selective pressures on the physical attributes of birds. Within ecologically similar or closely related taxa, migrants often possess longer, more pointed wings than sedentary individuals. I investigated whether the sympatric, ecologically similar Flammulated Owl (*Otus flammeolus*), a long-distance migrant, and Northern Saw-whet Owl (*Aegolius acadicus*), a species which may but does not always migrate long distances, possess wing morphology indicative of their different migratory strategies. When corrected for allometric differences between the two owl species, Flammulated Owls possessed shorter proximal primaries relative to Northern Saw-whet Owls, resulting in wings that are distinctly narrower and characterized by a relatively higher-aspect ratio. Conversely, wing pointedness, as indexed by the nearness of the wingtip to the leading edge of the wing, did not differ between species.

Introduction

Long-distance avian migrants face selective pressures on their physical attributes. Specifically, migratory birds tend to possess longer, more pointed wings than ecologically similar or closely related (even within) species with sedentary habits (Rayner 1988, Winkler & Leisler 1992, Senar et al. 1994, Marchetti et al. 1995, Mönkkönen 1995, Copete et al. 1999, Perez-Tris and Telleria 2001). Such adaptations likely relate to the increased lift and reduced drag associated with long, narrow high-aspect wings (Berthold 1996, Dingle 1996, Lockwood et al. 1998), which typically result from relatively long distal primaries and short proximal primaries (Rayner 1988, Winkler and Leisler 1992, Alerstam 1993, Lockwood et al. 1998). Furthermore, the optimal physical design for flight, specifically wing shape, is influenced by a variety of factors including habitat, prey, migration habits, even small morphological differences within a family can relate to differences in behavior and ecology (Norberg 1995).

The Flammulated Owl (*Otus flammeolus*) is a long-distance migrant (Balda et al. 1975, McCallum 1994) faced with a morphological tradeoff. Wing morphology adaptations expected of the Flammulated Owl contrast with the maneuverability (decreased turning radii and slower flight; Swaddle and Lockwood 2003) that is assumed to be needed to capture aerial insect prey in forested habitats (McCallum 1994).

In their areas of overlap in the western US, Northern Saw-whet Owls (*Aegoleus acadicus*) occupy habitats similar to Flammulated Owls during the breeding and migration season, and consume primarily small terrestrial prey (Rasmussen et al. 2008). Northern Saw-whet Owls, however, are thought to utilize a partial migration strategy in the western US (Lundberg 1988). A species exhibiting partial migration consists of several populations of individuals that each has different migratory behavior (Berthold 1996). In the case of Northen Saw-whet Owls, this typically involves no migration for some individuals, a short altitudinal migration by others, or regular long-distance latitudinal migratory movements (Rasmussen et al. 2008). Consequently, some Northern Saw-whet Owls may experience a morphological trade-off between migration and foraging similar to that of Flammulated Owls, while others may not. I investigated whether the sympatric, ecologically similar Flammulated Owl and Northern Saw-whet Owl exhibit wing morphology characteristics indicative of their different migratory strategies.

Methods

During the fall of 2003, I captured Flammulated Owls (*n* = 14) and Northern Saw-whet Owls (*n* = 100) in the Boise Mountains of southwestern Idaho; the study site and capture methodology are detailed elsewhere (Stock et al. 2006). For Flammulated Owls, I was unable to determine the sex of any individuals and aged only a few individuals. Consequently, I did not distinguish between Flammulated Owl sex or age classes. For Northern Saw-whet Owls, I assigned a sex to 60 (60%) individuals using a discriminant function based on wing chord and body mass (Brinker 2000). I categorized Northern Saw-whet Owls into three age classes according to the flight feather criteria detailed in Pyle (1997): hatching-year (HY; *n* = 81), second-year (SY; *n* = 15), and after second-year (ASY; *n* = 4). I excluded from analysis owls with molting flight feathers.

I measured the flattened length (± 0.5 mm) of each primary (P1 – P10, where P1 is the most proximal primary) on the right wing using a ruler with a thin nail fixed at zero. Allometric variations related to individual body size often invalidate comparisons of shape (Lleonart et al. 2000). Thus, using the methodology detailed by Senar et al. (1994) and justified by Lleonart et al. (2000), I standardized primary lengths (P1* – P10*) to a standard individual with a longest primary length of 110 mm. I calculated standardization parameters separately for each species, as well as for each sex class of Northern Saw-whet Owls, as the allometric relationship between body size and primary lengths can vary among species and between sexes in dimorphic species (Lleonart et al. 2000). Standardized primary lengths underlay the objective multivariate assessment of wing shape using Principal Components Analysis (PCA). Hereafter, any discussion of wing shape is restricted to the primaries, which is the portion of the wing measured in this study.

Statistical Analysis

I performed PCA on the covariance matrix of standardized primary lengths and compared PC scores between species, and among age and sex classes of Northern Saw-whet Owls using one-way and two-way ANOVA, respectively. I assessed sex-related differences in PC scores in Northern Saw-whet Owls by way of an *a priori* contrast between males and females only, thus excluding birds of unknown sex from the analysis. I conducted all analyses using SAS Version 8.2, and report all results as mean ± SE.

Results

Two principal components (PCs) explained 87% of the variation in standardized primary lengths (Table 1). PC1 represented increasing proximal primary (P1* – P5*) lengths; I interpreted this axis as wing broadness, with lower values indicative of a narrower, higher-aspect wing. PC2 represented increasing distal primary (P9* – P10*) length, particularly P10*; I interpreted this axis as wing pointedness (Lockwood et al. 1998), with higher values along this axis indicative of a wingtip closer to the leading edge of the wing.

Inter-specific Comparison

Flammulated Owls and Northern Saw-whet Owls differed dramatically in wing broadness (PC1: $F_{1,112} = 405.3$, $P < 0.001$). Specifically, Flammulated Owls (PC1: -13.59 ± 0.85) possessed shorter proximal primaries relative to Northern Saw-whet Owls (PC1: 1.90 ± 0.26; Figure 1). When considering standardized primary lengths, Flammulated Owl proximal primary lengths varied from 4.6 ± 0.4 mm (P5*) to 7.7 ± 0.4 mm (P2*) shorter than those of Northern Saw-whet Owls. The shorter proximal primaries in Flammulated Owls contribute to wings that are distinctly narrower and characterized by a relatively higher-aspect ratio than those of Northern Saw-whet Owls (Figure 2). Wing pointedness (PC2: 0.26 ± 0.64 and -0.04 ± 0.25 for Flammulated Owls and Northern Saw-whet Owls, respectively; $F_{1,112} = 0.2$, $P = 0.68$) did not differ between species.

Intra-specific Comparison

I found no relationship between wing broadness and Northern Saw-whet Owl age (PC1: $F_{2,95} = 0.4$, $P = 0.65$). However, wing broadness varied marginally between the sexes (PC1: $F_{1,95} = 3.6$, $P = 0.06$); males (PC1: 0.52 ± 0.71) exhibited a slightly narrower wing than females (PC1: 1.84 ± 0.59), although considerable overlap existed (Figure 3). There was no interaction between age and sex related to wing broadness (PC1: $F_{3,92} = 0.4$, $P = 0.78$). Like wing broadness, I found no relationship between wing pointedness and age (PC2: $F_{2,95} = 1.6$, $P = 0.20$). Marginal differences in wing shape again existed between the sexes of Northern Saw-whet Owls (PC2: $F_{1,95} = 3.3$, $P = 0.07$); females (PC2: 0.62 ± 0.54) exhibited a wing slightly closer to the leading edge of the wing than males (PC2: -0.55 ± 0.66), despite considerable overlap (Figure 4). There was no interaction between age and sex related to wing pointedness (PC2: $F_{3,92} = 0.8$, $P = 0.49$).

Interestingly, Flammulated Owls clustered into two distinct groups along the wing pointedness axis (PC2): those with relatively short P9* and P10* measurements (i.e., PC2 < -1.2; $n = 6$), and those with relatively long P9* and P10* measurements (i.e., PC2 > 0.8; $n = 8$).

Discussion

Inter-specific Comparison

Wing aspect ratio in Flammulated Owls and Northern Saw-whet Owls seemed to relate to each species' respective migratory habit. Specifically, Flammulated Owls possessed significantly longer and thinner wings than Northern Saw-whet Owls which displayed relatively long proximal primaries. The standardization of primary lengths corrects for allometric effects that could produce the observed differences in wing shape, although some amount of variation in wing shape likely relates to differences in ecology and phylogeny between the species.

Johnson (1997) provides measurements of owls that likely reflect morphological adaptations for pursuing and capturing prey; with short, broad wings enhancing maneuverability and long narrow wings providing endurance for long-distance flight. The Flammulated Owl and Northern Saw-whet Owl are often sympatric species in western North America and utilize similar breeding habitat. The hunting tactics of the two species also show similarities: Northern Saw-whet Owls frequently use low perches in forest openings or edges, detect prey auditorily and visually, and then pluck prey from the ground with their feet (Rasmussen et al. 2008); Flammulated Owls locate prey visually from a perch and capture prey aerially, hover glean, or pick it from the ground with feet or bill (McCallum 1994). Broad wings with rounded tips are thought to increase maneuverability when a bird is flying through obstacles like a forest under story (Lockwood et al. 1998); however more recent findings do not necessarily support the idea that wing roundedness improves maneuverability (Swaddle and Lockwood 2003). In any case, I theorize that selective pressures affecting wing shape as it relates to hunting behavior should result in a more similar wing shape between the two study species whether it be rounded or pointed. That is, all other factors being equal, Flammulated Owls and Northern Saw-whet Owls would require a similar wing shape if just for maneuverability in capturing prey and moving through breeding habitat. Since my findings in this study contradict this idea, I hypothesize that some other factor besides hunting behavior must be influencing the difference seen here between the two species

Within the Strigiformes, Flammulated Owls and Northern Saw-whet Owls are not closely related (Wink and Heidrich 1999), so phylogenetic differences could account for some portion of the observed differences in wing shape (Calmaestra and Moreno 2001). Exactly what portion of the wing shape differences is due to phylogeny is difficult to determine. Despite the potential influence of phylogeny on wing shape, the similar ecological adaptations of Flammulated and Northern Saw-whet Owls suggest that the migratory habits of Flammulated Owls resulted in some of the differences in selective pressure on wing morphology as it related to migration.

Intra-specific Comparison

Within Northern Saw-whet Owls, marginal differences along PC1 (wing aspect ratio) and PC2 (wing pointedness) were found between the sexes. While it is conceivable that wing morphology as it relates to migratory habit could differ between the sexes of Northern Saw-whet Owls, there is a large degree of overlap in both characteristics between the sexes. There could be some ecological reason for differential migration behavior between the sexes such as males remaining closer to the breeding grounds in order to secure preferred nesting sites. However, due to the variable migration of western Northern Saw-whets, it is likely that my samples included individuals with different migratory habits. Additionally the size dimorphism observed between male and female Northern Saw-whets could have contributed to the variation in my results. More study is warranted.

Primary measurements of Flammulated Owls revealed two distinct groups in relation to the length of P9* and P10* (PC2). This result could be a consequence of different patterns of primary molt found in hatch-year and adult Flammulated Owls. Specifically, the primary feathers are not replaced in the preformative molt of hatch-year Flammulated Owls, but the outer seven primaries (including P9 and P10) are replaced in all subsequent molts (Pyle 1997). Therefore, the two clusters of individuals observed along PC2 could represent two separate age groups of birds, hatch-years and adults. Given the difficulty of aging most Flammulated Owls, the relative length of P9 or P10, compared to another primary such as P7, may be worth exploring as a means of aging Flammulated Owls. Given the small sample of unknown age individuals, it is difficult to draw any definite conclusions, but further study of breeding individuals of known age is warranted.

Conclusions

This study was initiated and conducted just prior to the reclassification of owls in the *Otus* genus into the new *Megascops* genus, leaving the Flammulated Owl in its own genus (Banks et al. 2003). This, in combination with the fact that Northern Saw-whet Owls and Flammulated Owls are far separated on the Strigiformes phylogenetic tree (Wink and Heidrich 1999) detracts from the comparisons done in this study. There is a strong possibility that the differences seen in the two species here were as much a result of their genetic differences as any potential migration strategy. After conducting a study involving two relatively unrelated species I suggest others to use caution in their comparisons of species in similar relationships and be conservative in interpretation of their results.

Since few data exist regarding the two study species' migration in the western US, I maintain that wing morphology data can provide insight into differences in migratory habits between as well as within species. This study suggests that Flammulated Owls possess wings indicative of a more migratory lifestyle than do Northern Saw-whet Owls, in accordance with their expected migratory strategies as complete and partial migrants. This is a finding that I am not discounting and would encourage the further study of these owls and their status in the west. Certainly collaborative efforts would prove a more efficient means of study as the few sites that capture migrating Flammulated Owls typically catch them in relatively small numbers. Additionally, study of individuals of known age and sex may reveal differences in wing shape between sexes or migratory strategies within Northern Saw-whet Owls, or associated with age and sex in Flammulated Owls.

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Table 2.1. Results of PCA on standardized primary lengths of Flammulated (*n* = 14) and Northern Saw-whet Owls (n = 100). P1* represents the most proximal primary.

	Factor Loadings	
	PC1	PC2
P1*	0.50	-0.08
P2*	0.50	0.01
P3*	0.47	0.01
P4*	0.42	0.01
P5*	0.31	0.04
P6*	0.06	-0.03
P7*	0.01	-0.01
P8*	0.07	0.13
P9*	0.02	0.43
P10*	-0.01	0.89
Eigenvalue	33.3	6.0
Variance explained (%)	74	13

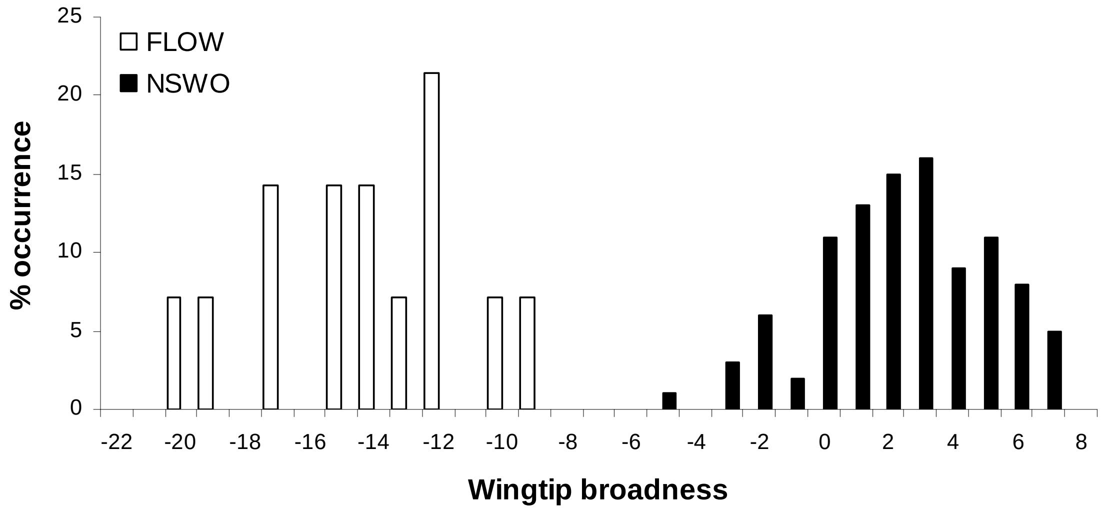

Figure 2.1. Frequency distribution (% occurrence) of Flammulated (*n* = 14; FLOW) and Northern Saw-whet (*n* = 100; NSWO) Owls along the first principal component axis representing wingtip broadness (see Table 1). Lower scores along this axis indicate a narrower, higher-aspect wing.

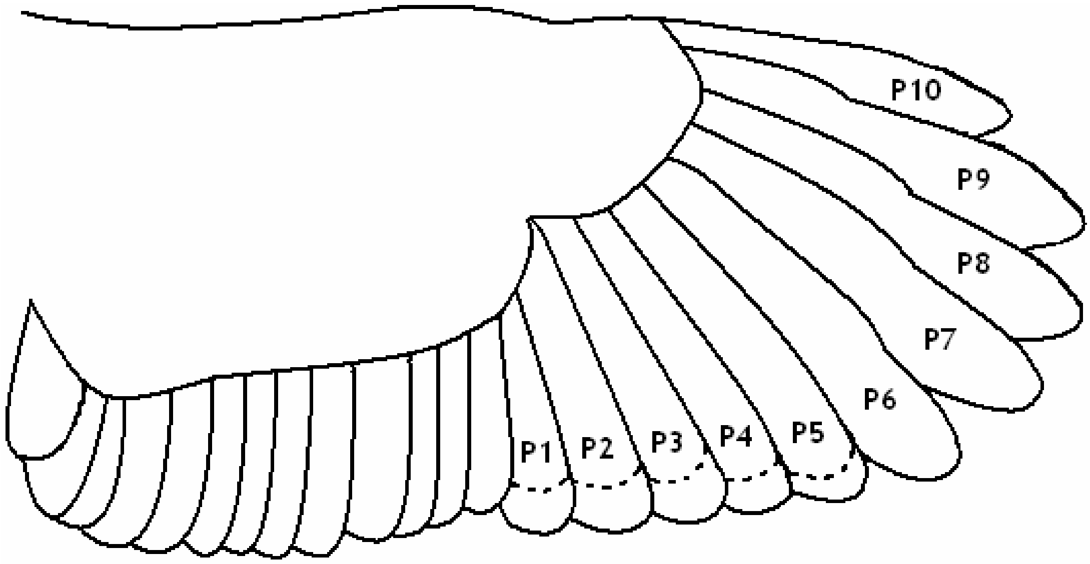

Figure 2.2. Standardized wing illustrating average difference in wingtip morphology between Flammulated (broken boundary) and Northern Saw-whet (continuous boundary) Owls resulting from differences in standardized primary lengths. Flammulated Owl wingtips are narrower proximally, resulting in a wingtip with a high aspect ratio relative to Northern Saw-whet Owls. Secondary feather lengths are not drawn to scale.

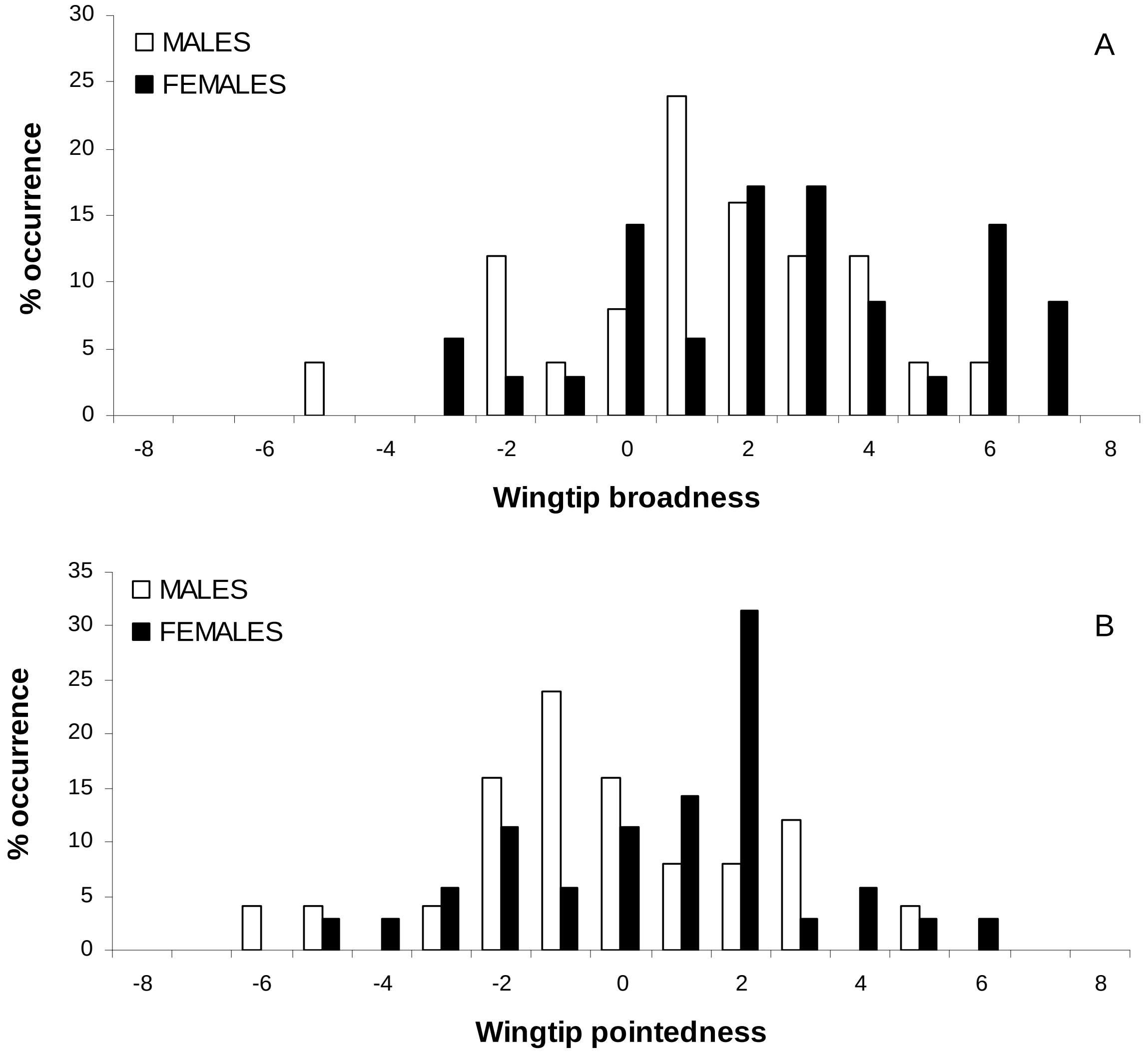

Figure 2.3. Frequency distribution (% occurrence) of male (*n* = 25) and female (*n* = 35) Northern Saw-whet Owls along the first principal component axis representing wingtip broadness (A; see Table 1) and the second principal component axis representing wing pointedness (B; see Table 1). Lower scores along the first axis indicate a narrower, higher-aspect wingtip, and higher scores along this axis indicate a wingtip nearer the leading edge of the wing.