

CHANGES IN HOME RANGE OF BREEDING AND POST-BREEDING MALE PEARLY-EYED THRASHERS IN THE LUQUILLO MOUNTAINS OF PUERTO RICO

José William Beltrán S.^{1,3}, Joseph M. Wunderle², Jr., & Wayne J. Arendt²

¹Department of Biology, University of Puerto Rico, Río Piedras Campus, PO Box 23360, San Juan, Puerto Rico 00931-3360, USA. *E-mail*: williambeltran2005@gmail.com

²International Institute of Tropical Forestry, USDA Forest Service, Sabana Field Research Station, HC 02 Box 6205 Luquillo, Puerto Rico 00773, USA.

Resumen. – Cambios en áreas de dominio vital en reproducción y post-reproducción en machos de Zorzal Pardo en las montañas de Luquillo, Puerto Rico. – Abundancia de alimento, periodo del año y estado reproductivo son factores importantes que afectan el área de dominio vital de aves. Entre el 23 de Enero y 28 de Noviembre de 2003, evaluamos las áreas de dominio vital y las áreas nucleares de actividad en 10 machos de zorzales pardos (*Margarops fuscatus*; Mimidae) radio-rastreados en el Bosque Experimental de Luquillo, noroeste de Puerto Rico. Encontramos diferencias significativas en el área de dominio vital entre los estados reproductivos. Los estados de polluelos y de huevos presentaron las mayores y menores áreas de dominio vital (medianas = 2,0 y 0,5 ha, respectivamente) y las áreas nucleares (medianas = 0,14 y 0,09 ha, respectivamente). La reducida área utilizada por machos durante el estado de polluelos podría estar relacionada con cambios de defensa territorial a alimentación de polluelos, siendo esta última relacionada con un aumento de presa animal en la dieta adulta para elevar el nivel de proteína accesible a la cría. Las áreas de dominio vital fueron mas grandes durante el periodo post-reproductivo (mediana = 17,9 ha, rango = 0,5–178,7 ha) que durante el periodo reproductivo (mediana = 2,1 ha, rango 1,3–7,7 ha), con diferencias significativas entre ambos periodos. Presumimos que el incremento de área de dominio vital durante post-reproducción fue una respuesta a la disminución en la abundancia de frutas de *Prestoea acuminata*, especialmente notoria al final del periodo reproductivo. No encontramos una correlación significativa entre la abundancia de frutas de *P. acuminata* y área de dominio vital, ni entre áreas nucleares de actividad y la abundancia de frutas. La carencia de correlaciones entre estas variables podría explicarse por la dieta omnívora y oportunista de los zorzales pardos.

Abstract. – Food abundance, time of year, and stage of the reproductive cycle are important factors affecting home range size in birds. Between 23 January and 28 November 2003, we determined the home range and core area sizes for 10 radio-tagged male Pearly-eyed Thrashers (*Margarops fuscatus*; Mimidae) within the Luquillo Experimental Forest, northeastern Puerto Rico. We found significant differences among the breeding stages in home range and core area sizes. Egg and nestling stages showed the largest and smallest home range sizes (medians = 2.0 and 0.5 ha, respectively) and core area sizes (median = 0.14 and 0.09 ha, respectively). The reduced area used by the male during the nestling stage may be attributable to a shift in the male's wandering behavior while the female incubates to the defense and feeding of nestlings. Home range sizes were significantly larger during the post-breeding period (median = 17.9 ha, range = 0.5–178.7 ha) than during the breeding period (median = 2.1 ha, range = 1.3–7.7 ha). We suggest that the increase in home range size during post-breeding season was a response to the abundance of palm fruits (*Prestoea acuminata*) which decreased during the breeding season. Although we found a positive correlation between number of nests with eggs and palm fruit abundance, there was no significant correlation between breeding period home range size and ripe fruit

density or core area size and ripe fruit density. Lack of correlation between the area used and fruit density may be due to the omnivorous and opportunistic diet of the thrasher. *Accepted 5 August 2010.*

Key words: Home range, breeding period, post-breeding period, fruit abundance, rain forest, reproductive stages, Pearly-eyed Thrasher, *Margarops fuscatus*.

INTRODUCTION

Home range size in birds can vary with a variety of factors including food abundance, time of year, and stage of the reproductive cycle (Krebs & Davies 1993, Dykstra *et al.* 2001, Vega-Rivera 2003). For example, studies comparing movements during the different stages of the nesting cycle have documented changes in home range size of breeding birds as energetic and nutritional demands change during the egg, chick, and fledgling stages (Møller 1990). In addition, home range size and habitat use following breeding can shift dramatically in the post-breeding period (Vega-Rivera 2003). Most of these studies, however, have been conducted in the north-temperate zone (Vega-Rivera 2003, Garza *et al.* 2005) with relatively few studies of area use or home range conducted on tropical birds (e.g., Lopes & Marini 2006, Brandt & Cresswell 2008) under conditions that may differ from the temperate zone (Stutchbury & Morton 2001).

The Pearly-eyed Thrasher (*Margarops fuscatus*), a Caribbean mimid, is an opportunistic omnivore for which changes in its home range are expected both within its six-month breeding season (Arendt 2000, 2006) and afterwards as food resources vary with changes in rainfall in the mountains of Puerto Rico (García-Martín *et al.* 1996). Although the thrasher feeds on a diversity of food items including frogs, lizards, and insects, as well as eggs and nestlings of other bird species, it also feeds heavily on fruit (Arendt 2000). Of the various fruits consumed by the thrasher, the fruit of the sierra palm (*Prestoea acuminata*) is an especially important food resource for adult and nestling thrashers, at least where

palms are abundant (Snyder *et al.* 1987, Arendt 2000). The breeding biology of the Pearly-eyed Thrasher has been well studied in the Luquillo Mountains (Arendt 1985a, 1985b, 1993, 2000, 2006). Radio telemetry, male homing experiments, and capture-recapture studies have documented year-round movements (including natal and reproductive dispersal) of adult and young thrashers in the Luquillo Mountains (Arendt 2006). Short-range movements (to areas adjacent to the forest, across Puerto Rico, and to nearby islands) and long-range, transmarine dispersal (Barbuda to Guadeloupe) have been recorded (Arendt 2006). However, more information is needed on thrasher home ranges, especially the use of core areas during breeding and post-breeding periods in the Luquillo Mountains and elsewhere.

The Pearly-eyed Thrasher has been characterized as a “supertramp” in part because it occurs on islands with depauperate bird communities from the central Bahamas to Puerto Rico and the Virgin Islands through the Lesser Antilles south to Bonaire (Arendt 2006). The species is aggressive and frequently competes with other bird species for cavity nest sites, as evident in its detrimental competition with the endangered Puerto Rican Parrot (*Amazona vittata*) for cavity nest sites (Snyder *et al.* 1987). Given these traits and the likelihood that thrasher home ranges would change over the course of the breeding season and afterwards, we conducted a study on the thrasher with the objective to: (1) compare home range and core area sizes among the breeding stages (egg, nestling, and fledgling); (2) determine if breeding home range and core area sizes are correlated with fruit density in the vicinity of the nest site; and (3)

compare home range and core areas during breeding and post-breeding periods. Our work focuses on males given their important role in territorial defense and the difficulties of capturing females without disrupting the nesting cycle. We predicted that male home ranges would be smallest during the nestling stage as the demands of territorial maintenance shifted to responsibilities of nestling care. Also, we expected that male home ranges would be inversely correlated with fruit density in the vicinity of the nest. Finally, we predicted that male home ranges would expand after breeding as males wandered more widely in search of food as fruit production declined after breeding.

STUDY AREA AND METHODS

This study was conducted in the El Yunque National Forest or Luquillo Experimental Forest (LEF), an 11,500 ha subtropical rain forest located in the Luquillo Mountains (120–1075 m a.s.l.) of northeastern Puerto Rico (18°19'N, 65°45'W). The LEF has four major forest types, which include the tabonuco, palo colorado, palm, and elfin forests (Wadsworth 1951). The four forest types are stratified mostly by elevation, ranging from tabonuco forest in the lowlands to elfin forest on the highest ridges. At mid elevation between these forest types are the palo colorado and palm forests in which our study was conducted. The palo colorado forest type encompasses 3318 ha and occurs at elevations ranging from 600–900 m a.s.l., and is named after the dominant palo colorado (*Cyrilla racemiflora*) trees. The sierra palm forest type is found in poorly drained sites and steep slopes at elevations above 750 m a.s.l., and covers 1942 ha of the LEF. The palo colorado and palm forests are found within the subtropical wet and lower montane wet and rain forest life zones of the Holdridge system (Ewel & Whitmore 1973).

Average annual rainfall ranges from 3537 mm in the lowlands to 4849 mm in the mountain peaks, with showers throughout the year, but a relatively dry period occurs between February to April (Scatena, http://luq.lternet.edu/research/projects/climate_hydrology_description.html). Our study was conducted in the Icacos Valley, located in the southeastern portion of the LEF at elevations from 610–750 m a.s.l. where a long-term study of Pearly-eyed Thrashers was conducted (Arendt 2006).

Trapping. We trapped 10 adult males at nest boxes during the early brood-rearing stage of each nest (when nestlings were about 5–10 days old) from 21 January to 24 June 2003. Each adult was caught using a small (20 x 20 x 25 cm) wooden box placed at the entrance of a nest box. All trapped individuals were marked with a distinctive combination of one aluminum and two color bands to facilitate identification in the field. Captured males were distinguished by the presence of a cloacal protuberance and the absence of a brood patch.

Each thrasher was followed by attaching a 3.8 g transmitter (Model PD-2 Holohil Systems, Ltd, Ontario, Canada), representing approximately 4% of the male body mass, and operating at a frequency of 164.185 to 164.800 MHz. Transmitters were attached using a backpack harness consisting of two loops of flexible steel wire covered with plastic, which passed beneath the legs and attached to the transmitter which rested on the dorsal portion of the synsacrum (Rappole & Tipton 1991). Each male was released after 30 to 50 min following capture and subsequent observations indicated that they had no difficulties flying.

Radio tracking began the day after capture and continued for approximately 120 days (normal time span of the transmitter battery) or until the male could no longer be detected.

We used a 3-element Yagi antenna and a hand-held receiver (Model TRX-2000S Wildlife Materials) to locate radio-tagged birds at intervals of 1–2 h during five days per week. A minimum 1-h interval was maintained between successive locations to avoid autocorrelation (White & Garrot 1990).

The location of each radio-tagged male was determined by triangulation, in which two people took simultaneous bearings from different sites where they could detect the strongest signal using a hand-held receiver. UTM coordinates in which bearings of the bird's position were recorded using a Global Positioning System (GPS) receiver (Trimble Pathfinder Pro XRS). All positions and the bearing lines were plotted using the GPS Pathfinder® Office program (Trimble Navigation Ltd.), which allowed us to determine the UTM coordinates of the bird's position where the two bearing lines intersected. Calibrations by Wunderle *et al.* (unpubl.) using triangulation on known signal source locations indicated that mean bearing error (in degrees) = 13.33 ± 0.02 , $n = 138$, which is equivalent to ± 12.01 m error at 50 m.

Determination of reproductive and post-reproductive period and breeding stages. We used the date on which adults ceased feeding fledglings (15 days after fledging) and when no reproductive signs were detected around nests to designate the end of the reproductive period and the beginning of the post-reproductive period. Each reproductive stage (i.e., eggs, nestlings, fledglings) was determined by daily visual inspection of nest boxes, when adults were absent. During the post-reproductive period, each nest box was checked every two weeks for signs of reproduction.

Analysis of movements. We determined home range sizes for each male based on the adaptive kernel (AK) model, which has an advantage when uncertainty is attributable to

locations on the edge of the distribution by smoothing the density function to a greater degree than the fixed kernel model (Worton 1989). We calculated both the 50% AK (henceforth core area) and the 95% AK. All estimates of home ranges and core areas were calculated using CALHOME (Kei *et al.* 1996) in which smoothing parameters were defined by least squares cross validation (Seaman & Powell 1996) and the grid size was selected automatically.

To calculate the home range and core areas for each reproductive stage we used the first 20 telemetry fix points for each male to standardize the number of fixes. To relate home range and core area to the abundance of ripe fruit each month we calculated home ranges and core areas based on the first 21 fixes obtained in a month for each male. For each radio-tagged male, we also calculated the average distance moved per hour (m/h) between successive locations as a measure of mobility rate. The overlap between home ranges (95% AK) of two neighboring males was estimated using Minta's (1993) index. Values range between 0 and 1, where 1 indicates a 100% overlap between two adjacent areas with the same size and location. The overlap between two adjacent home ranges was calculated using the "Intersect Polygons" routine from Arc-View version 3.2 (ESRI 1992) GIS program for breeding and post-breeding periods. For each bird, we used the 95% minimum convex polygon model (MCP) to generate cumulative curves of home range versus the cumulative number of fixes to identify the asymptote indicating that a sufficient number of fixes had been obtained to accurately characterize the home range size.

Abundance of ripe fruits. We estimated the abundance of ripe fruits on trees and shrubs between February and July 2003, in eight belt transects radiating from each thrasher nest

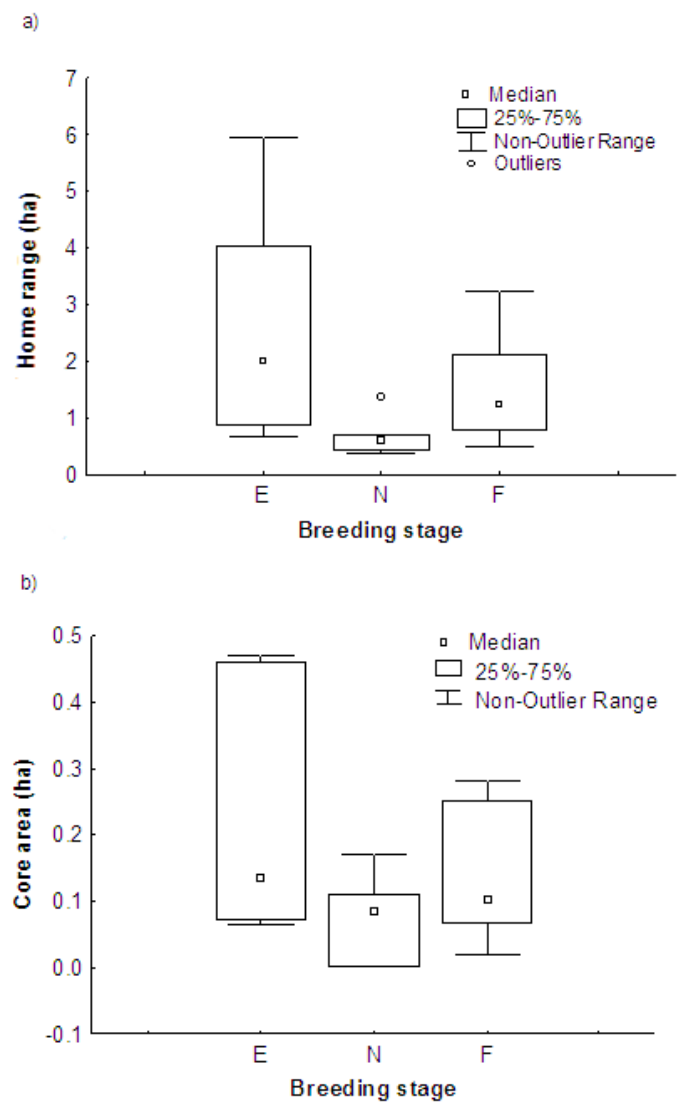


FIG. 1. Variation across egg (E), nestling (N), and fledgling (F) stages in (a) home range area (95% adaptive kernel) and (b) core area (50% adaptive kernel) for six radio-tagged male Pearly-eyed Thrashers in the Ica-cos Valley of the Luquillo Experimental Forest, Puerto Rico during February to May 2003. Adaptive kernel calculations were based on 20 telemetry fix points for each individual thrasher and each reproductive stage to allow comparisons among stages.

box. Each belt transect was 2 x 50 m in size and radiated away from the nest box in the N, NE, E, SE, S, SW, W, and NW directions. Within each belt transect, we estimated ripe

fruit abundance on trees and shrubs with a diameter > 3 cm at breast height (1.5 m) for species consumed by thrashers (Snyder *et al.* 1987) including: *Schefflera morototoni*, *Clusia clu-*

siodes, *Miconia* spp, *Margravia sintenessi*, *Psycotria berteriana*, *Cecropia scheberiana*, and *Prestoea acuminata*. To evaluate overall fruit abundance of *P. acuminata*, we used counts of these species obtained from a study on palm fruit phenology (Wunderle & Mercado, unpubl.) obtained during the same time period as our study. Abundance of palm fruits was obtained from two locations (1.5 km apart) within the thrasher study area. At each of the two palm phenology sites, number of infructescences with > 50% ripe fruits was counted on 100 marked sierra palms each month.

Statistical analysis. Statistical analyses followed Sokal & Rohlf (1995) and were conducted using the Statistica program (StatSoft 2000). Normality of each variable and homogeneity of variances were examined by Shapiro-Wilk test and Levene *F*-Test, respectively. Non-parametric tests were used when the assumptions of normality and homogeneity of variances were not met. In all statistical tests, a probability of 0.05 or less was accepted as significant, but we report higher values for descriptive purposes. Variation around the mean is indicated by the standard error (SE). Spearman rank correlation tests were used to determine whether there was a relationship between the number of nests with eggs and abundance of ripe palm fruits as well as a relation with monthly rainfall (mm). Friedman tests were used to compare variation among the three reproductive stages in home range size and core area. We used Mann Whitney *U*-tests to compare sizes of home ranges and core areas between reproductive and post-reproductive periods. The mobility (m/h) of radio-tagged males between reproductive and post-reproductive periods was analyzed with a *t*-test. Significance of differences for core areas and home range areas between reproductive and post-reproductive periods was tested using Mann-Whitney *U*-tests. Spearman rank correlation tests were used to exam-

ine the relationship between abundance of ripe fruits around nests with home range and core area sizes of radio-tagged males.

RESULTS

Male Pearly-eyed Thrashers were radio-tracked between 3.1 to 6.9 months, five of which were monitored during breeding and post-breeding periods, four during post-breeding only, and one during breeding only (Table 1). Cumulative home range or cumulative core area (100% convex polygon) graphed against cumulative number of telemetry fixes reached an asymptote for all, but one male (M9). During the breeding season, 60–80 fixes were sufficient to obtain accurate home range and core area estimates. In the post-breeding season, however, only 30–50 fixes were required for estimation of the home ranges and core area sizes for most males (7 of 11).

Home range, core area, and breeding stages. Home range size (Friedman test, $S = 7.0$, $df = 2$, $P = 0.03$; Fig. 1a) and core area size (Friedman test, $S = 7.0$, $df = 2$, $P = 0.03$; Fig. 1b) varied among the three breeding stages for the six radio-tagged male thrashers for which breeding-period data were available. The largest and smallest home range sizes occurred during the egg (median = 2.0 ha) and nestling (0.5 ha) stages (Mann-Whitney test, $U = 54$, $P = 0.02$; Fig. 1a). Home range and core areas did not vary significantly ($P > 0.05$) between the egg and fledgling stage or the nestling and fledgling stage.

Home range and core area size in relation to ripe fruit density. At six nesting sites, values of ripe fruit density were highly variable (range = 25–67,500 ripe fruits/ha) between February to July 2003. Ripe fruit density in nesting sites decreased over time, with the exception of M8 in which ripe fruit density increased from

TABLE 1. Duration of radio tracking (months) and movement parameters (m/h) during breeding and post-breeding periods for 10 radio-tagged male Pearly-eyed Thrashers studied from January to November 2003 in the Icaos Valley of the Luquillo Experimental Forest, Puerto Rico.

Male	Date of capture	Radiotracking (months)		# fixes	Mobility (m/h)	
		Breeding	Postbreeding		Breeding	Postbreeding
M1	23 April 2003	-	3.9	27	-	138.9
M2	23 January 2003	5.3	-	48	101.1	-
M3	30 May 2003	-	5.1	33	-	65.2
M4	6 May 2003	2.3	2.3	63	27.8	52.1
M5	6 June 2003	-	5.5	50	-	62.8
M6	21 January 2003	1.9	1.2	26	29.9	21.9
M7	23 April 2003	2	4.9	42	25.1	59.5
M8	19 February 2003	4	1.1	47	36.5	27.5
M9	5 March 2003	1.8	3.5	42	30.6	44.4
M10	2 June 2003	-	3.7	32	-	9.3

March to May and then declined (Fig. 2). Sierra palm showed the highest density of ripe fruits (>95% of the total of sample) in each month sampled. Ripe fruits of other plant species, including *Marcavia sintenisii*, *Schefflera morototoni*, *Miconia* sp., *Psychotria berteriana*, and *Cecropia scheberiana*, were present, but were less abundant. Overall, neither breeding period home range size and ripe fruit density (Spearman, $r_s = -0.20$, $df = 20$, $P = 0.39$) nor core area size and ripe fruit density (Spearman, $r_s = -0.34$, $df = 20$, $P = 0.12$) was correlated with ripe fruit density.

Home ranges and core areas between reproductive and post-reproductive seasons. All five radio-tagged male thrashers followed throughout the breeding and post-breeding periods showed changes in areas used between periods (Table 2). For example, home range sizes were larger during the post-breeding period (median = 17.9, range = 0.5–178.7 ha) than during the breeding period (median = 2.1, range = 1.3–7.7 ha; Mann-Whitney test, $U = 31$, $P = 0.049$).

Post-breeding core areas were larger (median = 1.38, range = 0.06–3.17 ha) than the breeding core areas (median = 0.23, range

= 0.2–0.34 ha; Mann-Whitney test, $U = 168$, $P = 0.08$). During the breeding season, all males showed more restricted movements around the nesting site. However, no significant differences in mobility (m/h) occurred between reproductive and post-reproductive periods ($t = -1.22$, $df = 9$, $P = 0.25$). Examination of male movements within their home ranges and core areas in the breeding and post-breeding periods indicates that the males concentrated almost all their activities around their nesting sites. For instance, during the breeding season the nest box was included within the home ranges and core areas for all males observed during that period ($n = 6$). Similarly, in the post-breeding period, most nest boxes (90 % of the total) were located within the male core areas.

Spatial distribution and overlap. In the breeding period, three of six radio-tagged males exhibited movements in two distinct areas (Fig. 3). However, of these three males, only M8 had separate home ranges in which both portions were exclusive of neighbors, while M7 overlapped with M9 in both portions (only in June; Minta's index = 0.38), and M2's home range entirely overlapped the M6 home range

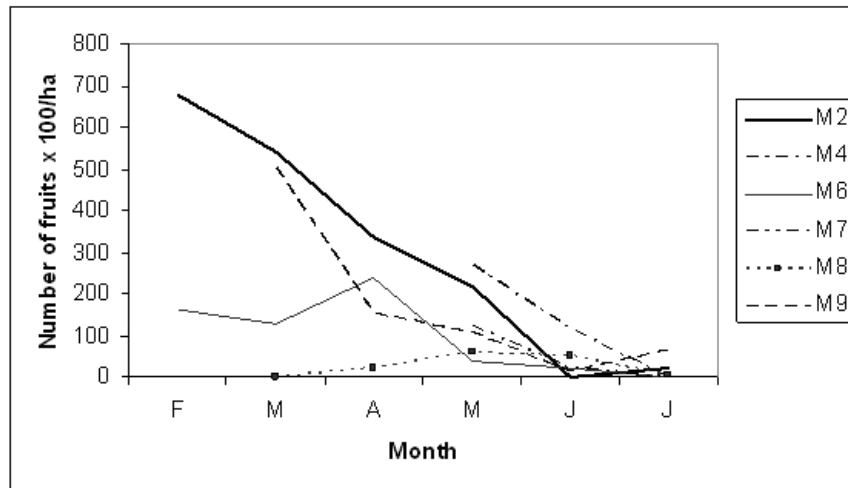


FIG. 2. Densities of ripe fruits (number of fruits/ha) around nesting boxes used by six radio-tagged male Pearly-eyed Thrashers from February to July 2003 in the Icacos Valley of the Luquillo Experimental Forest, Puerto Rico. Letter M and number indicate each individual male.

in one portion, but the other portion was exclusive of other males. Only males M8 and M4 had breeding home ranges that were exclusive of other males. After breeding, almost all males (90% of the total) expanded their home range areas resulting in overlap (range of Minta's index of 0.01–0.64) among home ranges of neighboring males (Fig. 4). In contrast to home ranges, core areas of neighboring males did not overlap and were used exclusively by each male in both the breeding and post-breeding periods. For each male, core areas varied little in location between breeding and post-breeding periods as evidenced by the relatively high overlap between the two seasons (among males, average Minta's index = 0.44 ± 0.08).

Breeding season, fruit abundance, and rainfall. Thrashers bred between January and July 2003 (Fig. 5a). The first peak of breeding occurred during the latter half of March when there was a relatively high number of fruiting sierra palms (Fig. 5b). A second breeding peak occurred during the latter half of May,

when the abundance of sierra palm fruit was lower (Figs. 5a, b). Both March and May were relatively dry (Fig. 5c). In contrast, April was a relatively wet month with a high abundance of fruiting palm trees. In April, three and four nests with eggs were found during the first and second biweekly sampling periods, respectively (Fig. 5a). The abundance of fruiting sierra palms was relatively high from January to April, but during the subsequent two months, abundance was lower. No fruiting palms were found from July to December 2003 (Fig. 5b). The number of nests with eggs increased with the abundance of fruiting sierra palms (Spearman, $r_s = 0.71$, $df = 11$, $P = 0.009$). However, there was no significant correlation between the abundance of fruiting sierra palms and total monthly rainfall (Spearman, $r_s = -0.08$, $df = 11$, $P = 0.8$).

DISCUSSION

The occurrence of larger male home range sizes during the egg stage than during the nestling or fledgling stages may in part be a

TABLE 2. Home range (95% adaptive kernel), core area (50% adaptive kernel), and number of telemetry fixes for 10 radio-tagged male Pearly-eyed Thrashers studied from January to November 2003 in the Icos Valley of the Luquillo Experimental Forest, Puerto Rico.

Male	Breeding			Postbreeding		
	Home range (ha)	Core area (ha)	# fixes	Home range (ha)	Core area (ha)	# fixes
M1	-	-	-	17.9	1.48	41
M2	7.7	0.34	211	-	-	-
M3	-	-	-	141.7	3.17	65
M4	2.2	0.19	101	9.9	1.69	65
M5	-	-	-	178.7	1.38	95
M6	1.9	0.13	127	0.5	0.06	24
M7	1.8	0.2	121	76	0.73	68
M8	4.3	0.3	244	2.8	0.74	24
M9	1.3	0.26	134	3.9	0.54	55
M10	-	-	-	26.2	2.48	58

strategy to protect food sources in advance of the latter two stages. This was supported by our observations that males' movements were concentrated along the home range boundaries presumably to evict intruding males. Breeders (both sexes) are known to spend much of their time disputing territorial boundaries during the early months of breeding, often causing injury and even death of the contenders (WJA, unpubl.). It is also likely, however, that male home ranges are larger during the egg stage when females are incubating, because males are then freed from mate and nest guarding and can seek opportunities for extra-pair copulations with neighboring females, which have not yet initiated a clutch. In addition, males may need to forage over larger areas because fewer plants have fruits to serve as a food source early in the breeding season (Snyder *et al.* 1987, Wunderle 1999).

Following the egg stage, the size of male home ranges and core areas contracted in the nestling stage as observed in other passerines (Odum & Kuenzler 1955, Möller 1990). This reduction in size may be attributable to a change in the male's behavior from wandering widely while the female incubates to feeding

nestlings. Although the male's contribution to nestling care generally is not as great as that of the female, males can make as many as half of the total nest visits to feed nestlings (WJA, unpubl.). In addition, the reduced area used by the male during the nestling stage observed in our study suggests that food supplies, which were protected by the male during the egg stage, were more than adequate for males to provision nestlings and themselves. Both sexes switch to a higher protein diet of mostly, animal prey during the chick-rearing stage when invertebrate and vertebrate prey items are abundant in close proximity to thrasher nests (Arendt 2006). Foraging within close proximity of the nest site at this stage by both members of the pair may have contributed to sexual dimorphism in bill size, a form of character displacement, which may have evolved to allow the sexes to exploit different-size food items thereby reducing competition (Arendt 2006).

Once nestlings fledged, male core areas increased in size, likely due to greater movements by males to obtain food for fledglings, especially given that fruit abundance declined in the vicinity of the nest during this stage. For example, after breeding in August 1982,

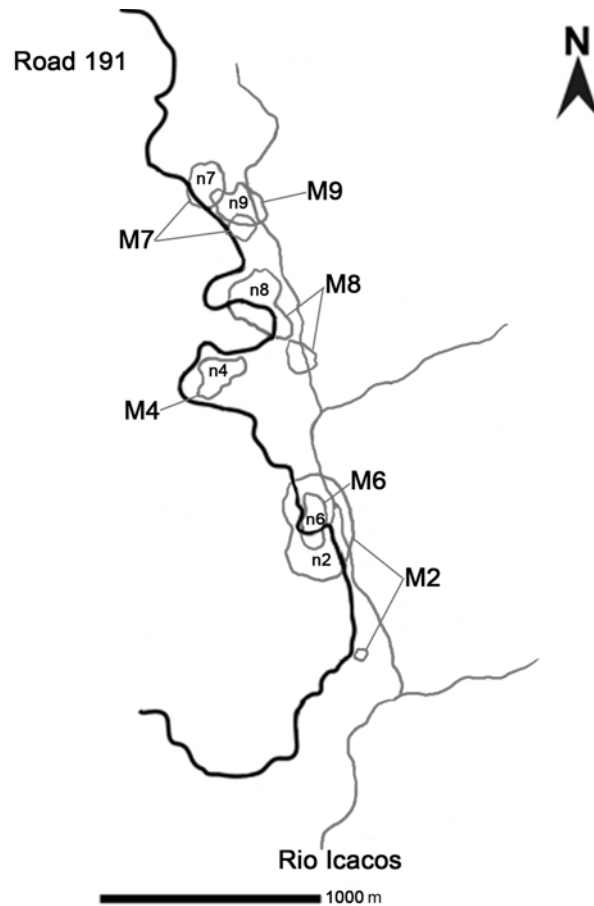


FIG. 3. Locations of 95% adaptive kernel home ranges during the breeding period (January-July 2003) of six male Pearly-eyed Thrashers determined by radio telemetry in the Icacos Valley of the Luquillo Experimental Forest, Puerto Rico. Letter M and numbers indicate each individual male. Letter n and numbers indicate locations of nest boxes for each male.

male and female thrashers were observed flying c. 600 m to feed with other thrashers ($n \approx 15$) on fruits of a large *Dacryodes excelsa* tree (WJA, pers. observ.). While in the fruiting tree there were no signs of aggression among the foragers. Also, as fledglings wander, males may increase their core areas to provide them with food and defense against intruding thrashers and other predators as noted in other passerines (Møller 1990, Dykstra *et al.* 2001).

During the breeding and post-breeding periods, nine of 10 nest boxes were included in the male home ranges and core areas, indicating high fidelity to a specific nest site. Long-term studies of thrashers here have shown high fidelity by males (92%) for nest boxes in subsequent years, and experiments with mounted thrashers used as “intruders” at nest boxes confirmed that both sexes defend their nest boxes during the non-breeding period (Arendt 2006). High site fidelity shown

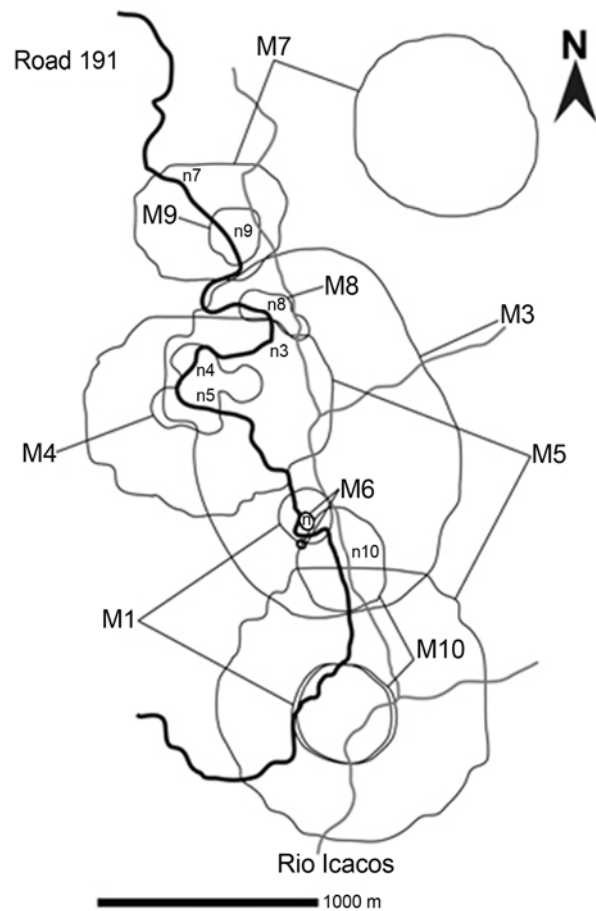


FIG. 4. Locations of the 95% adaptive kernel home ranges during the post-breeding period (March–November 2003) of nine male Pearly-eyed Thrashers determined by radio telemetry in the Icacos Valley of the Luquillo Experimental Forest, Puerto Rico. Letter M and numbers indicate each individual male. Letter n and numbers indicate locations of nest boxes for each male.

by males (and females) in this population results from the need to defend nest boxes and adequate breeding cavities, which are limited in availability and are critical to nest success under the wet conditions of the palo colorado forest. Similarly, other studies of secondary cavity nesters have also reported high rates of nest-cavity fidelity usually related to scarcity of natural cavities (Snyder *et al.* 1987, Waltman & Beissinger 1992, Berkunsky & Reboreda 2009). In the drier lowlands, Pearly-

eyed Thrashers use open nests (Arendt 2004) and there we expect that thrashers would show less fidelity to their specific nest sites, especially given that open nests may not be re-used in subsequent breeding seasons.

A significant finding of this study is that the male home range sizes during post-breeding period were larger than the sizes of home ranges during the breeding period, and unlike the breeding period, there was overlap across home ranges of neighboring post-breeding

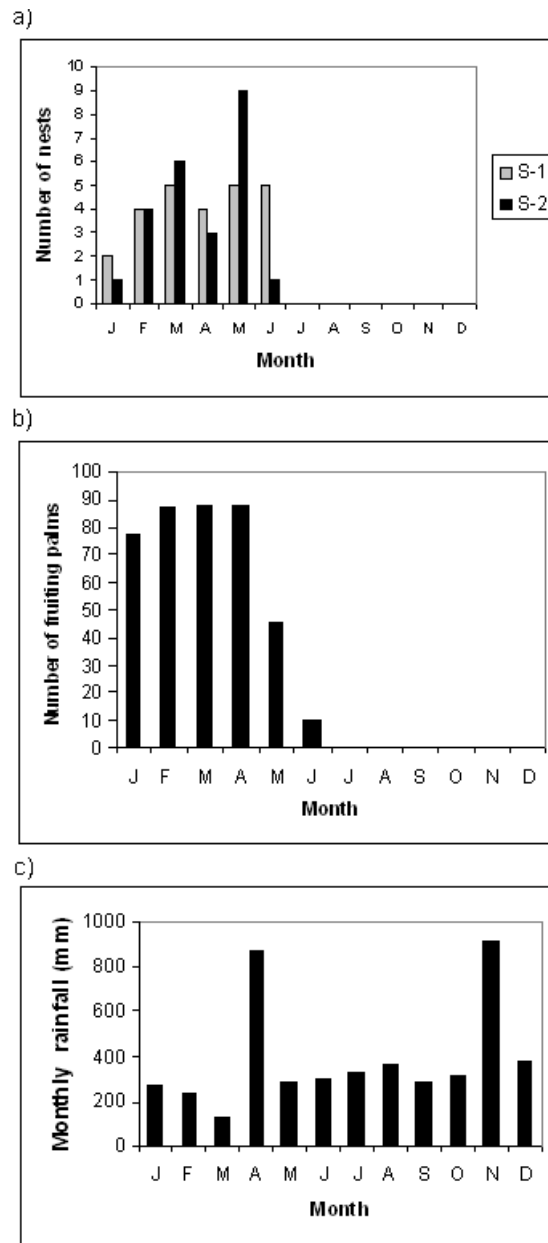


FIG. 5. Chronology of nesting, fruit abundance, and rainfall. (a) Number of active nests with at least one Pearly-eyed Thrasher egg based on biweekly sampling of 50 nest boxes during 2003 in the Icacos Valley, Luquillo Experimental Forest, Puerto Rico. S1 = first biweekly sampling period, S2 = second biweekly sampling period 2; (b) number of fruiting sierra palms along two trails located 1.5 km from the nesting study site in the Icacos Valley; (c) monthly rainfall (mm) at East Peak in 2003, located c. 3 km from nesting study site.

males. We presume that the increase in male thrasher post-breeding wandering was related to an increase in foraging in response to the decrease in palm fruit, which decreased in abundance during the breeding season. Similarly, other studies in tropical and temperate birds have found that home range sizes were larger after breeding than during the breeding season (Vega-Rivera *et al.* 2003, Garza *et al.* 2005, Wood *et al.* 2008).

The extensive breeding season (January–June) for Pearly-eyed Thrashers in this study was similar to that reported by Arendt (2000, 2006). The main breeding peaks occurred in the third and fourth weeks of March and May, respectively. Similarly, Arendt (2006) reported a breeding peak between April–March and May–June for the period 1979–2000, with little variation among years, with the exception of 2–3 breeding seasons following major hurricanes (Arendt 2006). The thrasher breeding season coincides with the availability of sierra palm fruit which, although variable, usually extends from October to May, with a peak in February (Bannister 1970, Wunderle 1999, Thompson-Baranello 2000).

Although we noted change in home ranges of post-breeding males, we did not see a correlation with food abundance during the breeding season. As opportunistic omnivores, breeding thrashers faced with low fruit abundance might concentrate their foraging searches on large insects, frogs, and lizards, without significantly changing the size of their home range. Alternatively, it is possible that our sampling design was inadequate to accurately measure the density of fruit in the thrasher home ranges and core areas. Furthermore, had we experimentally reduced the fruit supply in the home ranges or core areas we might have seen an increase in the size of thrasher home ranges and core areas as found in experimental reduction of food resources in territories of several temperate zone bird species (Hixon *et al.* 1983, Enoksson & Nis-

son 1983, Wasserman 1983, Eberhard & Ewald 1994). Food abundance alone, however, is probably not the only factor affecting home range size as population density is also a factor that can constrain the expansion of an individual's home range (Maher & Lott 2000). Therefore, expansion of a male thrasher's home range or territory in response to low fruit abundance may be constrained by the high density of territorial thrashers in this population (Arendt 2006). Thus it is possible that the thrasher's high population density in the palo colorado forest (Arendt 2006) constrains a male's ability to increase its foraging area while breeding in response to fluctuations in fruit availability.

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REFERENCES

- Arendt, W. J. 1985a. *Philornis* ectoparasitism of Pearly-eyed Thrashers. I. Impact on growth and development of nestlings. *Auk* 102: 270–280.
- Arendt, W. J. 1985b. *Philornis* ectoparasitism of Pearly-eyed Thrashers. II. Effects on adults and reproduction. *Auk* 102: 281–292.
- Arendt, W. J. 1993. The Pearly-eyed Thrasher: Distribution, ecology, and life-history strategy of an avian super-tramp. Ph.D. diss., Univ. of Wisconsin, Madison, Wisconsin.

- Arendt, W. J. 2000. Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery. *Ornitol. Neotrop.* 11: 13–63.
- Arendt, W. J. 2004. Open-and cavity-nesting traits merge in the evolution of the pearly-eyed thrasher (*Margarops fuscatus*). *Ornitol. Neotrop.* 15 (Suppl.): 455–465.
- Arendt, W. J. 2006. Adaptations of an avian super-tramp: distribution, ecology, and life-history strategy of the Pearly-eyed Thrasher (*Margarops fuscatus*). Gen. Tech. Rep. IITF-GTR-27. U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, San Juan, Puerto Rico.
- Bannister, B. A. 1970. Ecological life cycle of *Euterpe globosa* Gaerth. Pp B299–B323 in Odum, H. T., & R. F. Pigeon (eds.). A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico. Division of Technical Information, U.S. Atomic Energy Commission, Springfield, Virginia.
- Berkunsky, I., & J. C. Reboreda. 2009. Nest-site fidelity and cavity reoccupation by Blue-fronted Parrots *Amazona festiva* in the dry Chaco of Argentina. *Ibis* 151: 145–150.
- Brandt, M. J., & W. Cresswell. 2008. Breeding behaviour, home range and habitat selection in Rock Firefinches *Lagonosticta sanguinodorsalis* in the wet and dry season in central Nigeria. *Ibis* 150: 495–507.
- Dykstra, C. R., J. L. Hays, F. B. Daniels, & M. M. Simon. 2001. Home range and habitat use of suburban Red-shouldered Hawks in southwestern Ohio. *Wilson Bull.* 113: 308–316.
- Eberhard, J. R., & P. W. Ewald. 1994. Food availability, intrusion pressure, and territory size: An experimental study of Anna's Hummingbirds (*Calypte anna*). *Behav. Ecol. Sociobiol.* 34: 11–18.
- Enoksson, B., & S. G. Nilsson. 1983. Territory size and population density in relation to food supply in the Nuthatch *Sitta europaea* (Aves). *J. Anim. Ecol.* 52: 927–935.
- Environmental System & Research Institute (ESRI). 1992. Arc View 3.2 GIS software. Environmental System Research Institute Inc., Redland, California.
- Ewel, J. J., & J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U. S. Virgin Islands. Res. Pap. ITF-18, U.S. Forest Service, Río Piedras, Puerto Rico.
- García-Martinó, A. R., G. S. Warner, F. N. Scatena, & D. L. Civco. 1996. Rainfall, runoff, and elevation relationships in the Luquillo Mountains of Puerto Rico. *Caribb. J. Sci.* 32: 413–424.
- Garza, V., F. Suárez, J. Herranz, J. Traba, E. L. García De La Morena, M. B. Morales, R. González, & M. Castañeda. 2005. Home range, territoriality and habitat selection by the Dupont's Lark *Chersophilus duponti* during the breeding and postbreeding periods. *Ardeola* 52: 133–146.
- Hixon, M. A., F. L. Carpenter, & D. C. Paton. 1983. Territory area, flower density and time budgeting in hummingbirds: An experimental and theoretical analysis. *Am. Nat.* 122: 366–391.
- Kei, J. G., J. A. Baldwin, & C. J. Evans. 1996. CALHOME: A program for estimating animal home ranges. *Wildl. Soc. Bull.* 24: 342–344.
- Krebs, J. R., & N. B. Davies. 1993. An introduction to behavioural ecology. 3rd ed. Blackwell, Oxford, UK.
- Little, E. L., Jr., & F. H. Wadsworth. 1964. Common trees of Puerto Rico and the Virgin Islands. *Agricult. Handbook* 249, U. S. Dep. Agric, Government Printing Office, Washington, D. C.
- Lopes, L. E., & M. A. Marini. 2006. Home range and habitat use by *Suiriri affinis* and *Suiriri isleroum* (Aves: Tyrannidae) in the central Brazilian Cerrado. *Stud. Neotrop. Fauna Environ.* 41: 87–92.
- Maher, C. R., & D. F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. *Am. Midl. Nat.* 143: 1–29.
- Minta, S. C. 1993. Sexual differences in spatio-temporal interaction among badgers. *Oecologia* 96: 402–409.
- Møller, A. O. 1990. Changes in the size of breeding territories in relation to the nestling cycle. *Anim. Behav.* 40: 1070–1079.
- Odum, E. P., & E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. *Auk* 72: 128–137.
- Rappole, J. H., & A. R. Tipton. 1991. New harness design for attachment of radio transmitters to

- small passerines. *J. Field Ornithol.* 62: 335–337.
- Seaman, D. E., & R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators of home-range studies. *Ecology* 77: 2075–2085.
- Snyder, N. F. R., J. W. Wiley, & C. B. Kepler. 1987. The parrots of Luquillo: Natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Camarillo, California.
- Sokal, R. R., & F. J. Rohlf. 1995. *Biometry*. 3rd ed. W. H. Freeman, New York, New York.
- Statsoft. 2000. *STATISTICA* for Windows software. Statsoft, Inc., Tulsa, Oklahoma.
- Stutchbury, B. J. M., & E. S. Morton. 2001. *Behavioral ecology of tropical birds*. Academic Press, San Diego, California.
- Thompson-Baranello, J. J. 2000. Resource and population modeling of the Puerto Rican Parrot (*Amazona vittata*). M.S. thesis, Univ. of Puerto Rico, Río Piedras, Puerto Rico.
- Vega-Rivera, J. H., W. J. McShea, & J. H. Rappole. 2003. Comparison of breeding and post-breeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*). *Auk* 120: 632–644.
- Wadsworth, F. H. 1951. Forest management in the Luquillo Mountains. I. The setting. *Caribb. For.* 12: 93–114.
- Waltman, J. R., & S. R. Beissinger. 1992. Breeding behavior of the Green-rumped Parrotlet. *Wilson Bull.* 104: 65–84.
- Wasserman, F. E. 1983. Territories of Rufous-sided Towhees contain more than minimal food resources. *Wilson Bull.* 95: 664–667.
- White, G. C., & R. A. Garrot. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego, California.
- Wood, D. R., F. J. Vilella, & L. W. Burger, Jr. 2008. Red-cockaded Woodpecker home range use and macrohabitat selection in a loblolly-shortleaf pine forest. *Wilson J. Ornithol.* 120: 793–800.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70: 164–168.
- Wunderle, J. M., Jr. 1999. Pre- and post-hurricane fruit availability: implications for Puerto Rican Parrots in the Luquillo Mountains. *Caribb. J. Sci.* 35: 249–264.

