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Winter Behavior and Ecology of Eastern Bluebirds (*Sialia sialis*): Home Ranges, Habitat Use, and Effect of Weather on Foraging Behavior

Todd J. Weinkam
Eastern Kentucky University

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WINTER BEHAVIOR AND ECOLOGY OF EASTERN BLUEBIRDS (*Sialia sialis*): HOME
RANGES, HABITAT USE, AND EFFECT OF WEATHER ON FORAGING BEHAVIOR

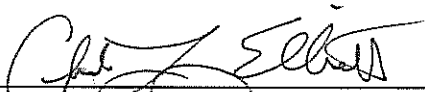
By

Todd J. Weinkam

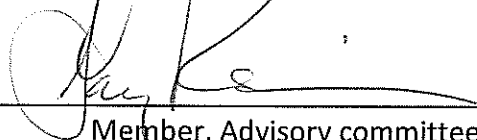
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Date

8 November 2013

WINTER BEHAVIOR AND ECOLOGY OF EASTERN BLUEBIRDS (*Sialia sialis*): HOME
RANGES, HABITAT USE, AND EFFECT OF WEATHER ON FORAGING BEHAVIOR

By:

Todd J. Weinkam

Bachelor of Science

Ohio University

Athens, Ohio

2008

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
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DEDICATION

This thesis is dedicated to my parents, Jerry and Marcia, without the support of whom my aspirations, educational and otherwise, would have been impossible.

To Cara, for her continuing encouragement every day.

And

To you, the reader: May you learn something interesting.

ACKNOWLEDGMENTS

I am grateful for the extensive help and guidance I've received throughout the process of this thesis. Dr. David Brown, your advice and support has propelled my learning to new levels. I'd also like to thank committee members Dr. Gary Ritchison, and Dr. Charles Elliott, for your invaluable advice. I extend thanks to Gregg Janos, for his diligence in the lab and his assistance in the field. My gratitude goes to the employees of the Blue Grass Army Depot for assisting me with access to the study site. Finally, I'd like to thank the men and women of science who have come before me, and whose work paved the way for this study.

ABSTRACT

Eastern bluebirds (*Sialia sialis*) are widespread across eastern North America, but populations appear to be susceptible to extreme winter weather. Declines in population following cold winters in states like Kentucky suggest the need to better understand winter-specific habitat requirements and behavioral responses to inclement weather. My objectives were to 1) describe the size and habitat composition of the home ranges of wintering bluebirds, and 2) examine the effects of weather (i.e., temperature, wind speed, and snow presence) on habitat occupancy, group size, and foraging behavior. My study was conducted at the Blue Grass Army Depot in Madison County, Kentucky. I radio-tracked 19 bluebirds during January and February 2010 and 2011 and recorded their locations, the size and composition (males vs. females) of groups, and foraging behavior. Mean home range size (\pm SE) was 29.2 ± 2.36 ha ($N = 9$), which is smaller than previously published estimates for wintering bluebirds. Home ranges consisted of an average (\pm SE) of $39.6 \pm 2.6\%$ wooded habitat and $60.4 \pm 2.6\%$ open habitat ($N = 9$), and edge habitat between these areas was likely an important additional component. Insectivory was the most frequently observed foraging behavior (>65% of all observations, $N = 235$), although shifts to frugivory were observed during periods of low temperatures, low wind speeds, and the presence of snow. Hackberry (*Celtis occidentalis*), mistletoe (*Phoradendron leucarpum*), and red cedar (*Juniperus virginiana*) were the most commonly consumed fruits, but high winds may restrict their potential as a food resource. High winds, when combined with low temperatures and substantial snow cover, potentially lower the efficiency of both insectivory and frugivory to sub-optimal levels, thus representing especially challenging winter conditions for bluebirds. In addition to changing foraging strategies, bluebirds appeared to respond to weather conditions by adjusting group sizes, a tactic which may enhance foraging efficiency, allow individuals to locate food resources, or both. These responses to weather occurred without an apparent shift in habitat occupancy, thus the ability of bluebirds to survive extreme winter weather may be constrained by available food resources and interacting weather conditions that may restrict foraging options.

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CHAPTER I

INTRODUCTION

A growing body of research has revealed that events occurring during the non-breeding season can significantly impact bird populations. Environmental factors and winter-specific resource constraints can be significant determinants of the behavior (Duriez et al. 2005, Diggs et al. 2011), abundance (Mehlman 1997, Meehan et al. 2004), and range limits (Gross & Price 2000, Zuckerberg et al. 2011) of birds. Density-independent factors like severe winter weather cause fluctuations in population size and impact winter survival and reproductive success in subsequent seasons (Porter et al. 1983, Sauer & Droege 1990). Differential habitat occupancy related to survival or winter strategies can have carryover effects at individual and population levels (Webster & Marra 2002, Norris et al. 2004, Studds et al. 2008). Our ability to predict and interpret these processes may be enhanced by a better understanding 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.

The behavior and ecology of birds during the non-breeding season has received disproportionately little research focus compared to the breeding season, despite its important influence on avian populations. Eastern bluebirds (*Sialia sialis*) have been widely studied during the breeding season (e.g., Pinkowski 1977a, b, Davis et al. 1994, Plissner & Gowaty 1995, Horn et al. 1996, Wood & Patton 2003, Godard et al. 2007), but

most of our knowledge of the winter ecology of eastern bluebirds (hereafter bluebirds) has been derived from anecdotal descriptions and inferences. Reports of bluebird mortality during harsh winter weather (Wilson & Stamm 1960, Pitts 1978) followed by observable population declines (Wilson 1962, Monroe 1978, Stamm 1979a, b, Sauer & Droege 1990) demonstrate the potential for winter weather to affect bluebird populations and underscore the importance of studying bluebird behavior and habitat use during this period. Wetzel and Krupa (2013) reported a positive correlation between mean winter temperature and bluebird abundance during subsequent breeding seasons in Kentucky, and suggested that bluebirds in Kentucky were particularly susceptible to cold winters.

Winters in temperate regions are characterized by low ambient temperatures and short days, creating metabolically demanding conditions for birds. Arthropods, an important food source for bluebirds, are not always available during winter, but bluebirds are known to include a wide variety of fruits in their winter diet (Pinkowski 1977b, Pitts 1979). The factors driving bluebirds to shift their diet have not been explicitly described, although it has been suggested that snow and ice are a major determinant of decreased food availability and subsequent bluebird mortality (Frazier & Nolan 1959, Pitts 1978). 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.

Another behavioral strategy of many wintering birds is to join flocks; larger groups allow individuals to spend more time foraging as a result of decreased anti-

predator vigilance by each individual. Groups may be expected to become larger 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 objectively described, although extremely large bluebird flocks have occasionally been reported during winter (Thomas 1946). Communal roosting by bluebirds during cold weather (Thomas 1946, Frazier & Nolan 1959, Pitts 1978) suggests that constraints on grouping behavior, such as resource-based territoriality, may be relaxed, at least for roosting birds, to help cope with unfavorable conditions. However, additional study is needed to better understand the conditions that contribute to fluctuations in group size.

Although several investigators have examined bluebird breeding habitat and nest box use (e.g., Sloan & Carlson 1980, Parren 1991, Plissner & Gowaty 1995, Horn et al. 1996, Stanback & Rockwell 2003), less is known about their winter habitat requirements and habitat use. Allen and Sweeney (1991) reported that winter home ranges of bluebirds in South Carolina averaged 113.1 ha in size, an almost ten-fold increase from that of the breeding season. They attributed this increase to greater winter energy requirements, decreased availability of arthropods, and the need for bluebirds to search for fruit in new areas. Allen and Sweeney (1991) also found that wintering bluebirds used edge habitat more than expected based on availability, and identified pine woodlands with an open understory as the single largest component of home ranges and the most often used habitat type. Conversely, wintering bluebirds in

their study rarely used dense pine stands, an alternative, but abundant habitat type in their study area.

Savereno (1991) studied non-breeding bluebirds during transitional periods between breeding/winter (September-October) and winter/breeding (March-April), and found that the average home range size was 28.0 ha. This estimate was determined using a maximum area curve (Odum & Kuenzler 1955) rather than the minimum convex polygon method (Mohr 1947) used by Allen and Sweeney (1991). Although these two contrasting methods of home range estimation make direct comparisons problematic, home ranges of bluebirds were consistently larger during non-breeding periods than during the breeding season regardless of the home range analysis method used. As also reported by Allen and Sweeney (1991), Savereno (1991) determined that open pine and edge habitats were used more than expected by bluebirds based on availability within the study area.

There are limits to the applicability of the results of previous studies because of regional differences in habitat availability. In addition, the use of kernel-based utilization distribution methods has improved the precision and biological relevance of home-range estimates over those derived from the minimum area method (Mohr 1947) used by Allen and Sweeney (1991) and by maximum area curves (Odum & Kuenzler 1955) used by Savereno (1991).

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 four decades, bluebird populations in central Kentucky have recently declined (Figure 1)¹ (Sauer et al. 2011). Mehlman (1997) demonstrated a trend for a decline in eastern bluebird abundance following the severe winters in the 1970s, but this effect varied across the species' range. Wetzel and Krupa (2013) identified a correlation between bluebird abundance in central Kentucky and mean temperature of preceding winters, and suggested that the susceptibility of bluebirds to extreme winter weather was partly responsible for the observed decline. Additional interacting factors such as nest-box competition (Wetzel & Krupa 2013) and the emergence of West Nile virus (*Flavivirus*) are likely involved in the decline (LaDeau et al. 2007), but the specific role of extreme winter weather and, more importantly, the ability of bluebirds to behaviorally mitigate such conditions (i.e., shifts in diet, group size, or habitat use) have yet to be identified.

Because unpredictable winter events are known to drive fluctuations of bluebird populations, identifying the habitat requirements and factors potentially limiting populations is important, especially within a regional context. The goals of my study were to describe the habitat composition and size of the winter home ranges of eastern bluebirds in the Bluegrass ecoregion of Kentucky, and to examine how weather influences bluebird habitat and space use, foraging decisions, group size, and group composition.

¹ All tables and figures located in appendix

CHAPTER II

METHODS

Study area. All field research was conducted at the U.S. Department of Defense Blue Grass Army Depot (BGAD), located in Madison County, KY (N 37.682054, W - 84.22122). The installation consists of approximately 5,907 ha, within which I focused on a study area of approximately 850 ha (Figure 2). Access to the area is restricted, and a population of eastern bluebirds and nest boxes (N = 75) that are often used for winter roosting were in place prior to this study. Both year-round residents and migrant bluebirds that breed at higher latitudes were presumably present during my study.

The study area is within the Outer Bluegrass region of the Interior Low Plateau physiographic region of Kentucky (Jones 2005). The climate is characterized as temperate, humid, and continental, and the landscape is gently rolling. Thomas (1994) described the BGAD in terms of three major vegetation types: pasture (2,568 ha; 74%), upland forest (506 ha; 14%), and bottomland forest (404 ha; 12%). The area where I studied bluebirds contained open fields and pastures dissected by woodlots, wooded stream corridors, roads, and buildings.

Telemetry and winter banding. I drove and walked throughout the study area during January and February of 2010 and 2011, locating bluebirds by sight and vocalizations. Once a flock of bluebirds was located, I erected a 12 m x 2.5 m (36 mm mesh) mist-net in the vicinity of the flock. A study skin of a male bluebird was placed on a low perch next to the net and audio playback of various bluebird songs, calls, and

distress vocalizations was used to attract bluebirds (Sloan & Carlson 1980). Audio playback was continued until one or more bluebirds were captured.

I captured and fitted 19 bluebirds with radio-transmitters during January and February 2010 (N = 11 birds, first capture on January 4, last capture on February 14) and 2011 (N = 8 birds, first capture on January 3, last capture on January 29). Radio-transmitters (Holohil, BD-2; 0.9 g; average = 2.5 ± 0.2 [SD] % of body mass) were attached using elastic nylon-string harnesses (Rappole & Tipton 1991, Naef-Daenzer 2007), and all birds were uniquely marked using one USGS numbered aluminum band and three color bands. The age of captured birds (second-year or after-second-year) was determined by examining the 10th primary coverts (Pitts 1985). Sex was determined using plumage characteristics. Individuals with rich blue upperparts and a contrasting chestnut throat, breast, and flanks were classified as males, whereas individuals with dull blue-gray upperparts and tail, gray wash over the back, and dull chestnut breasts were classified as females (Pyle 1997, Poole 2005). Radio-tagged birds were observed for up to several minutes after release until I was confident that the transmitter and harness did not impede mobility. Procedures related to the capture and handling of bluebirds were reviewed by Eastern Kentucky University's Institutional Animal Care and Use Committee and approved as Protocol #01-2010.

Each radio-tagged bluebird was tracked using a Yagi three-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. Radio-tracking was conducted during daylight (08:00-18:00 hrs), typically 4-6 days per week. I

used the homing method (Kenward 2001) to locate birds and visually confirmed their identity by sighting the bird's unique color bands or the transmitter's whip antenna. Upon locating a radio-tagged bird (hereafter, observation), I 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, all data were recorded from a distance (typically > 20 m) that appeared sufficient to avoid influencing the behavior of individuals or flocks.

Foraging observations (i.e., type of food bluebirds were searching for or consuming) were recorded whenever possible. Food type (typically arthropods or fruit; see Results section for a complete list of food items) was identified using binoculars). All bluebirds in a group, including radio-tagged birds, typically foraged for the same type of prey. Occasionally, however, two different food items were being consumed by bluebirds in a group (e.g., frugivory interrupted by sporadic ground-sallying by one or more group members). Discrete food categories (i.e., arthropods or fruit) were assigned later for analyses and, when two food items were being consumed, I assigned a category with a coin flip. I assumed bluebirds were foraging for arthropods when they exhibited their characteristic "fly-down" behavior (ground sallying; Goldman 1975) and this was often confirmed by observation of arthropod ingestion. The absence of leaves from most woody plants made instances of frugivory and type of fruit quickly discernible.

Individual bluebirds were typically observed in conspecific flocks in a relatively small area and, during observations of radio-tagged birds, an attempt was made to determine the size of the group and the sex of each group member. Discrete groups

were discerned by observing an area for several minutes until all or nearly all bluebirds were detected and an estimate obtained. Observations that included bluebirds of unknown sex were excluded from statistical analyses. Determination of flock 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 I report likely represent minimum group sizes.

My schedule for tracking radio-tagged bluebirds ensured that all were located the same number of times and at different times during each day of radio-tracking. After locating and observing each individual once, I began the process again by returning to the first individual and continuing until all birds were located again, or until field work was concluded for the day. The average (\pm SD) interval between same-day observations was 81 ± 73 min. In some instances, locations and observations of the same individual were determined successively (mean interval = 18.2 ± 6.9 (SD) min, $N = 54$) to increase sample sizes, but this method of sampling was used infrequently (i.e., no more than 5 locations per bird, per day were collected in this manner). I assumed that these successive observations were biologically independent because the interval between them was long enough that individuals could potentially traverse their entire home range (Lair 1987, Otis & White 1999, pers. obs.). Also, exclusive use of independent observations is unnecessary (Swihart and Slade 1997) and the accuracy and biological relevance of home-range estimates are enhanced by using consecutively collected locations (De Solla et al. 1999). Although relatively infrequent, bluebirds sometimes remained in the same location for an extended period and, when they did so, locations

were not determined consecutively. If I was unsuccessful at locating the signal of a focal bird, I drove throughout the study area and attempted to locate the signal from unobstructed vantage points. I searched until the bird was located or the remaining areas of the BGAD outside of the study area had been surveyed without success. This process continued each day of field work throughout the expected battery life of each transmitter.

Home range analysis. 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. Home range estimates were generated using a fixed kernel based utilization distribution (Silverman 1986, Worton 1989). Utilization distributions are more biologically meaningful than conventional minimum convex polygons (Mohr 1947), and have emerged as a powerful and popular method for depicting home ranges (e.g., Naef-Daenzer 1993, Thogmartin 2001, Hallworth et al. 2011). The fixed kernel technique is considered more accurate than adaptive kernel estimators, and the most robust overall (Worton 1995, Seaman & Powell 1996, Seaman et al. 1999, Walter et al. 2011).

Kernel density estimation (KDE) techniques produce utilization distributions (UD) based on the relative density of telemetry locations over an area (Van Winkle 1975). Home range estimates based on these utilization distributions portray integral nonuniform and multimodal qualities (Worton 1989), which describe animal activity patterns better than traditional methods such as minimum convex polygons (Mohr 1947).

I used the Geospatial Modelling Environment to conduct bluebird KDE analyses (Beyer 2012). Results of KDE analysis are sensitive to both the resolution of the evaluation area (grid size) and the bandwidth (Worton 1995, Seaman and Powell 1996, Walter et al. 2011). In my study, grid size appeared to have only a minor influence, whereas the bandwidth chosen was more important. A variety of bandwidth estimation methods exist, and there is consensus that no single method is appropriate for all applications (Gitzen et al. 2006, Walter et al. 2011). Many researchers have used the least-squares cross validation (LSCV) bandwidth estimator (Seaman et al. 1999, Barg et al. 2005, Hallworth et al. 2011), but it has been shown to perform poorly with low sample sizes or non-normal data (Worton 1987, Seaman & Powell 1996, Blundell et al. 2001, Hemson et al. 2005). I assessed several bandwidth techniques using my data and had mixed results; several bandwidth estimators (i.e., LSCV, biased cross validation [Scott et al. 1977], smoothed cross validation [Hall et al. 1992], plug-in [Woodroffe 1970], and fixed values > 30,000) resulted in obvious overestimation of home range area, with some resulting polygons larger than a minimum convex polygon. Conversely, fixed values < 10,000 were overly conservative and resulted in highly fragmented utilization distributions, often encompassing individual locations instead of groups of points that would better reflect areas of use. Based on these trials, I decided to use a fixed bandwidth value of 20,000 due to the lack of any obvious over or underestimation of home range estimates. The kernel density estimator tool in the program Geospatial Modeling Environment (Beyer 2011), a Program-R based supplement to ArcGIS, was used to generate KDE for all birds with > 20 locations (N = 9).

I depicted a home range boundary as the 95% isopleth of the kernel probability density function (Worton 1995, Howell and Chapman 1997, Seaman et al. 1999), thus, for this study I define a bluebird home range as the minimum area with a 95% probability of containing telemetry loci. The focal center or “core” of a home range, intended to represent areas of more intensive use (Samuel et al. 1985), is defined here by a 50% isopleth of the kernel probability function.

The indiscriminate capture of bluebirds used in my 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, five birds in 2010 appeared to occupy distinct, yet adjacent, home ranges. I calculated the percentage of overlapping area between these adjacent home ranges using ArcGIS.

Habitat analysis. Habitats were classified using satellite imagery and a maximum likelihood supervised image classification process (Thompson & Klassen 1980, Palmeirim 1988). The image classification tool in ArcMap 10 was used to classify each pixel of the 1-m resolution RGB satellite imagery map of the study area (U.S. Department of Agriculture 2006) to either 1) wooded or 2) open habitat types based on the color profiles of the pixels (see below). These two categories were selected after examining the study area within the 2006 National Land Cover Database (NLCD) (Fry et al. 2011); based on the nine categories of land cover present in those data, I determined that the most biologically relevant depiction of the study area suggested the combination of several categories of “open” habitat (e.g., pasture/hay field, grassland/herbaceous, or other open areas). Although differences among open habitat

types may exist, the NLCD provided only a coarse (e.g., 30-m resolution) and often inaccurate depiction of habitat in my study area, thus limiting its potential for reliably depicting bluebird habitat at a home-range scale. The two unique resulting habitat categories (wooded and open) were used as the basis for the image classification process.

Representative training samples of the satellite imagery, which are used in ArcMap to define the color profiles of the designated habitat categories, 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 two habitat category profiles. Three training samples totaling 10.5 ha of wooded areas (i.e., contiguous patches of forest, lone trees, and wooded corridors with no visible herbaceous vegetation) were used to define “wooded”, and 12 training samples of open habitat (i.e., areas absent of tree or shrub cover, including open fields and single-track gravel roads) totaling 14.2 ha were used to define “open” habitat. Based on the color profiles of these training samples, I assigned all pixels 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. This habitat map (Figure 3) was used to describe habitat composition of bluebird home ranges, and also to determine habitat use and distance to edge for each observation (see statistical analyses, below).

Weather data. Weather data were collected from an on-site weather monitoring station maintained by BGAD personnel. Air temperature and wind speed were recorded every 15 min, thus, no weather observations were more than 7 min removed from an instantaneous reading. Figure 4 depicts mean daily temperature during the study period. Snow depth (Figure 5) was recorded daily 53 km away at the Lexington Bluegrass Airport (N 38.04, W -84.61) and collected from the National Oceanic and Atmospheric Administration's National Climatic Data Center (www.ncdc.noaa.gov). These weather data were used as a basis for examining effects of weather on habitat use, group size, and foraging behavior (see statistical analyses, below).

Statistical analyses. Descriptive bluebird home range metrics including area, habitat composition, and overlap between adjacent home ranges were quantified using ArcGIS for both the 95% and 50% core home ranges. The habitat composition of home ranges was compared 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 minimum convex polygon bound by the most outward vertices of all bird home ranges over two years. I 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., ≥ 1 and 0 in, respectively, as recorded from the Lexington Bluegrass airport) using a Mann-Whitney U-test.

I used a nested ANOVA to investigate the potential effect of snow cover on the distance of each bluebird location to edge habitat (the boundary between open and wooded spaces), with individual birds used as nested variables to account for the

repeated sampling of individuals. I also used a nested ANOVA to examine the potential effect of freezing temperatures (i.e., $\leq 0^\circ\text{C}$ [range = $-10.7 - 0.0^\circ\text{C}$, and $0.1 - 16.1^\circ\text{C}$ for above freezing temperatures]) on bluebird group size, again with individual birds used as a nested variable. Similarly, group sizes were compared during periods of snow cover (≥ 1 in) and when snow was absent (0 in) using a nested ANOVA, with bird number nested in snow presence/absence. Observations were not included in these analyses when group size could not be determined. I compared the number of males and females in groups using a paired samples t-test. Sex composition of groups was also compared between periods of snow cover and when snow was absent using a repeated-measures ANOVA, with bird number nested in snow presence/absence. Observations were not included in these analyses when the sex of one or more group members was not determined.

I investigated the influence of snow cover, air temperature, and wind speed on the foraging behavior of bluebirds with a logistic regression analysis. For this analysis, foraging behavior was classified dichotomously as directed towards fruit or arthropod prey, and individuals were treated as a blocking variable to account for repeated sampling.

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

CHAPTER III

RESULTS

Nineteen individuals, including 15 males (7 SY and 8 ASY) and four females (2 SY and 2 ASY), were radio-tagged and tracked during January and February 2010 (11 individuals) and 2011 (8 individuals). Birds were tracked over an average span of 23 ± 15 (SD) days (range = 1 - 51), and locations of these birds were obtained on an average of 13 ± 9 (SD) days. I 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. At least three bluebirds with transmitters appeared to have been killed by predators (possibly either Sharp-shinned [*Accipiter striatus*] or Cooper's [*Accipiter cooperii*] hawks) as indicated by a transmitter located among or near numerous flight or contour feathers or other body parts. Those three birds were tracked for 11, 40, and 41 days, respectively, before transmitters were recovered. The other nine radios recovered on the ground or in foliage were attached to bluebirds for 21 ± 14 (SD) days (range = 5 - 42) before transmitters were recovered. Signals from the remaining seven radios could not be located during the tracking period and were not detected again or recovered. Those seven birds were tracked for 22 ± 18 (SD) days (range = 1 - 51) before the last observation took place.

In two cases, I combined the location data of two bluebirds for home range analyses. One pair of males in the same group of bluebirds was originally captured simultaneously and both were radio-tagged; 87% locations (N = 39) were shared by both birds (i.e., the two birds were typically found moving or foraging in the same group), and their overall and core home ranges showed almost complete overlap. The other two birds (a male and female) were also captured simultaneously, but were tracked over discrete time periods; the female was tracked for 14 days (16 – 29 January 2010; 16 total locations), after which the harness was recovered intact with no sign of the bluebird. In an attempt to potentially re-capture this bird, I erected a mist net in the same location of the original capture and initiated playback. The male was then captured at this location, radio-tagged, and tracked for 11 days (4 – 14 February 2010; 14 total locations) before apparently being predated. An exploratory home range analysis for the two birds revealed similar overall and core home ranges, again with substantial overlap. Because the two birds were originally captured together and subsequently used the same area, I combined their locations into a single home range analysis.

Including the two shared home ranges described above, there were nine bluebirds (or pairs) with > 20 location observations (average = 30.3 ± 7.5 [SD], range = 22 - 44). Of the nine birds (or pairs), seven were tracked during 2010 (including both pairs) and two during 2011. For these nine birds, the average home range area (95% utilization distribution) was 29.2 ± 2.4 ha (range = 16.3 – 42.3), and the average core home range area (50% utilization distribution) was 7.1 ± 0.6 ha (range = 3.8 – 9.9). Of

five birds with adjacent home ranges in 2010, an average of $9.4 \pm 2.5\%$ of the 95% home range estimate area was shared by neighboring birds. With the exception of the two pairs from 2010 whose location data were combined, core home ranges did not overlap. The two birds from 2011 whose home ranges were estimated occupied entirely distinct areas.

Eastern bluebird home ranges consisted of $39.6 \pm 2.6\%$ wooded habitat and $60.4 \pm 2.6\%$ open habitat ($N = 9$). 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 $41.1 \pm 3.5\%$ wooded habitat and $58.9 \pm 3.5\%$ open habitat ($N = 9$), which was not significantly different from the composition of habitats in the study area ($t_8 = 1.6$, $P = 0.16$).

The mean percentage of wooded area surrounding each observation (5-m radius) was $60.0 \pm 2.0\%$ ($N = 344$). 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 ($54.4 \pm 4.3\%$, $N = 94$) did not differ from that during periods when snow was absent ($63.1 \pm 2.5\%$, $N = 250$, $P = 0.14$ Mann-Whitney U-test). The distance of bluebirds to the edge of wooded habitat did not differ during periods of snow cover ($F_{1,91} = 0.01$, $P = 0.92$).

Focal bluebirds were almost always found in conspecific flocks (97% of observations). Average group size was 5 ± 0.1 individuals ($N=300$), with a maximum of 16 individuals observed in a flock that included a radio-tagged bird (Figure 7). 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 $0\text{ }^{\circ}\text{C}$ (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; $F_{1, 266} = 5.0$, $P = 0.027$). Although not included in the data of radio-tracked birds, extremely large groups of 60 or more bluebirds were occasionally observed during periods of snow cover and sub-freezing temperatures, but never during mild weather.

I obtained 235 observations of bluebirds foraging. Flocks were typically found with all members foraging on only one food item (91% of observations). The remaining 9% of observations were of flocks foraging on two food items, usually arthropods and fruit. Bluebirds consumed a variety of food items, including arthropods, hackberries (*Celtis occidentalis*), mistletoe berries (*Phoradendron leucarpum*), cedar berries (*Juniperus virginiana*), and, infrequently, other berries (black cherry; *Prunus serotina*, coralberry; *Symphoricarpos orbiculatus*, Japanese honeysuckle; *Lonicera japonica*, or poison ivy; *Toxicodendron radicans*). Arthropods were the most frequently consumed food item (>65% of observations for either year), and relative frequencies of frugivory varied during the two years (Table 1). Logistic regression analysis indicated that food type (arthropods or fruit) was influenced by air temperature (Wald's $X^2_1 = 14.5$, $P < 0.001$), wind speed (Wald's $X^2_1 = 8.2$, $P = 0.004$), and snow presence (Wald's $X^2_1 = 5.3$, P

= 0.021), with increased frugivory during observations with low temperatures, low wind speed, and the presence of snow.

CHAPTER IV

DISCUSSION

Home range and habitat use. The mean estimated 95% winter home range size of bluebirds in my 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 I used emphasizes focal areas of intensive use and minimizes the influence of distant, isolated loci. The mean size of 95% winter home ranges of bluebirds in my study was similar to that of bluebirds during transitional 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. My sample sizes were too small to examine the possible effects of sex and age on the size of bluebird winter ranges.

With the exception of two pairs in my study whose space use data were combined for home range analysis, I found little (95% home range estimates) or 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 (Safina & Utter 1989, Brown et al. 2000, Townsend et al. 2010). The distinct, minimally overlapping home ranges of bluebirds in my study may also represent resource-influenced territoriality, but, in this case, the territories appear to be specific to groups. The two pairs in my study that occupied almost identical home ranges suggest that bluebird groups (or certain pairs) persist during winter, but the specific roles of these relationships and other potential effects 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, the co-occurrence of a male and female within a home range in my study may be related to the winter maintenance of a breeding territory.

Home ranges of bluebirds in my study were composed of more open habitat than wooded, 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. I 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 and 95% home ranges. 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 only open and wooded habitat categories were considered in my calculation of home ranges, the similar amounts of open and wooded habitat in bluebird home ranges may indicate a preference for edge habitat.

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 my study appeared to be unchanged by snow presence. Brotons (1997) described how coal tits (*Parus ater*) responded to snow presence by changing foraging methods within a patch rather than seeking a new habitat, and my results suggest that bluebirds may respond to the presence of snow in a similar way. For example, Pinkowski (1977b) 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. Alternatively, my analyses may not have revealed actual changes in habitat use during snow cover (Type II

error) because of the distance between my study area and the location where snow cover data were collected (53 km). This distance could have produced inaccurate representations of snow cover in my study area, but the likelihood of such a discrepancy decreases during substantial snowfall events when bluebird behavior is presumably influenced the most. 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 shifts in diet or group size.

Foraging behavior. Bluebirds in my study were more likely to engage in frugivory when temperatures and wind speeds were low, and when snow cover was present. Low temperatures decrease arthropod activity (Mellanby 1939), making insectivory less reliable and possibly increasing the cost of this strategy to a suboptimal level. A behavioral shift to frugivory seems to be preferred during low temperatures. Snow presence also increased the occurrence of frugivory, although it is difficult to know whether snow presence or low temperature is more influential in this decision. Snow, along with low temperatures, reduces insect availability to bluebirds (Frazier and Nolan 1959, Pitts 1978), particularly by covering ground-active arthropods. However, the presence of snow (i.e., ≥ 1 in) did not absolutely prevent ground-foraging behavior; bluebirds in my study were often able to locate and forage on snow-free slopes within their home ranges (typically the south-facing sides of earthen bunkers or roadway medians), snow-free stream banks, or openings created by larger animals (e.g., wild turkeys, *Meleagris gallopavo*) for insectivory (pers. obs.). However, the presence of snow did appear to promote a shift in diet towards frugivory. Thus, the relative value of

fruit resources likely increases during periods of snow cover despite the ability of bluebirds to occasionally forage for insects in snow-free areas. Low temperatures without snow may similarly increase the relative value of fruits due to a decrease in insect activity, likely affecting foraging efficiency.

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 fruit in taller trees. Insectivory by bluebirds is possible from leeward edges and near the ground whereas frugivory is constrained spatially by the distribution of fruit. Mistletoe clusters, for example, were typically located on high tree branches where heat loss due to high winds would probably increase. Pinkowski (1977b) found no effect of wind speed on bluebird foraging height, but his analysis was apparently limited to “drop” feeding for arthropods across all seasons, so the relevance to my results is limited.

Bluebirds may cope with high winds by foraging for insects in more protected locations, such as lower to the ground, or the leeward side of wooded patches, but this option is likely constrained during low temperatures when insectivory is presumably less rewarding because of reduced availability of insects. The same is likely true when snow

is present, when frugivory seems to be preferable. 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 in my study area experience during winter.

The fruits most frequently consumed by bluebirds in my study differed between years. For example, 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. The availability of food was not determined during my study, so it is not possible to determine whether the relative abundances of these food items accounted for this pattern. However, anecdotal observations indicated that 2010 may have been a year of high mistletoe abundance. 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 (snow cover, low temperatures, or high wind speeds). Although bluebirds are known to consume at least 60 types of fruit in winter (Hoyo et al. 1992), fewer varieties are available at a particular site, and even fewer are available at any point in time during the winter. 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 1977b, Pitts 1978,

Savereno 1991). Bluebirds in my study were observed foraging on eight types of fruit, but relied principally on hackberry, mistletoe, and cedar berries. Although fruits are typically reported as important for wintering bluebirds, the three fruit varieties consumed most in my study (hackberry, mistletoe, and cedar) were entirely absent or made up only a minor dietary component for wintering bluebirds in Ohio (Morland 1978), South Carolina (Savereno 1991), and Tennessee (Pitts 1978, 1979). Assessing the value of specific fruit-bearing species to wintering bluebirds may be most useful when considered within a region.

Fecal samples were collected during the process of capturing and marking bluebirds in November 2009 and January 2010 and were used as part of a companion study on the winter diet of bluebirds (Janos 2011). This analysis revealed that arthropod segments, comprising at least six different orders, were the most common items in fecal samples, followed in decreasing order of occurrence by seeds of cedar, mistletoe, poison ivy, Japanese honeysuckle and an unidentified plant. Janos (2011) also found that seeds were more commonly found in fecal samples collected during periods with sub-freezing temperatures (Figure 8), again suggesting that bluebird diets shift toward fruit during periods with low temperatures, and reinforcing the value of these food resources during periods of inclement weather. Furthermore, the absence of hackberry seeds from any fecal samples collected during the winter of 2009/2010 (Janos 2011) supports my observation that little or no hackberry fruits were consumed during that winter, despite hackberry being a sizeable dietary component (24% of all foraging

observations) during the following winter. Thus, a diversity of fruit resources may be more important in some winters than an abundance of a single fruit-bearing species.

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 (Caraco 1979, Beauchamp 1998). Hogstad (1988) observed this effect among flocks of wintering willow tits (*Poecile montanus*) during cold days, and the observed increase in bluebird group size during freezing temperatures in my study may also be explained by this effect. Although group size of flocks with radio-tagged birds in my study differed between periods with freezing and above-freezing temperatures by an average of less than one (5 ± 0.2 and 4 ± 0.2 individuals, respectively), much larger flocks (>50 bluebirds) were occasionally observed during sub-freezing and snowing weather and may indicate a potential group-size effect. These large bluebird flocks were observed at least twice in my study area during periods when snow completely covered the ground, with bluebirds foraging in large patches of cedar trees. By assembling in such large numbers during inclement weather, bluebirds may be able to locate new food sources while simultaneously benefiting from a group-size effect. Large bluebird flocks have been sporadically reported elsewhere during winter (e.g., Thomas 1946), but are apparently rare events. Accounts of mountain bluebirds (*Sialia currucoides*) and western bluebirds (*Sialia mexicana*) assembling in large numbers around food sources during snowstorms (Allen

& Brewster 1883, Henderson 1903) may indicate a similar strategy for those species. Temporary flocking in large numbers during inclement weather may be related to the group size effect as well as an alternative strategy for locating food sources.

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., Ficken 1981, Elgar & Catterall 1982). However, if snow cover leads to increased frugivory, which is less energetically rewarding than insectivory, bluebirds would still benefit from a group-size effect that would allow greater foraging time. Thus, the two possibilities (a group-size effect, or a strategy for locating resources) to explain larger group size during unfavorable weather are not mutually exclusive.

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 in my study, it was not uncommon to repeatedly observe uniquely banded individuals together over a period of weeks. The two pairs of bluebirds in my study whose home range estimates showed considerable overlap may be an additional indication that group cohesiveness, as well as relatively consistent space use, can be maintained during the winter months. Additionally, my observations of extremely large bluebird flocks, and one instance of communal roosting during the day (19 bluebirds), demonstrate that rigid flock cohesiveness during winter is not always the case.

Increasing bluebird group size, whether by joining another flock or allowing new visitors, requires increased trespassing within home range boundaries. Such trespassing may be related to an interaction between foraging strategies and weather. During unfavorable weather, when group sizes increase, a shift toward frugivory may require individuals to seek new areas or groups that could ultimately have consequences for survival and territory establishment.

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APPENDIX:

TABLES AND FIGURES

Table 1. Summary of foraging observations of eastern bluebirds in 2010 (N = 139) and 2011 (N = 96).

Food category	Both years (%)	2010 (%)	2011 (%)
Arthropods	71.9	76.3	65.6
Hackberry	10.2	0.07	24
Mistletoe	8.5	13.7	1
Cedar	6	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.

	Wald's	P-value	Odds ratio
Low air temperature	14.5	<0.001	1.22
Low wind speed	8.16	0.004	1.77
Snow absence	5.32	0.021	0.29

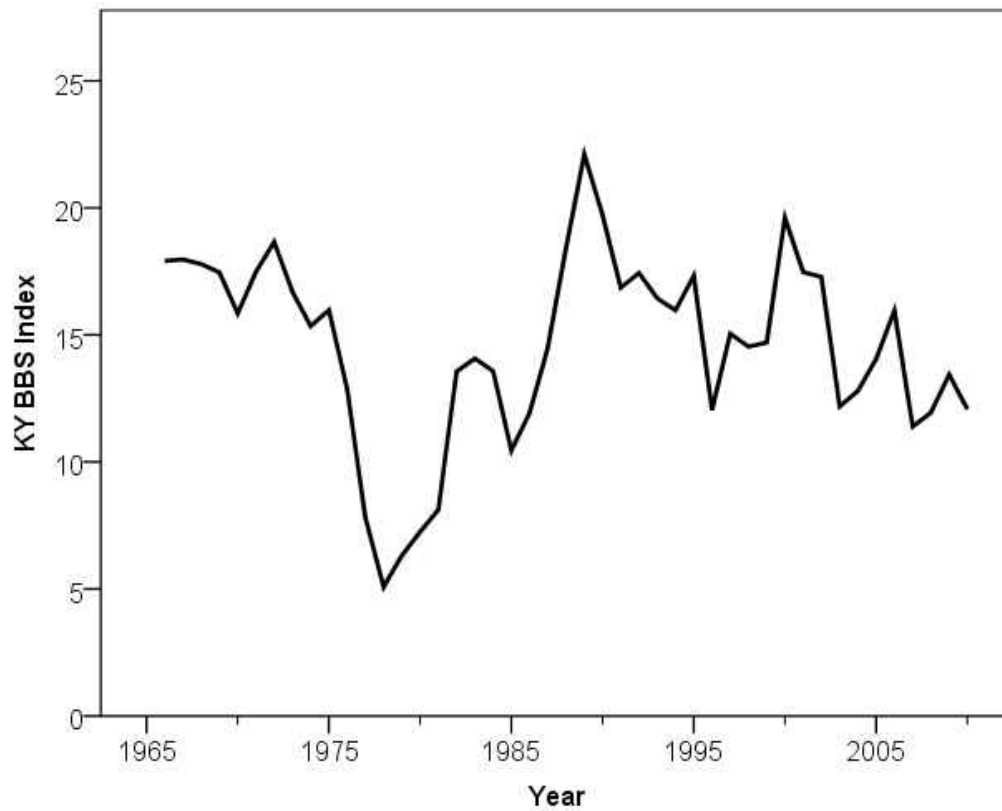


Figure 1. Eastern bluebird breeding bird survey indices (individuals per survey route) in Kentucky for the years from 1966 to 2010 (N = 1248). Source: Sauer, J.R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski, D. J., Jr., Link, W. A. 2011. The North American Breeding Bird Survey, Results and Analysis 1966–2010. Version 12.07.2011. USGS Patuxent Wildlife Research Center, Laurel, MD.

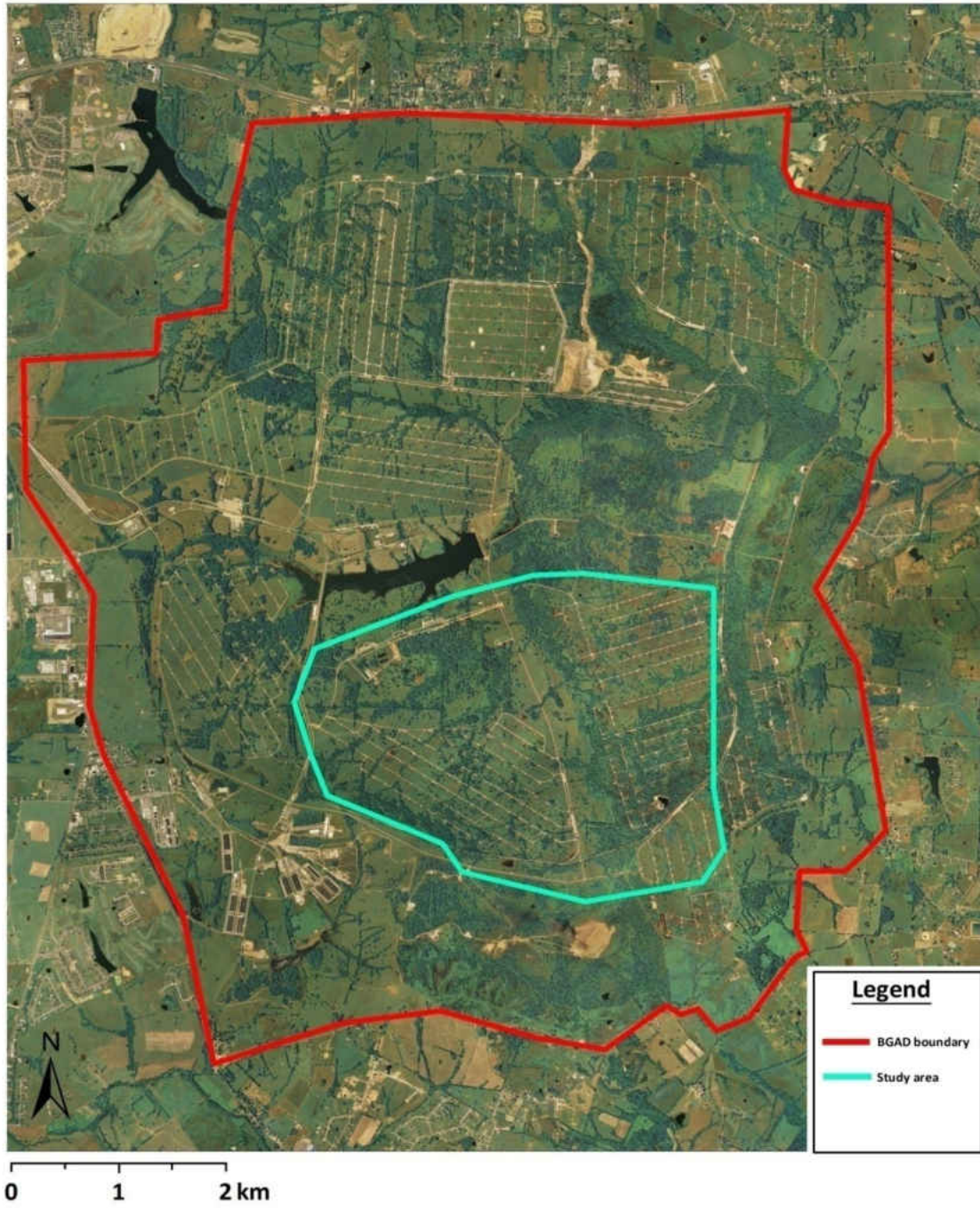


Figure 2. Map of the Bluegrass Army Depot and approximate study area

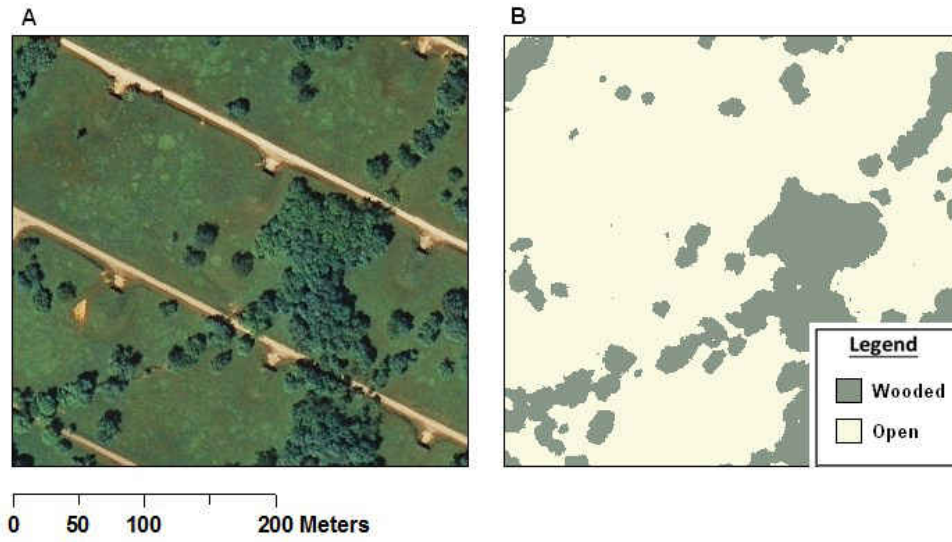


Figure 3. Example of typical bluebird habitat in my study area depicted with A) raw satellite orthography and B) habitat coverage derived from the image classification process.

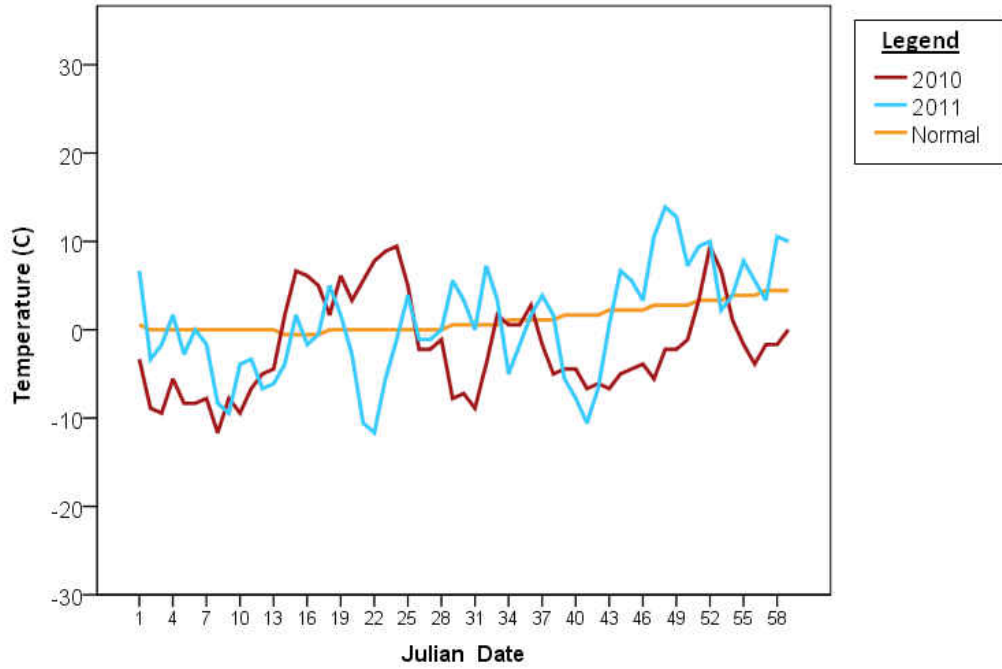


Figure 4. Mean daily temperature (Celsius) during January and February for 2010, 2011, and 30-year climate normal. Data from Lexington Bluegrass Airport.

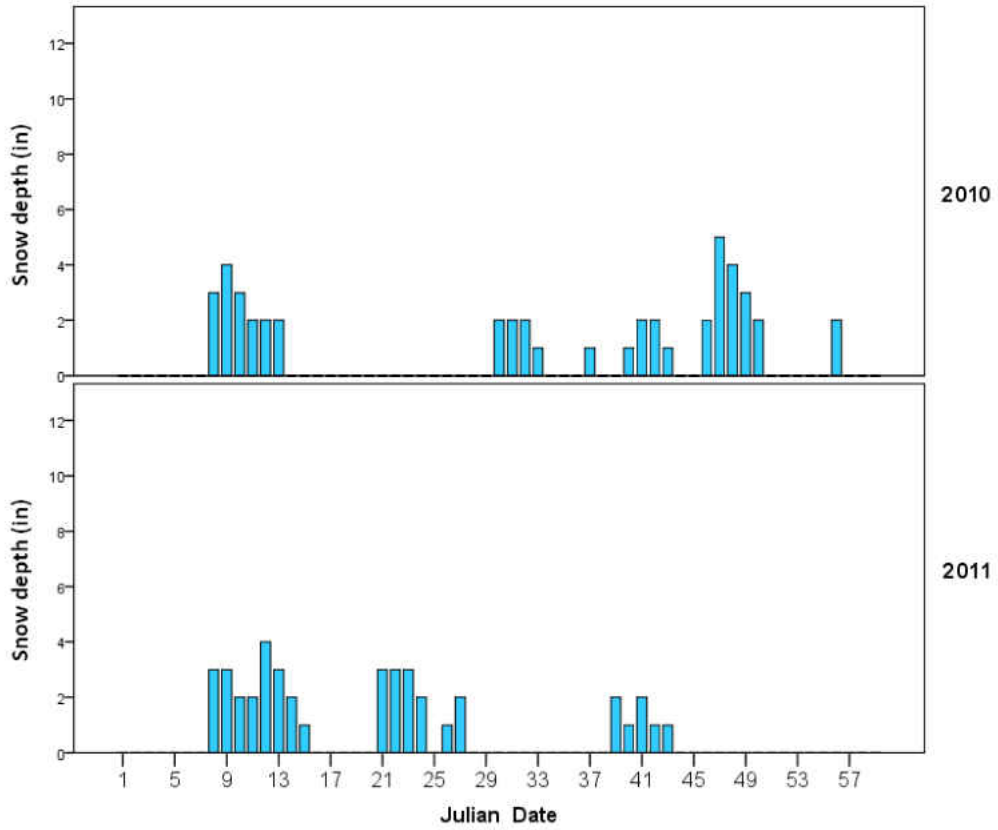


Figure 5. Snow depth at Lexington Bluegrass Airport during January and February for 2010 and 2011.

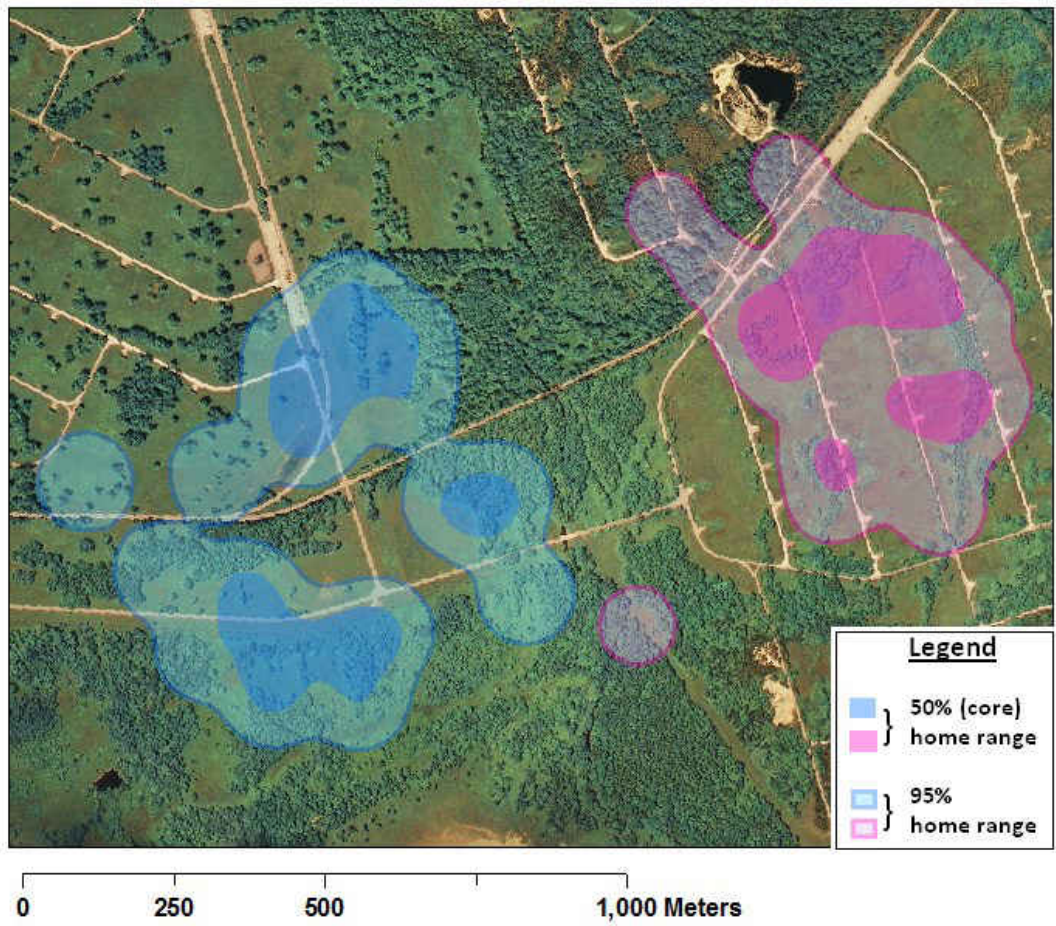


Figure 6. Example of 95% and 50% (core) home range estimates for two bluebirds in my study area.

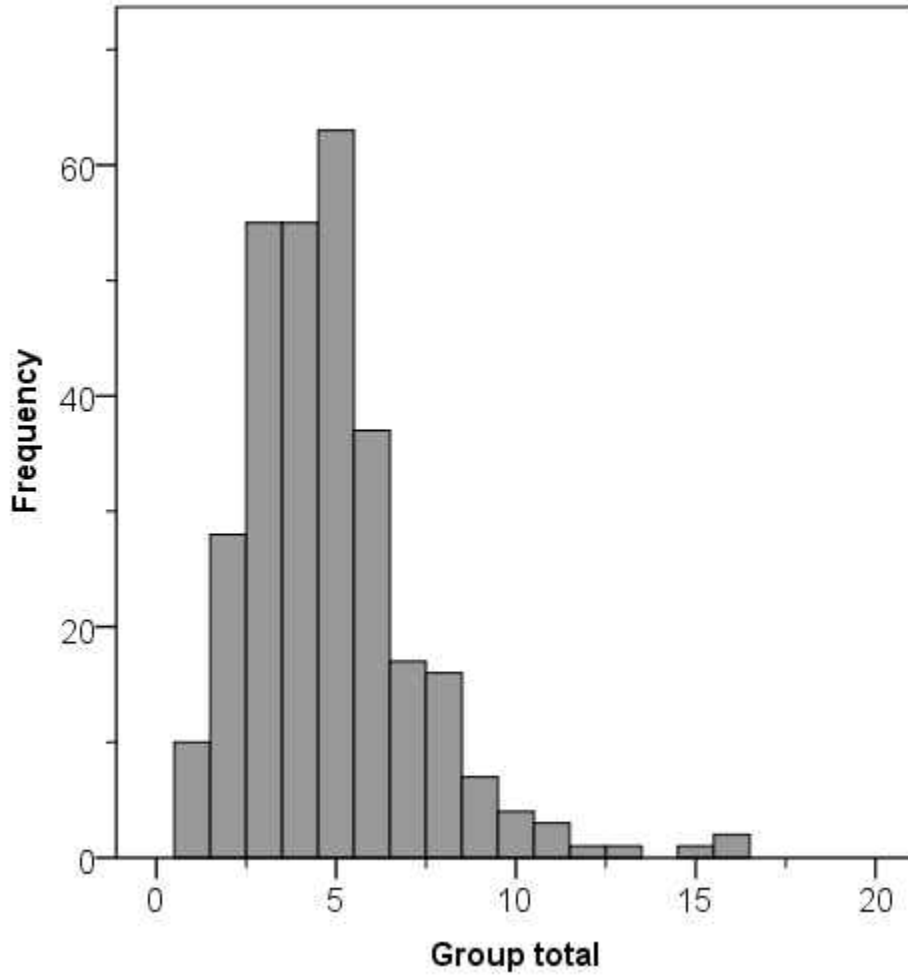


Figure 7. Histogram of bluebird group size (N = 300) during study period of 2010 and 2011.

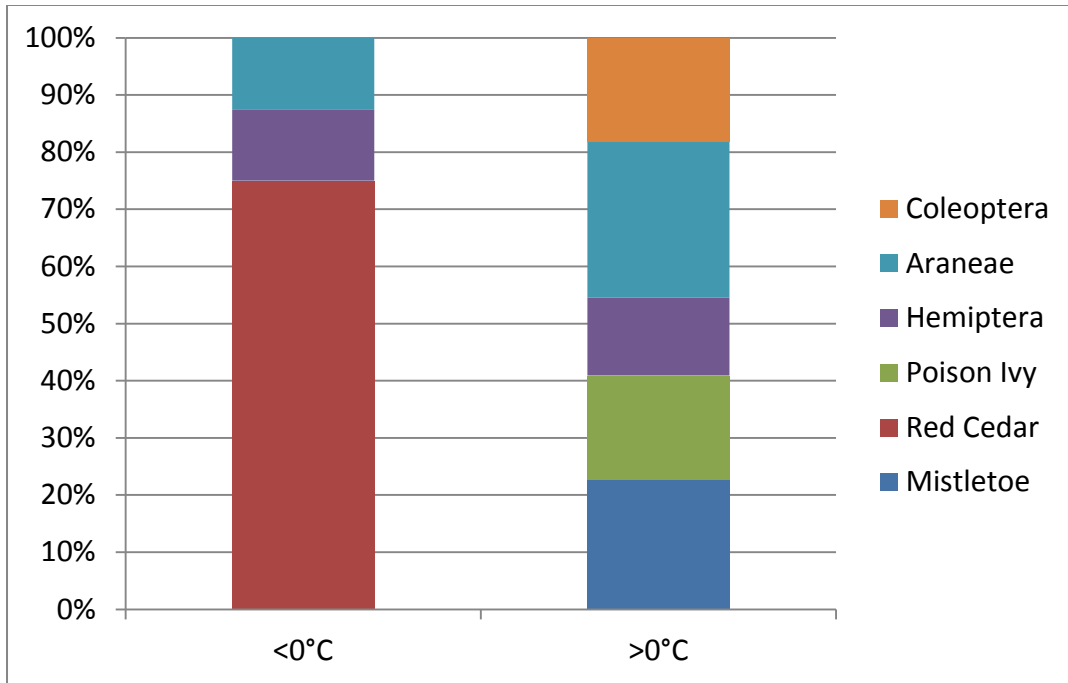


Figure 8. Percent occurrence of food items based on fecal sample analysis. Source: Janos, G. 2011. Wintering eastern bluebirds adjust habitat use, social behavior and diet, as determined by fecal sample analysis, during cold weather events. Honors Thesis, Eastern Kentucky University, Richmond.