Spatiotemporal Habitat Use by Breeding Flammulated Owls (*Psiloscops flammeolus*) in Colorado

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Abstract

Animals exist in landscape mosaics of high-quality and poor-quality habitat and evolution selects for behaviors that allow animals to occupy spaces that improve their fitness. Individuals employ innate and learned behaviors to select habitat over multiple spatial scales. Flammulated Owl (*Psiloscops flammeolus*) habitat selection has been studied with radio telemetry, but few studies have investigated Flammulated Owl habitat selection as a function of time. This investigation employed pinpoint GPS technology to identify changes in temporal/spatial habitat use by male Flammulated Owls 1) throughout a night of activity and 2) throughout a breeding season. During the 2017 summer breeding season, I deployed trackers on six territorial males in Pike National forest during their incubation and nestling stages, and I recorded GPS fixes during early and late-night activity. I compared understory and overstory characteristics between selected and available habitat, analyzed territory sizes based on temporal variables, and investigated patterns in their movement paths. Results suggested that Flammulated Owls select habitats with relatively high ground cover, but overstory was not significantly different between used and unused but available habitats. Results suggested that males employ different behavioral decisions based on the time of night and time during the breeding season. This study illustrated how Flammulated Owls shift their habitat use based on their energetic needs and resource availability as functions of time. In an increasingly unstable ecosystem, understanding how Flammulated Owls interact with their habitats is important in order to predict their responses to environmental disturbances and climate change.

Introduction

Vertebrates, as relatively large and mobile organisms, interact with their habitats at a conspicuous scale. They select habitats based on the relative availability of space and resources (Montgomery et al. 2013). Habitat use defines the general area on which animals occur not necessarily by choice, habitat selection encompasses the choices animals make in order to occur in a specific area, and habitat preference generalizes the type of habitat an entire species tends to prefer (Montgomery et al. 2013). Investigations into organisms' associations with particular habitats have been a dominant pursuit throughout ecological study in order to define relationships between demography and physical factors in environments (Huey 1991). Habitat selection and its effects on the survival and reproduction of individuals exemplifies how animals have evolved to occupy specific environments, because natural selection favors behaviors that result in the occupation of high quality habitat.

Habitat selection functions through a series of hierarchal choices made by individual animals that occur at decreasing scales. First-order habitat selection occurs at a geographic scale and contains all possible habitat on which a species could survive (Johnson 1980). Second-order habitat selection encompasses an individual's home range and the resources it needs to survive at specific times during its life history (Johnson 1980). Home ranges occupied during a breeding season, for example, sustain the survival and reproduction of a breeder in a population (Johnson 1980). Third-order habitat selection addresses the microhabitats individuals utilize to accomplish behaviors necessary for survival and reproduction (1980). Specific habitat characteristics are ideal for particular individual behaviors. For example, wolves (*Canis lupus*) in the northern Rockies select for habitats with shrub communities and high diversity for cover in order to successfully capture diverse prey species (Milakovic et al 2011). Fourth-order habitat selection relates to the daily spatial decisions individuals make within their ranges based on their immediate needs. For example, female Snowy Owls (*Nyctea scandiaca*) in Alberta defend winter territories that contain foraging habitat; they move between foraging habitat and ecotones throughout the day in order to acquire energy and defend their claimed resources (Boxall and Lein 1982).

Based on the presumption that evolution should favor animals that select habitats where energetic consumption outweighs energetic expenditure, optimal foraging theory established a model to predict the behaviors animals utilize to maximize energy input for energy output (Stephens 1986). Animals must acquire enough energy to persist and reproduce through foraging, and the behaviors associated with foraging require energetic output. The size of prey and search time dictate the amount of energy an individual must devote to foraging. The spatial distribution of prey within a system additionally constrains a predator's choices within a landscape (Mittelbach 1981). Habitats are heterogeneous, and some areas provide more resources and energy than others, and uneven resource availability within a landscape creates the need for an individual to move about their space efficiently (Mittelbach 1981). Animals that use space in a way that offsets energetic expenditure are more likely to successfully reproduce and feed into succeeding generations (Petren 2001). For this reason, habitat selection is especially important for breeding individuals.

Habitat selection at one order is limited by the selection at broader scales (Linkhart et al. 1998), and habitat use patterns occur at different spatial scales over varying temporal scales (Sutton et al. 2017). For example, the choices an animal makes at second-order level dictate the choices available at the third- and fourth-order. Snowshoe hares (*Lepus americanus*) were shown to move into suboptimal habitats as a response to increased population density (Kawaguchi and Desrochers 2018). When the hares occupied suboptimal habitats, their third- and fourth-ordered habitat selection were minimal because microhabitats for specific behaviors were simply unavailable. Additionally, individuals that occupied suboptimal habitats were significantly less productive than those that occupied more productive habitats (Kawaguchi and Desrochers 2018). The availability of high quality microhabitats within a home range, therefore, is a vital for successfully survival and reproduction.

Factors that affect habitat selection of individuals manifest in patterns expressed by populations. Landscapes provide different concentrations of resources over both time and space, creating a mosaic of habitat available to an individual (Mcnew et al. 2013). Due to an uneven availability of conditions and resources, animals make choices in response to perceived risk and reward (Mayor et al. 2009). MacArthur (1953) described that animal movements can be density-dependent, and populations are regulated by available habitat. In addition to the density of individuals in an area, the relative quality of a habitat influences the spaces animals occupy. The heterogeneous landscapes on which animals exist contain both “high-quality” and “poor-quality” habitat (Pulliam 1988). American pikas (*Ochotona princeps*, Lagomorpha) exhibit source-sink population structure in which birth rates exceed death rates in meadows (high-quality habitat) while birth rates fail to reach replacement levels in snowbeds (poor-quality habitat) (Kreuzer and Huntly 2003). Individuals emigrate from high-quality habitat into poor-quality habitat when carrying capacity is reached, a density-dependent reaction (2003).

A home range associated with second-order habitat selection sustains the survival of an individual and successful reproduction during breeding seasons (Johnson 1980). The sizes of home ranges are determined by the unique ways in which animals interact with their habitats based on their energetic needs. Energy is lost as a food chain progresses from primary production to tertiary consumption, thus apex predators have larger ranges than species that occupy lower trophic levels

(Golley 1960). Even within the same trophic levels, home range size varies between species based on species size, diet, and foraging strategies. The area of a home range encompasses the caloric needs of an individual, and large animals tend to have the largest home ranges (McNab 1963). Golden Eagles (*Aquila chrysaetos*) have relatively large home ranges compared to other raptors due to their size (Marzluff et al. 1997b). However, body mass and subsequent energetic requirements do not entirely account for home range sizes; the taxa and breadth of prey, which affect the distribution of those species, also influences the size of predator home ranges (Peery 2000). Marzluff et al. (1997a) noted that Prairie Falcons (*Falco mexicanus*) increased their home ranges when their prey shifted from ground squirrels to birds and reptiles, which are more sparsely distributed. Specialized predators that feed on only a few species tend to have larger home ranges than generalists with a wide prey base because they require more area to encounter their prey species (Peery 2000). Raptors that feed on birds tend to be less opportunistic than mammal-eating raptors, thus they range over larger areas (Peery 2000).

Understanding animals' home ranges contributes to understanding factors that influence choices they make at a landscape level and reveals the types of habitat on which they rely during a particular moment in their life history. It is important to quantify second order habitat selection and home range size because it can clarify how species interact with their spatial environments. Many methods estimate the size and shapes of home ranges using point location data acquired from radio-tracking or GPS-tracking, and they are based on distances between points or densities of locations. Minimum convex polygons (MCP) are one of the simplest ways to estimate home ranges (White and Garrot 1990), delineated by the smallest possible polygon that contains spatial points associated with an animal's movement. A second approach, kernel density, utilizes contours that enclose a specific proportion (usually 95%) of the entire probability density of all spatial points

(Katajisto and Moilanen 2004). While imperfect, analysis assumes uniform use of an enclosed area. The kernel density method offers an estimate of utilization distribution, showing the probability of an animal occurring at locations within the home range estimate, which offers a more complex analysis of an individual's home range than the MCP method. Methods of defining home range vary but all attempt to delineate the space individuals require at specific moments in their life history. Establishing the outer boundaries of a home range shows simplified estimations of second order habitat selection, but MCPs and 95% kernel contours do not necessarily lend insight into an individual's use of space within its home range (Harris et al 1990). Many species utilize space use in ways that cannot be fully understood through home range estimations alone (Breed et al. 2017). For example, Individuals can move between "core areas" that function as centers of use within the same home range. Kernel contours applied to distributions of data points that enclose a smaller proportion of points (50%) can be used to examine areas within home ranges that support intense use (Barg et al. 2005).

Within an animal's home range, habitat selection can be analyzed at a finer resolution in order to understand choices associated with microhabitat use. Ecologists have long sought to understand why animals disperse and why they move in particular ways within their home ranges (Johnson 1980). In its simplest form, movement is irregular and mimics the random dispersal that occurs at an atomic level in which one directional movement does not influenced a consecutive movement (Nathan et al. 2008). Random walk models can be employed to understand movement between location points (Bovet and Benhamou 1988). Animal movements have a partially random pattern, but the location of one point influences the location of a consecutive point. When direction is biased in some way, movement occurs as a correlated random walk. Animal movement paths can be understood through the distribution of changes of direction (location points) and the distribution of step lengths between consecutive points. Movement path characteristics can reflect energetic expenditure, and paths that are longer and less direct confer more energy spend moving across a landscape. Thus, habitat selection as a function of movement is important to study in order to understand how animals spend energy as they move around their systems to obtain energy (Shepard et al. 2013, Stephens 1986).

While landscape interactions have been extensively studied in birds, few studies have directly investigated temporal changes in habitat selection at multiple scales. As extremely mobile fauna, birds provide an important model to study habitat selection. Avifauna are wide-ranging and have a high potential to encounter many different habitat types, especially species that are long distance migrants (Cody 1985). For this reason, they express very specific and highly selective behaviors associated with habitat choice and usage. Predatory birds are especially influenced by landscape complexity because of their need to see, capture, and consume prey (Atuo and O'Connell 2017). Thus, a predatory bird's success depends on the characteristics of its habitat at multiple hierarchical orders. Species express varying levels of habitat specificity at different scales, and the landscapes and habitats they select are tightly related to behaviors associated with their life history (Linkhart et al. 1998). As a predatory, avian, long distance migrant, Flammulated Owls are an important model organism to investigate habitat selection as a function of time over multiple scales.

Flammulated Owls show high territory fidelity within and between seasons, which allows study of individual habitat selection throughout and between breeding seasons (Linkhart and Reynolds 2007). In Colorado, they occupy heterogeneous mixed conifer forests, which provides an opportunity to investigate the microhabitats they require for foraging, territorial defense, etc. (Linkhart et al. 1998). Flammulated Owls, as important indicator species in Ponderosa pine ecosystems (Linkhart et al. 1998), are important to study to investigate the system's stability. Additionally, they occupy a system that is an immediate concern for conservation (Yanco and Linkhart 2018). Natural fire cycles have historically been suppressed in Ponderosa pine ecosystems in Colorado, and the build-up of foliage and understory puts the system at risk for high severity forest fire (Veblen et al. 2000). Understanding how Flammulated Owls interact with their habitat over space and time is increasingly important to 1) predict potential impacts to their ecology following a severe disturbance and 2) address forest management practices to mitigate risk of high severity burns.

This study investigated the temporal changes in Flammulated Owl habitat selection in Colorado. Flammulated Owls have a breeding range that extends from the Rocky Mountains to the Pacific Coast Mountains, from central Mexico to southern Canada (Linkhart et al. 1998). Flammulated Owls that breed in the central and southern Rocky Mountains are migratory and winter in central and east-central Mexico near the Trans-Mexican Volcanic Belt Mountains. (Linkhart et al. 2016). They occupy landscapes of mixed-conifer forests that often contain oak and pinyon at low elevations and fir and quaking aspen at higher elevations. Linkhart et al. (2016) investigated habitat selection in Flammulated Owls in Colorado using radio telemetry and found that habitat use was affected by the distribution of old ponderosa pine (*Pinus ponderosa)* forests. They preferentially establish territories ranging between approximately 10-25 ha in forests containing old ponderosa pine/Douglas-fir (*Pseudostuga menziesii)* over other available overstory types (Linkhart et al. 1998).

Flammulated Owls aggressively defend their home ranges, so their territories are equivalent to their home ranges. Third order habitat selection in male Flammulated Owls encompasses the decisions they make to defend their territories and provide food for their mates, among other behaviors. As a territorial species, male Flammulated Owls aggressively defend their home range from conspecifics and sing territorial calls from large conifers on mid-slopes and ridge-tops (Linkhart and Reynolds 1987, 1998). As single-prey loaders, breeding male Flammulated Owls deliver one item of prey to their mate or nestlings at a time (Linkhart and Reynolds 1987). In order to meet their broods' energetic requirements, males visit foraging areas within their territories many times throughout the night. Linkhart et al. (1998) found that breeding males disproportionately use intensive foraging areas that contain old ponderosa pine and Douglas-fir over story. Males generally establish nests within intensive foraging areas, perhaps to minimize energy expenditure associated with travel time.

While much is understood about habitat selection in Flammulated Owls, few studies have addressed spatial decisions as a function of time. Males tend to visit the nest at a higher rate during the early evening and dawn than any other time during their nocturnal activity (Reynolds and Linkhart 1984). Additionally, foraging behaviors and subsequent prey delivery behaviors change throughout the breeding season. As the primary prey providers for a brood, breeding males experience increased energetic demands as eggs hatch and nestlings grow and develop (Linkhart and Reynolds 1987). During incubation, the male returns to the nest tree a few times throughout the night to feed the female who regulates the temperature of the eggs as they develop (Linkhart and Reynolds 1987). When the eggs begin to hatch, the male returns to the nest site at a higher rate to provide energy to the brood. After nestlings develop enough for thermoregulation, the female joins the male in foraging and delivering prey to the nest (Linkhart and Reynolds 1987). This is especially important as the calories required by the nestlings increases as they grow at a rapid rate.

The energetic demands faced by males throughout the breeding season could influence how they utilize the habitat within their territory. Few studies have quantified the changes in

Flammulated Owl habitat selection over time. Previous study into Flammulated Owl habitat selection relied on radio telemetry and on-site data collection (Linkhart et al. 1998). Many modern habitat selection studies have used satellite trackers to obtain high resolution spatial data on animal movements, but implementation of this technology to study Flammulated Owl movement has been limited by the species' small mass. Caccamise and Hedin (1985) recommended a tracker's mass should be less than 5% of a study individual's mass. This study utilized recently developed satellite trackers that are less than 2.0g, which is smaller than 5% of the average mass of a male Flammulated Owl (53.4 ± 0.6 g [SE], Linkhart and McCallum, 2013). This new tracking technology will add to the existing understanding of Flammulated Owl habitat selection by enabling us to acquire spatial movement information over a continuous time frame. With this capability, I set up a controlled data collection protocol over two distinct time scales; I compared habitat use between early- and late-night movements and between incubation (June) and the nestling period (July).

Understanding temporal changes in habitat selection offers important insight into the relationship between Flammlated Owls and the ponderosa pine/Douglas-fir ecosystem. I investigated temporal changes in Flammulated Owl habitat selection over two time frames: early- vs. late-night and incubation vs. nestling period. I attached Lotek GPS pinpoint-10s to six breeding males in the Manitou Experimental forest. I programmed the devices to collect spatial information during early- and late-night foraging over a span of four-six days during both incubation and the nestling period. I then compared the habitat in used and unused areas within the study birds' territories and compared second and third order habitat selection between incubation and the nestling stage and between early and late-night movements.

My research examined the following questions:

(1)Do used habitats differ from available but unused habitats within established territories? Based on previous research that found Flammulated Owls disproportionally use old ponderosa pine/Douglas fir over story to forage (Linkhart et al. 1998), I expected intensive use areas to contain more coniferous habitat than unused areas within the territory. I expected used areas to contain lower tree density and higher crown volume, both of which are characteristic to habitats associated with foraging and territorial defense (Linkhart et al. 1998). Because Flammulated Owls additionally forage at lower canopy levels, I expected ground cover to be higher in used areas than unused but available areas.

(2)Do breeding male Flammulated Owls use their habitats differently between incubation and the nestling period? Due to increased energetic demands on males as their broods hatch and develop, I expected males to capitalize on intensive use areas closer to nest sites to minimize energetic deficits associated with travel time (Stephens et al. 1986). I expected that home range estimates will be smaller later in the season, as males will most likely spend time delivering food to the nest. Smaller late season home ranges might correlate to energetic constraints Flammulated Owls face as single prey loaders. This contradicts other studies that show raptors expand their ranges as a response to higher energetic demands (Peery 2000). Additionally, I expected higher tortuosity later in the breeding season, reflecting a change in foraging strategy to compensate for a higher prey deliver rate. I expected males to move at a faster rate later in the season as a response to higher energetic demands as well.

(3)Do breeding male Flammulated Owls use their habitats differently early at different times throughout a night of activity? Field observations showed that males forage more aggressively in the evening and early morning than in the middle of the night (Reynolds and Linkhart 1984), and I expected that study males will spend more time in intensive use areas closer to the nest between 2000-2200 than 0100-0300. I expected home range estimates to be be smaller during early night foraging than late night foraging, exemplifying their use of potential foraging areas closer to their nest sites. Additionally, I expected tortuosity in movement to be higher early at night, reflecting a tighter usage of habitat as a possible early night foraging strategy. I expected the males to move about their habitats at a faster rate during early night foraging than late night foraging.

(4)Can GPS data loggers be employed to investigate habitat selection at multiple scales? I aimed to minimize the mass of any tracker I attached to study birds, and remote data collection small enough to deploy on Flammulated Owls was not available. Additionally, the trackers could not support solar rechargeable batteries. The Lotek pinpoint 10 GPS trackers stored a limited number of spatial points and eventually ran out of battery life. One of my main objectives was to evaluate the trackers' efficacy in estimating home ranges and examining habitat selection at a fine scale.

Methods

Study Area

I conducted my study between June and September in 2017 in the Manitou Experimental Forest in Teller Co, Colorado in Dr. Brian Linkhart's Flammulated Owl study sites. The territories I examined were located within two study sites: Missouri Gulch, bounded within 7.5 km^2 with a mean elevation of 2640+-64m, and Hotel Gultch bounded within a 5.5 km^2 area with a mean elevation of 2700+-74m. These two study sites are characterized by mixed ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudostuga menziesii*) forests. Quaking aspen (*Populus temuloides*) and blue spruce (*Picea pungens*) grow in the drainage bottoms, while ponderosa pines dominate ridgetops. Douglas firs occur on more mesic north-facing slopes, while ponderosa occur on xeric south-facing slopes. Ground cover is mostly comprised of kinnikinnick (*Arctostaphylos uva-ursi*), shrubby juniper (*Juniperus communis*), and grass species. Xeric slopes at lower elevations are characterized by ground cover comprised of broad leaf yucca (*Yucca baccata*) and Gambel's oak (*Quercus gambelii*).

Nest confirmation and male capture

A team of field assistants and I located active nests by examining trees with woodpecker-excavated cavities in historical Flammulated Owl territories in the Manitou Experimental forest. Nesting habitat has been under study in the Hotel Gulch study site since 1981 and in the Missouri Gulch since 2002. Most cavities available in the study sites are those excavated by woodpecker species like Northern Flickers (*Colaptes auratus*) and Williamson's Sapsuckers (*Sphyrapicus thyroideus*). Flammulated Owls most often select nesting cavities that are at least four-six cm in diameter in quaking aspens and Ponderosa pines. We observed behavior and employed a remotely monitored camera in order to confirm the presence of established nests. We tapped on trees with suitable cavities and noted the presence of a nest if a female Flammulated Owl appeared in the cavity entrance. If this tapping method did not illicit any activity, we extended wireless cameras mounted on Hastings™ poles into cavities to visually observe their contents (Hastings™ Hot Line Tools and Equipment http://www.hfgp.com/). Hastings™ poles were extended to heights between 1.5 and 15.2 meters, a range that included the majority of Flammulated Owl nests. The cameras mounted on the poles are about four-six cm in diameter and only fit into cavity entrances larger than the diameter of the camera. When these two methods did not reveal the presence of a nest in territories typically occupied by territorial males, we observed and listened for the owls' nocturnal activity, including vocalizations associated with territorial, courtship, and feeding behaviors (Linkhart and MacCallum 2013). By tracking male and female vocalizations, we zeroed in on nest habitats and visually confirmed the presence of nest trees.

Field assistants and I capitalized on the males' single prey loading behaviors in order to capture the males at their nest sites (Linkhart et al. 1998). Males, roosting in non-nest trees, returned to the nesting cavities to feed their mates during incubation and their broods during the nestling stage. We extended mist net capture bags mounted on Hastings poles to nest height and waited for the females and males to vocalize to one another (Reynolds and Linkhart 1984). Female begging elicited prey deliveries from the males, and the males entered the cavity with food. During the late nestling stage, females contributed to prey deliveries at night and begs from owlets elicited prey deliveries from both parents. We distinguished males from females by listening to vocalizations, the males having lower pitch calls than the females (Linkhart and MacCallum 2013). Once males entered nest cavities, we covered cavity entrances with the capture bags and waited for individuals to fly into the mist net material (Reynolds and Linkhart 1984). All six males were captured using this technique during the nestling stage and five males during incubation.

Field assistants and I captured one male (A2) using a lure-net at the periphery of its territory during incubation in mid-June. A lure-net functions to capture birds by drawing them into a nylon or polyester net set up at a strategic location. We set up a 6 x 3 m mist net on 4 m tall metal poles (Reynolds and Linkhart 1984). The mist net site was on a low slope characterized by open canopy with small conifers and quaking aspen in the immediate area. We set up the net at least 150 m away from owl nest sites to ensure I did not disturb incubating females. After raising the mist net, We played a previously recorded male territorial call on a speaker. Calls were obtained from xenocanto.org, a citizen science project that allows volunteers to record and publish bird calls. In order to draw the male towards the mist net, we alternated recorded territorial calls from different individuals, moved the speaker around the mist nest, and performed our own vocal imitations to encourage the male to fly into the mist net.

Tracker attachment

The team of field assistants and I attached GPS tracking devices (Lotek Wireless™, Pinpoint 10) to captured males in order to track their movements over time. we used a backpack method developed by Reynolds and Linkhart (1984) in order to secure the trackers between the owls' scapulars. As a modification to Reynolds and Linkhart's method, we attached the harness (7.71kg test, braided nylon fishing line, Stealth) to the tracker through the trackers' two superior wire loops (1984). The harness was secured over the owls' shoulders to connect on the ventral side just under the keel and the straps were crimped together. The harness was secured under the owls' wings to reconnect to the tracker on the dorsal surface. we threaded the harness straps through loop on the anterior side of the tracker and secured them with a square knot. A crimp was used to secure the attachment after the proper fit was accomplished. We used a mechanical pencil to test the fit, aiming to fit 1 cm of the tip underneath the harness at the keel and underneath the device. We used a double-loop style with dimensions of 12.5 cm (circumference) for the neck strap and 3.5 cm (length) for the breast strap, and 15 cm (circumference) for the body strap and the criss-cross style (overall length of 21.0 cm). We aimed to have the birds in hand no longer than 45 minutes. Study birds were released after attachment at the peripheries of their territories. We watched the birds for a minimum of five minutes in order to monitor their ability to fly with the trackers. To remove trackers, we recaptured the study birds using the two techniques described above and carefully used nail clippers to cut the harness straps securing the trackers.

GPS tracker schedules

The team of field assistants and I tracked the owls throughout their 2017 summer breeding season and obtained spatial data between late June and mid-July. Within this period, we deployed trackers on study birds at two specific points in order to compare incubation and nestling stage habitat selection. Flammulated Owls begin incubation in early June and enter the nestling stage early-mid July (Linkhart and MacCallum 2013). We aimed to deploy trackers in the middle of their incubation stage and in the middle of their nestling stage. I used the DLC-1 USB Interface reader and PinPoint Host installation from Biotrack™ to program the GPS trackers. I created a schedule for the trackers so they collected GPS coordinates, or "fixes," during early night activity and late-night activity. The trackers turned on and communicated with satellites every fifteen minutes between 0900 hr-1100 hr and 0100 hr-0300 hr, and they recorded fixes until the devices ran out of battery. The Lotek trackers have the ability to record 80 fixes in a best-case scenario;

the devices stay turned on until they communicate with enough satellites to triangulate a location. They take less time to find satellites when the time between fixes is minimized, but scheduling consecutive points takes up available pace in the trackers' software. I selected the schedule described above in order to maximize the battery life of the trackers and number of fixes.

Home Ranges

I estimated individuals' home ranges using ArcGIS (ArcGIS for Desktop v10.4.1). I used a kernel density analysis to figure the 95% home range estimates and 50% core range estimates of the six birds to estimated their home ranges during incubation and the nestling stage, as well as during early and late-night movements. I additionally figured minimum convex polygons (MCP) for each data set to estimate territory boundaries for each temporal variable. I referred to 50% core range estimates as intensive use areas (IUAs). IUAs under 500 m^2 were considered too small to sample, IUAs between 500 m^2 and 4000 m^2 were considered "small", and IUAs over 4000 m^2 were considered "large" IUAs. I randomly selected two sample points in each small IUA and four in each large IUA. In total, I established 50 random sample points in used habitat. I also established 50 random sample points outside IUAs and within MCPs to serve as the available but unused samples.

During September 2017, I quantified the over-story and understory of both used and unused habitats in the six territories of the study males. At each sample point, I located the nearest tree which served as a focal point for establishing line transects that extended five meters in all cardinal compass directions. At 0.5 meter intervals on each transect, I noted the presence or absence of ground cover. At each sample point, I also noted the most abundant understory plant species and assigned the slope position as either a drainage bottom, lower slope, higher slope, or ridge top. I found the nearest trees with a diameter at breast height (DBH) greater than and less than 20cm (Figure 1). To quantify forest overstory at each sample point, I used the point-quarter method to estimate tree density in each of the two size classes in quadrant aligned with the cardinal compass directions. Trees with DBH less than 20cm make up over levels in the forest and trees with DBH over 20cm make up the higher levels. For each nearest neighbor, I recorded the tree species, DBH, condition, and distance to the focal tree, tree height, and crown dimensions.

Data Analysis

I used ArcGIS (ArcGIS for Desktop v10.4.1) to analyze the distribution of fixes from the six deployed GPS trackers. For each male, I established minimum convex polygons (MCPs) and 95% and 50% kernel contours for spatial fixes collected during incubation and the nestling stage. Minimum convex polygons conferred the smallest area that contained all of the bird's locations, 95% kernel contours conferred a spatial estimate for where the bird spends 95% of its time, and 50% kernel contours conferred a spatial estimate of where the bird spends 50% of its time. I established these spatial estimations for four time periods: early night movements during incubation, late-night movements during incubation, early night movements during the nestling stage and late-night movements during the nestling stage.

I figured the areas of these estimations and used the statistical program Minitab to compare the areas of MCPs, 95% kernel contours, and 50% kernel contours based on temporal variables. My sample size was only six individuals, so I employed a nonparametric Kruskal-Wallis test to compare the median areas of home range estimations for early and late-night movements and for incubation and the nestling stage.

Habitat Quantification

I used a number of quantitative methods to analyze habitat data I collected in the field. I compared total crown volumes, crown volumes for trees over 20cm DBH, and crown volumes for trees <20cm DBH and tree densities between used and unused sample sites. For all statistical models, I examined distributions of residual variation and employed $\log_{10}$-transformations to non-normal data. I ran two sample t-tests to compare crown volumes and tree densities between selected and available but unused sample sites in order to investigate potential selection for habitat characteristics in the forest overstory. I additionally ran two sample t-tests to compare the percent cover between selected and available habitat at ground level, 0.5m, 1.0m, and 1.5m. P values less than 0.05 were considered significant. I additionally ran a binary logistic regression to test the predictable value for each habitat characteristic for habitat use.

Movement patterns

I utilized the statistical program R (version 3.4.1, r-project.org) to examine the movement path the six owls utilized for early and late-night movement and incubation and nestling stages. I examined movement paths, or the line connecting consecutive GPS coordinates, in order to compare energy spent in transit based on temporal variables. The three movement parameters I examined were 1) step length, or distance between fixes, 2) distance between fixes and nest sites, and 3) turn angles, or the angles between two step lengths (Figure 2). All statistics were performed on the combined fixes from all six of the study birds. I calculated step length, or distance between fixes, with the following model:

$$(X_k - X_{k-1})^2 + (Y_k - Y_{k-1})^2 = ST^2,$$

where X is the horizontal aspect of a coordinate, Y is the vertical aspect of a coordinate, k is the spatial point of interest, k-1 is the preceding point, and ST is the step length between k and k-1.

I excluded fixes collected more than fifteen minutes apart in order to control time as a variable. Step length conferred estimated speed of travel, and longer step lengths were associated with faster movement between two spatial fixes. I fit gamma distributions to step lengths and compared the models between temporal variables. I additionally figured the distance between each fix and the nest site (DTN) using a similar model:

$$(X_k - X_{nest})^2 + (Y_k - Y_{nest})^2 = DTN^2$$

Longer distances were associated with males spending more time in habitat further from their nest sites. I found turn angles (TA) between each fix by measuring the angle resulting from established step vectors using trigonometry (Figure 2).

$$1 - \cos^{-1}\frac{ST_k^2 + ST_{k-1}^2 - D}{2ST_kST_{k-1}} = TA,$$

where D is the distance between the end point of ST_k and the start point of $ST_{k-1.}$

In order to analyze fourth order habitat selection and movement patterns, I applied fitted models to the distributions of step lengths between points, distances between points and the nest site, and turn angles between points. I fit a gamma distribution to step lengths and compared the models between temporal variables. Turn angles conferred tortuosity of a bird's flight path, or the "turny-around-ness." Higher tortuosity suggests a bird is spending more energy than a less tortuous flight path. I fit gamma distributions to empirical SL and DTN distributions and a Cauchy distribution to empirical turn angle distributions. I ran randomization tests to compare the distributions between temporal scales. P values less than 0.05 were considered significant.

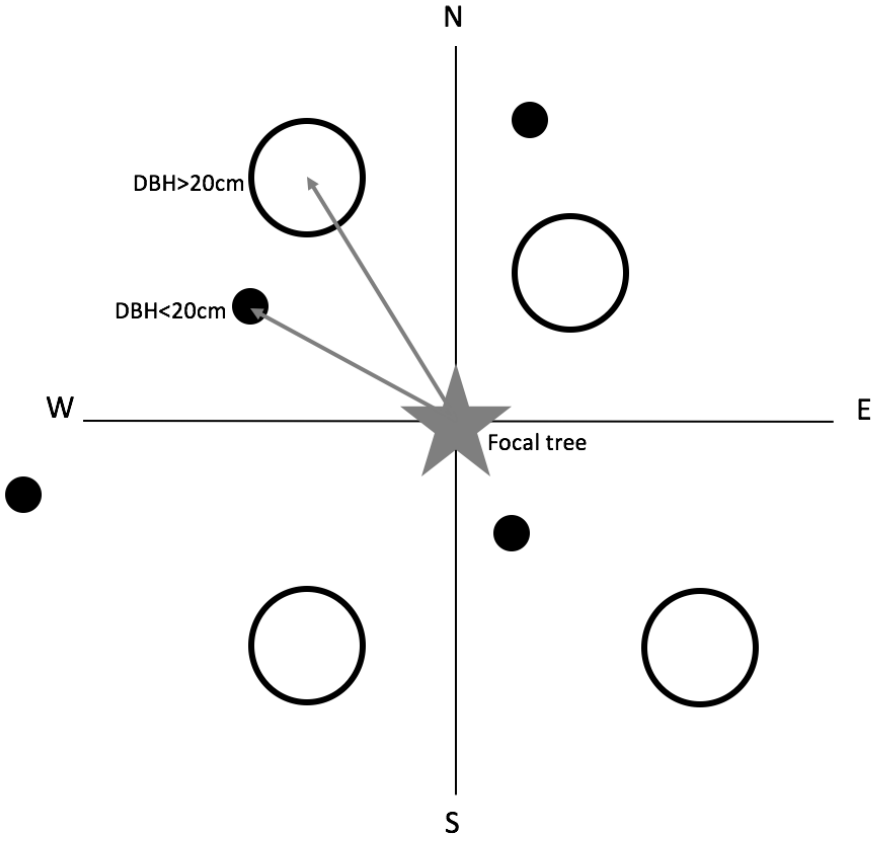


Figure 1. The point quarter analysis completed at each habitat sampling point. In each quadrant, the nearest trees with a DBH≥20cm and a DBH<20cm were selected. I identified each tree, recorded its height, crown dimensions, crown shape, and distance from focal tree. Along each transect (N/S and E/W), I tallied foliage every 1.0m along the transect from ground level, 0.5m, 1.0m, to 1.5m.

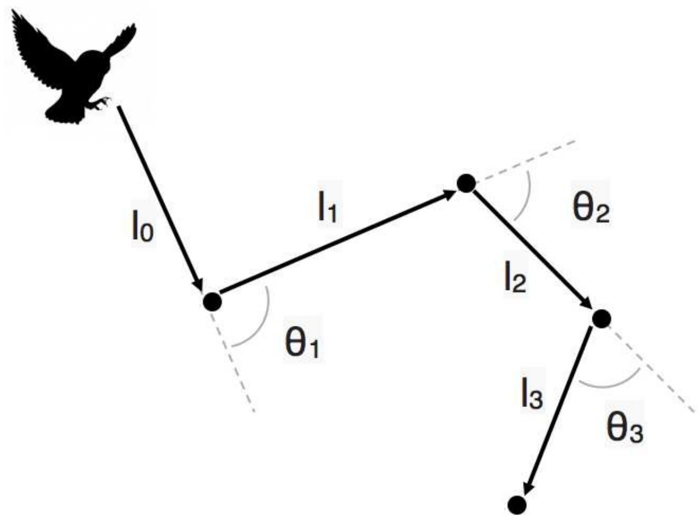


Figure 2. Step lengths (l) and turn angles (θ) in an owl's flight path. Figure is adapted from Thurfjell et al. (2014).

Results

Habitat Quantification

I did not find significant differences in overstory characteristics between selected and available sites (Figure 3). The average tree density in selected habitats was 334 $\frac{trees}{ha}$ +/-50.2SE and 379$\frac{trees}{ha}$+/-35.1 in available but unselected habitats. Tree density was not significantly different based on male owl use (t=1.18, df=97, p>0.2). The average total crown volume in selected habitats was 2719m^3+/-356 and 2236m^3+/-171 in available habitats, and total crown volumes were not significantly different based on use (t=-0.01, df=97, p>0.9). The average total crown volume for large trees (DBH>20cm) in selected habitats was 2259m^3+/-298 and 2608m^3 +/-541 in available habitats, and large tree crown volumes were not significantly different based on use (t=-0.01, df=97, p>0.9). The average total crown volume for small trees (DBH<20) in selected habitats was 1202m^3+/-228 and 139m^3+/-21 in available habitats, and small tree crown volumes were not significantly different based on use (t=-1.49, df=97, p>0.1).

I found a significant difference in ground cover at ground level, 0.5m, 1.0m, and 1.5m (Figure 4). At each level, ground cover was significantly higher in selected habitat than available but unused habitat.

The binary logistic regression showed that, when considered together, neither overstory nor understory characteristics were significant predictors for Flammulated Owl habitat use (p>0.05).

Home range estimations

Minimum convex polygons (MCPs) did not vary significantly between incubation and the nestling stages or early and late-night movements (Table 1). Trends showed that MCPs tended to be larger during the nestling stage than incubation and larger later at night than early at night.

The 95% kernel contours varied between early- and late-night movements and incubation and nestling stages (Table 1). The median 95% kernel contour was smallest for early night fixes collected during the nestling stage (Kruskal-Wallis, $p<0.05$). The largest median 95% kernel contour occurred for late night fixes collected during incubation (Kruskal-Wallis, $p<0.05$).

The male Flammulated Owls in this study tended to use more IUAs during incubation than the nestling stage (Figure 6-11). Four males used more IUAs during incubation than the nestling stage, one used two IUAs during both stages, and one used an additionally IUA during the nestling period. All males utilized IUAs around the nest site throughout the breeding season.

Movement Patterns

Fitted distributions to movement characteristics were not significantly different based on temporal variables (Figure 5). Step length fitted gamma distributions did not show significant variation between early- and late-night movements and between incubation and nestling stages (Figure 5). Fitted gamma distributions to distances between fixes and nest sites additionally did not show significant variation between early- and late-night foraging and between incubation and nestling stages. Cauchy distributions fitted to turn angle sample distributions did not show significant variation between early and late- night foraging and between incubation and nestling stages. Though insignificant, trends showed more frequent large angles and less frequent small angles during early night movements and the nestling stages, which suggests higher tortuosity in the owl movements for these temporal variables.

Nonparametric analysis of step lengths suggested that the median step length was shortest for fixes recorded during the nestling stage and early-night foraging ($p<0.05$). Longest step lengths appeared to occur during the incubation stage and late-night foraging. Step lengths between fixes were similar between incubation/early-night foraging and the nestling stage/late-night foraging. Nonparametric analysis of distance between fixes and nest sites suggested that the median distance to the nest was greatest for fixes recorded late at night during incubation ($p<0.05$). The smallest median distance occurred for early night fixes collected during the nestling stage, while the greatest distance between fixes and nest sites occurred for late night fixes collected during incubation. Median distance to the nest site was similar for early night fixes during incubation and late-night fixes during the nestling stage. Nonparametric tests did not show variation between median turn angles during early- and late-night foraging and between incubation and nestling stages ($p=0.4$).

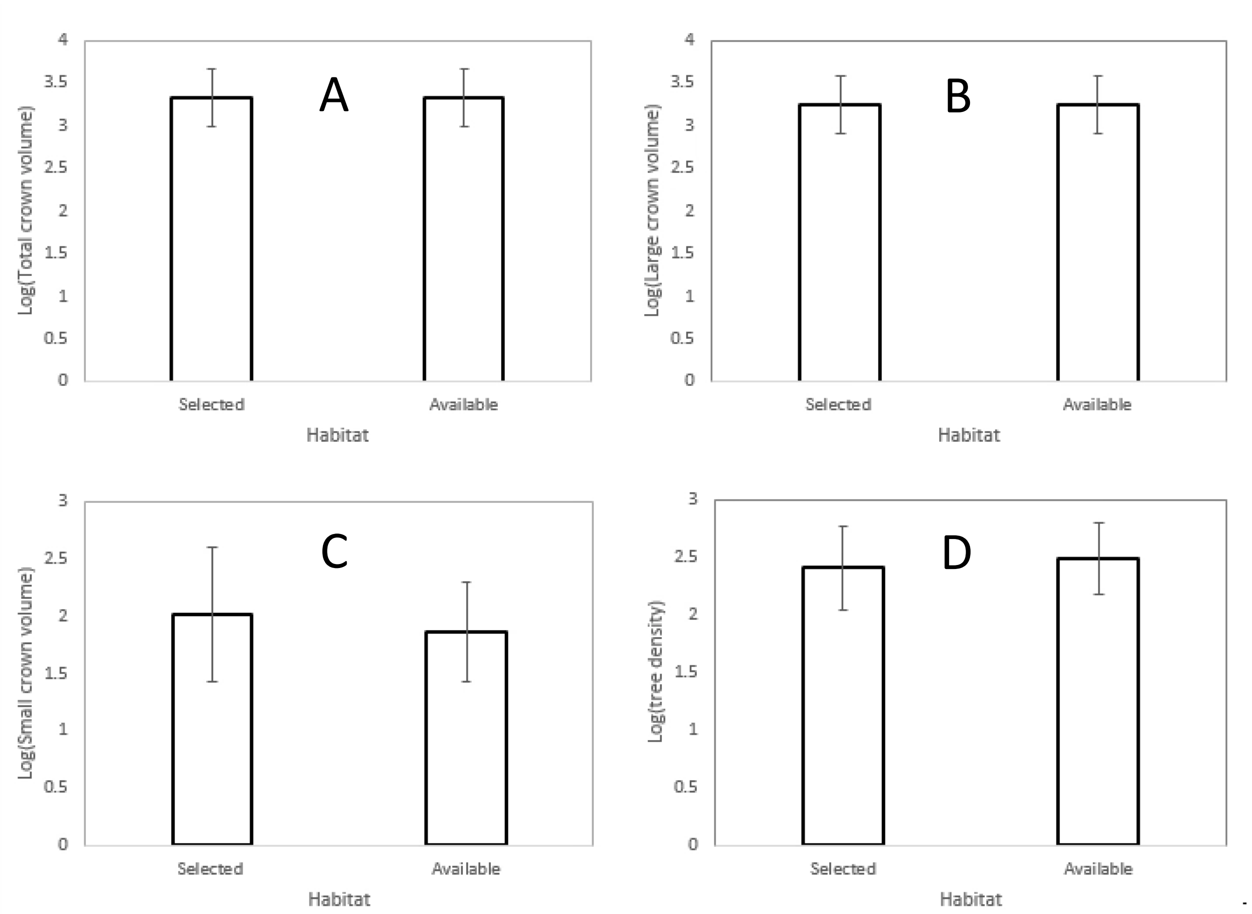


Figure 3. Habitat characteristics in used (selected) and unused (available) sample sites. Figure 3a shows that logarithmic transformed tree density did not vary between used and unused sample sites (p> 0.05). Figure 3b shows that logarithmic transformed total crown volume did not vary between used and unused sample sites (p> 0.05). Figure 3c shows that logarithmic transformed small tree crown volume did not vary between used and unused sample sites (p> 0.05). Figure 3d shows that logarithmic transformed large tree crown volume did not vary between used and unused sample sites (p> 0.05). Logarithmic transformations were utilized to normalize sample distributions.

C

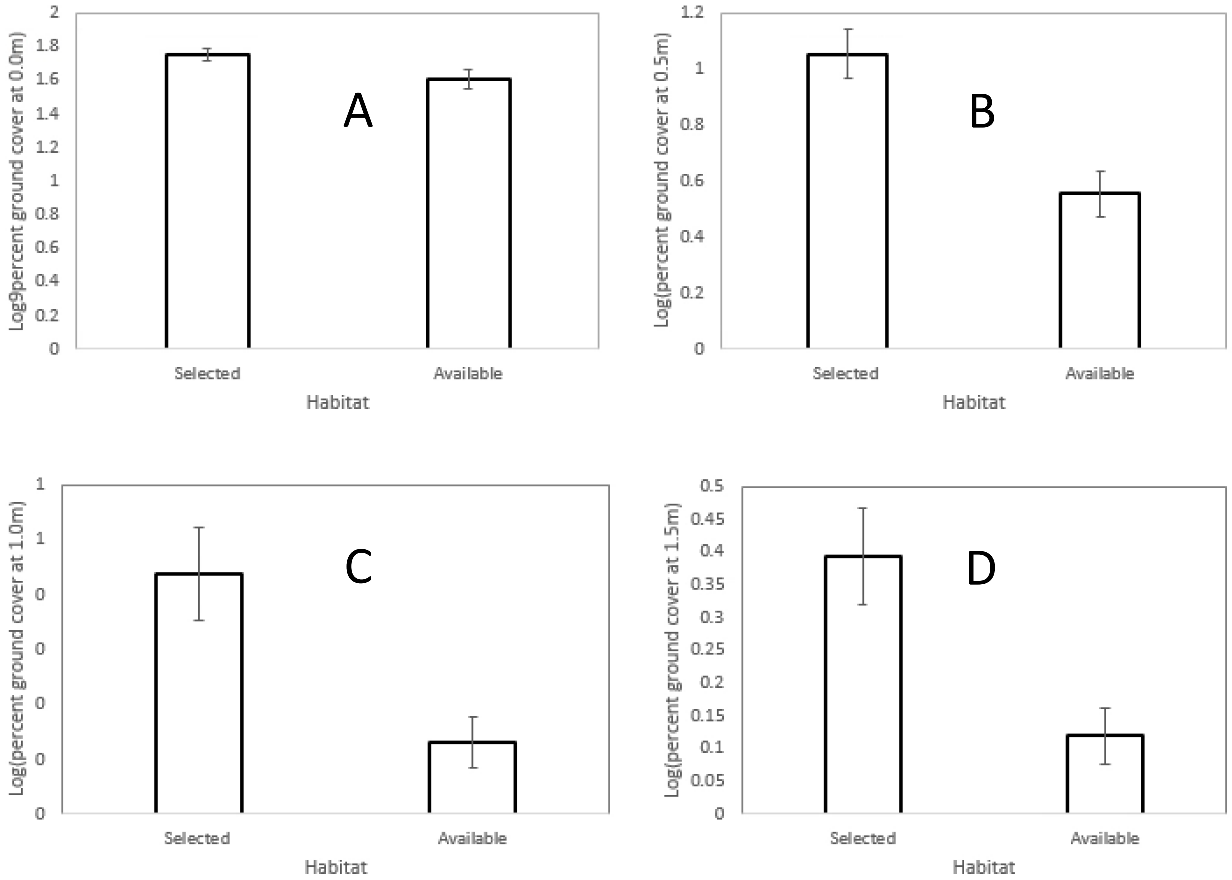
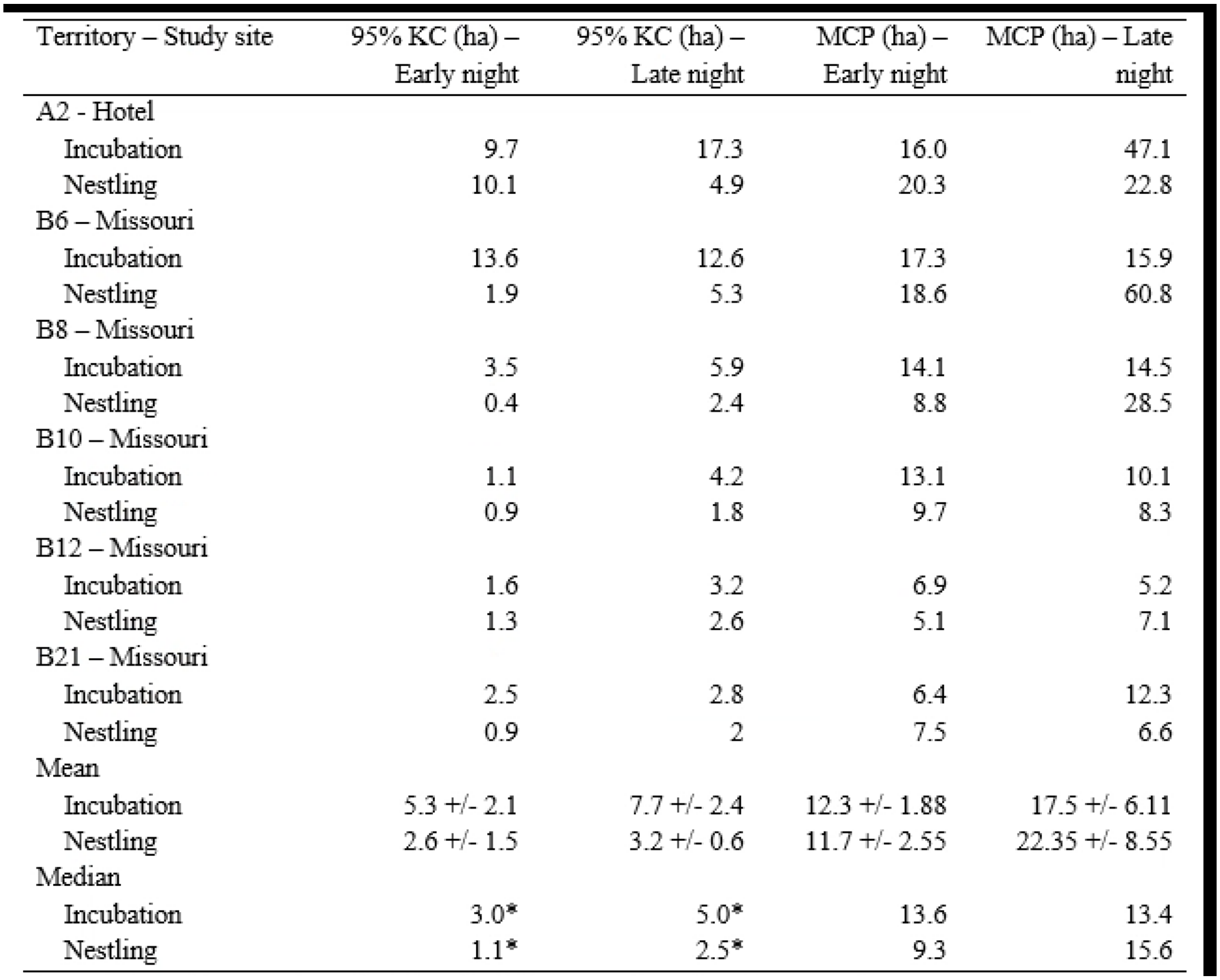


Figure 4. Ground cover in selected and available habitats. 4a shows that the logarithmic transformed percent ground cover varied between selected and available habitats at 0.0m (t=-2.21, df=87, p<0.05). 4b shows that the logarithmic transformed percent ground cover varied between habitats at 0.5m (t=-4.15, df=97, p<0.05). 4c shows that the logarithmic transformed percent ground cover varied between habitats at 1.0m (t=-3.20, df=74, p<0.05). 4d shows that the logarithmic transformed percent ground cover varied between habitats at 1.5m (t=-3.19, df=76, p<0.5).



Territory – Study site	95% KC (ha) – Early night	95% KC (ha) – Late night	MCP (ha) – Early night	MCP (ha) – Late night
A2 - Hotel				
Incubation	9.7	17.3	16.0	47.1
Nestling	10.1	4.9	20.3	22.8
B6 – Missouri				
Incubation	13.6	12.6	17.3	15.9
Nestling	1.9	5.3	18.6	60.8
B8 – Missouri				
Incubation	3.5	5.9	14.1	14.5
Nestling	0.4	2.4	8.8	28.5
B10 – Missouri				
Incubation	1.1	4.2	13.1	10.1
Nestling	0.9	1.8	9.7	8.3
B12 – Missouri				
Incubation	1.6	3.2	6.9	5.2
Nestling	1.3	2.6	5.1	7.1
B21 – Missouri				
Incubation	2.5	2.8	6.4	12.3
Nestling	0.9	2	7.5	6.6
Mean				
Incubation	5.3 +/- 2.1	7.7 +/- 2.4	12.3 +/- 1.88	17.5 +/- 6.11
Nestling	2.6 +/- 1.5	3.2 +/- 0.6	11.7 +/- 2.55	22.35 +/- 8.55
Median				
Incubation	3.0*	5.0*	13.6	13.4
Nestling	1.1*	2.5*	9.3	15.6

Table 1. Home range estimation sizes based on time of night and time during the breeding season. Nonparametric Kruskal-Wallis tests were employed to compare median 95% kernel contours (KC) and minimum convex polygons (MCP) based on temporal variables. $^*p<0.05$.

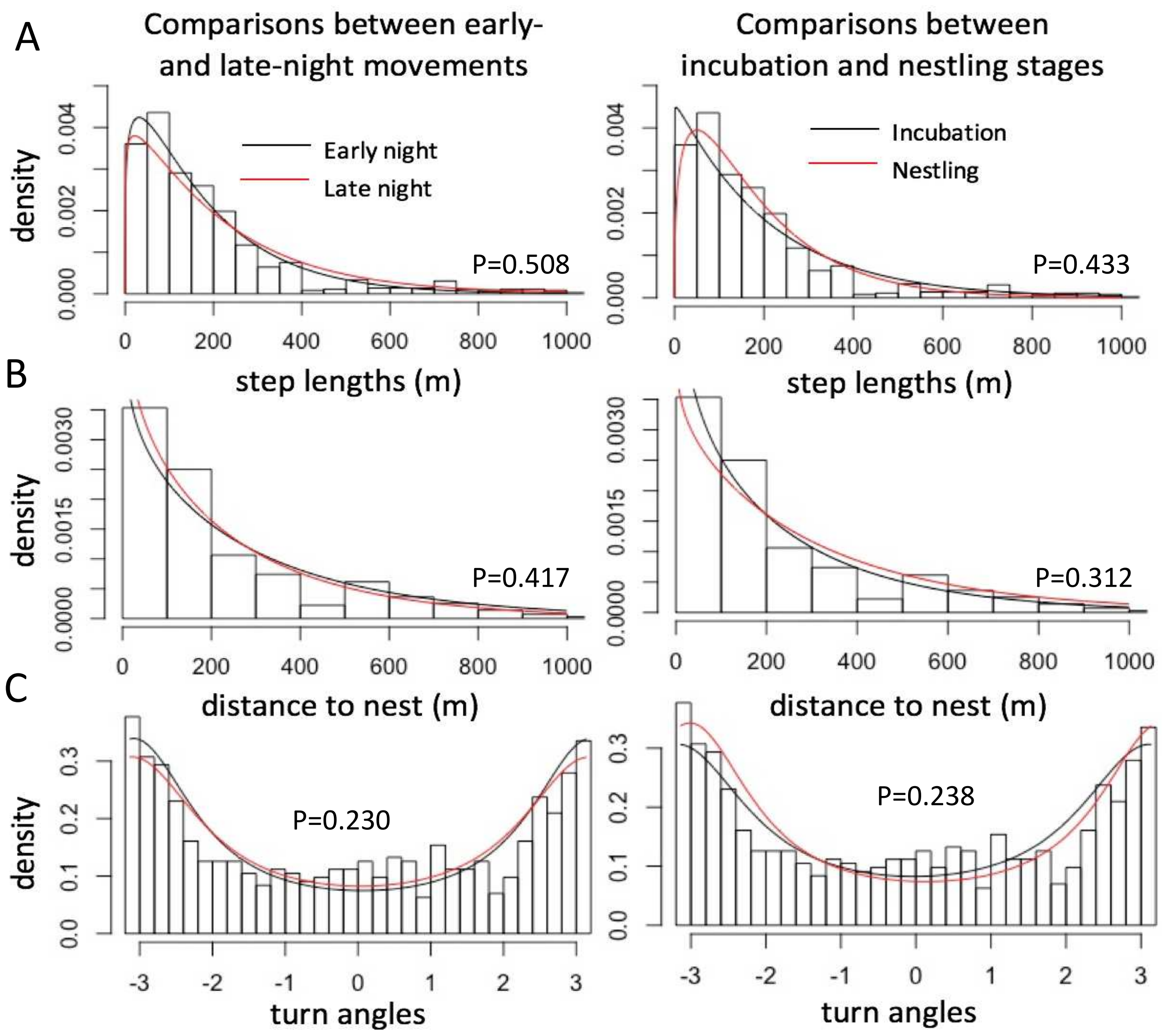


Figure 5. Fitted distributions to step lengths, distance to nest, and turn angles for multiple temporal variables. In these graphs, density represents the relative frequency of parameters. 5a shows that the distributions of step lengths (fitted gamma distributions) were not associated with either time of night or time during season ($p > 0.05$). 5b shows that the distributions of distances to nesting sites (fitted gamma distributions) were not associated with either time of night or time during season ($p>0.05$). 5c shows that the distributions of turn angles (fitted Cauchy distributions) were not associated with either time of night or time during season.

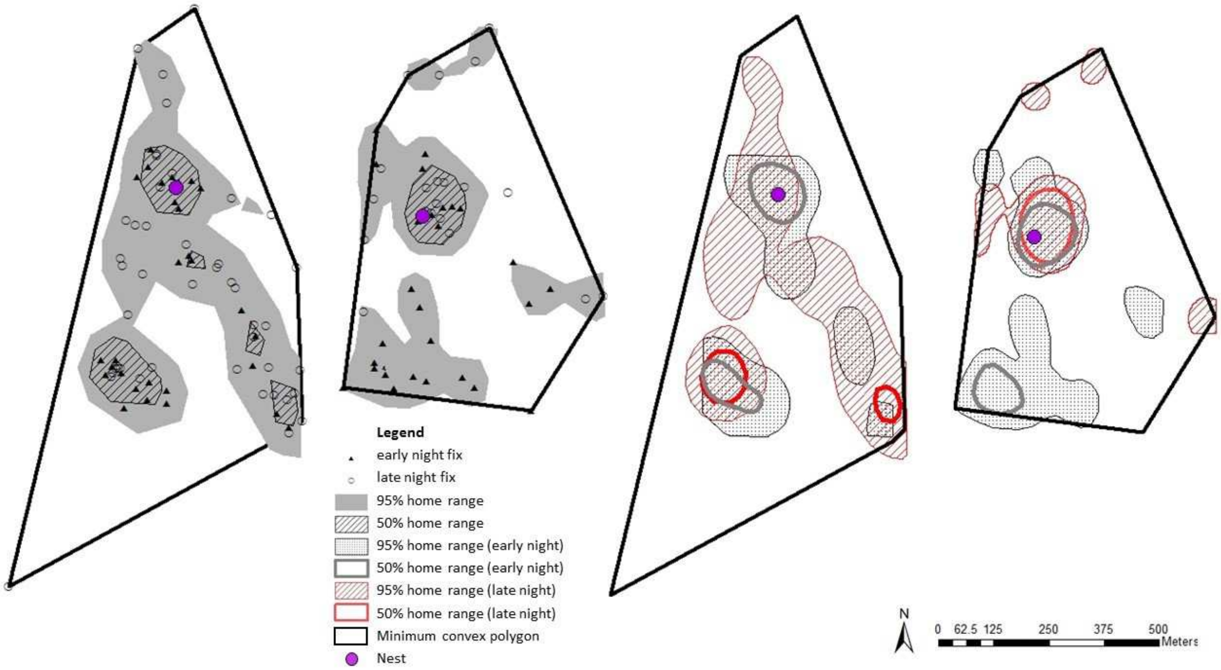


Figure 6. Home range use by male Flammulated Owl in the A2 territory. Triangle points represent fixes recorded early at night and the open circles represent fixes recorded late at night. The grey areas and barred grey areas represent 95% and 50% kernel contours, respectively, estimated without time of night considerations. Spotted grey and barred red areas represent 95% kernel contours estimated for early and late-night fixes, respectively. Grey outlined and red outlined areas represent 50% kernel contours estimated for early and late-night fixes, respectively. The black outlines represent delineations of Minimum convex polygons (MCPs), and the purple circles show the male's nest site. For the A2 male, both 95% kernel estimations and MCPs were smaller during the nestling stage than incubation. A 50% kernel contour remained present around the male's nest site throughout the entire breeding season. The male occupied less area early at night than late at night.

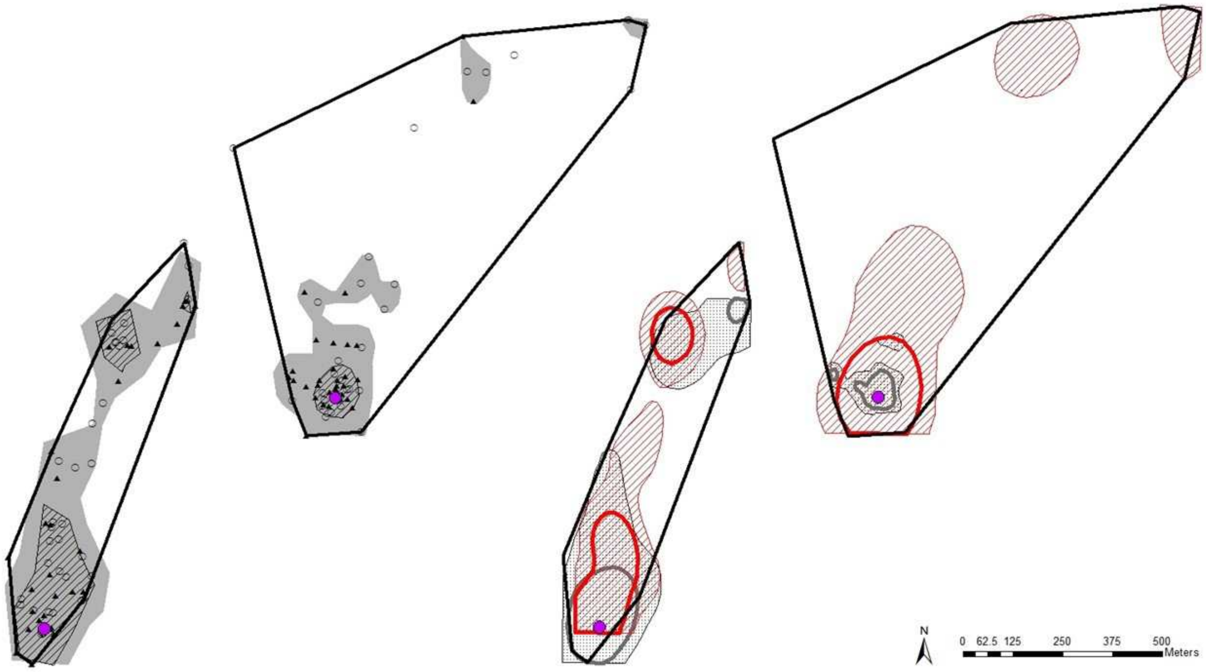


Figure 7. Home range use by male Flammulated Owl in the B6 territory. Triangle points represent fixes recorded early at night and the open circles represent fixes recorded late at night. The grey areas and barred grey areas represent 95% and 50% kernel contours, respectively, estimated without time of night considerations. Spotted grey and barred red areas represent 95% kernel contours estimated for early and late-night fixes, respectively. Grey outlined and red outlined areas represent 50% kernel contours estimated for early and late-night fixes, respectively. The black outlines represent delineations of Minimum convex polygons (MCPs), and the purple circles show the male's nest site. For the B6 male, the 95% kernel estimations were smaller and MCPs were larger during the nestling stage than incubation. A 50% kernel contour remained present around the male's nest site throughout the entire breeding season. The male occupied less area early at night than late at night.

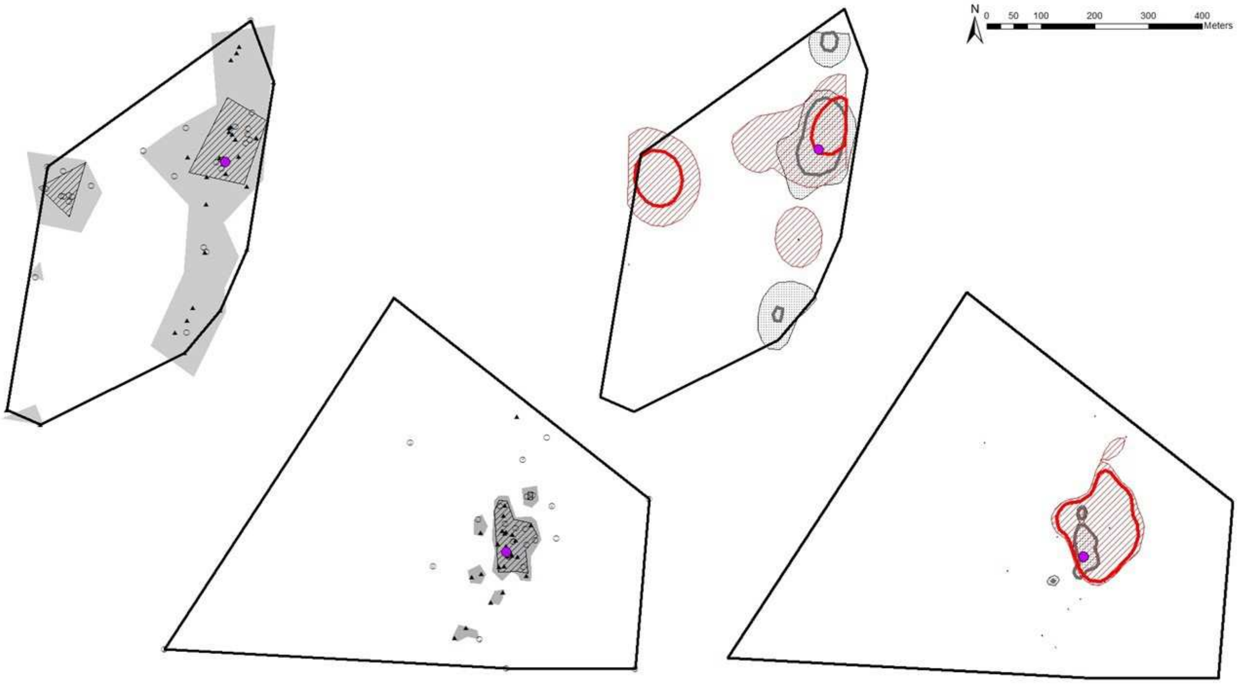


Figure 8. Home range use by male Flammulated Owl in the B8 territory. Triangle points represent fixes recorded early at night and the open circles represent fixes recorded late at night. The grey areas and barred grey areas represent 95% and 50% kernel contours, respectively, estimated without time of night considerations. Spotted grey and barred red areas represent 95% kernel contours estimated for early and late-night fixes, respectively. Grey outlined and red outlined areas represent 50% kernel contours estimated for early and late-night fixes, respectively. The black outlines represent delineations of Minimum convex polygons (MCPs), and the purple circles show the male's nest site. For the B8 male, the 95% kernel estimations were smaller and MCP were larger during the nestling stage than incubation. A 50% kernel contour remained present around the male's nest site throughout the entire breeding season. The male occupied less area early at night than late at night.

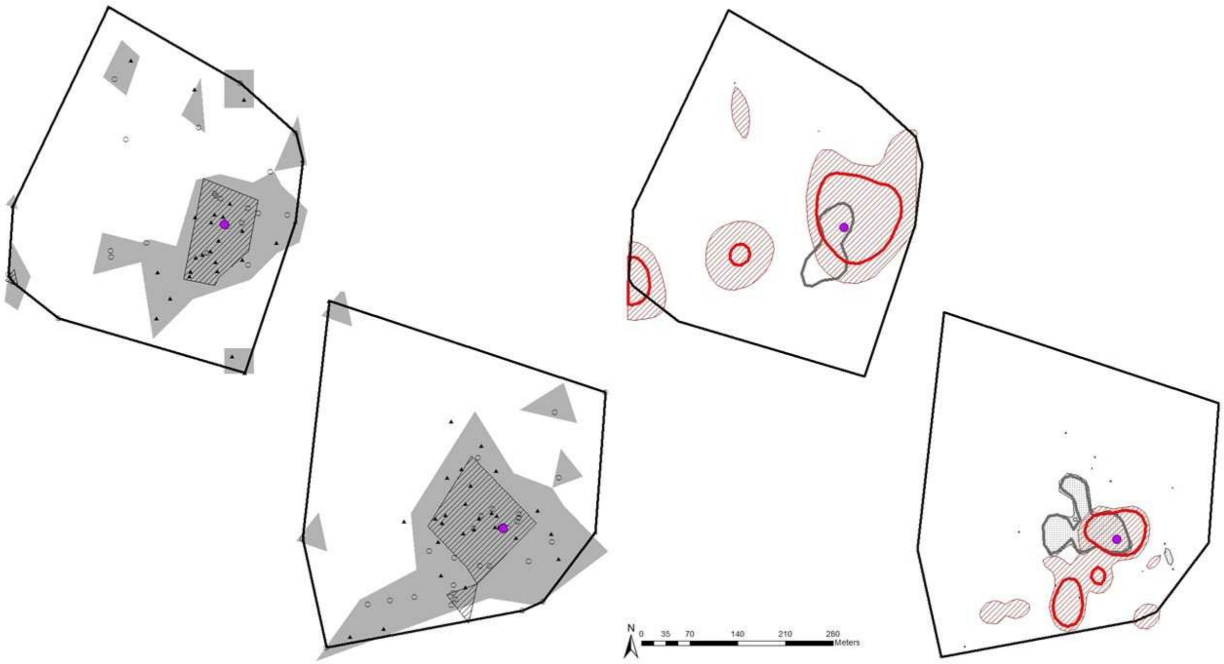


Figure 9. Home range use by male Flammulated Owl in the B10 territory. Triangle points represent fixes recorded early at night and the open circles represent fixes recorded late at night. The grey areas and barred grey areas represent 95% and 50% kernel contours, respectively, estimated without time of night considerations. Spotted grey and barred red areas represent 95% kernel contours estimated for early and late-night fixes, respectively. Grey outlined and red outlined areas represent 50% kernel contours estimated for early and late-night fixes, respectively. The black outlines represent delineations of Minimum convex polygons (MCPs), and the purple circles show the male's nest site. For the B10 male, both 95% kernel estimations and MCPs during the nestling stage than incubation. A 50% kernel contour remained present around the male's nest site throughout the entire breeding season. The male occupied less area early at night than late at night.

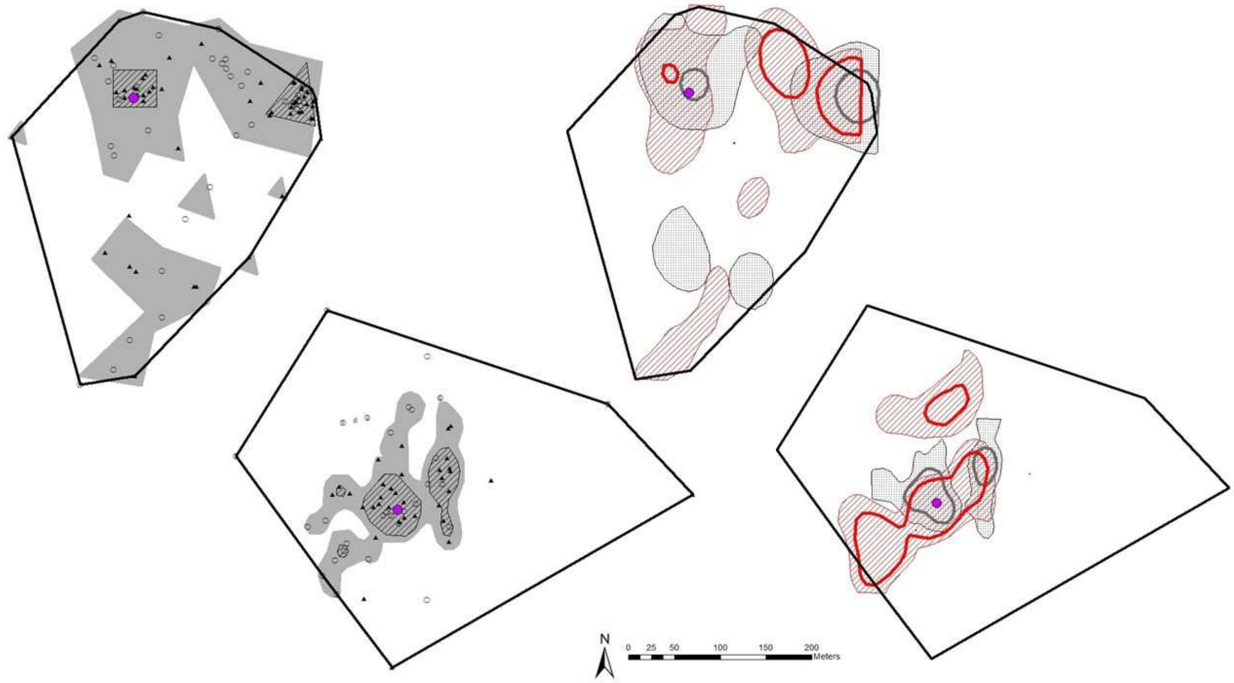


Figure 10. Home range use by male Flammulated Owl in the B12 territory. Triangle points represent fixes recorded early at night and the open circles represent fixes recorded late at night. The grey areas and barred grey areas represent 95% and 50% kernel contours, respectively, estimated without time of night considerations. Spotted grey and barred red areas represent 95% kernel contours estimated for early and late-night fixes, respectively. Grey outlined and red outlined areas represent 50% kernel contours estimated for early and late-night fixes, respectively. The black outlines represent delineations of Minimum convex polygons (MCPs), and the purple circles show the male's nest site. For the B12 male, the 95% kernel estimations were smaller and MCP were larger during the nestling stage than incubation. A 50% kernel contour remained present around the male's nest site throughout the entire breeding season. The male occupied less area early at night than late at night.

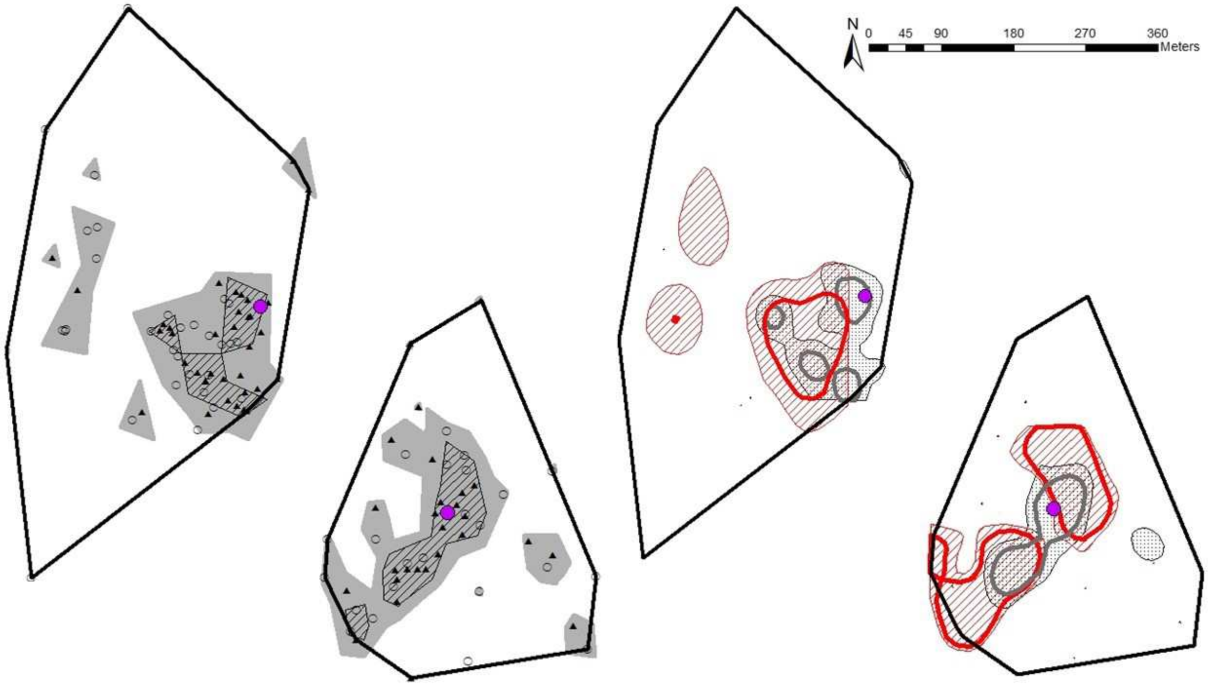


Figure 11. Home range use by male Flammulated Owl in the B21 territory. Triangle points represent fixes recorded early at night and the open circles represent fixes recorded late at night. The grey areas and barred grey areas represent 95% and 50% kernel contours, respectively, estimated without time of night considerations. Spotted grey and barred red areas represent 95% kernel contours estimated for early and late-night fixes, respectively. Grey outlined and red outlined areas represent 50% kernel contours estimated for early and late-night fixes, respectively. The black outlines represent delineations of Minimum convex polygons (MCPs), and the purple circles show the male's nest site. For the B21 male, both the 95% kernel estimations MCPs were smaller during the nestling stage than incubation. A 50% kernel contour remained present around the male's nest site throughout the entire breeding season. The male occupied less area early at night than late at night.

Discussion

Habitat quality and selection

My results suggested that habitat characteristics only varied between selected and available habitat at ground level and did not vary in overstory. This is inconsistent with previous work that shows males preferentially select habitats with old growth ponderosa pine and Douglas fir that are open with older trees (Linkhart et al. 1998). Results, however, are consistent with evidence of foraging habitat near the ground for Flammulated Owls.

This study did not show a clear difference in total crown volumes, total large tree crown volumes, and tree density between selected and available but unused areas within Flammulated Owl territories. This is inconsistent with prior studies on Flammulated Owl habitat selection that found a significant preference for forests with open habitat characterized by older ponderosa pines and Douglas firs (Linkhart et al. 1998). Linkhart and Reynolds (1998) showed that male Flammulated Owls use older trees with large crown volumes to forage and sing territorial calls, and their selected habitats were more open than available habitats. My findings might be a product of the limitations of the GPS trackers used in the field. While the trackers recorded fixes with 10m accuracy, this resolution was not high enough to distinguish among individual trees that were selectively used or not. Additionally, data points may have been recorded while owls were in transit and may not precisely reflect a used area. Previous study on Flammulated Owl habitat use utilized radio-telemetry, which allowed researchers to observe individual owls performing specific behaviors in confirmed locations (Linkhart et al. 1998). Because my study used the GPS trackers, location points were recorded without on-site researchers. This enabled continuous data collection but did not allow me to identify specific behaviors at each point.

While the lack of difference between selected and available habitat characteristics might have resulted from technical limitations, the apparent similarity in use vs. availability among habitat types could indicate the absence of third-order habitat selection from male Flammulated Owls in this study. Habitat selection at broader scales, such as the home range level, might preclude selection at the microhabitat level. The territories examined in this study historically have been less productive than other territories in the same study area, and males that established their territories in these suboptimal habitats might not have the ability to select microhabitats (Yanco and Linkhart 2018). Breeding males that established their territories in suboptimal habitat may have lacked variability within their home ranges to select microhabitats with significantly different habitat characteristics than available but unselected areas. LaHaye et al. (1997) investigated habitat selection in Spotted Owls (*Strix occidentalis*) and found that less productive pairs established territories in suboptimal habitats, and those individuals were pushed into less preferred habitats by territorial displacement. The 2002 Hayman fire in Colorado occurred near our study sites, and the disturbance might have displaced pairs from their original Hayman territories into suboptimal territories within Missouri Gulch (Yanco and Linkhart 2018). Future investigations should include territories of varying productivity within Missouri Gulch in order to clarify whether differences in demographic performance are associated with differences in habitat composition.

While crown volumes and tree densities did not vary between selected and available areas, I found significantly higher ground cover in selected habitat than available habitat from ground level, 0.5m, 1.0m, to 1.5m above ground level. Once explanation for these differences is that ground cover may provide an important microhabitat for foraging. Flammulated Owls forage not only in tree crowns but lower in the canopy as well. Researchers have observed the nocturnal predators make flights to the ground in order to capture items of prey (Linkhart and McCallum

2013). Flammulated Owls do not typically engage in ground foraging until mid-late breeding season, when they expand their moth-dominated diet to include orthopterans and coleopterans that exist near the ground (Linkhart and McCallum 2013). However, more research is necessary in order to directly relate selection for higher ground cover to prey availability.

Temporal foraging activity

I found variation in male Flammulated Owl habitat selection based on the time of night. 95% kernel contour estimations were larger during late night foraging than early night foraging, while MCP estimates did not seem to vary based on time of night. This concentrated habitat use occurred early at night when males have been shown to intensively forage (Reynolds and Linkhart 1984). The males may have occupied greater area later in the night because they spent less time and energy foraging and more energy performing other behaviors, perhaps foraging near the peripheries of their territories where they can also engage in territorial singing when conspecifics are heard (Linkhart et al. 1998). Thus, Flammulated Owls might employ specific nightly strategies to maximize energetic input for energetic output, capitalizing on peaks in prey activity early at night (Stephens et al. 1986). This is further supported by peak prey delivery rates; males (and females later in the breeding season) deliver items of prey much more frequent after sunset and before dawn than in the middle of the night (Linkhart and Reynolds 1987).

Several findings in my research suggest that male Flammulated Owls switch foraging strategies throughout the night. Step lengths tended to be longer during late night foraging than early night foraging, and median step lengths were longer later at night. Additionally, I found that individuals tended to spend time closer to the nest early at night throughout the entire breeding season, and their movements tended to be tighter with higher tortuosity. All of these attributes suggest that males make shorter movements closer to the nest with more dramatic changes in their directions earlier at night. In contrast, they seem to spend time further from the nest site and make longer, less dramatic movements late at night. This may be indicative of a switch in foraging strategy, a behavior employed by other nocturnal predators to maximize food intake based on prey activity (Arlettaz 1996). However, results of my study show only slight trends indicating different movements based on time of night, so further investigation is necessary. Additionally, temporal peaks in nightly moth activity in our study sites have not been quantified, so future research might investigate whether or not changes in foraging strategy are associated with changes in prey availability.

Energetic demands and space use

Home range analysis suggested a shift in home range use between incubation and nestling stages that parallels changes in energetic demands on breeding pairs. I found that minimum convex polygons (MCPs) tended to contain greater area during the nestling stage than incubation, while 95% kernel home ranges contained less area during the nestling stage. This discrepancy suggests that, while the males utilize more space overall later in the season, they concentrate most of their movements within a smaller area. Energetic demands on a breeding pair are much higher when they have owlets to feed (Linkhart and Reynolds 1987). The increased energetic demands during the nestling stage might illicit a change in foraging strategy that minimizes energetic expenditure associated with travel time (Stephens et al. 1986). Results additionally showed that intensive use areas (IUAs) changed between incubation and nestling stages. I found that males tended to use fewer IUAs during the nestling stage than incubation, with the exception of one individual, which suggests a switch to a more energetically efficient foraging strategy. IUAs remained constant around nest sites, which might indicate that pairs establish nests in good foraging habitat.

My 95% kernel home range estimates were significantly smaller during the nestling stage than incubation, which contradicts other studies that show the strong relationship between home-range size and energetic needs (Mace and Harvey 1983). Home range size in raptors has been linked to the species' size, prey taxa, and level of specialization (Peery 2000). Larger raptors tend to have larger home ranges. Bird-eating raptors have larger home ranges than mammal eating raptors, and insectivorous raptors have the smallest home ranges (Peery 2000). Northern Spotted Owl (*Strix occidentalis caurina*) home range sizes have been shown to depend on prey population densities, and owls occupying territories with more woods rats than flying squirrels have smaller home ranges (Zabel et al. 1995).

As relatively small insectivores, Flammulated Owls have smaller home ranges than raptors that eat other birds or mammals—the nocturnal Lepidoptera on which the small owls feed have larger population densities than mammalian and avian species that make up the diet of larger raptors. While male Flammulated Owls defend smaller territories than their larger avian relatives, the results of this study show a significant decrease in 95% kernel estimations throughout the breeding season. In contrast, larger raptors tend to utilize more space later in their breeding season. For example, research has shown Peregrine Falcon (*Falco peregrinus*) home ranges increase between the early and late nestling stage, which corresponds to a brood's increased energetic demands on its parents (Sokolov et al. 2014). The apparent difference between Flammulated Owls and larger raptors could be a consequence of single prey loading behavior in an insectivorous bird. Larger raptors, like peregrine falcons, that feed on large mammals or other birds return to their nests a few times each day because their prey sources are large and calorically sufficient to support a brood. Because Flammulated Owls feed on moths, a calorically limited prey, they return to their nests hundreds of times during the nestling stage to sustain growing broods (Linkhart and McCallum 2013). This behavior puts energetic constraints on the adult birds, which manifest in smaller home ranges estimations during the nesting stage than incubation.

While my results showed significantly larger nestling stage territories than incubation territories, the difference might also be a product of estimation techniques. The 95% kernel contour estimations produced islands of use, which does not biologically represent a home range. Future investigation might employ Brownian Bridge models, which merge islands of "use," in order to more accurately describe temporal habitat use of male Flammulated Owls during their breeding season.

GPS tracking as a technique

This study was one of the first to utilize GPS technology to investigate small raptor habitat selection. A primary goal of the study was to examine the efficacy of using the technology to track Flammulated Owl habitat use over time. Studies have used similar devices to investigate fine scale habitat selection in other model organisms, including Burrowing Owls (*Athene cunicularia*). Researchers utilized slightly larger GPS dataloggers to track Burrowing Owl movement within home ranges, and successfully identified foraging strategies (Marsh et al. 2014). My results showed that the GPS Lotek pinpoint-10s, while limited in their capacity to reflect fine scale habitat selection, successfully enabled us to estimate Flammulated Owl home ranges and core use areas. I programmed the data loggers to record locations at 15 min intervals between 2000-2200hr and 0100-0300hr until they ran out of battery. This schedule interval enabled us to investigate habitat use over the course of the entire breeding season and over the span of one night. I successfully managed to estimate the six males' home ranges and examine changes between incubation and the nestling stage and between early and late-night movements. Our estimations, however, exhibited a decent amount of variation. Additionally, different estimations yielded different patterns; MCPs did not significantly vary over time but tended to increase throughout the season. Kernel utilization distributions were significantly smaller early at night during the nestling stage. This pattern might be indicative of behavioral changes expressed by male flams, but also might reflect limitations of the programmed schedules on the GPS trackers.

The trackers enabled us to estimate higher order habitat use patterns, but they did not produce patterns conducive to fine scale analysis. Fitted distributions did not significantly vary based on time of night or time during season. Taken in 15 minute intervals, the data fixes reflect a simplified version of the individual's flight paths. In that time, the owls may have made movements that were not reflected in the collected GPS coordinates. Other studies that investigate higher order habitat selection in raptors use shorter intervals between points (Watson et al. 2014). Larger raptors can carry heavier equipment with remote sensing, enabling researchers to schedule fixes every few minutes or seconds to give a detailed, numerical description of movement. Similar investigation into Flammulated Owl movements might be limited until remote sensing technology becomes smaller.

Conclusion

Understanding the ways in which animals use their habitats offers important insights into the conservation of a system. Habitat selection dictates how individuals interact with their community, and studying those relationships can show the spatiotemporal importance of habitats to species (Mayor et al. 2009). Species can have uneven preference for specific microhabitats and strategically divide their spatial occupancy within a home range. Another species in the same system might prefer a particular microhabitat without a preference for a larger landscape (Sutton et al. 2017). Flammulated Owls in Colorado rely on ponderosa pine/Douglas fir forests that are at risk of high intensity forest fires due to centuries of fire suppression (Veblen et al. 2000). Not only has fire suppression interfered with the natural cycling that maintains habitat complexity and biodiversity, it has led to the accumulation of debris and foliage that acts as efficient forest fire fuel (2000). Throughout their breeding season, Flammulated Owls maintain intensive use areas within their habitats and around their nest. They more intensely utilize smaller areas later in their breeding seasons when energetic demands on breeding pairs are high, but they make trips to the peripheries of their territories. Thus, breeding pairs rely heavily on all aspects of their Ponderosa pine/Douglas fir habitats to produce viable young.

It is important to understand the forest characteristics that Flammulated Owls use in order to address new fire management strategies. This study 1) describes how Flammulated Owls change their movement strategy between early and late-night activity and 2) describes how habitat selection varies between incubation and the nestling stage. Without components of the forest that enable their success throughout their life history, conservation of this species' habitat would be significantly compromised.

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