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# Movement and Space Use by Coastal Rosy Boas (*Lichanura trivirgata roseofusca*) in Coastal Southern California

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ABSTRACT.—**We studied the movement ecology of Coastal Rosy Boas (*Lichanura roseofusca*) by radio tracking 17 animals across four sites for up to four years. The typical movement pattern included many short distance moves with rare long distance movements. These skewed distributions made the mean a poor descriptor of movement and this is likely a common issue in other studies. Sexes had similar movement patterns and moved less frequently and shorter distances per day during cooler seasons. Rare long-distance movements occurred primarily in the spring. Propensity to move and mean distance moved per day varied across sites. Home-range size increased with additional fixes even after four years and had a seasonal pattern, increasing during warmer seasons and remaining stable or shrinking during cooler seasons. Despite using novel habitat in sequential years, nearly all individuals used the same general area over longer periods of time. Finally, individuals of both sexes had high levels of spatial overlap. The results indicate for *L. roseofusca* (1) Individual variability in movement is more the rule than the exception; (2) Common seasonal patterns in movement and space use do exist; (3) Home-range sizes vary through time yet remain in the same general location; and (4) A lack of territoriality and considerable overlap in space use exist.**

The spacing of individuals, as well as the frequency and distance of their movements, affects population dynamics. Empirical studies indicate spatial dispersion and movement affect population size and trajectory at multiple scales: from metapopulation dynamics in butterflies (Fahrig and Paloheimo, 1987; Hanski et al., 1995) and salamanders (Trenham et al., 2001), to source-sink dynamics in grasses (Keddy, 1981, 1982; Watkinson et al., 1989), and to ideal free habitat selection in small mammals (Diffendorfer, 1998) and birds (Doncaster et al., 1997).

In addition to affecting population dynamics, dispersion patterns and movement often reflect ecological, behavioral, or social interactions among individuals (Huffaker, 1958; Wynne-Edwards, 1967; Pusey, 1987; Pulliam, 1988; Danielson, 1991, 1992). Thus, natural selection likely has strong impacts on many aspects of movement, ranging from physiological and anatomical adaptations enhancing movement ability, to selection for the propensity to disperse (Holt, 2003).

Given difficulties inherent in measuring snake movements and the relatively recent use of radiotelemetry techniques, no general theory of snake movement exists to define explicit, testable hypotheses. Indeed, after reviewing over 50 papers on snake movements, Macartney et al. (1988) suggested the number of variables affecting movement patterns and the lack of specific analyses of movement precluded any general conclusions. Although numerous subsequent studies exist, snake ecologists are still in the formative stages of understanding snake spatial ecology.

Factors affecting snake movement include the particular ectothermic physiology of a species and the need to find locations suitable for thermoregulation (Huey et al., 1989; Dorcas and Peterson, 1998; Whitaker and Shine, 2002; Pringle et al., 2003; Whitaker and Shine, 2003). Many snake species move long distances to and from seasonal hibernacula, returning to specific locations during stressful conditions while foraging elsewhere during favorable conditions. During reproductive activity, a number of studies found increased movement in males, presumably seeking mates (Jenkins et al., 2001). In addition, females often travel to a particular location with a preferred thermal environment and reduce

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activity when gravid (Brown and Weatherhead, 2000).

In perhaps the most comprehensive review of snake movement ecology, Gregory et al. (1987) suggested the spatial pattern and density of critical resources (hibernacula, ponds, prey, etc.) may best explain major patterns in movement. Gregory et al. (1987) argued snake dispersion should be nonrandom given a lack of evidence for territoriality and given the formation of seasonal or short-term aggregations. Habitat selection for favorable conditions may result in short-term aggregations as snakes thermoregulate or select areas of high prey density (Reinert, 1993; Whitaker and Shine, 2003). Larger, longer-term aggregations may result from mating (Aleksiuk and Gregory, 1974), overwintering (Gregory, 1984), stressful conditions (Aleksiuk, 1977), and communal oviposition or reproduction such as aggregations of gravid females (Duvall et al., 1985).

The Coastal Rosy Boa (*Lichnura trivirgata roseofusca*) is one of two boid species native to the United States (Stebbins, 2003). Until recently, little data existed about spatial ecology, activity patterns or even basic natural history information of rosy boas (Rodriguez-Robles et al., 1999). In an unpublished 1996 report to the Arizona Game and Fish Department, D. A. Parizek, P. C. Rosen, C. R. Schwalbe, and C. H. Lowe provided data on movement, habitat selection, and activity patterns of six rosy boas collected using telemetry. Dorcas (1995) studied the thermal ecology of Rubber Boas (*Charina bottae*), providing detailed information on daily activity patterns and body temperature (Dorcas et al., 1997; Dorcas and Peterson, 1998). Coastal populations of rosy boas exist in a rapidly fragmenting landscape (Hunter et al., 2003), and understanding spatially explicit movements is necessary for evaluating reserve sizes and for long-term management of this species (Case and Fisher, 2001). Here, we extend work on the spatial ecology of rosy boas by analyzing radiotelemetry data from 17 individuals at four sites over four years. We report results related to movement, individual spacing and overlap, and seasonal changes in movement patterns. Data on thermal ecology and habitat selection of rosy boas will be presented in other publications.

## MATERIALS AND METHODS

*Study Sites.*—We began in May 1999 by collecting animals using visual searches, road surveys, and pitfall arrays used in a monitoring project (Fisher and Case, 2000). We added snakes to the study during the first three years, so some individuals were tracked for longer periods than others.

We studied animals at four locations in San Diego and Riverside Counties, all dominated by coastal sage scrub: (1) WAP, San Diego Wild Animal Park, San Diego County, CA (33.09465°N, 116.98253°W, 140–255 m elevation) managed by the Zoological Society; (2) MT, San Diego County Mission Trails Regional Park, San Diego County, CA (32.81066°N and 117.03789°W, 165–215 m elevation); (3) CNM, Cabrillo National Monument, San Diego County, CA (32.66912°N and 117.24107°W, 22–109 m elevation); this single boa, collected by CNM staff, was the only rosy boa observed at CNM despite eight years of reptile and amphibian monitoring (Fisher and Case, 2000; Case and Fisher, 2001) and given a lack of historic observations, was likely a released captive; and (4) SM. Santa Margarita Ecological Reserve, Riverside County, CA (33.45768°N and 117.17044°W, 790–1120 m elevation).

*Telemetry.*—We used receivers from Wildlife Materials, Inc. (TRX-1000S), AVM Instrument Co. (LA12-Q), Telonics, Inc. (TR-4 and TR-5), and RA-2AK (Telonics, Inc.) directional antennas. To ensure transmitters weighed less than 5% of a snake's body mass (Hardy and Greene, 1999), we used two types of transmitters by Holohil Systems Ltd. Smaller snakes received the SB-2 (5.5 g, 9 × 19 mm), whereas larger snakes received the temperature sensitive SI-2T (9.5g, 10 × 33 mm).

Surgical procedures used throughout the study followed the guidelines described by Reinert and Cundall (1982) and Hardy and Greene (1999) and had approval by the Animal Use Committee of San Diego State University (protocol 99-011F). C. Rochester, and later L. Young, DVM (San Diego Zoo) performed all implants. We released snakes at the site of collection a few days after surgery, as minimizing time in captivity increases postsurgical survival (Hardy and Greene, 1999).

*Field Protocols.*—Sampling effort varied as snake activity patterns changed seasonally. During the spring and summer, we located individuals two to four times per week but only once or twice a week during winter and fall. We recorded GPS locations directly above the snake (whether above or belowground) with a GPS handheld unit (Garmin 12-XL or Trimble GeoExplorer3, UTM coordinate system, ~1.5 m accuracy).

*Statistical Analyses.*—We analyzed the data for differences in movement, by sex, season, and site. We defined each season as: Winter (21 December to 20 March), Spring (21 March through 20 June), Summer (21 June to 20 September), and Fall (21 September to 20 December).

We used the Animal Movement extension (Hooge and Eichenlaub, 1997) in ArcView 3.3 to estimate home-range size. For comparison with older studies of snake home-range size, we calculated 100% minimum convex polygons (MCP) but also calculated kernel home-range (KHR) sizes because these are more accurate estimators of home-range size (Seaman and Powell, 1996). We report both adaptive and fixed kernel estimates but estimated home-range overlap with fixed kernel estimates. For KHR, we used least-squares cross-validation to determine the smoothing factor (Seaman and Powell, 1996; Blundell et al., 2001). For the overlap analyses, we defined each year from 21–20 December and used these data to calculate an annual home range with the area shared by sequential annual home ranges considered overlap.

Because movement data were extremely skewed, we analyzed two components. First, the proportion of fixes resulting in movements addressed the question "what factors affect the chance an animal moves?" Second, we analyzed the distances moved per day, but only when movement occurred, by excluding distances of zero and asked "when animals moved, how far did they move?" We calculated the proportion of possible fixes resulting in moves ("proportional movement") for each individual then used *t*-tests or ANOVA to test for differences across treatments. Because the accuracy of our GPS unit was ~1.5 m, we considered distances between successive locations greater than 3 m as movement. Because we typically found animals below ground, we do not feel we could appreciably increase the level of spatial accuracy using other techniques.

As recommended by Gregory et al. (1987), we estimated distance moved per day and distance moved per fix. However, we found a strong correlation between these two estimates of movement so we only analyzed movement per day by sex, season, or site.

Distance moved per day can be calculated in two ways. First, dividing the total distance moved by an individual during the entire study by the total number of days produces a single, overall estimate. Second, estimating the distance moved per day across sequential pairs of fixes (distance moved between two fixes divided by the number of days between the fixes) produces a distribution of distances allowing the calculation of mean (typically), median, mode and variance. Both methods occur in the literature, often reported as "average distance moved per day." However the two methods do not always produce the same estimate. For example, if an animal moved 2, 3, 2, and 1 units in 1, 4, 8, and 2 days, its overall distance/day = $(2 + 3 + 2 + 1)/(1 + 4 + 8 + 2)$ or 8 units/15 days = 0.5333, but the mean distance moved per day equals the mean of $(2/1, 3/4, 2/8, 1/2) = (2 + 0.75 + 0.25 + 0.5)/4 = 0.875$. We advocate estimating sequential distances moved per day and then using estimators of central tendency, variability, and skewness to describe and compare the distributions.

We estimated sequential movements per day, excluding periods of no movement, then compared it between sexes, sites, or seasons using *t*-tests or ANOVAs. Even after removing distances of zero, the distances moved per day were highly skewed, so we used 4th-root transformations to meet the assumptions of normality.

The data contained high levels of temporal correlation: if an animal moved a short distance in one time period, it likely moved a similar short distance the following time period. To avoid psuedoreplication, we used individuals as replicates. Thus, our statistical tests often compared "means of means" because we averaged movements for an individual within a season, or site, and used individuals as the unit of replication in the appropriate statistical test. Given our opportunistic sampling effort, we did not have adequate sample sizes to statistically analyze all combinations of sex, site, and season. Therefore, we performed less complex one- and two-way analyses when appropriate. Finally, we used correlations to check for relationships between individual body size and distance moved per day.

## RESULTS

We captured 25 snakes, implanted transmitters in 21, and obtained sufficient movement data from 17 (Table 1). The fates of implanted animals varied with most surviving during the study. The four unused individuals died, were eaten, or disappeared from the study area before we could gather a sufficient set of fixes (Table 1). We located the 17 snakes 1169 times. As a result of cumulatively adding snakes to the study, implantation dates, total number of days tracked, and total number of locations varied substantially across individuals (Table 1). On average, snakes were located 1.3 times per week. Sampling effort varied by location and by season (Table 2) resulting partly from the closer geographic proximity of WAP and MT.

*Proportional Movement.*—Males and females had similar proportional movement ($t = -0.268$, df = 15, $P = 0.793$, Table 3, column C); thus, we combined data across sexes to investigate seasonal and site effects. Although movement occurred in all months, the probability of an animal moving declined sharply in the winter ($F = 3.567$, df = 3, 57, $P = 0.02$, Winter: mean ± SE = 0.277 ± 0.070, $N = 13$, Spring: 0.573 ± 0.065, $N = 15$, Summer: 0.512 ± 0.061, $N = 17$, Fall: 0.494 ± 0.063, $N = 16$). At WAP and MT (sites with multiple individuals captured in each season) we performed a two-way ANOVA using site and season as explanatory variables, combining data across sexes. As with the full dataset,

TABLE 1. Summary statistics. ID refers to an individual's identification. Implant date includes recapture and transmitter replacement datesFate is the disposition of the animal at the end of the study. A = Alive and Active, P = Predated, D = Dead because of complications, U = unknown disposition.

| Study site | ID | Sex | Implant date | Days monitored | Number of fixes | Fixes per week | Fate |
|---|---|---|---|---|---|---|---|
| Cabrillo National Monument (CNM) | | | | | | | |
| | CNM-1 | M | 5/99<br>8/99<br>5/00 | 507 | 65 | 0.9 | A |
| Mission Trails Regional Park (MT) | | | | | | | |
| | MT-1 | F | 7/99 | 441 | 76 | 1.2 | A |
| | MT-2 | M | 7/99 | 55 | 12 | 1.5 | U |
| | MT-3 | F | 3/00 | 216 | 34 | 1.1 | A |
| | MT-4 | F | 3/00 | 214 | 35 | 1.1 | A |
| | MT-5 | F | 3/00 | 203 | 36 | 1.2 | A |
| Santa Margarita Ecological Reserve (SM) | | | | | | | |
| | SM-1 | F | 5/99<br>4/00 | 484 | 81 | 1.2 | A |
| | SM-2 | M | 5/99 | | | | P |
| | SM-3 | M | 5/99 | | | | P |
| Wild Animal Park (WAP) | | | | | | | |
| | WAP-1 | M | 5/99<br>4/00<br>9/01 | 1146 | 162 | 1.0 | A |
| | WAP-2 | M | 5/99<br>5/00 | 501 | 108 | 1.5 | A |
| | WAP-3 | M | 6/99 | 214 | 41 | 1.3 | P |
| | WAP-4 | M | 6/99<br>1/00 | 485 | 87 | 1.2 | A |
| | WAP-6 | M | 9/99 | | | | D |
| | WAP-7 | F | 3/00 | 859 | 102 | 0.8 | A |
| | WAP-9 | F | 4/00 | 488 | 70 | 1.0 | A |
| | WAP-10 | M | 5/00<br>9/01 | 783 | 81 | 0.7 | A |
| | WAP-11 | F | 5/00<br>10/01 | 744 | 81 | 0.8 | A |
| | WAP-12 | F | 6/00<br>10/01 | 530 | 62 | 0.8 | A |
| | WAP-15 | M | 4/01 | 428 | 36 | 0.6 | A |

proportional movement showed a trend toward declining in the winter (Season; $F = 2.438$, df = 3,45, $P = 0.077$). However, mean proportional movement was higher at WAP (0.517 ± 0.040, $N = 38$) than at MT (0.327 ± 0.067, $N = 15$, $F = 8.515$, df = 1,45, $P = 0.005$), and this difference did not change with season (Site × Season; $F = 0.221$, df = 3,45, $P = 0.881$).

We compared the single individuals at SMER and CNM to the average proportional movement at both MT and WAP using one-sample $t$-tests. The male boa at CNM had a higher proportion of fixes that were movements (0.64) than the boas at either WAP (0.52 ± 0.04, $N = 10$; $t = -2.478$, df = 9, $P = 0.035$) or MT (0.29 ± 0.04, $N = 5$; $t = -5.880$, df = 4, $P = 0.004$). The female at SMER had a higher proportion of fixes that were movements (0.56) than the boas at MT ($t = -4.028$, df = 4, $P = 0.016$) but not WAP ($t = -0.769$, df = 9, $P = 0.462$).

*Distances Moved.*—Frequent short distance movements and rare, long moves resulted in right skewed distributions of distances moved per day for all individuals across all sites (Fig. 1). Summary statistics for all snakes show how the skewness and the method of calculation influence our perception of snake movement (Table 3). For example, mean distance moved per day and mean distance moved per move were greater than median values in nearly all cases. Given the influence of rare long-distance movements, overall meters moved per day (total m moved/total days) was typically smaller than mean distance moved per day (Table 3, column F vs. column G). We used mean distance moved per day in all other calculations.

Excluding cases of no movement, we found positive correlations between distances moved between fixes and distances moved per day in 12

TABLE 2. Total number of fixes by site, season, and sex. Wild Animal Park had sufficient sampling to investigate sex by season interactions. See Table 1 and text for site abbreviations. The number of individual snakes making up the fixes is shown in parentheses.

| | | Study site | | | |
|---|---|---|---|---|---|
| Season | Sex | CNM | MT | SM | WAP |
| Fall | Female | 0 | 16 (4) | 10 (1) | 50 (4) |
| | Male | 15 (1) | 0 | 0 | 114 (6) |
| Winter | Female | 0 | 16 (4) | 5 (1) | 51 (4) |
| | Male | 8 (1) | 0 | 0 | 68 (5) |
| Spring | Female | 0 | 98 (4) | 32 (1) | 101 (4) |
| | Male | 23 (1) | 0 | 0 | 152 (5) |
| Summer | Female | 0 | 51 (4) | 33 (1) | 108 (4) |
| | Male | 19(1) | 12 (1) | 0 | 175 (6) |
| Total number of snakes | | 1 | 5 | 1 | 10 |

of 14 individuals (Table 4). These results indicate when animals moved longer distances, they actually moved farther per day and not that long periods between fixes resulted in long-distance movements. Including distances of zero between fixes increased the correlation coefficients and the sample sizes, making all correlations statistically significant.

Male and female rosy boas had similar distances moved per day (Table 4), and body size did not affect distances moved per day. Like proportional movement, average distance moved per day declined with cool weather ($F = 3.355$, df = 3, 53, $P = 0.026$; Table 4). When considered with the low amounts of proportional movement in the winter, the data show rosy boas not only moved much less frequently but also at slower rates during the Winter.

Long-distance movements occurred predominantly in Spring, with 78 of the 114 farthest 1% of the distances moved per day in the Spring, 28 in the Summer, six in the Fall, and two in the Winter. We found no evidence of sexual bias in these movements with females accounting for 48% (55 of 114) of the long movements.

*Home-Range Size and Novel Habitat.*—Minimum convex polygons (MCP) and kernel home range (KHR) methods produced different estimates of annual home-range size but showed similar patterns of change with increasing numbers of fixes and with season. Home-range size tended to increase with additional fixes for all individuals (Fig. 2A,B) regardless of home-range

TABLE 3. Summary movement statistics for all individuals, both sexes and each season. Summary statistics in columns G, H, I, and J used the entire history of movements for an individual including movements of zero. Standard errors bound mean values. For those rows with means by sex and season, the values are the averages across individuals and represent untransformed values tested in the ANOVAs. Values in parentheses in the column "Sex" represent sample sizes.

| | | A | B | C | D | E | F | G | H | I | J |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ID | Sex | Observed moves | Possible moves | Proportional movement = A/B | Total meters moved | Days | Meters per day = D/E | Mean meters per day ± SE | Median meters per day | Mean meters per move ± SE | Median meters per move |
| CNM-1 | M | 41 | 64 | 0.64 | 2038 | 507 | 4.02 | 6.0 ± 1.3 | 1.8 | 31.8 ± 6.5 | 9.3 |
| MT-1 | F | 26 | 75 | 0.35 | 802 | 441 | 1.82 | 2.9 ± 1.1 | 0.0 | 10.7 ± 2.8 | 0.0 |
| MT-2 | M | 4 | 11 | 0.36 | 174 | 55 | 3.16 | 1.9 ± 1.1 | 0.0 | 15.8 ± 11.2 | 0.0 |
| MT-3 | F | 15 | 33 | 0.45 | 353 | 216 | 1.63 | 2.1 ± 1.1 | 0.0 | 10.7 ± 3.5 | 0.0 |
| MT-4 | F | 9 | 34 | 0.26 | 313 | 214 | 1.46 | 2.0 ± 0.8 | 0.0 | 9.2 ± 3.4 | 0.0 |
| MT-5 | F | 18 | 35 | 0.51 | 570 | 203 | 2.81 | 4.8 ± 1.3 | 0.5 | 16.2 ± 3.9 | 1.0 |
| SM-1 | F | 44 | 80 | 0.56 | 912 | 484 | 1.88 | 3.1 ± 0.7 | 0.5 | 11.7 ± 2.2 | 2.0 |
| WAP-1 | M | 96 | 161 | 0.60 | 2803 | 1146 | 2.45 | 3.5 ± 0.6 | 0.8 | 17.6 ± 2.4 | 6.0 |
| WAP-2 | M | 30 | 107 | 0.29 | 921 | 501 | 1.84 | 1.8 ± 0.5 | 0.0 | 8.9 ± 2.2 | 0.0 |
| WAP-3 | M | 12 | 40 | 0.30 | 190 | 214 | 0.89 | 0.7 ± 0.3 | 0.0 | 4.8 ± 2.2 | 0.0 |
| WAP-4 | M | 37 | 86 | 0.43 | 770 | 485 | 1.59 | 2.7 ± 0.8 | 0.0 | 9.1 ± 1.8 | 0.0 |
| WAP-7 | F | 55 | 101 | 0.56 | 1094 | 859 | 1.27 | 1.7 ± 0.3 | 0.3 | 11.2 ± 2.0 | 3.8 |
| WAP-9 | F | 40 | 69 | 0.59 | 1721 | 488 | 3.53 | 4.7 ± 1.0 | 1.0 | 25.3 ± 5.9 | 4.7 |
| WAP-10 | M | 50 | 80 | 0.63 | 1162 | 783 | 1.48 | 1.9 ± 0.3 | 0.4 | 14.5 ± 2.2 | 5.3 |
| WAP-11 | F | 42 | 80 | 0.53 | 1002 | 744 | 1.35 | 1.9 ± 0.5 | 0.1 | 12.7 ± 2.4 | 0.9 |
| WAP-12 | F | 33 | 61 | 0.54 | 656 | 530 | 1.24 | 1.6 ± 0.4 | 0.1 | 10.8 ± 2.5 | 1.6 |
| WAP-15 | M | 27 | 35 | 0.77 | 1705 | 428 | 3.98 | 4.1 ± 1.0 | 1.7 | 48.7 ± 12.0 | 15.8 |
| Males | (8) | | | 0.50 ± 0.06 | | | | 2.8 ± 0.59 | | 34.5 ± 5.7 | |
| Females | (9) | | | 0.48 ± 0.04 | | | | 2.8 ± 0.41 | | 27.6 ± 2.7 | |
| Fall | (16) | | | 0.49 ± 0.06 | | | | 10.4 ± 2.3 | | 19.5 ± 2.9 | |
| Winter | (13) | | | 0.28 ± 0.07 | | | | 8.3 ± 5.3 | | 16.5 ± 5.1 | |
| Spring | (15) | | | 0.57 ± 0.06 | | | | 22.9 ± 3.8 | | 39.5 ± 5.0 | |
| Summer | (17) | | | 0.51 ± 0.07 | | | | 16.9 ± 3.2 | | 29.8 ± 4.1 | |

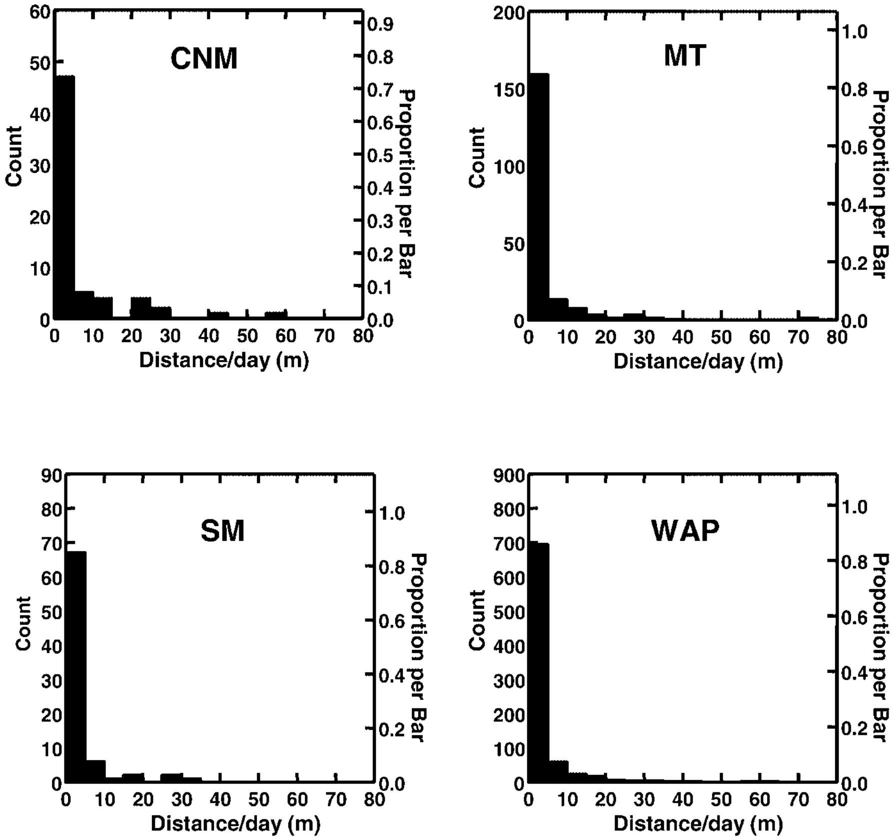

FIG. 1. Frequency histograms of distances moved per day (m) for each of the four study sites. In areas with multiple animals (MT and WAP), data were combined across all individuals resulting in the higher number of total events.

estimator. However, except for the likely released CNM-1, home-range size never exceeded 1.5 ha.

In some cases, the estimate of home-range size declined with additional fixes. Estimators removing a small percentage of the extreme data (95% AK, or FK) sometimes added locations near the center of the home range during periods of no movement, resulting in the removal of outlying points and reductions in home-range size (Fig. 2A). Increases in home-range size typically slowed or stopped during the winter because animals rarely moved (Fig. 2B).

Home-range size increased between years for nine snakes, remained approximately the same for two, and declined for one individual. In some cases, changes were attributed to smaller or larger sample sizes between years, but in general home-range sizes varied between individuals and showed no annual patterns. Given the dynamic nature of home-range size and its dependence on sample size and season of data collection, we did not compare home-range size by sex, season, site, or body size.

In many cases, snakes added considerable amounts of additional area to their home range from one year to the next (mean ± SE % novel habitat in 2000 = 70.7 ± 13.2, $N$ = 6; 2002 = 73.2 ± 5.1, $N$ =6; 2003 = 64.6 ± 11.4, $N$ = 5). Despite the addition of habitat, snakes also remained in the same general area over long periods of time reusing substantial areas from previous years. For example, WAP-1 and WAP-10 kept their home ranges in the same general location each year, despite large amounts of novel habitat between years and different directions of change in home range size (WAP-1 decreased, but WAP-10 increased; Fig. 3).

Although we did not quantify home-range overlap, snakes at WAP and MT showed overlap and sympatric space use (Fig. 4). At WAP, 12 snakes (10 radiotracked snakes, and two other small rosy boas) occurred within a 5.6-ha area. There were 26 instances of individual snakes occurring within 5 m of each other. On five occasions, two rosy boas were found together, and in most cases, the two snakes differed in sex.

One pair of snakes (WAP-2, WAP-9), was first found together in March 2001 and again in May 2001. The pair then remained together until mid-June 2001, moving over a 100 m distance.

## Discussion

This research highlights four patterns in rosy boa spatial ecology. First, individual variation in movement and space use is more a rule than an exception. Second, despite this variation, common patterns exist regarding seasonality of movement and right-skewed movement distributions. Third, rosy boa home ranges vary in size through time but remain in the same general location. Fourth, our data strongly suggest rosy boas do not show territoriality, and considerable overlap is common.

*Individual Variation.*—Despite consistent seasonal changes in movement, individual snakes exhibited high levels of variation in the daily timing of activity, proportional movement, and distances moved per day. For example, proportional movement at WAP varied from 0.29–0.77, whereas mean distance moved per day varied from 15.8–63.2 m. We do not know whether such differential spatial activity is common across snake species. For example, Shine (1987) also found individual variability in *Pseudechis porphyriacus*, whereas Plummer and Mills (2000) reported similar home range size and movement patterns among resident *Heterodon platirhinos*.

In our study, differences across individuals in the proportion of fixes collected during active and inactive seasons undoubtedly explain some of this variation. Shine (1987) suggested the large geographic extent of his study and a severe drought may have contributed to the observed variability across individuals. In our study, even animals coexisting within the same study site showed relatively large differences in space use and movement. Furthermore, we found no evidence body size affected space use. Thus, additional factors, such as reproductive activity, physiological state, or the density of rodents and rodent burrows within a home range, may have impacted space use.

*Seasonality and Skewness in Movement.*—Similar to Secor (1992), we found a decline in movement and activity during colder winter months. Surprisingly, the boas remained somewhat active during the fall, with rates of proportional movement similar to those in the spring and summer but with lower distances moved per day. Although rare, we observed boas above ground during November, December, and January. Other snake species in southern California may show less activity during cooler seasons than boas. For example, radio-tracked Red Diamond Rattlesnakes (*Crotalus ruber ruber*) studied concomitantly at WAP entered dens in mid-November and remained inactive typically until March (T. K. Brown, unpubl. data). Similarly, recent telemetry work on *Masticophis flagellum* showed animals below ground and inactive by September (M. J. Mitrovitch, unpubl. data). Also, Klauber (1939) found snake road kills began in March, peaked in May, and declined through September.

TABLE 4. Correlation coefficients between the distance moved (m) between fixes and the distance moved per day (m/day) when animals moved (movements of zero excluded). For each interval between a fix, we calculated both the distance moved and the distance moved per day. Sample size refers to the total number of intervals (total number of fixes = 1) used in each correlation.

| Individual | Correlation coefficient | $N$ | $P$ |
|---|---|---|---|
| CNM-1 | 0.748 | 41 | <0.001 |
| MT-1 | 0.603 | 26 | 0.001 |
| MT-2 | 0.478 | 4 | 0.522 |
| MT-3 | 0.615 | 15 | 0.015 |
| MT-4 | 0.591 | 9 | 0.093 |
| MT-5 | 0.504 | 18 | 0.033 |
| SM-1 | 0.832 | 44 | 0.001 |
| WAP-1 | 0.684 | 96 | 0.001 |
| WAP-2 | 0.562 | 30 | 0.001 |
| WAP-3 | 0.171 | 12 | 0.595 |
| WAP-4 | 0.571 | 37 | 0.001 |
| WAP-7 | 0.647 | 55 | 0.001 |
| WAP-9 | 0.840 | 40 | 0.001 |
| WAP-10 | 0.756 | 50 | 0.001 |
| WAP-11 | 0.451 | 42 | 0.03 |
| WAP-12 | 0.808 | 33 | 0.001 |
| WAP-15 | 0.860 | 27 | 0.001 |

We observed right-skewed distributions in movement distances for all individuals; similar to those reported for *H. platirhinos* (Plummer and Mills, 2000). Right-skewed movement distributions are likely common in many species (see summarized case studies in Nathan et al., 2003), including small mammals (Diffendorfer et al., 1996), birds (Conner et al., 1997), butterflies (Baguette, 2003), plants (van der Pijl, 1982), and snakes (Plummer and Mills, 2000). Causes for right skewness include processes causing both the high frequency of short distance movements and processes causing rarer, longer movements.

For snakes, sleep and its associated inactivity, the ubiquity of some centrality in space use (i.e., home ranges or territories), and risk of predation all contribute to shorter distance movements. Movement patterns expressing a tendency to return toward a central location may be common in snakes because many recent studies, including ours, report such patterns (Shine, 1987; Webb and Shine, 1997; Reinert and Rupert, 1999; Johnson, 2000; Plummer and Mills, 2000; Whitaker and

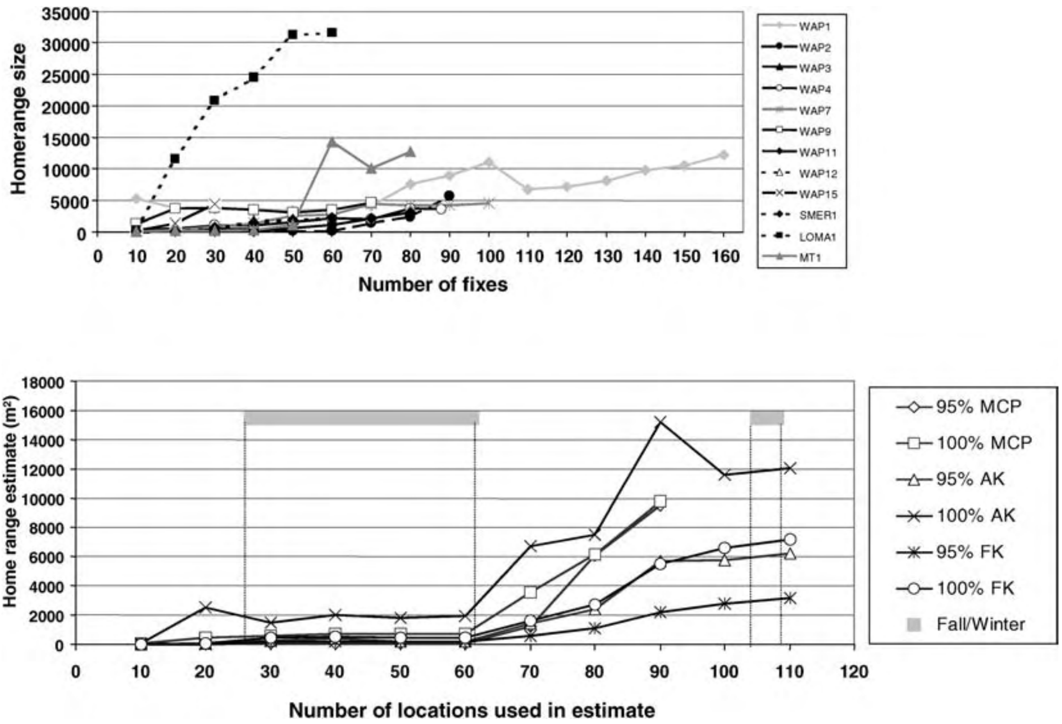

FIG. 2. Increase in home-range size estimated using the 95% adaptive kernel method with increased numbers of fixes. (A) represents all snakes across all time periods. (B) shows home-range size with increasing numbers of fixes for WAP 2. Home range was calculated using 95% or 100% of the data and either Minimum Convex Polygon (MCP), Adaptive Kernel (AK), or Fixed Kernel (FK) method. The gray bar at the top of the figure represents fall and winter. Other snakes showed similar patterns.

Shine, 2003). Although difficult to study, predation risk likely increases with time spent above ground and perhaps moving. For example, Reinert and Rupert (1999) showed declines in survivorship with longer distance movements for *Crotalus horridus*, and Bonnet et al. (1999) showed snake species with longer distance movements experienced greater mortality than sedentary species. As for rare, longer distance movements, factors have been reported for a number of snake species including searching for mates and migrating to seasonal hibernacula or gestation sites.

We spent considerable time on the issue of skewness because it should impact the statistics chosen and how one reports and analyzes movement data. Comparing movement patterns between species or between populations is surely a powerful tool for developing our understanding of snake movement ecology. However, building on Shine's (1987) recommendations, authors must report appropriate statistics given the properties of their movement data. Even recently, authors report estimates of distances moved per day using the two different methods described in Table 3 (i.e., columns F vs. G in this paper, see Ashton 2003), which give different values when data are skewed.

We suggest future work report frequency distributions of movements (instead of simply their summary statistics) because the shapes of these distributions likely reflect a rich summation of trade-offs affected by both longer-term natural selection as well as more proximate environmental factors. Reporting only summary statistics may hide patterns evident in the shapes of these distributions. Contrasting how these distributions change through time, across degraded habitats, or across species and determining the processes causing their shape may lead to valuable insights.

*Variability in Home-Range Size.*—Regardless of the estimation method, we found home-range size increased with additional locations for all snakes and animals typically used substantial amounts of novel habitat each year. However, snakes tracked multiple years remained in the same general area, and only one snake had a home-range size greater than 1.5 ha, even after four years of data. Furthermore, within a period

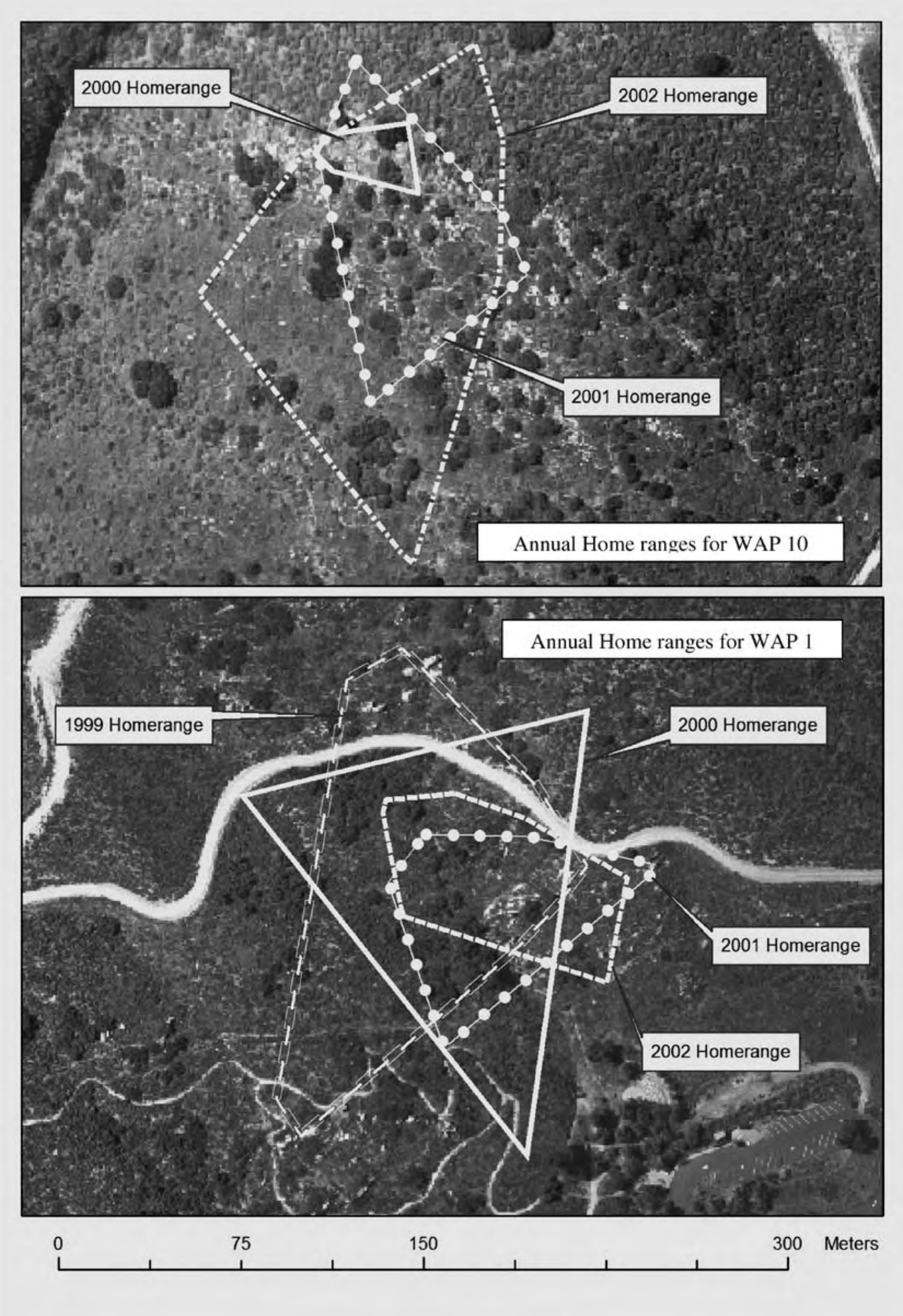

FIG. 3. Annual 100% minimum convex polygon home ranges for two male rosy boas at the Wild Animal Park. The home ranges show considerable overlap across years.

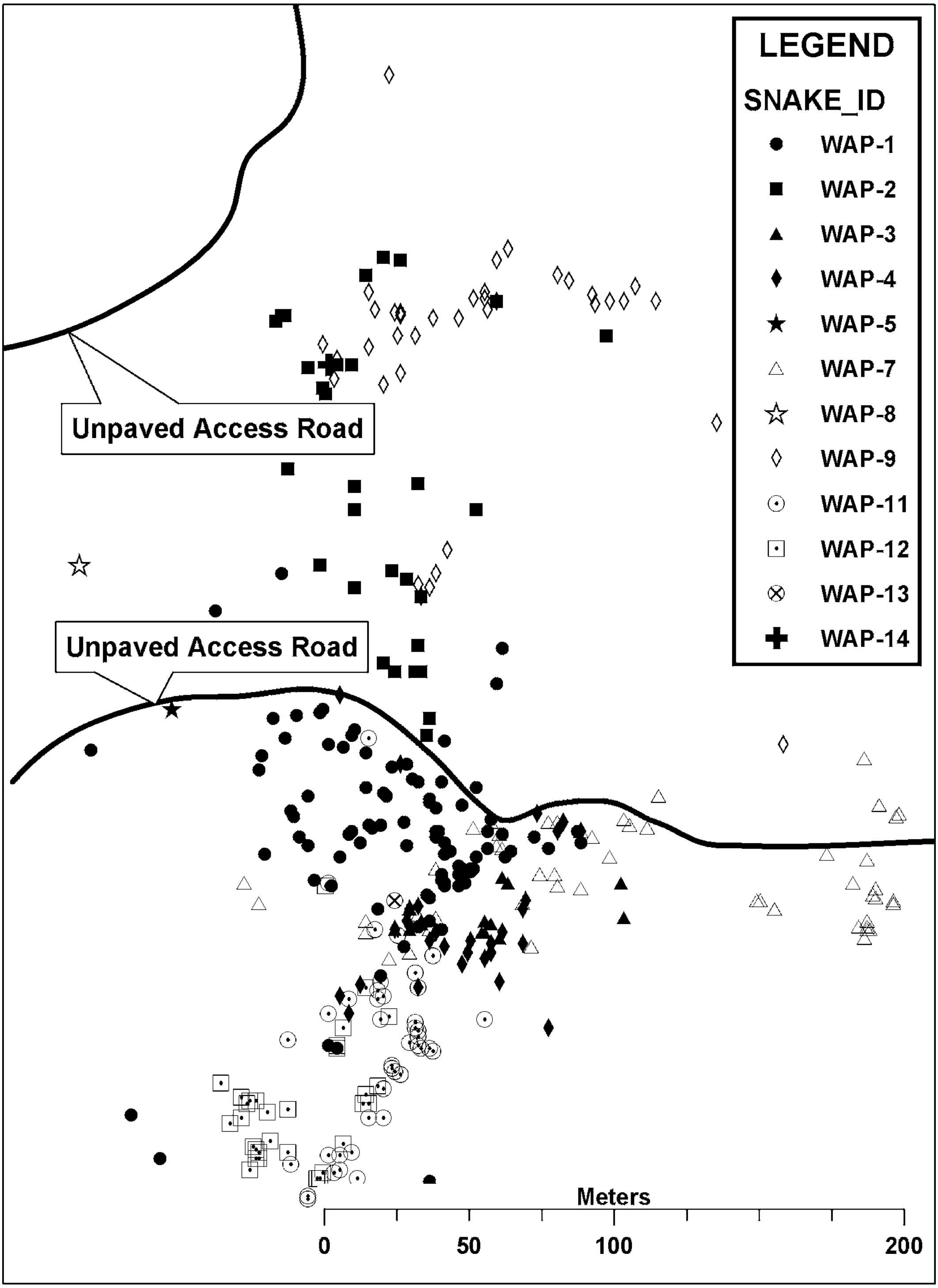

FIG. 4. Locations of 10 rosy boas tracked at the Wild Animal Park showing high levels of spatial overlap. Solid symbols are male snakes, and open symbols are female snakes.

of activity (spring and fall) snakes returned to particular sites and reused areas where they had already traveled. Thus, even with the rare long-distance movements, individuals had relatively fixed home ranges.

Notably, the home-range sizes for the boas in our study were smaller, relative to similarly sized snakes. Parizek et al.'s report (D. A. Parizek, P. C. Rose, C. R. Schwalbe, and C. H. Lowe, 1996, unpubl.) indicated an average Minimum Convex Polygon for six Mexican Rosy Boas (*Charina trivirgata trivirgata*) radio tracked for ~1 yr in Arizona of 1.8 ha ± 0.52, very similar to our findings. We compared our home-range sizes to those reported by MacCartney et al. (1988) for similarly sized species with similar sampling efforts (species with larger home ranges but comparatively smaller sampling efforts were included but not vice versa). Of these 13 species, only three had smaller reported home ranges than the rosy boas (*Carphophis amoenus*, *Coronella austriaca*, and *Vipera aspis*). Within these 13 species, home ranges varied from 207.4 ha for *Crotalus horridus* to 0.18 ha for *V. aspis*, indicating factors beyond body size likely influence home-range size. Perhaps selective forces shaping the spatial ecology of different species and phylogenetic constraints explain the majority of this variation. Teasing apart the interplay between species plasticity and natural selection on movement patterns should lead to a greater understanding of the factors determining the large amounts of variation in snake movement patterns.

*Lack of Territoriality and Habitat Use.*—The observed spatial overlap among individuals and the multiple instances of sharing particular sites strongly suggest rosy boas are not territorial. In their 1996 unpublished study, D. A. Parizek, P. C. Rose, C. R. Schwalbe, and C. H. Lowe, found overlap in six Mexican Rosy Boas in Arizona. M. E. Dorcas (pers. comm.) also found considerable overlap and sharing of particular locations for rubber boas (*Charnia bottae*) observing six gravid females basking on one rock within 0.5 m of each other. We repeatedly found boas together with no evidence of conspecific avoidance as was seen for Stephens' banded snakes (*Hoplocephalus stephensii*; Fitzgerald et al., 2002).

Unlike the avoidance seen between male *Pituophis catenifer* (Rodriguez-Robles, 2003) or the spring time avoidance observed in male *Hoplocephalus bungaroides* (Webb and Shine, 1997), we found male rosy boas together with no sign of combat or displacement behavior throughout the entire study.

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# Ecology and Reproduction of *Anolis capito* in Rain Forest of Southeastern Nicaragua

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**ABSTRACT.—We studied the ecology of *Anolis capito* in the rain forest of southeastern Nicaragua during late dry season of 1993. These cryptic anoles live low on trunks in shaded rain forest and are active throughout the day but appear to spend most of their time in shade. Body temperatures averaged 28.8 ± 0.5°C, which is 1.3°C higher than substrate temperatures and 1.7°C higher than air temperatures. Females were larger and reach sexual maturity at a larger SVL than males. Females in late dry season often contain two oviductal eggs that differed in shell condition indicating that they were not ovulated simultaneously. Females had evidence of as many as four clutches (two oviductal eggs and two different-sized enlarged vitellogenic follicles) suggesting rapid clutch production. The diet consists of a variety of invertebrates, with grasshoppers, homopterans, insect larvae, and roaches dominating volumetrically. On average, these lizards contained 1.6 ± 0.1 prey items. Prey size varied with lizard size, but no sexual differences existed. These lizards appear to capture a small number of large prey. Many ecological and life-history traits of *A. capito* are similar to those of other *Anolis* lizards suggesting an historical origin.**

As more and more tropical forest regions experience deforestation or other habitat modification, ecological studies of individual species, species assemblages, communities, and entire ecosystems increase in importance. Establishing the "value" of tropical ecosystems requires data on resident species such that decisions on forest "development" can be made with the best possible ecological information. Descriptive ecological studies of lizards are important because "(1) basic ecological data are lacking for most species; (2) ecological data provide the basis for understanding the role of each species in

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complex ecosystems; (3) ecological data can be used in phylogenetic analyses that synthesize data from many studies and trace the evolutionary history of such traits; and (4) ecological data provide an arsenal for defending the value of natural ecosystems when drastic habitat alteration is considered" (Vitt et al., 2003a).

Central American moist forests are among the Earth's most endangered ecoregions (Mittermeier et al., 2000) and have experienced rapid conversion to agriculture following deforestation even though detailed studies on many resident species are lacking. The natural history of many Central American rain forest species has been summarized by various authors (Rand and Myers, 1990; see chapters in Janzen, 1983), and a number of detailed ecological studies have provided insight into the value of individual species for understanding biological processes (e.g., Andrews and Rand, 1984; Andrews et al., 1983; Guyer, 1988a,b). The vast majority of studies on Caribbean rain forest lizards have taken place in Costa Rica or Panama, most likely a result of ease of access, availability of well-equipped field stations, and a high level of funding that has been directed toward studies in these two areas. Studies in other regions should be of particular interest because they provide a yardstick against which to examine geographic variation in ecological traits.

In an earlier paper, we compared ecology of all lizard species occurring just north of the Río San Juan in Nicaragua (Vitt and Zani, 1998). The primary intent of that paper was to provide a community-level analysis of rainforest lizard diets, with very little detail on individual species. In this paper, we describe the ecology of one species, *Anolis capito* in much more detail. Although *A. capito* (as *Norops capito*) was listed as a species occurring in rain forest of Costa Rica by Scott et al. (1983) and indicated as a potential predator on another anole (*Anolis polylepis*) by Andrews (1983), no ecological information was included. Savage (2002) described *A. capito* as an anole inhabiting "relatively undisturbed Lowland Moist and Wet Forests and Premontane Wet Forest and Rainforest." It is arboreal, perching low on tree trunks, a thermoconformer, and reproduces year round (see also Fitch 1975; Corn, 1981; Fitch and Seigel, 1984). *Anolis capito* is a species for which little detailed ecological data have been published.

## MATERIALS AND METHODS

*Study Site, Sampling, Microhabitats, Activity, and Thermal Ecology.*—We conducted this study in Caribbean rainforest near the north bank of the Río San Juan in Río San Juan Province, Nicaragua, between 13 March and 20 April of 1993 (Vitt and Zani, 1998), which is late in the dry season. Most of the study site was undisturbed, but a few small patches of slightly disturbed forest were included in our sampling. For each lizard, we recorded habitat (primary or secondary forest), microhabitat (tree trunks or leaf litter; although other microhabitats were available, none was used by *A. capito*), and height off ground and perch (trunk) diameter in centimeters. We also recorded whether lizards were in sun, shade, or active under clouds. We collected all lizards by hand. Within 30 sec of capture, we took lizard body temperature ($T_b$) with a Miller-Weber rapid-register thermometer. We also recorded air ($T_a$) and substrate ($T_{ss}$) temperatures at the point of capture. Upon return to our field laboratory, we euthanized lizards with a lethal injection of Nembutal.

*Morphology and Reproduction.*—We took the following relevant measurements on all lizards prior to fixation: snout-vent length (SVL), tail length, and length of regenerated tail portion (if any) to 1.0 mm with a metric rule; total mass (0.1 g) with Pesola spring balances; head width, length, and height, body width and height, and hindleg length (0.1 mm) with dial calipers. We individually tagged all lizards and preserved them in 10% formalin. Within two weeks of capture, lizards were dissected and sex was determined on the basis of reproductive organs. Males were considered sexually mature if they contained enlarged testes and distended epididymides. Females were considered sexually mature if they contained vitellogenic follicles and/or oviductal eggs. We counted the number of oviductal eggs, assigned them to left or right oviduct, and measured (length and width to 0.01 mm), towel dried, and weighed them to 0.1g. We noted whether shell was present or absent. We calculated oviductal egg volume as:

$$V = \pi L W^2 (3c^2 + 14c + 35)/210,$$

where $L$ is egg length, $W$ is egg width, and $c = \lambda (\sqrt{E} - 1)$. We estimated $E$ for individual eggs by dividing egg length by width and $\lambda$ was estimated as 0.25 by comparing the shape of *A. capito* eggs with models in Maritz and Douglas (1994). We also counted and measured vitellogenic follicles and noted whether they were in the left or right ovary. We estimated relative clutch mass as oviductal egg mass/body mass (Vitt and Congdon, 1978). Finally, we estimated the minimum number of clutches a female could produce by totaling up the number of oviductal eggs and enlarged vitellogenic follicles.

We performed a Mann-Whitney $U$-test on SVL and mass of adults to test for sexual dimorphism in size. To test for sexual differences in other morphological traits, we $\log_{10}$-transformed all morphological variables. We then performed analyses of covariance (ANCOVA) on each morphological variable with SVL as the covariate and sex as the class variable.

*Diet.*—We removed stomachs from lizards, separated prey items on a Petri dish, identified them to family level when possible (all were identified at least to order), and measured length and width of each prey item to 0.1 mm with dial calipers. Prey categories for analysis were: Collembola, Orthoptera, Blattaria, Phasmatida, Homoptera, Coleoptera, Lepidoptera, Diptera, ants, insect larvae, spiders, Diplopoda, Chilopoda, Isopoda, and lizards. We estimated volumes of individual prey with the formula for a prolate spheroid:

$$V = 4/3\pi(L/2)(W/2)^2,$$

where $L$ = prey length and $W$ = prey width. We consider this a reasonable procedure because prey in the stomach are tightly packed, with limbs and wings pressed against the body, thus presenting the minimum possible volume. We used the computer program BugRun, a 4th dimension–based analysis, to produce the dietary summary, calculate mean prey size (length, width, and volume) for each lizard, estimate stomach volume based on total prey volume, and calculate niche breadth using the inverse of Simpson's (1949) measure (Pianka, 1975):

$$\beta = 1/\sum_{i=1}^{n} p_i^2,$$

where $p$ is the proportional utilization of each prey type $i$. Niche breadth values (β) vary from 1 (exclusive use of a single prey type) to $n$ (even use of all prey). Output from BugRun includes a summary of mean prey length, width, and volume for each individual lizard.

We examined the effect of lizard size on prey size and number of prey eaten by first $\log_{10}$-transforming mean prey volume, number of prey per stomach, and lizard size data and then performing a regression analysis on the $\log_{10}$ transformed variables with $\log_{10}$-SVL as the independent variable. We compared prey size and number of prey eaten between sexes with an ANCOVA with lizard $\log_{10}$-SVL as the covariate and sex as the class variable.

All lizards were ultimately transferred to 70% ethanol for permanent storage and deposited in the Sam Noble Oklahoma Museum of Natural History (OMNH) or the National Museum of Nicaragua in Managua. Means are presented throughout ± 1 SE.

## RESULTS AND DISCUSSION

*Habitat Use and Thermal Ecology.*—In lowland rainforest of southeastern Nicaragua, *A. capito* occurs in undisturbed and slightly disturbed rain forest, where it resides low on trunks of relatively small trees. Among 26 individuals for which we collected habitat and microhabitat data, 24 (92.3%) were in primary forest, and two (7.7%) were in secondary forest. Individuals are most frequently observed off the ground, but they occasionally descend to the ground, most likely to capture insects (see Savage, 2002). Nineteen (73.1%) of those were first observed on tree trunks, and seven (26.9%) were on leaf litter. The 19 on tree trunks averaged 45.8 ± 7.2 (12–120) cm off the ground. Diameter of trunks on which lizards were found averaged 7.9 ± 3.0 (1–60) cm. Four of 22 (18.2%) lizards were in sun when first observed, 16 (72.7%) were in shade, and two (9.1%) were active under clouds. Lizards were found on tree trunks or in leaf litter through most of the day (Fig. 1). They are cryptic in morphology and color, resembling a patch of lichens on the tree trunk.

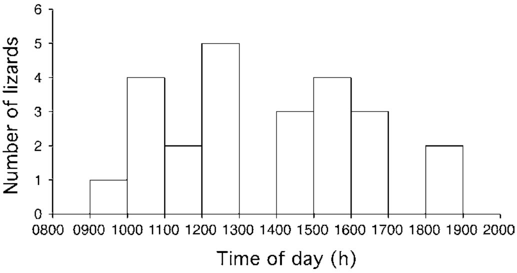

FIG. 1. Daily activity cycle of *Anolis capito* in southeastern Nicaragua based on field observations of active lizards.

Body temperatures ($T_b$) of 16 lizards averaged 28.9 ± 0.4°C with corresponding $T_{ss}$ and $T_a$ averaging 27.7 ± 0.4°C and 27.4 ± 0.5°C, respectively. Although a significant relationship existed between lizard $T_b$ and both $T_{ss}$ ($R^2 = 0.662$, $F_{1,15} = 19.8$, $P = 0.0001$) and $T_a$ ($R^2 = 0.425$, $F_{1,15} = 12.1$, $P = 0.0037$), lizard $T_b$ averaged 1.3 ± 0.3°C higher than $T_{ss}$ and 1.5 ± 0.3°C above $T_a$. The relationship between $T_b$ and $T_{ss}$ is $T_b = 11.011 + 0.647$ ($T_{ss}$). Even though lizard $T_b$ was tightly correlated with $T_{ss}$ and $T_a$, lizard $T_b$ averages slightly higher than $T_{ss}$ or $T_a$ suggesting that some basking takes place for heat gain. This is also suggested by observations that 18% of lizards were first encountered in sun. $T_b$ is low relative to many Neotropical lizard species that occupy forest clearings or treefalls (e.g., *Ameiva festiva*, Vitt and Zani, 1996a; *Kentropyx calcarata* and *Mabuya nigropunctata*, Vitt et al., 1997a), but similar to lizards that occupy shaded microhabitats within undisturbed rain forest (e.g., *Anolis nitens* [as *Anolis chrysolepis*], Vitt and Zani, 1996b; Vitt et al., 2001; *Anolis trachyderma*, Vitt et al., 2002; *Gonatodes hasemani* and *Gonatodes humeralis*, Vitt et al., 1997b, 2000; *Neusticurus juruazensis* and *Neusticurus ecpleopus*; Vitt and

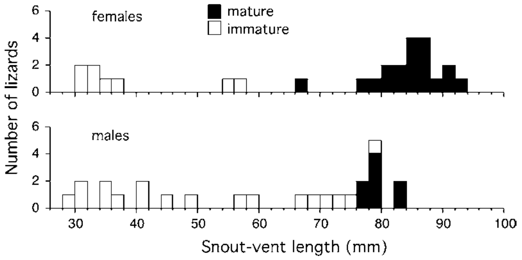

FIG. 2. Distribution of SVL for *Anolis capito* in southeastern Nicaragua.

Avila-Pires, 1998; Vitt et al., 1998). Thus, for the most part, our quantitative data are consistent with Savage's (2002) qualitative description of habitat use and thermal ecology of *A. capito.*

*Morphology.*—Thirty captured females averaged 70.3 ± 4.3 mm SVL (Fig. 2) and weighed 9.2 ± 1.1 g. The largest female measured 92 mm SVL (Fig. 2) and weighed 15.5 g. Twenty-nine males captured averaged 59.5 mm SVL and weighed 5.6 ± 0.8 g. The largest male measured 82 mm SVL and weighed 11.2 g. Among adult lizards, females had larger SVL (Mann-Whitney $U$, $Z = -4.2$, $P < 0.0001$) and mass (Mann-Whitney $U$, $Z = -4.4$, $P < 0.0001$) than males. Adult females averaged 84.8 ± 0.9 mm SVL and weighed 12.8 ± 0.4 g. Adult males averaged 77.1 ± 1.0 mm SVL and weighed 9.4 ± 0.5 g. No sexual differences were detected in mass (ANCOVA, $F_{1,49} = 2.7$, $P = 0.1066$), head width (ANCOVA, $F_{1,49} = 2.5$, $P = 0.1202$), or head length (ANCOVA, $F_{1,49} = 2.5$, $P = 0.1170$) independent of those associated with differences in SVL. However, males had longer forelegs and hind legs than females independent of SVL (ANCOVA, all $P$-values $< 0.001$). Thus the only apparent sexual dimorphism appears to be in adult body size (SVL and mass) and relative limb lengths. Similar sexual differences have been observed in some other lizard species (e.g., three subspecies of *Anolis nitens*; Vitt et al., 2001). The function of relatively longer limbs in male lizards remains unknown, but may be associated with bobbing, dewlap extension, and other social behaviors of males that involve lifting the front part of the body. Consequently, it may be attributable to sexual selection if males with relatively longer forelimbs have greater reproductive success as a result. This remains to be determined. Male *A. capito* reach sexual maturity at a smaller size than females, which might account for their smaller size through life. When males are the larger sex, sexual dimorphism usually is attributed to sexual selection (e.g., Jenssen, 1970; Stamps, 1983; Vitt et al., 1995). In *Anolis* species with females larger than males (e.g., Vitt et al., 2001, 2002, 2003a), large female size may allow females to produce larger eggs (see Andrews and Rand, 1974) and it could allow more rapid clutch production. Apparently, in *A. capito*, as in some other anoles (e.g., *A. nebulosus*; Ramírez-Bautista and Vitt, 1997), the advantages to large male size (increased ability to secure mates; Ruby, 1981) outweigh the advantages to large female size (e.g., ability to produce larger eggs or produce eggs at a more rapid rate; Andrews and Rand, 1974).

*Reproduction.*—Seventeen females contained one of several possible combinations of oviductal eggs and enlarged vitellogenic follicles. Eight contained two oviductal eggs, one with shell and one without, and one contained two shelled oviductal eggs. In the latter, one egg had a more developed shell than the other. Among the 17 reproductive females, nine contained a combination of oviductal eggs and vitellogenic follicles suggesting a minimum of three clutches and eight showed similar evidence of four clutches (two oviductal eggs and two enlarged vitellogenic follicles). Overall mean number of minimum potential clutches was 3.5 ± 0.13. Presence of two oviductal eggs and, in many instances, two additional vitellogenic follicles (four sequential clutches) in female *A. capito* suggests that clutches may be produced in rapid succession. Although we do not know the amount of time between clutches in *A. capito*, some anoles are known to produce an egg every seven days (Andrews, 1985). Rapid clutch production may reflect seasonally high abundance of resources (Ballinger, 1977). Alternately, some combination of day length, temperature, and moisture may signal that the dry season is coming to an end, and as a result, females begin producing clutches in rapid succession. If so, then high resources associated with the wet season may be most important for hatchlings. Andrews and Sexton (1981) found that warm temperatures, which signaled drought conditions, caused *A. limifrons* and *A. auratus* to curtail reproduction. Thus reproductive response to immediate environmental conditions appears likely in *A. capito* as well.

The difference in size of shelled versus unshelled oviductal eggs was reflected mostly in egg length (Table 1) which translated into large differences in egg volume and mass; freshly ovulated eggs did not differ in width from shelled eggs ready to be deposited. Among females with two oviductal eggs, only one was in each oviduct. Both the difference in presence of shell and size indicates that each oviductal egg was ovulated at a different time (allochronic pattern of Smith et al., 1973). Mass of shelled oviductal eggs was not correlated with lizard SVL ($r_s = 0.078$, $P = 0.837$) or lizard mass ($r_s = 0.231$, $P = 0.540$).

Reproduction in *A. capito* appears similar to most anoles studied. Eggs ovulated allochroni-

TABLE 1. Body size and reproductive characteristics of female *Anolis capito* containing two oviductal eggs. In all cases but one, one oviductal egg (first clutch) had a shell; the other did not (second clutch). For the individual containing two eggs with shells in different stages, we considered the more developed shelled egg as the first clutch. These females averaged 85.3 ± 1.6 mm SVL and weighed 13.5 ± 1.5 g in total mass. Oviductal eggs elongate but do not change width as they mature. First eggs averaged 0.16 ± 0.032 g heavier than second eggs.

| Characteristic | First clutch | Second clutch | *F*-value | *P*-value |
|---|---|---|---|---|
| Egg mass (g) | 0.60 ± 0.03 | 0.44 ± 0.30 | 18.8 | 0.0007 |
| Egg length (mm) | 17.46 ± 0.49 | 15.45 ± 0.35 | 11.6 | 0.0053 |
| Egg width (mm) | 7.95 ± 0.16 | 7.28 ± 0.34 | 2.5 | 0.1392 |
| Egg volume ($mm^3$) | 606.07 ± 24.30 | 453.47 ± 39.62 | 10.8 | 0.0054 |
| | 1 egg | 2 eggs | *F*-value | *P*-value |
| Relative clutch mass | 0.045 ± 0.003 | 0.077 ± 0.004 | 46.9 | $< 0.0001$ |

cally (Smith et al., 1973) in rapid succession (e.g., Gordon, 1956; Tinkle, 1969; Andrews, 1985), based on the observation that two eggs with different shell conditions were often present (one in each oviduct) and two vitellogenic follicles (one in each ovary) were also present. Thus, clutch size based on number of eggs produced during an oviposition event is one egg (Fitch, 1970, 1982; Tinkle et al., 1970). This points to the importance of closely examining condition of oviductal eggs in lizards to be certain that the number of eggs estimated for a clutch in dissected females accurately reflects the number of eggs that will be deposited in a single oviposition event. In anoles, clutch size is a single egg even though more than one egg may be represented in oviducts. Like other anoles (Tinkle et al., 1970; Vitt and Congdon, 1978; Vitt and Price, 1982), RCM is low if the single shelled egg is used for the calculation. If both oviductal eggs are used, RCM is still relatively low compared to lizards that produce clutches of several or many eggs.

*Diet.*—A variety of insects and other invertebrates were eaten by *A. capito*. Forty-three lizards contained 67 individual prey comprising 15 different prey types. Prey averaged 15.42 ± 0.98 (2.84–39.64) mm in length, 4.00 ± 0.25 (0.67–10.78) mm in width, and 199.75 ± 35.15 (0.88–1813.23) $mm^3$ in volume. In general, these lizards ate few, relatively large prey items. Prey size varies considerably among *Anolis* lizards, with some Central American species, such as *A. limifrons* and *A. humilis* and South American species such as *A. fuscoauratus* eating many small prey and others, such as *A. biporcatus* and *A. capito* eating a few relatively large prey (Vitt and Zani, 1998). *Anolis* lizards that eat large prey often eat small lizards as well (e.g., Savage 2002; Vitt et al., 2003a,b). On average, lizards contained 1.6 ± 0.1 (range 1–4) prey items. The diet of *A. capito* was dominated numerically by insect larvae and grasshoppers (Table 2). Volumetrically, grasshoppers, homopterans, insect larvae, and roaches dominated. Insect larvae and grasshoppers were eaten by most of the lizards

TABLE 2. Summary of the diet of *Anolis capito* from southeastern Nicaragua.

| Prey type | *N* | % *N* | Volume | % Vol. | Frequency |
|---|---|---|---|---|---|
| Collembola | 4 | 5.97 | 14.52 | 0.11 | 2 |
| Orthoptera | 12 | 17.91 | 3356.51 | 25.08 | 12 |
| Blattaria | 5 | 7.46 | 1580.91 | 11.81 | 5 |
| Phasmatida | 2 | 2.99 | 433.31 | 3.24 | 2 |
| Homoptera | 3 | 4.48 | 3296.64 | 24.63 | 2 |
| Coleoptera | 5 | 7.46 | 714.34 | 5.34 | 5 |
| Lepidoptera | 2 | 2.99 | 134.3 | 1.00 | 2 |
| Diptera | 3 | 4.48 | 321.8 | 2.40 | 3 |
| Ants | 3 | 4.48 | 16.57 | 0.12 | 3 |
| Insect larvae | 17 | 25.37 | 1604.49 | 11.99 | 15 |
| Spiders | 3 | 4.48 | 969.88 | 7.25 | 3 |
| Diplopoda | 5 | 7.46 | 375.72 | 2.81 | 5 |
| Chilopoda | 1 | 1.49 | 163.89 | 1.22 | 1 |
| Isopoda | 1 | 1.49 | 96.65 | 0.72 | 1 |
| Lizards | 1 | 1.49 | 303.62 | 2.27 | 1 |
| SUMS | 67 | 100 | 13383.15 | 100 | — |
| Niche breadths | | 7.86 | | 6.13 | |

sampled. Mean prey volume per lizard was correlated with lizard SVL ($F_{1,39}$ = 91.4, $P <$ 0.0001), but no sexual differences in mean prey volume independent of SVL were found (ANCOVA, with SVL as covariate and sex as the class variable, $F_{1,39} = 0.08$, $P = 0.7854$). Likewise, no sexual difference in number of prey independent of SVL was apparent (ANCOVA, with SVL as covariate and sex as the class variable, $F_{1,39}$ = 1.32, $P$ = 0.2581). A significant relationship existed between stomach contents volume and lizard SVL ($R^2 = 0.71$, $F_{1,41} = 105.3$, $P < 0.0001$), but little variation exists in stomach contents volume independent of SVL. Thus smaller lizards were equally as full as larger lizards. The equation describing the relationship between lizard size and full stomach volume is: $\log_{10}$ stomach volume = 3.627 ($\log_{10}$-SVL) –4.368. This, coupled with the observation that all captured lizards had prey in their stomachs, suggests that they typically were in positive energy balance (Huey et al., 2001).

## CONCLUSIONS

Many ecological and life-history traits of *A. capito* are similar to those of certain other *Anolis* lizards. These include arboreality restricted to tree trunks, shade dwelling, relatively low active body temperatures, and lichen-like cryptic morphology. Still other characteristics are similar to those of all anoles, including allochronic ovulation of eggs and oviposition of a single egg at a time. These similarities likely reflect characteristics of ancestors of *A. capito* at varying levels within the evolutionary history of anoles (e.g., Vitt et al., 2003c). A phylogenetic analysis of ecological traits of anoles may identify the origins of ecological traits within anoles, shedding considerable light on their ecological history.

Habitat modification that reduces the canopy, exposing more of the forest floor to sun likely would have a detrimental effect on populations of *A. capito* because *A. capito* possess a set of ecological traits (shade seeking, low $T_b$, trunk dwelling) associated with presence of tropical rainforest. The observation that these lizards are not found in open habitat patches alone suggests their dependency on relatively undisturbed rainforest. This species will likely disappear with elimination of rainforest canopy.

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