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IMPACTS OF VARIATION IN FOOD AVAILABILITY ON SPATIAL HABITAT USE IN BREEDING AND NON-BREEDING RED CROSSBILLS (*LOXIA CURVIROSTRA*)

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ABSTRACT

Movement patterns, habitat use, and reproductive behavior are among many attributes impacted by the distribution of resources within habitats. Our study used radio telemetry to investigate the relationship between food availability and movement patterns of breeding and non-breeding red crossbills (*Loxia curvirostra*). Crossbills were captured and tracked in different seasons and under conifer seed mast and non-mast conditions. Telemetry data were used to generate statistical models to analyze spatial habitat use. Total linear distance traveled per total area of the home range was used as a comparative measure of activity within home ranges across specimens. We found a significant increase in within-home range activity during mast years. Birds rearing young exhibited greater within-home range activity than non-breeding birds. Total distance traveled was significantly greater in summer than in winter. Our results suggest greater activity under high food conditions.

INTRODUCTION

Animal movement is vital to the fitness of species, population dynamics, and stability of resources in ecosystems. Movement is essential for survival and, as such, shapes how organisms evolve over time. The ability of an animal to secure resources requires energy spent searching and is reflected in their movement patterns (Lundberg & Moberg, 2003). Whether to find food, mate, or migrate to a more productive area, the movement of animals throughout their habitats is crucial to their survival and ability to reproduce. Likewise, movement patterns can have far-reaching impacts on human activities, such as agriculture production and spread of disease (Powell, 2000). Our understanding of the factors that determine habitat use in animals can help inform issues of public

health, land management, conservation of natural resources, and preservation of populations, particularly in the context of progressive human encroachment throughout the natural world.

Animals typically exhibit non-random movement confined to specific regions considered to be secure in resources and will show fidelity to areas with resource benefits that exceed the costs of locating, harvesting, or protecting them (Powell, 2000). Animals may migrate between locations seasonally as resources diminish, or they may relocate as metabolic conditions change across different developmental or reproductive phases. The area within an animal's cognitive map that is used to fulfill its resource requirements is typically referred to as its home range (Powell & Mitchell, 2012). Home ranges tend to maintain relatively defined boundaries when conditions are stable but are subject to change due to factors such as variability in food availability or competition (Spencer et al., 1990). Further, home ranges may differ across species and conspecifics depending on the mobility of the individual, its current metabolic needs, and resource distribution (Gautestad & Mysterud, 1993). For example, as resources become more scarce in winter, species such as coyotes (*Canis latrans*) exhibit exclusivity to the areas within their home ranges that contain their most vital resources, thus decreasing the size of the home range (Person & Hirth, 1991).

The home range size and general activity of an animal can also be affected by resource distribution and metabolic needs. Northern flickers (*Colaptes auratus*) show an increase in home range size under more favorable food conditions and while raising young (Elchuk & Wiebe, 2003) – perhaps reflecting the high needs of developing young or the benefits of exploration when resources are abundant. In contrast, some captive migratory songbird species show increased activity when under relatively severe food stress and decreased activity when food is abundant (Ferreti et al., 2019; Cornelius et al., 2010, 2018; Astheimer et al., 1992). This is presumed to reflect increased searching behavior for limited resources and may translate to a larger home range size when food is very limited. These differences highlight the complexity surrounding spatial habitat use and food availability, which may not impact home range size linearly.

Seasonal change is another factor that may affect spatial habitat use and movement in songbirds because of the often-large changes in food abundance and thermoregulatory conditions. These changes can subsequently affect their choice to reproduce (Elchuk & Wiebe, 2003). American redstarts (*Setophaga ruticilla*) under winter food stress are known to either abandon their territories or remain within a limited home range size when food supply is more limited, but, in consequence,

they suffer decreased body condition and delay their migration departure time (Cooper et al., 2015). It is possible that home ranges become smaller when resource conditions become poorer as birds try to reduce the energy costs of foraging - unless they become physiologically stressed (e.g., if the food resources become extremely limited) - at which point they may abandon territories completely. Tropical kingbirds (*Tyrannus melancholicus*) show a trend indicating smaller home range sizes in the non-breeding season (Jahn et al., 2010). Further, common cuckoos (*Cuculus canorus*) show a large increase in home range size while raising young when food is abundant (Williams et al., 2015). Indeed, most songbirds are highly seasonal breeders, breeding only in the spring or summer when resources are abundant and environmental conditions are relatively benign. It can therefore be difficult to differentiate the impacts of resource requirements to support breeding from the impacts of seasonal differences in resource distribution on movement dynamics in songbird species (Hahn, 1998).

Birds that breed across multiple seasons can provide insight into seasonal effects on habitat use due to their year-round presence in environments that are seasonally heterogeneous. The red crossbill (*Loxia curvirostra*) is an opportunistic breeder that can often breed in both summer and winter due to its consistent access to food across seasons (Cornelius et al., 2011). Crossbills are specialized feeders and will feed on conifer seeds that are produced regionally by masting conifer species every few years (Bock & Lepthien, 1976). Because of the unpredictable nature of the masting conifer species they prey upon, crossbills are nomadic migrants and may use predictive cues to move between regions to find crops (Cornelius & Hahn, 2012). These changes in food availability have a significant impact on population density and breeding status (e.g., high density and breeding in a mast year versus low density and non-breeding in a non-mast year) and may, ultimately, play key roles in the shaping of home ranges and spatial habitat use.

The purpose of this study is to investigate the effects of changes in food availability on spatial habitat use of the red crossbill across the winter and summer seasons, across conifer masting status, and under different reproductive conditions. We hypothesized that seasonal and annual differences in food distribution would cause changes in spatial habitat use as crossbills search for food to meet energy demands. We used total distance traveled divided by total area of the home range as a comparative measure of habitat use. We tested four predictions related to this hypothesis. First, we predicted that crossbills would move a lesser distance per

home range area during non-masting years when food is less abundant if birds forage more efficiently to conserve energy (P1-Conifer Masting Status). Second, we predicted that crossbills raising young would travel a greater distance per home range area given that they must provision nestlings frequently, which requires transit between foraging areas and the nest (P2-Reproductive Status). Third, we predicted crossbills would have a smaller, more confined home range area when needing to meet increased thermoregulatory demand more efficiently in winter, given that conditions are colder and daylight available for foraging is reduced (P3-Seasonal Energy), and that non-breeding crossbills would feature less distance traveled per home range area in winter relative to summer when conditions are significantly more energetically costly (P3-Seasonal Breeding). To test these predictions, we analyzed GPS-tracked telemetry data collected from red crossbills in Wyoming across different seasons and food conditions.

METHODS

Study Site

Our study was based in Moose, WY, in Grand Teton National Park, which hosts a population of red crossbills that fluctuates from high to low density due to the occasional production of huge seed crops by masting conifers. These include blue spruce (*Picea pungens*), Engelmann spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*), as well as the more consistent, but low-yield cone crop-producing lodgepole pine (*Pinus contorta*). Telemetry data were collected during the summer of 2009 and winter of 2010, when masting conifers failed to produce seeds, and thus, crossbills generally did not breed; and again during the summer of 2016 and winter of 2017, when there was a huge mast crop of Douglas fir and blue spruce on which crossbills fed abundantly. Data were collected in or near the southern end of Grand Teton National Park in four general areas: Phillips Pass (43.547852, -110.932116), a high-elevation montane, Engelmann spruce- and Douglas fir-dominant habitat; Devil's Staircase (43.722010, -110.898479), a high-elevation montane, Engelmann spruce- and Douglas fir-dominant habitat; the Murie Center (43.649812, -110.728167), a high-elevation valley floor, blue spruce dominant-habitat; and Signal Mountain (43.847805, -110.567908), a high-elevation valley floor, lodgepole pine- and Douglas fir-dominant habitat.

Capture and Tracking Methods

Red crossbills were captured using live decoy lures and mist nets so that they could be fitted with continuous-tone radio transmitters. We tracked 14 birds during the summer and 10 birds during the winter of the low-cone and non-breeding year of 2009-2010. We tracked seven birds during the summer and nine birds during the winter of the high-cone and breeding year of 2016-2017. Birds were removed immediately from mist nets following capture for morphometric data collection and radio attachment. We measured unflattened wing chord, tarsus, and keel lengths to the nearest 0.1 mm using dial calipers to estimate body size and measured body mass to the nearest 0.5 g using a Pesola spring scale. Fat stores were visually estimated on a scale of 0-5 for both the furcular and abdominal cavities, and data were collated for analysis (Cornelius & Hahn, 2012). Reproductive condition was described in females as the presence or absence of a brood patch and as the length of the cloacal protuberance in males (Cornelius et al., 2011) and was confirmed during tracking by behavioral observations. Birds that were feeding nestlings or fledglings were further classified as raising young. Due to the speed and sometimes secretive parental behavior of some of the tracked crossbills, the probability of false negatives was higher than false positives when classified as raising or not raising young. Males with large cloacal protuberances, but whose nests could not be identified during tracking, were thus classified as “suspected breeders.”

To track and assess habitat use, a small, continuous-tone radio transmitter (0.6 g from Sparrow Systems, Chicago, IL) was attached to the back of the bird using a glue-on attachment method. Red crossbills were released within 30 minutes of capture and were then tracked by investigators wearing Garmin GPS devices for 48 hours or for as long as they were able to be tracked before their signal was lost – presumably because they moved out of the study location. GPS coordinates were recorded every 30 seconds by the GPS units during the original data collection and tracks were subsequently “down-sampled” to reduce movement error caused by GPS error during location triangulation. Given the short 48-hour tracking time and the frequent movement of birds between foraging trees, we reduced the sampling rate to one GPS point every three minutes. Although this had the potential to overestimate total distance traveled if birds did not move between trees for long periods of time (e.g., the sum of GPS error during repeated triangulation of a stationary bird), it minimized the omission of small but frequent movements between nearby trees.

Analyzing Movement and Spatial Habitat Use

Telemetry data were imported to RStudio (v. 1.2.5033) to create kernel density estimations (henceforth, KDE) using the package *rhr* to analyze spatial patterns of habitat use for each tracked individual. KDEs display habitat use distributions and incorporate modifiable probability contours to examine the extent of habitat use and to provide a comparative view of home range size (ha) under different seasonal and reproductive conditions. A ratio of total linear distance moved per hectare of home range was used as a comparative measure of activity within the home range that allowed for another metric by which to compare habitat use. KDEs were drawn with a 95% density isopleth to delineate the total home range size. We calculated the average total linear distance moved per 24 hours for each bird, which provided a measure for how far birds moved within their home range. Finally, distance moved per hour of daylight was used as a comparative measure of activity from summer to winter.

After quantifying several parameters that described spatial use (i.e., total linear distance traveled, home range area), we used t-tests ($\alpha = 0.05$) and ANOVA to evaluate whether spatial parameters were impacted by season, seed crop size (year), or reproductive condition. Ultimately, 29 of the original 35 tracked individuals were used in analysis because some of the birds we tracked had too few telemetry locations. While we collected nearly 1,000 telemetry locations for each bird, some had fewer than 150 locations and would not have provided reliable information.

RESULTS

Conifer Masting Status

There was no significant difference in home range size or total km traveled between masting conditions ($t = 0.22$; $p = 0.828$; $t = 0.16$; $p = 0.18$; respectively); however, the distance traveled per home range area was nearly five times greater under masting conditions than in non-masting conditions ($t = -2.38$; $p = 0.0157$). Under non-masting conditions, total distance traveled per home range area was close to 0.1 km/ha (Fig. 1); whereas birds tracked during mast years exhibited a higher average of around 0.5 km/ha.

Crossbill Reproductive Status

Home range size of crossbills raising young was smaller than those not raising young ($t = -1.71$; $p = 0.053$; Fig. 2; Fig. 3). Crossbills that were

confirmed to be raising young featured greater distance traveled per home range area than non-breeders ($F = 2.06$; $p = 0.0044$; Fig. 4). Only one bird was found raising an egg and this bird exhibited a home range size of 112.03 ha. The average distance traveled by crossbills raising young was 15.69 km, while non-breeding crossbills traveled on average 11.71 km.

Figure 1. Distance traveled relative to home range size of red crossbills across conifer masting conditions. Home range sizes determined by 95% KDE. Boxplots represent ratio distributions. The central bar indicates the mean, the box indicates the 25-75% interquartile range, and bars indicate the 95% confidence interval

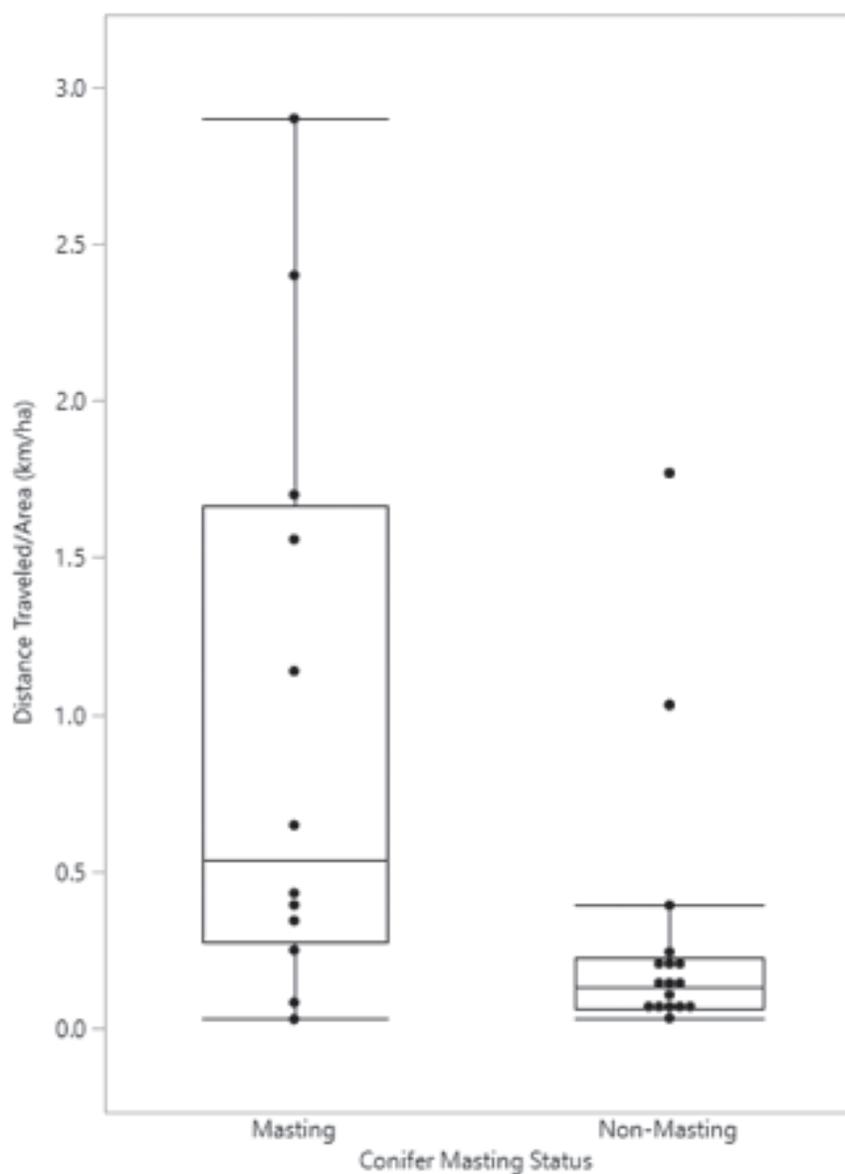
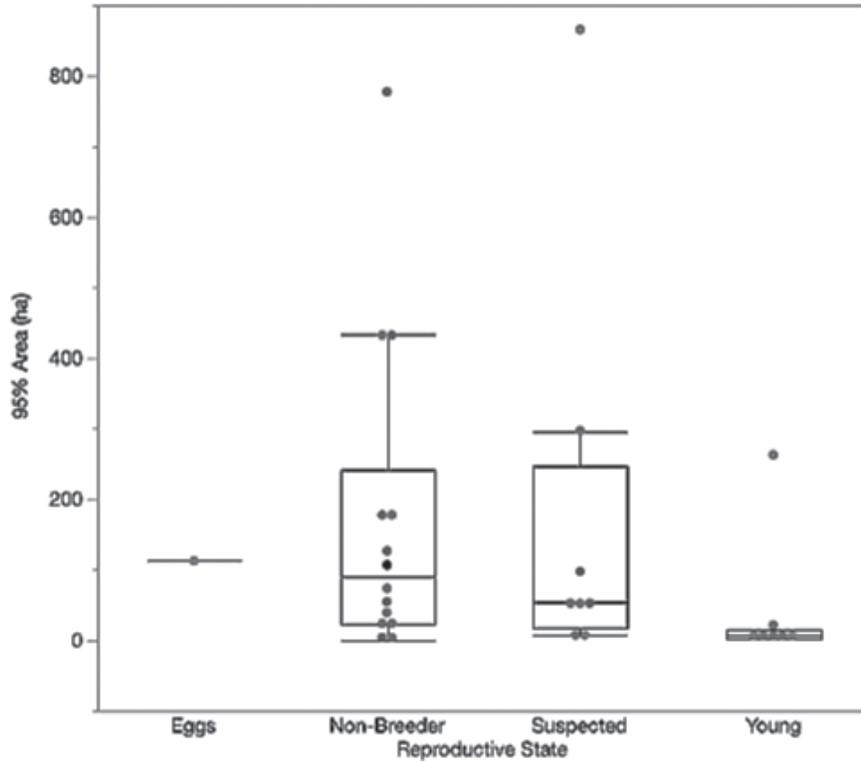


Figure 2. Home range size of free-living red crossbills across different reproductive states ($n = 29$). Home range sizes determined by 95% KDE. Boxplots represent ratio distributions. The central bar indicates the mean, the box indicates the 25-75% interquartile range, and bars indicate the 95% confidence interval



Season

Average home range size tended to be larger in summer than in winter (Summer Mean = 283.70 ± 75.82 ha, Winter Mean = 86.50 ± 32.28 ha; $t = -1.533$; $p = 0.072$; Fig. 3). We found no significant effect of season on distance traveled per home range area ($t = 0.188$; $p = 0.574$; Fig. 5). Distance traveled per hour of daylight was also unaffected by season ($t = -1.639$; $p = 0.106$; Fig. 6). There was an increase in distance traveled in summer as opposed to winter ($t = -2.16$; $p = 0.0244$; Fig. 7).

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Figure 3. Home range boundaries of four red crossbills drawn with a 95% density isopleth. Maps correspond to different reproductive states and seasons

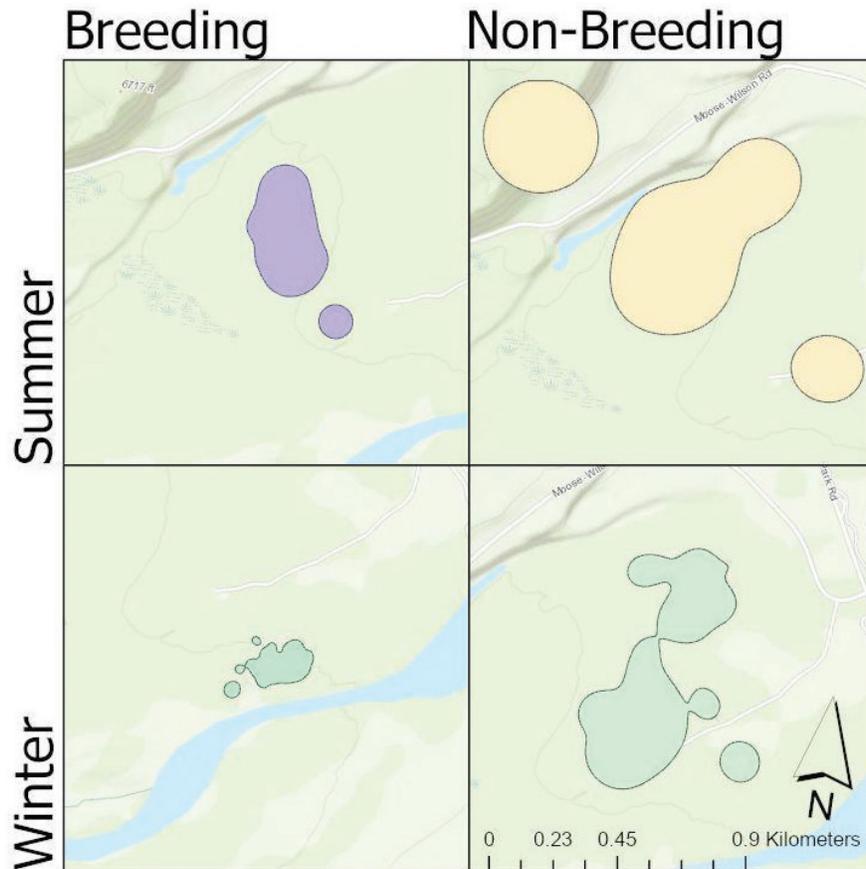
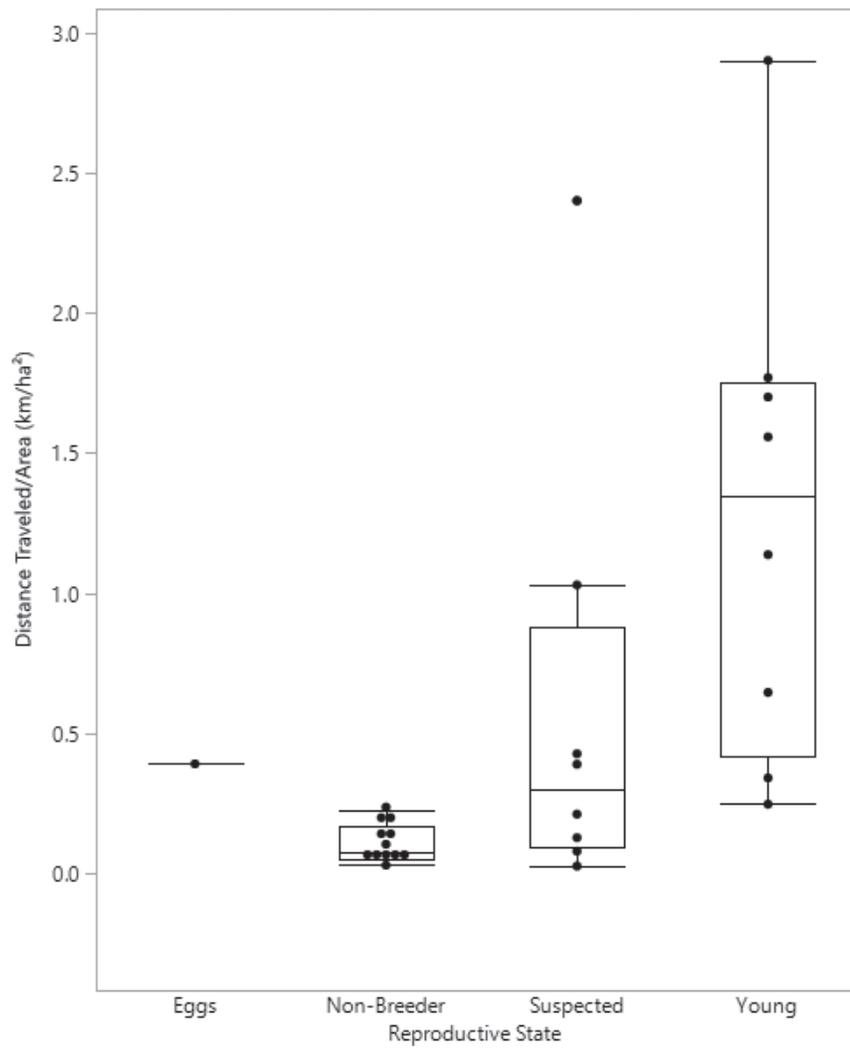


Figure 4. Distance traveled relative to home range size of free-living red crossbills across different reproductive states ($n = 29$). Home range sizes determined by 95% KDE. Boxplots represent ratio distributions. The central bar indicates the mean, the box indicates the 25-75% interquartile range, and bars indicate the 95% confidence interval



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Figure 5. Distance traveled relative to home range size of red crossbills across seasons ($n = 29$). Home range sizes determined by 95% KDE. Boxplots represent ratio distributions. The central bar indicates the mean, the box indicates the 25-75% interquartile range, and bars indicate the 95% confidence interval

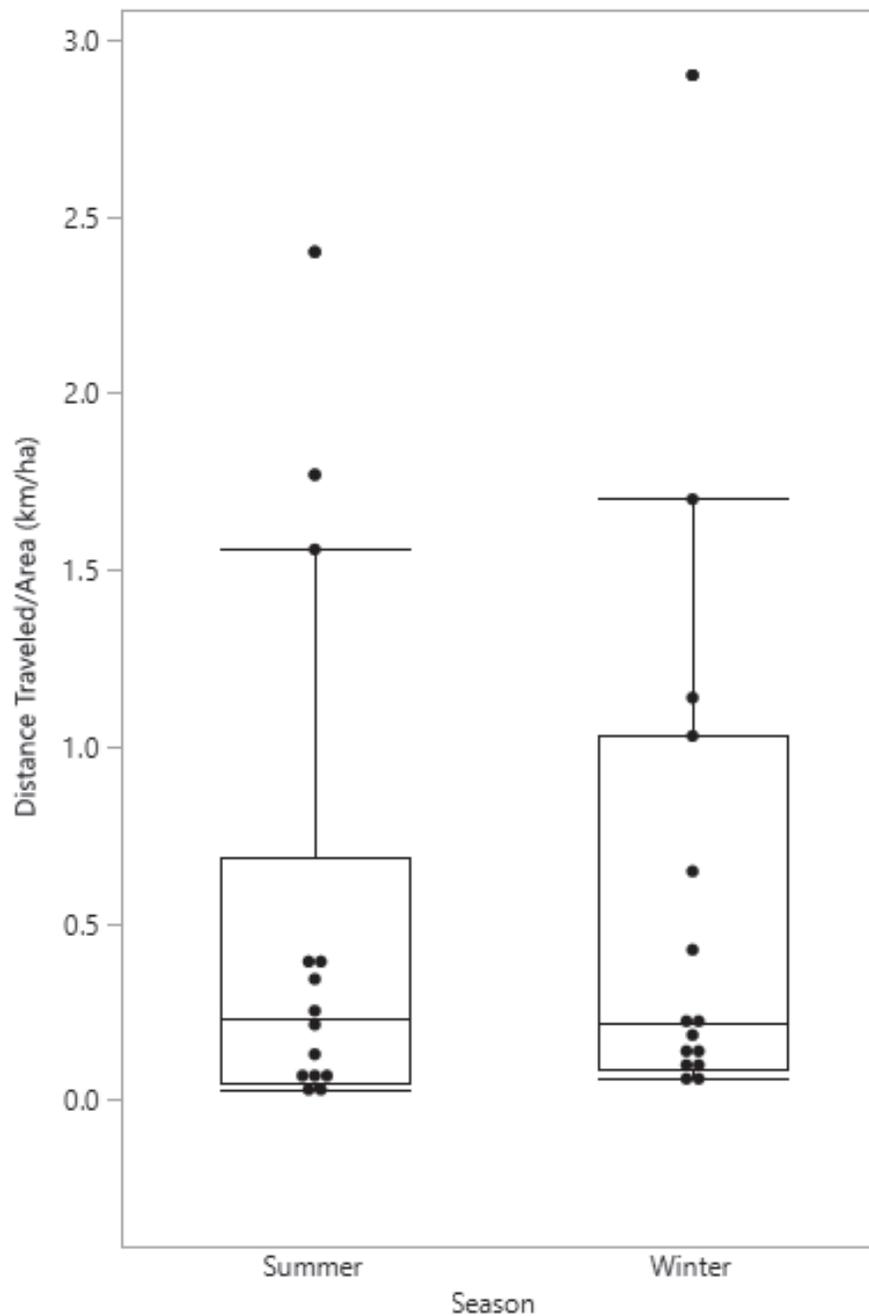
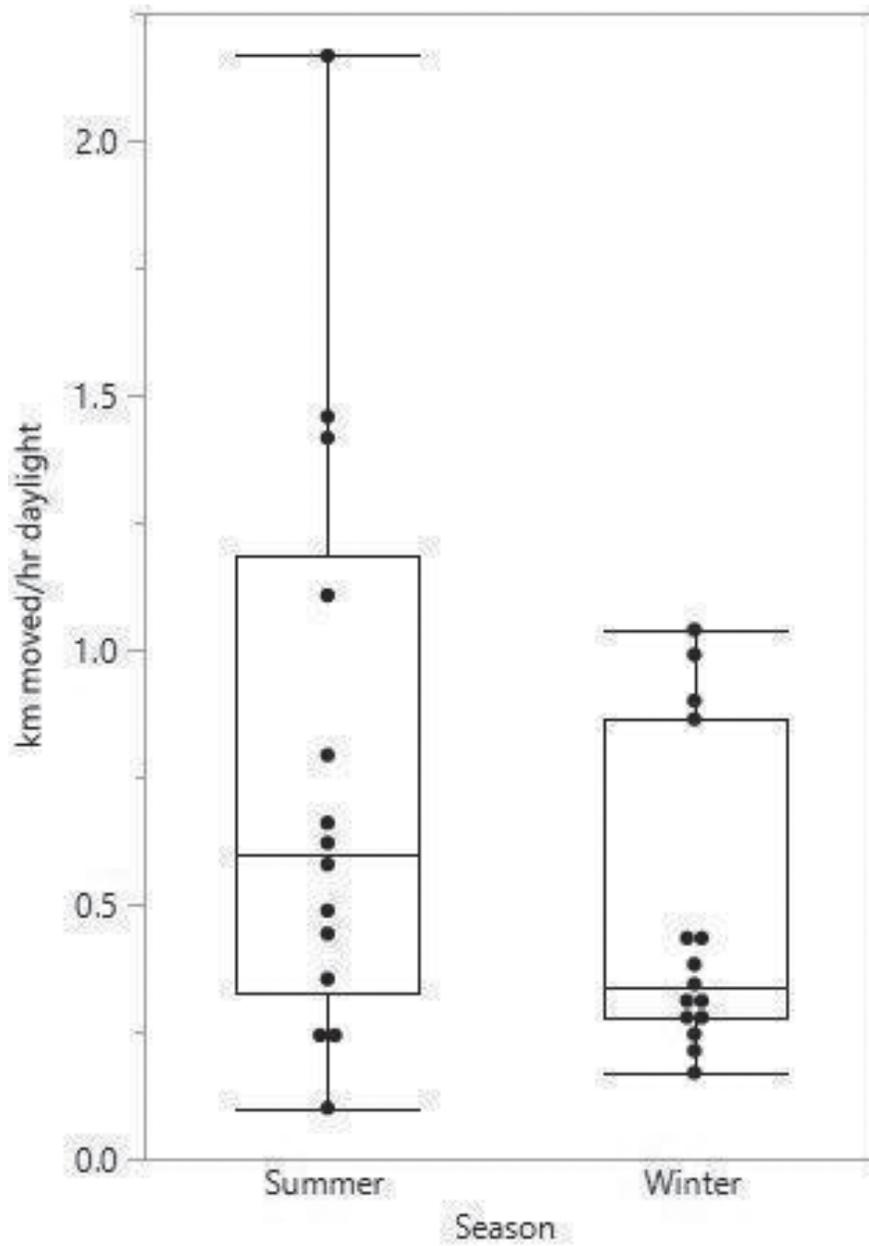
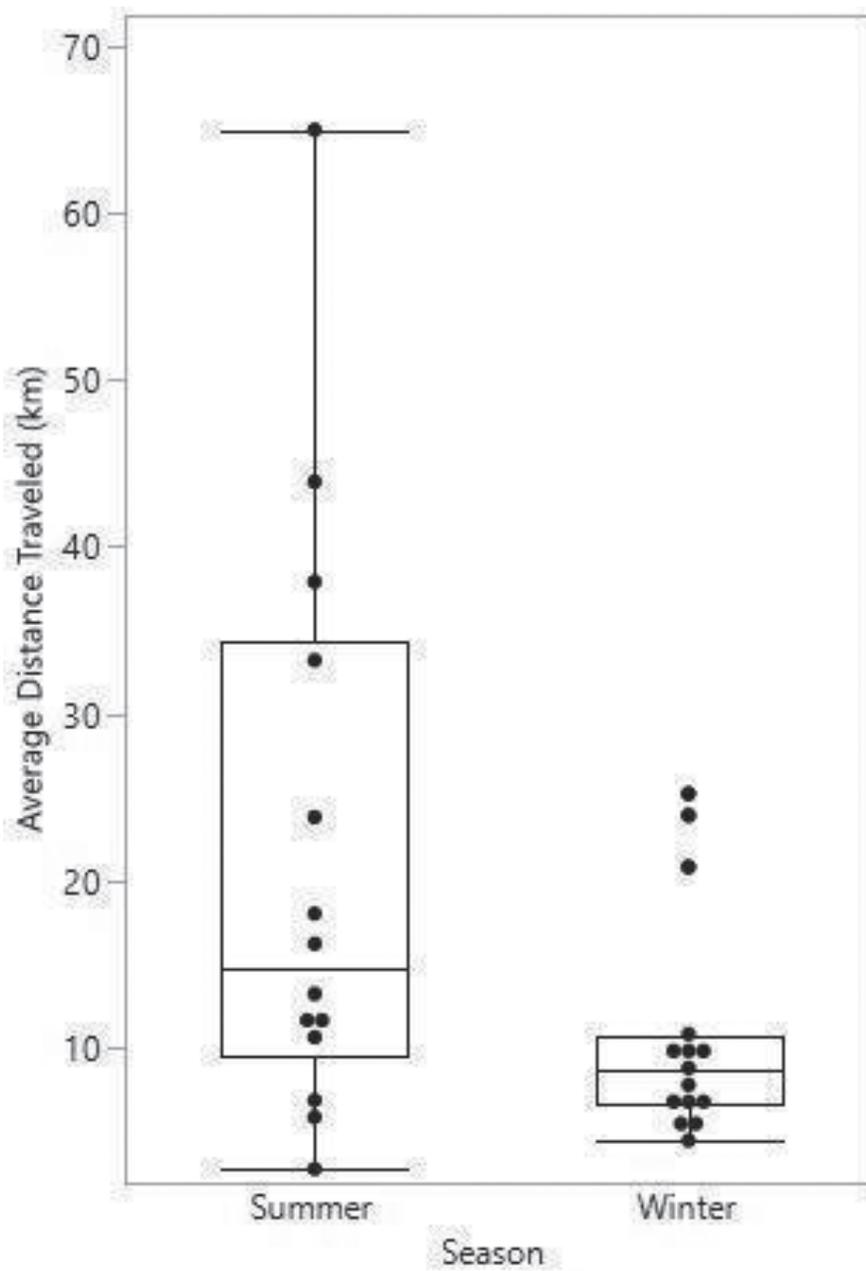


Figure 6. Distance traveled per hour of daylight in red crossbills across seasons ($n = 29$). Boxplots represent ratio distributions. The central bar indicates the mean, the box indicates the 25-75% interquartile range, and bars indicate the 95% confidence interval



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Figure 7. Average distance traveled of red crossbills across seasons ($n = 29$). Boxplots represent value distributions. The central bar indicates the mean, the box indicates the 25-75% interquartile range, and bars indicate the 95% confidence interval



DISCUSSION

Crossbills had smaller home ranges but still traveled the same total distance during masting seed crop years. Together this meant that birds traveled a greater distance within their home range during masting conditions, supporting the hypothesis that differences in food distribution may impact spatial habitat use in red crossbills. These findings agreed with our prediction that crossbills would reduce movement within their home range as they forage more efficiently when food is more limited and, conversely, would increase movement within their home range when food was abundant and birds were likely breeding. Crossbills facing low food resources may need to use a larger home range to find sufficient resources, but they are apparently also able to move more efficiently by reducing the frequency of transits between patchy resources. Red crossbills have shown fidelity to areas with specific conifer species based on their profitability (rate of seed intake) and will relocate to find different species and eventually different areas entirely as profitability decreases (Benkman, 1987). Our findings disagree with reports from another study that found smaller home ranges under low food conditions in the red-headed woodpecker (Vukovich & Kilgo, 2013); however, crossbills are known to breed when seeds are abundant during mast years, and the feeding of young may complicate the relationship we found between food availability and spatial habitat use.

We found a greater distance traveled relative to home range size and a far smaller home range in crossbills raising young than in non-breeding birds. This supported the prediction that crossbills would exhibit greater total movement within their home range when needing to provision nestlings. Males must feed themselves, their mates, and any developing young, especially in winter when young are unable to thermoregulate and the female is nest-bound. Provisioning thus appears to result in many trips from the nest to nearby foraging locations, which inflates distance traveled relative to home range size. This requires strong familiarity with immediate surroundings and, combined with the energetically costly endeavor of raising young in the winter, may explain the observed reduction in home range with more localized foraging. The need to maintain close proximity to the nest and to make many trips to locate food are reflected by these results and are supported by a study examining differences in home range size of white storks (*Ciconia ciconia*), which show greater home range sizes when not raising young (Zurell et al., 2018). Conversely, another study of Venezuelan troupials (*Icterus*

icterus) found no significant difference in territory size as a function of reproductive status (Odom et al., 2019). However, their omnivorous diet, in which they feed insects to their young, may impact habitat use differently than patchy seed distribution.

Few studies have addressed potential variation in territory sizes of birds that are raising young that have not yet hatched. The individual that we tracked during the egg incubation stage featured a home range size intermediate between those with young and those without. The minimal sample size ($n = 1$) cannot be used to make any broad conclusions, but it is interesting that the home range size was intermediate to non-breeders and those raising nestlings given that males supporting an incubating female needed only to feed their mates rather than additional growing nestlings. Clearly this warrants further research. Additionally, the suspected breeders (i.e., those birds for which we could not confirm a nest during the masting year) showed a cluster of points for distance traveled per home range size that were most similar to non-breeders, but a few individuals had much higher levels that may have been consistent with frequent trips to a central nest location. This commuting behavior may therefore be a metric by which researchers could confirm breeding without having to locate a nest in future studies. Finally, the variation observed within individuals feeding nestlings was quite large and may reflect differences in local resource distribution or habitat quality, whereby some individuals were required to transit much further between resource patches and the nest.

The only significant effect of season on spatial habitat use was in total distance traveled. Home range size did not vary greatly between seasons though there was a weak indication that winter yielded smaller territory sizes. Additionally, there was no significant difference between distance traveled relative to home range across seasons. The data failed to support our third prediction that crossbills would exhibit smaller home ranges and less movement within their home ranges to account for increased thermoregulatory demand and energetic costs of surviving winter. A study of black-throated finches (*Poephila cincta*) similarly showed no change in home range size across season (Rechetelo et al., 2016). Impacts of season on home range size is certain to be specific to the habitats in which each species winters and summers. One possible reason for the similarity in home range sizes and movement within home ranges across seasons in crossbills could be the increased ease of access to seeds in cones as the season progresses (Benkman, 1987). Seeds may be easier to access during winter as cones mature and the scales open. This may

partially compensate for the increasing energetic costs of thermoregulation in winter. Though seeds may also disperse from cones once the scales open and become unavailable to crossbills, the foraging efficiency will be dependent upon multiple factors and may vary across years. There are also fewer predators that remain resident at high elevation in winter, potentially allowing for sustained levels of movement throughout home ranges. Red crossbills are also non-territorial, which may reduce the impact of season on home range size given that they may not be directly competing for resources (Hahn, 1998).

Spatial patterns of habitat use under different food distributions and energy demands offer valuable insight into factors behind animal movement. Our study is the only study examining patterns of habitat use and foraging behavior in a nomadic migrant and opportunistically breeding bird, and it revealed that breeding had the strongest impact on metrics of spatial habitat use. As season seemed to have little effect on red crossbill behavior, this species may be used as a model in future studies investigating different stimuli on behavior across seasons. Understanding the drivers of spatial habitat use are important for understanding how animals meet their needs to survive and reproduce under very different environmental conditions. The findings from this study may be applicable for similar species that fulfill valuable ecological niches, such as pollination and seed dispersal. Having comprehensive insight into their decision-making is crucial for conservation efforts given that the continued reshaping of the natural world for commercial use will continue to disrupt services these species provide.

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