Movements and habitat selection of Short-eared Owls (*Asio flammeus*) in North America

Movimentos e seleção de habitat da coruja-do-nabal (*Asio flammeus*) na América do Norte

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ABSTRACT

Effective conservation and management of Short-eared Owls (*Asio flammeus*) requires an understanding of population size, distribution, and linkages, as well as habitat requirements. Research in North America over the past decade has advanced knowledge of these subjects, though many gaps remain. Data on Short-eared Owl movements were historically limited to banding recoveries, with only 54 records since 1923, mostly short- or medium-distance recoveries (mean 308 km; maximum 2,002 km). More recently, satellite telemetry of 26 Short-eared Owls from Alaska revealed long-distance fall migration (ranging from 3,205 to 6,886 km) to a broadly dispersed wintering range, and low site fidelity in owls that returned northward in spring. Our satellite telemetry research on 13 individuals wintering in New York also found long-distance spring migration to breeding grounds (ranging from 1,751 to 1,938 km), but with more consistent population connectivity. While Short-eared Owls are generally considered to use a broad range of open habitat types from tundra to grassland to wetland, very little of this habitat in North America is occupied at any given time, suggesting that more specific preferences exist. A study of wintering Short-eared Owls in New York revealed that ground roosts were associated with significantly greater thatch depth, grass cover, maximum grass and forb height, number of

vertical strata, and vegetation diversity; foraging occurred preferentially in fields with an abundance of vole runways and high forb cover. Similarly, research in Ontario found Short-eared Owls nesting in loose aggregations in areas with taller grasses. Larger concentrations of dozens to hundreds of Short-eared Owls are occasionally reported at various locations across North America. Multiple irruptions have been recorded at Beaverhill Lake in central Alberta, where maximum abundance correlates with vole abundance, in turn triggered by a peak crop of plants such as alfalfa (*Medicago sativa*) and foxtail barley (*Hordeum jubatum*). Expanded documentation of irruptions and satellite tracking of individuals at such locations is considered a research priority.

Keywords: Asio flammeus, banding, habitat use, irruptions, telemetry

RESUMO

A conservação e gestão eficazes da coruja-do-nabal (Asio flammeus) implicam o conhecimento da sua dimensão populacional, distribuição e ligações, bem como dos seus requisitos de habitat. Ao longo da última década, a investigação na América do Norte produziu conhecimento sobre estes assuntos, embora ainda existam algumas lacunas. Os dados sobre os movimentos de coruja-do-nabal estão historicamente limitados a recapturas de aves anilhadas, havendo apenas 54 registos desde 1923, na sua maioria recapturas de curta ou média distância (média 308 km; máximo 2,002 km). Mais recentemente, 26 corujas-do-nabal do Alasca seguidas através de telemetria de satélite revelaram uma migração outonal de longa distância (variando de 3,205 a 6,886 km) para uma área de invernada amplamente dispersa, e reduzida fidelidade ao local de nidificação em corujas que regressavam ao norte na primavera. O nosso estudo de telemetria de satélite com 13 indivíduos invernantes em Nova Iorque também registou migração de longa distância na primavera para áreas de reprodução (variando de 1,751 a 1,938 km), embora com uma conectividade populacional mais consistente. Apesar de se considerar que a coruja-donabal utiliza uma ampla gama de habitats abertos, desde a tundra a pastagens e zonas húmidas, esses não são os habitats mais ocupados na América do Norte, sugerindo a existência de uma preferência de habitat mais específica. Um estudo com corujas-do-nabal invernantes em Nova Iorque revelou que os poisos ao nível do solo estavam associados com maior profundidade de palha, coberto herbáceo, altura máxima do coberto herbáceo e pastagem, número de estratos verticais e diversidade da vegetação. A alimentação ocorreu preferencialmente em campos com abundância de trilhos de micromamíferos e maior altura da pastagem. Da mesma forma, estudos em Ontario revelaram que a coruja-do-nabal nidifica em grupos dispersos em áreas com erva mais alta. Grandes concentrações de dezenas a centenas de corujas-donabal são reportadas ocasionalmente em vários locais na América do Norte. Foram registadas várias irrupções no lago Beaverhill, no centro de Alberta, onde a abundância máxima está correlacionada com a abundância de micromamíferos que, por sua vez, é potenciada pelo pico de abundância de culturas como luzerna (Medicago sativa) e cevada-marítima (Hordeum jubatum). Nesses locais, a documentação das irrupções e o seguimento dos indivíduos por satélite são considerados prioritários para a investigação.

Palavras-chave: anilhagem, Asio flammeus, irrupções, telemetria, uso de habitat

Introduction

Knowledge about the movements of Short-eared Owls (*Asio flammeus*) in North America was historically limited to banding data. Of over 3,200 individuals banded since 1923, only 54 (1.7%) have been recovered, at a mean distance of 308 km (range 0 to 2,002 km) from their original location (L. Laurin pers. comm.). Recently, the first published satellite telemetry study of Short-eared Owls in North America documented individuals from Alaska covering much greater distances, ranging from 3,205 to 6,886 km (Johnson et al. 2017).

Occasional large gatherings of Short-eared Owls presumably represent individuals converging from a broader area, but these have mostly been sparsely documented. Habitat preferences are somewhat better described, although much of what is known comes from a few mostly local studies (e.g., Clark 1975, Holt 1992, Dechant et al. 1999, Swengel & Swengel 2014) that may not fully represent the species across its wide range. Although most strongly associated with grasslands, Short-eared Owls can be found in a variety of other open habitats such as tundra, shrublands, and croplands (Wiggins et al. 2006), but the relative importance of these habitat types and the features within them that particularly influence their suitability for Short-eared Owls remain poorly understood (Booms et al. 2014).

Long-term declines in Short-eared Owl populations have been recorded across much of North America over at least the past 50 years, but the species has not yet been the focus of much conservation effort (Holt 1986; Wiggins et al. 2006; National Audubon Society 2010; Pardieck et al. 2017). Part of the challenge is that numbers appear to fluctuate naturally, making it difficult to assess whether changes represent true declines at either a local or regional scale; this is exacerbated by a limited understanding of how populations are linked on a regional or continental scale. Gaps in fine-scale knowledge of habitat preferences also hinder effective conservation management efforts (Booms et al. 2014).

Our objectives were to: 1) document longdistance movements of Short-eared Owls in eastern North America to compare with results from Alaska and identify key locations and regional linkages; 2) summarize and interpret knowledge about irruptions of Short-eared Owls; 3) build on existing knowledge of breeding and wintering habitat, with a focus on fine-scale habitat features used by Short-eared Owls; and 4) provide recommendations for further study in support of conservation and management.

Methods

Satellite telemetry

We deployed 13 Argos satellite platform transmitter terminals (PTTs) on wintering Short-eared Owls at six sites in New York state, from Buffalo (43°13'N, 78°32'W) to Washington (43°14'N, 73°33'W) and Greene (42°22'N, 73°48'W) counties, from 2006 to 2013. The PTTs were 12 g solar powered units (Microwave Telemetry, Columbia, Maryland, USA), equipped with motion, temperature, and battery voltage sensors. All owls outfitted with PTTs were adults. Based on wing chord, they comprised five males, four females, one probable male, one probable female, and two of unknown sex.

Owls were captured with bal-chatri traps, bow-nets, or mist nets near roosts, with either European Starlings (*Sturnus vulgaris*) or House Mice (*Mus musculus*) as bait (Bloom et al. 2007), and sometimes supplemented with MP3 players broadcasting mouse vocalizations. We attached PTTs with a backpack harness of 4 mm wide Tefloncoated nylon ribbon (Bally Ribbon Mills, Bally, Pennsylvania, USA), as per Steenhof et al. (2006). Known females had a mean mass of 383 g (range 355 to 405 g), whereas males had a mean mass of 335 g (range 311 to 396 g); the PTTs and associated harnesses were on average 3.0% (range 2.4 to 3.5%) of the mass of females and 3.5% (range 3.3 to 3.8%) of males.

We programmed the PTT duty cycle to be 10 hours on and 48 hours off, beginning at time of deployment. We received standard and auxiliary location data via the Argos System (www.argos-system.org) and CLS America (www.clsamerica.com). These were filtered through a systematic hybrid algorithm to remove implausible locations (Douglas et al. 2012). We retained location classes 1, 2, and 3, as well as auxiliary locations (classes 0, A, B, and Z) if they were within 5 km of another location, resultant movement rates were <80 km/h, and changes in direction were not suspiciously acute. We analyzed the best quality location during each duty cycle. We assumed PTT failure when transmission stopped after a period of poor quality data or low battery voltage readings and considered mortality to be probable when a PTT transmitted continuously from a single location, the motion sensor indicated it was stationary, or the temperature sensor reflected ambient conditions.

We defined fall and spring movement periods as beginning when owls were consistently moving away from summer and winter areas and ending when changes in position were reduced to localized multidirectional movements. We considered stopovers to be locations migratory temporarily used by owls in fall or spring, where they moved <35 km within 48 hours. Because PTTs were not transmitting every day, we estimated departure and arrival dates as the midpoint of transmission gaps <= 7 days but did not estimate them for longer gaps. We determined total displacement by measuring the straight-line distance between wintering and presumed breeding locations.

Irruptions

We reviewed all available eBird data to date (as of September 2017) for peaks in occurrence by generating "high count" figures across all years for each state, province, and territory (e.g., eBird 2017). For each jurisdiction, we noted the three highest totals reported, and the corresponding week of the year.

For Alberta, we collected information on winter irruptions of Short-eared Owls from a variety of sources including published literature, volunteer programs (Christmas Bird Counts and dead raptors turned in to Alberta Sustainable Resource Development), Alberta Birds Facebook page, and unpublished data including field notes from naturalists and wildlife biologists. We defined an irruption as more than 10 individuals observed in a small geographic area over a span of at least one month.

During the winter 2005-2006 and 2015-2016 irruptions of Short-eared Owls at Beaverhill Lake, Alberta (53°23' N 112°36' W) we collected data during daylight hours from a viewing blind at Francis Point, looking north over the lake. We also compiled records from others in the local birding community, with requested data including date and time of observations, where observations took place, time spent observing, number of owls observed, and type of optics (Priestley et al. 2008; Priestley and Crosland unpublished data).

We assessed the maximum number of owls observed each day through the two winters, and the number of owls observed versus time to sunset. Because sunset varied considerably throughout the season, we transformed the time that owls were observed into the number of minutes before sunset.

Habitat use

We used coordinated surveys and radio telemetry to study habitat use and home range at 11 primary wintering sites across New York State during the winters of 2007-2008 and 2012-2013. Visual surveys were conducted by trained observers every second week from December through March and took place between one hour before sunset and one half-hour after sunset.

We primarily captured owls using bow nets, but also used bal-chatri traps, noose "carpets", dho-gaza nets, and mist nets (Bloom et al. 2007). Owls (n=76) were fitted with VHF backpack style transmitters (LL Electronics, frequency range 150-152 Hz, 6-7 g; Holohil, frequency range 216-217 Hz, 8-9 g) and banded with standard USFWS leg bands. We obtained locations for these owls while they were present on wintering areas, typically at three-day intervals. We surveyed during daylight hours (30 minutes before sunrise to 30 minutes after sunset) to identify roost locations, and again for several hours during the night when owls were active.

We conducted all home-range data analyses using Biotas Version 2 (2005), and all statistical analyses using MS Excel (2013). Owls observed over a period of less than two weeks, with fewer than 10-15 individual locations, or with very few foraging locations (n=18) were omitted from detailed analysis. Home range calculations were initially performed for 31 owls from eight sites using minimum convex polygons based on both triangulation data and visual observations. However, we considered owls to have home ranges only if the cumulative area of their home ranges, calculated incrementally from three locations to the maximum number of locations collected, appeared to approach an asymptote. Incremental area analyses were conducted by visual inspection. Using this approach, ten owls were eliminated from home range analysis. For the remaining 21 owls analyzed

for this report, we collected an average of 45 points per individual owl (range=20-93). We estimated 95% utilization distributions for each individual, omitting occasional sallies to locations outside of the general use area (Hansteen et al. 1997). We calculated spatiotemporal independence of points for each owl using a Mantel's U test, which performs Monte-Carlo simulations to calculate the permutation variance of the frequency of locations near one another across time (Eckley and Curtin 2012). All data on home range sizes were In-transformed to approximate a normal distribution prior to further analyses.

We assessed habitat selection by using plot-based field measurements and landscape-level GIS data (ArcMap Version 10.2). We evaluated whether sites selected for diurnal roosts differed from those used only (or primarily) for foraging, or from randomly selected sites not used for either foraging or roosting. We collected habitat data from multiple fields in at least one year at eight of the 11 primary study areas and obtained landscape-level measurements for at least one year from two or more fields at seven of the 11 primary study areas. We used visual observation and radio-telemetry to locate owls to identify general roost locations, as well as fields used by owls for foraging. Fields never or only very rarely used by foraging owls were also identified. More precise roost locations were later obtained by walking into roost areas when owls were not present and finding cast pellets or feces.

We defined ground roosts as being centered at the location of cast pellets or whitewash. We randomly selected the center of plots used or not used for foraging from within fields delineated by GIS. Randomly selected plots typically numbered 20 per field, whereas roost plots were generally fewer and equal to the number of pellets/ whitewash locations. Field-based plot measurements included % cover in grasses, forbs, and bare ground within square meter quadrats, and % cover of shrubs or trees within a 5 m radius of the plot center. Maximum vegetation height was measured by recording the presence or absence of vegetation within each of six height intervals (0-10 cm, 10-25 cm, 25-50 cm, 50-75 cm, 75-100 cm, >100 cm) along with a measurement of thatch depth. A vegetation growth diversity measure was developed by multiplying the number of vegetation growth forms by the number of strata with vegetation contacts at each plot. Soil moisture was defined at each plot as inundated (standing water), saturated (wet to touch), or unsaturated (dry). Lastly, the number of distinct small mammal runways within each quadrat was recorded. For conifer roost locations (n=3), data recorded included the height, diameter at breast height, and species of the roost tree, the height where owls roosted (based on whitewash on tree branches, or branch location immediately above pellets on the ground), and azimuth to the center of the conifer.

Landscape-level measurements included a) % cover for a variety of land cover types within both a 0.5 km and 1.6 km radius of the center of a roost, foraging field, or nonuse field (defined as being within the home range of an owl, but with no telemetry or visual records), b) nearest distance to a variety of habitat features, and c) a measure of linear habitats not well measured as % cover such as ditches, fence lines, and road edges (Tables 1, 2, & 3). Fields that were used by owls for both roosting and foraging were used twice or treated separately in the analysis. Sample sizes for landscape level measurements are much smaller than for plot measurements as this aspect was developed later during this study. Fewer non-use fields were available for analysis because it was difficult to document that fields were not used. We used one-way ANOVAs to look for significant differences in vegetation for foraging, roosting, and non-use areas. Some tests violated the

assumption of homogeneity of variances, but nonparametric tests gave similar results, so we report ANOVA results here. Tukey HSD post-hoc tests are reported as well.

To better understand micro-scale habitat selection by breeding Short-eared Owls, we assessed habitat surrounding active nest sites on Amherst Island (44°08' N 76°43' W) and Wolfe Island (44°10' N 76°22' W), Ontario, in 2009 and 2010, as described in Keyes et al. (2016). We documented the dominant vascular plant species within a 4 m radius of each nest and surveyed 1 m^2 quadrats over the nest and at 5, 10, 15, 25, and 50 m intervals along transects to the east, south, west, and north (Bonham 1989). Keyes et al. (2016) also estimated vegetation composition and average height for each quadrat and recorded the distance from each nest to the nearest waterbody, building, and fence.

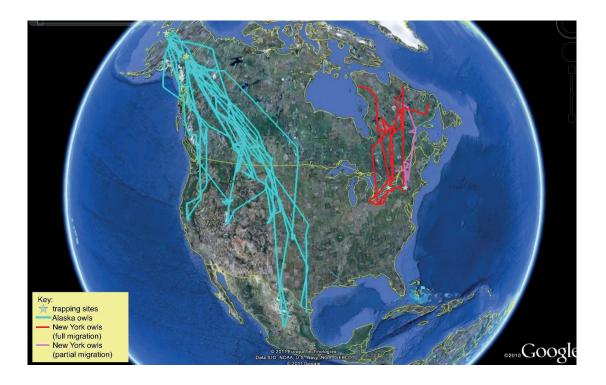
Results

Satellite telemetry

Estimated departure dates of owls carrying PTTs ranged from early to mid-March to late April, similar to data from our study's VHF-tracked owls, which had last detection dates on the wintering area beginning in March (n=8), peaking in April (n=10), and as late as May 7 (n=1). Of the 13 owls satellite-tracked from wintering areas in New York, transmitter failure or mortality occurred for six owls before spring migration was completed. Two other owls were tracked until mid-late May, by which time one was in southern Quebec (326 km from its wintering site) and the other was in western Labrador (1,375 km), but transmissions ended too soon to determine whether these had settled on a breeding home range.

Of the five owls that provided data throughout summer, three departed their wintering sites to the north or northeast, with Figure 1 - Satellite telemetry tracks from Short-eared Owls (*Asio flammeus*) trapped at wintering grounds in New York, compared with satellite telemetry tracks of Short-eared Owls from breeding grounds in Alaska from Johnson et al. (2017).

Figura 1 - Percursos determinados por telemetria de satélite de corujas-do-nabal (*Asio flammeus*) capturadas em locais de invernada em Nova Iorque, em comparação com os percursos de corujas-do-nabal provenientes de locais de reprodução no Alasca segundo Johnson et al. (2017).

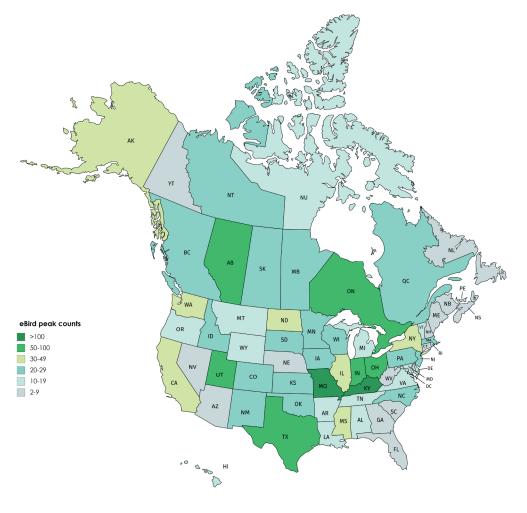


two individuals wintering in Washington County in 2007 and 2010 that migrated north to the Lake Champlain area before continuing into Quebec. Another, captured in Niagara County, moved northeast into southern Ontario and then on to northern Quebec (Fig. 1). The other two owls departed to the west, heading south of Lake Erie and into Ohio prior to crossing north over Ontario and into Quebec. Four of these owls settled on summer territories between mid-May and early July - two of them in western Labrador, another in northern Labrador, and the fourth nearby in northern Quebec, adjacent to Ungava Bay. Their mean straight-line distance from wintering to breeding area was 1,835 km (range 1,751 to 1,938 km). The fifth owl stopped over in southern Ontario between 25 April and 2

May, then continued into central Quebec, where it was detected at numerous locations from mid-June through mid-September.

Transmitters for two owls continued to function longer. One of these, captured in Washington County in 2006, had a single detection on March 12 in Sullivan County, approximately 180 km south of where it had spent the previous winter. Another owl, originally captured in Greene County in 2009, had a single detection on March 12 the following year in Ohio, where it had spent much of April during its spring migration the previous year; it also was detected the following summer in far northern Quebec, approximately 750 km northeast of its location the previous year. In addition, three VHF-tracked owls returned to New York in a subsequent winter. One owl captured in Figure 2 - All-time peak counts of Short-eared Owls (Asio flammeus) in the eBird database for each state, province, and territory in the United States and Canada.

Figura 2 - Contagens de máximos totais de corujas-do-nabal (Asio flammeus) na base de dados eBird para cada estado, província e território nos Estados Unidos e Canadá.



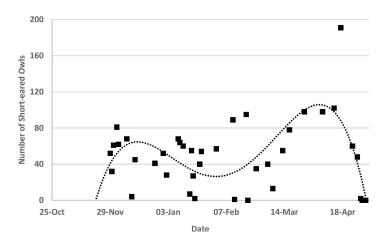
Created with mapchart.net

Niagara County on 8 February 2008 was recaptured at the same site on 17 February 2010. Another originally captured at a site south of Rochester on 22 January 2010, returned the following year and spent the winter at another regular wintering site approximately 15 km west of the original capture site. The third returning owl was originally captured 27 December 2009 in wetlands near the Montezuma Wildlife Refuge, Wayne County, and a single radio detection was obtained the following winter on 13 December 2010 at a location on the refuge, approximately 10 km from the original capture location.

Irruptions

Data from eBird up to September 2017 revealed that peak counts of 30 or more Short-eared Owls have been recorded in 13 states and 2 provinces, ranging from Alaska and New York to Texas and Mississippi (Fig. 2). Peak counts mostly occurred in Figure 3 - The maximum number of Short-eared Owls (*Asio flammeus*) counted on each survey day during winter 2005/06 at Beaverhill Lake, Alberta.

Figura 3 - Número máximo diário de corujas-do-nabal (Asio flammeus) durante o inverno de 2005/06 no Lago Beaverhill, Alberta.



winter (December through March), except in North Dakota (1 April), Utah (15 May), and Alaska (8 August). Similarly, 80% of the top three counts for each of these 15 states and provinces were in winter. The aforementioned three states accounted for most of the other exceptions (the other being Alberta, 15 April).

The top two counts were 126 at the Sinclair Unit of Peabody Wildlife Management Area in Kentucky (4 February 1996) and 125 in Dade County, Missouri (31 January 2010). These appear to have been exceptional records, as the second highest counts for Kentucky and Missouri are 20 and 31, respectively.

There is a long history of documented Short-eared Owl irruptions in Alberta. Randall (1925) described a spike in Shorteared Owl abundance and reproductive output in southern Alberta in 1925, associated with a peak in vole numbers. In 1931-32, 'thousands' of Short-eared Owls ate 'mice' that thrived in grain stocks in the central part of the province (Farley in Bent 1938). In winter 1988-89, an invasion occurred in central Alberta, with peak counts of up to 30 owls during December and January. Meadow Voles (*Microtus pennsylvanicus*) were prevalent in uncut alfalfa (*Medicago sativa*) fields at this time, and comprised the only prey remains found in 25 owl pellets that were collected and dissected (E. Wallace & G. Holroyd pers. comm.).

In summer 1997, J. Schmutz & K. Clayton (pers. comm.) reported a Shorteared Owl irruption in southern Alberta. They observed 15 Short-eared Owls in an area where they had observed, on average, less than one owl per year from 1984 to 1996. This corresponded with a rate of 2.6 voles/100 trap nights in 1997, compared to 0.3 in 1996 (J. Schmutz & K. Clayton pers. comm.).

The two largest irruptions documented in Alberta were both at Beaverhill Lake, in the winters of 2005-2006 and 2015-2016. We compiled 46 sightings from Beaverhill Lake in winter 2005-2006, covering 29 days between 29 November and 27 April (Fig. 3). The number of owls counted was variable, peaking at 191 on 17 April and as low as 0 on 20 February; however, the monthly maximum counts were all at least 70. We found the average number of owls observed

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Figure 4 - Number of Short-eared Owls (Asio flammeus) detected versus time before sunset during winter 2005/06 at Beaverhill Lake, Alberta.

Figura 4 - Número de corujas-do-nabal (Asio flammeus) detetadas versus o tempo antes do ocaso durante o inverno de 2005/06 no Lago Beaverhill, Alberta.

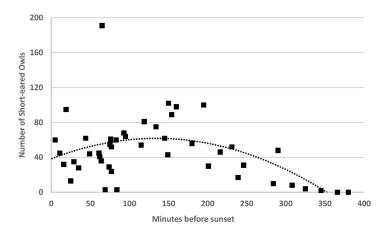
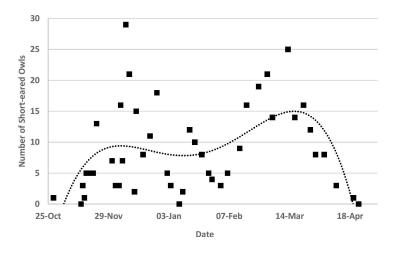


Figure 5 - The maximum number of Short-eared Owls (Asio flammeus) counted on each survey day during winter 2015-16 at Beaverhill Lake, Alberta.

Figura 5 - Número máximo diário de corujas-do-nabal (Asio flammeus) durante o inverno de 2015/16 no Lago Beaverhill, Alberta.



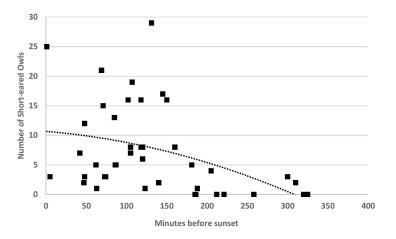
increased through the winter (r=0.39, P<0.01), but tapered off sharply in late April; despite the availability of seemingly suitable nesting habitat, no owls were observed during the subsequent breeding season. We received eight other records of Short-eared Owls from other parts of Alberta during the winter of 2005-2006,

but none of them involved large numbers.

Owls were observed foraging at all times of the day but were more frequently observed 50-100 minutes before civil twilight (Fig. 4) (Priestley et al. 2008). There was no linear relationship between number of owls observed and time of day (P=0.94) (Priestley et al. 2008), however the

Figure 6 - Number of Short-eared Owls (Asio flammeus) detected versus time before sunset during winter 2015-16 at Beaverhill Lake, Alberta; the line represents the best fit of abundance relative to time before sunset.

Figura 6 - Número de corujas-do-nabal (Asio flammeus) detetadas versus o tempo antes do ocaso durante o inverno de 2015/16 no Lago Beaverhill, Alberta.



highest count was made 65 minutes before civil twilight.

During the 2015-2016 irruption at Beaverhill Lake, we compiled 54 owl surveys covering 51 days between 28 October and 3 May (Fig. 5). Owl numbers were lower than in 2005-2006 and were variable but appeared to show two peaks, one in early December (n=29) and the other in the middle of March (n=25). We found the number of owls observed increased as the time of day approached sunset (Fig. 6; r=0.43, P<0.01). On one occasion, two birders went out searching for Short-eared owls at 12:00 and observed none, but 25 individuals were counted beginning at 14:00.

Habitat use

For 21 telemetry-marked owls the average number of days from date of capture to last date detected by telemetry was 53 days (range 26-112). Home ranges for these 21 owls ranged from 49.3 to 1,256.1 ha (mean 217.7 ha, single SE limits 173.6 & 273.0).

Grass cover was most dominant at

roosting sites and least abundant at nonuse sites, forb cover was more than twice as extensive at foraging sites compared to elsewhere, shrub and tree cover were low throughout all areas, and bare ground was scarce except at non-use sites (Table 1). Vole runways were over 8 times more numerous at foraging sites than roosting sites and 12 times more than at non-use sites (Table 1). The number of vegetation strata and overall vegetation diversity were higher at roostingonly sites than elsewhere (Table 2).

Ground roost locations had significantly greater thatch depth, grass cover, maximum grass height, maximum forb height, number of vertical strata, and vegetation diversity (forms and strata) compared to both foraging fields and non-use fields (Table 3). Fields used for foraging had a significantly greater number of vole runways and significantly greater forb cover than either roost fields or non-use fields. Fields used for foraging also had significantly greater thatch depth, grass cover, maximum height of grass and forbs, and vegetation diversity compared to non-use fields. Non-use fields had a significantly greater amount of bare ground Table 1 - Vegetation height and cover and vole runways at Short-eared Owl (Asio flammeus) field plots in New York.

Tabela 1 - Altura e cobertura da vegetação e trilhos de ratos-cegos nas parcelas ocupadas por coruja-do-nabal (Asio flama	neus)
em Nova Iorque.	

	Foraging only (<i>n</i> =661)		Roosting only (<i>n</i> =183)		Roosting/ Foraging (n=58)		Non-use (<i>n</i> =181)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Grass cover (%)	78.80	27.79	91.35	15.65	83.64	27.57	44.01	42.74
Grass maximum height (cm)	26.36	26.94	57.27	38.11	31.77	18.47	13.99	12.72
Forb cover (%)	16.07	24.20	6.23	11.18	8.95	19.62	8.05	15.03
Forb maximum height (cm)	41.04	34.79	52.30	37.30	96.25	44.23	8.50	9.32
Shrub cover (%)	1.97	8.70	2.21	8.61	0.03	0.26	0.47	3.05
Shrub maximum height (cm)	60.17	71.23	56.14	68.74	0.00	0.00	0.00	0.00
Tree cover (%)	0.08	0.78	0.01	0.19	0.00	0.00	0.00	0.00
Bare ground cover (%)	3.17	10.89	1.89	10.07	6.64	18.86	44.34	39.47
# Vole runways	2.28	3.40	0.27	1.38	1.32	1.49	0.18	0.76

Table 2 - Vegetation growth forms and strata at Short-eared Owl (Asio flammeus) field plots in New York.

Tabela 2 - Formas de crescimento da vegetação e estratos nas parcelas ocupadas pela coruja-do-nabal (Asio flammeus) em Nova Iorque.

	Foraging only (n=631)		Roosting only (n=183)		Roosting/ Foraging (n=19)		Non-use (n=125)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Number of growth forms	1.95	0.78	1.81	0.68	1.84	0.69	1.12	0.73
Number of strata	1.77	1.15	2.96	1.41	1.37	0.76	1.58	1.11
Diversity (forms x strata)	3.88	3.83	5.25	2.85	2.58	1.39	2.12	1.59
Thatch depth (cm)	4.92	3.87	5.91	5.53	7.16	6.94	1.49	3.03

compared to both fields used for roosting and fields used for foraging. In addition, soil was inundated more frequently at roost sites than at foraging sites, and unsaturated more frequently at foraging sites than at roost sites (Table 4; $X_2^2 = 65.74$, *P*<0.0001).

At some roost locations, pellets were found in pockets between vegetation where taller vegetation provided a backdrop. Plant species observed providing these conditions included: common reed (*Phragmites australis*), reed canary grass (*Phalaris arundinacea*), purple loosestrife (*Lythrum salicaria*), and various species of rushes (*Juncus spp.*), sedges (*Carex spp.*), and cattails (*Typha spp.*). Notably, these are all wetland species, which may correlate with the finding of more frequent soil inundation at roost plots.

At three of the 11 study areas, Short-eared

Table 3 - Statistical comparison of vegetation growth forms and strata at Short-eared Owl (*Asio flammeus*) field plots in New York.

Tabela 3 - Comparação estatística das formas de crescimento e estratos da vegetação em parcelas ocupadas pela coruja-do-nabal (*Asio flammeus*) em Nova Iorque.em Nova Iorque.

VARIABLE	F	df	Р	NON-USE VS. FORAGING	ROOSTING VS. FORAGING	ROOSTING VS. NON-USE
Grass cover (%)	134.1	1021, 2	< 0.0001	<0.0001	< 0.0001	< 0.0001
Grass maximum height (cm)	121.20	934, 2	< 0.0001	< 0.0001	< 0.0001	<0.0001
Forb cover (%)	21.55	1021, 2	< 0.0001	<0.0001	< 0.0001	0.9396
Forb maximum height (cm)	43.66	985, 2	< 0.0001	<0.0001	0.9572	< 0.0001
Shrub cover (%)	2.885	1020, 2	0.0563	0.0643	0.9347	0.0963
Shrub maximum height (cm)	9.623	929, 2	< 0.0001	0.0003	0.4748	0.0001
Tree cover (%)	1.44	980, 2	0.2370	0.3597	0.4215	0.9802
Tree maximum height (cm)	1.012	890, 2	0.3640	0.6392	0.4340	1.0000
Bare ground cover (%)	343.6	1011, 2	< 0.0001	< 0.0001	0.7102	< 0.0001
# Vole runways	52.46	933, 2	< 0.0001	<0.0001	< 0.0001	0.9599
Number of growth forms	63.01	936, 2	< 0.0001	< 0.0001	0.0653	< 0.0001
Number of strata	77.75	936, 2	< 0.0001	0.2459	< 0.0001	<0.0001
Diversity (forms x strata)	31.03	936, 2	< 0.0001	< 0.0001	< 0.0001	<0.0001
Thatch depth (cm)	52.38	932, 2	< 0.0001	<0.0001	<0.0001	< 0.0001

Table 4 - Soil moisture counts for Short-eared Owl (Asio flammeus) habitat characterization in New York.

Tabela 4 - Valores de humidade do solo para caracterização do habitat da coruja-do-nabal (Asio flammeus) em Nova Iorque.

	INUNDATED	SATURATED	UNSATURATED	TOTAL
Foraging	25 (4.0%)	368 (58.6%)	235 (37.4%)	628
Roost	37 (20.7%)	109 (60.9%)	33 (18.4%)	179
Total	62	477	268	807

Owls roosted almost exclusively in conifers. These roosts were within one of three roost site types: Christmas tree farms or tree clusters, tree rows, and lone conifers. Roost trees therein included eastern white pine (*Pinus strobus*), Scots pine (*Pinus sylvestris*), white fir (*Abies concolor*), and blue spruce (*Picea pungens*). Individual roost tree height ranged from 0.6 to 8.0 m, with site roost tree height averages as follows: Christmas tree farms or tree clusters = 4.1 m; tree rows = 3.5 m; and lone conifers = 8.0 m. The average diameter at breast height of the roost trees at the three sites were 8.2, 10.3, and 17.5 cm, respectively. Roost heights averaged 1.1, 1.4, and 2.3 m, respectively, and were typically on the leeward (i.e., east/ northeast) side of a given tree.

At the landscape level, public roads were not significantly farther from roosting sites $(470.4 \pm 319.7 \text{ m})$ than from foraging sites $(250.2 \pm 184.9 \text{ m}; t_{8.13} = -1.88, P = 0.097).$ Perennial water sources were almost significantly closer to roosting sites (305.4 \pm 314.7 m) than to foraging sites (651.4 \pm 632.3 m; $t_{22,34}$ =2.07, P=0.050). The areal extent of grassland was not significantly greater within 0.5 km of foraging vs. roosting sites $(131.2 \pm 41.1 \text{ ha vs. } 76.7 \pm 10.1 \text{ hz})$ 70.0 ha, $t_{8.17}$ =2.12, P=0.066) but it was significantly greater within 1.6 km of foraging vs. roosting sites (910.8 ± 492.9 ha vs. 335.8 \pm 454.3 ha, $t_{9.48}$ =2.98, P=0.015). Analysis of landscape level data for non-use and roosting categories was not conducted due to low sample sizes.

Seven active nests were studied on Amherst and Wolfe Islands in Ontario in 2009 and 2010 (Keyes et al. 2016). In 2009, three of them were clustered within 2 km of each other in the south-central part of Amherst Island, while in 2010, another three were also within 2 km of each other on the eastern part of Amherst Island, ~5 km from the previous year's concentration. Five of the nests were in grazed grassland, with one each in a hayfield and a fallow field. Five of the seven nests were near grid wire fencing with wooden posts. All four nests that survived to nestling stage were within 540 m of a marsh or pond (mean 366 ± 181 m; range 175-540 m) and most were within 1,000 m of an occupied human residence (mean 767 ± 526 m; range 370-1,500 m).

Birdsfoot trefoil (*Lotus corniculatus*) and cow vetch (*Vicia sativa*) were found at five of the seven nests, Canada goldenrod (*Solidago canadensis*) and reed canary grass (*Phalaris arundinacea*) were observed at four nests, and smooth brome (*Bromus inermis*), red clover (*Trifolium pratense*), redtop (*Agrostis gigantea*), timothy (*Phleum pratense*), thistle (*Carduus spp., Cirsium spp., Silybum spp.*), and sedge species (*Carex spp.*) were each documented at three nests (Keyes et al. 2016). Vegetation was taller and grass cover was greater (70 \pm 13%) surrounding nests than at any other survey quadrants, whereas forb cover and bare ground were more frequent away from nests (Keyes et al. 2016).

Discussion

Until recently, Short-eared Owl movement data were largely limited to band recoveries and mostly indicated short to moderate distance displacement (mean 308 km, L. Laurin pers. comm.). Initial satellite telemetry research in the early 2000s documented longer movements (e.g., ~1,500 km from Saskatchewan to Iowa, Migration Research Foundation 2007; ~1,900 km from southern Ontario to northern Quebec, Bird Studies Canada 2011; >2,000 km from central Alberta to Kansas, G. Holroyd & H. Trefry, unpub. data), but sample sizes were small and possibly not representative of populations. Johnson et al. (2017) showed that long-distance movement is typical for Short-eared Owls breeding in Alaska, with seven individuals tracked throughout fall migration traveling between 3,205 and 6,886 km (mean 4,722 ± 1,156 km) over a span of 61 to 147 d (mean 85.2 ± 31.8 d). Although migration routes were concentrated through western Yukon as well as southeastern Alberta and southern Saskatchewan, winter locations of these owls varied widely, spanning 21° of latitude from Montana to Texas, and 24° of longitude from California to Kansas; two other owls were farther south near Zacatecas, Mexico, and still on the move when transmissions ended. In contrast, the mean distance between wintering and breeding areas by New York owls (1,835 km) was more comparable to the previous result from southern Ontario, and there was much tighter migratory connectivity, with all of the owls occupying summer home ranges in Labrador or central-northern Quebec.

The lack of breeding site fidelity shown by western Short-eared Owls is like that observed for PTT-marked Burrowing Owls (Athene cunicularia) (Holroyd & Trefry 2011; Holroyd et al. 2011) and Snowy Owls (Bubo scandiaca) (Fuller et al. 2003; Therrien et al. 2012). Like Snowy Owls, Short-eared Owls are rodent specialists, and presumably select their breeding areas annually in response to asynchronous fluctuations in prey populations (Kalela 1962; Korpimäki & Norrdahl 1991; Pitelka & Batzli 2007). Although owls from Alaska ranged widely, all stayed west of 95°W, whereas all of the owls from New York remained east of the upper Great Lakes. This is consistent with band recovery data, in which all Short-eared Owls banded in the Pacific or Atlantic flyways were recovered in the same flyway, whereas those from the Central and Mississippi flyways were occasionally encountered in adjacent flyways. This suggests that although Short-eared Owls are considered nomadic and breeding concentrations appear to shift considerably from year to year, there may be a divide in North America between western and eastern populations.

Satellite telemetry has also revealed the importance of stopover locations to Shorteared Owls. To some extent, pauses in migration that we observed were likely associated with encountering headwinds. However, the extended duration of several stays and the clustering of stopover sites suggests that some regions may be of particular value for this species and warrants further investigation. In particular, western Yukon and southeastern Alberta appear to be particularly important for western Shorteared Owls (Johnson et al. 2017), while corresponding areas in the east include the shorelines of Lake Erie and Lake Ontario, as well as parts of central Quebec.

Insights from our satellite telemetry research were somewhat constrained by using a less frequent transmission duty cycle designed to prolong PTT lifespan. While this had minimal influence on our ability to describe timing and displacement of longdistance movements, it yielded limited data for assessing habitat use at stopover locations and documenting fine-scale migration route details. The recent availability of lightweight GPS transmitters that can be safely worn by Short-eared Owls allows for much more precise documentation of habitat use (e.g., Calladine 2017), and we recommend the use of this technology for future study of Shorteared Owl movements.

Our VHF telemetry research provided the first estimates of winter home range size (mean 218 ha) for Short-eared Owls which were more than triple the mean size of breeding home ranges reported by Wiggins et al. (2006). There was, however, considerable variability in home range size. Many factors could drive winter range size, including small mammal densities, snow cover, and interspecific and intraspecific competition; results can also be influenced by sampling effort. At some sites, there were individuals, possibly subdominant, with much greater home ranges. Winter home range sizes for Short-eared Owls in Taiwan (Tseng et al. 2017) averaged nearly twice as large as in our study. The owls in Taiwan possibly differed in that they moved between different core areas every few days, whereas in our study, most owls that were tracked for longer periods of time remained in the same area throughout the winter months. However, we lost track of some individuals over the course of our study, so it is possible they also moved between different core areas.

Our results highlighted several distinctions between roosting and foraging locations. There was strong selection of foraging habitat with higher forb cover and greater vole activity. Typical ground roost sites in New York had tall, diverse, herbaceous cover and owls roosted at low heights in low to mid-height conifer trees. In his study of wintering Short-eared Owls in New York, Clark (1975) documented roosting in a quarry, a gravel pit, stubble fields, and conifer groves; Bosakowski (1986) also reported the use of conifer roosts. While we found three roost sites with conifers, most roost sites in our study were on the ground either in old fields that had not been mowed for several years, or in hayfields that had not been mowed in late summer or fall. This supports the conclusion that wintering Short-eared Owls in New York prefer fields with taller, thicker, more diverse vegetation for ground roosting which provides owls with shelter from wind and protection from mammalian predators. During our study, we found the remains of several Northern Harriers (Circus hudsonius), which also roost on the ground, and tracks indicated Coyote (Canis latrans) as the likely predator in each case. In Taiwan, Tseng et al. (2017) also found owls roosting in tall grasslands and suggested avoidance of predators as one possible factor in roost site selection.

While avoidance of areas with human activity might be a factor in roost selection, two of the three conifer roosts observed in this study were near residences or barns, and others have been noted in New York State since the completion of our study. Similarly, during winter surveys we conducted on Amherst Island, Ontario, in January 2010, we found a roost of 18 Short-eared Owls in a red cedar (Juniperus virginianus) 3 m from an occupied residence. Availability of suitably-sized conifers for roosting may be limited in some areas, and the importance of shelter may outweigh the occasional disturbance by people and or pets, especially during extreme weather, when buildings may provide additional shelter from the elements.

The significantly higher number of vole runways in foraging plots is expected, given that voles are a primary prey item, and fluctuations in vole abundance have long been recognized as influencing Short-eared Owl numbers (e.g., Goddard 1935, Elton 1942). Most non-use fields identified were row crop fields or closely cut hayfields, which likely support lower prey densities.

High concentrations of voles are likely also at the basis of periodic concentrations of Short-eared Owls. Beaverhill Lake has been drying out since the late 1990s, with 2005 being the driest year since the early 1950s. In the summer of 2005, foxtail (Hordeum jubatum) barlev colonized extensive portions of the dry lake bed. The prevailing northwest winds carried seeds to the southern shore of the lake and collected in piles >1 m high. As a result, microtine abundance, particularly Meadow Voles, spiked sharply, presumably in response to the increase in seeds as a source of food. In addition, below-average snowfall resulted in shallow snow cover, allowing Short-eared Owls access to the voles.

Despite the large number of Short-eared Owls present at Beaverhill Lake over a span of several months, there were occasions when very few or even none were observed. Although it is possible that there was some movement of birds within the region, sightings were not reported from surrounding areas. Moreover, same-day differences in counts suggest that variation in numbers was primarily a function of detectability, which in turn was highest within the last 1-2 hours of daylight. Our experience highlights how easy it is to overlook even unusually large concentrations of Short-eared Owls, and the importance of surveying late in the afternoon to optimize detection at wintering sites.

Although large numbers of Short-eared Owls remained at Beaverhill Lake into April in both 2006 and 2016, no local evidence of breeding was observed in either year, despite the availability of apparently suitable nesting habitat. Similarly, habitat across much of Amherst and Wolfe Islands appears suitable for breeding, yet nesting records were largely clustered in different areas in consecutive years of our study. These results suggest that there are important factors in habitat site selection that remain poorly understood and require further research. Our findings that Short-eared Owls preferentially nested adjacent to taller vegetation and near wooden fence posts are likely just site-specific details superimposed on other criteria considered by the owls.

Our research, as summarized in this report and Gahbauer et al. (2021), has addressed aspects of the three Short-eared Owl conservation research priorities identified by Booms et al. (2014), namely better defining important habitat, improving population monitoring, and describing seasonal and annual movements. Our habitat studies highlight that, both in summer and winter, Short-eared Owls have some very specific microhabitat preferences, although these may well differ across the range of the species and warrant further investigation in other locations. Our telemetry results reinforced the belief that Short-eared Owls are highly mobile and have nomadic tendencies, although we discovered an apparent divide between eastern and western populations, with more consistency in movements in eastern North America.

The potential for ecological and behavioural differences between western and eastern North American Short-eared Owls may have implications for conservation and management and warrants additional study. Satellite telemetry of owls wintering in the US Midwest may be particularly important to target, since this is an area with relatively large wintering numbers, but the linkages to breeding areas remain unclear. Strong consideration should also be given to PTT-tagging owls during irruptions to investigate the area over which individuals from such congregations subsequently disperse. Stable isotope analysis of feathers collected from owls during winter irruptions would provide insights as to where the sampled feathers were grown, clarifying whether individuals from different breeding areas gather at such locations. More detailed and standardized study of the irruptions themselves is needed to better understand how owl numbers and activity levels vary in relation to time of day, season, and weather conditions. We recommend heightened awareness of the importance of irruptions to understanding Short-eared Owl ecology, and coordination of research and communication

efforts across North America to track these occurrences over time and space. The use of GPS transmitters for any future satellite telemetry research will provide highly detailed location data that can be used to address questions like those above, as well as helping to continue refining our understanding of key habitat requirements in different parts of the species' range.

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References

Bent, A.C. 1938. Life histories of North American Birds of Prey (Part 2). Orders Falconiformes and Strigiformes. Bulletin of the US Natural Museum (170). viii+482 pp.

- Bird Studies Canada. 2011. Monitoring Short-eared Owls. Website: http://www. birdscanada.org/research/speciesatrisk/ seow/ (accessed December 2017).
- Bloom, P.H., W.S. Clark & J.W. Kidd. 2007. Capture techniques. In: Bird, D.M. & K.L. Bildstein (eds.) Raptor research and management techniques. Hancock House Publishers, Blaine, Washington, pp 193-220.
- Bonham, C.D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons, Toronto, Ontario.
- Booms, T.L., G.L. Holroyd, M.A. Gahbauer, H.E. Trefry, D.A. Wiggins, D.W. Holt, J.A. Johnson, S.B. Lewis, M.D. Larson, K.L. Keyes & S. Swengel. 2014. Assessing the status and conservation priorities of the Short-eared Owl in North America. Journal of Wildlife Management 78: 772-778.
- Bosakowski, T. 1986. Short-eared owl winter roosting strategies. American Birds 40: 237-240.
- Calladine, J. 2017. Short-eared Owls Asio flammeus: sensitivities to changes of land use in upland Britain. World Owl Conference, Evora, Portugal.
- Clark, R.J. 1975. A field study of the Short-Eared Owl, *Asio flammeus* (Pontoppidan), in North America. Wildlife Monographs 47: 3-67.
- Dechant, D.J., M.L. Sondreal, D.H. Johnson, L.D. Igl, C.M. Goldade, M.P. Nenneman & B.R. Euliss. 1999. Effects of management practices on grassland birds: Short-eared Owl. Northern Prairie Wildlife Research Center, Jamestown, North Dakota.

- Douglas, D.C., R. Weinzierl, S.C. Davidson, R. Kays, M. Wikelski & G. Bohrer. 2012. Moderating Argos location errors in animal tracking data. Methods in Ecology and Evolution 3: 999-1007.
- eBird. 2017. Short-eared Owl High Counts for Kentucky, 1900-2017. Website: https://ebird.org/barchart?r=US-KY&bmo=1&emo=12&byr=1900&eyr=2017&spp=sheowl (accessed December 2017).
- Eckley, D.C. & K.M. Curtin. 2012. Evaluating the spatiotemporal clustering of traffic incidents. Computers, Environment and Urban Systems 7: 70-81.
- Elton, C. 1942. Voles, mice and lemmings: problems in population dynamics. Oxford University Press, London, 496 pp.
- Fuller, M.R., D. Holt & L. Schueck. 2003. Snowy Owl movements: variation on the migration theme. In: Berthold, P., E. Gwinner & E. Sonnenschein (eds.) Avian migration. Springer Verlag, Berlin, pp. 359-366.
- Gahbauer, M.A., R.A. Miller, N. Paprocki,
 A. Morici, A.C. Smith & D.A. Wiggins.
 2021. Status and monitoring of Shorteared Owls (*Asio flammeus*) in North and South America. In: Roque, I., Duncan,
 J.R., Johnson, D.H. & Van Nieuwenhuyse,
 D. (eds) Proceedings of the 2017 World Owl Conference. Évora, Portugal. Airo 29: 115-142.
- Goddard, T.R. 1935. A census of Short-eared Owls (*Asio f. flammeus*) at Newcastleton Roxburghshire, 1935. Journal of Animal Ecology 4: 289-290
- Hansteen, T.L., H.P. Andreassen & R.A. Ims. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. Journal of Wildlife Management 61: 280-290.

- Holroyd, G. & H. Trefry. 2011. 5G PTT demonstrates dispersal hypothesis in burrowing owls. Microwave Telemetry Inc., Columbia, Maryland. Tracker News 12(1): 8.
- Holroyd, G.L., C. Conway & H.E. Trefry. 2011. Breeding Dispersal of a Burrowing Owl from Arizona to Saskatchewan. Wilson Journal of Ornithology 123: 378-381.
- Holt, D.W. 1986. Status report: the Shorteared Owl in the northeast. Eyas 9: 3-5.
- Holt, D.W. 1992. Notes on short-eared owl (*Asio flammeus*) nest sites, reproduction, and territory size in coastal Massachusetts. Canadian Field-Naturalist 106: 352-356.
- Johnson, J.A., T.L. Booms, L.H. DeCicco & D.C. Douglas. 2017. Seasonal movements of the Short-eared Owl (*Asio flammeus*) in western North America as revealed by satellite telemetry. Journal of Raptor Research 51: 115-128.
- 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.
- Keyes, K.L., M.A. Gahbauer & D.M. Bird. 2016. Aspects of the breeding ecology of Short-eared Owls (*Asio flammeus*) on Amherst and Wolfe Islands, Eastern Ontario. Journal of Raptor Research 50: 121-124.
- Korpimäki, E. & K. Norrdahl. 1991. Numerical and functional responses of Kestrels, Short-eared Owls, and Long-eared Owls to vole densities. Ecology 72: 814–826.
- Laurin, L. 2018. Short-eared Owl banding recovery database export. Bird Banding

Office, Canadian Wildlife Service, Ottawa, Ontario.

- Leasure, S.M. & D.W. Holt. 1991. Techniques for locating and capturing nesting female Short-eared Owls (*Asio flammeus*). North American Bird Bander 16: 32-33.
- Migration Research Foundation. 2007. Shorteared Owl: Results. Website: http://www. migrationresearch.org/research/shortear/track2007.html (accessed December 2017).
- National Audubon Society. 2010. The Christmas Bird Count Historical Results [Online]. Website: http://www.christmasbirdcount.org (accessed December 2017).
- Pardieck, K.L., D.J. Ziolkowski Jr., M. Lutmerding, K. Campbell & M.-A.R. Hudson. 2017. North American Breeding Bird Survey Dataset 1966 - 2016, version 2016.0. U.S. Geological Survey, Patuxent Wildlife Research Center. Website: www.pwrc.usgs. gov/BBS/RawData/ (accessed December 2017).
- Pitelka, F.A. & G.O. Batzli. 2007. Population cycles of lemmings near Barrow, Alaska: a historical review. Acta Theriologica 52: 323-336.
- Priestley, D.L., G.L. Holroyd & C.E. Priestley. 2008. Short-eared owl invasion at Beaverhill Lake, AB, winter 2005-06. Blue Jay 66: 131-138.
- Randall, T.E. 1925. Abnormally large clutches of eggs of Short-eared Owl (Asio flammeus). Canadian Field-Naturalist 39: 194.
- Steenhof, K., K.K. Bates, M.R. Fuller, M.N. Kochert, J.O. McKinley & P.M. Lukacs. 2006. Effects of radio-marking on Prairie Falcons: attachment failures provide

insights about survival. Wildlife Society Bulletin 34: 116-126.

- Swengel, S.R. & A.B. Swengel. 2014. Shorteared owl abundance and conservation recommendations in relation to site and vegetative characteristics, with notes on northern harriers. Passenger Pigeon 76: 51-68.
- Therrien, J-F., G. Gauthier & J. Bety. 2012. Survival and reproduction of adult Snowy Owls tracked by satellite. Journal of Wildlife Management 76: 1562-1567.
- Tseng, W., W-L. Lin & S-M. Lin. 2017. Wintering ecology and nomadic movement patterns of short-eared owls *Asio flammeus* on a subtropical island. Bird Study 64: 317-327.
- Wiggins, D.A., D.W. Holt & S.M. Leasure. 2006. Short-eared Owl (Asio flammeus), The Birds of North America Online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca NY. Website: http://bna.birds.cornell.edu/bna/species/062 (accessed December 2017).