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SPATIAL DYNAMICS OF THE RED-TAILED HAWK IN THE LUQUILLO MOUNTAINS OF PUERTO RICO

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ABSTRACT.—The Red-tailed Hawk (*Buteo jamaicensis*) is a top predator of upland ecosystems in the Greater Antilles. Little information exists on the ecology of the insular forms of this widely distributed species. We studied movements and resource use of the Red-tailed Hawk from 2000 to 2002 in the montane forests of northeastern Puerto Rico. We captured 32 and used 21 radio-marked Red-tailed Hawks to delineate home range, core area shifts, and macrohabitat use in the Luquillo Mountains. Red-tailed Hawks in the Luquillo Mountains frequently perched near the top of canopy emergent trees and were characterized by wide-ranging capabilities and extensive spatial overlap. Home range size averaged 5,022.6 ± 832.1 ha (305–11,288 ha) and core areas averaged 564.8 ± 90.7 ha (150–1,230 ha). This species had large mean weekly movements (3,286.2 ± 348.5 m) and a preference for roadside habitats. Our findings suggest fragmentation of contiguous forest outside protected areas in Puerto Rico may benefit the Red-tailed Hawk. *Received 28 February 2012. Accepted 21 May 2012.*

Oceanic islands are recognized as important repositories of biodiversity and are a critical component of global conservation strategies (Myers et al. 2000, Donázar et al. 2002). Raptors have key roles in the food web of oceanic island ecosystems given the virtual absence of native mammalian predators (Losos and Ricklefs 2009). The Red-tailed Hawk (*Buteo jamaicensis*) is one of the most widespread raptors in the Americas (Johnsgard 1990, Preston and Beane 2009). The eastern Caribbean region of Puerto Rico and the Virgin Islands (east to St. Kitts and Nevis) represents the southeastern limit of the species' geographic range where the non-migratory subspecies *B. jamaicensis jamaicensis* occurs (Raffaele et al. 1998, Preston and Beane 2009). This species is common in coastal and upland forests of Puerto Rico where it coexists with six other resident raptors including the endangered subspecies of the Broad-winged Hawk (*B. platypterus brunnescens*) and Sharp-shinned Hawk (*Accipiter striatus venator*), Turkey Vulture (*Cathartes aura*), Puerto Rican Screech-Owl (*Otus nudipes*), Short-eared Owl (*Asio flammeus*), and American Kestrel (*Falco sparverius*). Little is known about the ecology of the Red-tailed Hawk in its neotropical range, including the Caribbean (Bildstein et al. 1998, Raffaele et al. 1998). A number of studies have examined movements of Red-tailed Hawks in North America, but information on spatial dynamics in neotropical environments is mostly absent. A limited number of studies have been conducted of the Red-tailed Hawk in the Luquillo Mountains, including dispersal of juveniles from natal areas and temporal stability of territories in portions of El Yunque National Forest (Santana and Temple 1988, Boal et al. 2003).

Our objectives were to: (1) quantify Red-tailed Hawk spatial dynamics, and (2) habitat use in the Luquillo Mountains, namely El Yunque National Forest and surrounding private lands. Specifically, we report annual and seasonal home ranges and movements, including shifts in core area use, and provide information on resource selection at the macrohabitat level.

METHODS

Study Area.—Our study was conducted in the Luquillo Mountains of northeastern Puerto Rico including El Yunque National Forest (18° 10′ N, 65° 30′ W) and adjacent private lands (Fig. 1). El Yunque National Forest (El Yunque) encompasses 11,332 ha of subtropical rainforest in northeast Puerto Rico with elevations ranging from 20 to 1,079 m. Mean annual precipitation is 200–500 cm, increasing with elevation. Wind speed at the highest elevations averages 18 km/hr. The vegetation structure of El Yunque reflects forest regeneration following agricultural abandonment and seral responses to hurricane-induced disturbances (Foster et al. 1999).

El Yunque encompasses five life zones characterized by four dominant forest types along an elevation gradient (Wunderle and Arendt 2011). Life zones include: subtropical moist forest (< 200 m asl) dominated by palma real

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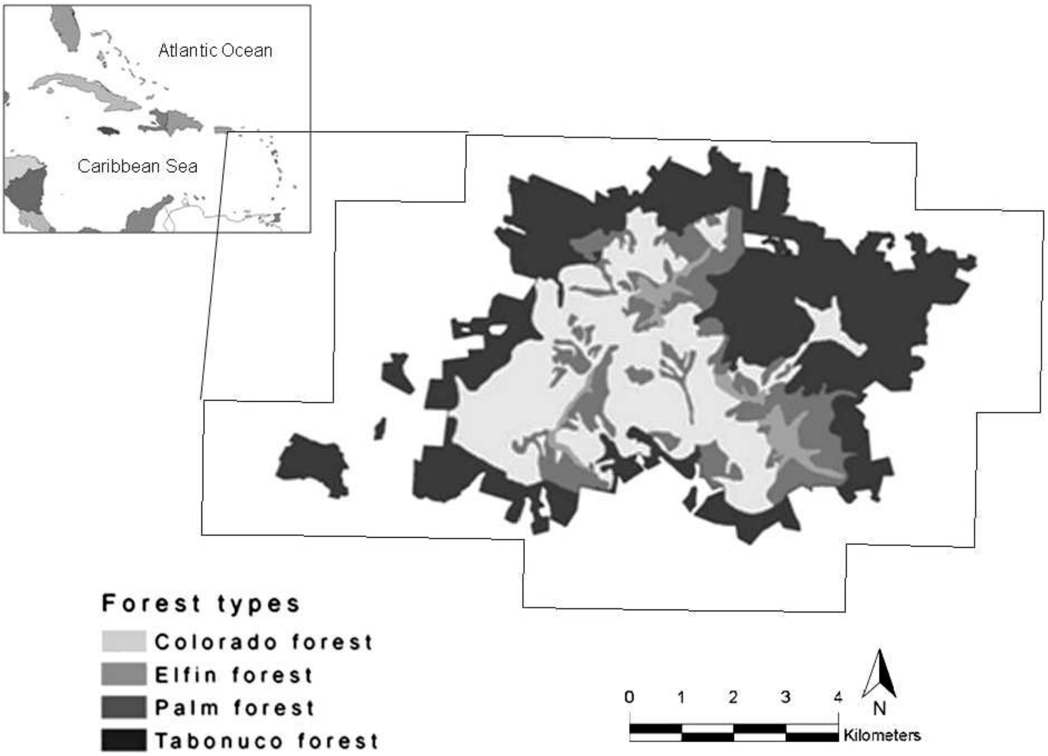

FIG. 1. El Yunque National Forest including reserve proclamation area boundary and forest types (adapted from Wunderle and Arendt 2011).

(*Roystonea borinquena*) and roble blanco (*Tabebuia heterophylla*), subtropical wet forest (200–600 m asl) dominated by tabonuco (*Dacryodes excelsa*), subtropical rain forest (> 450 m asl) dominated by palma de sierra (*Prestoea montana*) on steep slopes, subtropical lower montane wet forest (601–900 m asl) characterized by palo colorado (*Cyrilla racemiflora*), and subtropical lower montane rainforest dominated by dwarf cloud forest on high peaks and ridges (750–1,079 m asl).

Trapping and Radio-tracking.—We trapped hatch-year (HY), after-hatch year (AHY), second-year (SY), and after-second year (ASY) Red-tailed Hawks in the Luquillo Mountains during May 2000–May 2002 using bal-chatri traps and bow nets (Thorstrom 1996, Vekasy et al. 2002). Bow nets were baited with adult Rock Pigeons (*Columba livia*) captured in the center of nearby towns and bal-chatri traps were baited with young Helmeted Guineafowl (*Numida meleagris*) purchased from local suppliers. We placed bal-chatri traps along roads and established three stations for bow-net trapping. Trapping stations were on private lands west of the El Yunque boundaries, in the Mameyes River Valley at 300 m elevation in tabonuco forest, and in the Icacos River Valley at 650 m elevation in palo colorado forest.

We banded all captured hawks after recording mass and body measurements with a USGS band on the right leg and color-coded band on the left leg. We instrumented Red-tailed Hawks with radio transmitters using a Teflon backpack harness designed to break away from a center point over the keel (Vekasy et al. 2002, Klavitter et al. 2003). Radio transmitters (Holohil RI-2CP; Carp, Ontario, Canada) had a life expectancy of ~1.5 years and were programmed with a 24-hr activity switch. The 19-g harness and transmitter packages averaged ~2.2% of body mass. Individuals for which the radio transmitter exceeded 3% of body weight were measured, banded, and released (Vekasy et al. 2002). We conducted telemetry accuracy tests prior to tracking to evaluate the equipment and estimate observer-based location error. We estimated location error by placing radio transmitters on the ground and on canopy-level observation platforms at known distances and azimuths. We measured azimuths to transmitters from telemetry stations with known Universal Transverse Mercator (UTM) coordinates, and compared true azimuths to measured azimuths to calculate mean azimuth error. We used homing whenever possible to obtain visual locations of radio-marked hawks and minimize telemetry error.

We located birds 1–3 times weekly by homing and conducted systematic searches using omni-directional antennas mounted on trucks to locate radio-marked hawks that had ranged outside our search area (Samuel and Fuller 1994). We recorded UTM coordinates when a radio-marked hawk was visually located with a portable Global Positioning System (GPS), recorded compass bearing to the hawk, and measured distance in meters with a range finder. Homing minimized location and azimuth errors from telemetry tests ($\sim 2^{\circ}$) and allowed behavioral observations. We searched for radio-marked hawks during a random time period (0700–1100, 1101–1500, 1501–1900 hrs) every other location to reduce location bias by time of day. We generated UTM coordinates for all locations once fieldwork was completed (White and Garrott 1990, SAS 2001).

Statistical Analyses.—We calculated the minimum number of locations for home ranges to reach an asymptote prior to analysis by randomly selecting locations for six hawks with the greatest number of locations to create home ranges. We plotted each home range area by the number of locations to assess when home range area reached an asymptote. We pooled years for home range estimates due to the relatively small sample size (n = 21) of radio-marked hawks available for analyses.

All spatial analyses were conducted using ArcView 3.2 Animal Movements extension Version 2.04 (Hooge and Eichenlaub 1999). We estimated mean home range, mean weekly movements, and core area changes for the breeding (15 Dec–30 Jun) and non-breeding (1 Jul–14 Dec) seasons. We also estimated maximum distance traveled from trapping station and 50% fixed-kernel breeding season centroids for all individuals during the study. Home ranges were calculated using the fixed-kernel estimator with least squares cross validation (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001). Distances moved from breeding season centroids by paired Red-tailed Hawks were examined to learn if movements increased as energetic demands of nestlings and fledglings increased. We examined distances moved by juveniles to measure dispersal distances following the post-fledgling dependency period. We used mixed-model ANOVA to test whether home range and weekly movements differed between age and gender (SAS Institute 2001). Seasonal core area shifts of Red-tailed Hawks among breeding and non-breeding seasons were calculated using a multiple response permutation procedure (MRPP) in Program BLOSSOM (Cade and Richards 1999).

We used Euclidean Distance analysis to assess Red-tailed Hawk patterns of habitat use (Conner et al. 2003, Bingham and Brennan 2004). We used the Animal Movements extension to generate 1,000 random points within the home range of each hawk then overlaid each home range and random-point home range on the landcover of El Yunque and surrounding lands. We calculated distance from each hawk location and random point to the closest representative of each vegetation type by querying one vegetation type at a time (ESRI 2001). We used MANOVA to test differences in means of the ratio vectors (Conner and Plowman 2001). Paired t-tests were used to test disproportionately-used habitats and a ranking matrix of all possible pair-wise comparisons constructed to rank habitat types. All values are reported as mean $\pm$ SE (range); results were considered significant when $P \leq 0.05$.

RESULTS

We captured 32 Red-tailed Hawks in the Luquillo Mountains during our study of which 27 were radiomarked and 21 were used for analyses (Table 1). A minimum of 25 locations was required for home ranges to reach asymptote. We excluded two outlier individuals from analyses; a juvenile male (RTHA 13) and an unpaired second-year female (RTHA 7). The outlier juvenile male exhibited the greatest home range (28,791 ha), ranging beyond the Luquillo Mountains to the Sierra de Cayey, 40 km to the southwest (Table 1). Red-tailed Hawks were monitored for an average of 5.9 $\pm$ 0.9 months (2–14), yielding an average of 46.7 $\pm$ 5.7 (24–110) locations per individual.

We located hawks perched 62.3% (n = 628) of the time, most frequently near the top of canopy emergent trees. Maximum distance from trapping sites averaged 10,660 $\pm$ 1,291.3 m (range = 6,875–17,490 m). Home range of Red-tailed

TABLE 1. Red-tailed Hawks captured and radiomarked, and home ranges in the Luquillo Mountains, Puerto Rico.

Bird	Capture date	Months tracked	Number of locations	Gender[a]	Age[b]	Home range[c]	Core area[d]
1	6/20/00	8	79	U	AHY	8,635	520
2	6/29/00	2	29	U	SY	2,849	427
4	3/05/01	14	84	F	ASY	1,320	236
5	3/07/01	14	110	M	ASY	1,483	150
6	3/12/01	11	65	M	AHY	2,317	312
7	4/03/01	5	32	F	SY	14,734	1,883
8	5/04/01	8	63	F	AHY	5,724	598
9	5/14/01	12	69	F	AHY	1,408	190
12	7/06/01	7	44	F	HY	1,853	317
13	7/13/01	10	60	M	HY	28,791	3,601
14	7/13/01	7	42	F	HY	7,401	519
15	2/14/02	5	33	F	ASY	8,854	1,226
16	2/20/02	5	50	F	AHY	8,644	925
17	3/12/02	4	37	M	SY	1,312	210
18	3/14/02	3	37	M	ASY	11,288	1,230
19	4/04/02	3	37	F	ASY	7,228	1,047
20	5/15/02	2	37	M	HY	1,660	149
21	5/16/02	2	37	M	HY	532	69
22	5/20/02	2	37	F	HY	571	62
23	5/31/02	2	37	F	HY	305	40
24	5/31/02	2	37	F	HY	362	80

[a] Gender: U = unknown, F = female, M = male.
[b] Age: HY = hatch-year, AHY = after-hatch year, SY = second-year, ASY = after-second year.
[c] Home range: 95% fixed kernel (ha).
[d] Core area: 50% fixed kernel (ha).

Hawks in the Luquillo Mountains averaged 5,022.6 ± 832.1 ha (305–11,288 ha) and core areas averaged 564.8 ± 90.7 ha (150–1,230 ha). The home range of paired Red-tailed Hawks averaged 4,584 ± 420.6 ha (1,312–11,288 ha) for males and 5,219.7 ± 1,395 ha (1,320–8,854 ha) for females. Home range of juvenile males (1,096 ha) was more than twice that of juvenile females (412.6 ha). Breeding season home range of Red-tailed Hawks did not differ by age ($F_{1,5}$ = 0.83, $P = 0.40$) or gender ($F_{1,5} = 0.02$, $P = 0.89$). Red-tailed Hawks in the Luquillo Mountains exhibited high spatial overlap and essentially complete coverage of El Yunque (Fig. 2).

Weekly movements averaged 3,063.1 ± 348.5 m (range = 1,652–5,090 m). Movements of juveniles during the post-fledging dependency period averaged 1,348 ± 264.2 m (Table 2). Red-tailed Hawk weekly movements during the breeding season did not differ by age ($F_{1,6}$ = 0.01, $P = 0.93$) nor gender ($F_{1,6} = 0.46$, P = 0.52). We detected shifts in Red-tailed Hawk core area use (Table 3). The breeding season core area used by one after-second-year female (RTHA 4) decreased 69% ($\delta = -6.53$, $P \leq 0.001$) from 2001 (205 ha) to 2002 (64 ha) and differed from the non-breeding season to the breeding season ($\delta = -8.90$, $P \leq 0.001$). Similarly, one adult male (RTHA 5) shifted core area used from the breeding to non-breeding season ($\delta = -4.81$, $P = 0.002$) and from non-breeding season to breeding season ($\delta = -4.29$, $P = 0.003$). A juvenile male (RTHA 13) exhibited the greatest shift in core area ($\delta = -7.37$, $P \leq 0.001$). Red-tailed Hawks in the Luquillo Mountains exhibited non-random patterns in habitat use (Wilks' λ = 0.1346, $F_{10,6} = 3.86$, $P = 0.05$) and used roadside habitats more than palo colorado forest (P = 0.001), agriculture ($P = 0.002$), rivers (P = 0.002), and pasture ($P = 0.005$). Roadside habitats were used more than wetlands ($P <$ 0.001), urban ($P < 0.001$), sierra palm forest (P = 0.001), and subtropical moist forest ($P = 0.001$).

DISCUSSION

Neotropical buteos generally search from perches and initiate attacks once prey is detected (Panasci and Whitacre 2000). Retention of perch hunting behavior has been documented in other insular forms of the Red-tailed Hawk and closely related species including the Hawaiian Hawk (*B. solitarius*) (Walter 1990, Klavitter et al. 2003). This behavior may be facilitated by the availability of perches in tropical forests (Wunderle 1997).

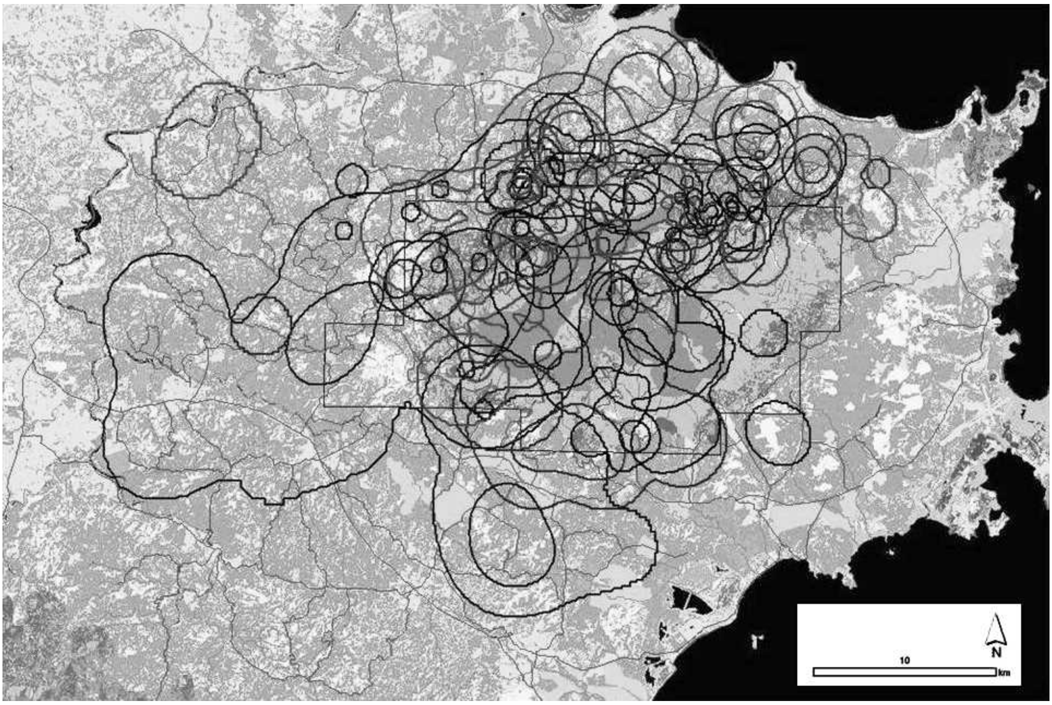

FIG. 2. Composite of 21 Red-tailed Hawk home ranges in the Luquillo Mountains depicting high spatial overlap and virtually complete coverage of El Yunque National Forest, Puerto Rico.

Most visual locations of radio-marked individuals were near the top of canopy emergent trees, suggesting Red-tailed Hawks in the Luquillo Mountains readily use perches with an unobstructed view of their surroundings. This may facilitate territory defense and improved hunting success in the dense forest canopy of El Yunque and the fragmented woodlands in surrounding private lands. However, we repeatedly ($n = 27$) observed Red-tailed Hawks in El Yunque hunting from a soar and making long stoops at Scaly-naped Pigeons (*Patagioenas squamosa*) and small flocks of the critically endangered Puerto Rican Parrot (*Amazona vittata*). White et al. (2005) reported predation by Red-tailed Hawks was one of the primary mortality factors for parrots in El Yunque. We also observed Red-tailed Hawks soaring with rats in their talons in El Yunque and adjacent lands. Previous studies have documented high abundance of columbids and rodents in El Yunque (Zwank and Layton 1989, Rivera-Milán 1992).

Red-tailed Hawks in the Luquillo Mountains are smaller in body size compared to continental conspecifics, reflecting the 'island rule' concept of body size variation in terrestrial vertebrates of oceanic islands (Lomolino 2005, Vilella 2007). Annual home range was large compared to mainland counterparts and other similar-sized raptors of the Americas (Reynolds et al. 1994, Walls et al. 1999). Similarly, breeding season home ranges were larger than reported for continental subspecies (Andersen and Rongstad 1989, Smith et al. 2003). The largest home range (28,791 ha) was exhibited by an unpaired juvenile male, a pattern observed in other conspecifics (Bloom et al. 1993).

Home ranges of Red-tailed Hawks in El Yunque were markedly different from previously reported estimates of territory sizes (Santana and Temple 1988, Boal et al. 2003). Boal et al. (2003) reported Red-tailed Hawk breeding territories in the eastern portions of El Yunque averaged 124.3 ha. The authors also argued there was little temporal change in the spatial distribution of territories and considerable boundary overlap over a 26-year period. Our results indicated Red-tailed Hawks in the Luquillo Mountains use large areas throughout the year. Core areas within Red-tailed Hawk home ranges averaged 564.8 ha, almost five

TABLE 2. Distance from trap sites and weekly movements of Red-tailed Hawks in the Luquillo Mountains, Puerto Rico.

Bird ID	Gender[a]	Age[b]	Max D[c] (m)	B-MWM[d] (m)	NB-MWM[e] (m)	MWM[f] (m)
1	U	AHY	6,875	3,263	3,058	3,481
2	U	AHY	7,348		2,119	2,119
4	F	ASY	8,881	1,595	1,913	1,652
5	M	ASY	6,454	2,048	1,580	2,166
6	M	AHY	9,629	3,730	2,095	2,599
7	F	AHY	17,490	4,573	5,039	4,651
8	F	AHY	10,248	2,906	2,873	2,975
9	F	AHY	16,008	2,327	1,312	2,090
12	F	HY	8,014		3,028	3,258
13	M	HY	39,942	6,791	6,782	6,705
14	F	HY	8,089		3,758	3,628
15	F	ASY	16,576	5,090		5,090
16	F	AHY	8,096	3,754		3,819
17	M	AHY	8,818	2,073		1,954
18	M	ASY	15,308	3,967		3,967
19	F	ASY	12,066	4,085		4,085
20	M	HY	5,179			2,286
21	M	HY	5,276			1,188
22	F	HY	3,194			1,470
23	F	HY	1,959			877
24	F	HY	2,104			919

[a] Gender: U = unknown, F = female, M = male.
[b] Age: HY = hatch-year, AHY = after-hatch year, ASY = after-second year.
[c] Maximum distance from trap site.
[d] Breeding season mean weekly movement.
[e] Non-breeding season mean weekly movement.
[f] Annual mean weekly movement.

times greater than territory sizes reported by Boal et al. (2003), a difference we attribute to the benefits of radiotelemetry. Territory sizes of Broad-winged Hawk pairs measured by spot mapping (74.3 ha) in the Rio Abajo Forest of north-central Puerto Rico were considerably smaller than home range estimates (213.1 ha) obtained from radiotelemetry (Vilella and Hengstenberg 2006). Radiotelemetry generates improved estimates of animal space use compared to visual estimation techniques (i.e., spot mapping) because individual birds can be tracked and observed continuously below or above the canopy over extended periods of time. However, most estimates of home range size for neotropical raptors with few exceptions (Valdez 2009) have relied on territory mapping and ground surveys, not radiotelemetry (Mader

TABLE 3. Distance between centroids and core area shifts from breeding to non-breeding season for six Red-tailed Hawks in El Yunque National Forest, Puerto Rico.

Bird ID	Gender[a]	Age[b]	ST[c]	DIST1[d]	DIST2[e]	DIST3[f]
4	F	ASY	P	422.5	699*	569*
5	M	ASY	P	1,750.7*	1,385*	367
6	M	AHY	P	1,013.1		
8	F	AHY	P	276.8		
9	F	AHY	P		87.3*	
13	M	HY	N		6,265.2*	

[a] Gender: F = female, M = male.
[b] Age: HY = hatch-year, AHY = after-hatch year, ASY = after-second year.
[c] Status: P = paired, N = not paired.
[d] DIST1 = distance (m) 2001 breeding season centroid to 2002 non-breeding season centroid.
[e] DIST2 = distance (m) 2001 non-breeding season centroid to 2002 breeding season centroid.
[f] DIST3 = distance (m) 2001 breeding season to 2002 breeding season centroid.
* Significant core use area shifts estimated by Multi- Response Permutation Procedure.

1982, Thiollay 1989, Panasci and Whitacre 2002). The extensive spatial overlap of home ranges during our study suggests that, while Red-tailed Hawk pairs may be highly territorial in the immediate area around their nest, individuals may move and forage over communally-shared space. This may be a result of reduced competition from the absence of other species of similar-sized raptors (i.e., ecological release) provided by the isolation of an oceanic island setting and the soaring conditions in the Luquillo Mountains (McNab 1994, Vilella 2007).

Home range size in raptors increases with body mass and is influenced by prey composition in the diet (Peery 2000). Moreover, home range size may be a function of prey availability, dominance status, and territory acquisition. Female Red-tailed Hawks in the Luquillo Mountains are considerably larger than males averaging 199 g more, suggesting they may be dominant during interactions. Garcelon (1990) showed larger females displaced smaller males during observed interactions. Dominance and aggression in raptors enhances territory acquisition and access to limited resources in temperate regions (Janes 1994, Shelley et al. 2004).

Studies on resource availability of Red-tailed Hawk prey in El Yunque have not been conducted, but previous research suggests diet varies with elevation. Santana and Temple (1988) reported Red-tailed Hawks in lowland habitats outside El Yunque consumed mostly mammals such as small Indian mongoose (*Herpestes auropunctatue*) and rats (*Rattus* spp.) in contrast to the high elevation rain and cloud forests of El Yunque where they relied on amphibians, reptiles, and birds taken from the canopy. Food delivery rates by parents to nestlings can also be impeded by rainfall and fog, contributing to nest failure at high elevations (Santana and Temple 1988).

We documented substantial home range overlap among radio-marked hawks during our study (Fig. 2). Valdez (2009) reported a slight home range overlap among five species of *Micrastur* forest falcons in the Peruvian Amazon. The Red-shouldered Hawk (*B. lineatus*) exhibited limited amount of overlap between adjacent home ranges in urban and suburban environments (Dykstra et al. 2001). Alternatively, home ranges of nesting Red-tailed Hawks in Wisconsin overlapped extensively (Stout et al. 2006). The extent of spatial overlap exhibited by Red-tailed Hawks in the Luquillo Mountains may be related to high population density, as well as distribution and availability of prey (Zwank and Layton 1989, Rivera-Milán 1992, Boal et al. 2003, Nimitz 2005).

Red-tailed Hawks in the Luquillo Mountains moved considerable distances between weekly locations, averaging 3,063 m per movement (Table 2). Paired females had slightly greater weekly movements compared to paired males and may have been related to dominance status. Unpaired individuals of some raptor species exhibit larger home ranges and movement between weekly locations (Bloom et al. 1993). Male juvenile Red-tailed Hawks in our study had larger average mean weekly movements than juvenile females during the post-fledging dependency period. This could be related to earlier flight feather development and active dispersal of juvenile males (Hargis et al. 1994, Marzluff et al. 1997). Radio-marked hawks frequently exhibited long distance flights (4–7 km) within a short-time period ($\leq$4 min) and readily used areas inside and outside El Yunque. This may reflect the soaring conditions in the Luquillo Mountains and the generalist nature of the species (Snyder et al. 1987, Bildstein et al. 1998). We detected shifts in core area use for Red-tailed Hawks within and between years (Table 3). Large range use shifts have been reported for Northern Goshawk (*A. gentilis*) outside the breeding season (Hargis et al. 1994, Drennan and Beier 2003). Resource depression in core areas and habitat alteration can also influence shifts in range use by raptors (Jaksić 1988, Rodríguez-Estrella et al. 1998).

Red-tailed Hawks in El Yunque and surrounding lands were associated with roadside habitats. Roadside vegetation in the Luquillo Mountains is characterized by an open canopy of pioneering tree species (e.g., *Cecropia peltata*) and a sun-tolerant understory dominated by early succession plants and ferns (Lugo and Gucinski 2000). Compared to the surrounding dense forest vegetation, openings along riparian forest and roads in the contiguous forest of El Yunque and fragmented lowlands may facilitate resource acquisition and benefit Red-tailed Hawks (Preston 1990). We frequently observed hawks hunting along rivers, roads, and in pastures. The Red-tailed Hawk is considered a habitat generalist throughout its range; our findings suggest fragmentation of contiguous forest outside protected areas may benefit Red-tailed Hawks. Additional research on

Red-tailed Hawks in the Caribbean will improve our understanding of the ecological role of this upper level predator in the terrestrial ecosystems of the Greater Antilles.

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LITERATURE CITED

ANDERSEN, D. E. AND O. J. RONGSTAD. 1989. Home range estimates of Red-tailed Hawks based on random and systematic locations. Journal of Wildlife Management 53:802–807.

BILDSTEIN, K. L., W. SCHELSKY, J. ZALLES, AND S. ELLIS. 1998. Conservation status of tropical raptors. Journal of Raptor Research 32:3–18.

BINGHAM, R. L. AND L. A. BRENNAN. 2004. Comparison of Type 1 error rates for statistical analysis of resource selection. Journal of Wildlife Management 68:206–212.

BLOOM, P. H., M. D. MCCRARY, AND M. J. GIBSON. 1993. Red-shouldered Hawk home range and habitat use in southern California. Journal of Wildlife Management 57:258–265.

BOAL, C. W., H. A. SNYDER, B. D. BIBLES, AND T. S. ESTABROOK. 2003. Temporal and spatial stability of Red-tailed Hawk territories in the Luquillo Experimental Forest, Puerto Rico. Journal of Raptor Research 37:277–285.

CADE, B. S. AND J. RICHARDS. 1999. User manual for Blossom Statistical Software. USGS, Fort Collins Science Center, Fort Collins, Colorado, USA.

CONNER, L. M. AND B. W. PLOWMAN. 2001. Using Euclidean Distances to assess nonrandom habitat use. Pages 275–290 *in* Radio tracking and animal populations (J. J. Millspaugh and J. M. Marzluff, Editors). Academic Press, San Diego California, USA.

CONNER, L. M., M. D. SMITH, AND L. W. BURGER. 2003. A comparison of distance based and classification based analyses of habitat use. Ecology 84:526–531.

DONÁZAR, J. A., C. J. PALACIOS, L. GANGOSO, O. CEBALLOS, M. J. GONZÁLEZ, AND F. HIRALDO. 2002. Conservation status and limiting factors in the endangered population of Egyptian Vulture (*Neophron percnopterus*) in the Canary Islands. Biological Conservation 107:89–97.

DRENNAN, J. E. AND P. BEIER. 2003. Forest structure and prey abundance in winter habitat of Northern Goshawks. Journal of Wildlife Management 67:177–184.

DYKSTRA, C. R., J. L. HAYS, F. B. DANIEL, AND M. M. SIMON. 2001. Home range and habitat use of suburban Red-shouldered Hawks in southwestern Ohio. Wilson Bulletin 113:308–316.

ESRI. 2001. Getting to know ArcGIS desktop. Environmental Systems Research Institute Inc., Redlands, California, USA.

FOSTER, D. R., M. FLUET, AND E. R. BOOSE. 1999. Human or natural disturbance: landscape scale dynamics of the tropical forests of Puerto Rico. Ecological Applications 9:555–572.

GARCELON, D. K. 1990. Observations of aggressive interactions by Bald Eagles of known age and sex. Condor 92:532–534

HARGIS, C. D., C. MCCARTHY, AND R. D. PERLOFF. 1994. Home ranges and habitats of Northern Goshawks in eastern California. Studies in Avian Biology 16:66–74.

HOOGE, P. N. AND B. EICHENLAUB. 1999. Animal Movements extension for ArcView, Version 2.04. USGS, Alaska Biological Science Center, Anchorage, USA.

JAKSIĆ, F. M. 1988. Trophic structure of some Nearctic, neotropical and Palearctic owl assemblages: potential roles of diet opportunism, interspecific interference, and resource depression. Journal of Raptor Research 22:44–52.

JANES, S. W. 1994. Partial loss of Red-tailed Hawk territories to Swainson's Hawks: relations to habitat. Condor 96:52–57.

JOHNSGARD, P. A. 1990. Hawks, eagles and falcons of North America. Smithsonian Institution Press, Washington, D.C., USA.

KERNOHAN, B. J., R. A. GITZEN, AND J. J. MILLSPAUGH. 2001. Analysis of animal space use and movements. Pages 125–166 *in* Radio tracking and animal populations (J. J. Millspaugh and J. M. Marzluff, Editors). Academic Press, San Diego California, USA.

KLAVITTER, J. L., J. M. MARZLUFF, AND M. S. VEKASY. 2003. Abundance and demography of the Hawaiian Hawk (*Buteo solitarius*): is delisting warranted? Journal of Wildlife Management 67:165–185.

LOMOLINO, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32:1683–1699.

LOSOS, J. B. AND R. E. RICKLEFS. 2009. Adaptation and diversification on islands. Nature 453:830–836.

LUGO, A. E. AND H. GUCINSKI. 2000. Function, effects, and management of forest roads. Forest Ecology and Management 133:249–262.

MADER, W. J. 1982. Ecology and breeding habits of the Savanna Hawk in the Llanos of Venezuela. Condor 84:261–271.

MARZLUFF, J. M., B. A. KIMSEY, L. S. SCHUECK, M. E. MCFADZEN, M. S. VEKASY, AND J. C. BEDNARZ. 1997. The influence of habitat, prey abundance, sex, and breeding success on the ranging behavior of Prairie Falcons. Condor 99:567–584.

McNab, B. K. 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. American Naturalist 144:643–660.

Myers, N., R. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Nimitz, W. F. 2005. Use and movement patterns of the Red-tailed Hawk *Buteo jamaicensis* in occupied Puerto Rican parrot *Amazona vittata* habitat. Thesis. Mississippi State University, Mississippi State, USA.

Panasci, T. and D. Whitacre. 2000. Diet and foraging behavior of nesting Roadside Hawks in Petén, Guatemala. Wilson Bulletin 112:555–558.

Panasci, T. and D. Whitacre. 2002. Roadside Hawk breeding ecology in forest and farming landscapes. Wilson Bulletin 114:114–121.

Peery, M. Z. 2000. Factors affecting interspecies variation in home range size of raptors. Auk 117:511–517.

Preston, C. R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. Condor 92:107–112.

Preston, C. R. and R. D. Beane. 2009. Red-tailed Hawk (*Buteo jamaicensis*). The birds of North America. Number 52.

Raffaele, H., J. W. Wiley, O. H. Garrido, A. Keith, and J. Raffaele. 1998. A guide to the birds of the West Indies. Princeton University Press, Princeton, New Jersey, USA.

Reynolds, R. T., S. M. Joy, and D. G. Leslie. 1994. Nest productivity, fidelity and spacing of Northern Goshawks in northern Arizona. Studies in Avian Biology 16:106–113.

Rivera-Milán, F. F. 1992. Distribution and abundance patterns of columbids in Puerto Rico. Condor 94:224–238.

Rodríguez-Estrella, R., J. A. Donázar, and F. Hiraldo. 1998. Raptors as indicators of environmental change in Baja California Sur, Mexico. Conservation Biology 12:921–925.

Samuel, M. D. and M. R. Fuller. 1994. Wildlife radiotelemetry. Pages 370–418 *in* Research and management techniques for wildlife and habitats (T. A. Bookout, Editor). Fifth Edition. The Wildlife Society, Bethesda, Maryland, USA.

Santana, E. C. and S. A. Temple. 1988. Breeding biology and diet of Red-tailed Hawks in Puerto Rico. Biotropica 20:151–160.

SAS Institute. 2001. SAS/STAT user's guide, Version 8.2. SAS Institute Inc., Cary, North Carolina, USA.

Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Shelley, E. L., M. Y. U. Tanaka, A. R. Ratnathicam, and D. T. Blumstien. 2004. Can Lanchester's laws help explain interspecific dominance in birds? Condor 106:395–400.

Smith, R. N., S. H. Anderson, S. L. Cain, and J. R. Dunk. 2003. Habitat and nest site use by Red-tailed Hawks in northwestern Wyoming. Journal of Raptor Research 37:219–227.

Snyder, N. F. R., J. W. Wiley, and C. B. Kepler. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, California, USA.

Stout, W. E., S. A. Temple, and J. M. Papp. 2006. Landscape correlates of reproductive success for an urban-suburban Red-tailed Hawk population. Journal of Wildlife Management 70:989–997.

Thiollay, J. M. 1989. Censusing of diurnal raptors in a primary rain forest: comparative methods and species detectability. Journal of Raptor Research 23:72–84.

Thorstrom, R. K. 1996. Methods for capturing tropical forest birds of prey. Wildlife Society Bulletin 24:516–520.

Valdez, M. U. 2009. The secretive forest-falcons of Amazonian Peru: windows into their ecology. Dissertation. University of Washington, Seattle, USA.

Vekasy, M. S., J. P. Smith, and L. Carver. 2002. HawkWatch International trapping and banding manual. HawkWatch International, Salt Lake City, Utah, USA.

Vilella, F. J. 2007. Ecography of the Red-tailed Hawk (*Buteo jamaicensis jamaicensis*) in Puerto Rico. Pages 122–133 *in* Neotropical raptors (K. L. Bildstein, D. R. Barbier, and A. Zimmerman, Editors). Raptor Conservation Science Series Number 1. Hawk Mountain Sanctuary, Orwigsburg, Pennsylvania, USA.

Vilella, F. J. and D. W. Hengstenberg. 2006. Broad-winged Hawk movements and habitat use in a moist limestone forest of Puerto Rico. Ornitología Neotropical 17:563–579.

Walls, S. S., S. Manosa, R. M. Fuller, K. H. Hodder, and R. E. Kenward. 1999. Is early dispersal enterprise or exile? Evidence from radio-tagged buzzards. Journal of Avian Biology 30:407–415.

Walter, H. S. 1990. Small viable population: the Red-tailed Hawk of Socorro Island. Conservation Biology 4:441–445.

White, G. C. and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

White, T. H., J. A. Collazo, and F. J. Vilella. 2005. Survival of captive-reared Puerto Rican Parrots released in the Caribbean National Forest. Condor 107:424–432.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.

Wunderle Jr., J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223–235.

Wunderle Jr., J. M. and W. J. Arendt. 2011. Avian studies and research opportunities in the Luquillo Experimental Forest: a tropical rain forest in Puerto Rico. Forest Ecology and Management 262:33–48.

Zwank, P. J. and B. W. Layton. 1989. Black rats as potential Puerto Rican Parrot nest predators. Caribbean Journal of Science 25:13–20.