Caribbean Journal of Science, Vol. 40, No. 3, 343–352, 2004

Foraging Behavior, Home Range, Movements and Activity Patterns of *Epicrates inornatus* (Boidae) at Mata de Plátano Reserve in Arecibo, Puerto Rico

ALBERTO R. PUENTE-ROLÓN AND FERNANDO J. BIRD-PICÓ

[1]*Department of Biology, University of Puerto Rico, Mayagüez, Puerto Rico, corresponding author: albertonski@hotmail.com*

ABSTRACT.—**Observations of foraging behavior of the Puerto Rican boa (*Epicrates inornatus*) were performed at a cave entrance beginning one hour before sunset until one hour after sunrise. Boas captured bats from 1745 h to 0600 h, but most captures were between 1900 and 2400 h. The most common preyed bats were *Erophylla sezekorni*, *Mormoops blainivillii*, *Pteronotus quadridens* and *Monophyllus redmanii*, while *Brachyphylla cavernarum* was rarely caught. The average prey handling time was 12.53 min. The Radiotelemetry was used to determine the home range, activity and movements of *E. inornatus*. Eleven snakes (six females and five males) were fitted with transmitters. Using the minimum convex polygon method, the average home range area for females and males was 7,890 m^2 ± 6614 m^2 and 5,000 m^2 ± 4,102 m^2, respectively. These were not significantly different. Ten of the radio-tracked snakes returned at least twice to the cave. Females were active during 29 ± 7.2% (n = 89) of the observations, and the males were 36 ± 12.5% (n = 66). Movement by *E. inornatus* has notable implications for surveys and site assessment. Sites should be managed to ensure that all features needed by the species are available within relatively discrete patches; thus, feeding and thermoregulatory requirements and the provision of shelter and protection should all be available within a limited area.**

KEYWORDS.—**Puerto Rican boa, radiotelemetry, serpentes, wildlife, endangered species**

INTRODUCTION

The Puerto Rican boa, *Epicrates inornatus*, is the largest native snake in Puerto Rico. Grant (1933) made the first reference to the apparent scarcity of this snake in Puerto Rico. In 1970, the species was designated as endangered and was legally protected by the Endangered Species Act of 1973, as amended. The recent consensus among herpetologists is that the boa is not as rare as previously thought (Pérez-Rivera and Vélez 1978; Reagan 1984; Bird-Picó 1994), and Moreno (1991) recommended changing its status from Endangered to Threatened. Bird-Picó (1994) suggested that the species should be maintained in its current status until further studies regarding aspects of its biology and ecology are carried out. The decrease boa population is attributed predominantly to human impact. Habitat loss, mongoose predation, poaching for oil extraction, and killing because of innate fear, religious prejudice, or ignorance are the main factors affecting the species (Reagan and Zucca 1982). However, quantitative information on the effect of these factors in boa populations is needed, and most of the published information regarding these aspects is anecdotal rather than rigorously scientific (Stejneger 1904; Grant 1933; Rivero 1998). Valuable population data such as age structure, population turnover rates, foraging rates and strategies, home range, and seasonal activities are essential to evaluate the status of this species.

The secretive habits and cryptic coloration of this species, and the rough terrain and dense forest of its habitat, make it difficult to study individuals for extended periods. For this reason, radiotelemetry was chosen as a technique. Radiotelemetry is an efficient and appropriate technique for obtaining life history information, because it enables researchers to study behavior and movement in the wild, causing minimal stress to the animal (Reinert and Cundall 1982; Weatherhead and Anderka 1984). Radiotelemetry has the potential to provide basic information needed for the conservation and management of the Puerto Rican boa.

Our objectives were to: (1) document foraging behavior, and (2) to determine home-range, movements, and activity patterns of the Puerto Rican Boa at Mata de Plátano Reserve in Arecibo, Puerto Rico.

MATERIALS AND METHODS

Study site

Mata de Plátano Natural Reserve is located 7 km southwest of Arecibo in the limestone karst region of north central Puerto Rico. The Reserve lies within the sub-tropical moist forest life zone. This zone covers 58% of the total area of Puerto Rico and has a precipitation regime between 100 and 220 cm per year with a canopy height of about 20 m (Ewel and Whitmore 1973).

Cueva de los Culebrones is located within the Reserve (2037658.159N, 740229.926E, Universal Transverse Mercantor coordinates), and is classified as a hot cave. The only entrance faces 77° NE and is 5 m wide, 3 m in height and 8 m in depth. The main passage is 182 m long and consists of three rooms distributed along a main tunnel. Within 20 m of the entrance, two small rooms branch off the main passage. The third and largest room is located 80 m from the entrance. The cave is inhabited by five species of bats with a wide range of average body masses: *Brachyphylla cavernarum* (40 g), *Erophylla sezekorni* (16.1 g), *Monophyllus redmani* (8.7 g), *Mormoops blainvillii* (8.6 g), and *Pteronotus quadridens* (4.8 g). The total population of these five species has been estimated as 300,000 individuals (Rodríguez-Durán pers. comm.). At this cave, Rodríguez and Reagan (1984) reported bat predation by the Puerto Rican boas.

Foraging behavior at the cave entrance

Observations at the entrance of the cave started one hour before sunset and continued until one hour after sunrise. Fifty-one visits were made from March 1994 through January 1996. Snakes were monitored continuously using a headlamp fitted with a red filter. Observations were made using a Moonlight Man 30K Night Vision Binocular and a Moonlight Man 1400 Night Vision Scope. Data on prey capture and manipulation, perch position, number of individuals, and interactions between individuals were gathered. Blood samples were retrieved for future DNA analysis.

Radiotelemetry

Nine snakes (4 males, 5 females) were captured at the entrance, inside, and in the vicinity of Cueva de los Culebrones. A female *E. inornatus* was captured in a *Citrus* sp. tree 550 m from the cave entrance and was included in the study. Another snake, a male captured in Mayagüez, was also included in the study. Sex, snout-vent length (SVL), and mass of the snakes were recorded.

Two types of transmitters were used: an SB2 model (AVM Instrument Co., Livermore, California) coated with a 1:1 mixture of paraffin and beeswax with a final package mass of 39 g, and an SI-2T model (Holohil Systems Ltd., Ontario, Canada) with a package mass of 9 g. Transmitters operated at frequencies between 150.000 and 151.999 MHz.

The units were surgically implanted in the body cavity following the procedure of Reinert and Cundall (1982). Implanted snakes were held in captivity for two weeks after surgery for recovery and then were transported to the cave entrance and released. An implanted animal identification microchip system or passive integrated transponder tag (AVID, Norco, California) identified additional snakes captured at the study site.

Activity

Snakes were located every 48 hours and tracked for ten months using an Advanced Telemetry Systems receiver (Isanti, Minnesota) and a hand-held three-element Yagi antenna. Snake activity at the time of location (basking, moving, eating, denning in cavity or burrow), date and time were recorded at each location. Even if a snake could not be seen, its location could be determined within an area of 0.5 m^2. At each location, snakes were considered inactive if their location was < 5 m from the previous day's location and active if their location was > 5 m from the previous day's location. This information was transformed and a t-Test applied to compare activity of males and females. Global Positioning System (GPS) locations were taken with a Trimble GPS Pathfinder Pro XR unit to determine the precise location of the radio-tracked snakes. These locations were used for calculating home range.

Home range determination

The minimum convex polygon method (Hayne 1949; Jennrich and Turner 1969) and the harmonic mean measure (Dixon and Chapman 1980) were used to describe home range. Estimates of home range were calculated with the home range analysis software Calhome (Kie et al. 1994). The term home range was used for the area to which an animal normally confines its movements (Burt 1943).

Minimum convex polygons were chosen for the analyses because of their extensive use in other studies of reptilian spatial use (Rose 1982; Gregory et al. 1987; Burns and Heatwole 1998). Harmonic mean home range area was delineated by the 95% isopleth, and core activity area by the 50% isopleth. Reproductive period was determined from the available literature. Area used during the reproductive period from March to October and non-reproductive period was calculated using the coordinates of all males and females during these periods. Home range size, mean distance per move, and mean distance moved per day were tested for difference between the sexes with the t- Test. The relationship of snout-vent length and home range was analyzed using Spearman Correlation. Two-way ANOVA tests were applied to assess whether use of substrates differed between males and females during the study period.

RESULTS

Foraging behavior

Epicrates inornatus began occupying hunting perches at the entrance of the cave at 1730 h. Snakes were captured from 1745 h to 0600 h, but mostly between 1900 and 2400 h. At the entrance of the cave, snakes hung 75% or more of their bodies from a vine, branch, or limestone outcropping, making a side to side movement. When bats flew close or collided with them, the boas attempted a capture by a quick upward swing with their mouths open. Once a boa had captured a bat, it threw two coils around it with the snake's head inside the coil. After killing the bat, the snake swallowed it either head first, tail first, or from either side. Inside the cave, snakes hunted actively during the bats' reproductive season from April to July.

During the study period, one-hundred and twenty bat captures were observed at the cave entrance. Most (117) of the observations involved predation of one of the four smaller bat species (*Erophylla sezekorni, Mormoops blainvillii, Pteronotus quadridens, Monophyllus redmani*) present at the study site. Only three observations involved *Brachyphylla cavernarum,* a larger species. Predation success depended on the perching position occupied by a snake (Fig. 1). The most frequently used perch category consisted of the wall limestone outcroppings, followed by a looped root, and the vines across the center of cave the opening. The looped root, located in the midst of the bats flight path as they exited or entered the cave, was the site with more bat captures by the boas. Only one individual occupied this perch at a time, whereas two or more snakes simultaneously occupied the other locations at various times. Competition for the loop root as a hunting spot was observed.

Usually, the individual that occupied this perch during the day was the one that occupied it at feeding time. Interference between individuals resulted in confrontation in which both individuals abandoned their hunting postures and faced each other snout to snout for the remainder of the

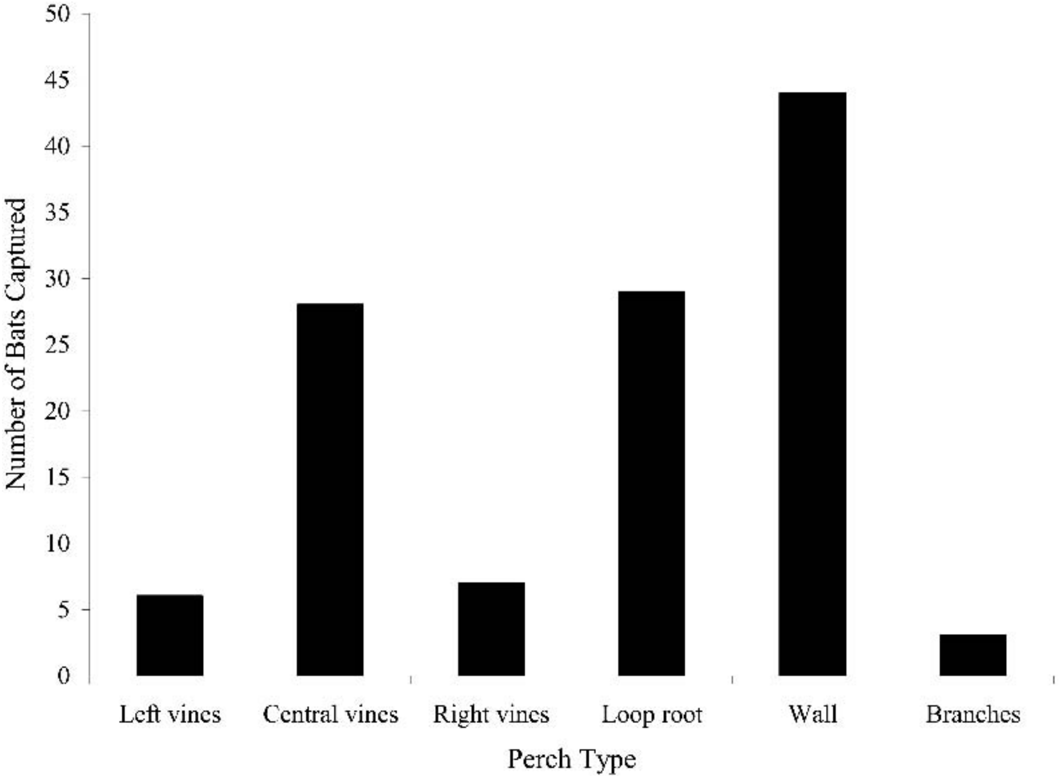

FIG. 1. Number of bats captured by snakes at different foraging perches at Cueva de los Culebrones, Mata de Platano Reserve, Arecibo, Puerto Rico

night. The least successful perches (least captures) were vines at the left and right edge of the entrance (Fig. 1). These perches were higher than the exit/entrance route used by the bats.

The maximum number of bats we observed captured on a single night was 14 by 10 boas, while the mean was 2.3 bats per night (n = 120 captures). The maximum number of captures by one individual was four bats in a single night. The average handling time was 12.53 ± 6.5 minutes. Excluding *B. cavernarum,* (the largest species), prey manipulation averaged 11.5 minutes while for *B. cavernarum* averaged 40.6 minutes.

We observed four piracies in which the prey was *E. sezekorni*. In three of these events, one or two snakes perching close to the successful hunter provoked the interference. The interference resulted in loss of the prey after about 30-45 minutes, with the opponents pulling and pushing each other. In one event, the intruder coiled around the successful hunter at 0100 h. The prey was released after 15 minutes and both the hunter and pirate remained coiled until 0600 h when they separated. In only one of the four piracy events was the hunter able to retain its prey successfully. It later manipulated and swallowed the prey. We offered each lost prey item to resting snakes and it was readily accepted.

The largest snake marked with a pit tag was a female (140 cm SVL, 22.8 cm tail length), whereas the smallest one was a male (45 cm SVL, 12 cm tail). Log transformed regressions of weight and length did not differ significantly between the sexes (t = –0.589, DF = 24, P = 0.556)

Home range

Eleven *E. inornatus* (six females, five males) were located at least 25 times over a ten-month period. Home range areas varied from 138.9 m^2 to 18,380 m^2. Convex

TABLE 1. Time spent (%) at each location by females (n = 6) and males (n = 5) during the study period at Mata de Plátano Reserve, Arecibo, PR.

	Time spent (%) at each location								
	Cave entrance	Inside cave	Ground	Rock wall	Tree	Under litter	Cavity	Log	Abandoned structure
Females									
Mean	.16	25	24	21	08	04	14	.33	03
SE	.16	11	10	07	03	04	04	.33	03
Males									
Mean	11	09	17	01	25	20	03	08	05
SE	05	05	05	.06	12	07	02	04	05

polygon home ranges of males and females did not differ significantly (t = 0.847, DF = 9, P = 0.419) and were not correlated with size (Spearman correlation coefficient = −0.358, N = 10, P = 0.252). However, females had larger mean home range areas (7,890 m^2 ± 6614 m^2) than males (5,000 m^2 ± 4,102 m^2). Average harmonic means for radio tracked males was 2,964 m^2 (with range from 246 m^2 to 6911 m^2) and for females was 3,365 m^2 (with range from 104 m^2 to 9729 m^2). Male and female harmonic means were not significantly different (t = 0.195, DF = 9, P = 0.850). Male 50% core activity area (ranging from 20 m^2 to 653 m^2) and female core area ± (ranging from 6 m^2 to 664 m^2) did not differ statistically (t = −0.218, DF = 9, P = 0.832).

Mean distance per move was 47.9 m ± 18 m for females and 51.5 m ± 24 m for males, and did not differ significantly between the sexes (t = −0.269, DF = 9, P = 0.794). Mean distance traveled per day was 83 m ± 51 for males and 99 m ± 88 m for females and the difference was not significant (t = 0.365, DF = 9, P = 0.723). The area used during non-reproductive time (November to February) by all radio-tracked males was 1,322 m^2 and 22,119 m^2 for females. During the reproductive period (March to October), the area used by males was 18,500 m^2 and by females 16,940 m^2. Mean time spent by snakes at the same location was 37.4 ± 38.3 days with range from 5 to 53 consecutive days for males and 47 ± 34.7 days with range from 2 to 96 days for females.

Activity patterns

Females were active during 29 ± 7.2% of the observations (n = 89), whereas males were active during 36 ± 12.5% (n = 66). Differences between the sexes were not significant (t = −1.230, DF = 9, P = 0.246). The average proportion of time females were active was 23 ± 6.6% during the reproductive period and 6 ± 3.7% during the non-reproductive period. Males were more active during the reproductive period (32 ± 12%) than during the non-reproductive period (5 ± 4%). Although males tended to be more active than females during the reproductive period, the difference between the sexes was not significant (t = −1.549, DF = 9, P = 0.156).

Females had changed location 24.5% of the observations and males 35.6%. Males spent more time at rock walls, trees, and on the ground; females spent more time inside the cave, on the ground and on rock walls (Table 1). Relationships between sex and location were not significant (F = 0.860, DF = 7, P = 0.542). However, percent of time spent by both sexes for eight locations, for which data were sufficient for analyses, were significantly different (F = 4.572, DF = 7, P = 0.000). Rock walls, trees, cavities, ground, and inside the cave were sites occupied significantly more often than under litter, logs, and the cave entrance (orthogonal contrast, F = 28.4, DF = 1, P = 0.000).

Movements

Males radio-tracked revisited the cave from two to eleven times ($\text{mean}_{\text{visits}}$ = 4.8) during the study period. Five of the six females tracked revisited the cave from 2-7 times ($\text{mean}_{\text{visits}}$ = 4.2). The only female that did not return to the cave was initially captured in a *Citrus* sp. tree 550 m from the cave entrance and released at the cave entrance. Within a two-week period, it had returned to the area where it was originally captured and continued moving in the same area for the rest of the study period. One male included in the study was relocated at the study site from the western part of the island (Mayagüez) in order to document preliminary information of translocation effect on the specie. Its movements were short and it stayed near the area of release during the study period. In general, the movements by ten of the snakes were confined principally to two areas. Four snakes moved to the haystack hills areas facing the cave entrance, whereas five snakes moved to the haystack hills located behind the cave entrance.

DISCUSSION

Foraging behavior

Predation on bats is known for other Caribbean *Epicrates* such as the Cuban boa, *Epicrates angulifer* (Hardy 1957; Silva-Taboada 1979) and the Jamaican boa, *Epicrates subflavus* (Prior and Gibbson 1997). The hunting strategy of *E. inornatus* is similar to that observed in *E. subflavus* but different from that of *E. angulifer*. *Epicrates angulifer* can be found foraging on the floor of the caves and at heat traps within the caves, feeding mostly on *Phyllonycteris poeyi*, the ecological equivalent of *Erophylla sezekorni* in Puerto Rico (Silva-Taboada pers. comm.).

Rodríguez-Durán (1996) reported *E. inornatus* hunting bats in four other caves in Puerto Rico, and reported that boas did not start hunting at the onset of bat activity. His observations contrast with our findings that snakes start hunting as bats begin exiting the cave. The fact that most of the prey items involved *Erophylla sezekorni* suggest that prey density may be a crucial factor for *E. inornatus*. Of the approximately 300,000 individuals at the cave, the highest number of individuals is that of *E. sezekorni* (Rodríguez-Durán 1996). Thus, the boas seems to capitalize not on the weight of this species (15 g), as opposed to the other available species ranging from five to nine grams, but rather on the number of bats that are exiting or entering the cave at a given time. This observation coincides with those of Henderson et al. (1987) and Schwartz and Ogren (1956) regarding opportunistic feeding when preys are readily available.

When foraging for bats the difference in feeding strategies among *E. angulifer, E. inornatus,* and *E. subflavus* involves differences in their energetic expenditure. *E. angulifer* hunts on the floor close to the heat trap within the cave, which serves as a funnel for bats entering and exiting, but *E. inornatus* and *E. subflavus* occupy perches and have their bodies in a vertical position while hunting for prey. The energetic, morphological, physiological adaptations that are necessary for these actions are demanding (Lillywhite and Henderson 1993). Thus, compensating these events with periods of rest or digesting for several days might be important.

Home range, activity patterns and movements

Most of the studies of home ranges of snakes have not found significant differences in home range sizes between the sexes (Clark 1970, 1974; Freedman and Catling 1979; Goddard 1980; Plummer 1981b; Michot 1981; Reinert and Kodrich 1983; Burns and Heatwole 1998). There has been only one study that we are aware in which females had significantly larger home ranges than males (*Natrix natrix,* Madsen 1984). Gregory et al. (1987) reported that in some studies males exhibited a greater home range than females, but either the methods used to calculate home range lacked credibility or there was no test for differences. No significant sexual differences in home-range size were found for *E. inornatus* during the present study, although a tendency for females to have a larger mean home range was observed. On going studies of movements of *E. inornatus* in other areas show females with a larger home range area (Puente-Rolón unpublished data).

Stickel and Cope (1947) suggested that home ranges in highly productive habitats are smaller than those in less productive habitats. Michot (1981) found, for the water snakes *Neroida* spp., small home range size in Lousiana where the predominant prey was fish. Fish occurred in great concentrations and water snake predation on them had little impact on prey population density. However, Madsen (1984) found a greater home range size for water snakes (*Natrix natrix*) where they fed on amphibians occurring in much lower densities than the prey populations of the water snakes in Louisiana. Cueva de los Culebrones represents a highly productive habitat, where food is concentrated in a particular area and is available to the snakes. This may explain why individuals of *E. inornatus* in Mata de Plátanos Reserve were confined to the proximity of the cave. In areas where food resources are more dispersed or in lower densities *E. inornatus* needs larger home ranges (Puente-Rolón unpublished data).

Bonnet et al. (1994), Brown (1991), and Diller and Wallace (1984) found that body reserves were important for vitellogenesis in many species of snakes. Three of the radio-tracked females were gravid during the study period. We observed a reduction in their movements, compared to those of non-gravid females; also, gravid females spent the day basking in rock walls. Garland and Arnold (1983) noted that pregnancy in squamates involved more changes than a mere increase in body mass. In studies with gravid garter snakes (*Thamnophis sirtalis*), Birchard et al. (1984) found that heart rate and oxygen consumption increased during the gestation period. All the changes during development of the offspring result in a decrease in locomotion ability that may be more complex and variable than that seen during a comparable increase in mass following feeding (Seigel et al. 1987).

Males of E. *inornatus* showed high activity during the reproductive period. Gibbons and Semlitsch (1987) and Gregory et al. (1987) determined that there is an increase in movements in response to mate searching, like that observed in *E. inornatus.* Studies with viperids showed that feeding in males decreases during the mating period (Bea et al. 1992; Bonnet and Naulleau 1996). This enables males to optimize their search, investing their time in seeking mates rather than in foraging and digestion.

Epicrates inornatus spent most of the study inactive; a substantial part of the activity that did take place occurred during the reproductive period. Montgomery and Rand (1978) found that when a *Boa constrictor* was located, at hourly or shorter intervals during the day and night, the snake was usually inactive. For an ectotherm, movement greatly increases metabolic rate (Bennett 1982). It is energetically and metabolically beneficial for a reptile to minimize its movements. Lower energy expenditure results in a decreased need to actively forage for food (Gent and Spellerberg 1993). One of the primary concerns of an ectotherm is the maintenance of body temperature. Thus, movement may be a response to local factors, perhaps determined by thermoregulatory needs or movement between places offering shelter.

Rock walls were an important location for *E. inornatus.* These provide a thermoregulatory site during the morning and before sunset periods (pers. obs.). Selection of a thermally heterogeneous environment may allow behavioral thermoregulation and avoidance of extreme temperatures through only small movements (Gent and Spellerberg 1993). Also, these areas are important as a food resource. Mancina and Llanes-Sosa (1997) reported predation on the cave swallow (*Hirundo fulva*) by the Cuban boa (*Epicrates angulifer*) at rock walls. Although these behaviors have not been reported for *E. inornatus*, we have observed snakes at rock walls supporting many nests of cave swallow.

The interior and floor of the cave were important for the females. The cave offers a meeting place where snakes can choose mates and copulate. Afterwards, females can spend time inside the cave eating, thermo-regulating, and eliminating ectoparasites in the water pools (pers. obs).

The fact that ten E. *inornatus* returned to the cave more than once indicated good knowledge of the habitat. Recognition of visual landmarks was important in short movements for snakes, whereas chemosensory cues play a major role in the trailing behavior of conspecific snakes, especially trailing of females by males during the mating season (Gregory et al. 1987).

Landreth (1973) found that when *Crotalus atrox* were released in a strange habitat, they reacted differently from local animals and continued to move in direct courses, usually returning to the area where they had been captured. This seems to be true for the snake captured far from the cave and released at the cave. However, *E. inornatus* relocated from another municipality remained near the release point. Parker and Brown (1980) established that homing success by *Masticophis t. taeniatus* and *Pituophis malanoleucus deserticola* was inversely correlated with displacement distance. Gregory et. al. (1987) concluded that many snakes' species are sometimes capable of homing over short distances.

The movements exhibited by *Epicrates inornatus* have notable implications for surveys and site assessments. This means that observations of *E. inornatus* in a particular site may under represent the total population that uses the area. Also, the low movements of this species in a highly productive habitat indicate these animals are likely to remain within a specific area for prolonged periods. Sites, therefore, should be managed to ensure that all features needed by the species are available within relative discrete patches. Thus, feeding and thermoregulatory requirements and the provision of shelter and protection should be available within a limited area.

Acknowledgments.—We thank Jeffrey Lee and Vince of the Tall Timbers Research Station and Dr. Wes Burger and Dr. Francisco Vilella of Mississippi State University for training in use of telemetry. We are grateful to the following people who helped and/or advice in various aspects of this proyect: Peter Tolson, Wynona Shellabarger, Edgardo Rivera, Luis Figueroa, personnel at the Juan A. Rivero Zoo, Ciudadanos del Karso, Inc., Jaime Collazo, Leopoldo Miranda, Speleological Society of Puerto Rico, Efraín Mercado, Allen R. Lewis, José G. Rodríguez, students in the Special Problems course, North Carolina State University field assistants (Humus Team), Anahí Vale, and Carlos Rodríguez. The Department of Natural Resources and the Environment (DNRE) and the US Fish and Wildlife Service provided permits to pursue the research. The Department of Biology at the University of Puerto Rico at Mayagüez Campus provided a teaching assistantship during the study. Dr. Harold Heatwole critically reviewed the manuscript. This research was supported by a Cooperative Agreement from the US Fish and Wildlife Services (#1448-0004-95-9162) and the US Forest Service (Grant # IITF-96-G-001).

LITERATURED CITED

Bea, A., F. Brana, J. P. Baron, and H. Saint Girons. 1992. Regimes et cycles Alimentaires des Viperes europeenes (Reptilia, Viperidae). *An. Biol.* 31:25-44.

Bennett, A. F. 1982. The energetics of reptilian activity. In *Biology of the Reptilia*, ed. C. Gans, and F. H. Pough, Vol. 13, 155-199. N. Y.: Academic Press.

Birchard, G. F., C. P. Black, G. W. Schuett, and V. Black. 1984. Influence of pregnancy on oxygen consumption, heart rate and hematology in the garter snake: implications for the cost of reproduction in live bearing reptiles. *Comp. Biochem. Physiol.* 77A: 519-523.

Bird-Picó, F. J. 1994. *Final Report on Epicrates inornatus survey throughout Puerto Rico.* Cooperative Agreement between U.S. Department of Interior, Fish & Wildlife Service and the Department of Biology, University of Puerto Rico, Mayagüez Campus #14-16-0004-92-958.

Bonnet, X., and G. Naulleau. 1996. Are body reserves important for reproduction in male dark green snakes? (Colubridae: *Coluber viridiflavus*). *Herpetologica* 52(2):137-146.

Bonnet, X., G. Naulleau, and R. Mauget. 1994. The influence of body condition on 17-beta estradiol levels in relation to vitellogenesis in female *Vipera aspis* (Reptilia, Viperidae). *Gen. Comp. Endocrinol.* 93:424-437.

Bureau of Sport Fisheries and Wildlife. 1973. *Threatened Wildlife of the United States*. Bureau of Sport Fisheries and Wildlife Resourse Publ.

Burns, G., and H. Heatwole. 1998. Home range and habitat use of the olive sea snake *Aipysurus laevis*, on the great barrier reef, Australia. *J. of Herpetology* 32(3): 350-358.

Burt, W. H. 1943. Territoriality and home range concept as applied to mammals. *J. Mammal.* 24:347-352.

Clark, D. R. Jr. 1970. Ecological study of the worm snake, *Carphophis vermis* Univ. Kans. Publ. Mus. Nat. Hist. 19:85-194.

Clark, D. R., Jr. 1974. The western ribbon snake (*Thamnophis proximus*): Ecology of a Texas population. *Herpetologica* 30:372-379.

Diller, L. V., and R. L. Wallace. 1984. Reproductive biology of the northern Pacific rattlesnake (*Crotalus viridis oreganus*). *Herpetologica* 40:182-193.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61: 1040-1044.

Ewel, J. J., and J. L. Whitmore. 1973. *The ecological life zones of Puerto Rico and the U.S. Virgin Islands*. Forest Serv. Research Pap. ITF-8, USDA.

Freedman, B., and P. M. Catling. 1979. Movements of sympatric species of snakes at Amherstburg, Ontario. *Canadian Field Naturalist* 93(4):399-404.

Garland, T. Jr., and S. J. Arnold. 1983. Effects of a full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). *Copeia* (4): 1092-1096.

Gent. A. H., and I. F. Spellerberg. 1993. Movement rates of the smooth snake *Coronella austriaca* (Colubridae): a radio-telemetric study. *Herpetological Journal* 3:140-146.

Gibbons, J. W., and R. D. Semlitsch. 1987. Activity patterns. In *Snakes: ecology and evolutionary biology*, ed. A. Seigel, J. T. Collins, and S. S. Novak, 396-421. New York: MacMillan Publ. Co.

Goddard, P. 1980. Limited movement areas and spatial behavior in the smooth snake *Coronella austriaca* in southern England. In *Proceedings of the European Herpetological Symposium*, ed. J. Coborn, 25-40.

Grant, C. 1933. Notes on *Epicrates inornatus*. *Copeia* 1933:224-225.

Gregory, P. T., and K. W. Steward. 1975. Long distance dispersal and feeding strategy of the red sided garter snake (*Thamnophis sirtalis parietalis*) in the interlake of Manitoba. *Can. J. Zoo.* 53:238-245.

Gregory, P. T., J. M. Macartney, and K. W. Larsen. 1987. Spatial patterns and movements. In *Snakes: ecology and evolutionary biology*, ed. A. Seigel, J. T. Collins, and S. S. Novak, 366-395. New York: MacMillan Publ. Co.

Hardy, J. D. 1957. Bat predation by the Cuban boa (*Epicrates angulifer*). *Copeia* 1957:151-152.

Hayne, D. W. 1949. Calculation of size of home range. *J. Mammal.* 30:1-18.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of non circular home range. *Theoret. Biol.* 22:227-237.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1994. *Calhome: home range analysis program. Electronic User's Manual*. Fresno and Albany, California: U. S. For. Serv.

Landreth, H. F. 1973. Orientation and behavior of the rattlesnake, *Crotalus atrox*. *Copeia* 1973 (1):26-31.

Lillywhite, H. B., and R. W. Henderson. 1993. Behavioral and functional ecology of arboreal snakes. In *Snakes: ecology and evolutionary biology*, ed. A. Seigel, and J. T. Collins, 1-48. New York: McGraw-Hill, Inc.

Madsen, T. 1984. Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweden. *Copeia* 1984 (3):707-713.

Mancina, C. A., and A. Llanes-Sosa. 1997. Indicios de depredación de huevos de *Hirundo fulva* (Passeriformes: Hirundinidae) por *Epicrates angulifer* (Serpentes: Boidae). *El Pitirre*. 10 (3):95-96.

Michot, T. 1981. Thermal and spatial ecology of three species of water snakes (*Nerodia*) in a Louisiana swamp. Ph D. diss. Louisiana State University.

Montgomery, G. G., and A. S. Rand. 1978. Movements, body temperature and hunting strategy of a *Boa constrictor*. *Copeia* (3):532-533.

Moreno, J. A. 1991. Accounts of those species considered to be concern. In *Status y Distribución de los reptiles y anfibios de la región de Puerto Rico*, ed. J. A. Moreno, 9-10. Puerto Rico: Publ. Científica Miscelánea No. 1 DRN de Puerto Rico.

Nowak, E. M. 1997. Effects and effectiveness of rattlesnake relocation at a national Monument in central Arizona. In *Proceedings of 77 annual meeting of American Society of Ichthyologist and Herpetologist*, Seattle, Washington.

Parker, W. S., and W. S. Brown. 1980. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucos deserticola*, in northern Utah, Milw. Publi. Mus. Publ. Biol. Geol. 7:1-104.

Pérez-Rivera, R. A., and M. J. Vélez. 1978. Notas sobre algunas culebras de Puerto Rico. *Science-Ciencia* 6(1):68-73.

Plumer, M. V. 1981b. Habitat utilization, diet and movements of a temperate arboreal Snakes (*Opheodrys aertivus*). *J. Herpetol.* 15:425-432.

Prestt, I. 1971. An ecological study of the viper (*Vipera berus*) in southern Britain. *J. Zool. Lond*. 164:373-418.

Prior, K. A., and R. C. Gibbson. 1997. Observation on the foraging behavior of the Jamaica Boa, *Epicatres subflavus*. *Herp. Review.* 28(2):72.

Reagan, D. P. 1984. Ecology of the Puerto Rican Boa (*Epicrates inornatus*) in the Luquillo Mountains of Puerto Rico. *Caribb. J. Sci.* 20 (3-4):119-126.

Reagan, D. P., and C. P. Zucca. 1982. *Inventory of the Puerto Rican boa (Epicrates inornatus) in the Caribbean National Forest*. CEER T-136, 42 pp.

Reinert, H. K., and D. Cundall. 1982. An improved surgical implication method for radiotracking snakes. *Copeia* (3): 702-705.

Reinert, H. K., and W. R. Kodrich. 1983. Movements and habitat utilization by the massasauga, *Sistrurus catenatus catenatus*. *Copeia* 16:162-171.

Rivero, J. A. 1998. *Los anfibios y reptiles de Puerto Rico*. San Juan, Puerto Rico: Universidad de Puerto Rico, Editorial Universitaria.

Rodríguez-Durán, A. 1996. Foraging ecology of the Puerto Rican boa (*Epicatres inornatus*): bat predation, carrion feeding and piracy. *J. Herpetol.* 30:533-536.

Rodríguez, G., and D. A. Reagan. 1984. Bat predation by the Puerto Rican boa, *Epicrates inornatus*. *Copeia* (1): 219-220.

Rose, B. 1982. Lizard home ranges: methodology and functions. *J. Herpetol*. 16: 253-269.

Schwartz, A., and L. H. Ogren. 1956. A collection of reptiles and amphibians from Cuba, with the description of two new forms. *Herpetologica* 12:91-110.

Seigel, R. A., M. M. Huggins, and N. B. Ford. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologica* 73:481-485.

Silva-Taboada, G. 1979. *Los murciélagos de Cuba*. Cuba: Acad. de Ciencias de Cuba. Stejneger, L. 1904. *The Herpetology of Porto Rico*. Rpt. U.S. Nat. Mus. 1904: 521-720.

Stickel, W. H., and J. B. Cope. 1947. The home ranges and wanderings of snakes. *Copeia* (2): 127-135.

Weatherhead, P. J., and F. W. Anderka. 1984. An improved radio transmitter and implantation for snakes. *J. Herpetol.* 8:264-269.