Migration timing and routes, and wintering areas of Flammulated Owls

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ABSTRACT. Determining patterns in annual movements of animals is an important component of population ecology, particularly for migratory birds where migration timing and routes, and wintering habitats have key bearing on population dynamics. From 2009 to 2011, we used light-level geolocators to document the migratory movements of Flammulated Owls (*Psiloscops flammeolus*). Four males departed from breeding areas in Colorado for fall migration between ≤5 and 21 October, arrived in wintering areas in Mexico between 11 October and 3 November, departed from wintering areas from ≤6 to 21 April, and returned to Colorado between 15 and 21 May. Core wintering areas for three males were located in the Trans-Mexican Volcanic Belt Mountains in the states of Jalisco, Michoacán, and Puebla in central and east-central Mexico, and the core area for the other male was in the Sierra Madre Oriental Mountains in Tamaulipas. The mean distance from breeding to wintering centroids was 2057 ± 128 km (SE). During fall migration, two males took a southeastern path to eastern Mexico, and two males took a path due south to central Mexico. In contrast, during spring migration, all four males traveled north from Mexico along the Sierra Madre Oriental Mountains to the Rio Grande Valley and north through New Mexico. The first stopovers in fall and last stopovers in spring were the longest in duration for all males and located 300–400 km from breeding areas. Final spring stopovers may have allowed male Flammulated Owls to fine tune the timing of their return to high-elevation breeding areas where late snows are not uncommon. One male tracked in both years had similar migration routes, timing, and wintering areas each year. Core wintering and final stopover areas were located primarily in coniferous forests and woodlands, particularly pine-oak forests, suggesting that these are important habitats for Flammulated Owls throughout their annual cycle.

RESUMEN. **El calendario y las rutas de migración, y las zonas de invernada de *Psiloscops flammeolus***
La determinación de los patrones de movimientos anuales de los animales es un componente importante de la ecología de la población, especialmente para las aves migratorias donde el calendario y las rutas de migración y las zonas de invernada tienen una influencia clave en la dinámica de poblaciones. Desde 2009–2011, se utilizó geolocalizadores sensibles a la luz para documentar los movimientos migratorios de tecolotes flameados (*Psiloscops flammeolus*). Cuatro machos abandonaron las zonas de reproducción en Colorado para la migración de otoño entre el 5 al 21 de octubre, luego llegaron al sitio de invernada en México entre el 11 de octubre y el 3 de noviembre, y finalmente abandonaron los sitios de invernada entre el 6 al 21 de abril y regresaron a Colorado entre el 15 y el 21 de mayo. Para tres machos las zonas núcleo de invernada fueron localizadas en las montañas del Cinturón Volcánico Trans-Mexicanos en los estados de Jalisco, Michoacán y Puebla en el centro y el centro-este de México. La zona núcleo del otro macho fue ubicada en las montañas de la Sierra Madre Oriental en Tamaulipas. La distancia media entre las centroides de las zonas de cría e invernada era 2057 ± 128 (SE) km. Durante la migración de otoño, dos machos tomaron una ruta sudeste hasta el este de México, y otros dos machos tomaron una ruta al sur hasta el centro de México. Durante la migración de primavera, en cambio, los cuatro machos viajaron al norte desde México a lo largo de las montañas de la Sierra Madre Oriental en el Valle del Río Grande y al norte a través de Nuevo México. En el curso de migración en otoño y en primavera, las primeras paradas fueron los más largos de duración de todas paradas de los machos y estaban situados entre 300 y 400 km de las zonas de reproducción. Las paradas finales de primavera pueden haber permitido los búhos machos a ajustar el momento de su regreso a las zonas de cría a altitud elevada, donde no es raro que nieva a fines de la primavera. Un macho seguido en ambos años tenía el calendario, las rutas de migración, y las zonas de invernada similares cada año. Zonas núcleo de invernada y de paradas definitiva fueron localizadas principalmente en bosques de coníferas y en bosques de pino y encino en

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particular, lo que sugiere que estos bosques son hábitats importantes para *Psiloscops flammeolus* a lo largo de su ciclo anual.

An understanding of factors affecting the population ecology of migratory birds requires information about the entire annual cycle and, for most species, less is known about the non-breeding season (Faaborg et al. 2010). Choices of migration routes and timing, as well as habitats associated with stopovers and wintering destinations, may strongly affect patterns of abundance, survival, and reproduction (Sillett and Holmes 2002, Norris et al. 2004), and may be mediated by connectivity between breeding and wintering areas (Trierweiler et al. 2014), body condition (Marra et al. 1998), and environmental conditions (Sillett et al. 2000). Given their direct bearing on population dynamics, movement patterns and habitat associations during migration have important implications for the conservation and management of bird populations.

Despite their significance, information about migratory movements and habitats has been particularly difficult to acquire for small migratory birds because of the limited number of recoveries of bands, and weight constraints of radio- and satellite-transmitters (Linkhart et al. 1998, Bridge et al. 2011). Stable hydrogen isotopes have proven valuable for estimating latitude of breeding (Hallworth et al. 2013) and non-breeding areas (Hobson et al. 2004), but not for estimating longitude (Bowen et al. 2005), and cannot be used to infer migration routes or timing. However, photosensitive geolocators have become sufficiently lightweight in the past decade to yield a growing body of data on annual movements of small (<50 g) birds, including Black Swifts (*Cypseloides niger borealis*; Beason et al. 2012), Wood Thrushes (*Hylocichla mustelina*; Stutchbury et al. 2009), and Kirtland's Warblers (*Setophaga kirdlandii*; Ewert et al. 2012).

Flammulated Owls (*Psiloscops flammeolus*) are small, insectivorous raptors that breed in coniferous forests in western North America (Linkhart and McCallum 2013). Although early researchers considered these owls to be non-migratory (Phillips 1942), Winter (1974) provided evidence that at least northern populations were migratory, based on their apparent absence from breeding areas during the winter months (Phillips 1942), fall vagrancy

(Woolfenden 1970), lack of evidence for torpor (Banks 1964, Ligon 1969), and lack of strong plumage variation across their range, in contrast to sedentary species of owls (Marshall 1967). More recently, evidence indicating that Flammulated Owls are long-distance migrants has included high gene flow among populations (Arsenault et al. 2005, Mika 2010), high body condition scores or significant gains in mass during pre-migratory or migratory periods (Linkhart and Reynolds 1987, DeLong 2006, Stock et al. 2006), and a latitudinal cline in wing length (Marshall 1967, Smith et al. 2012), which is correlated with migration distance (Wiedenfeld 1991). However, still lacking is information about migratory timing and routes, and winter destinations. Winter records exist from southern Mexico to El Salvador (Linkhart and McCallum 2013), but the migratory status of these owls was unknown.

Habitat use by Flammulated Owls outside of the breeding season is poorly understood. As secondary cavity-nesters (Linkhart and McCallum 2013), breeding owls are most often associated with the distribution of yellow pine (sub-family *Ponderosae*), particularly ponderosa (*Pinus ponderosa*) and Jeffrey pine (*P. jeffreyi*; Linkhart et al. 1998, Nelson et al. 2009), although they also breed in dry conifer forests dominated by other pines and Douglas-fir (*Pseudotsuga menziesii*; Howie and Ritcey 1987, Dunham et al. 1996), and in quaking aspen (*Populus tremuloides*) forests (Marti 1997). Owls captured at fall banding stations in Nevada, New Mexico, and Idaho were associated with mixed-conifer or dry forests containing pine (DeLong et al. 2005, Stock et al. 2006, Smith et al. 2012), and owls were netted in pinyon-juniper (*P. edulis-Juniperus* sp.) woodlands in spring in New Mexico (Balda et al. 1975), but the extent to which these forests served as breeding vs. stopover habitat needs clarification. Winter records in Mexico and Central America were associated with pine-oak forests (Linkhart and McCallum 2013), but, as noted, owls in these forests may have been year-round residents.

Taken collectively, available data suggest that coniferous forests, often containing pine, are important for Flammulated Owls throughout

their annual cycle. If corroborated, this association raises concerns because pine forests have incurred dramatic structural and floristic changes resulting from overgrazing, logging, and fire suppression in the southwestern United States (Brown and Wu 2005), and illegal logging and habitat conversion in Mexico and Central America (Cairns et al. 2000, Brower et al. 2002). Given the status of Flammulated Owls as sensitive or a conservation concern in the United States (Witt 2005, USFWS 2008), a species of special concern in Canada (COSEWIC 2010), and a priority species for assessing effects of habitat changes in western forests (Donovan et al. 2002), determining habitat associations during the non-breeding season is important for clarifying their conservation needs.

We used geolocators to study the migration of male Flammulated Owls captured on breeding territories in Colorado from 2009 to 2011. Specifically, our objectives were to determine (1) the routes and timing of fall and spring migration, (2) the locations of wintering areas, and (3) habitats associated with wintering areas and select stopover sites.

METHODS

Study areas. We captured owls in three study areas (500 ha each) on the Pike National Forest in central Colorado, all of which are part of long-term investigations of habitat use and demography (Linkhart et al. 2006, Linkhart and Reynolds 2007). Study areas were 5–15 km apart, and had a mean latitude of 39.1°N and mean longitude of 105.1°W. Forests consisted of ponderosa pine/Douglas-fir on ridgetops and south-facing slopes, Douglas-fir on north-facing slopes, and quaking aspen in drainages. Elevations ranged from 2550 to 2855 m.

Locating and capturing owls. We targeted breeding males for geolocator attachment because they are more readily captured than unpaired males (Linkhart and Reynolds 1997), and because they are more likely to be recaptured than females because of their greater fidelity to breeding territories (93% for males vs. 56% for females; Linkhart and Reynolds 2007). We captured males during nestling and post-fledging periods (July and August; Reynolds and Linkhart 1984) at nests or in mist nets accompanied by playback of the territorial calls of males.

Data collection. We deployed 16 geolocators assembled by British Antarctic Survey (BAS), including six units of model Mk14S in 2009 and 10 units of Mk12S in 2010. Geolocators were programmed to measure ambient light levels every minute and store the maximum light level during each 2-min (Mk12S model) or 10-min period (Mk14S model). The dimensions of the Mk14S model were 20 × 9 × 5.5 mm and they weighed 1.5 g, and the dimensions of the Mk12S model were 20 × 8 × 4 mm with a weight of 0.9 g; both models had a light sensor mounted at the end of a 30-mm stalk angled at 30° to ensure the sensor cleared the feathers. Both models had two small metal loops on the posterior end for activating and downloading data via PC computer.

We attached geolocators to owls using back-pack harnesses, similar to those used for attaching radio-transmitters to Flammulated Owls (Reynolds and Linkhart 1984, Linkhart et al. 1998). We used two 12-cm-long lengths of flat polyester elastic braid (3.1 mm) as harness material. Each length was tied to posts on the anterior end of geolocators, passed over the shoulders and crossed on the breast, brought beneath the wings and tied to the posterior loops on geolocators. We then secured the harness ends and harness crossing with Gorilla™ glue. Geolocators with the harness had a total weight of either 1.9 g (Mk14S model) or 1.3 g (Mk12S), representing 2.5–3.7% of the mean breeding mass of males (53.4 ± 0.6 g [SE]; Linkhart and McCallum 2013), well within the recommended guidelines (Cochran 1980, Caccamise and Hedin 1985). We deployed most geolocators (94%; 15 of 16) during the nestling period; one was deployed after the male's owlets fledged. After attaching geolocators, which required 20–30 min, males typically flew to perches and preened and tugged at harness straps for 10–30 min before returning to normal behaviors. We observed five males during portions of one to four nights before their owlets fledged; all of these males exhibited normal flight behavior, and light sensor stocks on all geolocators (and harness on one male that we recaptured on three separate nights) appeared to be in their original positions. Nest-cavity entrances of all males were sufficiently large (6–8 cm diameter) to prevent geolocators from catching or rubbing when males entered or exited cavities.

Data analysis. We employed BASTRAK software (ver. 18) to download and process data

from geolocators. Internal clocks of most geolocators incurred little drift over deployment (<4 min/yr), and we used DECOMPRESSOR to correct for such drift. However, one geolocator (on male 64737) incurred considerable clock drift (32 min) over its ~1 yr deployment. We attempted to correct this error, which only affected longitude of locations, by adding sufficient time (6 min) to the true download time so that mean longitude of adjusted locations (after performing TRANSEDIT2; below) from June to August matched the longitude of the breeding area (105.1°W). This shifted longitude of this male's locations during deployment by 1.5° west.

We used TRANSEDIT2 to evaluate ambient light conditions associated with each datum and to calculate daily times of sunrise and sunset. To capture light levels associated with dusk/dawn light transitions (approximately $-5°$), we used a light transition threshold of two, which minimized likelihood of extraneous shading events affecting calculations of day length. We also evaluated each data file in TRANSEDIT2 and identified shading events that artificially created sunrises and sunsets, and excluded these from analysis. We used geospatial data from Colorado breeding areas to calculate sun elevation angles and ground-truth location estimates. Sunrise and sunset transitions were determined based on a sun elevation angle of -3.9 to $-4.2°$, depending on individual geolocators. Longitude is determined by calculating the absolute time of local midnight/noon and latitude by comparing night/day length. We used only noon locations in our determinations of daily and seasonal locations because, based on the activity at fall migration stations (DeLong 2006, Stock et al. 2006), we assumed owls migrated at night and remained stationary at day roosts. Based on the comparisons of mean latitude ($39.05 \pm 0.16°$; $N = 3$ owls) and longitude ($-104.83 \pm 0.16°$) for calculated geolocator locations of males on breeding areas from June to August to known locations of males on breeding areas, we determined that geolocator locations had a mean error of 43.2 ± 6.7 km during breeding. Because distinguishing between night/day length on dates around equinoxes is not possible, we excluded locations ±15 d around equinoxes for determining latitude. After excluding locations owing to equinox periods and light-level interference, we had an average of 229.3 ± 6.6 locations for three males that carried geolocators

for ~1 yr, and 620 locations for one male that carried a geolocator for ~2 yr. We used an average of 99.0 ± 4.3 locations/owl (range = 89–112) to map wintering areas.

We identified dates of departure from breeding areas and wintering areas based on shifts of longitude greater than 2° in a direction consistent with migration (*sensu* Stanley et al. 2012) during the period ±15 d of equinoxes. However, for males that moved due north or south from breeding or wintering areas, we identified dates of departure based on shifts of latitude >2° in a direction consistent with migration. We defined a stopover as an area where males remained stationary for ≥2 d (*sensu* Stutchbury et al. 2009, Delmore et al. 2012), and locations were clustered within a radius of ±200 km (rounded mean error reported by Phillips et al. 2004). A few solitary locations were identified as stopovers, but only if they were >200 km from other locations, and their positions were consistent with the chronology and direction of migration. We mapped locations and measured distances in ARCMAP (ESRI 2012). To evaluate spatial relationships and biotic community associations, we identified aggregations at stopovers and wintering areas using Kernel Density in Spatial Analyst (ARCMAP), and set the search radius at 200 km and grid size at 2 km (*sensu* Bächler et al. 2010). We calculated kernels for stopovers with ≥5 locations, and used the entirety of winter locations for kernel calculations. We used Isopleth in Geospatial Modeling Environment (Beyer 2012) to generate 50% (referred to as "core areas" hereafter), 75%, and 90% density polygons on kernel raster data. We evaluated biotic community composition within core areas at stopover sites and wintering areas using a digitized, ecologically based map of biotic communities of North America (Brown et al. 2007; community descriptions in Brown et al. 1998). Values are presented as means $\pm$ SE.

RESULTS

We recovered four geolocators from males recaptured in 2011 on Colorado breeding territories, including one of six geolocators attached in 2009 and three of 10 attached in 2010. The 2009 geolocator was carried by male 64514 for 731 d, whereas the 2010 geolocators were carried for 332, 349, and 364 d, respectively. Overall

recovery rate for males with geolocators (4 of 16; 25%) was lower than the return rate for males with leg bands only from 2009 to 2011 (90.5%, 19 of 21) and from 1981 to 2003 (84%, 81 of 97; Linkhart and Reynolds 2007). However, all recaptured males appeared in good physical condition and had greater mass (mean = 56.9 ± 2.2 g) than when geolocators were attached (51.0 ± 2.6 g; paired t_3 = −3.2, P = 0.05), including male 64514, whose mass increased 13% from 2009 to 2011. After removal of geolocators, we observed small areas of worn feathers and/or new pin feathers where geolocators and harnesses had rested, but noted no evidence of skin abrasions, scar tissue, or injuries. Two of the recaptured males were tending nests with eggs and two were tending nests with owlets, and all owlets fledged from the four nests.

Males left breeding areas and began fall migration between 5 and 21 October in 2009 and 2010; the departure date of one male could not be determined in 2010 because of its proximity to the equinox (Table 1). Three males with known departure dates left breeding areas within a 6-d period over 2 yr (5 October in 2009, and 10 and 11 October in 2010; Table 1). After departing, initial stopover sites of all males were located 300–400 km from breeding areas and clustered within a 100-km radius in east-central New Mexico (Fig. 1). Duration of this stopover (mean = 7.0 ± 2.7 d, range = 2–13 d; Table 1) was the longest in duration during fall migration, and the habitat in core stopover areas consisted primarily of shortgrass prairie (70 ± 12%) and conifer woodland or forest (15 ± 13%). Migration pathways of males diverged after stopover. Two males (64654 and 64737) moved southeast, with stopovers near the lower Rio Grande River Valley, and then continuing south through the Sierra Madre Oriental Mountains to wintering areas in eastern Mexico (Fig. 1). The two other males (64514 in 2009, and 64614) flew due south, with stopovers in southern New Mexico or west Texas, and then continuing along the Mexican Plateau to wintering areas in central Mexico (Fig. 1). Because of persistent shading events, we were unable to determine the locations of fall stopovers for male 64514 in 2010. Total duration of fall migration ranged from 1 to 3 weeks (Table 1), and the mean duration of stopovers (range = 4 – 8) was 2.4 ± 0.6 d (range = 1–13 days) (Fig. 1). Males arrived at wintering areas between 11 October and 3 November, with

Table 1. Phenology of fall and spring migration, and mean degrees latitude and longitude (±SE) for centroids of 50% kernel density wintering areas, initial fall stopover areas, and final spring stopover areas for four male Flammulated Owls with geolocators from 2009 to 2011. Means are presented ± SE.

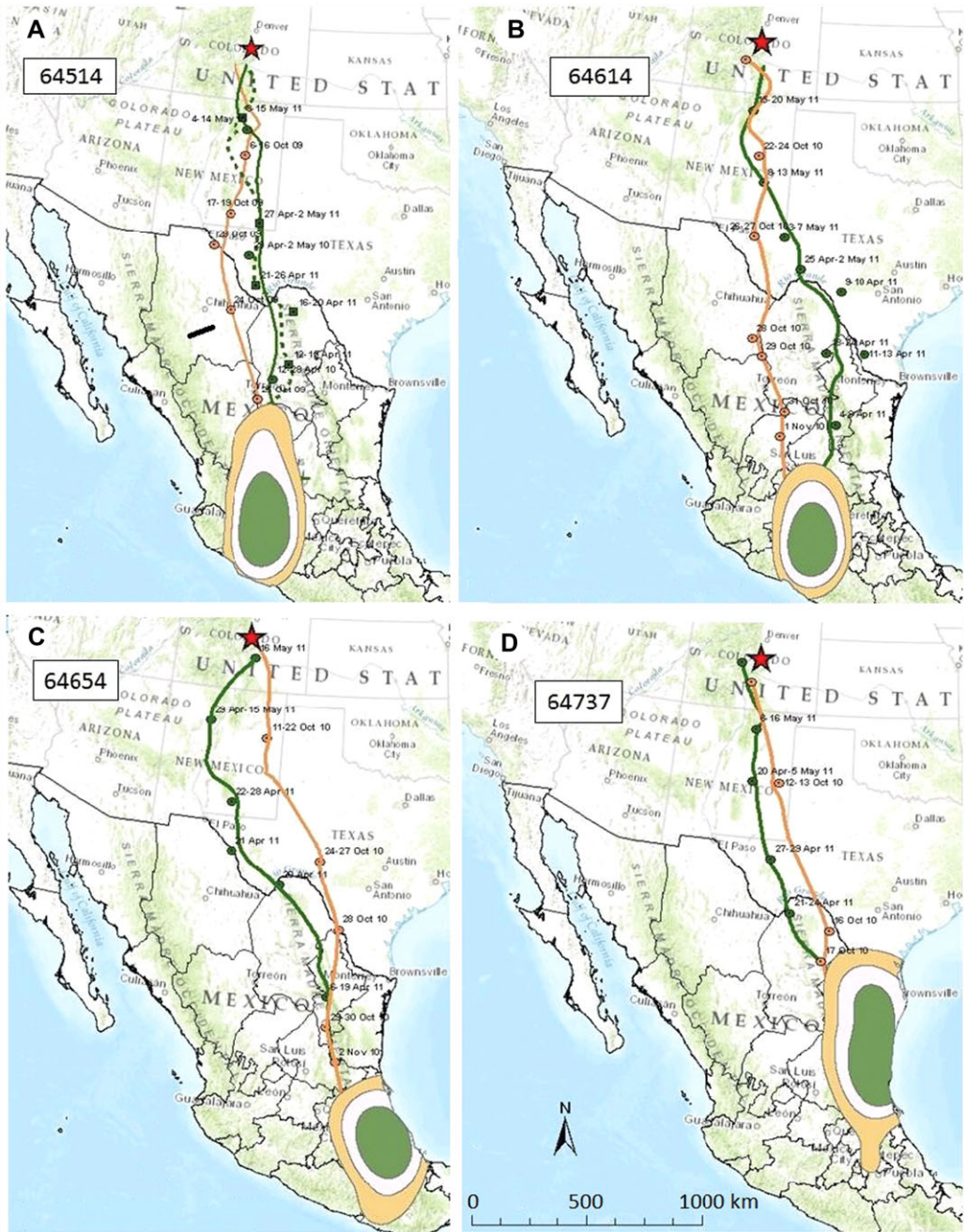| | Fall migration | | | | Wintering area | | | | Spring migration | | | |
| | | Initial stopover | | | | | | | Final stopover | | | |
ID	Depart CO	Duration	Latitude	Longitude	Arrive	Latitude	Longitude	Depart	Duration	Latitude	Longitude	Arrive CO
64514 (2009–2010)	5 October	6–16 October	34.8 ± 0.4	−104.8 ± 0.2	27 October	20.4 ± 0.1	−102.6 ± 0.1	13 April	4–14 May	36.3 ± 0.6	−104.7 ± 0.5	15 May
64514 (2010–2011)	≤5 October	–	–	–	11 October	22.1 ± 0.1	−102.4 ± 0.1	12 April	3–15 May	36.3 ± 0.3	−105.2 ± 0.3	16 May
64614 (2010–2011)	19–21 October	22–24 October	34.6 ± 0.4	−104.6 ± 0.3	2 November	19.5 ± 0.1	−101.0 ± 0.1	≤6 April	15–20 May	36.3 ± 0.3	−105.2 ± 0.4	21 May
64654 (2010–2011)	10 October	11–22 October	35.2 ± 0.3	−103.8 ± 0.2	3 November	19.5 ± 0.1	−97.6 ± 0.1	≤6 April	29 April to 15 May	35.5 ± 0.2	−106.8 ± 0.1	16 May
64737 (2010–2011)	11 October	12–13 October	34.2 ± 0.4	−103.6 ± 0.2	18 October	23.9 ± 0.2	−98.6 ± 0.1	21 April	6–16 May	36.3 ± 0.2	−105.0 ± 0.2	17 May

Fig. 1. Migration routes during fall (light yellow lines) and spring (dark green lines), and wintering areas (polygons) of four male Flammulated Owls marked with geolocators on breeding areas in central Colorado in 2009 and 2010. Wintering areas are expressed by kernel density contours (50%, 75%, and 90%). (A) Male 64514 was tracked from 2009 to 2011 so that there are two routes for spring migration (solid line for 2009–2010, and dashed line for 2010–2011), but only one route (2009–2010) for fall migration; (B) male 64614; (C) male 64654; and (D) male 64737.

Table 2. Biotic community composition (%) within 50% kernel density areas in wintering areas in Mexico of four male Flammulated Owls with geolocators from 2009 to 2011. Superscripts refer to biotic communities described by Brown et al. (1998).

	Biotic community				
ID	Evergreen forest/woodland[a]	Dry deciduous forest[b]	Thornscrub[c]	Grassland[d]	Miscellaneous[e]
64514 (2009–2010)	26.2	12.2	8.2	53.4	–
64514 (2010–2011)	12.0	0	18.4	69.6	–
64514 Mean (2 yr)	19.1	6.1	13.3	61.5	–
64614 (2010–2011)	38.3	14.7	12.6	34.3	–
64654 (2010–2011)	61.0	19.0	2.0	12.7	7.4
64737 (2010–2011)	17.3	35.0	42.3	4.2	1.1
Mean	34.0	18.7	17.6	28.2	2.1

[a]Transvolcanic evergreen forest and woodland; Madrean evergreen forest and woodland; Guerreran evergreen forest and woodland; Veracruz evergreen forest.
[b]Guerreran dry deciduous forest; Sinaloan dry deciduous forest; Tamaulipan semi-deciduous forest.
[c]Guerreran thornscrub; Tamaulipan thornscrub.
[d]Semi-desert grassland.
[e]Veracruz cloud forest; Veracruz evergreen rain forest.

male 64514 arriving 16 d earlier in 2010 than in 2009 (Table 1).

Core wintering areas for three males were located in the Trans-Mexican Volcanic Belt Mountains, with one core area centered near the Sierra Madre Occidental Mountains in Jalisco and west Michoacán, one in central Michoacán, and one near the Sierra Madre Oriental Mountains in Puebla (Fig. 1). The core wintering area for the remaining male was located near the northern Sierra Madre Oriental Mountains in Tamaulipas (Fig. 1). Between 2009–2010 and 2010–2011, 90% kernel wintering areas for male 64514 overlapped by 85% and core wintering areas overlapped by 44% (Fig. 1). Habitat within core wintering areas of all males reflected the heterogeneous topography of the mountainous regions, with evergreen forest and woodland most common (34 ± 10%), followed by grassland (28 ± 13%; Table 2).

Mean distance between centroids of breeding areas and wintering areas was 2057 ± 128 km (range = 1760–2306 km), and the rate of travel during fall migration for males with known departure/arrival dates was 97 km/d (male 64514 in 2009) and 293 km/d (male 64737). Duration on wintering areas for two males with known departure/arrival dates was 183 d (male 64514 in 2010) and 185 d (male 64737) and, for other males, it was ~4–5 mo (Table 1). Departure dates from wintering areas varied by ≥15 d, with the latest departure on 21 April by a

male (64737) that wintered farthest north, and departures by male 64514 differed by just one day between years (Table 1).

Spring migration routes differed from fall routes, with all males following a similar pathway north from Mexico along the Sierra Madre Oriental Mountains to the Rio Grande Valley, and north through New Mexico to breeding areas in Colorado (Fig. 1). Total duration of spring migration ranged from 4 to 8 weeks (Table 1), and the mean duration of stopovers (range = 3–8) was 7.2 ± 0.9 d (range = 1–17 days) (Fig. 1). Rate of travel during spring migration for three males (including male 64514 in 2010 and 2011) with known departure/arrival dates ranged from 57 to 68 km/d. Excluding final stopovers, core areas of prolonged (≥5 d) stopovers were primarily associated with mountain ranges and the Rio Grande Valley, and consisted of desert scrub (43 ± 7%), semi-desert grassland (25 ± 5%), thornscrub (14 ± 6%), and evergreen forest and woodland (6 ± 2%) habitat.

Final spring stopover sites for all males were located in northern New Mexico, ~300 km from breeding areas, and these stopovers were most prolonged of both migrations (mean = 11.6 ± 1.8 d, range = 6–17 d; Fig. 1, Table 1). Stopover locations for three males, including male 64514 in 2010 and 2011, were clustered in a 300-km^2 area in the southern Sangre de Cristo Mountains, and the stopover location for the

other male (64654) was located 200 km further west in the Jemez Mountains (Fig. 1, Table 1). Core stopover areas consisted primarily of Great Basin conifer woodland (34 ± 3%), shortgrass prairie (32 ± 2%), and Rocky Mountain conifer forest (22 ± 2%) habitat. After leaving these final stopover sites, all males arrived in breeding areas within a 6-d span in mid-May, with one day separating the arrival dates of male 64514 in 2010 and 2011 (Table 1).

DISCUSSION

Our study is first to report on migration routes and timing, and wintering destinations of Flammulated Owls. Core wintering areas for three of four males, all of which bred in central Colorado, were located in central and east-central Mexico and were associated with the Trans-Mexican Volcanic Belt Mountains in Jalisco, Michoacán, and Puebla; the core area for the other male was associated with the northern Sierra Madre Oriental Mountains in Tamaulipas. Our results support Marshall's (1997) suggestion that Flammulated Owls (*P. f. frontalis*) that breed in the Great Basin and central and southern Rocky Mountains winter in central and southern Mexico.

Our results also indicate that Flammulated Owls have one of the longest migrations (~2000 km) among North American owls. Other owls, including Snowy Owls (*Bubo scandiacus*; Holt et al. 2015), and Long-eared Owls (*Asio otus*; Marks et al. 1996), exhibit nomadic movements or irruptive migrations that may be longer than 2000 km between breeding and wintering areas, but only Burrowing Owls (*Athene cunicularia*) have populations whose annual migrations between Canada and Mexico may exceed this distance (Holroyd et al. 2010).

Overstory vegetation in core wintering areas consisted primarily of evergreen forest and woodland communities, which are dominated by stands of pine-oak across the Volcanic Belt region of central Mexico (Nixon 1993, Styles 1993). In the central state of Michoacán, where portions of core wintering areas of two males were located, one of us (BDL) captured and/or heard numerous singing males in pine-oak forests at elevations of 2000–2500 m from January to March in 2008 and 2015, whereas few owls were detected in adjacent forest types at higher elevations (B. Linkhart, unpubl. data).

Analyses of stable isotopes in feathers of owls captured in these pine-oak forests indicated occupancy by resident owls and at least one migrant owl (B. Linkhart, unpubl. data). Given the anthropogenic threats facing pine-oak forests in Mexico (see references cited in Introduction), additional study is needed to determine the extent to which migratory owls winter in these forests.

Fall and spring migrations were marked by several temporal and spatial patterns. For owls whose dates of departure could be determined, three males left breeding areas in mid-October and two males left wintering areas in mid-April. At least during fall migration, proximate cues associated with departure likely reflect insect abundance, particularly moths, which are the principal prey of Flammulated Owls during the breeding season in Colorado (Reynolds and Linkhart 1987), but become increasingly scarce by early October when night temperatures regularly fall below 0°C (B. Linkhart, pers. obs.). Indeed, fall departures were followed immediately by the longest stopover of the fall migration, with all males located 300–400 km from breeding areas at lower elevations in eastern New Mexico where food was likely more abundant.

Fall and spring migrations differed both in their flight pathways and duration, with males taking two different routes in the fall, but similar routes north in the spring. Other investigators have reported distinct seasonal pathways by migrants (Egevang et al. 2010), including "loop migrations" in the western (Delmore et al. 2012) and eastern hemispheres (Schmaljohann et al. 2012). In part related to the more direct migration by owls in the fall, spring migration was, on average, twice as long in duration as fall migration, primarily because the mean duration of spring stopovers was nearly three times longer. This pattern differs from the pattern of many migrants, where spring migration is more abbreviated as birds attempt to establish early residency on breeding territories (Stutchbury et al. 2009, Heckscher et al. 2011, Seavy et al. 2012, but see Callo et al. 2013). However, owls arriving too early on high-elevation breeding territories in Colorado may face severe consequences because late cold snaps and spring snowstorms may greatly decrease insect availability for extended periods (B. Linkhart, pers. obs.). For long-distance migrants, prey abundance and/or

temperature may function critically as cues at stopover locations for adjusting the timing of arrival in breeding areas (Marra et al. 2005, Newton 2006, Balbontín et al. 2009). Indeed, final stopovers of male Flammulated Owls in our study, which were the most prolonged of both migrations, were followed immediately by arrival in breeding areas. Arrival dates of males differed by just 6 d over 2 yr, despite variation in departure dates from wintering areas of at least 15 d.

The longest (≥5 d) stopovers during spring migration were located in mountains, suggesting that coniferous forests and woodlands were important habitats for resting and refueling. The clustered locations of the final stopover sites in northern New Mexico were in areas primarily associated with Great Basin conifer woodland, a lower-elevation forest dominated by pinyon-juniper (B. Linkhart, pers. obs.) and Rocky Mountain conifer forests. Based on mistnetting data from New Mexico and Arizona, Balda et al. (1975) suggested that Flammulated Owls may use lower-elevation forests when migrating north, but ponderosa pine forests, where sampling revealed a greater abundance of large-bodied moths in the fall, when migrating south. If true, this may explain the unmarked male Flammulated Owls heard singing in low elevation pine-oak woodlands, but not in higher-elevation mixed-conifer forest, in northern New Mexico in April 1986 (B. Linkhart, unpubl. data). We found no evidence of prolonged fall stopovers by males in ponderosa pine forests during fall migration, as suggested by Balda et al. (1975), suggesting that primarily hatch-year owls of local or regional origin, rather than adults, stopover for extended periods in these forests. This may explain why hatch-year Flammulated Owls were trapped more frequently than adults at fall banding stations in New Mexico where ponderosa pine was common (DeLong 2006).

Coupled with breeding areas, biotic communities in core wintering areas, and at least the longest stopovers, provide further evidence that Flammulated Owls are associated with pine-dominated forests throughout their annual cycle. Given the similarity in physiognomy of pine forests on wintering areas, stopover sites, and breeding areas, Flammulated Owls may have evolved behaviors to exploit similar habitats during both the breeding and non-breeding seasons.

In Colorado, radio-tagged male Flammulated Owls preferentially foraged by gleaning moths within spacious crowns of large conifers that were also used for territorial singing and day-roosting (Linkhart et al. 1998).

The degree to which core wintering areas of males were distributed across Mexico suggests diffuse migratory connectivity between breeding and wintering areas (*sensu* Webster and Marra 2005) of *P. f. frontalis*, and may underlie evidence for high gene flow among widely distributed breeding populations (Arsenault et al. 2005, Mika 2010). Larger sample sizes are needed to clarify juxtaposition of wintering areas, and elucidate patterns of connectivity between wintering and breeding areas, among populations and across all sub-species of Flammulated Owls because the extent of connectivity may have important conservation implications (Trierweiler et al. 2014). We found evidence of strong convergence in spring migration routes among males, despite disparity in the locations of core wintering areas, possibly reflecting limited availability of suitable stopover locations for owls while migrating through xeric landscapes in the southwestern United States and Mexico. Although other long-distance migrants also show evidence of restricted migration routes (Phillips 1975, Trierweiler et al. 2014), some species have more variable migration pathways (Delmore et al. 2012, Stanley et al. 2012). Climate change may impose increased restrictions on selection of suitable stopover sites by Flammulated Owls in coming decades because projections for warmer, drier conditions (IPCC 2013) may reduce or modify distributions of coniferous forests and woodlands in this region (Hanson and Weltzin 2000).

Reports of repeat migrations by individuals are rare, and our repeat tracking of one male (64514) revealed considerable overlap in estimates of wintering areas and spring migration routes over 2 yr. Whether this reflected actual reuse of the same local habitats is unknown, but male Flammulated Owls are known to exhibit strong fidelity to breeding territories (Linkhart and Reynolds 2007) as well as foraging habitats within territories (Linkhart et al. 1998), and other migratory birds with strong fidelity to breeding territories also exhibit fidelity to wintering areas (Mouritsen 2003, Wunderle et al. 2010). The apparent reuse of spring migration stopover sites and routes between years by the

male in our study is consistent with patterns exhibited by some species of birds (Stanley et al. 2012, Trierweiler et al. 2014), but not others (Cantos and Telleria 1994, Merom et al. 2000, Alerstam et al. 2006), where individuals show flexibility in use of migration routes in consecutive years.

The recovery rate of geolocators (25%) in our study was much lower than return rates of males with only leg bands. Besides one male found dead ~50 km from his breeding territory in late fall (BDL, unpubl. data), we were uncertain whether males that were not recovered had died during migration or emigrated. However, the absence of any males returning to breeding areas without geolocators, coupled with high fidelity to breeding territories (Linkhart and Reynolds 2007), suggest that the owls had not survived migration. The results of other studies of the impacts of geolocators on birds have been equivocal (Gómez et al. 2014, Pollet et al. 2014), indicating that further study is needed to develop optimal taxon-specific marking practices.

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