Habitat Use and Foraging Behavior of Eastern Bluebirds (Sialia sialis) in Relation to Winter Weather

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Todd J. Weinkam[1], Gregg A. Janos[1], and David R. Brown[1,*]

Abstract - Population declines of songbirds following severe winters draw attention to a need to better understand behavioral responses to inclement weather. We used observations of radio-tracked *Sialia sialis* (Eastern Bluebird) wintering in Kentucky to examine the effects of weather on habitat use, group size, foraging behavior, and diet. Home ranges were smaller than published estimates, and consisted of more open than wooded habitat, in proportion to availability. Although habitat use appeared unchanged during inclement weather, Bluebirds increased group sizes, and shifted from insectivory to frugivory during periods of sub-freezing temperatures and snow cover. Fecal analysis confirmed the weather-driven shift of diet. Inclement winter weather likely lowers the efficiency of insectivory, leading to changes in social and foraging behaviors.

Introduction

Environmental factors and winter-specific resource constraints can affect the behavior (Duriez et al. 2005), abundance (Meehan et al. 2004), and range limits (Zuckerberg et al. 2011) of birds. Severe winter weather can reduce winter survival, population size, and impact reproductive success in subsequent seasons (Porter et al. 1983, Sauer and Droege 1990). Our ability to predict and interpret these processes may be enhanced by a better understanding of winter-specific habitat and resource requirements. Specifically, information about the interactions between weather, habitat, and behavior may help explain how winter events influence population patterns.

Sialia sialis L. (Eastern Bluebird, hereafter Bluebird) have been widely studied during the breeding season (Gowaty and Plissner 2015), but much less is known about their winter ecology. Reports of Bluebird mortality during harsh winter weather (Pitts 1978, Wilson and Stamm 1960) followed by observable population declines (Monroe 1978; Palmer-Ball 2015; Sauer and Droege 1990; Stamm 1979a, b; Wilson 1962) demonstrate the potential for winter weather to affect their populations. Recently, Wetzel and Krupa (2013) reported a positive correlation between mean winter temperature and Bluebird abundance during subsequent breeding seasons in central Kentucky, and suggested that the Bluebird population there may be particularly susceptible to cold winters, in part because most birds are residents.

Although several investigators have examined Bluebird breeding habitat use (e.g., Plissner and Gowaty 1995, Sloan and Carlson 1980, Stanback and Rockwell 2003), less is known about use of habitat during the winter. Allen and Sweeney

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(1991) reported that winter home ranges of Bluebirds in South Carolina averaged 113.1 ha in size, an almost 10-fold increase from that of the breeding season. They attributed this increase to greater winter energy requirements, and the need to search outside their home range for food. Allen and Sweeney (1991) also found that wintering Bluebirds used edge habitat more than expected based on availability.

Region-specific information on habitat requirements and animal behaviors is important because population responses to environmental stimuli can vary across a species' range (Mehlman 1997, Whittingham et al. 2007). For instance, despite a trend for increasing Bluebird abundance nationally over the past 4 decades, Bluebird populations in central Kentucky have recently declined (Sauer et al. 2014). Mehlman (1997) demonstrated a trend for a decline in Bluebird abundance following a series of severe winters in the 1970s, but this effect varied across the species' range.

Many wintering birds join flocks; larger groups allow individuals to spend more time foraging as a result of decreased anti-predator vigilance by each individual, and may enhance the efficiency of finding food (Morse 1970, Sridhar et al. 2009). Group size may increase during periods of higher energetic demands (Caraco 1979), such as those imposed by inclement winter weather. Factors that might contribute to adjustments in group size by Bluebirds during unfavorable weather have not been described.

Winters in temperate regions can create metabolically demanding conditions for birds. Arthropods, an important food source for Bluebirds, are not always available during winter, and Bluebirds include a wide variety of fruits in their winter diet (Pinkowski 1977, Pitts 1979). Fruit is a critical component of the diet of many other wintering neo-temperate bird species (Baird 1980), but its relative importance for bluebirds is not clear. Snow is likely to affect availability of ground-active arthropods, whereas ice, which can accumulate on tree branches during freezing-rain events, may also impact fruit availability, and has been shown to disproportionately affect the abundance of tree foraging bird species in subsequent years as compared to open-habitat, ground-foraging species (Blais et al. 2001). If fruit is an important food resource for Bluebirds in winter, identifying and describing conditions that cause a shift to frugivory is important for better understanding the ability of Bluebirds to survive such conditions.

Because unpredictable winter events are correlated with fluctuations of Bluebird populations   (Gowaty and Plissner 2015, Wetzel and Krupa 2013), identifying the habitat requirements and factors potentially limiting populations is important, especially within a regional context since Bluebird population changes are spatially variable (Mehlman 1997, Sauer et al. 2014). The goals of this study were to describe the habitat composition and size of the winter home ranges of Bluebirds in the Bluegrass ecoregion of Kentucky, and to examine how weather influences Bluebird habitat and space use, group size, group composition, foraging decisions, and diet. We used radio-telemetry to locate individual Bluebirds throughout the winter, and then related their behaviors to habitat availability and weather conditions.

Field-site Description

All field research was conducted at the US Department of Defense Blue Grass Army Depot (BGAD), located in Madison County, KY (37°40'55"N, 84°13'16"W; Fig. 1). The installation consists of ~5907 ha, within which we focused on a study area of ~850 ha containing open fields and pastures dissected by woodlots, wooded stream corridors, roads, and buildings. The local population of Bluebirds presumably included both residents and migrant Bluebirds that breed at higher latitudes.
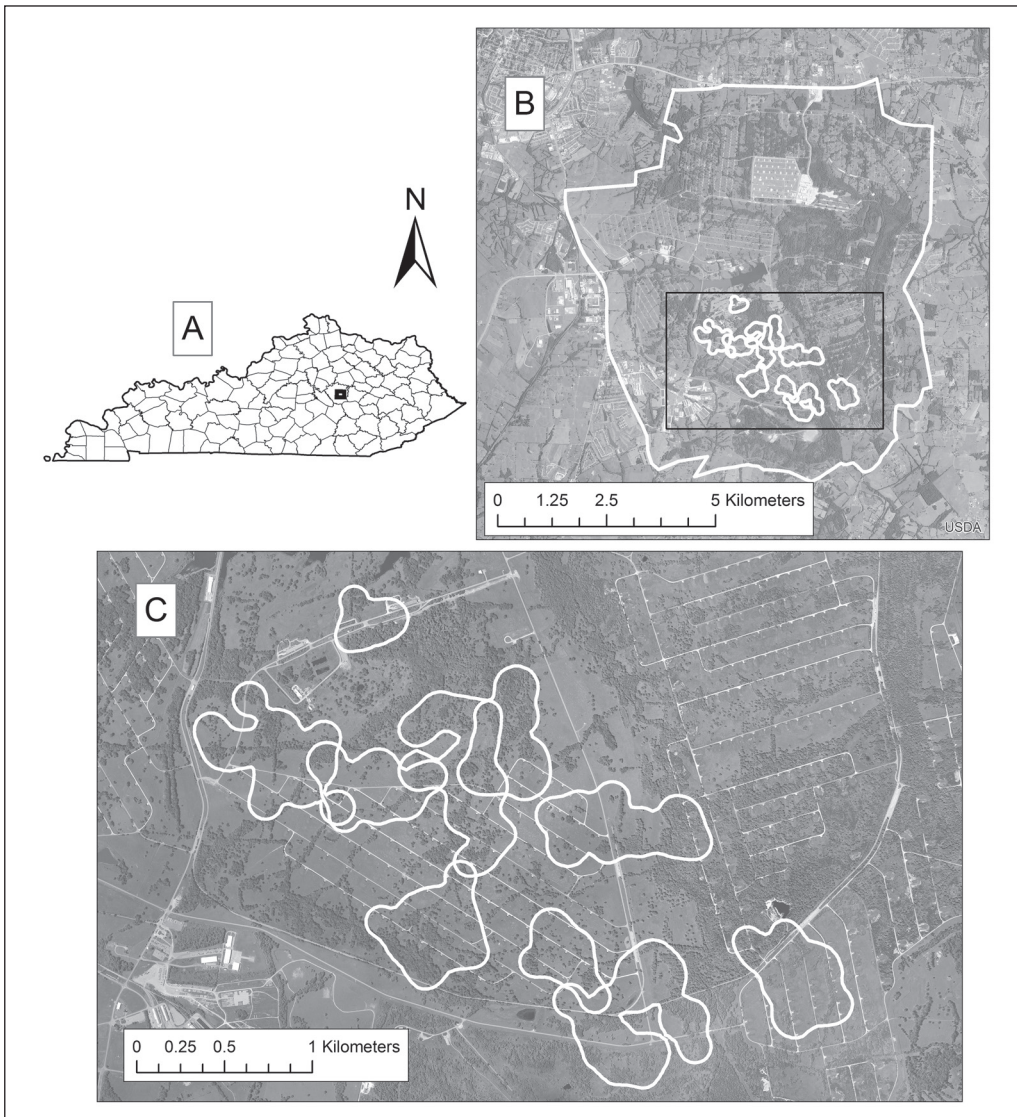

Figure 1. (A) Location of study area within the state of Kentucky. (B) Home ranges (95% kernel isopleths) of Bluebirds within the Bluegrass Army Depot (white boundary line), and (C) at a larger geographic scale within the study area.

Methods

During January–February of 2010 and 2011, we located Bluebirds across the study area and used 12 m x 2.5 m x 36 mm mist-nets to capture 1 or more birds in each observed group. We used playback of Bluebird vocalizations to attract birds into the mist-nets. We used elastic nylon-string harnesses (Rappole and Tipton 1991) to attach radio-transmitters (Holohil, BD-2; 0.9 g; average = 2.5 ± 0.2 [SD] % of body mass) to 19 Bluebirds (2010: n = 11 birds, 2011: n = 8 birds), and uniquely marked each bird using 1 USGS numbered aluminum band and 3 color bands. We determined the age of captured birds (second-year [SY] or after-second-year [ASY]) by examining the 10th primary coverts (Pitts 1985), and the sex of the birds by using plumage characteristics (Pyle 1997). Each radio-tagged Bluebird was tracked during daylight (08:00–18:00 hrs), typically 4–6 days per week, using a Yagi 3-element antenna and Telonics TR-4 receiver (Telonics, Inc., Mesa, AZ) for the duration of the transmitter battery life (60 days), or until transmitters fell off, or birds were depredated. We used a homing method to locate birds and visually confirmed their identity by sighting color bands or the transmitter's whip antenna. Upon locating a radio-tagged bird, we used a portable GPS/data management device (Trimble Juno SB; Trimble Navigation Ltd., Sunnyvale, CA) to record the individual's geo-referenced location, date, and time. During each observation, we recorded all data from a distance (typically >20 m) that appeared sufficient to avoid influencing the behavior of individuals or flocks. The average (± SD) interval between same-day observations was 81 ± 73 min.

Foraging observations were recorded whenever possible as part of radio-tracking and began as soon as birds were visually located. Radio-telemetry allowed us to locate birds from a distance (typically 25−100 m). Observations lasted 2−5 minutes and were conducted on all birds visible in the group. The average (± SD) number of observations per group was 21 ± 5. Observations occurred throughout the day, with an average (± SD) of 30 ± 11 per daylight hour. All Bluebirds in a group typically foraged for the same type of prey. Foraging directed at arthropods was treated as a single category because of difficulty identifying prey. We assumed Bluebirds were foraging for arthropods when they exhibited their characteristic drop-foraging behavior (ground sallying; Goldman 1975) and this assumption was often confirmed by observation of arthropod ingestion. The absence of leaves from most woody plants made instances of frugivory and type of fruit consumed quickly discernible. Frugivory was recorded based on plant species, and we later combined all such instances into a single category for analysis. Occasionally 2 different food items were being consumed by Bluebirds in a group (e.g., frugivory interrupted by sporadic drop-foraging by one or more group members), in which case we used the dominant foraging mode to assign food type.

Individual Bluebirds were typically observed in conspecific groups in a relatively small area. We estimated the size of the group and the sex of each group member during observations of radio-tagged birds. Determination of group size was often facilitated by extended flights of the entire group into open habitat, but estimates made in forest habitat or when movements were minimal may be biased

towards lower numbers. Thus, the estimates reported here likely represent minimum group sizes.

We opportunistically collected fecal samples while banding birds and stored them on filter paper. Dried fecal samples were scraped into a petri dish for sorting and identification. Working under a dissecting microscope, we dripped small amounts of ethyl alcohol (70%) into the dishes and separated seeds, arthropod parts, and other materials using forceps and probes (Burger et. al. 1999). Arthropods were sorted and identified to Order using references by Ralph et al. (1985), Borror et al. (1989), and Burger et al. (1999), and counted based on the number of heads, or pairs of mandibles, wings, elytra, chelicerae, or other distinguishable body segments. For example, a head capsule was counted as one individual and every two mandibles of particular taxa were counted as one individual. We sorted by species and counted all seeds found in the samples. To identify seeds, we used reference material including books (Jones 2005), the seed collection of the EKU Herbarium, and dissected field collections from the study area. We also consulted with an entomologist (A. Braccia, Eastern Kentucky University, Richmond, KY, pers. comm.) and a botanist (R. Jones, Eastern Kentucky University, Richmond, KY, pers. comm.) for verification.

All GPS locations were downloaded into ArcMap version 10.0 (ESRI, Redlands, CA) and projected using the NAD 1983 state plane (feet) Kentucky coordinate system. We generated home-range estimates using kernel density estimation (KDE) techniques that produce utilization distributions (UD) based on the relative density of telemetry locations over an area. We used the Geospatial Modelling Environment (Beyer 2012), a Program-R based supplement to ArcGIS, to conduct KDE analyses for all birds with >20 locations ($n = 9$). Results of KDE analysis are sensitive to both the resolution of the evaluation area (grid size) and the bandwidth (Seaman and Powell 1996). We used a fixed-bandwidth value of 20,000 for all analysis because it provided a suitable balance between over- and under-estimation of home ranges. We depicted a home-range boundary as the 95% isopleth of the kernel probability density function (Seaman et al. 1999). The core home-range area, representing areas of intensive use, is defined here by a 50% isopleth of the kernel probability function.

The nonselective capture of Bluebirds used in our sampling design excluded many individuals present in the study area, so comprehensive insight of Bluebird home range overlap across the study area was not possible. However, 5 birds in 2010 appeared to occupy distinct, yet adjacent, home ranges. We calculated the percentage of overlapping area between these adjacent home ranges using ArcGIS.

We used satellite imagery and a maximum-likelihood supervised image-classification process to categorize habitats (Palmeirim 1988), employing the image classification tool in ArcMap 10.0 to designate each pixel of the 1-m–resolution RGB satellite image of the study area (US Department of Agriculture, 2006) as either (1) wooded or (2) open habitat types based on the color profiles of the pixels. Representative training samples of the satellite imagery were selected using unambiguous areas of land cover within the study area and then further

adjusted to minimize overlap within resultant scatterplots of the red, green, and blue visual spectra for the 2 habitat category profiles. Based on the color profiles of these training samples, we assigned all pixels in the study area to either open or wooded categories. Further correction of the resulting raster image map (e.g., removal of artifacts such as improperly categorized shadows) was completed manually using Adobe Photoshop CS (version 5.1, Adobe™) and referencing the original satellite imagery.

Weather data were collected from an on-site weather monitoring station maintained by the US Army. Air temperature and wind speed were recorded every 15 min; thus, no weather observations were more than 7 min removed from an instantaneous reading. Snow depth was recorded daily 53 km north at the Lexington Bluegrass Airport (38°2' 23.99"N, 84°36'35.99"W) and collected from the National Oceanic and Atmospheric Administration's National Climatic Data Center (www. ncdc.noaa.gov).

Statistical analysis

We quantified descriptive Bluebird 95% and 50% home-range metrics including area, habitat composition, and overlap between adjacent home ranges with ArcGIS. We compared the habitat composition of home ranges to that of all unused habitat in the study area using a one-sample *t*-test. In this case, the study area was defined as a polygon bound by the most-outward vertices of all bird home ranges over 2 years. We quantified the habitat surrounding each bird location within a 5-m radius to determine habitat use at each location. These data were used to compare habitat use both when snow cover was and was not present (i.e., ≥ 2.54 and 0 cm, respectively, as recorded from the Lexington Bluegrass airport) using a Mann-Whitney U-test.

We used a nested-ANOVA to investigate the potential effect of snow cover on the distance of birds to edge habitat (the boundary between open and wooded spaces). For this analysis, we were interested in whether Bluebirds preferentially used edge habitats during periods of snow cover. To account for the repeated observations of individuals, each Bluebird location was nested by the identity of its group as determined by the individual radio-tagged bird that was used to find the group. Thus, group identity is based on the radio-tagged individual. We also used a nested-ANOVA to examine the potential effect of freezing temperatures (i.e., ≤ 0 °C) on Bluebird group size, again with each observation nested within group identity, as based on individual radio-tagged birds. Similarly, group sizes were compared during periods of snow cover (≥ 2.54 cm) and when snow was absent (0 cm) using a nested-ANOVA, with each observation of group size nested within a flock represented by the radio-tagged bird. We used a paired samples *t*-test to compare the number of males and females in groups. Sex composition of groups was also compared between periods of snow cover and when snow was absent using a nested-ANOVA, with the count of each sex nested within the flock as represented by the radio-tagged bird. Observations were not included in these analyses when the sex of one or more group members was not determined.

To test for influence of snow cover, air temperature, and wind speed on the foraging behavior of Bluebirds, we used a logistic regression analysis. For this

analysis, foraging behavior, the response variable, was classified dichotomously as directed towards fruit or arthropod prey. Group identity, as determined by the presence of a radio-tagged individual, was included as a random effect to account for repeated sampling.

For diet, we report the percent occurrence of taxa (i.e., the percent of samples in which a taxa occurs; Rosenberg et. al. 1990). To test for differences in diet based on weather, we used a 2 x 2 contingency table analysis to compare the relative occurrence of fecal samples with and without seeds when the temperatures were greater or less than 0 °C.

All analyses were performed using SPSS v. 18.0 (SPSS Statistics 2009). All means are reported ± SE, unless otherwise noted. Statistical significance was accepted at $\alpha = 0.05$.

Results

There were 21 and 19 days of snow cover of ≥2.54 cm during January–February of 2010 and 2011, respectively (Fig. 2). Daytime temperatures averaged 31.2 °C and 31.5 °C during January–February of 2010 and 2011, respectively.

We radio-tagged and tracked 19 individuals, including 15 males (7 SY and 8 ASY) and 4 females (2 SY and 2 ASY), for an average span of 23 ± 15 (SD) days (range = 1–51). We obtained an average of 20 ± 13 (SD) locations per individual (range = 2–44). Each day of tracking yielded an average of 1.7 ± 0.6 (SD) locations per individual.

Twelve of the 19 radio-transmitters were subsequently recovered either on the ground or among foliage. Whereas most of the recovered transmitters appeared to have fallen off (the birds were later re-sighted), at least 3 Bluebirds with transmitters appeared to have been killed by predators as indicated by a transmitter located among or near numerous feathers or other body parts.

In 2 cases, location data of 2 Bluebirds were combined for analyses. One pair of males from the same group was captured and radio-tagged simultaneously; 87% of 39 locations were shared by both birds (i.e., the two birds were typically found moving or foraging together). The other 2 birds (a male and female) were also captured simultaneously, but were tracked over separate time periods; the female was tracked for 14 days, after which the radio-tag fell off. We then recaptured and radio-tagged the male at the same location, and tracked it for 11 days. An exploratory home-range analysis for the 2 birds revealed nearly identical overall and core home ranges, so we combined their locations into a single home-range analysis.

Including the 2 shared home ranges described above, 9 Bluebirds (or pairs) had >20 location observations (average = 30.3 ± 7.5 [SD], range = 22–44). For these 9 birds, the average home-range area (95% utilization distribution) was 29.2 ± 2.4 ha (range = 16.3–42.3 ha), and the average core home-range area (50% utilization distribution) was 7.1 ± 0.6 ha (range = 3.8–9.9 ha) (Fig. 1). Of 5 birds that had an adjacent home range, an average of 9.4 ± 2.5% of the 95% home-range–estimate area was shared by neighboring birds. Core home ranges did not overlap.

Bluebird home ranges consisted of 39.6 ± 2.6% wooded habitat and 60.4 ± 2.6% open habitat. The percentage of wooded habitat within home ranges did not differ significantly from the overall percentage of wooded habitat in the entire study area (35.7%) (t_8 = 1.5, P = 0.18). Similarly, core home-range areas consisted of 41.1 ± 3.5% wooded habitat and 58.9 ± 3.5% open habitat, which was not significantly different from the composition of available habitat in the study area (t_8 = 1.6, P = 0.16).

The mean percentage of wooded area surrounding each observation (5-m radius) was 60.0 ± 2.0% (n = 344). Habitat within the 5-m radius around each point was frequently either entirely (100%) wooded or entirely open (0% wooded). The mean percentage of wooded habitat per observation (5-m radius) during periods of snow cover (54.4 ± 4.3%, n = 94) did not differ from that during periods when snow was
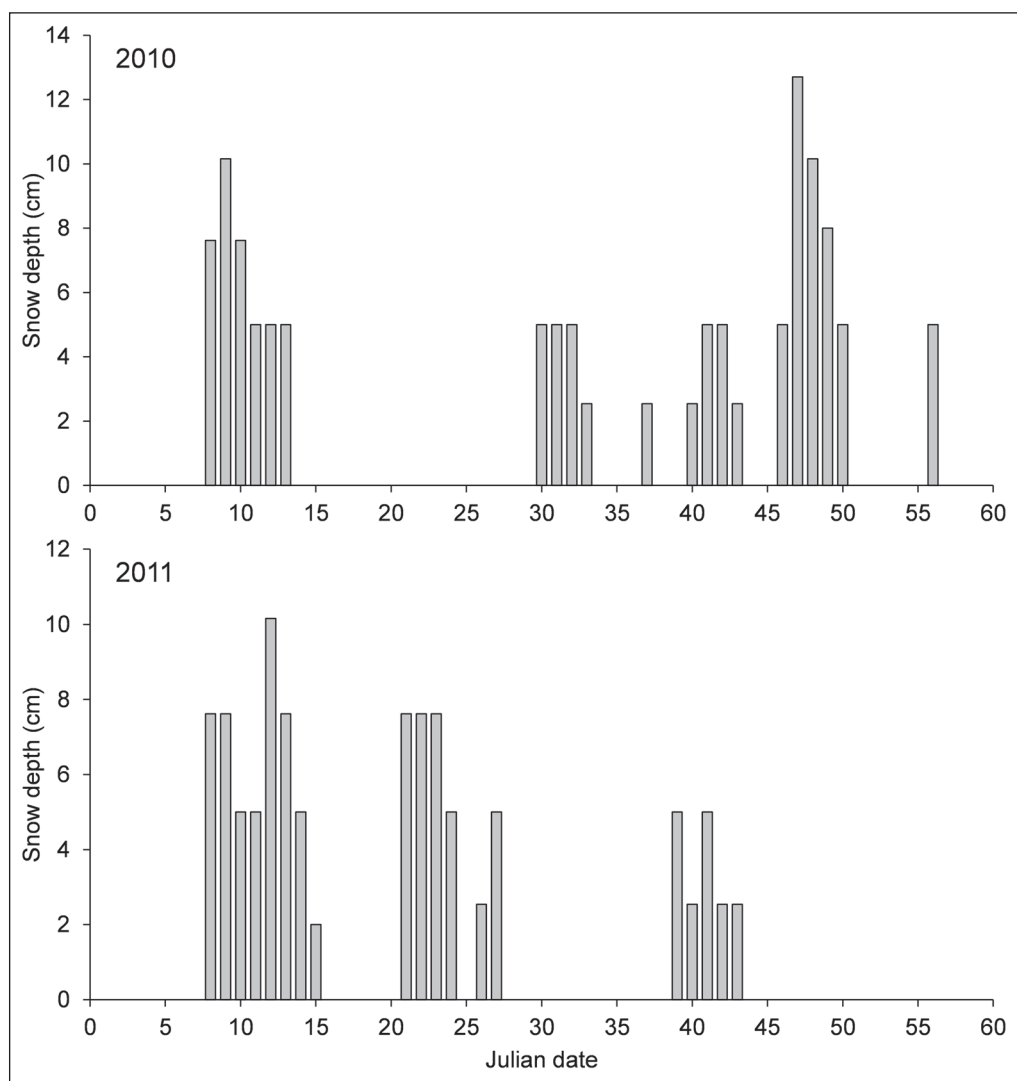

Figure 2. Snow depth at Lexington Bluegrass Airport during January–February of 2010 and 2011.

absent (63.1 ± 2.5%, n = 250) (Mann-Whitney U-test: P = 0.14). The distance of Bluebirds to the edge of wooded habitat did not differ during periods of snow cover ($F_{1,91}$ = 0.01, P = 0.92).

Radio-tagged Bluebirds were almost always found in conspecific groups (97% of observations). Average group size was 5 ± 0.1 individuals (n = 300), with a maximum of 16 individuals observed in a group that included a radio-tagged bird (Fig. 3). Groups included more males (2 ± 0.1) than females (1 ± 0.1) (t_{272} = 20.0, P < 0.001), and the presence of snow cover did not influence the sex composition of groups ($F_{1,83}$ = 2.6, P = 0.11). Mean Bluebird group size during below-freezing temperatures (5 ± 0.2 individuals) was larger than when temperatures were above 0 °C (4 ± 0.2 individuals) ($F_{1,62}$ = 4.8, P = 0.032). Similarly, group size during periods of snow cover (6 ± 0.3 individuals) was larger than that when snow was absent (5 ± 0.1 individuals) ($F_{1,266}$ = 5.0, P = 0.02).

Flocks were typically found with all members foraging on either arthropods or fruit (91% of n = 235 observations), but not both. Most foraging attempts were directed at arthropods (>65% of observations for either year), and relative frequencies of frugivory for different fruits varied between years, with *Phoradendron leucarpum* Raf. (Oak Mistletoe) most common in 2010, and *Celtis occidentalis* L. (Hackberry) the most common in 2011 (Table 1). Logistic regression analysis indicated that frugivory was more likely than foraging on arthropods during observations with low temperatures, low wind speed, and the presence of snow (Table 2).

Analysis of fecal samples from 33 birds included 105 items identified from 7 arthropod orders (Mesostigmata, Araneae, Orthoptera, Hemiptera, Hymenoptera,
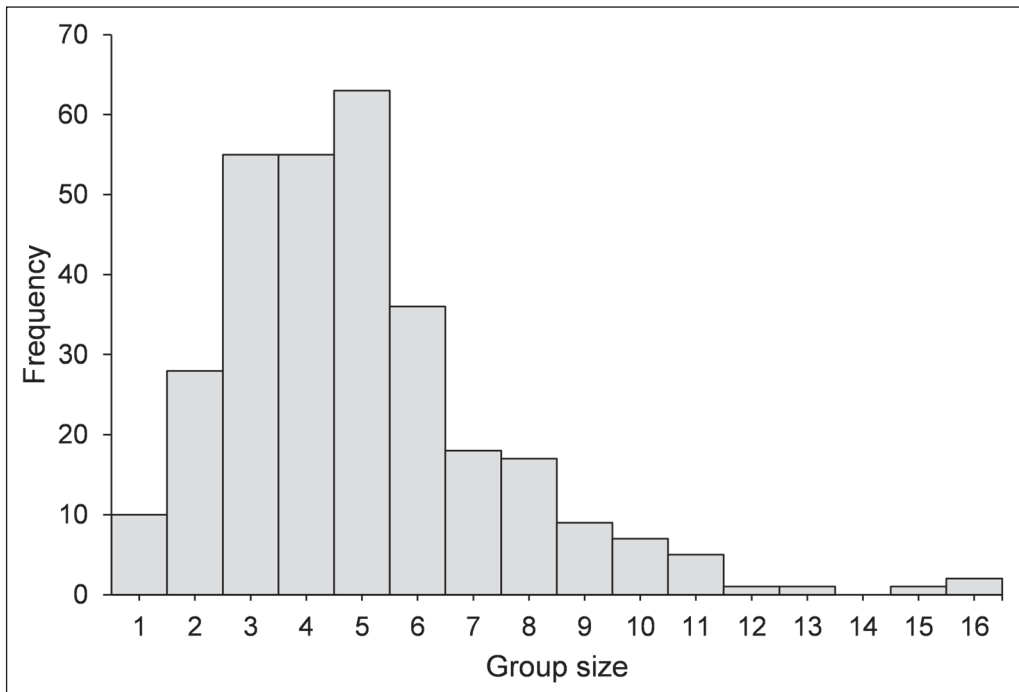

Figure 3. Eastern Bluebird group sizes (n = 300) during January–February of 2010 and 2011.

Coleoptera, and Lepidoptera) and 5 species of seeds (Table 1). Seeds represented 60% of all items and occurred in 22 samples. There was an equal frequency of fecal samples that contained only arthropods (33%), only fruit seeds (33%), and both arthropods and fruit seeds (33%). Fecal samples collected when the temperature was below 0 °C ($n = 20$) were 4.4 times more likely to have seeds present than samples collected at higher temperatures ($n = 13$) ($\chi^2 = 4.06$, $P = 0.04$, Fig. 4).

Table 1. Percent foraging observations of Eastern Bluebirds in 2010 ($n = 139$), 2011 ($n = 96$), and in both years combined among different food categories. Other fruit included *Prunus serotine* Ehrhart (Black Cherry), *Symphoricarpos orbiculatus* Moench(Coralberry), *Lonicera japonica* Thunb. (Japanese Honeysuckle)*, and *Toxicodendron radicans* L. (Poison Ivy)*. Plant species with an asterisk were also detected in fecal samples.

Food category	Both years (%)	2010 (%)	2011 (%)
Arthropods	71.9	76.3	65.6
Hackberry*	10.2	0.1	24.0
Oak Mistletoe*	8.5	13.7	1.0
Red Cedar*	6.0	7.9	3.1
Other fruit	3.4	1.4	6.3

Table 2. Results of logistic regression analysis on forage type (fruit or arthropods) by weather conditions. Low air temperature, low wind speed, and snow presence increased the likelihood that eastern bluebirds foraged on fruit. Group identity was included as random variable to account for repeated measurements so coefficients and odds ratio are not reported.

	Wald's	*P*-value	*B*	95% CI Lower	95% CI Upper	Odds ratio
Low air temperature	14.5	<0.001	0.19	0.09	0.29	1.22
Low wind speed	8.2	0.004	0.57	0.18	0.96	1.77
Snow presence	5.3	0.020	1.23	0.18	2.28	3.44
Group identity	13.0	0.791	-	-	-	-

Figure 4. Percent of fecal samples with seeds present (i.e., only seeds, or seeds and arthropods) or with only arthropods collected from Eastern Bluebirds during January–February of 2010 and 2011 when temperatures were above or below freezing.
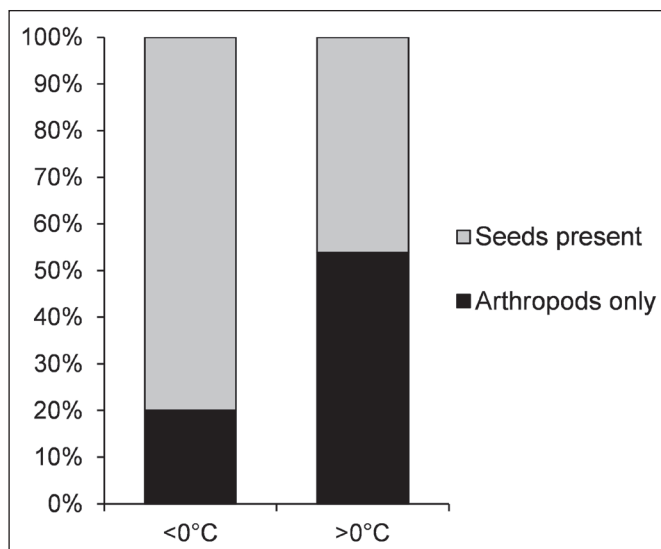
Discussion

Home range and habitat use

The mean estimated 95% winter home range size of Bluebirds in this study (29.2 ha) was smaller than that reported by Allen and Sweeney (1991) in South Carolina (113.1 ha). However, this difference is likely at least partially due to the use of different home-range estimation techniques; the minimum convex polygon method used by Allen and Sweeney (1991) is known to overestimate home-range sizes (Anderson 1982), whereas the kernel-based utilization distribution that we used emphasizes focal areas of intensive use and minimizes the influence of distant, isolated locations (i.e., outliers). The mean size of 95% winter home ranges of Bluebirds in this study was similar to that of Bluebirds during seasonal transition periods (i.e., August–November and February–April) described by Savereno (1991) in South Carolina (28.0 ha). In his study, home-range area was calculated using cumulative area curves (Odum and Kuenzler 1955), which is more comparable to the kernel-based utilization distribution used in this study than the minimum convex polygon method. Our sample size was too small to examine the possible effects of sex and age on the size of Bluebird winter home ranges.

With the exception of 2 pairs whose space use data were combined for home-range analysis, we found little (95% home-range estimates) and no (core home-range estimates) overlap in the home ranges of Bluebirds. Territory maintenance and defense during the non-breeding season has been documented in resident and migratory bird species, and is typically driven by variation in the abundance of limited food resources (Brown et al. 2000, Safina and Utter 1989, Townsend et al. 2010). The distinct, minimally overlapping home ranges of Bluebirds in this study may also represent resource-influenced territoriality, but, in this case, the territories appear to be specific to groups. The 2 pairs that occupied almost identical home ranges over 45 days of radio-tracking suggest that Bluebird groups (or certain pairs) persist for extended periods of the winter , but the specific roles of these relationships and other potential effects of group behavior on space use of wintering Bluebirds have yet to be determined. It is also possible that winter territoriality is related to defense of breeding territories. Thomas (1946) noted that wintering Bluebirds in Arkansas sometimes engaged in intraspecific competition (i.e., fighting and singing) around nest boxes, suggesting that defense of nest sites may occur throughout the year, though to a lesser degree in winter. Thus, in some populations, the co-occurrence of a male and female within home ranges may be related to the winter maintenance of a breeding territory.

Home ranges of Bluebirds in this study were composed of more open habitat than wooded habitat, although wooded areas made up almost 40% of home ranges. Habitat structure was not measured in this study, but, in all cases, home ranges included a heterogeneous mixture of both open and wooded areas, including lone trees and wooded corridors. We found no difference in habitat composition between Bluebird home ranges and the study area outside of those home ranges, and also no difference in habitat composition between core (50%) and 95% home ranges. Because we used radio-telemetry to locate birds, our observations should not be

biased by differences in detectability between habitats. Allen and Sweeney (1990) and Savereno (1991) reported that wintering Bluebirds in South Carolina used edge habitat more than expected, and Levey et al. (2008), also in South Carolina, found that movement along edges was preferred by wintering Bluebirds over using open space within corridors. Because we only categorized open and wooded habitat, our data cannot test if Bluebirds prefer edge habitat, as has been found in other studies (Allen and Sweeney 1990, Levey et al. 2008, Savereno 1991).

Mean distance to edge did not change during periods of snow cover, nor did the mean percentage of wooded habitat within a 5-m radius. These results suggest that Bluebirds do not dramatically shift habitat occupancy during periods of snow cover, and that their presumed preference for edge habitat is unaffected. Petit (1989) demonstrated that wintering woodland birds move into habitat patches with greater cover (i.e., mature pine stands) during harsh weather, but habitat occupancy by Bluebirds in this study appeared to be unchanged by snow cover of at least 2.54 cm in depth. Brotons (1997) described how *Parus ater* L. (Coal Tit) responded to snow presence by changing foraging methods within a patch rather than seeking a new habitat, and our results suggest that Bluebirds may respond to the presence of snow in a similar way. For example, Pinkowski (1977) described a positive relationship between Bluebird foraging height and temperature as well as sunshine percentage (i.e., the proportion of time that shadows were cast), possibly as a response to changing insect detectability related to weather. In that scenario, a change of habitat as temperatures drop may be unnecessary to meet immediate foraging needs, requiring only a behavioral response within the habitat. Even a shift toward frugivory may not require movement to a new habitat (e.g., into a wooded area) if fruits are available nearby. Despite no apparent change in habitat occupancy during snow cover, Bluebirds may cope with unfavorable weather and its associated energetic demands in other ways, such as by shifting diet or group size. Several studies have documented communal night roosts in trees and bird houses during cold weather and snowstorms (Forbush 1929, Frazier and Nolan 1959, Pitts 1978, Thomas 1946), suggesting weather influences bluebird habitat use and group size during nighttime. Because of site access limitations during the night, we were unable to include such behavior as part of this study, although we did observe a daytime roost in a tree of 19 individuals during a severe winter storm.

Foraging behavior

Bluebirds in this study were more likely to engage in frugivory when temperatures and wind speeds were low, and when snow cover was present, with snow cover having the strongest effect. Low temperatures decrease arthropod activity (Mellanby 1939), and snow reduces insect availability to Bluebirds (Frazier and Nolan 1959, Pitts 1978), particularly by covering ground-active arthropods. Since drop foraging is the most common foraging method used by Bluebirds in all seasons (Gowaty and Plissner 2015), it's not surprising that snow cover causes a shift to alternative methods. Together, low temperatures and snow cover may make insectivory less reliable and possibly increase the cost of this strategy to a suboptimal level. Increased frugivory when wind speeds were low may indicate an ability of

Bluebirds to manage thermal stress by altering foraging behavior. Grubb (1975) found that several species of woodland birds foraged at lower heights during periods of high wind (i.e., 2–3 m/s), and suggested that birds seek areas of low thermal stress (i.e., closer to the ground) under windy conditions. Similarly, birds have been shown to avoid windward edges of habitat patches and favor leeward edges (Dolby and Grubb 1999). High winds may encourage insectivory and discourage frugivory as a way to minimize thermal loss to wind, which would likely increase when Bluebirds forage for fruits high in trees. Both Oak Mistletoe and Hackberry fruit, the 2 most common targets of frugivory, were typically located well above ground level. The presence of high wind may limit the ability of Bluebirds to forage efficiently during low temperatures and snow cover; so, when combined, these factors may create the most energetically demanding (and behaviorally restrictive) conditions that Bluebirds experience during winter.

The fruits most frequently consumed by Bluebirds in this study differed between years. For example, based on observational data we found that Oak Mistletoe frugivory accounted for 13.7% of all foraging observations in 2010, and only 1% in 2011. Instances of Hackberry frugivory displayed an opposite pattern with 0.07% and 24.0% of all observations in 2010 and 2011, respectively. Although both are native species, Oak Mistletoe tends to have relatively high lipid content (Stiles 1993), whereas Hackberry has low levels of lipids (Johnson et al. 1985, Stiles 1980). The availability of food was not determined in this study, so it is not possible to determine whether the relative abundances of these food items accounted for this pattern. Nonetheless, the composition of fruit in the diet of wintering Bluebirds occupying the same general area can differ considerably between years. Therefore, the relative value of any one fruit resource over another may vary annually, just as the relative value of fruit over arthropods may depend on immediate weather circumstances. Although Bluebirds are known to consume at least 60 types of fruit in winter (Hoyo et al. 1992). Most winter studies of Bluebirds in temperate North America document the consumption of fewer than 10 fruit species, most of which represent only a minor dietary component (Morland 1978, Pinkowski 1977, Pitts 1978, Savereno, 1991). We observed Bluebirds foraging on 7 types of fruit, but most foraging was directed toward fruit of Hackberry, Mistletoe, and *Juniperus virginiana* L. (Red Cedar). Although fruits have been reported as important for wintering Bluebirds elsewhere, these 3 species were absent or only a minor dietary component for wintering Bluebirds in Ohio (Morland 1978), South Carolina (Savereno 1991), and Tennessee (Pitts 1979), suggesting regional or temporal differences, likely based on availability.

Arthropod segments, comprising at least 7 different orders, were the most common items in fecal samples, followed in decreasing order of occurrence by seeds of Red Cedar, Oak Mistletoe, Poison Ivy, and Japanese Honeysuckle. Seeds were more commonly found in fecal samples collected during periods with sub-freezing temperatures reinforcing our conclusions from foraging observations that Bluebird diets shift toward fruit during periods with low temperatures.

Group size

If the metabolic costs of birds increase during unfavorable weather conditions (i.e., low temperature), individuals may have to spend more time foraging to meet metabolic demands. One strategy for increasing an individual's foraging time is termed the "group-size effect", whereby individual foraging time can increase with flock size as a result of improved collective anti-predator vigilance (Beauchamp 1998, Caraco 1979). Hogstad (1988) observed this effect among flocks of wintering *Poecile montanus* von Baldenstein (Willow Tit) during cold days. Large Bluebird flocks during snowstorms have been sporadically reported elsewhere during winter (e.g., Thomas 1946), including accounts of *Sialia currucoides* Bechstein (Mountain Bluebird) and *Sialia Mexicana* Swainson (Western Bluebird) (Allen and Brewster 1883, Henderson 1903). By assembling in larger numbers during inclement weather, Bluebirds may be able to locate new food sources while simultaneously benefiting from a group-size effect. Because Bluebird group size was larger during periods with snow cover, when frugivory was also higher, increased flocking behavior as a strategy to locate fruit resources seems possible (e.g., Elgar and Catterall 1982, Ficken 1981).

Thomas (1946) described "roaming and shifting" among Bluebird flocks during winter, suggesting a lack of cohesiveness within Bluebird groups. Although accurately estimating group membership was not always possible, it was not uncommon to repeatedly observe the same uniquely banded individuals together over a period of weeks. The 2 pairs of Bluebirds whose home-range estimates showed considerable overlap is an additional indication that group cohesiveness, as well as stable territoriality, can be maintained during the winter months. So it appears that Bluebirds maintain winter territories in small groups through most of the winter, but group membership may change, particularly during periods of inclement weather when group size increases. More work is needed to understand how group size and membership is related to foraging.

Our results suggest Bluebirds respond to inclement winter weather by changing foraging behaviors and increasing group size; however, it remains to be determined how these responses are driven by the distribution of food, their ability to find resources, predator avoidance, and even thermoregulation (e.g., communal roosting). Although we detected no mortality as a result of winter weather, our sample size to do so was small. Winter weather may lead to mortality by reducing food availability and contributing to physiological stress through heat loss. Concurrent changes in foraging and space-use behavior may also make birds more vulnerable to predation. We found evidence for changes in behavior in response to weather, but more work is needed to understand the population-level impacts.

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