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Spatial Ecology of Puerto Rican Boas (*Epicrates inornatus*) in a Hurricane Impacted Forest[1]

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ABSTRACT

Spatial ecology of Puerto Rican boas (*Epicrates inornatus*, Boidae) was studied with radiotelemetry in a subtropical wet forest recovering from a major hurricane (7–9 yr previous) when Hurricane Georges struck. Different boas were studied during three periods relative to Hurricane Georges: before only; before and after; and after only. Mean daily movement per month increased throughout the three periods, indicating that the boas moved more after the storm than before. Radio-tagged boas also became more visible to observers after the hurricane. Throughout the three periods, the sexes differed in movements, with males moving greater distances per move and moving more frequently than females. Males showed a bimodal peak of movement during April and June in contrast to the females' July peak. Sexes did not differ in annual home range size, which had a median value of 8.5 ha (range = 2.0–105.5 ha, *N* = 18) for 95 percent adaptive kernal. Females spent more time on or below ground than did males, which were mostly arboreal. Trees used by boas had larger diameters and more vines than random trees. Hurricane winds that strip leaves, vines, and branches from trees may reduce cover for boas and limit access to arboreal sites, at least for several years until succession brings about recovery with increased vine growth. Boas were especially difficult to observe; telemetrically monitored boas were detected visually at an average of only 15 percent of their fix sites, indicating that the species is more abundant than generally perceived.

RESUMEN

La ecología espacial de las boas Puertorriqueñas (*Epicrates inornatus*; Boidae) fue estudiada con radio telemetría en un bosque subtropical lluvioso, en recuperación de un fuerte huracán (7–9 años antes) cuando el Huracán Georges azotó la isla. Varias boas fueron estudiadas durante tres períodos relativos al Huracán Georges: antes, antes y después, y después del huracán. El desplazamiento diario promedio por mes se incrementó a lo largo de los tres períodos, indicando que las boas se desplazaron más después que antes de la tormenta. Las boas con radio transmisor eran más visibles a los observadores después del huracán. El desplazamiento de los sexos difirió a lo largo de los tres períodos, recorriendo los machos mayor distancia por movimiento y desplazándose con mayor frecuencia que las hembras. Los machos mostraron un desplazamiento bimodal, con picos en abril y junio, en contraste de las hembras donde el pico fue en julio. Los sexos no difirieron en el tamaño del territorio, el cual presenta una mediana de 8.5 ha (intervalo = 2.0–105.5 ha, *N* = 18) para el 95 por ciento adaptive kernal. Las hembras pasaron mayor tiempo encima o bajo tierra que los machos, los cuales eran principalmente arbóreos. Los árboles utilizados por las boas tenían un diámetro mayor y más lianas que árboles escogidos al azar. Los vientos huracanados que despojan a los árboles de sus hojas, lianas y ramas, pueden reducir la cobertura de las boas y limitar su acceso a ubicaciones arbóreas al menos por varios años hasta que la sucesión traiga consigo recuperación en incremento del crecimiento de lianas. Las boas estudiadas fueron especialmente difíciles de observar; boas seguidas con telemetría fueron detectadas visualmente en promedio en sólo el 15 por ciento de las veces buscadas, indicando que la especie posiblemente sea más abundante de lo que se percibe.

Key words: *Boidae; disturbance ecology;* Epicrates inornatus*; habitat use; home range; hurricane effects; Puerto Rico; vines.*

TROPICAL CYCLONES OR HURRICANES occur with sufficient frequency in some tropical areas to be major factors in determining the structure and composition of biotic communities (Wadsworth & Englerth 1959, Odum 1970, Walker *et al.* 1991). Although direct effects of hurricanes are often initially evident as mortality resulting from exposure

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to high winds and rainfall, indirect effects may have the longest lasting impacts on populations (reviewed in Walker *et al.* 1991, Wiley & Wunderle 1994). Indirect effects include loss of food supplies or substrates for foraging or resting, as well as the loss of cover for nesting, roosting, or hiding. Animals may respond to these indirect effects by shifting their diet or moving into less damaged locations, habitats, or sites within a habitat. Also, hurricanes can set back plant succession, creating a mosaic of patches at different successional stages. Thus, in regions with frequent hurricanes, natural selection should favor habitat and diet generalists.

A high hurricane frequency is characteristic of Caribbean islands such as Puerto Rico, where a hurricane strikes approximately every ten years (Wadsworth & Englerth 1959), resulting in forests adapted to withstand frequent storms (Odum 1970, Doyle 1981). Within these forests are animals with broad habitat and diet breadths (Reagan & Waide 1996), including the endemic Puerto Rican boa (*Epicrates inornatus*). The boa is widespread in a variety of habitats from sea level to 400 m (Reagan 1984), where its prey includes various invertebrates, lizards, rats, bats, and birds (Reagan 1984, Rodriguez & Reagan 1984, Rodriguez Duran 1996, Wiley 2003). Formerly common (Schwartz & Henderson 1991), the boa is believed to have declined in both population size and distribution during a period of intense deforestation on Puerto Rico in the late 1800s (U.S. Fish and Wildlife Service 1986). This decline and apparent rarity prompted the federal government to list the boa as endangered (Bureau of Sports Fisheries and Wildlife 1973). Recent observations indicate that the species may be more abundant and less endangered than initially thought (Pérez Rivera & Vélez 1978, Pérez Rivera 1979, Reagan 1984, Moreno 1991). The Puerto Rican boa's biology, however, is poorly known, especially its movements, home range characteristics, and habitat use, all of which are important for evaluating the species' status and devising conservation strategies.

Few studies have been conducted on movements and habitat use by Neotropical snakes relative to their diversity, abundance, and ecological importance as predators. A relevant example has come from the work of Tolson (1988) and Chandler and Tolson (1990) on the Virgin Islands boa (*Epicrates monensis granti*), which is related to the Puerto Rican boa. These studies have indicated that closed canopy woodland in which branches of neighboring trees interlock are important habitat requirements for this arboreal species. Such studies are lacking for the Puerto Rican boa, although activity and movements of Puerto Rican boas concentrated around a cave entrance to feed on bats were studied by Puente Rolón (1999). These studies provide valuable comparative information for our radiotelemetry studies on the Puerto Rican boa that were conducted with the objective of describing the boa's (1) movements and home range and (2) habitat use. Our study was initiated in a forest still recovering from Hurricane Hugo (7 yr previous) and was underway when Hurricane Georges struck the forest. These storms enabled us to study the movements, home range, and habitat use of the Puerto Rican boa in a forest during the latter stages of hurricane recovery (7–9 yr) and to document the boa's response to a major hurricane and its aftermath.

METHODS

STUDY SITE.—This study was conducted in the Luquillo Experimental Forest (LEF) of eastern Puerto Rico. The LEF has been classified into four major forest types including tabonuco, colorado, palm, and elfin forest (Wadsworth 1951). These four forest types are generally stratified by elevation. Below 600 m where this study was conducted, is the tabonuco forest named for the predominant tree (*Dacryodes excelsa*). This forest type covers *ca* 70 percent of the LEF and is found within the subtropical wet forest zone (Ewel & Whitmore 1973).

The LEF has a warm and humid subtropical maritime climate (Scatena, http://luq.lternet.edu). Monthly temperatures range from *ca* 23.5°C in January to 27°C during September in the tabonuco forest. The prevailing easterly trade winds drop rain as they rise over the mountains, causing rainfall to increase with elevation and resulting in an average of 3537 mm per year in the lowlands to 4849 mm per year on the mountain peaks. Rainfall occurs in every month, although a drier period typically occurs from February to April.

Hurricanes are the dominant natural disturbance affecting the LEF (Scatena, http://luq.lternet.edu), and approximately once every ten years a hurricane passes sufficiently near the island to cause severe, but localized, damage. On an average of once every 50 to 60 years, hurricanes pass directly over the LEF causing widespread damage. Seven years before initiation of this study, on 18 September 1989, Hurricane Hugo struck the LEF (Scatena & Larsen 1991). During our study, Hurricane Georges struck the LEF on 21 September 1998 with sustained winds of 184 km per hour

(U.S. Geological Service 1999), causing substantial damage to the forest (Ostertag *et al.* 2003). Storm force winds struck the forest for *ca* 26 hours (J. Wunderle, pers. obs.).

METHODS.—Field studies of boas were conducted in the tabonuco forest of the LEF from 8 October 1996 to 9 July 2001. Boas were found incidentally during the daylight and evening hours (1130–2130h) while walking or driving in the forest to sites with telemetrically monitored boas. All boas were captured by hand and subsequently weighed. Snout–vent length (SVL) and total length were measured. Sex was determined by cloacal probing. To enable individual identification of boas not used in the telemetry studies, we injected 70 boas with transponders or pit tags (Avid® microchip identification system) between 9 April 1997 and 7 August 2001 and released them at their capture sites.

TELEMETRY AND MOVEMENTS.—Twenty-four snakes (12 females, 12 males) were monitored using 9 g transmitters (model SI-2T, Holohil Systems, Ltd., Ontario, Canada) operating at frequencies between 164.040 and 164.825 MHz. Transmitters were surgically implanted into the body cavity by a veterinarian following the procedures of Reinert and Cundall (1982). Following surgery, snakes were held for two weeks before release. Once released at the capture site, snake positions were located using a handheld 3-element Yagi antenna and a Falcon Five® receiver or a Wildlife Materials® TRX-2000S receiver. Snakes located with telemetry were often not visible, but snake locations were verified to within an approximate area of 2 m^2 projected on the ground by circling the site and taking additional telemetry readings to verify the boa's position. Observations of transmitter-bearing boas at night were facilitated by use of a handheld spotlight.

Twenty-four snakes were relocated with telemetry (designated as a fix) at an average interval of 4.3 days (range = 3.6–5.6 d). Telemetrically tracked snakes were found at least once during the day (1130–1830h) and again during the night (1831–2130h) at least twice weekly. Most day and night fixes were obtained on separate days, but when day and night fixes occurred on the same day, random elimination of one of the fixes from analyses was done to ensure that all fixes occurred on separate days. Inclement weather and difficulties in locating some individuals made it impossible to locate snakes at fixed intervals. With the exception of snakes that died during the study, snakes were followed for periods of approximately one year (345–465 d; Table 1).

Once a snake was located, data on date, time, weather, snake location (tree, ground/underground, or other), visibility of the snake (visible vs. not visible), and mobility (immobile vs. moving) were recorded. Finally, each snake location was also noted on a field sketch map and marked with flagging for later determination of geographic coordinates.

Geographic coordinates for all snake locations were obtained with a global positioning system (GPS) using a Trimble GPS Pathfinder® Pro XRS receiver with an accuracy of ±1 m. The coordinates of all snake fixes were plotted on maps with Trimble Pathfinder Office software and used to determine distance between fix sites.

We calculated several different movement indices. Total distance moved was calculated by summing the linear distances between successive relocation sites. Mean daily movement per fix was calculated by taking the mean of each linear distance between successive fixes divided by the number of days between the two fixes. Mean daily movement per move was first calculated by determining the linear distance between successive fixes in which the snake moved and dividing each by the number of days between the two fixes and then determining the mean of these values. These measures are minima and dependent on the frequency of relocation; however, because our relocations were frequent and consistent, we believe this was not a problem.

As a measure of minimum immobility time, we calculated the mean number of days between fixes in which no movement between fixes (>5 m) was detected. Preliminary studies in which boa movements were monitored daily indicated that the snakes did not make brief movements (>5 m) and then return to the preceding fix site within a few days (3–7 d). Thus, it is unlikely that the boas made movements that were undetected within our sampling interval of three to six days between fixes.

Home range, defined as the area to which an animal normally confines its movements (Burt 1943), was described with both the minimum convex polygon (Southwood 1966, Jennrich & Turner 1969) and adaptive kernal (Worton 1989) methods. We used the CALHOME program (Kie *et al.* 1996) to determine the shape and size of home ranges (95%) and core areas (50%). Optimal bandwidths for adaptive kernal (henceforth AK) home range calculations were automatically set by the CALHOME program (Kie *et al.* 1996). Minimum convex polygons (henceforth MCP) were calculated without special treatment for outliers and are re-

TABLE 1. *Movement parameters for 18 Puerto Rican boas tracked with radiotelemetry for approximately one year each in the Luquillo Experimental Forest. All terms are defined in the Methods section.*

Snake	SV Length (cm)	Release Date	Days Tracked	No. Fixes	Total Dist. Moved (m)	Mean Daily Move (m/fix)	Mean Daily Move (m/move)	Mean Days Immobile
Females								
S040A	171	15/10/96	386	77	5612	9.7	19.7	10.8
I169A	147	18/3/97	468	96	2578	7.5	14.1	11.1
E465A	115	28/7/97	380	87	2424	8.1	14.3	7.6
M491O	145	28/7/97	345	83	3436	14.1	24.8	10.7
V541A	175	26/1/98	386	95	4189	12.0	23.6	8.3
M586S	163	20/4/98	420	102	4062	10.1	21.5	14.9
B641I	150	20/7/98	380	93	5452	18.9	28.1	8.2
M399A	136	13/4/99	369	88	3535	11.4	21.2	12.6
M069A	168	23/6/99	385	94	3858	3.1	21.6	17.1
Males								
C145A	95	18/3/97	426	76	3402	10.6	15.5	8.5
R235L	128	12/5/97	450	96	6335	17.8	37.0	12.8
R127O	136	12/5/97	462	85	7245	15.9	27.7	8.0
R423O	138	26/1/98	378	104	6598	7.7	35.9	8.8
C614O	148	20/4/98	407	105	6292	6.6	29.4	7.1
B270O	141	23/6/99	407	91	8786	25.9	42.6	10.8
V330R	155	23/6/99	384	97	5806	17.8	27.8	6.7
B350A	136	16/5/00	365	86	4266	15.6	31.9	8.6
S101I	152	31/5/00	404	98	7204	19.2	39.1	11.1

ported with the number of locations to facilitate comparison with earlier studies.

Vegetation characteristics.—Vegetation characteristics were quantified in 16 m diameter circles (0.02 ha) centered on broadleaf trees in which immobile boas were found. Trees and associated vegetation used by boas were compared to randomly selected broadleaf trees and associated vegetation in similar size circles.

Within each 16 m circle, we measured stems of all standing (living and dead) broadleaf trees and saplings greater than or equal to 3 cm diameter measured 1.3 m from the base (DBH). Palms and tree fern stems were measured at the their base. Shrub, palm, and vine density at breast height was estimated along four 8 m transects running in the cardinal directions from the center tree. Understory density was determined by an observer walking along transects and counting all stems (<3 cm) touching the observer's body and outstretched arms at breast height. The contributions of broadleaf shrubs, vines, and palms were recorded separately.

A point quarter method (henceforth PQM) was used to quantify both the distance and size of the nearest broadleaf tree, palm, and free vine (unattached to trunk) to the central tree. Percent canopy cover and ground cover were determined at 2 m intervals along the four 8 m transects radiating in the cardinal directions from the central tree. An observer stood at each point and sighted vertically up (canopy cover) and down (ground cover) through a 4 cm diameter tube and estimated the percent cover of live vegetation.

Species, when known, of the central tree was recorded as well as DBH, tree height, and height to first branch, which were measured with a clinometer. Number of vine stems growing on the central tree was counted. Vines attached to the trunk were counted separately from vines unattached to the trunk. Also, the extent of crown connection of the central tree to the crowns of neighboring trees was estimated on a scale of 1 to 4. A rank of 1 indicated the central tree had a crown fully contiguous (100%) with surrounding crowns; 2 was a crown that was highly contiguous (75%); 3 was a crown that was moderately contiguous (50%); and 4 had little or no continuity (<25%) with neighbors. Site elevation (msl) of the central tree was also determined.

The study was initially designed to sample the first 15 different fixes in which an individual boa occupied a broadleaf tree and a corresponding random broadleaf tree. Each random broadleaf tree (DBH > 10 cm) was selected by moving in a random direction and distance (≤100 m) from each snake tree; however, Hurricane Georges struck before all samples could be completed, resulting in an unbalanced design of random tree sites relative to snake tree sites. The 71 measured random tree sites were dispersed throughout the home ranges of nine boas (4 females; 5 males) for which snake tree samples ($N = 93$) were also obtained. All vegetation measurements were collected before the arrival of Hurricane Georges.

Data Analysis.—Analyses of movement and home range were based on 18 snakes for which we had approximately one year of telemetry data (Table 1). These included seven boas (4 females, 3 males) for which telemetry studies were completed before the arrival of Hurricane Georges (21 September 1998); however, telemetry studies of five boas (3 females, 2 males) were underway when the hurricane struck the LEF and thus enabled both before and after comparisons with the same animals. Finally, movements of six boas (2 females, 4 males) were studied only after the storm. Therefore, different boas were studied in the three different tracking periods relative to the storm: pre-hurricane, hurricane, and post-hurricane. An additional six boas were also studied with radiotelemetry in these periods (pre-hurricane, 3 boas; hurricane, 1 boa; post-hurricane, 2 boas), but due to mortality they were tracked for periods of less than one year.

Statistical analyses followed Sokal and Rohlf (1981), unless otherwise noted. Parametric tests were run on SAS (1999) and nonparametric tests on SYSTAT (SYSTAT 1992). Normality of data was checked using the Shapiro–Wilk statistic, and homogeneity of variances was checked using the Levene F-test. All analyses with proportions were done with and without arcsine transformation. In no cases were conclusions different using the transformation; hence, all results are reported using untransformed data.

Two-factor ANOVAs were performed to determine if mean daily movement per fix, mean daily movement per move, and mean number of days immobile differed between sexes and among boa tracking periods (pre-hurricane, hurricane, post-hurricane). Three-factor ANOVAs were used to determine if proportion of fixes on the ground, proportion of fixes in which boas were observed, and proportion of fixes in which boas were moving differed between sexes, among tracking periods, and between day (1130–1830h) and night (1831–2130h).

Three-factor ANOVAs were used to determine if mean daily movement per month and proportion of fixes on the ground differed between sexes, among tracking periods, and among months. Two-factor ANOVA was used to determine if minimum immobility days varied with sex and month. The factor "time" in the ANOVAs was treated separately as a random or fixed effect and found to have no effect on the conclusions. We report the values as a fixed effect.

Nonparametric tests were used when the data were not normal and variances were not equivalent (Sokal & Rohlf 1981). For example, Mann–Whitney *U*-tests were used to compare median male and female home range sizes based on both 95 and 50 percent AKs. Median AK home ranges sizes (both 95 and 50%) for all boas (males and females) were compared among the pre-hurricane, hurricane, and post-hurricane periods by use of a Kruskal–Wallis test.

Standard deviation (SD) was used to describe variation around a mean and standard error (SE) was used to facilitate comparison between means. In all analyses, a probability of type I error of 0.05 or less was considered significant, but greater values are shown for descriptive purposes.

Equality of vegetation sample variances from boa and random plots was tested with an *F*-test and *t*-tests calculated according to equality or inequality of sample variances. Assumptions of normal distribution were violated for some of the vegetation variables; however, because sample sizes were large, parametric *t*-tests were used. We found that results of the nonparametric Wilcoxon rank sum test were consistent with the *t*-test results and we therefore report only the *t*-test results. Although we report the *P* values for 10 of the 24 different vegetation variables compared between boa and random plots, we also indicate the variables that differ significantly between plots with the Bonferroni correction for multiple comparisons (Miller 1981).

Principal component analysis (PCA) was used to assess vegetation differences between boa plots and random plots. A matrix of all vegetation variables from random circles was inspected to evaluate the strength of Pearson correlations between two vegetation variables. Only vegetation variables with an $r < 0.50$ were used in the PCA. The PCA variables used in the analysis were the variables that had a significant ($P < 0.05$) difference between random and boa plots and include central tree DBH, height, number of free vines, number of attached vines, and canopy continuity, as well as PQM for nearest broadleaf tree distance, PQM for nearest free vine distance, PQM for nearest free vine diameter and understory density, and mean percent canopy cover over the circle.

RESULTS

Characteristics of the snakes.—Radiotelemetry studies of Puerto Rican boas were conducted in the tabonuco forest of the LEF from 8 October 1996 to 9 July 2001. Twenty-four boas (12 females, 12 males) were monitored during this period. Areas used by telemetrically tracked boas ranged in elevation from 65 m (individual B270O) to 438 m (individual S040A). Six boas (3 females, 3 males) died before one year and were excluded from movement and home range calculations, although some yielded sufficient data for other analyses. Mean SVL for the 18 boas used in movement and home range studies (Tables 1 and 2) averaged 144.4 cm (range = 95–175 cm; male $\bar{x}$ = 136.6 cm ± 5.9 SE; female $\bar{x}$ = 152.2 cm ± 6.4 SE).

Reproductive status of the telemetrically monitored boas was known in only a few cases. For example, one monitored female (V541A) was observed copulating in a stream on 6 May 1998, although it was never verified that it actually gave birth. On 15 May 2001, a male (B350A) was found copulating with an unmarked female. Six female boas gave birth during the study with a mean parturition date of 29 September (range = 23 Sept.–7 Oct.). Two of these females carried transmitters and gave birth (young observed) in the field (M586S, 2 Oct. 1998; M069A, 7 Oct. 1999).

Daily movement per fix.—Eighteen boas monitored for approximately one year moved an average of 12.9 m ± 5.7 SD daily between fixes (Table 1). No significant ($F_{1,\,12} = 3.36$, $P = 0.09$) difference in daily movement per fix was found between males ($\bar{x}$ = 15.2 m ± 2.0 SE) and females ($\bar{x}$ = 10.5 m ± 1.5 SE); however, a significant interaction between sex and period was found ($F_{1,\,12} = 7.13$, $P = 0.009$). This interaction indicates that mean daily movement per fix by males was greater than those for females in the pre- and post-hurricane periods (pre-hurricane $\bar{x}$ = 14.8 m ± 2.2 SE vs. $\bar{x}$ = 9.9 m + 1.5 SE; post-hurricane $\bar{x}$ = 19.6 m ± 2.2 SE vs. $\bar{x}$ = 7.3 m ± 4.2 SE), but in the hurricane period males moved less than females ($\bar{x}$ = 7.2 m ± 0.6 SE vs. $\bar{x}$ = 13.7 m ± 2.7 SE).

Although some individuals changed behavior following the hurricane, responses of individual boas to the storm were not consistent. For example,

TABLE 2. *Number of locations and home range sizes (ha) based on 95 percent adaptive kernal (AK), 50 percent adaptive kernal (AK), 95 percent minimum convex polygon (MCP), and 50 percent minimum convex polygon (MCP) calculations for 18 Puerto Rican boas tracked for approximately one year each in the Luquillo Experimental Forest. Details on date of release and number of days followed are summarized in Table 1.*

	Home Range Size (ha)				
Snake	Locations	95% AK	50% AK	95% MCP	50% MCP
Females					
S040A	28	66.8	4.7	44.7	4.2
I169A	19	2.4	0.1	0.7	0.02
E465A	33	2.0	0.1	1.2	0.3
M491O	28	3.8	0.5	1.7	0.3
V541A	40	43.1	2.8	19.0	9.7
M586S	41	17.1	3.2	13.7	8.1
B641I	47	8.4	1.4	5.4	1.6
M399A	25	3.8	0.1	1.8	0.3
M069A	42	6.7	1.0	4.4	1.1
Males					
C145A	44	3.6	0.6	2.6	1.2
R235L	30	8.0	0.3	5.6	2.8
R127O	37	8.6	1.4	5.6	1.9
R423O	44	5.8	0.8	4.9	2.7
C614O	49	11.8	2.2	7.5	2.5
B270O	45	105.5	3.8	68.1	3.8
V330R	54	12.3	1.7	6.2	2.5
B350A	34	9.1	0.9	5.9	1.8
S101I	40	19.7	1.4	12.9	8.5

the median daily movement per fix of the female M586S was significantly (Mann–Whitney U = 820.0, $P = 0.001$) higher after the storm than before (0.0 m/d/fix vs. 7.3 m/d/fix). This response, however, may have been unrelated to the hurricane and was due to changes in movement associated with the birth of young (6 Oct. 1998) shortly after the storm.

DAILY MOVEMENT PER MOVE.—Boas moved an average of 26.4 m ± 8.5 SD daily per move (Table 1). Sexes differed significantly ($F_{1,\ 12} = 10.66$, $P = 0.007$) in average daily movement per move, with males moving greater distances per move than females ($\bar{x} = 31.9$ m ± 2.7 SE vs. $\bar{x} = 21.0$ m ± 1.5 SE). A hurricane effect was not detected as no significant difference in mean daily movement per move was detected among the three periods ($F_{2,\ 12} = 1.78$, $P = 0.21$). Also, no significant interaction ($P > 0.05$) was detected between the study period and sex. Following the hurricane, however, a female (B641I) showed a significant (Mann–Whitney $U = 314.0$, $P = 0.05$) decrease in median daily movement per move (39.8 m before vs. 21.6 m after).

IMMOBILITY.—Boas located by telemetry were immobile much of the time as evident in a mean of 10.2 ± 2.8 SD consecutive days without movement between fixes (Table 1). Sexes differed significantly ($F_{1,\ 12} = 5.09$, $P = 0.04$) in immobility, with females remaining immobile for more days on average than males (11.3 d ± 1.1 SE vs. 9.2 d ± 0.7 SE). No effect of the hurricane was detected ($F_{2,\ 12} = 1.85$, $P = 0.20$) in the minimum number of days a boa was immobile. No significant ($P > 0.05$) interaction was found between study periods and sex.

Twenty boas were detected moving during only an average of 6.0 percent ± 6.0 SD of the fixes, with sexes showing similar values ($\bar{x} = 6.5\%$ ± 1.5 SE, 10 males; $\bar{x} = 5.3\%$ ± 1.0 SE, 10 females; $F_{1,\ 28} = 1.85$, $P = 0.18$). Movement of boas during a fix was observed significantly ($F_{1,\ 28} = 25.23$, $P < 0.001$) more often at night ($\bar{x} = 9.7\%$ ± 1.5 SE) than during daylight hours ($\bar{x} = 2.4\%$ ± 0.4 SE). The hurricane appeared to have no effect on the percentage of fixes in which movement was detected ($F_{2,\ 28} = 1.41$, $P = 0.26$). No significant interactions ($P > 0.05$) were found between sex and time of day or study period, and the three-way interaction was not significant.

MONTHLY MOVEMENT.—Mean daily movement per month varied significantly among months ($F_{11,\ 143} = 2.66$, $P = 0.004$). Sex differences in mean daily

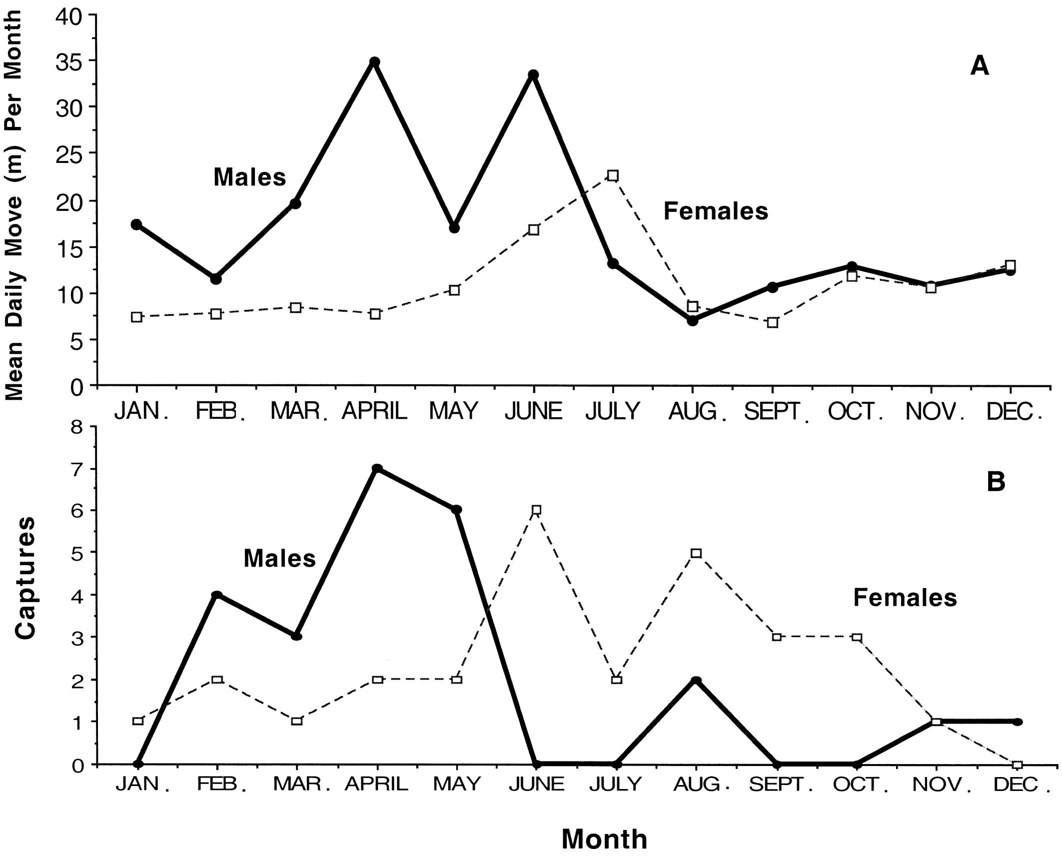

FIGURE 1. Seasonal movement and activity of Puerto Rican boas in the Luquillo Experimental Forest. Upper graph (A) shows the mean daily movement (m) per month for nine male and nine female boas tracked with radiotelemetry for approximately one year in the LEF as summarized in Table 1. Lower graph (B) shows captures of boas on roads in the LEF.

movement per month were significant ($F_{1,\ 143}$ = 11.06, P =0.001), with greater values for males ($\bar{x}$ = 16.7 m/d/mo ± 1.6 SE) than females ($\bar{x}$ = 11.0 m/d/mo ± 0.9 SE). A significant ($F_{11,\ 143}$ =1.92, P = 0.04) interaction between sex and month was detected, with males showing a bimodal peak in monthly movement during April and June in contrast to females in which monthly movement peaked in July (Fig. 1A). These peaks approximately correspond to peaks in monthly captures of males and females on roads in the LEF (Fig. 1B). Capture dates of male and female boas arranged sequentially differed (Runs test Z = 2.96, P = 0.003), with a predominance of male captures early in the year followed by mostly female captures.

The hurricane had a significant effect ($F_{2,\ 143}$ = 3.91, P = 0.02) on monthly movements of boas as evident by a progressive increase in mean monthly movements among periods (pre-hurricane, $\bar{x}$ = 10.7 m/d/mo ± 1.1 SE; hurricane, $\bar{x}$ = 14.9 m/d/mo ± 1.3 SE; post-hurricane, $\bar{x}$ = 16.8 m/d/mo ± 2.2 SE). No significant interaction (P > 0.05) was found between sex and month or sex and study period, and there was no significant three-way interaction.

HOME RANGE.—Cumulative 95 percent AK home range size graphed against cumulative fix or date reached an asymptote within a year of radio-tracking for 15 of 18 boas (Figs. 2 and 3). Despite approximately one year of radio-tracking, an asymptote was never reached for the 95 percent AK home range of the female S040A and two males (B270O and C145A). Home range size was not significantly correlated with the number of days tracked for the 18 boas (95% AK, Spearman r = 0.14, P = 0.57; 95% MCP, Spearman r = 0.18, P = 0.47) or separately for males and females (P

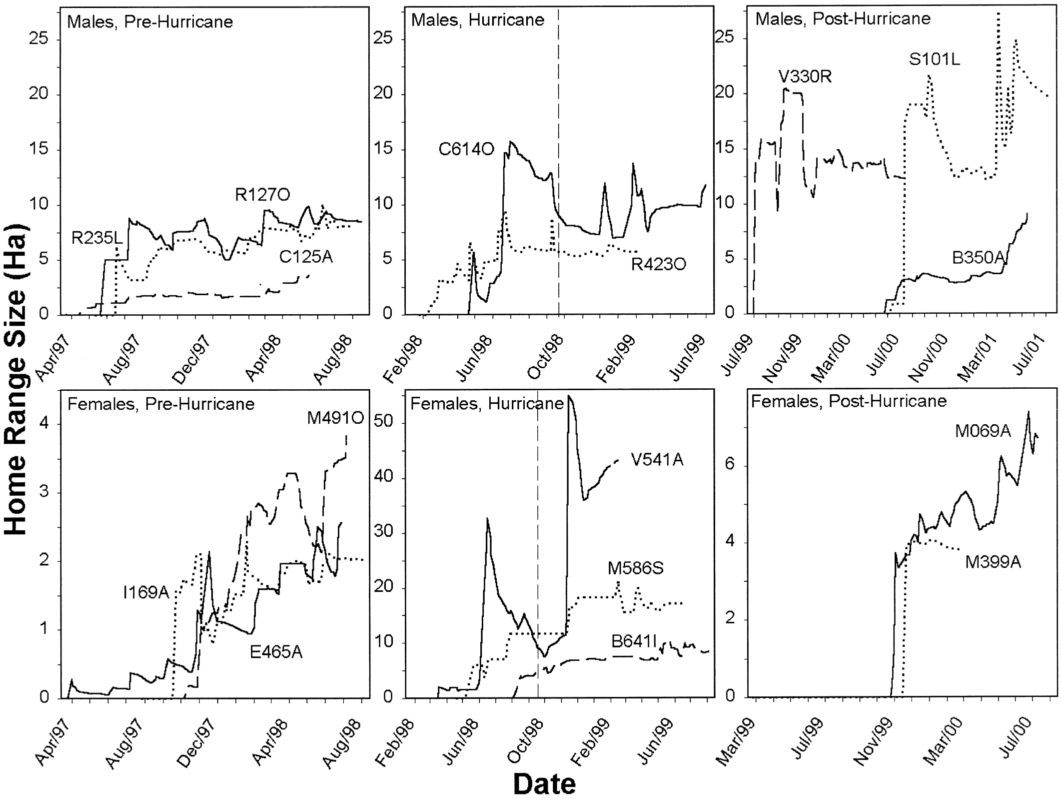

FIGURE 2. Cumulative 95 percent adaptive kernal home range size for 16 Puerto Rican boas followed with radiotelemetry for approximately one year each in the Luquillo Experimental Forest. Upper graphs show males in the pre-hurricane, hurricane, and post-hurricane periods. Lower graphs show females in the same periods, but note different scales on the *y*-axis for each period. Occurrence of Hurricane Georges (21 September 1998) is indicated by the vertical dashed line in the middle panel of both upper and lower graphs. See Table 1 for details on tracking and movements for individual boas.

> 0.05). Home ranges of individual boas shifted considerably in size and geographic position over the approximately one-year period in which snakes were followed. Expansion of home range size was expected to correspond with the increased boa movements documented during the reproductive period and in some cases was observed, especially for males (*e.g.*, C145A, C614O, R423O, R127O, B270O) but less frequently for females (*e.g.*, M069A).

Fidelity to a specific site was usually low, as boas only revisited (*i.e.*, return to <5 m from a site) a small percentage of the sites in the home range during the approximately one year each boa was studied. For example, during movements by nine males, 13 percent of the sites was revisited once, 4 percent of the sites was revisited twice, and 1 percent of the sites was revisited on three occasions. Similarly for females, 16 percent of the sites was revisited once, 6 percent of the sites was revisited twice, 1 percent of the sites was revisited three times, and 2 percent of the sites was revisited four times.

For the two males followed through Hurricane Georges, home range size changed little between pre- and post-hurricane periods (Fig. 2). In contrast, expansion of home range size was evident in two of three females shortly after Hurricane Georges (Fig. 2), although home range size expansion may have been due to increased movements following parturition. One female (M586S) gave birth shortly (2 Oct. 1998) after the hurricane, and a second (V541A) is suspected to have given birth in September or early October 1998.

The median home range size for 18 boas (9 males, 9 females) with approximately one year of telemetry data (Table 2) was 8.5 and 5.6 ha for the 95 and 50 percent AK, respectively, and 5.6 and

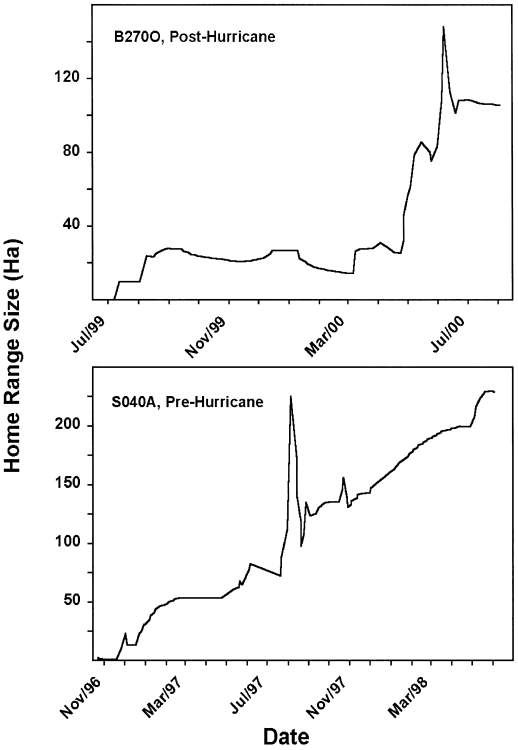

FIGURE 3. Cumulative 95 percent adaptive kernal home range size for two Puerto Rican boas followed with radiotelemetry for approximately one year each in the Luquillo Experimental Forest. Upper graph shows a male (B270O) tracked in the post-hurricane period and lower graph shows a female (S040A) tracked in the pre-hurricane period. See Table 1 for details on tracking and movements for individual boas.

2.2 ha for the 95 and 50 percent MCP home ranges, respectively. Median home range size did not differ significantly between the sexes for either AK calculation (95%, 9.1 ha for males vs. 6.7 ha for females, Mann–Whitney $U = 51.0$, $P = 0.35$; 50%, 1.4 ha for males vs. 1.2 ha for females; Mann–Whitney $U = 46.0$, $P = 0.63$).

A significant positive correlation (Spearman $r = 0.61$, $P = 0.007$) was found between boa SVL and 95 percent AK home range size for the 18 boas; however, the correlation between length and 95 percent AK home range size was not significant in females (Spearman $r = 0.32$, $P = 0.40$) or males (Spearman $r = -0.23$, $P = 0.56$).

Although the trend was for median AK home ranges of all boas to increase during each time period for the 95 percent AK (pre-hurricane, 3.8 ha; hurricane, 11.8 ha; post-hurricane, 10.7 ha) and the 50 percent AK (pre-hurricane, 0.5 ha; hurricane, 1.4; post-hurricane, 1.2 ha), the differences were not significant (for 95%, Kruskal–Wallis = 3.62, $P = 0.16$; for 50% Kruskal-Wallis = 1.88, $P = 0.39$).

BOA HABITAT USE: FIX LOCATIONS.—Although boas were located in a variety of microhabitats in the LEF, the highest mean (±SD) percentage of fixes for 20 telemetrically followed boas occurred in live broadleaf trees (52.8% ± 30.1) followed by ground or belowground sites (34.9% ± 25.9). Other sites less frequently occupied by telemetrically tracked boas included vine enclosed broadleaf trees and shrubs (6.5% ± 8.6); vine tangles (1.7% ± 2.4); sierra palm, *Prestoea acuminata* (1.0% ± 2.1); tree ferns, *Cyathea* spp. (0.8% ± 2.3); bamboo, *Bambusa vulgaris* (0.8% ± 2.9); dead trees (0.7% ± 2.1); stream (0.4% ± 0.8); building (0.3% ± 1.2); and miscellaneous cultivated plants (0.1% ± 0.2).

VISUAL DETECTABILITY.—Even when we were within a few meters of telemetrically monitored boas, it was difficult to observe them; we observed boas ($N = 20$) during an average of only 15.3 percent ± 8.6 SD of the fixes. Visibility of radio-tagged boas at fix sites did not differ significantly ($F_{2,\,28} = 1.05$, $P = 0.31$) between day ($\bar{x} = 14.1\% \pm 2.2$ SE) and night ($\bar{x} = 16.5\ \% \pm 1.7$ SE). Nor were sex differences in visual detection during fixes apparent (male $\bar{x} = 15.9\% \pm 1.9$ SE; female $\bar{x} = 14.6\% \pm 2.0$ SE; $F_{1,\,28} = 0.03$, $P = 0.87$); however, the percentage of fixes in which boas were visible changed significantly ($F_{2,\,28} = 3.62$, $P = 0.04$) among study periods, indicating that radio-tagged boas became more visible to observers after the hurricane. For example, boas became progressively more visible during fixes in the pre-hurricane (10.8% ± 1.5 SE), hurricane (15.6% ± 2.2 SE), and post-hurricane (19.6% ± 2.7 SE) periods. No significant interactions ($P > 0.05$) were detected between sex and time of day or study period, and no three-way interaction was found.

ARBOREAL VS. TERRESTRIAL SITES.—Boas were located both above (arboreal) and on or below ground (terrestrial), with an average of 35.0 percent ± 26.1 SD of the fixes in terrestrial sites for 20 boas. The sexes differed significantly ($F_{1,\,28} = 26.66$, $P < 0.001$), with females spending more time on or below ground ($\bar{x} = 53.9\% \pm 7.9$ SE of fixes) than males ($\bar{x} = 19.5\% \pm 3.3$ SE of fixes). The mean percentage of terrestrial fixes did not vary significantly with time of day (day, $\bar{x} = 33.5\% \pm 5.8$ SE ; night, $\bar{x} = 36.5\% \pm 6.0$ SE; $F_{1,\,28} = 0.25$, $P =$

0.62) or study period (pre-hurricane $\bar{x}$ = 33.4 ± 7.5 SE; hurricane $\bar{x}$ = 44.9 ± 6.6 SE; post-hurricane $\bar{x}$ = 28.1% ± 7.0 SE, $F_{2,\ 28}$ = 1.51, P = 0.24). No significant interactions ($P > 0.05$) were detected between sex and time of day or study period, and no three-way interaction was found; however, of the boas followed in the hurricane period, one female (B641I) in a heavily damaged area showed a significant post-hurricane shift to the ground (35.3% of 17 fixes terrestrial before vs. 85.7% of 77 fixes after; G = 17.0, df = 1, $P <$ 0.001).

Boa use of terrestrial sites on a monthly basis was consistent with the previous terrestrial use findings. Annual variation in monthly use of terrestrial sites was not observed ($F_{11,\ 143}$ = 0.49, P = 0.90); however, sex differences in mean percentage of terrestrial fixes per month were significant ($F_{1,\ 143}$ = 58.5, $P <$ 0.001), and as found previously, females were more frequently encountered in terrestrial sites than males (54.2% ± 3.5 SE fixes/mo vs. 17.4% ± 2.3 SE fixes/mo). Hurricane effects were not apparent in monthly use of terrestrial sites as the mean percentage of terrestrial fixes per month did not vary significantly ($F_{2,\ 143}$ = 0.66, P = 0.52) among the three periods (pre-hurricane, $\bar{x}$ = 35.9% ± 4.1 SE; hurricane $\bar{x}$ = 42.8% ± 4.3 SE; post-hurricane, $\bar{x}$ = 29.5% ± 4.0 SE). No significant interactions ($P > 0.05$) were found between sex and month or study period, and no three-way interaction was evident.

BOA TREES VS. RANDOM TREES.—Broadleaf trees in which boas were located by radiotelemetry differed from randomly selected broadleaf trees in a number of traits (Table 3). For example, trees with boas differed from random trees by having larger diameter trunks (DBH); being taller; having more crown contact with neighboring crowns; being closer to other broadleaf trees; being surrounded by a higher density of understory vegetation; and having a lower percentage canopy cover than random trees. It was vine cover, however, that especially characterized trees used by boas, as these trees had more vines (both attached and unattached to the trunk) and the nearest free vines were closer to the trunk and had larger diameters than vines on randomly selected trees.

Both random and boa trees were ordinated with PCA to assess differences in ten vegetation characteristics between boa and random plots. The first three principal components accounted for 58.1 percent of the variation in trees and associated vegetation (Table 4), with PC1 contributing 26.7 percent, PC2 contributing 19.2 percent, and PC3 contributing 12.1 percent. For PC1, DBH and vine coverage had the highest positive loadings and the most influential negative loadings were canopy continuity score (the inverse of canopy connectedness) and PQM vine distance (nearest distance to vine stem). This indicates that as a tree's DBH and vine coverage increase, the degree of canopy connectedness increases and distance to nearest vine stems decreases. For PC2, understory density, PQM broadleaf tree distance, and number of free vines had high positive loadings and the high negative loadings were mean percent canopy cover and tree height. This component was related to light and spacing. The reduced canopy cover indicates a more open stand in which trees tend to be shorter. Also, a more open canopy implies a greater distance between competing trees, denser understory, and more vine growth. Finally, for PC3, canopy continuity had a high positive loading and mean percent canopy cover had a high negative loading, indicating that this component was related to tree canopy and associated characteristics.

A graph of the first two principal components shows clustering of the random trees with the boa trees dispersed in a semicircle around the random trees (Fig. 4). The boa trees tend to fall to the right of the random trees on PC1 (more vines, larger DBH, and denser understory), although separation along PC2 is less distinct. This graph indicates a difference in vegetation characteristics between random and boa trees and shows that random trees were more homogeneous, at least for the measures used in this study.

DISCUSSION

SEX DIFFERENCES IN MOVEMENT.—Sex differences in movements were detected as found in previous studies (Gibbons & Semlitsch 1987). On both a per move basis (mean daily movement per move) and monthly basis (mean daily movement per month), males moved farther than females and a similar trend was found for mean daily movement per fix. In contrast to males, females were immobile for significantly longer average time periods. The sexes did not differ significantly in home range size (95% AK), although our sample sizes were small (potentially limiting statistical power).

Puerto Rican boa movements were consistent with previous studies in reflecting a seasonal pattern of reproduction, with mating in Caribbean *Epicrates* from January through May (Tolson & Henderson 1993). Within the LEF, mating is be-

TABLE 3. *Mean ± SD of vegetation variables measured in 0.02 ha circular plots centered on broadleaf trees in which Puerto Rican boas were found with radiotelemetry and randomly selected broadleaf trees in the Luquillo Experimental Forest. Measurements were obtained in 93 circular plots at sites used by 9 boas and 71 randomly selected circular plots prior to Hurricane Georges (21 September 1998). Shown are vegetation variables that differed between boa and random plots with* P < 0.05. *With the Bonferroni correction, only the first three variables were statistically significant at* P < 0.05. *The vegetation variables are defined in the Methods section.*

Vegetation Variable	Boa Plot $\bar{x}$ ± SD	Random Plot $\bar{x}$ ± SD	*P*-value
Tree DBH (cm)	52.7 ± 49.8	23.9 ± 20.4	<0.001
Vines attached to trunk	33.0 ± 59.0	3.3 ± 8.4	<0.001
PQM nearest free vine distance (m)	0.9 ± 1.6	2.8 ± 1.8	<0.001
Number of free vines per tree	65.5 ± 120.8	18.1 ± 79.3	0.003
Tree height (m)	16.1 ± 6.9	13.3 ± 4.9	0.005
Understory density (stems <3 cm)	147.5 ± 143.6	95.3 ± 121.7	0.01
Vegetation continuity index	2.7 ± 1.0	3.1 ± 1.0	0.02
PQM nearest free vine DBH (cm)	2.2 ± 1.0	1.9 ± 0.7	0.02
PQM nearest broadleaf tree	2.7 ± 1.0	3.0 ± 0.9	0.03
Percent canopy cover	81.9 ± 12.9	86.2 ± 13.5	0.04

lieved to occur at the beginning of the wet season during April–May (Grant 1932, Reagan 1984), which we confirmed (*e.g.,* copulating pairs on 6 and 15 May). Furthermore, our observations on the birth of young during September–October support an April–May mating period based on a 153- to 176- day gestation period (Huff 1978). Corresponding with this mating period was our finding of an increase in male boa movements from April through June, suggesting that males actively search for females at this time. Active searching by males for more sedentary females is a common courtship tactic, particularly in solitary snakes (Gibbons & Semlitsch 1987). It is less obvious why female movements peaked in July following the male peak, but it may partly represent increased foraging to sustain embryo growth as well as a shift to environments appropriate for gestation and parturition.

The April to July peak in boa movements also approximately corresponded to the period of reproductive activity in some boa prey at the LEF, which may increase prey abundance and vulnerability. For example, juvenile black rats (*Rattus rattus*) are most abundant in the tabonuco forest from April to August (Weinbren *et al.* 1970). Similarly, the peak of avian breeding occurs during March–July (Waide 1996).

Our inability to verify the reproductive status of most females and small sample sizes of telemetrically followed females prevented us from statistically comparing behavior of gravid and non-gravid females. But in general, female boas were immobile for more days and were located more frequently on the ground than males, as might be expected given constraints or requirements of gestation.

Gravid females of *Epicrates* spp. are known to

TABLE 4. *Eigenvectors for the first three principal components from a principal component analysis of ten vegetation variables measured in 71 circular plots (0.02 ha each) centered on random broadleaf trees and 93 circular plots (0.02 ha each) centered on broadleaf trees used by nine Puerto Rican boas tracked with radiotelemetry in the Luquillo Experimental Forest. The vegetation variables are defined in the text of the Methods section.*

Variable	PC1	PC2	PC3
Tree DBH	0.464	−0.195	0.253
Tree height	0.282	−0.383	0.281
Number of free vines	0.426	0.355	−0.183
Vines attached to trunk	0.520	0.126	0.011
Vegetative continuity index	−0.209	0.112	0.590
PQM nearest broadleaf tree	0.022	0.308	−0.356
PQM nearest vine distance	−0.364	0.115	0.080
PQM vine DBH	0.120	−0.328	0.222
Understory density	0.237	0.473	0.189
Percent canopy cover	0.070	−0.471	−0.506
Eigenvalue	2.67	1.92	1.22
Percent of variance accounted for	26.7	19.2	12.1

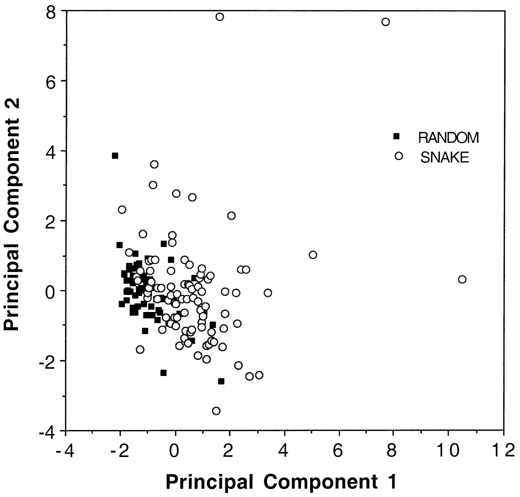

FIGURE 4. Graph of principal component 1 against principal component 2 for Puerto Rican boa tree plots compared with random tree plots measured before Hurricane Georges in the Luquillo Experimental Forest.

use exposed terrestrial debris piles for thermoregulation (Tolson & Henderson 1993) and this may contribute to greater use of ground sites by female boas. Consistent with this was a female (M069A) that showed a marked shift to ground use when gravid (97% of fixes) compared to its non-gravid period (23% of fixes). Less marked was the ground shift made by V641A during the period of its suspected gestation (39% of fixes vs. 22% of fixes); however, a shift to ground sites was not observed in another gravid female (M586S), possibly because about half of its time was spent at ground sites anyway (51% of 39 fixes, gravid vs. 57% of 64 fixes, non-gestation).

Immobility of gravid females was expected due to reduced locomotor performance of gravid snakes, especially before parturition (Seigel *et al.* 1987). Reduction in movement was indeed evident in the minimum immobile periods of 60 and 118 days each documented prior to parturition in the two females of known reproductive status. The female for which parturition was suspected but never verified (V541A) had a minimum immobile period of 9 days just prior to suspected parturition, although a 14-day minimum immobile period also occurred during the predicted gestation period.

Foraging.—Although seasonality of boa movements in the LEF may be mostly attributable to reproductive behavior, the overall patterns of movement likely reflect foraging behavior. Alternation of immobile periods with active movement as observed in this study is consistent with an opportunistic foraging strategy involving both active search and ambush strategies of a generalist predator. We suspect that prey were occasionally ambushed by boas during immobile periods as well as captured while moving (searching?) between sites. Whereas captive juvenile boas are known to actively search for *Anolis* lizards (Bloxam 1981), boas of the size range in our study were believed to be opportunistically preying upon a mix of endothermic prey such as birds, bats, and rats (Reagan 1984, Rodriguez & Reagan 1984, Tolson & Henderson 1993, Wiley 2003). With the exception of a Puerto Rican Bullfinch (*Loxigilla portoricensis*) feather found in a boa fecal pellet, we were unable to verify boa diets in the LEF.

Boa movements elsewhere.—Snakes foraging in productive food patches are expected to have smaller home ranges than those in less productive patches (Stickel & Cope 1947). Consistent with this prediction are the studies of boas at a bat cave in the karst region of north–central Puerto Rico (Puente Rolón 1999) that indicate smaller home range sizes than those in the LEF. Although telemetry fixes were obtained more frequently at the cave site than in the LEF (48 h vs. 4–5 d) and boas were studied for fewer months (10 vs. 12) it is likely that the substantial differences in home range size between the two sites resulted mostly from differences in prey abundance and dispersion. Minimum convex polygon home ranges at the cave site were relatively small (male $\bar{x}$ = 5000 m^2 based on $\bar{x}$ = 66 locations; female $\bar{x}$ = 7890 m^2 based on $\bar{x}$ = 89 locations) compared with the 95 percent MCP obtained in the LEF (male $\bar{x}$ = 133,000 m^2 based on $\bar{x}$ = 42 locations; female $\bar{x}$ = 103,000 m^2 based on $\bar{x}$ = 34 locations). These differences in boa home range size are consistent with an expectation of smaller home ranges associated with a rich food source, represented by abundant bats in the cave, in contrast to the larger home ranges in the LEF where prey are likely more widely dispersed and occur in lower densities.

Habitat use.—As is characteristic of *Epicrates* (Tolson & Henderson 1993), Puerto Rican boas were opportunistic in their use of habitat. The boa was found in a wide array of locations from terrestrial to arboreal sites, with males encountered more frequently in arboreal sites and females more commonly at terrestrial sites. As previously mentioned, thermoregulation requirements of gravid females may contribute to use of exposed terrestrial debris piles. The role of thermoregulation, however, in microhabitat selection is largely unknown, although both sexes were observed basking in both terrestrial and arboreal sites with body temperatures elevated 1–5°C above ambient temperatures (Rogowitz & Wunderle, pers. obs.).

Vine coverage was one of the most distinctive traits of broadleaf trees used by boas, as has been observed in other arboreal snakes (Shine & Fitzgerald 1996, Fitzgerald *et al.* 2002). Vines are important for gaining access to trees from either the ground or from other trees or shrubs and provide dense cover for foraging and resting. Moreover, vines are more abundant on large trees in the LEF (Brokaw *et al.* 2002), which partially explains the presence of boas in trees of larger DBH relative to randomly sampled trees. Also, big trees are likely to provide larger diameter perches used by heavier snakes (Henderson & Winstel 1995). In addition, tree cavities, which may be used by boas for resting or locating prey, are more common and bigger in trees with larger DBHs (Snyder *et al.* 1987). Also, large trees may have bigger crowns, increasing the likelihood of contacting the crowns of neighboring trees and thereby providing the vegetation continuity required for arboreal snake movements in the canopy (Plummer 1981, Tolson 1988, Henderson & Winstel 1995). Rarity of vegetative continuity, including vine coverage, and structural aspects may have limited boa use of palms and tree ferns despite their abundance in the LEF.

Given the importance of vegetative continuity and vine cover for movement of arboreal snakes, prey species should avoid sites with such traits if possible. Indeed, Snow (1976) has suggested that some species of tropical forest birds nest in isolated trees without vines or canopy continuity to avoid nest predators, including snakes. The risk of nesting in snake-accessible sites is evident in Jamaica where parrots nesting in cavities in trees covered with vines or with high canopy connectivity were more likely to fail, due to chick losses, than in cavity trees lacking these traits (Koenig 1999, 2001). The evidence, independent of vegetation traits, strongly suggested to Koenig (1999, 2001) that nestling losses were due to predation by the Jamaican boa (*Epicrates subflavus*), which is further supported by our boa observations.

HURRICANE EFFECTS.—Post-hurricane increases in movement were expected as boas shifted from heavily damaged to less damaged sites in response to changes in foliage cover and prey abundance. Hurricane winds were expected to radically alter the thermal environment for arboreal snakes by defoliating trees while simultaneously removing flowers, fruits, seeds, and substrates required by their prey (reviewed in Wiley & Wunderle 1994). Boa prey, such as birds, may move from heavily damaged sites to less damaged sites after hurricanes. Black rats may have also shifted habitats in response to hurricane damage, as we observed more rats in the LEF for several months after the storm than previously. Therefore, our findings of increased movements of boas over the three study periods, at least on a monthly basis, are consistent with an expectation of greater movement in response to hurricane alterations in cover and prey distributions. Given more boa movement and reduced foliage cover after the hurricane, it was not surprising that telemetrically monitored boas were seen more frequently after than before the storm, potentially increasing their predation risk and exposure to harassment by mobbing birds (Mercado *et al.* 2002).

Although damage to the LEF from Hurricane Georges was extensive and widespread (Ostertag *et al.* 2003), patches of undamaged forest were evident throughout in protected valleys and on leeward slopes after the storm. These undamaged forest patches likely served as important post-hurricane refugia for the boas, but made it difficult for us to quantify overall effects of the storm on individual boas. For example, structural damage and defoliation were highly variable among the home ranges of telemetrically tracked boas followed through the hurricane, which may explain why the responses of individual boas to the hurricane were not consistent. One of our boas apparently died shortly after the hurricane. A male (D566D) was last detected moving ten days after the storm in a heavily damaged area, and no further movement was detected until the transmitter battery died two months later. Increased post-hurricane movement and home range expansion was documented in one female (M586S), although it is likely that the increased movement was in response to behavioral changes associated with parturition 16 days after the storm. Similarly, a post-hurricane increase in home range size for another female (V541A) may have also been related to behavioral changes associated with parturition suspected shortly after the storm (copulation observed, but parturition not documented). Both a decrease in movement and shift from arboreal to terrestrial sites were found in another female (B641I) after the hurricane. Thus, among the individual boas followed through the storm, hurricane effects are suspected in one boa mortality and decreased movement and shift to ground sites by a female, while increased movements or home range expansions by two females were likely a result of behavioral changes related to parturition shortly after the storm.

Hurricanes can have substantial effects on vegetation and forest structure (Walker *et al.* 1991), thereby altering features important for boa habitat use. For example, vines are especially susceptible to hurricane damage, as found in the LEF when 75 percent of 36 tagged *Marcgravia sintenisii* vines were blown out of trees by Hurricane Hugo and subsequently died (Wunderle 1999). In the immediate aftermath of hurricanes, the loss of vines may make many trees inaccessible and less attractive to boas and their prey. Moreover, loss of branches to storm damage greatly reduces the connectivity of canopy trees, further restricting arboreal movements of boas. Thus, restricted access and reduced cover limit the post-hurricane availability of arboreal sites for boas, at least for several years until succession brings about recovery, often with increased vine growth.

POPULATION STATUS.—The 72 Puerto Rican boas captured during this study suggest a larger population of boas in the lowlands of the LEF than expected based on the species' official designation as endangered (Bureau of Sports Fisheries And Wildlife 1973). Much of the boa's apparent rarity undoubtedly relates to observers' difficulties in visually detecting the species in forests. As we found, boas were especially cryptic as evidenced by our failure to visually detect telemetrically tracked boas during an average of 85 percent of our fixes. Given this detection difficulty in forests, it is likely that the boa is more abundant than generally perceived. Indeed, others have questioned the endangered designation for the boa, citing its widespread distribution on the island (Pérez Rivera & Vélez 1978, Pérez Rivera 1979, Reagan 1984, Moreno 1991). Obviously, studies of boa population density are needed to clarify the species' status (Moreno 1991); however, the widespread movements of the boa as documented in their relatively large home ranges and our recapture of only 1 of 70 transponder-bearing individuals, suggest that such density studies will require searches for marked boas over considerable areas (10–100 ha).

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