Seasonal Movements of the Short-Eared Owl (Asio flammeus) in Western North America as Revealed by Satellite Telemetry

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SEASONAL MOVEMENTS OF THE SHORT-EARED OWL (*ASIO FLAMMEUS*) IN WESTERN NORTH AMERICA AS REVEALED BY SATELLITE TELEMETRY

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ABSTRACT.—The Short-eared Owl (*Asio flammeus*) is a widespread raptor whose abundance and distribution fluctuates in response to the varying amplitudes of its prey, which are predominately microtines. Previous efforts to describe the seasonal movements of Short-eared Owls have been hindered by few band recoveries and the species' cryptic and irruptive behavior. We attached satellite transmitters to adult Short-eared Owls at breeding areas in western and interior Alaska in June 2009 and July 2010, and tracked their movements for up to 19 mo. Owls initiated long-distance southward movements from Alaska and most followed a corridor east of the Rocky Mountains into the Prairie provinces and Great Plains states. Four owls followed a coastal route west of the Rocky Mountains, including one owl that crossed the Gulf of Alaska. Completed autumn migration distances ranged from 3205–6886 km (mean = 4722 ± 1156 km [SD]). Wintering areas spanned 21° of latitude from central Montana to southern Texas, and 24° of longitude from central California to western Kansas. Subsequent seasonal migrations were generally northward in spring and southward in autumn; these movements were comparatively short-distance (mean = 767.5 ± 517.4 km [SD]) and the owls exhibited low site fidelity. The Short-eared Owls we tracked from two relatively local breeding areas in Alaska used a patchwork of diverse open habitats across a large area of North America, which highlights that effective conservation of this species requires a collaborative, continental-scale focus.

KEY WORDS: *Short-eared Owl*; Asio flammeus; *migration*; *movements*; *satellite telemetry*.

MOVIMIENTOS ESTACIONALES DE *ASIO FLAMMEUS* EN EL OESTE DE AMÉRICA DEL NORTE REVELADOS POR TELEMETRÍA SATELITAL

RESUMEN.—*Asio flammeus* es un ave rapaz de amplia distribución cuya abundancia y distribución fluctúa en respuesta a la variabilidad de sus presas, las cuales son predominantemente roedores microtinos. Los esfuerzos previos para describir los movimientos estacionales de *A. flammeus* se vieron obstaculizados por la recuperación de pocas anillas y por el comportamiento críptico e irruptivo de la especie. Equipamos con transmisores satelitales a individuos adultos de *A. flammeus* en áreas de cría en el oeste y el interior de Alaska en junio del 2009 y julio del 2010, y seguimos sus movimientos hasta 19 meses. Los búhos iniciaron sus movimientos de larga distancia desde Alaska hacia el sur y la mayoría siguió un corredor ubicado al este de las Montañas Rocosas hacia las provincias de las Praderas y los estados de las Grandes Llanuras. Cuatro individuos siguieron una ruta costera al oeste de las Montañas Rocosas, incluyendo un búho que cruzó el Golfo de Alaska. Las distancias completas de la migración de otoño oscilaron entre 3205 y 6886 km

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(promedio = 4722 ± 1156 km [DE]). Las áreas de invernada abarcaron desde los 21° de latitud desde el centro de Montana hasta el sur de Tejas y 24° de longitud desde el centro de California hasta el oeste de Kansas. Las migraciones estacionales posteriores fueron en general hacia el norte en primavera y hacia el sur en otoño; comparativamente, estos movimientos fueron de corta distancia (promedio = 767.5 ± 517.4 km [DE]) y los búhos mostraron una baja fidelidad al sitio. Los individuos de *A. flammeus* seguidos, pertenecientes a dos áreas reproductivas relativamente locales, utilizaron un mosaico diverso de hábitats abiertos a lo largo de una gran área de América del Norte, lo que remarca que la conservación efectiva de esta especie requiere de un enfoque colaborativo a escala continental.

[Traducción del equipo editorial]

Migration involves the movements of animals to exploit peaks of spatially and temporally variable resources and avoid seasonal resource depletion (Alerstam et al. 2003). To carry out these movements, individuals embark on journeys that may span several months and long distances, during which they encounter diverse environmental conditions and risks. Among the numerous migratory behaviors that have been defined (see Newton 2008), here we consider two broad categories: obligate and facultative (Berthold 2001). Obligate migratory behavior is characterized by consistency. Timing, routes, and distances travelled are most often similar each year, and fidelity to sites used during breeding, wintering, and migratory periods is relatively high. Obligate migratory behavior is considered to be adaptive given predictable environmental conditions and resources. Examples of obligate migratory species include both short- and long-distance, complete seasonal migrants (Berthold 2001, Newton 2008).

In contrast, facultative migratory behavior is distinguished by irregularity. Populations may remain near breeding areas for the entire nonbreeding season or until they are forced to depart by severe weather or a scarcity of food. Others may initiate migration, but their movements to wintering areas are in direct response to prevailing weather and resource conditions. Facultative migratory behavior is adaptive when spatial and temporal variability of resources is high. Examples of facultative migration include partial, irruptive, and nomadic migrants (Newton 2012).

One species that exhibits facultative migratory behavior is the Short-eared Owl (*Asio flammeus*), a widespread raptor whose abundance and distribution fluctuates in response to the varying amplitudes of its prey, which are predominately microtines (Clark 1975, Holt 1993). For example, Short-eared Owls breeding in Finland increased from 0 to 49 pairs in a 47-km^2 study area during a 5-yr period, in response to

a 44-fold increase in the spring density of *Microtus* voles (Korpimäki and Norrdahl 1991). Individuals breeding at northern latitudes are thought to be highly migratory because winter snow cover limits access to prey (Clark 1975, Sonerud 1986). In contrast, individuals breeding at temperate latitudes may maintain year-round territories (Mikkola 1983).

Previous attempts to evaluate Short-eared Owl migration ecology have been hindered by scarce band recoveries, which may reflect low fidelity to breeding and nonbreeding areas. Of the 3200 owls banded in North America since 1922, only 15 (<1%) were recovered >100 km from where they were banded (U.S. Geological Survey 2014). Consequently, the migratory routes, timing, and behavior of the Short-eared Owl are largely unknown (Wiggins et al. 2006). There is a pressing need to better understand this species' biology: multiple lines of evidence (e.g., Breeding Bird Surveys, Christmas Bird Counts, and conservation assessments) suggest that North America's population of Short-eared Owls has undergone a long-term, range-wide decline since at least 1966 (Holt 1986, Wiggins et al. 2006, Booms et al. 2014).

In this study, we used satellite transmitters to track adult Short-eared Owls as they moved from two summering areas in Alaska. Our objective was to investigate general migratory behavior, including migration routes, stopover and wintering areas, habitat use, timing and rate of migration, and the influence of wind on migration activity.

METHODS

We deployed Argos satellite transmitters (PTTs) at two locations with high densities of Short-eared Owls. In 2009, we worked in northwestern Alaska on Seward Peninsula near Nome (64°30.0′N, 164°30.0′W). In 2010, we worked in interior Alaska at the Minto Flats State Game Refuge (64°54.0′N, 149°0.0′W) and in the Mosquito and West Fork

drainages of the Fortymile River (63°48.0′N, 142°54.0′W).

During 4–24 June 2009, we captured 14 adults using roadside bal-chatri traps baited with live mice (*Mus domesticus*; Bloom et al. 2007) or mist nets placed over incubating females (Leasure and Holt 1991). During 12–16 July 2010, we captured 12 adults using a net-gun deployed from a helicopter as described in Booms et al. (2010).

We used 12-g solar-powered PTTs (Microwave Telemetry, Columbia, MD U.S.A.) glued atop a 2-mm-thick 5 × 7 cm neoprene (2009) or closed-cell foam (2010) pad to keep the feathers from obscuring solar cells. We deployed PTTs using a backpack-style harness made of 4-mm-wide Teflon-coated nylon ribbon (Bally Ribbon Mills, Bally, PA U.S.A.) and fitted each bird following Steenhof et al. (2006). The mass of the transmitter compared to an

individual owl's body mass averaged 3.0% (range = 2.5–3.4%) for 2009 and 3.4% (range = 3.1–3.6%) for 2010 (Table 1). Molecular sexing indicated that all owls tagged on Seward Peninsula were females and 10 of 12 owls tagged at interior sites were males.

Data Collection and Filtering. PTTs were programmed to transmit for 10 hr and turn off for a 40-hr recharging period. Standard and auxiliary location classes (LC) were derived by the Argos System (www.argos-system.org) and disseminated by CLS America (www.clsamerica.com). We used a systematic hybrid filtering algorithm to remove implausible Argos locations (Douglas et al. 2012). Filtering criteria considered location quality class, distance moved, movement rate, and turning angle. Locations were retained if their LC was 1, 2, or 3. Auxiliary locations (LCs 0, A, B, and Z) within 5 km of a preceding or subsequent location were retained

Table 1. Capture and tracking information for 26 Short-eared Owls outfitted with satellite transmitters on Seward Peninsula and in interior Alaska in 2009 and 2010.

Sex[a]	Mass (g)	Capture Location	Tracking Dates	Tracking Period (d)	Cumulative Travel Distance (km)	Filtered Argos Locations (n)	Fate
Female	383	Nome	24 Jun 2009–18 Nov 2009	147	7759	51	PTT failure
Female	396	Nome	23 Jun 2009–15 Feb 2011	602	7348	148	PTT failure
Female	417	Nome	20 Jun 2009–14 Oct 2009	116	627	48	PTT failure
Female	362	Nome	22 Jun 2009–10 Oct 2009	110	409	45	Probable mortality
Female	402	Nome	20 Jun 2009–30 Oct 2009	132	3148	46	Probable mortality
Female	412	Nome	23 Jun 2009–14 Dec 2010	539	5452	191	PTT failure
Female	370	Nome	16 Jun 2009–9 Dec 2009	177	7462	66	Probable mortality
Female	420	Nome	16 Jun 2009–25 Oct 2009	131	4067	56	Probable mortality
Female	390	Nome	15 Jun 2009–02 Nov 2009	140	1726	47	Probable mortality
Female	486	Nome	4 Jun 2009–27 May 2010	357	7920	124	Probable mortality
Female	397	Nome	19 Jun 2009–11 Oct 2009	114	3467	49	Confirmed mortality
Female	414	Nome	20 Jun 2009–7 Oct 2009	109	1750	46	Probable mortality
Female	392	Nome	19 Jun 2009–11 Dec 2009	175	6553	45	Probable mortality
Female	406	Nome	19 Jun 2009–9 Nov 2009	143	3626	57	Probable mortality
Female	350	Interior	12 Jul 2010–6 Oct 2010	86	97	31	PTT failure
Male	360	Interior	13 Jul 2010–26 Jan 2011	197	4672	32	Confirmed mortality
Male	330	Interior	13 Jul 2010–4 Aug 2010	22	382	8	Probable mortality
Male	360	Interior	13 Jul 2010–12 Oct 2011	456	7023	132	PTT failure
Male	365	Interior	14 Jul 2010–25 Mar 2011	254	3793	89	Probable mortality
Male	350	Interior	15 Jul 2010–10 Sept 2010	57	2789	23	Probable mortality
Male	340	Interior	15 Jul 2010–17 Dec 2010	155	2484	31	Confirmed mortality
Male	330	Interior	15 Jul 2010–28 Sept 2010	75	34	32	Probable mortality
Female	340	Interior	15 Jul 2010–15 Dec 2010	154	6013	36	Probable mortality
Male	345	Interior	16 Jul 2010–8 Nov 2010	115	1816	25	Confirmed mortality
Male	335	Interior	16 Jul 2010–20 Nov 2010	127	3180	28	Probable mortality
Male	380	Interior	16 Jul 2010–25 Aug 2010	40	18	17	Probable mortality

[a] Molecularly determined.

by virtue of spatial redundancy, and remaining auxiliary locations were included only if resultant movement rates were <80 km/hr and the internal angles (α, in degrees) formed by preceding and subsequent vectors (of lengths d1 and d2 km) were not suspiciously acute ($\alpha > -25 + \beta \times \ln[\text{minimum}$ (d1,d2)], where $\beta = 15$). We assigned $\beta = 15$ because it performed well for our specific tracking data during both stationary and migratory periods. PTTs reported a total of 19,709 standard and auxiliary locations; 3757 (19%) of the auxiliary class locations were removed by filtering. We further filtered locations by retaining only the best quality location (highest LC) per duty cycle. This resulted in 1503 total locations (92% standard quality) and 8–191 locations per owl (mean = 57.8 ± 44.0 [SD] locations). Root-mean-square location errors, as estimated by Douglas et al. (2012), were 1.0, 2.5, and 4.3 km for unfiltered LCs 3, 2, and 1, respectively, and 6.3, 4.2, 6.2, and 5.2 km for filtered LCs 0, A, B, and Z, respectively.

PTTs were equipped with sensors that monitored motion, temperature, and battery voltage. We estimated causes of tracking termination following Klaassen et al. (2014). We considered PTT failure likely when the loss of contact was preceded by an extended period of poor transmission performance or low battery voltage. Probable mortality occurred when the PTT transmitted continuously from the same location, the motion sensor stopped incrementing, and the temperature sensor emulated ambient conditions. In any of these circumstances, we retained an owl's last active location. We attempted to recover motionless transmitters to assess an owl's fate and potential cause of mortality as soon as was logistically feasible.

Movement Patterns. We defined four seasonal periods to describe Short-eared Owl movements. Autumn and spring movement periods began when new locations showed that owls were consistently moving away from summer and winter areas, and ended when the owls started making only localized multidirectional movements. Owls tended to be relatively sedentary during summer and winter in between the spring and autumn movement periods. We classified migratory stopovers as periods during spring or autumn when owls temporarily occupied a localized area, which we defined as moving <35 km within 48 hr. Because transmitters were not active every day, we could not always determine the exact dates of departure and arrival. We estimated departure and arrival dates as the midpoint of transmission gaps ≤7 d, but did not estimate departure and arrival dates based on gaps >7 d.

We investigated ground speed (km/hr) by constructing all pairwise vectors with LC 3, 2, or 1 endpoints that spanned 2–10 hr. We examined diurnal movement patterns by assigning the more probable movement vectors (those >5 km/hr) to daytime (0600–1800 H) or nighttime (1800–0600 H) based on the vector's midpoint local time. We report cumulative distance moved based on the subset of filtered locations with the highest quality location for each transmitter duty cycle. We calculated all distances as great-circle-routes (i.e., orthodromes). We calculated local time for a given location by offsetting its Greenwich Mean Time (GMT) by −1 hr for each 15° of west longitude.

We evaluated wind conditions when owls undertook substantive movements and during stopovers. We extracted wind speed and direction at 10 m aboveground from the National Centers for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) daily datasets (Mesinger et al. 2006) with 3-hr periodicity as described in Rutledge et al. (2006). For substantive owl movements, we considered tracking vectors that exceeded 500 km during 50–80 hr (movement between two sequential transmitter duty cycles). We averaged the NARR wind data over the duration of the movement vector, within an area along the flight path buffered laterally to each side by one-quarter of the flight-path length. At stopover sites, we averaged the NARR wind data for the duration of the stopover. Because our diurnal analysis indicated that owls moved primarily at night, we restricted the wind data to the local nocturnal period (i.e., 1800–0600 H). Following Kemp et al. (2012), we calculated a tailwind index (TWI) using the averaged u (east/west) and v (north/south) wind-vector components (m/s), and the compass direction of migration (ω) as indicated by the tracking data:

$$\text{TWI} = \text{sqrt}(u^2 + v^2)$$

$$* \cos\left(\left(\left(\arctan(u,v)*(180/\pi)\right) - \omega\right)\right.$$

$$\left. * \left(\pi/180\right)\right).$$

The tailwind index expresses the amount of the wind vector that is parallel to the direction of the

birds' movement, where positive values represent a favorable tailwind and negative values a headwind.

We evaluated general patterns of habitat use during migratory stopover and seasonal stationary periods by first creating a buffer around each location, with radius equal to the root-mean-square error of the estimated location accuracy of the relevant LC. We extracted general habitat characteristics by overlaying each buffer on the North American Land Change Monitoring System (NALCMS. 2010). We standardized the extracted habitat information using an inverse-area scaling, in which smaller buffers with higher location accuracy were given a higher proportional weight than larger buffers with lower location accuracy. We performed all spatial mapping and analyses in ArcMap 10 (ESRI 2011). Unless otherwise noted, descriptions of movements are based on all birds combined across years and capture locations. Summary statistics are presented as the range followed parenthetically by the mean ± SD.

RESULTS

We tracked owls for all or a portion of the following periods: summer (26 owls), autumn (24 owls), winter (five owls), spring (three owls), second summer (three owls), and second autumn (two owls). Transmissions ceased abruptly soon after deployment for two interior owls.

Autumn Migration. Fourteen owls departed summer ranges on Seward Peninsula during a 47-d period from 8 August to 25 September (mean departure date 3 September ± 12.7 d). Seven interior owls began autumn migration during a 15-d period from 31 July to 15 August (3 August ± 5.9 d). Owls that migrated from interior sites departed an average of 30 d earlier than owls that migrated from Seward Peninsula.

Seven owls dispersed from Seward Peninsula in a predominantly southeasterly direction, and their movements converged within approximately an 85-km-wide zone in interior Alaska that encompassed the Tanana River valley and the primary 2010 interior capture location (Fig. 1A). Four other owls deviated from this pattern (Fig. 1A). One owl flew northeast from Seward Peninsula across the northern Yukon Territory before orienting to the southeast. Three owls veered to the south and crossed the Alaska Range into coastal southcentral Alaska.

Movements of most Seward Peninsula and interior owls ($n = 14$) converged in a 200–400-km-wide zone east of the Rocky Mountains, extending through the Yukon Territory, northeastern British Columbia, Alberta, and southwestern Saskatchewan (Fig. 1A). One interior owl deviated from this corridor and migrated through the Northwest Territories and southern Manitoba. Four Seward Peninsula owls flew mostly west of the Rocky Mountains, including one owl that crossed 850 km of open water over the Gulf of Alaska. An interior owl was relocated in southern British Columbia after a 48-d data gap, which also suggested a southward trajectory west of the Rocky Mountains.

Among 11 owls that crossed the Canadian border into the conterminous United States, nine migrated through Montana and western North Dakota and two migrated through central Washington (Fig. 1A). Seven owls completed their autumn migrations in 61–147 d (85.2 ± 31.8 d) and settled on winter ranges between 22 October and 27 December. The duration of autumn migration averaged more than 1.5 times longer for three interior owls (104 ± 36.9 d) than it did for four Seward Peninsula owls (63 ± 15.1 d). Winter destinations for these seven owls spanned 21° of latitude from central Montana to southern Texas, and 24° of longitude from central California to western Kansas (Fig. 1A).

Completed autumn migrations spanned 3205–6886 km (4722 ± 1156 km) and were on average longer for owls originating on Seward Peninsula (5280 ± 1185.8 km) than for owls originating at interior sites (3979 ± 672.2 km). Other migration tracks terminated prematurely because of owl mortality or transmitter failure. Notably, the transmitters of one owl captured on Seward Peninsula and one owl captured at an interior location both failed when the owls were within 35 km of each other in Zacatecas, Mexico, after the owls had travelled 6008 and 7057 km, respectively (Fig. 1A). A third owl traveled 6553 km from Seward Peninsula to southern Texas before its transmitter failed (Fig. 1A).

Peak movements occurred almost entirely at night between 1800 and 0600 H local time (Fig. 2). Owls migrated at rates of 44.5–340.7 km/d (146.5 ± 101.2 km/d). Estimates of in-flight ground speed reached as high as 40 km/hr (Fig. 2). Substantial movements (≥ 500 km in <3 d) during autumn migration occurred when the wind speed and direction along the flight corridor were slightly favorable (i.e., a light tailwind) or neutral (Fig. 3), but long-distance movements did not necessarily appear dependent
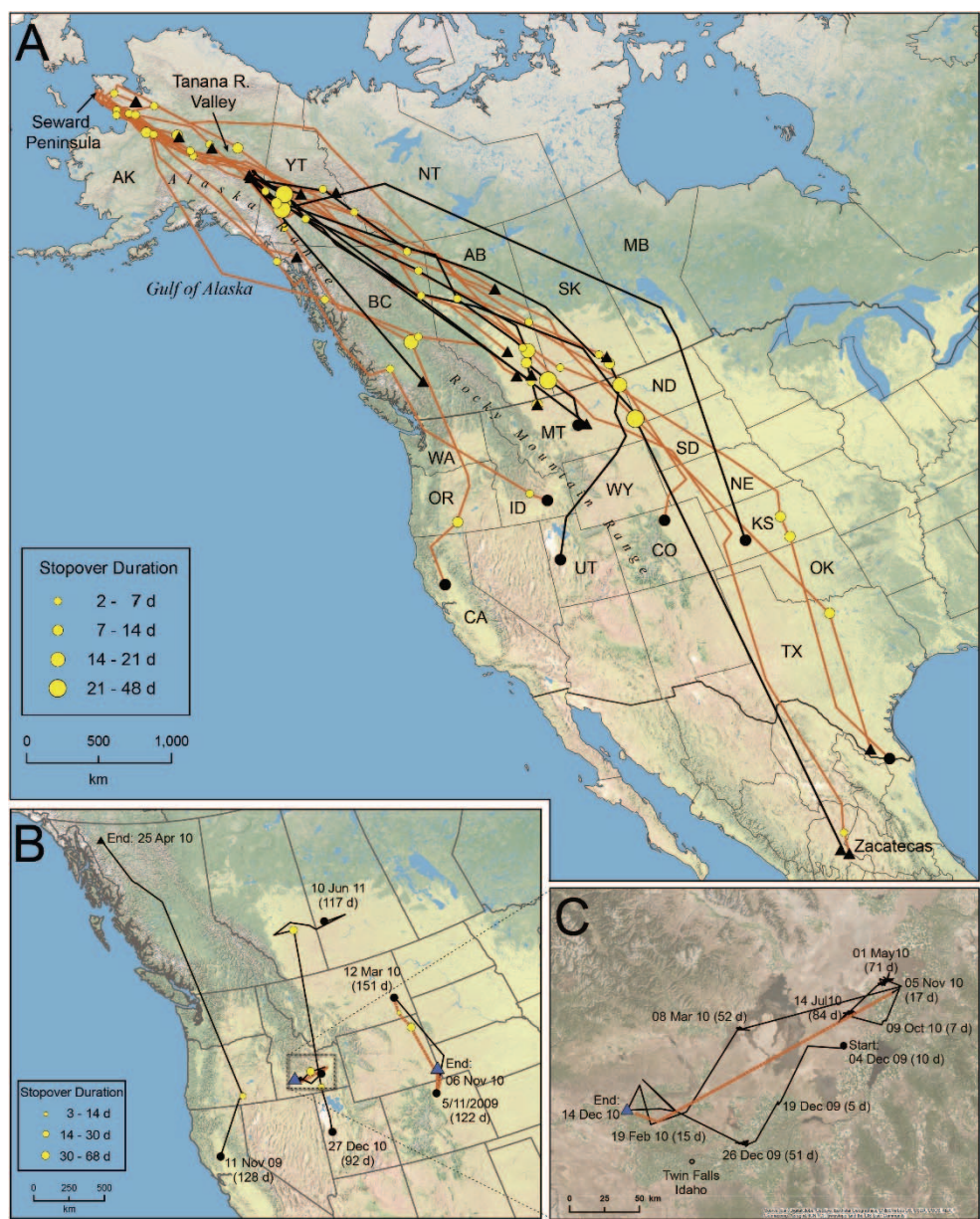
Figure 1.   (A) Autumn movements of 14 Short-eared Owls captured on Seward Peninsula (orange lines) and 12 owls captured at two sites in interior (black lines) Alaska. Yellow dots denote location and duration of stopovers. Triangles denote last known location of partial migratory tracks, and dots denote locations where owls completed migration. (B) Seasonal movements of four Short-eared Owls following first documented winter period. Black and orange lines delineate spring and autumn migration routes, respectively. Other symbols are as for (A). (C) Movements of one owl that remained in southern Idaho for a full year after migrating south from Alaska. For all maps, orthodromes are depicted as straight lines in this gnomonic map projection.
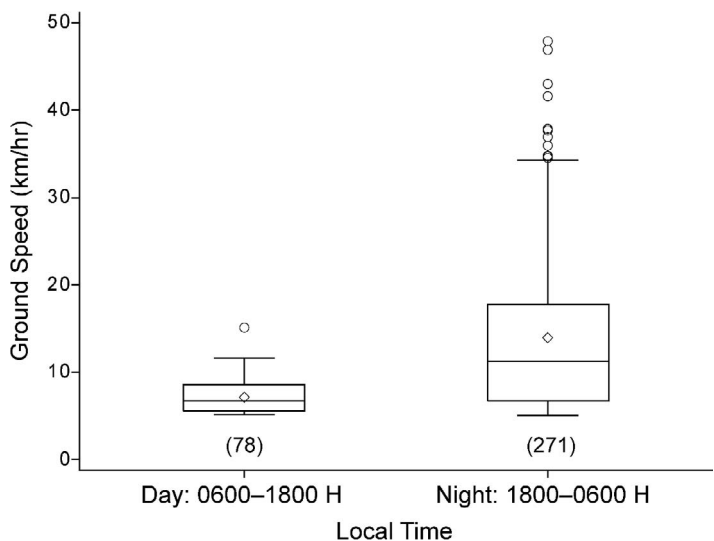
Figure 2. Tracking speeds of Short-eared Owls during local daytime and nighttime hours. More and faster movements occurred at night. To represent movements of flying owls, samples (in parentheses) were limited to vectors of 2–10 hr duration that were bounded by standard quality Argos locations (LC 3, 2, or 1) and represented ground speeds >5 km/hr. The upper range of tracking speeds (35–45 km/hr) represents conservative (straight line) maximum estimates of sustained (2–10 hr) movement rates over the landscape. Boxes span the interquartile range (IQR), whiskers extend to 1.5 times the IQR, means are denoted with diamonds, and medians with horizontal lines.
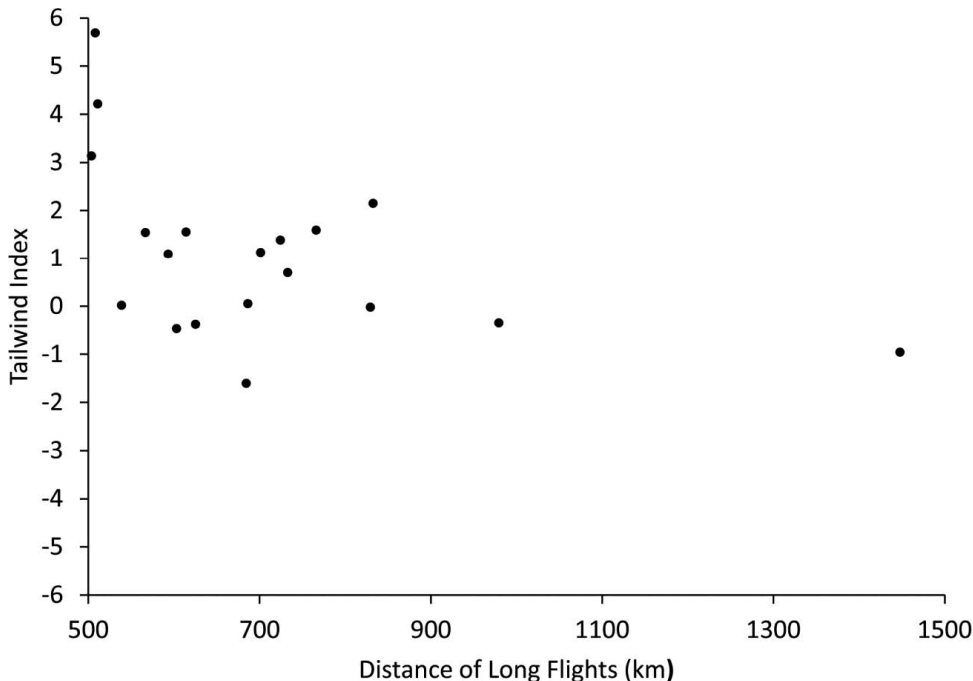

Figure 3. Long-distance movements (50–80 hr and >500 km) of Short-eared Owls in relation to wind conditions. Positive values represent tailwinds and negative values represent headwinds.

on tailwinds. Notably, however, the owl that crossed the Gulf of Alaska followed a trough of low pressure that generally provided favorable tailwinds throughout most of the >800-km overwater flight (Fig. 4).

All seven owls that completed autumn migration made one or more stops along their southbound routes (4.1 ± 1.3 stops per owl; Fig. 1A). Length of stay ranged from 2–48 d (11.7 ± 14.8 d) and the combined duration of autumn stopovers ranged from 18–75 d (47.3 ± 19.1 d). Stopovers accounted for 29–58% (46.9 ± 10.9%) of the total migration periods for individual owls. The total duration of stopovers was >1.5 times longer for interior owls (61 ± 17.8 d, $n=3$) than for Seward Peninsula owls (37.0 ± 13.9 d, $n=4$). Excluding stopovers, interior owls took slightly longer to complete their autumn migrations (43.3 d ± 28 d) than Seward Peninsula owls (34.2 ± 14.3 d). Shorter stopovers often

A. 18 October 2009 0900 H
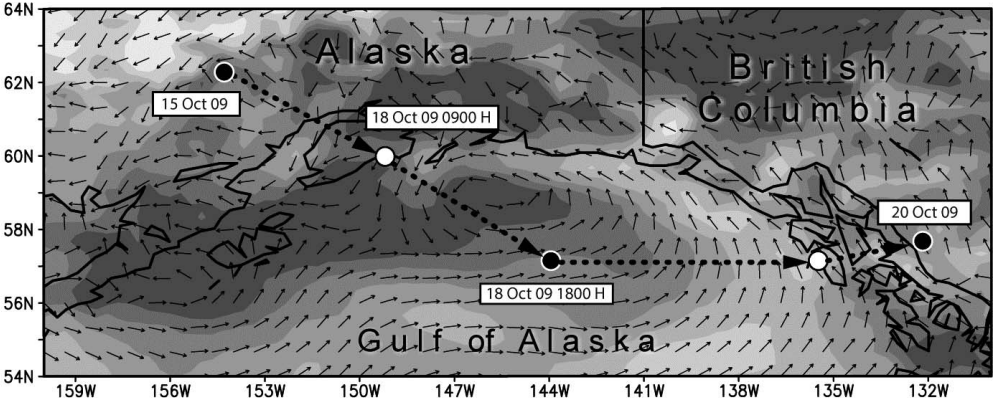
B. 19 October 2009 0300 H

Wind Speed

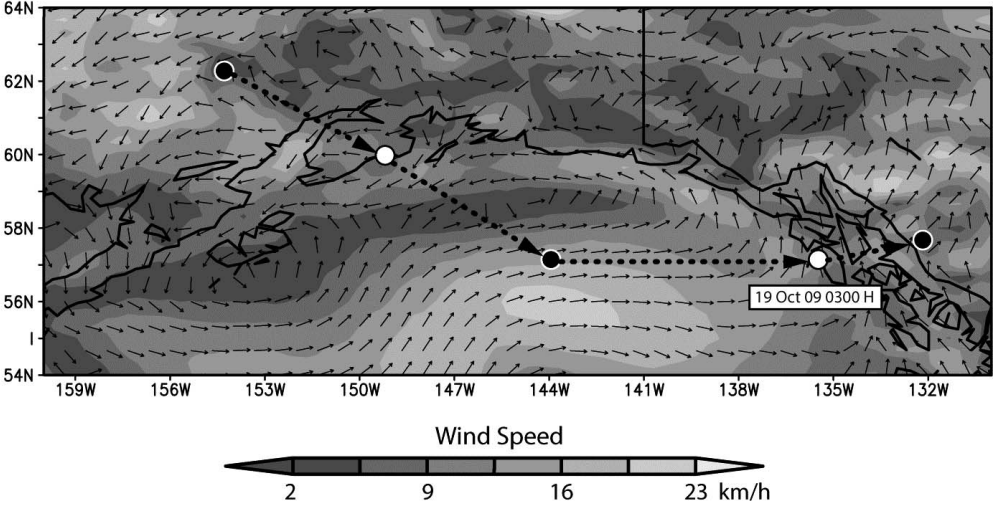2   9   16   23 km/h

Figure 4. Near-surface (1000 millibar) wind conditions (National Oceanographic and Atmospheric Administration 2016) during the flight of a Short-eared Owl over the Gulf of Alaska. Black dots are Argos satellite tracking locations and white dots are estimated locations for the beginning and end of the open-water crossing. (A) Beginning wind conditions when the owl encountered a low pressure system in the northern Gulf of Alaska and appeared to follow tailwinds around the southern side of the low. (B) Ending wind conditions showing a trough of easterly tailwinds that prevailed as the owl completed the second half of the crossing.

coincided with the occurrence of headwinds, whereas the average tailwind index was neutral during long stopovers (>14 d; Fig. 5).

Owls occupied primarily open habitats during stopovers, including grasslands and shrublands (64 ± 19.8% of the area occupied by individual owls), and croplands (21 ± 21.3%), but they also occupied stopover areas that contained forest habitat (15 ± 11.5%).

Winter. We tracked four owls during a complete winter period, ranging in length from 92–162 d (134 ± 31.3 d). Three owls that originated on Seward Peninsula wintered in central California, southern Idaho, and northern Colorado, and one interior owl wintered in western Utah (Fig. 1B). We tracked a fifth owl, which travelled from interior Alaska to central Montana, for only a portion of the winter season. Four owls were relatively sedentary during winter, remaining within a <20-km radius, whereas one owl moved among several sites within a 100-km radius.

Owls wintered in a variety of open habitats. Three owls in southern Idaho, central Montana, and northern Colorado occupied a mixture of natural and introduced grasslands (52 ± 16.3% of occupied area), croplands (43 ± 17.7%), and natural shrublands (5 ± 1.3%). Two other owls occupied almost

exclusively croplands in the Central Valley of California (99% of occupied area) and shrublands in southern Utah (98% of occupied area).

Spring Migration. Three owls initiated spring migration between 30 March and 30 April (12 April ± 15.9 d), traveled 115–1375 km (743 ± 630.1 km) from their wintering areas, and settled on summer ranges in southern Idaho, eastern Montana, and southern Alberta (Fig. 1B). The fourth owl departed on 20 March and traveled 2461 km from central California to northern British Columbia paralleling its southward migration route, at which point its transmitter failed (Fig. 1B).

The owl that traveled between western Utah and southern Alberta made one 15-d stop in southern Idaho, during which time it occupied croplands (54% of occupied area), natural shrublands (23%), and natural grasslands (23%).

Summer. We tracked three owls throughout a second summer. A female that wintered in western Utah arrived in eastern Montana on 10 April and remained there for 121 d. A female that wintered in southern Idaho moved to a nearby summering area in southeastern Idaho on 1 May and remained there for 161 d (Fig. 1C). The timing, length of stay, and movement patterns of these two females suggested
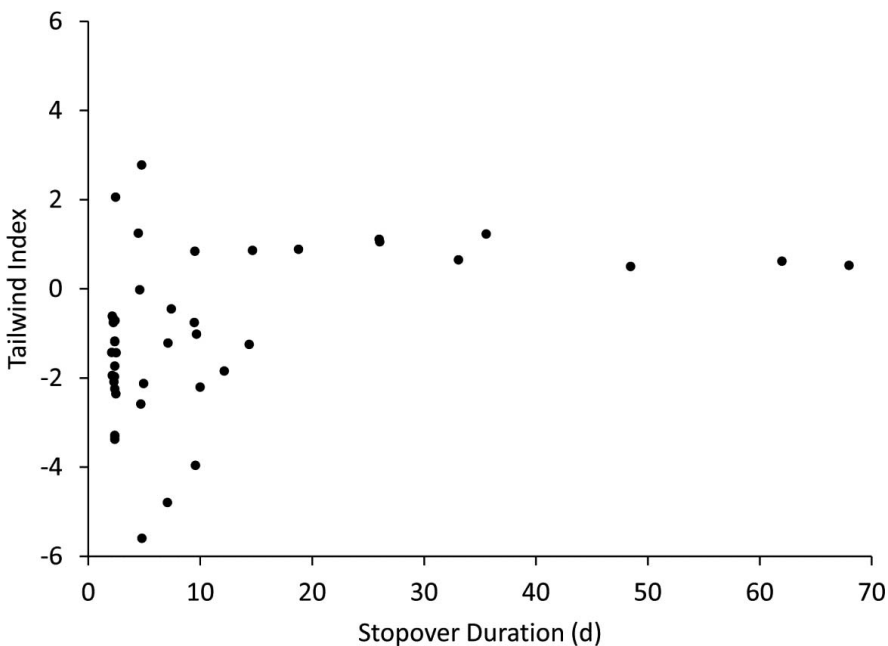

Figure 5. Migratory stopover duration of Short-eared Owls in relation to wind conditions. Positive values represent tailwinds and negative values represent headwinds.

that they may have nested. In contrast, a male that wintered in western Utah arrived in southeastern Alberta on 30 April, and spent the summer moving among several locations in southeastern Alberta and southwestern Saskatchewan (Fig. 1B).

The two females occupied predominantly natural habitats in summer: natural grasslands (83%) and croplands (17%) in eastern Montana, and a mosaic of natural shrublands (86%), natural grasslands (10%), and cultivated croplands (4%) in southern Idaho. In contrast, the male in Alberta occupied primarily croplands (86%) and less often natural grasslands (14%).

Second Autumn Migration. On 9 October, the female in southern Idaho began a series of short movements in the vicinity of her summer range, and she was last located on 14 December in her previous wintering area (Fig. 1C). The female in eastern Montana departed her summer range on 9 August, spent 83 d migrating south to her previous winter location in northern Colorado, and then moved 175 km north into southeastern Wyoming, where she remained until her transmitter failed on 15 February. She made one stop for 68 d in grassland (92% of occupied area) and shrubland (8%) habitats in northeastern Wyoming. The southern Alberta/Saskatchewan male was still on his summer range when transmitter failure occurred on 12 October (Fig. 1B).

Fate of PTTs and Owls. Sensor data and PTT recoveries indicated that 20 of 26 owls probably (13 owls) or definitely (seven owls) died during the study. Two owls died near capture sites before migrating south, 13 died during the first autumn migration, three during winter, one in spring, and one during the second autumn migration. The total travel distance and duration from deployment locations to the locations of probable or confirmed mortalities averaged 2591 ± 1729 km and 125 ± 50 d.

We found owl remains at six of seven sites where we recovered PTTs. At the seventh site, we found only a chewed harness. Evidence at recovery locations, such as plucked feathers, bones with attached tendons stripped of meat, and proximity of perches, suggested that raptor predation was the likely cause of death for four owls; however, we could not rule out post-mortality scavenging. Sensor data suggested that six PTTs were on live owls when the batteries failed, four during the first autumn migration period and two during the subsequent winter.

DISCUSSION

Adult Short-eared Owls initiated long-distance southward migrations from high-latitude summer areas in Alaska. Subsequent migrations between mid-latitude winter and summer ranges were typically northward in spring and southward in autumn, but were comparatively short-distance. Two owls did not migrate at all from their mid-latitude summer areas during the second autumn. This variety of movement strategies is typical among facultative (including irruptive and partial) migrants. Presumably, long-distance movements from Alaska allowed owls to avoid snow cover that inhibits access to prey (Baker and Brooks 1981, Sonerud 1986), while subsequent movements were a flexible response to prevailing environmental conditions (Newton 2012).

The tracked owls wintered across a large area of the western U.S.A., and we detected no apparent differences in the wintering areas used by birds from the two capture areas. Owls from interior Alaska often used areas that were close to those used the previous year by owls from Seward Peninsula. None of the tracked owls moved east of 95°W longitude, suggesting owls that summer in Alaska tend to remain in the Central and Pacific flyways. This pattern is also evident in limited band recovery data (U.S. Geological Survey 2014). Short-eared Owls banded in the Pacific and Atlantic flyways were always recovered in the same flyway, whereas owls banded in the Central and Mississippi flyways were usually recovered within the same flyway, but also rarely in neighboring flyways. Furthermore, movement data from a few Short-eared Owls tracked with PTTs in southern Alberta (G. Holroyd and H. Trefry pers. comm.) and from larger samples of owls tracked in eastern Ontario (D. Badzinski pers. comm.) and southern New York (New York State Department of Environmental Conservation pers. comm.) provided little evidence of movements between flyways, and no marked birds from eastern North America moved west of the Mississippi River. Overall, results from telemetry and banding studies suggest a migratory divide in breeding origins of Short-eared Owls wintering west and east of the Mississippi River.

The Short-eared Owls we tracked exhibited no fidelity to summer ranges. None of the four owls that completed spring migration returned to Alaska; however, one owl's incomplete spring migration suggested a possible attempt to return to Alaska.

Although our findings are limited by a small sample size, limited tracking durations, and potential adverse effects of PTTs, they are generally consistent with the findings of other studies. Of 23 adult female Short-eared Owls banded during the breeding season in Montana between 1987–1993, none were recaptured there in a subsequent summer (Wiggins et al. 2006). Another microtine specialist, the Snowy Owl (*Bubo scandiacus*), also exhibits low fidelity to breeding areas. Adult female Snowy Owls tracked with PTTs did not return to breeding areas where they were captured (Fuller et al. 2003, Therrien et al. 2012).

Rodent specialists like the Short-eared Owl might have low fidelity to breeding areas because rodent populations fluctuate asynchronously across large landscapes (Kalela 1962, Pitelka and Batzli 2007). The species' mobility, behavioral flexibility, and ability to locate abundant prey would facilitate high reproductive outputs under optimal conditions; Short-eared Owl clutch sizes can reach 11 eggs during peak vole cycles (Korpimäki 1984, Wiggins et al. 2006). Furthermore, although Short-eared Owls were unusually abundant on Seward Peninsula in 2009, owl density was dramatically lower during 2010–2015 (J. Johnson unpubl. data). The irruptive numeric response of Short-eared Owls is often synchronous with microtine population increases (Korpimäki and Norrdahl 1991) and return rates are lower when vole numbers crash than they are when vole numbers are increasing (Village 1987). This evidence leads us to speculate that the low owl numbers recently observed on Seward Peninsula reflected low prey densities.

Among the Short-eared Owls in this study, the only evidence of interannual site fidelity was two females that temporarily returned to their previous wintering locations in Idaho and Colorado. Similarly, some adult Short-eared Owls tracked with PTTs in New York and eastern Ontario returned to within 25 km of their original winter capture location (D. Badsinski pers. comm., New York State Department of Environmental Conservation pers. comm.). Adult female Snowy Owls also appear to show relatively high fidelity to winter ranges; in one study, 19 of 122 (17%) females (but no males) returned in a following winter (Holt et al. 2015). How differing prey populations influence regional variation in movements and range fidelity, and the relative levels of winter and summer range fidelity, warrant further study.

Although completed autumn migrations from sites in interior Alaska averaged 1200 km shorter than those from Seward Peninsula, interior owls took longer to complete their autumn migrations, primarily because of longer duration stopovers. All owls used multiple stopover areas, sometimes for extended periods. Similar to other facultative migrants (Newton 2012), these stopover periods were likely associated with replenishing reserves and pausing during unfavorable weather. Our results showed that stopovers <14 d often coincided with moderate headwinds. In contrast, the average wind conditions during longer stopovers were generally favorable, suggesting that long stopovers were associated with resting and refueling, or perhaps other activities such as opportunistic range exploration.

Some owls remained sedentary during winter while other owls moved across large areas, underscoring that Short-eared Owls are opportunistic. If adequate numbers of prey are present throughout the winter, owls may adopt a sedentary winter strategy. Conversely, if prey availability is low or drops, because of either low abundance or deep snow reducing accessibility, owls may adopt a nomadic strategy of searching large areas for more suitable conditions. More information on prey abundance, foraging behavior, and energetic requirements is needed to understand how changes in environmental conditions influence facultative behaviors like nomadism.

Potential Mortality/Transmitter Effects. Placing a transmitter on a bird affects it in some, usually unknown, manner ranging from short-term behavioral modifications to potentially long-term physical effects, including death (Reynolds et al. 2004, Steenhof et al. 2006, Barron et al. 2010). Attributes of Short-eared Owls that may make them sensitive to transmitters include light wing-loading and an aspect ratio maximized for slow buoyant flight, forward thrust just above stalling speed, and aerial agility (D. Holt pers. comm.). We observed no obvious direct negative effects of transmitters on owls encountered during a 7–23 d post-deployment period on Seward Peninsula. Three of the owls were nesting females that continued to incubate eggs or brood young. Furthermore, the chronology and movement patterns of two females suggested that they successfully nested during the second summer tracking period.

Most (92%) owls survived the initial summer period, but then the mortality rate increased

substantially during autumn migration. Our results are consistent with other studies that have documented higher mortality rates for raptors during migration than during stationary periods. The mortality rate for adult Ospreys (*Pandion haliaetus*), Marsh Harriers (*Circus aeruginosus*), and Montagu's Harriers (*Circus pygargus*) was six times higher during migratory periods than during stationary periods (Klaassen et al. 2014). Reduced apparent survival of Burrowing Owls (*Athene cunicularia*) was related to an increased number of storms during autumn and spring migration (Wellicome et al. 2014).

We acknowledge that PTTs could have contributed to higher mortality by reducing the owls' maneuverability and increasing their susceptibility to predation or accidents. Nevertheless, raptor predation was suspected as the cause of death for most recovered owls and, although the natural predation rates are unknown, several raptor species are known to prey on Short-eared Owls in North America, including Rough-legged Hawks (*Buteo lagopus*; Bechard and Swem 2002), Gyrfalcons (*Falco rusticolis*; Booms et al. 2008), Peregrine Falcons (*Falco peregrinus*; Sooter 1942), Snowy Owls (Murie 1929, Levin et al. 1977), and Great Horned Owls (*Bubo virginianus*; Killpack 1951). Short-eared Owl remains are regularly observed in raptor nests in western Alaska, and with increasing frequency in years of high owl abundance (T. Booms unpubl. data). On one occasion, remains of eight Short-eared Owls were found in a single Peregrine Falcon nest in northern Alaska (T. Swem pers. comm.). The morphologically and behaviorally similar Long-eared Owl (*Asio otus*) is the most frequent victim of raptor predation among European owls (Mikkola 1976, Marks et al. 1994).

Booms et al. (2014) listed raptor predation as a likely secondary threat facing Short-eared Owls in North America. Populations of some open-landscape or edge-associated species of potential predators (e.g., Peregrine Falcon and Red-tailed Hawk [*Buteo jamaicensis*]) have increased concurrent with a decline in Short-eared Owls (Sauer et al. 2012). Thus, although we cannot rule out PTTs having exacerbated the risk, the evidence gathered during this study and previously by others is consistent with raptor predation being an important source of mortality for Short-eared Owls that probably contributed to the high mortality observed during this study.

Management Implications. Multiple lines of evidence indicate a long-term, range-wide decline in the abundance of Short-eared Owls in North America since at least 1966 (Holt 1986, Wiggins et al. 2006, Sauer et al. 2012). Loss of native grasslands and shrublands is believed to be one of the primary causes of the decline (Wiggins et al. 2006, Booms et al. 2014). This and other studies demonstrate that Short-eared Owls are capable of exploiting a wide range of open habitats, including croplands, grasslands, and shrublands (Wiggins et al. 2006). Assessing the comparative value of different habitat types for Short-eared Owls during different parts of their annual cycle is an important area for future research. Additionally, although brief tracking periods and few multiyear samples limited relevant insight, the owls we tracked demonstrated little interannual range fidelity. Hence, the available information suggests that Short-eared Owls occupy areas across larger spatiotemporal scales than we typically consider when assessing a species' dependence on a particular parcel of land. The Short-eared Owls we tracked used a patchwork of diverse open habitats across a large area of western North America, which demonstrates that effective conservation of this species requires a continental perspective (Booms et al. 2014). Furthermore, our study highlights that areas used intermittently among years by Short-eared Owls should not necessarily be classified by managers as of low importance.

Although the causes of mortality in this study were not readily apparent, the high number of owl deaths during autumn migration suggests that the stresses of long-distance migration may play a major role in determining Short-eared Owl demography. A better understanding of seasonal and overall survival rates, and the factors influencing them, is an important missing component to conserving Short-eared Owl populations. Further, we interpret the timing and location of mortalities to suggest that conservation measures may be most needed at latitudes south of Alaska where the majority of mortalities occurred.

Literature Cited

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long distance migration: evolution and determinants. *Oikos* 103:247–260.

Baker, J.A. and R.J. Brooks. 1981. Raptor and vole populations at an airport. *Journal of Wildlife Management* 45:390–396.

Barron, D.G., J.D. Brawn, and P.J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behavior and ecology. *Methods in Ecology and Evolution* 1:180–187.

Bechard, M.J. and T.R. Swem. 2002. Rough-legged Hawk (*Buteo lagopus*). *In* P.G. Rodewald [Ed.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NY U.S.A. https://birdsna.org/Species-Account/bna/species/rolhaw (last accessed 22 September 2016).

Berthold, P. 2001. Bird migration: a general survey. Oxford University Press, Oxford, U.K.

Bloom, P.H., J.A. Smallwood, L.S. Young, and M.N. Kochert. 2007. Capture techniques. Pages 193–219 *in* D.M. Bird and K.L. Bildstein [Eds.], Raptor research and management techniques. Hancock House Publishers Ltd., Surrey, BC Canada.

Booms, T.L., T.J. Cade, and N.J. Clum. 2008. Gyrfalcon (*Falco rusticolus*). *In* P.G. Rodewald [Ed.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NY U.S.A. https://birdsna.org/Species-Account/bna/species/gyrfal (last accessed 22 September 2016).

———, G.L. Holroyd, M.A. Gahbauer, H.E. Trefry, D.A. Wiggins, D.W. Holt, J.A. Johnson, S.B. Lewis, M. Larson, K. Keyes, and S. Swengel. 2014. Assessing the status and conservation priorities of the Short-eared Owl in North America. *Journal of Wildlife Management* 78:772–778.

———, J.S. Whitman, and C.L. Gardner. 2010. Utility of helicopters for Short-eared Owl nest searches and surveys. *Journal of Raptor Research* 44:247–248.

Clark, R.J. 1975. A field study of the Short-eared Owl, *Asio flammeus* (Pontoppidan), in North America. *Wildlife Monographs* 47:1–67.

Douglas, D.C., R. Weinzierl, S.C. Davidson, R. Kays, M. Wikelski, and G. Bohrer. 2012. Moderating Argos location errors in animal tracking data. *Methods in Ecology and Evolution* 3:999–1007.

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute. Redlands, CA U.S.A.

Fuller, M., D. Holt, and L. Schueck. 2003. Snowy Owl movements: variation on the migration theme. Pages 359–366 *in* P. Berthold, E. Gwinner, and E. Sonnenschein [Eds.], Avian migration. Springer Berlin Heidelberg, Germany.

Holt, D.W. 1986. Status report: the Short-eared Owl in the northeast. *Eyas* 9:3–5.

———. 1993. Breeding season diet of Short-eared Owls from Massachusetts. *Wilson Bulletin* 105:490–496.

———, M.D. Larson N. Smith, D.L. Evans, and D.F. Parmalee. 2015. Snowy Owl (*Bubo scandiacus*). *In* P.G. Rodewald [Ed.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NY U.S.A. https://birdsna.org/Species-Account/bna/species/snoowl1 (last accessed 11 January 2017).

Kalela, O. 1962. On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. *Annales Academiae Scientiarum Fennicae Series Biologica* 66:1–38.

Kemp, M.U., E.E. van Loon, J. Shamoun-Baranes, and W. Bouten. 2012. RNCEP: global weather and climate data at your fingertips. *Methods in Ecology and Evolution* 3:65–70.

Killpack, M.L. 1951. Short-eared Owl eaten by horned owl. *Condor* 53:262.

Klaassen, R.H.G., M. Hake, R. Strandberg, B.J. Koks, C. Trierweiler, K.M. Exo, F. Barlein, and T. Alerstam. 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology* 83:176–184.

Korpimäki, E. 1984. Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland. *Annales Zoologici Fennici* 21:287–293.

——— and K. Norrdahl. 1991. Numerical and functional responses of kestrels, Short-eared Owls, and Long-eared Owls to vole densities. *Ecology* 72:814–826.

Leasure, S.M. and D.W. Holt. 1991. Techniques for locating and capturing nesting female Short-eared Owls (*Asio flammeus*). *North American Bird Bander* 16:32–33.

Levin, S.A., J.E. Levin, and R.T. Paine. 1977. Snowy Owl predation on Short-eared Owls. *Condor* 79:395.

Marks, J.S., D.L. Evans, and D.W. Holt. 1994. Long-eared Owl (*Asio otus*). *In* P.G. Rodewald [Ed.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NY U.S.A. https://birdsna.org/Species-Account/bna/species/loeowl (last accessed 22 September 2016).

Mesinger, F.G. DiMego, E. Kalnay, K. Mitchell, P.C. Shafran, W. Ebisuzaki, D. Jović, J. Woollen, E. Rogers, E.H. Berbery, M.B. Ek, Y. Fan, R. Grumbine, W. Higgins, H. Li, Y. Lin, G. Manikin, D. Parrish, and W. Shi. 2006. North American regional reanalysis. *Bulletin American Meteorological Society* 87:343–360.

Mikkola, H. 1976. Owls killing and killed by other owls and raptors in Europe. *British Birds* 69:144–154.

———. 1983. The owls of Europe. Buteo Books, Vermillion, SD U.S.A.

MURIE, O.J. 1929. Nesting of the Snowy Owl. *Condor* 31:3–12.

NATIONAL OCEANOGRAPHIC AND ATMOSPHERIC ADMINISTRATION. 2016. Monthly/seasonal maps and composites: NCEP/NCAR reanalysis and other datasets. NOAA, Washington, DC U.S.A. http://www.esrl.noaa.gov/psd/cgi-bin/data/composites/printpage.pl (last accessed 22 September 2016).

NORTH AMERICAN LAND CHANGE MONITORING SYSTEM. 2010. Land cover, 2010. Commission for Environmental Cooperation, Montreal, QC Canada. http://www.cec.org/tools-and-resources/map-files/land-cover-2010 (last accessed 22 September 2016).

NEWTON, I. 2008. The migration ecology of birds. Elsevier, London, U.K.

———. 2012. Obligate and facultative migration in birds: ecological aspects. *Journal of Ornithology* 153:171–180.

PITELKA, F.A. AND G.O. BATZLI. 2007. Population cycles of lemmings near Barrow, Alaska: a historical review. *Acta Theriologica* 52:323–336.

REYNOLDS, R.T., G.C. WHITE, S.M. JOY, AND R.W. MANNAN. 2004. Effects of radiotransmitters on Northern Goshawks: do tailmounts lower survival of breeding males? *Journal of Wildlife Management* 68:25–32.

RUTLEDGE, G.K., J. ALPERT, AND W. EBUISAKI. 2006. NOMADS: a climate and weather model archive at the National Oceanic and Atmospheric Administration. *Bulletin American Meteorological Society* 87:327–341.

SAUER, J.R., J.E. HINES, J.E. FALLON, K.L. PARDIECK, D.J. ZIOLKOWSKI, JR., AND W.A. LINK. 2012. The North American Breeding Bird Survey, results and analysis 1966–2011. Version 07.0302013. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, U.S.A. http://www.mbr-pwrc.usgs.gov/bbs/bbs.html (last accessed 1 November 2014).

SONERUD, G.A. 1986. Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. *Ecography* 9:33–47.

SOOTER, C.A. 1942. Duck hawk takes Short-eared Owl. *Condor* 44:182.

STEENHOF, K., K.K. BATES, M.R. FULLER, M.N. KOCHERT, J.O. MCKINLEY, AND P.M. LUKACS. 2006. Effects of radiomarking on Prairie Falcons: attachment failures provide insights about survival. *Wildlife Society Bulletin* 34:116–126.

THERRIEN, J.F., G. GAUTHIER, AND J. BÊTY. 2012. Survival and reproduction of adult Snowy Owls tracked by satellite. *Journal of Wildlife Management* 76:1562–1567.

U.S. GEOLOGICAL SURVEY. 2014. Summaries of banding and encounter data. Bird Banding Laboratory, Patuxent Wildlife Research Center, Laurel, MD U.S.A.

VILLAGE, A. 1987. Numbers, territory size and turnover of Short-eared Owls *Asio flammeus* in relation to vole abundance. *Ornis Scandinavica* 18:198–204.

WELLICOME, T.I., R.J. FISHER, R.G. POULIN, L.D. TODD, E.M. BAYNE, D.T.T. FLOCKHART, J.K. SCHUMTZ, K. DE SMET, AND P.C. JAMES. 2014. Apparent survival of adult Burrowing Owls that breed in Canada is influenced by weather during migration and on their wintering grounds. *Condor* 116:446–458.

WIGGINS, D.A., D.W. HOLT, AND S.M. LEASURE. 2006. Short-eared Owl (*Asio flammeus*). *In* P.G. Rodewald [ED.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NY U.S.A. https://birdsna.org/Species-Account/bna/species/sheowl (last accessed 22 September 2016).