



WINTER TERRITORIALITY AND SPATIAL BEHAVIOR OF BICKNELL'S THRUSH (*CATHARUS BICKNELLI*) AT TWO ECOLOGICALLY DISTINCT SITES IN THE DOMINICAN REPUBLIC

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ABSTRACT.—We used radiotelemetry to investigate the spatial behavior of wintering Bicknell's Thrushes (*Catharus bicknelli*) at a mid-elevation rainforest site and a high-elevation cloud-forest site in the Dominican Republic. We also analyzed blood stable carbon isotopes and fecal samples to compare thrush diets at these two floristically and climatically distinct sites. Birds consumed a primarily fruit-based diet at the mid-elevation site and a primarily arthropod-based diet at the high-elevation site. Despite these dietary differences, individuals at both sites defended and maintained exclusive, minimally overlapping core use areas and home ranges. The mean size of both core use areas and home ranges was similar between males and females and between adults and first-winter birds. Presence of nonterritorial or “floater” individuals was low at both sites (2.7% and 5.6%). Birds at the arthropod-dominated site were observed significantly more often on or within 1 m of the ground than birds at the fruit-heavy site, which were more often observed in the mid-canopy structure above 2 m. Birds at both sites displayed agonistic behaviors toward conspecifics and toward playback of conspecific vocalizations. Exclusive territoriality was the predominant winter social system, and we suggest that both arthropods and fruit are defensible resources for wintering Bicknell's Thrushes. Received 31 August 2009, accepted 13 January 2010.

Key words: Bicknell's Thrush, *Catharus bicknelli*, Nearctic–Neotropical migrant, nonbreeding diet, radiotelemetry, winter social system.

Territorialidad y Comportamiento Espacial de *Catharus bicknelli* Durante el Invierno en Dos Sitios Ecológicamente Distintos en la República Dominicana

RESUMEN.—Utilizamos radiotelegrafía para investigar el comportamiento espacial de individuos invernantes de la especie *Catharus bicknelli* en un bosque húmedo ubicado a elevaciones medias y en un bosque nublado de alta elevación en la República Dominicana. También analizamos isótopos estables de carbono en la sangre y muestras fecales para comparar la dieta de las aves entre estos dos sitios, que son florística y climáticamente distintos. Las aves consumieron una dieta principalmente basada en frutos en el sitio de elevaciones medias y una principalmente basada en artrópodos en el de elevaciones altas. A pesar de esas diferencias dietarias, los individuos de ambos sitios defendieron y mantuvieron áreas nucleares de uso y ámbitos hogareños exclusivos, con mínima superposición. El tamaño medio de tanto las áreas nucleares de uso como de los ámbitos hogareños fue similar entre machos y hembras, y entre adultos y aves en su primer invierno. La presencia de individuos no territoriales o “flotantes” fue baja en ambos sitios (2.7% y 5.6%). Las aves del sitio dominado por artrópodos se observaron con una frecuencia significativamente mayor en el suelo o a 1 m de éste que las aves del sitio dominado por frutas, las cuales se observaron con mayor frecuencia en la estructura del dosel medio por encima de 2 m. Las aves de ambos sitios exhibieron comportamientos agresivos ante individuos coespecíficos y ante la reproducción de vocalizaciones coespecíficas grabadas previamente. La territorialidad exclusiva fue el sistema social predominante del invierno y sugerimos que tanto los artrópodos como las frutas son recursos defendibles por parte de los individuos invernantes de *C. bicknelli*.

SEVERAL STUDIES OF Neotropical migrants have shown that winter space use and social organization are linked closely to resource selection (Morton 1971, Jones et al. 2000, Brown and Sherry 2008). Greenberg and Salewski (2005) reviewed a large number of natural-history observations and found that social gregariousness on the

wintering grounds is strongly associated with use of flower and fruit resources, whereas exclusive territoriality is linked closely to an arthropod-based diet. These differences in spatial behavior hinge on defensibility of the respective resources. For species that rely on an arthropod-based diet, the energetic gains from securing

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exclusive occupancy of an arthropod-rich area presumably outweigh the costs of territorial vigilance. By contrast, for species that rely on fruit or flower resources that are patchy, ephemeral, and widely dispersed across the landscape, territoriality is unlikely to be an energetically profitable strategy. When fruit or flower resources are concentrated and available throughout the winter period, however, certain species defend discrete territories around these resources (e.g., George 1986, Latta and Faaborg 2002, Skórka et al. 2006). Aggressive competition for control of space is therefore expected to occur only when resources are concentrated and defensible, with energetic gains from the critical resource exceeding the costs of territorial maintenance (Brown 1964).

Fretwell's (1972) ideal despotic distribution model for territorial species predicts that habitats with optimal levels of critical resources will be occupied by behaviorally dominant birds to the exclusion of subordinates. Further, Sherry and Holmes (1996) suggested that this competition for optimal winter territories may be an important factor limiting populations of Neotropical–Nearctic migrant songbirds. As wintering birds compete for the highest-quality sites, subdominant individuals (often smaller-bodied females and first-winter birds) may be forced to inhabit lower-quality sites or adopt a nonterritorial “floater” strategy (Marra et al. 1993, Winker 1998, Brown and Long 2007). The consequences for these subdominant individuals can include lowered body condition, decreased annual survival, and later arrival on breeding grounds with reduced reproductive success (Latta and Faaborg 2001, Marra and Holmes 2001, Norris et al. 2004). Winter territoriality, therefore, can play an important role in population regulation of migrant species, with implications for conservation and management of winter habitats (Sherry and Holmes 1996).

Despite this broad understanding of the importance of winter-season events, detailed studies of the winter spatial behavior of Neotropical–Nearctic migrant landbirds have been conducted on only a small subset of species, mainly paruline warblers that inhabit mostly dry, drought-prone habitats (e.g., Strong and Sherry 2000, Latta and Faaborg 2001, Marra and Holmes 2001). To fully understand the potential influence of winter space-use patterns on overall population dynamics, detailed species-by-species studies that encompass an array of habitats of variable quality are needed (Greenberg and Salewski 2005). Variation in habitat quality across the landscape, particularly in terms of food availability, may exert a key influence on the spatial structure and consequent population limitations of migrant songbirds (Strong and Sherry 2000, Johnson and Sherry 2001, Brown and Sherry 2006).

We used radiotelemetry and direct observation to monitor the agonistic behavior, space-use patterns, diet, and microhabitat use of Bicknell's Thrushes (*Catharus bicknelli*) wintering in the Dominican Republic. This rare, range-restricted species is one of eastern North America's long-distance migrants of highest conservation concern (Pashley et al. 2000, Wells 2007), and it is classified as globally “vulnerable” by the International Union for the Conservation of Nature (BirdLife International 2000). Bicknell's Thrushes winter in remote, relatively undisturbed wet broadleaf forest in the Greater Antilles, and Hispaniola is believed to support the majority of the global wintering population (Rimmer et al. 2001).

Our study took place at two floristically and climatically distinct sites—one in high-elevation, undisturbed cloud forest and

the other in mid-elevation, second-growth rainforest. Preliminary field observations and analysis of fecal samples suggested that birds at the mid-elevation site primarily consumed fruit, whereas the diet of birds at the high-elevation site consisted primarily of arthropods. We predicted that birds at the fruit-dominated site would show little to no territoriality as they tracked spatially ephemeral resources. By contrast, we predicted that birds at the arthropod-dominated site would defend and maintain exclusive territories based on behavioral dominance interactions. We additionally hypothesized that females and first-winter birds within this territorial system would be less likely to compete successfully with larger-bodied, more aggressive adult males and would be more likely to adopt a floater strategy. Our specific objectives were to (1) compare thrush space-use patterns in distinct habitat types that provide different dietary resources and (2) investigate differences in microhabitat use, space-use strategy, home-range size, and amount of spatial overlap between the sexes and age classes.

METHODS

Field methods.—Over the course of 4 years, during the boreal winters of 2005–2008, we conducted field work at two ~80-ha study sites, one in high-elevation cloud forest and the other in mid-elevation rainforest in the Dominican Republic. The two sites are located in the southwestern and north-central areas of the country, respectively, and are ~185 km apart. The southwestern site, Pueblo Viejo (hereafter “PUVI”), occupies primary, undisturbed montane cloud forest at 1,600–1,800 m elevation in the Sierra de Bahoruco National Park (18°12'N, –71°32'W). The site is characterized by a dense understory composed largely of vine tangles from storm-related blow-downs, complete canopy cover with trees reaching heights between 15 and 20 m, and an abundance of lianas and epiphytes (Veloz 2007). Dominant canopy trees include *Didymopanax tremulus*, *Ocotea acarina*, *Myrsine nubicola*, *Calypttranthes nummularia*, *Meliosma impresa*, and *Turpinia picardae*. Common understory and mid-canopy tree species include *Psychotria balteweckii*, *Palicourea alpine*, and *Cestrum coelophlebium*. The north-central site, Loma La Canela (hereafter “LOCA”) is situated in the Cordillera Septentrional at elevations of 350–600 m and is part of the Loma Quita Espuela Scientific Reserve (19°25'N, –70°8'W). This rainforest site has undergone periodic selective logging and small-scale shifting agriculture within the past 100 years and is a mosaic of early- and late-successional regenerating broadleaf forest with small patches (about 10–20 ha) of undisturbed primary forest at the highest elevations (Sanchez and Hager 1997). The LOCA site has a relatively more open understory than PUVI and fewer dense vine tangles. Canopy cover is 80–90%, and common canopy trees include *Ocotea leucoxylo*, *Byrsonima spicat*, *Mora abbotii*, *Schefflera morototoni*, *Ormosia krugii*, *Prestoea montana*, *Alchorneopsis portoricensis*, *Casaria arborea*, *Miconia mirabilis*, *Miconia punctata*, *Chionanthus domingensis*, *Gomidesia lindeniana*, *Pouteria domingensis*, and *Turpinia occidentalis*. These trees reach heights of 12–15 m in regenerating forest and up to 25 m in primary forest. A mid-canopy group of smaller understory trees that reach 3–5 m in height include *Alsophila brooksii*, *Cyathea arborea*, *Cnemidaria horrida*, *Lasianthus lanceolatus*, *Miconia samanensis*, and *Psychotria berteriana*.

We captured Bicknell's Thrushes in 6- and 12-m, 36-mm-mesh mist nets by both passive netting and playback of conspecific vocalizations. The proportions of males and females were similar between passive and playback netting, and the same proportion of nonterritorial birds was captured by both methods. The aggressiveness of the birds' responses to playbacks during the minutes before being captured was quantified on a scale of 1 to 4, where 1 = individual responds silently before capture, without counter-calling; 2 = individual responds with counter-calling *beer* note; 3 = individual responds with high-pitched *beer* note and growl call; and 4 = individual responds by counter-singing to playback of song.

Birds were measured and weighed to the nearest 0.1 g, and 50–80 μ L of blood was collected in heparinized capillary tubes via brachial venipuncture using sterile 27-gauge hypodermic needles. Blood was used for DNA extraction to determine sex, and for analysis of stable isotope composition. Blood for sex determination was preserved in Queen's lysis buffer (Seutin et al. 1991), whereas blood for stable isotope analysis was centrifuged to separate plasma and red blood cells; these were stored in sealed glass vials and frozen. We also collected fecal samples from clean cotton bags that we used to transport and hold individual birds during mist-netting operations. Samples were collected from 95% of captured birds at LOCA and 64% of captured birds at PUVI, and all samples were stored in 95% ethyl alcohol.

All birds were fitted with 1.2-g radiotransmitters (Model BD-2G; Holohil Systems, Carp, Ontario), which constituted <5% of the average wintering Bicknell's Thrush's mass of 26.7 g, using the backpack harness method (Rappole and Tipton 1991). We obtained locations of radiotagged individuals with Wildlife Materials TXR-1000 receivers and three-element hand-held Yagi antennas (White and Garrott 1990). Location data were collected by "burst sampling," a technique that allows many observations to be taken in a short amount of time, balancing the goals of defining habitat use of individuals with the logistical constraints of a limited field schedule (Barg et al. 2005). Observations within a burst are separated by a short, regular time interval sufficient to allow the target species to cross from one border of its territory to another (Dunn and Gipson 1977, Lair 1987). In the present study, a burst consisted of 1–4 h, with locations recorded every 5 min. Over the course of the 20–30 days of field time available, 5–11 bursts were conducted for each individual (mean bursts per individual = 7.7 ± 2.8 [SD]). All bursts combined for each bird produced 30–64 fixes (mean fixes per individual = 40.1 ± 9.1), within the recommended number of observations for kernel home range estimates (Seaman et al. 1999). Simple linear regression analysis showed that the number of bursts was not significantly correlated with estimates of core use areas ($F = 0.59$, $df = 52$, $P = 0.45$) or of 90% kernel home ranges ($F = 2.29$, $df = 52$, $P = 0.14$). Bursts took place during both morning and afternoon for all individuals.

All locations were determined by stealth homing (White and Garrott 1990). Birds were quietly approached, and location coordinates (Universal Transverse Mercator, datum WGS 84) were recorded using hand-held global positioning system units (Garmin GPSmap 76) with an average accuracy of ± 8.5 m. A beacon study was conducted to determine the strength of signal for varying distances from a stationary transmitter in thick understory cover and at various vertical forest strata. For each location

fix, we characterized the microhabitat as being composed of (1) dense vine tangles, (2) open forest, or (3) mixed forest with both open and dense understory. When direct observations were possible, we recorded the individual's use of forest strata by categorizing observations as on or within 1 m of the forest floor, in the understory between 2 and 4 m, or in the mid-canopy higher than 4 m. With the exception of nocturnal roosting, birds were never observed in the upper canopy (Townsend et al. 2009). We also recorded any agonistic behaviors between individuals and in response to playback of conspecific song.

Spatial analyses.—Home ranges were modeled with fixed-kernel use distributions using the Animal Movement extension to ARCVIEW, version 3.2 (Hooge and Eichenlaub 2000). Kernel techniques assess the relative frequency of an animal's locations, or its "utilization distribution" (Van Winkle 1975), and produce a probabilistic characterization of an individual's spatial boundaries (Worton 1989). We assessed the 90% and 50% kernel home range (KHR) isopleths of each individual, using the least-squares cross-validation method to arrive at an optimum smoothing parameter value (Seaman et al. 1999). We avoided the 95% isopleths because of evidence that this distribution can overestimate boundaries (Börger et al. 2006). The 90% KHR therefore represents the maximum likelihood of encountering an individual within the bordered space, hereafter "home range," whereas the 50% KHR represents a core area of intensive use within the home range, hereafter "core use area" (Howell and Chapman 1997). We also utilized the minimum convex polygon (MCP) to describe the total space used by individual birds. The MCP home-range estimate is based on the same utilization distribution, but unlike the KHR estimate, the MCP simply draws a polygon that connects points on the periphery of the utilization distribution. MCP estimates are considered less biologically meaningful than KHR estimates because of the potential for including large areas rarely used by individuals (Harris et al. 1990). We include MCP estimates to facilitate comparisons of our data with those of several previous telemetry studies on forest thrushes (e.g., Winker et al. 1990, Brown et al. 2000).

We assessed the intensity of the use of core areas by calculating the percentage of territorial space (percent territory) and the percentage of total locations (percent use) contained within each core use area (Samuel et al. 1985, Barg et al. 2005). Finally, we assessed the proportion of spatial (but not temporal) overlap between neighbor pairs for all core use areas and home ranges by both site and year.

Laboratory analyses.—Blood plasma was freeze dried in the laboratory before being weighed (100–800 μ g) into preweighed tin boats. To analyze stable isotope contents, samples were combusted in a Costech ECS 4010 elemental analyzer coupled to a Thermo-Finnigan Delta XL Plus isotope ratio mass spectrometer. Stable carbon isotope ($\delta^{13}\text{C}$) values are reported in standard format in parts per thousands (per mil, ‰) in relation to Vienna Pee Dee Belemnite. Accuracy and precision of measurement were independently verified using NIST sucrose and peach leaves. Daily precision of instrument was verified by repeated analysis of the laboratory standards (fish muscle, acetanilide, and spinach). The estimated analytical precision was ± 0.2 per mil. More depleted levels of $\delta^{13}\text{C}$ are indicative of a fruit-based diet, whereas enriched values indicate an arthropod-based diet (Herrera et al. 2001).

Fecal samples were examined under a dissecting microscope to determine percentage arthropod vs. fruit composition. Samples were categorized on the basis of presence or absence of fruit material or arthropod parts for comparison in two separate logistic regression models, following the analysis procedure of Strong et al. (2005) for wintering Hermit Thrush (*Catharus guttatus*) fecal samples. For the first model, sample categories were “contains arthropods,” which included samples with both fruit and arthropods, or “no arthropods.” In the second model, sample categories were “contains fruit,” again including samples with both fruit and arthropods, or “no fruit.” In both models we included the independent variables site, year, season (early = January to mid-February, late = March), sex of the individual, and all two-way interactions. Although fecal samples do not provide a complete dietary picture, they yield useful information via the complete or near-complete passage of seeds and hard arthropod body parts such as wings and chitin (Ralph et al. 1985, Strong et al. 2005) and are used in this study as an index of bulk consumption rather than as a detailed assay of individual dietary items.

Whole blood collected in lysis buffer was used to extract DNA using Perfect gDNA Blood Mini kits (Eppendorf) following the manufacturer’s protocol. Homologous sections of sex-chromosome-based chromo-helicase-DNA-binding (CHD) genes were then amplified by polymerase chain reaction (PCR). When viewed on a gel, PCR product from males shows a single CHD-Z band, whereas PCR product from females displays a second CHD-W band (Griffiths et al. 1998).

Statistical analyses.—All data were tested for normality and log-transformed when necessary. Because of extreme zero-inflation in each of these data sets, nonparametric Kruskal-Wallis tests were performed on measures of microhabitat use and neighbor overlap. Logistic regression models were used to compare contents of fecal samples between sites. Standard least-squares regression analysis of variance tests (ANOVA) were performed on all other data. All data were analyzed using the statistical program JMP, version 7.0 (SAS Institute, Cary, North Carolina). Results are presented as means ± SE.

RESULTS

Diet.—We collected 18 fecal samples at LOCA and 25 at PUVI over 3 years. Beetle carapaces, arthropod legs, chitin, and wings of diptera and hymenoptera species dominated the contents of PUVI samples, whereas seeds were rare. The LOCA samples were predominantly composed of fruit seeds, skin, and pulp, whereas arthropod body parts were rare. Most of the seeds in LOCA samples could not be identified to species because we lacked reference materials. However, seeds of a known common food source at LOCA for which we had reference material, *Psychotria berteriana*, appeared in 32% of samples. For the logistic regression model with fecal-sample content categories “contains arthropods” ($n = 23$) and “no arthropods” ($n = 20$), only site was important for predicting presence of arthropods. Significantly more fecal samples from PUVI than from LOCA contained arthropods ($\chi^2 = 32.5$, $df = 1$, $P < 0.001$). For the model with fecal-sample content categories “contains fruit” ($n = 30$) and “no fruit” ($n = 13$), significantly more fecal samples from LOCA than from PUVI contained fruit ($\chi^2 = 29.1$, $df = 1$, $P < 0.001$). No other variables in the model were important for predicting fecal-sample contents. More than 72% of fecal samples from PUVI contained exclusively arthropod parts, whereas 80% of samples from LOCA contained exclusively fruit material. Analysis of stable carbon isotopes in blood plasma showed more depleted $\delta^{13}C$ at LOCA ($n = 4$; $-27.1 \pm 0.4\text{‰}$) than at PUVI ($n = 5$; $-23.9 \pm 0.3\text{‰}$) (ANOVA effect_{site} = $-1.635 \pm 0.254\text{‰}$, $F = 40.97$, $P < 0.001$).

Territoriality.—Fifty-eight birds were fitted with radiotransmitters: 39 at PUVI and 19 at LOCA. Two of the 39 PUVI birds and one of the 19 LOCA birds were depredated before we were able to determine territorial status; thus, 55 radiotagged birds were successfully tracked at both sites (Table 1). We defined floaters as birds that moved >500 m from the point of original capture and subsequently moved broadly over the landscape. Only one of 37 (2.7%) birds at PUVI, a first-winter male, and one of 18 (5.6%) birds at LOCA, a first-winter female, were nonterritorial floaters. We were unable to track either of these two individuals to a discrete location at any time during the study. All other birds were

TABLE 1. Estimates (mean ± SE) of core use area, 90% kernel home ranges (KHR), and minimum convex polygon (MCP) home ranges in hectares for Bicknell’s Thrushes wintering at Pueblo Viejo (PUVI), a high-elevation cloud forest site, and Canela (LOCA), a mid-elevation rainforest site in the Dominican Republic, 2005–2008 (n = number of individuals, M = male, F = female, Ad = adult, and FW = first-winter).

Site	Sex	Age	n	Core use area	90% KHR	MCP
PUVI	M	Ad	15	0.323 ± 0.049	1.571 ± 0.207	1.725 ± 0.204
PUVI	M	FW	10	0.352 ± 0.116	1.738 ± 0.465	1.744 ± 0.359
PUVI	F	Ad	5	0.189 ± 0.068	1.082 ± 0.314	1.656 ± 0.583
PUVI	F	FW	6	0.204 ± 0.054	1.308 ± 0.285	1.618 ± 0.300
LOCA	M	Ad	7	0.313 ± 0.089	1.179 ± 0.289	1.193 ± 0.257
LOCA	M	FW	5	0.388 ± 0.118	1.720 ± 0.380	3.182 ± 1.127
LOCA	F	Ad	4	0.226 ± 0.067	0.783 ± 0.252	0.823 ± 0.256
LOCA	F	FW	1	0.230	0.759	0.722
All Ad	M	—	22	0.320 ± 0.043	1.446 ± 0.169	1.555 ± 0.167
All FW	M	—	15	0.364 ± 0.084	1.732 ± 0.326	2.223 ± 0.457
All Ad	F	—	9	0.206 ± 0.045	0.949 ± 0.202	1.286 ± 0.356
All FW	F	—	7	0.207 ± 0.046	1.230 ± 0.253	1.490 ± 0.284

invariably tracked to defined, unvarying spaces during each burst session, with zero failures to locate individuals.

Territorial behavior was observed at both sites. Crepuscular vocalizations were a primary agonistic behavior. These consisted of counter-calling *beer* notes issued by neighboring individuals. Counter-calling interactions occasionally included higher-pitched, rising *beer* notes and growl calls as two or more birds approached each other along territorial boundaries. During playback of conspecific song, aggressiveness scores were measured for 32 individuals at LOCA and 31 individuals at PUVI. Playback of *beer* notes elicited aggressive counter-calling in 68% of quantified responses, whereas playback of typical breeding-grounds song elicited phrases of song otherwise not heard on the winter grounds in 17.5% of all quantified responses. Aggressiveness score means did not differ between the sites and were 1.8 ± 0.2 at LOCA and 2.1 ± 0.2 at PUVI ($t = 0.96$, $P = 0.34$). Because of the densely vegetated habitat, direct observations of physical displays were exceedingly rare. However, during playback of conspecific vocalizations, individuals were occasionally observed tail- and wing-flicking and crest-raising as they approached the amplifier.

Overlap of core use areas was minimal at both sites, with 14% of neighbor pairs overlapping at PUVI and 29% at LOCA. Overlap of core use areas averaged $3.1 \pm 1.4\%$ of total core area at PUVI and $5.2 \pm 1.9\%$ at LOCA, with no significant between-site difference in magnitude of overlap (Kruskal-Wallis score $\text{mean}_{\text{PUVI}} = 49.3$, score $\text{mean}_{\text{LOCA}} = 57.4$, $\chi^2 = 3.43$, $df = 1$, $P = 0.064$). Overlap of home ranges was higher than that of core use areas, with 64% of neighbor birds overlapping at PUVI and 79% at LOCA. Mean overlap of home ranges at PUVI was $12.2 \pm 1.8\%$ of individual territorial space while at LOCA mean overlap was $18.6 \pm 4.7\%$. There was no significant difference in the magnitude of territorial overlap between sites (Kruskal-Wallis score $\text{mean}_{\text{PUVI}} = 49.2$, score $\text{mean}_{\text{LOCA}} = 57.5$, $\chi^2 = 1.66$, $df = 1$, $P = 0.198$).

There were no differences between sites in individual estimates of core use areas, 90% KHRs, or MCPs (core use area $\text{effect}_{\text{site}} = 0.061 \pm 0.109$, $F = 0.316$, $P = 0.577$; 90% KHR $\text{effect}_{\text{site}} = -0.094 \pm 0.098$, $F = 0.0910$, $P = 0.345$; MCP $\text{effect}_{\text{site}} = -0.094 \pm 0.101$, $F = 0.882$, $P = 0.352$). Core use areas and home ranges of females tended to be smaller than those of males at both sites (Fig. 1 and Table 1), with the largest difference occurring between male and female core use areas. However, these trends were not significant (core use area $\text{effect}_{\text{sex}} = -0.214 \pm 0.110$, $F = 3.760$, $P = 0.058$; 90% KHR $\text{effect}_{\text{sex}} = -0.176 \pm 0.099$, $F = 3.145$, $P = 0.082$; MCP $\text{effect}_{\text{sex}} = -0.137 \pm 0.102$, $F = 1.812$, $P = 0.185$). For all females combined ($n = 16$), the mean size of core use areas was 0.21 ± 0.03 ha, that of 90% KHRs was 1.07 ± 0.16 ha, and that of mean MCPs was 1.38 ± 0.23 ha. For all males combined ($n = 37$), mean size of core use area was 0.34 ± 0.04 ha, that of 90% KHRs was 1.56 ± 0.17 ha, and that of MCPs was 1.83 ± 0.21 ha. No detectable differences existed between adults and first-winter birds in mean estimates of core use areas, 90% KHRs, or MCPs (core use area $\text{effect}_{\text{age}} = 0.037 \pm 0.103$, $F = 0.131$, $P = 0.719$; 90% KHR $\text{effect}_{\text{age}} = -0.048 \pm 0.093$, $F = 0.269$, $P = 0.606$; MCP $\text{effect}_{\text{age}} = -0.099 \pm 0.095$, $F = 1.103$, $P = 0.299$; Fig. 2). For all birds combined ($n = 53$), the mean size of core use areas was 0.30 ± 0.03 ha, that of 90% KHRs was 1.41 ± 0.13 ha, and that of MCPs was 1.69 ± 0.17 ha.

Measures of habitat use.—Data from both sexes were combined to compare measures of habitat use between the sites. The

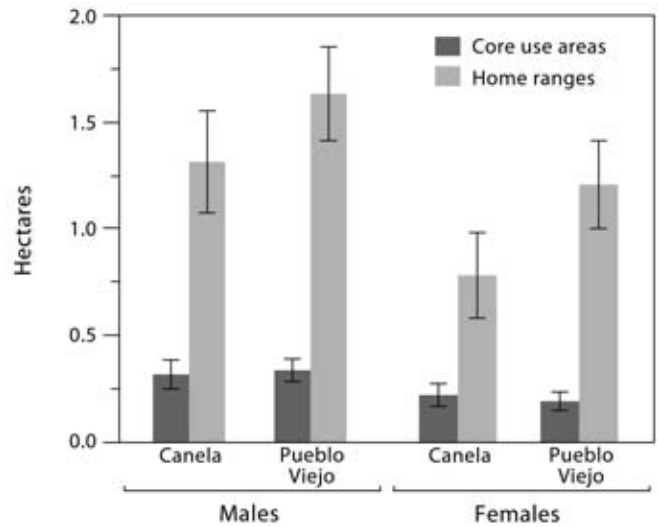


FIG. 1. Estimates of core use areas and home ranges of male and female Bicknell's Thrushes wintering at a mid-elevation rainforest site (Canela: $n = 12$ males, 5 females) and a high-elevation cloud-forest site (Pueblo Viejo: $n = 25$ males, 11 females) in the Dominican Republic during the boreal winters of 2005–2008. Error bars = SE.

mean percentage of total locations contained within the core use area (percent use) was significantly greater at LOCA than at PUVI (percent use $\text{effect}_{\text{site}} = 0.070 \pm 0.016$, $F = 19.934$, $P < 0.001$; Table 2). Additionally, the percentage of the total home range encompassed by the core use area (percent territory) was significantly greater at LOCA than at PUVI (percent territory $\text{effect}_{\text{site}} = 0.033 \pm 0.008$, $F = 16.934$, $P < 0.001$; Table 2). Intensity of use (percent use/percent

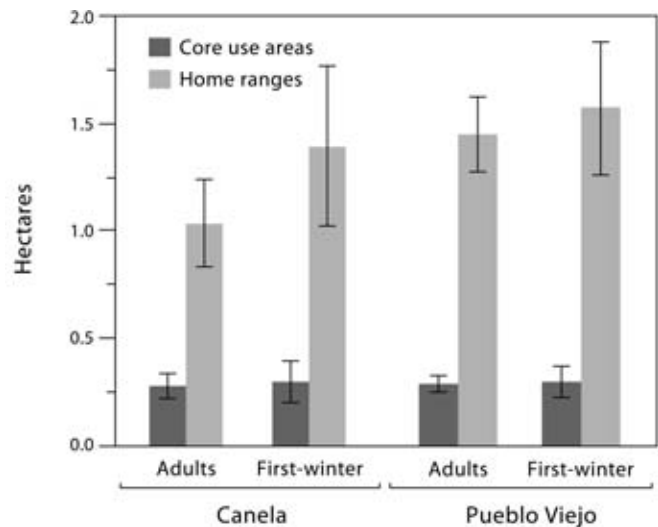


FIG. 2. Estimates of core use areas and home ranges of adult and first-winter Bicknell's Thrushes wintering at a mid-elevation rainforest site (Canela: $n = 11$ adults, 6 first-winter birds) and a high-elevation cloud-forest site (Pueblo Viejo: $n = 20$ adults, 16 first-winter birds) in the Dominican Republic during the boreal winters of 2005–2008. Error bars = SE.

TABLE 2. Intensity of use of core use areas by Bicknell's Thrushes at two wintering sites, Canela (LOCA) and Pueblo Viejo (PUVI), in the Dominican Republic, 2005–2008.

Site	Sex	<i>n</i>	Percent use (%) ^a (Mean ± SE)	Percent territory (%) ^b (Mean ± SE)	Intensity ^c (Mean ± SE)
LOCA	M	12	59.8 ± 3.0	24.1 ± 1.8	2.5 ± 0.1
LOCA	F	5	64.5 ± 5.5	29.3 ± 2.2	2.2 ± 0.1
PUVI	M	25	49.0 ± 2.2	20.0 ± 1.1	2.6 ± 0.1
PUVI	F	11	41.0 ± 2.8	15.9 ± 1.0	2.6 ± 0.1

^aPercentage of total locations contained within the core use area.

^bPercentage of territory (90% kernel home range) encompassed by the core use area.

^cPercent use/percent territory.

territory) did not differ between the two sites (intensity effect_{site} = 0.047 ± 0.058, $F = 0.654$, $P = 0.423$; Table 2).

Microhabitat preferences of birds at the two sites did not differ significantly as measured by percentage of fixes in the three microhabitat types (Kruskal-Wallis tests, all $P > 0.05$). More than 50% of fixes for all birds at both sites occurred in dense thickets that usually consisted of vine tangles growing in gaps left by fallen trees (Table 3). We recorded 59 min of direct observations of 19 birds at PUVI and 48 min of 9 individuals at LOCA. Birds at PUVI were observed significantly more often on the ground or utilizing substrate within 1 m of the ground than birds at LOCA (Kruskal-Wallis score, PUVI mean = 17.1, LOCA mean = 9.2, $\chi^2 = 6.2$, $df = 1$, $P = 0.01$; Table 3), whereas birds at LOCA were observed utilizing mid-canopy trees at heights >4 m more often than birds at PUVI (Kruskal-Wallis score, LOCA mean = 19.9, PUVI mean = 11.9, $\chi^2 = 6.5$, $df = 1$, $P = 0.01$; Table 3).

DISCUSSION

Diet and site-based spatial behavior.—Food availability and habitat-specific diet may act as proximate drivers of space-use strategies for wintering songbirds (Greenberg and Salewski 2005). Our analyses of the diet of wintering Bicknell's Thrushes strongly suggested that birds at LOCA consumed primarily fruit whereas those at PUVI consumed primarily arthropods. Blood plasma samples, which reflect diet over short periods (1–5 days; Hobson and Clark 1993, Podlesak et al. 2005), were indicative of a fruit-heavy diet for LOCA because they showed significantly more depleted $\delta^{13}\text{C}$ values (Herrera et al. 2001, Podlesak et al. 2005). Similarly, fecal samples from LOCA were significantly more likely to contain fruit than the arthropod-filled samples from PUVI.

Given the dietary differences between LOCA and PUVI, we expected birds at LOCA to be less territorial than those at PUVI as they tracked an ephemeral and presumably non-economically defensible food resource, as has been shown in other frugivorous migrant songbirds (e.g., Greenberg 1979, Morton 1980, Levey and Stiles 1992). We suspected that PUVI birds, in contrast, would establish and maintain strictly defended territories containing arthropod biomass sufficient for self-maintenance throughout the winter. However, birds at both sites defended minimally overlapping, exclusive-use territories that did not vary in size between sites. This suggests that fruit at LOCA was a defensible resource with predictable, season-long availability. Our observations of the fruiting phenology of a common mid-canopy tree, *Psychotria berteriana*, in which we frequently observed Bicknell's Thrushes foraging, support this possibility. We documented several individual *P. berteriana* simultaneously bearing ripe fruit, flowers, and spent fruiting stems in January, February, and March of all years, which suggests a reliable and potentially defensible resource. Studies of other wintering migrants have shown a similar phenomenon of territoriality when fruiting trees consistently bear fruit over the course of the nonbreeding period (e.g., George 1986, Bates 1992, Latta and Faaborg 2002, Skórka et al. 2006). It is also possible that predator avoidance could drive territoriality at LOCA. However, we find this explanation unlikely because diurnal avian predators occur at low densities at this study site (J. M. Townsend pers. obs.). Nocturnal rats (*Rattus* spp.) are known to depredate Bicknell's Thrushes at LOCA (Townsend et al. 2009), but it is unclear how maintenance of diurnal territories would serve in avoiding these predators. We suggest that the evidence most strongly supports territorial defense of fruit resources at LOCA. Future studies should more thoroughly quantify the fruiting phenology of *P. berteriana*, investigate interspecific competition for this fruit, and assess the fat and lipid contents of fruits to determine their energetic value to wintering thrushes.

Although the size of core use areas and home ranges did not differ between sites, other metrics of space-use behavior did, and these likely reflect site-based dietary differences. Birds were more frequently observed within 1 m of the forest floor at PUVI than at LOCA, whereas birds at LOCA were found more frequently at forest strata >4 m high than birds at PUVI (Table 3). This finding probably reflects differences in foraging ecology at the two sites. Mid-canopy fruiting trees were rare at PUVI, and most direct foraging observations were of birds hunting along the forest floor by passive wait-and-strike foraging or by leaf-lifting (J. M. Townsend pers. obs.). At LOCA, by contrast, mid-canopy fruit was abundant, and birds were frequently observed taking fruit from hanging

TABLE 3. Percentage (± SE) of fixes of radiotagged Bicknell's Thrushes by microhabitat and percentage of direct observations by forest strata at a mid-elevation rainforest site, Canela (LOCA), and a high-elevation cloud-forest site, Pueblo Viejo (PUVI), in the Dominican Republic, 2005–2008. Asterisk indicates significant difference between sites ($P < 0.05$)

Site	<i>n</i>	Forest strata			<i>n</i>	Microhabitat type		
		0–2 m*	2–4 m	>4 m*		Thicket	Mixed	Open
LOCA	9	38.9 ± 11.2	33.3 ± 8.5	27.8 ± 14.7	12	52.2 ± 8.4	26.5 ± 8.9	21.2 ± 9.1
PUVI	19	76.3 ± 7.3	18.4 ± 7.1	5.3 ± 3.6	35	69.3 ± 4.8	19.6 ± 4.7	11.1 ± 2.5

clusters by hover-gleaning or by walking lateral branches. Although fruit predominated in the diet of LOCA birds, we also observed birds at this site on or near the forest floor, where their ground-foraging tactics in search of arthropods varied little from those used by birds at PUVI and on the breeding grounds (Rimmer et al. 2001). We further suspect that ground-foraging Bicknell's Thrushes at LOCA scavenged fallen fruit from the upper canopy, as did several species of doves at this site (J. M. Townsend pers. obs.). We found seeds of fruits not known from mid-canopy trees in fecal samples of LOCA birds, and we posit that these fell from the upper canopy. We did not detect diurnal use of the upper canopy by radiotagged birds during the study.

Birds at the two sites did not differ significantly in the intensity of use (percent use/percent territory) of their core use areas. Although the percentage of total fixes that fell within the core use area (percent use) was higher at LOCA, so too was the percentage of total territorial space encompassed by the core area (percent territory). The difference expressed in the variation in percent use and percent territory between the sites was essentially a measure of how dispersed our fixes of individual birds were across their total territorial space: locations were more spatially clustered at PUVI than at LOCA. We suspect that this spatial clustering of points at PUVI reflected a preference for thickets with shelter and high arthropod abundance. Birds at PUVI may have been more sedentary than those at LOCA. A high-nutrient arthropod diet may have allowed birds at PUVI to restrict foraging to a smaller area than fruit-eating LOCA birds were able to do. At LOCA, we did not observe any fruiting trees with a superabundance of fruit that might have enabled individuals to maintain highly concentrated territories (Latta and Faaborg 2002). *Psychotria berteriana* is a small understory or mid-canopy tree that grows to heights of 2–5 m at LOCA, and it seems likely that individuals would need to visit multiple trees to meet nutritional demands. It is possible, therefore, that LOCA birds may have been forced to move more widely within their territorial space as they foraged for fruit away from thickets and vine tangles. Birds at both sites showed a preference for thickets, in that >50% of all locations at both sites occurred in dense microhabitat (Table 3). Birds at LOCA appeared to move across open space to find and exploit open-forest fruit but still preferentially sought the shelter of dense forest and restricted most of their daily movements to this microhabitat.

Core use areas at both sites overlapped minimally, with 86% of PUVI neighbor pairs and 71% of LOCA neighbor pairs showing no overlap along their core use borders. Where core use areas overlapped, the shared area was very small (3.1% and 5.2% mean overlap of total core use area at PUVI and LOCA, respectively). At both sites, home ranges overlapped more extensively than core use areas, but the magnitude of territorial overlap was again low (mean overlap 12.2% and 18.6% at PUVI and LOCA, respectively). Importantly, these estimates are of spatial overlap only and do not represent potential temporal overlap. We were logistically unable to simultaneously track neighboring birds on a consistent basis. During two mornings of simultaneous tracking of three neighboring birds at PUVI, however, we did not detect any instances of temporal overlap within the same geographic area. Further, we rarely captured more than one individual during playback of conspecific song. Together these observations suggest that birds at both sites avoided contact, both spatially and temporally.

Spatial behavior of sex and age classes.—Both females and first-winter birds established territories in the same habitat as adult males and maintained unchanging adjacent boundaries with adult males during the period of study. The size of first-winter birds' core use areas and home ranges did not differ from those of adults. Females tended to have smaller core use areas and home ranges than males (Fig. 1 and Table 1), but variability was high and the differences were not significant. Similar studies of radiotagged wintering Hermit Thrushes ($n = 34$; Brown et al. 2000) and Willow Flycatchers (*Empidonax traillii*; $n = 39$; Koronkiewicz et al. 2006) also detected no differences in territory size between males and females.

Combining data from both sites, we estimate that mean core use areas of Bicknell's Thrushes in the Dominican Republic are 0.30 ± 0.23 ha in size, mean 90% KHRs are 1.41 ± 0.93 ha, and mean MCPs are 1.69 ± 1.21 ha. Winker et al. (1990) reported much smaller mean MCPs for Wood Thrush (*Hylocichla mustelina*) in Mexico (0.44 ha), as did Brown et al. (2000) for Hermit Thrush in Louisiana (0.55 ha), although caution must be used in comparing home-range estimates between studies (Kernohan et al. 2001). For both of these species, it was suggested that habitat was saturated and that subordinate birds were forced to adopt a floater strategy, phenomena that we did not observe in Bicknell's Thrush. We identified only two floating individuals, one at each site. This rate of floater occurrence (2.7% at PUVI, 5.6% at LOCA) is lower than rates reported in other telemetry-based studies of wintering songbirds. Rappole et al. (1989) found 44% of wintering Wood Thrushes in Mexico to be floaters, whereas 14% of wintering Hermit Thrushes in Louisiana (Brown et al. 2000) and 8–17% of wintering Ovenbirds (*Seiurus aurocapilla*) in Jamaica (Brown and Sherry 2008) were categorized as floaters. The low rates of floater behavior among Bicknell's Thrushes in the present study indicate that most individuals, regardless of age or sex, establish territories.

We suggest that Bicknell's Thrush territories are maintained to defend exclusive access to food supply and that both fruit and arthropods constitute defensible resources for wintering thrushes in the Dominican Republic. Future studies should investigate fitness consequences of winter residence at sites with a fruit-heavy resource base versus those with a greater abundance of available arthropods. Between-habitat variation in fitness, combined with more detailed investigations of food resources, could contribute to our understanding of how winter food availability contributes to population limitation in migrant songbirds.

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