The Mating Behavior of *Iguana iguana*

GORDON H. RODDA

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ABSTRACT

Rodda, Gordon H. The Mating Behavior of *Iguana iguana*. *Smithsonian Contributions to Zoology*, number 534, 40 pages, 18 figures, 11 tables, 1992.—Over a 19 month period I observed the social behaviors of individually recognized green iguanas, *Iguana iguana*, at three sites in the llanos of Venezuela. The behavior of iguanas outside the mating season differed from that seen during the mating season in three major ways: (1) during normal waking hours outside the breeding season, adult iguanas spent the majority of time immobile, apparently resting; (2) their interactions involved fewer high intensity displays; and (3) their day to day movements were often nomadic.

During the mating season, one site was watched continuously during daylight hours (iguanas sleep throughout the night), allowing a complete count of all copulation attempts (N = 250) and territorial interactions. At all sites, dominant males controlled access to small mating territories. Within the territories there did not appear to be any resources needed by females or their offspring. Thus, females could choose mates directly on the basis of male phenotype. Females aggregated in the mating territories of the largest males and mated preferentially with them. Territorial males copulated only once per day, although on several occasions more than one resident female was receptive on the same day. A few small nonterritorial males exhibited pseudofemale behavior (i.e., they abstained from sexual competition), but most nonterritorial males stayed on the periphery of mating territories and attempted to force copulations on unguarded females (peripheral male behavior). Uncooperative females were mounted by as many as three males simultaneously. Females resisted 95% of the 200 observed mating attempts by peripheral males, but only 56% of the attempts by territorial males (N = 43). The selectivity of the females probably increased the genetic representation of the territorial males in the next generation. During the mating season females maintained a dominance hierarchy among themselves. Low ranked females tended to be excluded from preferred mating territories. In this system, both sexes may be subjected to sexual selection. I hypothesize that the ecological factors responsible for the unusual mating system are related to the lack of defendable resources, the iguana's folivory, and the high density of iguanas present in preferred mating areas.

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Contents

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Gordon H. Rodda

Introduction

When Darwin used Henry Spencer's phrase "survival of the fittest" he unwittingly reinforced a common misunderstanding that natural selection maximizes survival. As he knew, it does not; natural selection maximizes reproductive success within the environment in which the organism is customarily found. For this reason, the biological circumstances under which reproduction occurs in nature are of critical interest to biologists. It is surprising, therefore, that so little effort has been made to observe mating under field conditions. Although anurans have attracted a fair amount of attention due to the ease with which the advertising males may be located (Howard, 1978; Ryan, 1985), there are few studies of mating reptiles in the wild. For example, there are only eight published studies reporting to have seen at least 15 complete lizard copulations in the field (see "Forced Copulations"). We cannot hope to understand the evolution of reptiles without better comparative data on the factors that affect reproductive success.

In studying adaptation, the comparative method is usually applied interspecifically in the hope that the trait of interest will be free to covary with the causal factor and that all other traits will be identical or irrelevant. This is unlikely. Intraspecific comparisons, on the other hand, are less influenced by phylogenetic confounds and can provide a well-matched test of adaptation if the trait of interest is found to vary between populations.

The green iguana, *Iguana iguana*, is well suited to interpopulational comparisons of its mating behavior because the species is widely distributed and easily observed. In addition to being diurnal and sedentary, the iguana mates in exposed locations (in trees) and its mating behavior appears to rely almost exclusively on vision, a modality readily monitored by human observers. Dugan (1980; 1982b) described mating behavior of green iguanas from a small island (Flamenco) in the Gulf of Panama. Males displayed with characteristic headbobs, then jockeyed for possession of exclusive mating territories. Mating territories included no resources needed by females; they provided only space to mate. Precopulatory females visited several territories. One to four females selected the mating territory of each large male, and over 90% of the females eventually copulated there. Medium-size males rarely controlled territories with a female. Small males (which resemble females morphologically) obtained a few copulations by entering territories undetected and forcing copulations when the resident male was occupied or out of view.

The major goals of the present study were to provide a relatively complete record of mating behaviors in the green iguana and to compare the results of this study with the study of Panamanian iguanas by Dugan. In the llanos of Venezuela, iguanas often inhabit areas with scattered trees and discontinuous canopy, facilitating visual observation and recognition of individual iguanas. Dugan studied a large number of mating territories, each for short periods of the day. Dugan never observed males to mate more than once per day or to eat during the mating season. However, because she reported that feeding takes about 20 min per day and that copulation lasts about 7 min, it is possible that these behaviors might have occurred when the animals were not under observation. Also, Dugan was not able to identify the individual female iguanas under study. By subjecting a smaller number of known individuals to continuous scrutiny, I was able to unequivocally determine the frequencies and context of selected rare, but potentially significant, behaviors. In combination with Dugan's work, these data provide the most detailed observations available for the mating behavior of a reptile.

This monograph is divided into four parts, each with a "Results" and "Discussion." To provide a context, the first short section, "Nonbreeding Behavior," describes typical green iguana behavior outside the breeding season. The second section, "General Mating Behavior," gives a general description of reproductive behaviors leading to copulation. (Some postcopulatory reproductive behaviors are described in Rodda (1990) and Rodda and Grajal (1990).) The third and fourth sections focus on two aspects of mating that present unresolved theoretical problems: "Forced Copulations" and "Female Dominance Relations." The methods section below describes the methods used throughout.

Gordon H. Rodda, National Ecology Research Center, 4512 McMurray Ave., Fort Collins, Colorado, 80525.

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Materials and Methods

My field assistants and I observed iguanas in the central llanos of Venezuela from June 1982 to January 1984. A blind was set up 50–100 m from 2–8 mating territories at each of three sites: El Frio, Guacimos, and Masaguaral. The areas chosen for observation had iguanas bearing sufficient natural markings that it was not necessary to capture iguanas for individual recognition (Rodda et al., 1988). The primary character used for individual recognition was the morphology of the damaged or unusual dorsal-crest scales. Crest scales are visible from both sides of the animal and each scale was distinguishable on the basis of length (14 character states), attitude (6 states), curvature (6 states), and tip type (6 states; Rodda et al., 1988). Color pattern, tail regrowth, and other morphological idiosyncrasies provided supplemental recognition characters.

The three major study sites were observed periodically throughout the year. A fourth, "La Guanota," was observed opportunistically from a darkened automobile "blind" for information on gross population movements. At Guacimos, one mating territory was observed from before dawn until after dark throughout the 1983 copulation season to provide an uninterrupted record of mating behaviors. To verify that the results from this intensively monitored territory were representative, seven other Guacimos territories were scanned periodically throughout the day from the same blind. In addition, the Masaguaral and El Frio blinds each were used for several hours a day periodically during the 1982 and 1983 mating seasons. The Masaguaral site included two mating territories and was monitored almost every day during mating. At El Frio, the two territories within the study site were monitored for a few days each month. In sum, one Guacimos territory was observed continuously and eleven more territories (at Guacimos, Masaguaral, and El Frio) were observed with varying degrees of thoroughness for one or two mating seasons. Because the sampling intensity varied from site to site, the results that follow are not presented uniformly nor are all cases listed for each site. In some cases, simple descriptive statistics, such as the mean basking time, are reported for an appropriate subsample of the data set. In every case where changes among sites, individuals, or seasons were observed, these differences were analyzed with the most appropriate sample available. The omission of a site from the results simply reflects an inadequate data base from the omitted site with reference to the question at hand. All contrary results are noted.

Subjecting one site to continuous observations for an entire mating season increases the opportunity for detecting rare but significant events such as copulations. The disadvantage of this technique is that a small number of individuals are sampled repeatedly. When analyzing measurements taken repeatedly from the same individuals, I attempted to use repeated measures ANOVAs whenever possible (unless noted, analyses were executed with the Statistical Analysis System (SAS) computer package). If repeated measures ANOVAs were not suitable, I attempted to use each individual's mean score for comparisons or to statistically pair comparisons across individuals and test for differences in each individual's behavior among two or more conditions. When it was possible to quantify the total amount of the variance contributed by individual identity, the contribution usually was found to be less than 15%. The most difficult problem of sample size arose in the analysis of dominant male behavior, because only one dominant male was monitored continuously. In this case, the general applicability of conclusions is based on similarity between the intensively monitored male's behavior and that of the 11 other territorial males that were monitored less intensively.

Study Sites

The Guacimos, La Guanota, and Masaguaral sites were located in the mixed savanna/woodland of the central llanos of Venezuela (habitat described in Neville, 1972). The Guacimos site (8.575°N, 67.605°W), on the ranch "Hato Masaguaral" along the western margin of a lake, Lagunas Guacimos, was observed during all daylight hours from 30 November to 24 December 1983, and at varying hours of the day from 4 October 1983 to 12 January 1984, for a total of 756.5 h. Because iguanas sleep throughout the night (Flanigan, 1973), the more than 40,000 behaviors recorded at Guacimos are a complete record for the copulation season and a comprehensive record for several weeks immediately preceeding and following the copulation season. One hundred twenty-three individual iguanas were seen at the Guacimos site during our observations.

The Masaguaral site (8.564°N, 67.588°W), about 3 km SE of Guacimos at the edge of a seasonal marsh, was observed at varying hours on 258 days from 12 September 1982 to 23 December 1983, for a total of 527.6 h. Almost all of the

observations included the 2 h preceeding sunset, an interval that yielded the greatest number of observable interactions among the iguanas. At Masaguaral we saw a total of 65 individual iguanas during 1982 and 73 during 1983. About half of the observations (138 days, 278.4 h) occurred during October–December, the months of mating activity.

The La Guanota site (6.92°N, 67.52°W) was located on the ranch "Hato La Guanota," immediately upstream from San Fernando de Apure, about 80 km south of the Hato Masaguaral sites. The vegetation was similar to that in the above-mentioned study sites, but the trees were not near a water body. The iguanas were viewed for 1–2 h on each of 7 visits to the site from November 1982 to September 1983 (14 individuals seen).

The El Frio site (7.812°N, 68.897°W), about 160 km SW of the Hato Masaguaral sites, was in a narrow gallery forest among the savannas of the low llanos on the ranch "Hato El Frio" (habitat described by Tamayo, 1964). The study trees, at the edge of an impounded stream, were observed at varying hours on 41 days between 22 September 1982 and 30 December 1983, for a total of 91.7 h. About half of the observations (21 days, 53.3 h) occurred during the mating season months of October–December. We saw 28 individual iguanas in 1982 and 37 in 1983.

Behavioral Methods

Four observers attempted to record all copulations, interactions, and movements within the study sites (typically a space of about 10 × 10 × 10 m). Headbob displays were recorded whenever possible. The fraction of the displays that were not recorded was estimated by comparing the written record with cine films of 44 sequences of interactions filmed during the peak of mating activity. Slow motion analysis of the films revealed that all copulations, interactions, and movements in the sample had been recorded, but only 66% (40 out of 61) of the displays had been noted. The estimated display totals reported in this paper are extrapolations from the tabulated counts. No statistical tests were performed on the extrapolated totals. Values given in the form $x \pm y$ are the mean ± 1 SE. Parametric tests were corrected for nonhomogeneity of variances when appropriate.

At the beginning of the study, a few animals were captured and marked with colored beads, but these animals subsequently exhibited aberrant behavior (Rodda et al., 1988). Consequently, capture and marking was discontinued and all adult iguanas were recognized individually by their unique patterns of color and crest-scale damage or loss (Rodda et al., 1988). For the identifications made by more than one observer, interrater agreement exceeded 99.7% ($N > 1000$).

The relative sizes of individuals were determined by noting which animal of a pair was larger whenever two individuals rested on a branch perpendicular to the observer. At Guacimos these pairings yielded 304 comparisons that were related to absolute dimensions from measurements of nine individuals captured at the conclusion of the study. The nine measured animals included the smallest and largest resident females as well as the second largest male; thus, the sizes of all of the residents at Guacimos are fairly precisely known because they are anchored by absolute measurements. The sizes of iguanas at the other sites are less precisely known, but each animal was readily classified as small, medium, or large based on their approximate absolute size based on direct observation, and on 219 (Masaguaral) or 35 (El Frio) relative size comparisons anchored with measurements of three individuals of extreme size.

Sexing was based on external dimorphisms; dorsal-crest spines, head size, and femoral pore size are larger in males (Dugan, 1980; Fitch and Henderson, 1977; Rodda, 1991). No nominal "males" became gravid and all nominal "females" did so.

The positions of each iguana in a tree were recorded with reference to one of the mapped perches in the study site (207 perches were mapped in the intensively monitored tree at Guacimos). Absolute distances between animals were computed only for Guacimos, where the tree and its environs were photographed at a distance of 30 m from 18 equally spaced positions (0°–340° × 20°). A calibrated reference rod of known dimensions was centrally located in each photograph. When the apparent positions of each perch in each photograph were arrayed by the angle of the photograph, the horizontal and vertical coordinates closely approximated sine functions. Using SAS nonlinear curve-fitting program for a sine function, I obtained a least squares fit for each perch in each dimension. The phase angle in vertical and horizontal dimensions indicated the angle of the perch viewed from above. The horizontal and vertical coordinate amplitudes gave the height of the perch and its distance from the reference rod, respectively. Distances between adjacent perches were computed using the Pythagorean theorem and distances among more distant perches were computed from the string of perches through which the iguana moved as it traversed the tree. This computation was greatly aided by the relatively limited number of pathways available to iguanas in this particular site.

Operational Definitions.—"Perch," "approach," "interaction," and "copulation attempt" have special meanings in this paper. A "perch" was an iguana-size segment of a tree limb or branch that was habitually used by resting iguanas. Initially, each limb was divided into 10, 20, or 100 equal sectors, depending on the limb's absolute length. Records of the positions of resting iguanas were accumulated until clusters of positions became clearly evident for each limb. Perches were based on the modal position within clusters, with the restriction that each perch was sufficiently distant from the immediately adjacent perch that occupancy of one would not physically preclude occupancy of the adjacent perch.

An "approach" was a movement of an iguana from a more distant site to within 2 m of a specific iguana. A frequency histogram of interindividual spacings at Guacimos was

bimodal with an intervening minimum at 2.0 m, indicating that most iguanas stopped moving at a distance either larger or smaller than 2.0 m.

An "interaction" was said to begin if either (1) one iguana approached another, or (2) one animal elicited a reaction from another by bobbing or some other decisive action (e.g., biting). An interaction was said to have ended when either (1) the animals were no longer adjacent, or (2) 5 min had elapsed without any noticeable action. If the interaction involved more than two iguanas and the roles of the various iguanas were unclear the interaction was not scored. This occurred primarily when iguana densities were very high, so that the absolute number of interactions reported at high densities is an underestimate. Each interaction was scored on a scale of 1–5 for its outcome, with a "1" indicating that the approacher had fled rapidly from the site of the interaction (usually leaving the tree), and "5" indicating that the approached animal had fled rapidly (usually by jumping out of the tree). The interactions scored as 1 or 5 were categorized as "high intensity"; the other interactions were termed "low intensity." A "2" indicated that neither animal moved, a "3" indicated a slow or delayed upward movement of the approached animal (the modal response), and a "4" indicated a rapid but short distance movement of the approached animal (usually a displacement of a few perches). These scores are asymmetrical with reference to direction of travel, because both iguanas were incrementally moving upward. A slow upward movement ("3") was the norm and appeared to be a socially neutral outcome.

A "copulation attempt" occurred when a male mounted another iguana. In two cases out of 250 a male mounted another male, which I assumed to be a mistake, because the attempt was quickly broken off and no other evidence of homosexual behavior was seen.

I use "mating" season to include the date of all behaviors preliminary to and including copulation; "copulation" season to include only the dates from earliest to latest copulation; and "breeding" season to include the seasons of both mating and postzygotic parental care (in this case, through oviposition).

Nonbreeding Behavior

RESULTS

The behavior of iguanas outside the mating season differed from that seen during the mating season in three major ways: (1) during normal waking hours outside the breeding season, adult iguanas spent the majority of the time immobile, apparently resting; (2) their interactions involved fewer high intensity displays; and (3) their day to day movements were somewhat nomadic, with less attachment to a specific sleeping tree.

DAILY ACTIVITY PATTERN.—When sleeping, the iguanas usually lay horizontally (23% of 509 sleep site selections) or with head up (75% of 509). Of 115 horizontal perch uses, I recorded about twice as many (75 vs 40) with the head pointed away from the base of the limb as pointed toward the limb base. Although iguanas prefer to sleep at the ends of branches and they prefer branches that extend over water, they showed no preference for specific branch angles or diameters (from 1.5 cm diameter vines up to about 18 cm diameter limbs).

Iguanas slept throughout the night, as indicated by (1) continuously closed eyes, (2) greater arousal thresholds, and (3) continuous immobility. On 59 nights at Guacimos we observed 697 iguanas positions both at dusk and the following dawn. None of the iguanas changed perches. Iguanas became immobile at dusk even if they were in the middle of social interactions when it became dark. The only circumstance in which we observed iguanas sleeping on top of each other was when the top individual had been climbing over the other at nightfall. On one of three such occasions a pair of iguanas were in the midst of a violent fight at dusk. The fight was not resumed at dawn; instead the iguanas disengaged and basked separately.

The iguanas opened their eyes before sunrise, but they did not move until direct sunlight provided an opportunity for them to bask. In emergent trees, this produced a peak of activity at sunrise. For example, from 5 to 20 November 1983 at the Guacimos site I recorded 92 movements in the 15 min interval that included sunrise, compared to only 9 movements during the 15 min interval 1 h later when the iguanas were in the midst of basking. I noticed, but did not quantify, exceptional wariness among the iguanas early in the day; flight distances of iguanas in trees seemed to be about 90 m at dawn compared to 50–60 m after the iguanas warmed up.

The iguanas routinely basked in a head down position. I was unable to determine if this was related specifically to basking or was simply a result of their morning descent of the tree. As they warmed, the iguanas made a series of short, intermittent moves toward the base of their sleeping tree. Excluding the mating season at Guacimos, the average time of departure of large female iguanas from their sleeping trees was 4.09 ± 0.30 h after sunrise (N = 134 departures). Small iguanas usually left before larger ones.

I found it difficult to keep track of individual iguanas as they were foraging on the ground and in nearby trees and shrubs. Therefore, it was not possible to quantify the average time per day spent foraging. However, it was evident that much, if not most, of the foraging occurred on ground herbs and low shrubs. The iguanas quickly returned to the trees whenever humans or foxes approached to within 100–200 m, but it was uncommon for undisturbed iguanas to be high in trees during midday. During midday, the iguanas spent the majority of their time resting. I never saw individuals foraging for a period of greater than 30 min.

Unless disturbed by predators, the iguanas began returning to their sleeping trees two to three hours before sunset. Large iguanas usually arrived before the smaller ones ($F = 6.16$; df = 1,25; $P = 0.020$), but arrival times did not differ between the sexes ($F = 0.61$; df = 1,25; $P = 0.44$). The mean arrival time for the 25 iguanas present at Guacimos in October 1983 (this sample is characteristic of nonmating conditions) was 2.3 h

before sunset for large iguanas and 1.7 h before sunset for small iguanas (i.e., < 350 mm snout-vent length (SVL)). The time of their last move of the day (to sleeping perches) did not vary between sizes ($F = 0.65$; df = 1,32; $P = 0.43$) or sexes ($F = 0.85$; df = 1,32; $P = 0.36$). The average settling time for October 1983 at Guacimos was 0.4 h before sunset. The latest iguana movement in a study area occurred about 0.3 h after sunset regardless of season, but movements after sunset were rare and almost inevitably a result of unfinished interactions between neighbors.

Almost all interactions between nonbreeding iguanas were of low intensity and the outcome usually was predictable on the basis of which iguana was higher in the tree. Individual identities or relative sizes seemed unimportant. A typical afternoon interaction was initiated by an iguana climbing a branch at a slow pace until it reached a point immediately below a resting iguana. In a sample of 226 nonbreeding interactions, the approaching animal gave a headbob in 31% of the cases and the approached animal gave a headbob in 41% (the difference in these proportions was not significant ($G = 1.48$; df = 1; $P = 0.22$). Of these nonbreeding headbobs, 42% were given after the animals had separated and the outcome of the interaction was already apparent (see also "Female Dominance Relations"). I considered four classes of situations for the analysis of headbobs among nonbreeding females (there was insufficient data for the analysis of interactions among nonbreeding males): (1) headbob given before or during an interaction in which the approaching iguana was repulsed, (2) headbob given after an interaction in which the approacher was repulsed, (3) headbob given before or during an interaction in which the approacher prevailed, and (4) headbob given after an interaction in which the approacher prevailed. In the three latter cases there was no significant association between winning and headbobbing. In the first case, the iguana giving a headbob was significantly more likely to be the victor ($G = 38.9$; df = 1; $P < 0.001$).

In nonbreeding season interactions (N = 290) the modal outcome (33%) was no response (i.e., both iguanas remained stationary). However, if an iguana did move, it was much more likely that the animal that was initially stationary would move (55% vs 12%). In about 5% of the cases, the higher animal did not respond to being approached, but the lower animal eventually continued on its way by walking across the back of the higher iguana. The usual response of the walked-upon iguana was to "scratch" or tail arch at the other animal as it passed by, or to bob after the interaction. A "scratch" consisted of swinging the forelimb in the general direction of the other iguana. One or both forelimbs might be used. These movements appeared to be ritualized, as the nominal recipient rarely was touched by the "scratching" animal and no damage was ever done.

I was unable to discern a hierarchy among the iguana individuals based on their success in convincing other iguanas to move ahead when they were ascending the study trees outside of the breeding season (see also "Female Dominance Relations"). At least three factors would make it difficult to identify individual relations if such exist outside the breeding season: (1) a majority of interactions did not have a decisive outcome, (2) the physical asymmetry in interactions (the higher animal usually moves) tended to obscure individual relations, and (3) as iguanas wander more during the nonbreeding season, there are few opportunities for two individuals to interact repeatedly. This wandering habit not only makes it unlikely that specific dyads would be observed repeatedly, but it also minimizes the opportunities for iguanas to develop consistent dominance relationships among themselves.

POPULATION CHARACTERISTICS.—Iguana densities differed among the sites in Venezuela and from the densities in Panama reported by Dugan (1980:32-37; 1982a; 1982b). Unfortunately, it was not appropriate to quantify the densities at the sites I studied in units of individuals per ha, as reported by Dugan. Dugan's site was a small, forested, coastal island over which the iguanas were relatively evenly dispersed. My sites, like most iguana habitats, were strips of trees along water courses. The iguanas foraged in adjacent shrubs and on the ground in the surrounding savannas, but they took refuge almost exclusively in the narrow tree corridors that rarely exceeded the canopy of one tree in width. Iguanas rarely ventured more than 50 m from riparian shrubs and most iguana activity occurred within 15 m. Another indicator of limited movement is the mean daily movement totals for Guacimos of 111 m ($n = 1$ large male for 10 days) and 135 m ($n = 6$ large females, each for 10 days). If one assumes a riparian iguana's habitat to be a tree canopy width of 10 m and a 50 m band of adjacent savanna, the strips of trees illustrated in Figure 1 yield the linear and areal density estimates shown in Table 1. The

TABLE 1.— Nonmating season population sizes of iguanas in the territories shown in Figure 1. Letters in parentheses are territories in Figure 1.

	El Frio	Masaguaral	Guacimos
Mean numbers of sleeping iguanas	1.8(A)	2.3(C)	10(AF)
	4.8(P)	3.2(AZ)	4.5(AG)
			8(AL)
			7(BF)
			4.5(BJ)
			5.5(BZ)
			17(C)
			12.4(H)
Total for site*	6.6	6.4	~80
Est. area of sleeping trees (hectares (ha))	0.02	0.01	0.035
Est. adjacent foraging area (ha)	0.10	0.05	0.175
Length of shoreline (km)	0.021	0.01	0.035
Linear density (iguanas/km)	314	640	2285
Areal density (iguanas/ha) (area is sum of sleeping and foraging area)	55	107	364

* Does not equal sum of territory totals because many iguanas slept in areas that did not become a mating territory.

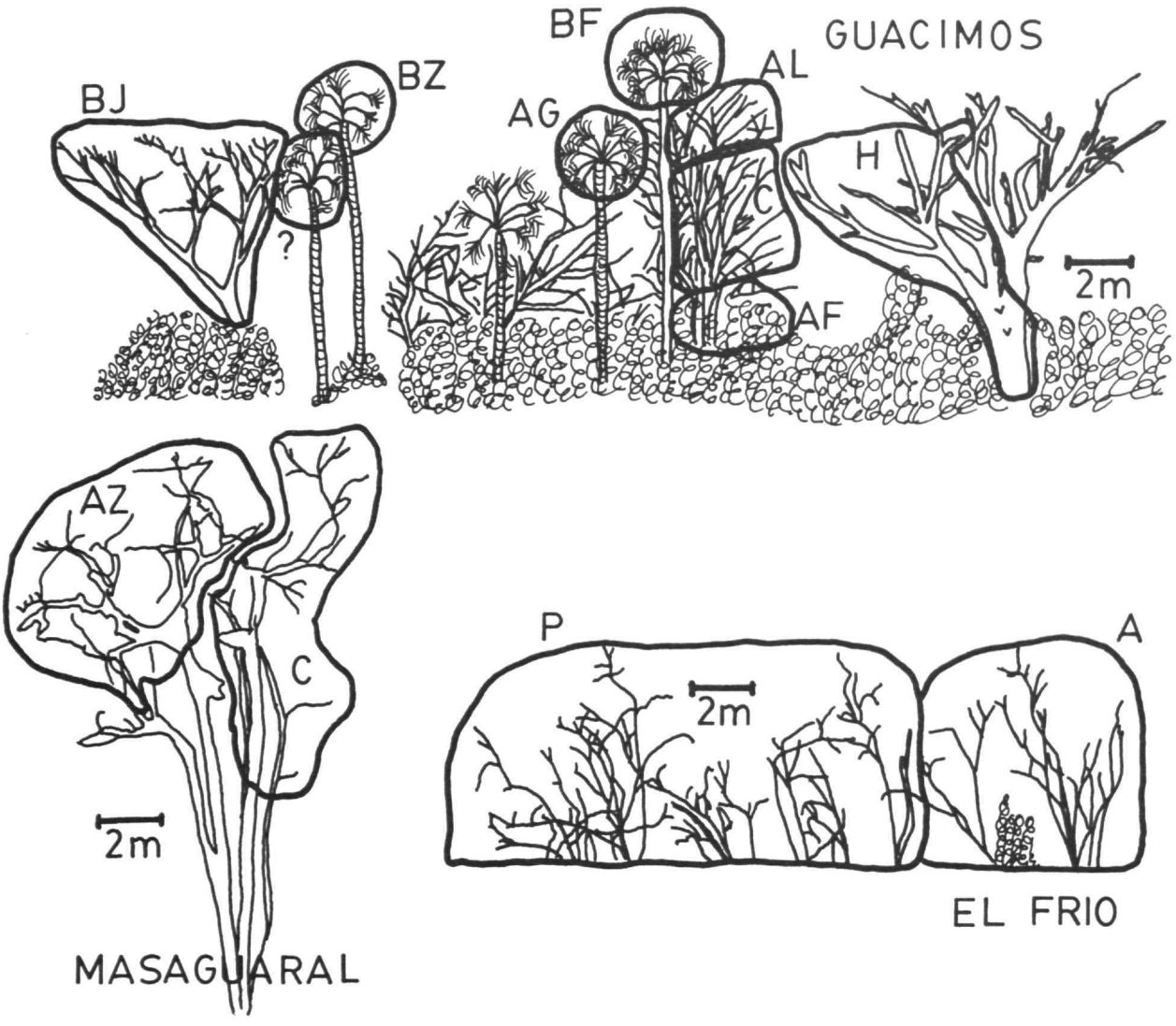

FIGURE 1.—The study sites showing modal territory boundaries (males identified by letter codes). Each of the trees illustrated was approximately cylindrical and most projected out over the adjacent shoreline during the late dry and early wet seasons. During the late wet and early dry (mating) seasons the water rose and submerged the tree bases. The tree, including the territory of male H at Guacimos, was monitored continuously during the copulation season.

values in Table 1 exclude hatchling iguanas, for which no census figures were attempted. The census figures are mean totals of iguanas sighted at dusk in the illustrated trees outside of the mating season.

At three of four sites, population turnover (daily percent of study population changing sleeping perch to a place outside of the monitored area) was relatively higher outside of the copulation season (Satterthwaite's approximation of t for unequal variances = 12.5; df = 210.4; $P < 0.0011$), while El Frio exhibited near-zero population turnover at any time. At La Guanota, all iguanas abandoned the trees used for breeding near the beginning of the rainy season but returned to this area by the middle of the rainy season. At all sites, males and females had different patterns of movements, with females changing locations more often than males throughout the year (Table 2; paired t-test comparing monthly means at each site $t = 3.13$; df = 24; $P = 0.0022$).

Females were more numerous than males (average female/

TABLE 2.—Mean percent returns at three sites. Higher means indicate greater average site fidelity from night to night.

Time of year	El Frio		Guacimos		Masaguaral	
	male	female	male	female	male	female
Nonbreeding season						
mean	100	88	66	61	61	33
nights	13	13	20	20	84	86
SE	0.0	0.9	8.1	4.1	4.6	3.7
Breeding season						
mean	96	84	76	80	70	55
nights	14	14	69	69	116	116
SE	0.8	1.1	2.7	2.0	3.4	3.5
Overall						
mean	98	86	74	76	66	45
nights	27	27	89	89	200	202
SE	0.3	0.5	2.8	2.0	2.8	2.6

male sex ratios among nonmating iguanas measured at dusk: 3.4 at El Frio, 2.3 at Masaguaral, 2.3 at Guacimos). Males were slightly larger than females (adequate data are available only for Guacimos during the mating season: male/female length ratio = 1.1).

DISCUSSION OF NONBREEDING BEHAVIOR

Iguanas usually find plenty of edible leaves in their immediate vicinity (Rand, 1978). Moreover, an iguana's gut has room for only modest additions each day, as passage times are lengthy (average 6.9 days for this population; D. Brust, pers. comm.). Dugan's (1982b) estimate of daily foraging time of 20 min is consistent with the 30 min maximum that I observed. Unlike the large insectivorous lizards in the study areas (e.g., *Tupinambis*), iguanas readily interrupted their foraging in response to distant approaches of a potential predator (Rodda and Burghardt, 1985). Finding enough to eat does not appear to be a major problem for iguanas, but leaves have relatively little extractable food energy. Thus, it is not surprising that these lizards conserve energy (Dugan and Wiewandt, 1982). Most of their day is devoted to basking. Nonbreeding iguanas bask for about 4 hours in their sleeping tree in the morning and another 2–3 hours in the afternoon. They are immobile for most of the time that they are out of their sleeping tree. Stamps (1983) characterized the Iguaninae as being "relatively phlegmatic"; perhaps they are better thought of as being quiescently vigilant.

Nonmating iguanas are relatively tolerant of the proximity of other iguanas. Typically, agonistic interactions are low in intensity, involve few displays, and occur only as they ascend the sleeping trees. They exhibited no defense of territories or other exclusive use areas. Their mild protests to being passed by another iguana along a branch did not extend to defense of a specific perch. Once an iguana had passed another, the two resumed a relaxed posture and showed no tendency to challenge each other. Suitable perches did not seem to be limiting.

Two lines of evidence suggest that headbobs often were given for a purpose other than winning the interaction immediately at hand: (1) the overall lack of association between displays and success in interactions, and (2) the frequent display of headbobs after the iguanas had separated following an interaction (see "Female Dominance Relations").

The iguanas' tendency to sleep in a head up posture and bask in a head down posture may have a physiological basis. Clark and Gillingham (1990) argued that the head up sleeping posture adopted by two species of *Anolis* maximized nocturnal vigilance by keeping the anoles' heads toward the limb base, thereby expediting detection of climbing predators. This rationale is not directly applicable to the pattern of sleep postures in iguanas, as iguanas on horizontal perches more often slept with their heads pointing away from the limb base.

Although nearly all iguanas slept in a horizontal or head up posture, most basked horizontally or with the head down. Head down basking might facilitate warming of the head and increase early morning motor coordination. Smaller iguanas can warm up faster than larger animals while basking, which presumably accounts for their leaving the sleeping tree sooner and returning later than the larger adults.

The density of iguanas in the Guacimos study area was higher than reported in Central America (Dugan, 1980:32–37; Van Devender, 1982). Density is known to affect social interactions; for example, terrritorial animals may shift to a hierarchy at sufficiently high densities (Brattstrom, 1974; Wilson, 1975). However, density did not appear to influence the behavior of nonbreeding iguanas, as the behavior at all sites was similar.

The lower site fidelity of females compared to males is consistent with Dugan's (1982b) observation that female home ranges were larger than those of males year round. Dugan suggested that the males may be maintaining residence status in

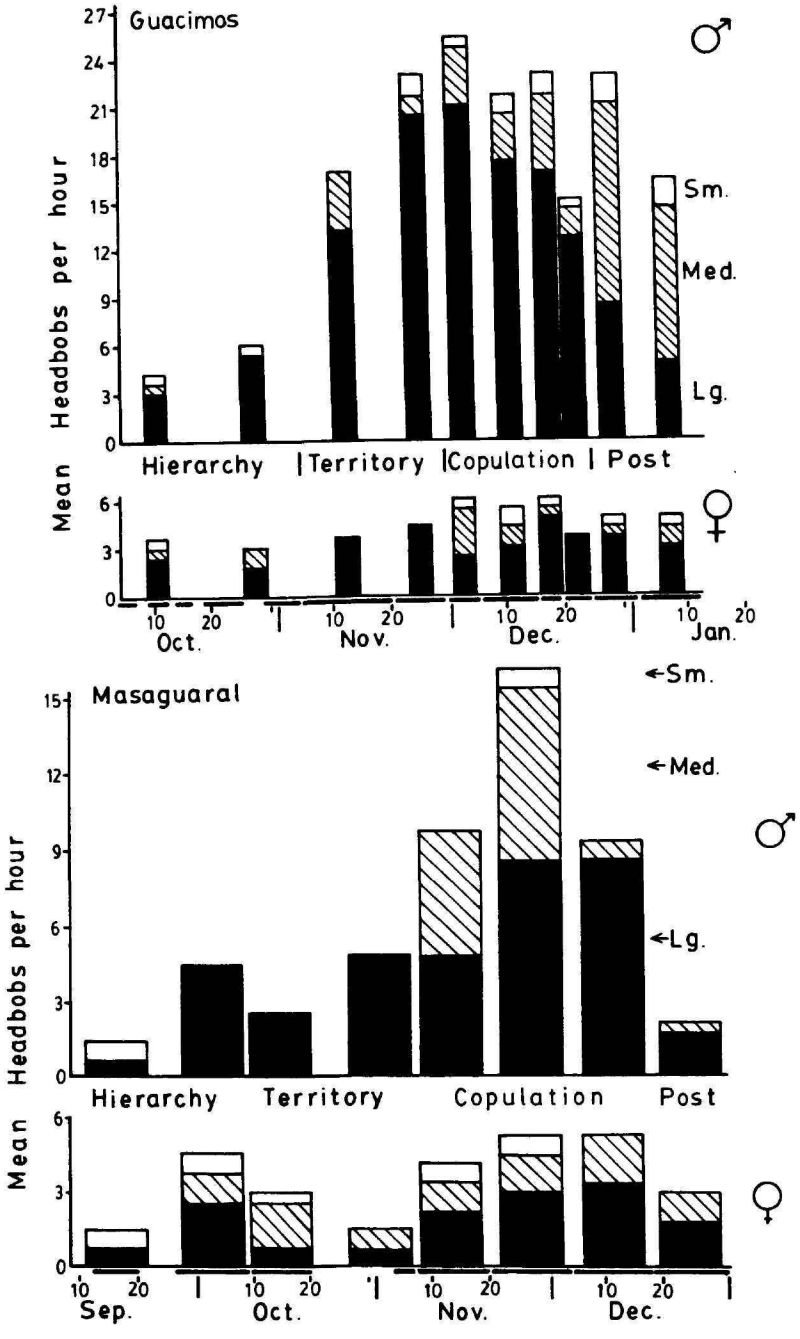

FIGURE 2.—Seasonal changes in headbob frequencies at two sites during the 2 h preceding dusk. Each bar subsection represents the mean headbob rate per hour for individuals of the indicated class. Note that the axes are scaled differently for the two sites/years, which had different densities and mating phenologies and therefore cannot be compared quantitatively. The thick horizontal lines at the base of each bar represent the days sampled at each site for this and subsequent figures. Sampling intervals at Masaguaral were chosen by dividing the range of dates into eight equal intervals. Sampling intervals at Guacimos were based on the major behavior events occurring in the population, as described in the text.

an area that will be defended during the mating season. The higher number of females present at all times of year suggests that mortality may be higher among adult males. This was the case among road-killed iguanas reported by Rodda (1990); the excess deaths of males (largly peripheral males) occurred during the mating season (see also Harris, 1982).

General Mating Behavior

Results

MALE HIERARCHY FORMATION.—The first event of the mating season was the gradual emergence of a male dominance hierarchy. Initially, males distorted their daily movements so as to avoid the immediate neighborhood of larger males. This was accompanied by an increase in the frequency and vigor of headbob displays (Figure 2). The intensities of interactions gradually increased (Figure 3), although large male iguanas continued to sleep in trees with other large male iguanas.

In these Venezuelan populations, the males did not develop a facial/mandibular reddening, as is characteristic of mating iguanas elsewhere (Dugan, 1980:31). In addition, males in the study areas did not acquire the tan, orange, or gold body color often found in Central America (Swanson, 1950; Alvarez del Toro, 1982:85; Fitch and Henderson, 1977).

TERRITORY FORMATION.—The year-round home ranges of the males I observed often contained several sites that eventually would become mating territories. Thus, territory formation involved both the selection of a mating territory and the establishment of defended boundaries for the chosen site. In the beginning of November, territorial defense was intermittent; a male would display for a few hours or days and then abruptly abandon an uncontested territory to try elsewhere. Often a male would defend a territory for a few hours after dawn and before dusk (when the largest number of females were present), but not at other times of day. Territories were most often abandoned when few females were present. Territories tended to be established around the highest concentrations of females ("hot spots"). Surprisingly, some males at Guacimos continued to try to establish territories until nearly the end of the copulation season. Usually, no females would enter such a late territory and all of the very late territories were abandoned after a few days of unsuccessful displaying. In one case at Guacimos, however, part of a highly

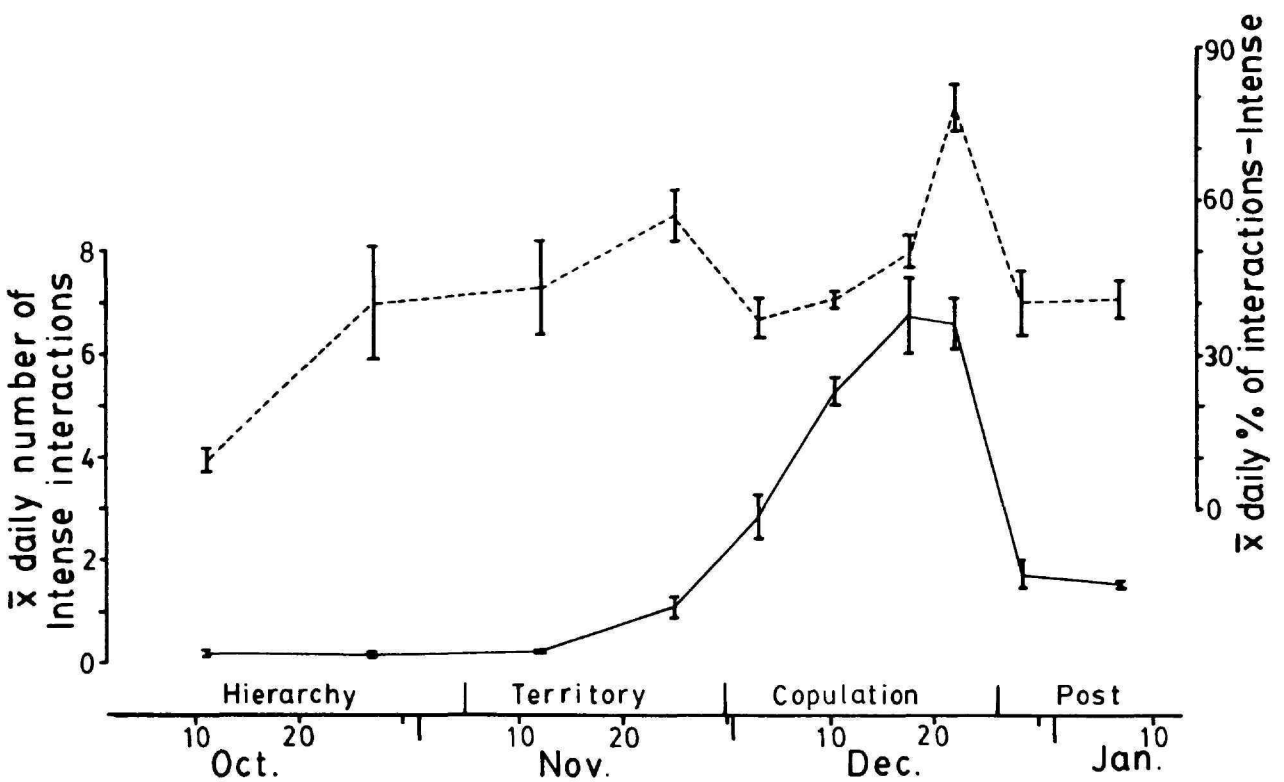

FIGURE 3.—The number (solid line) and percentages (dashed line) of total male:male interactions that resulted in outcomes of the highest intensity levels (1 or 5) during the 2 h preceding dusk at Guacimos. Vertical bars are ± 1 SE, based on daily samples.

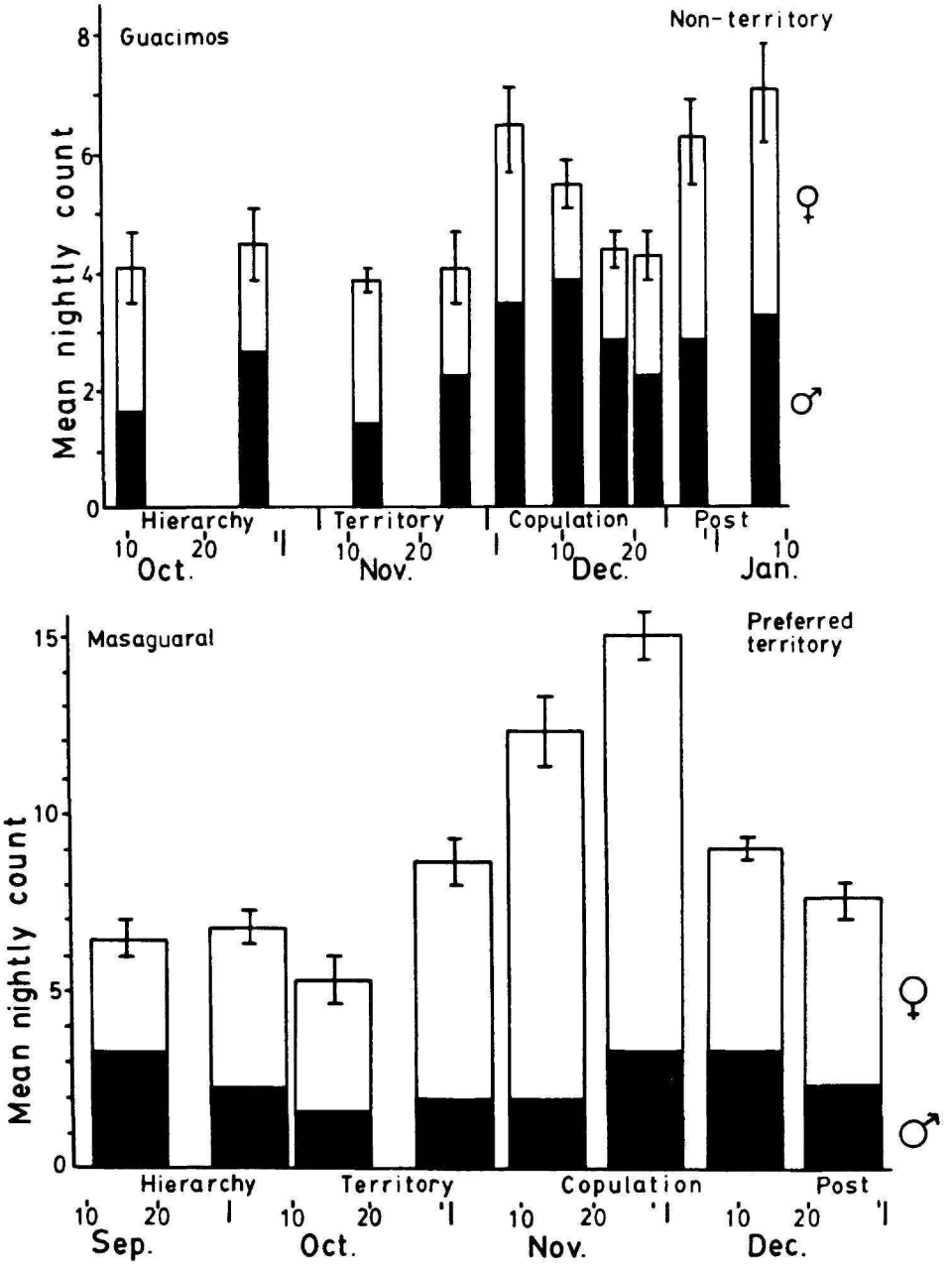

FIGURE 4.—Seasonal changes in numbers of iguanas sleeping in a nonterritorial tree and in a preferred territory, contrasting the population trends in the two areas (both prime habitat) during the copulation period. Solid bars represent the mean numbers of males; open bars represent the females. The error bars are for the total.

successful male's territory was usurped by a newly territorial male about one-third of the way through the copulation season. In contrast to the unstable territorial boundaries at Guacimos, only two major changes in territory were noted at the two other sites in two years. In one case, a male at Masaguaral (C in Figure 1) lost use of several of its foreclaws, presumably due to

an injury suffered in intermale combat. As it became unable to reliably climb smooth-barked trees, it was no longer able to defend its entire territory. The abandoned part of its territory was then incorporated into the adjacent male's territory. The following year the same male, still without use of some of its foreclaws, attempted to establish a territory in another tree at the Masaguaral site. However, it failed to attract any females and it abandoned the territory after a few days. Only very minor boundary changes occurred after territory formation in both years at El Frio.

The longest male:male interactions occurred in November, as territories were being formed. One fight, qualitatively similar to those that have been described for captive iguanas (Peracca, 1891), involved 45 min of vigorous wrestling and biting of extremities, but most fights lasted less than 30 sec.

Territorial males ceased foraging once territorial defense was maintained throughout the day. At El Frio both territories contained a few leaves of *Nectandra pichurum*, a preferred food, which one male ate occasionally during long pauses between interactions. However, this male ate little and continued to lose weight noticeably. Territorial defense often involved regular patrolling of the mating territory, presumably to intercept intruding males and to court females (see below).

As territories became established and small males were excluded, females began to aggregate in the territories of the largest males (Figure 4). In the territory of male H at Guacimos, little change in female density occurred following territory establishment by the area's second largest male (Figure 5). The tree that became H's territory was heavily used by females prior to establishment of territories.

Small individuals of both sexes generally were excluded from preferred mating territories (Guacimos: males $t = 4.24$, $df = 50$, $P = 0.0001$; females t for unequal variances $= 3.24$, $df = 16.3$, $P = 0.0051$). However, the exclusion was more stringent for males, resulting in the sexual size (length) dimorphism for preferred mating territories being more extreme (e.g., H terr. −1.3) than it was for the population at large (1.1).

As the territorial boundaries solidified, female use of the territories stabilized, with a high percentage of females returning to the same territory in which they spent the previous night (Figure 6). Some small males that did not display or remain in a territory during the day nonetheless often slept within another male's territory, arriving late and leaving early (Figure 7). The resident males did not attack or chase these small males. High numbers of females combined with the exclusion of small males during the middle of the day produced an elevated female:male territory sex ratio, which I term the

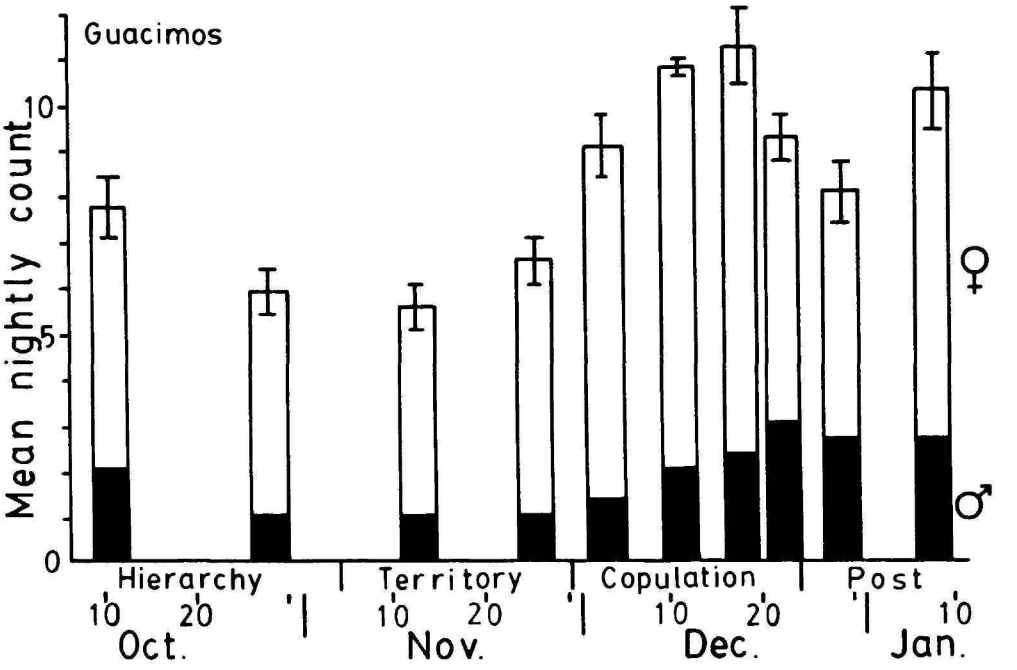

FIGURE 5.—Seasonal changes in numbers of iguanas sleeping in the intensively monitored territory of male H at Guacimos. Legend as in Figure 4.

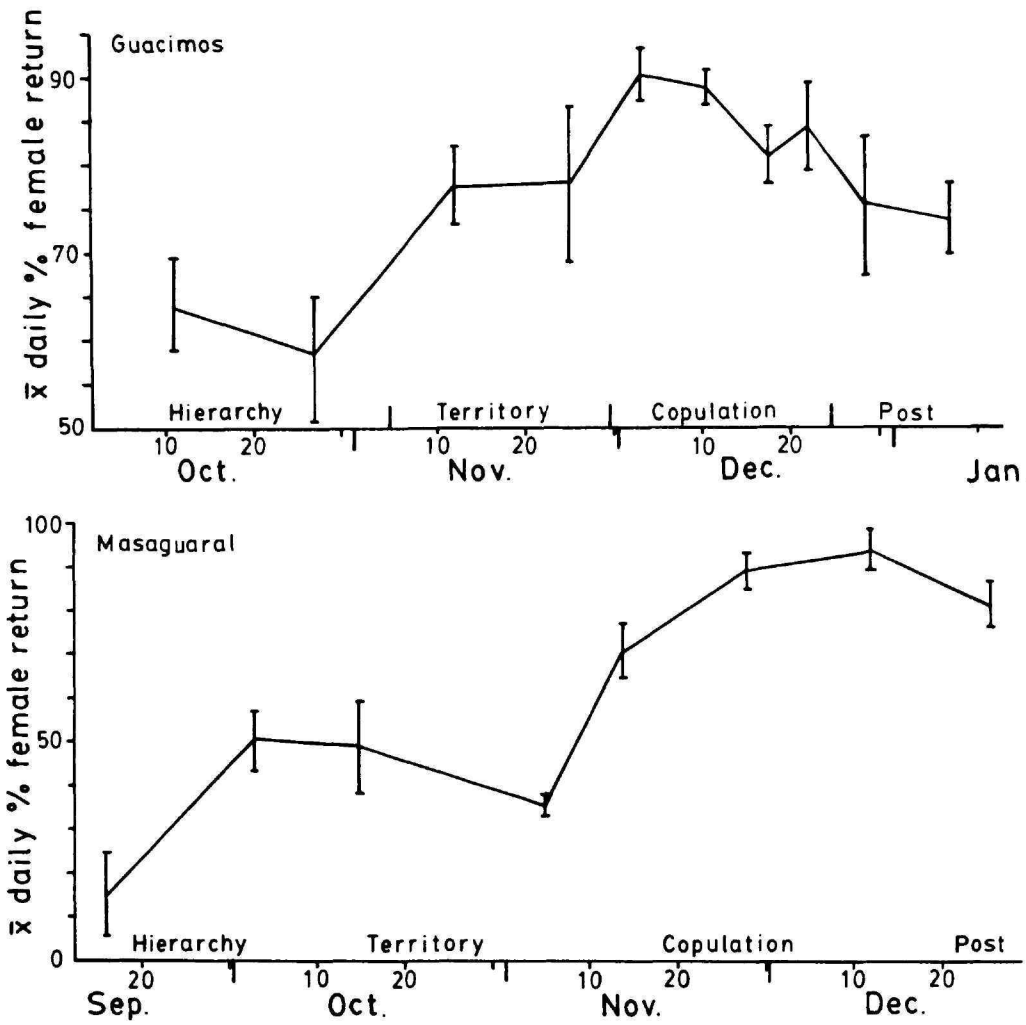

FIGURE 6.—Percent female returns at two sites during the mating season. Vertical bars are ± 1 SE.

operational sex ratio or OSR (cf., Emlen and Oring, 1977). The presence of small males reduced the OSR at dawn and dusk during the copulation season (Figure 8). Nevertheless, an increase in OSR occurred during the mating season at all sites (Figure 9).

COPULATION SEASON.—Prior to the copulation season, female iguanas left their sleeping trees each morning. As their body cavities began to fill with developing ova, they stopped feeding and remained in the tree during the day (Figure 10). Midday occupancy of territories coincided with the onset of copulation, but preceded the cessation of feeding by a mean of 7.5 ± 4.1 days (N = 7). The study territories were selected for their leaflessness and thus females moving into these territories may have been subjected to greater midday insolation (cf. Beuchat, 1988). However, females in heavily foliated territories were observed to follow the same pattern of remaining in their territories throughout the day. Females that remained in a mating territory were subjected to fewer mounting attempts by peripheral males. However, as the copulation season progressed, peripheral males increased the number of their intrusions into mating territories (see below).

At Guacimos (1983), the first copulation attempt and first copulation occurred on 30 November. At Masaguaral (1982), the first observed copulation attempt was on 19 November and the first observed copulation was on 20 November. At Guacimos, the territorial male obtained most of the copulations that occurred during the first half of the copulation season (Figure 11).

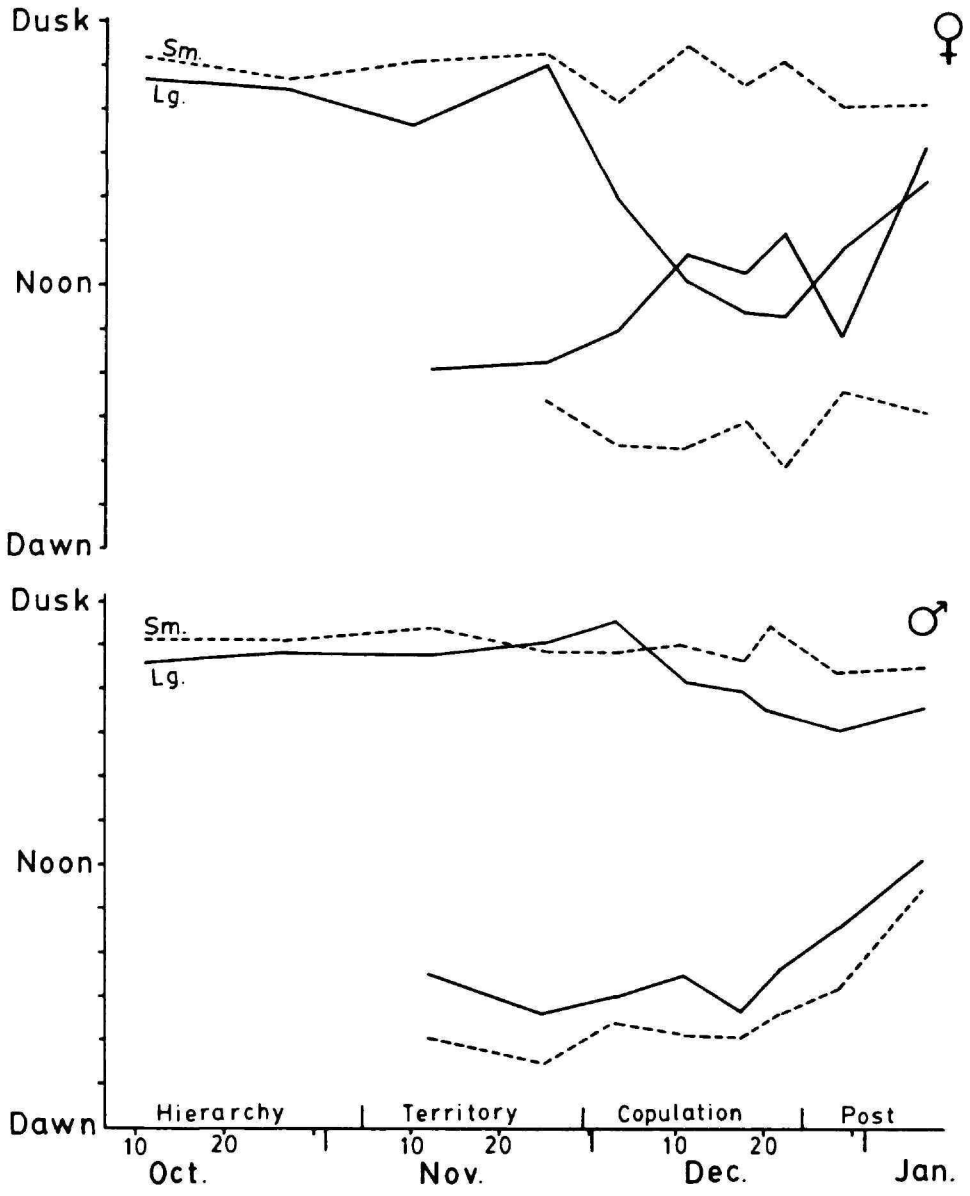

FIGURE 7.—Mean arrival and departure times by size, sex, and season in the intensively monitored tree at Guacimos. The times for small and medium iguanas have been pooled. The mean arrival and departure times for large females (solid lines) intersect during the copulation season because most females remained in the tree throughout the day. In this and subsequent figures showing time of day using the notations dawn-noon-dusk, the times are given in hours relative to sunrise and sunset for the days sampled (the noon "hour" expands or contracts between 1.64 and 1.83 h in length to accommodate the seasonal changes in day length).

Once a territory was established, the roles of mature males fell into three classes: pseudofemale, peripheral, and territorial. Pseudofemales were small adult males that behaved as females. Generally they did not display, attempt to copulate, nor did they spend their days at the periphery of another male's territory, intruding when possible. Small males regardless of social status gave very few headbobs (Figure 2), whereas pseudofemales were conspicuously undemonstrative even for small iguanas. I

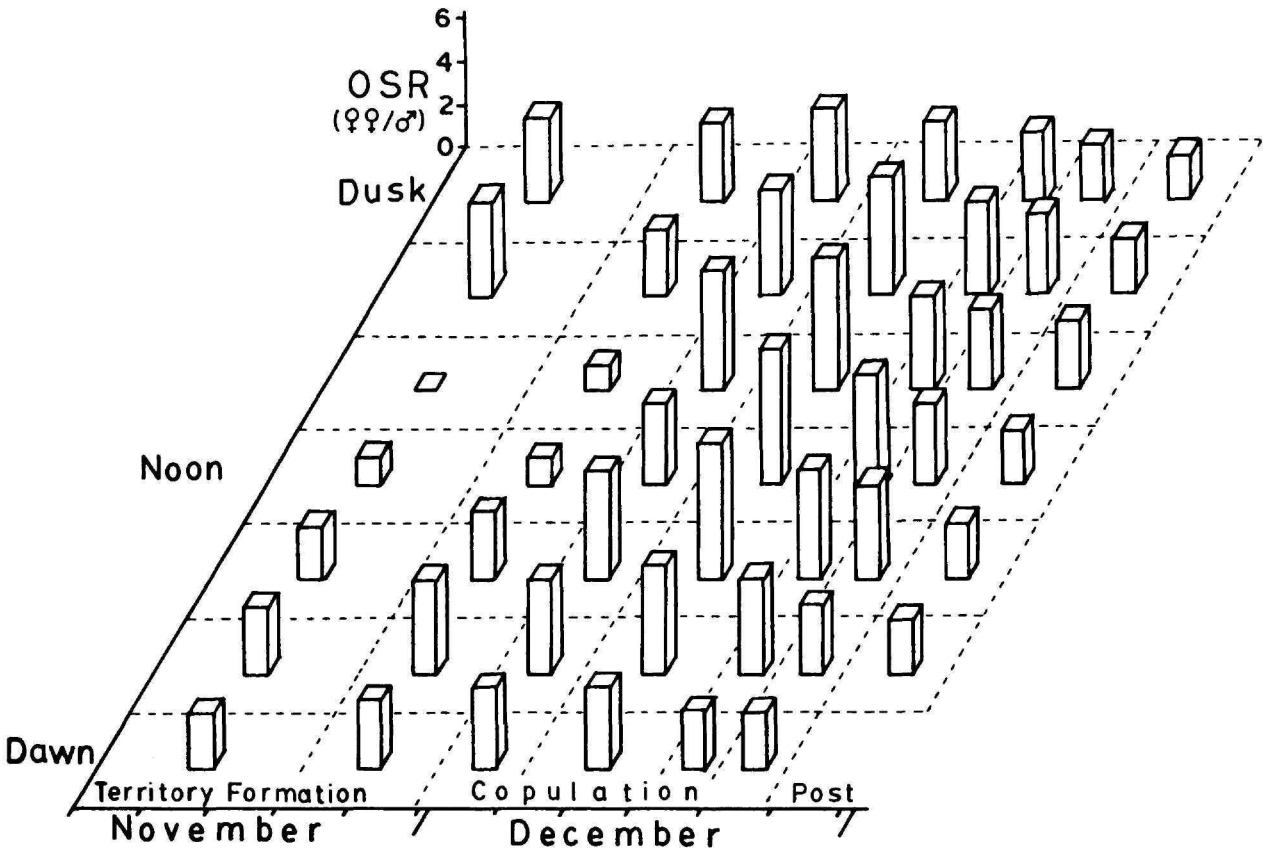

FIGURE 8.—OSR by season and time of day for the intensively monitored territory at Guacimos.

saw pseudofemale behavior in only two situations: (1) at Masaguaral in 1982, a pseudofemale habitually occupied a tiny side branch off the trunk of the largest tree (Figure 1), at a place just below the major branching of the crown, where the territorial male normally perched; and (2) in several territories, pseudofemales entered the territory just before dusk and were the first to leave in the morning (see Figure 7). On several occasions large or medium males attempted to mount such pseudofemales at dusk, but the pseudofemales fled. I believe that pseudofemales often were mistaken for females by other iguanas of both sexes.

The distinctive feature of peripheral males was their characteristic location (at the edge of a territory) and their repeated attempts to force copulations, either by a transient foray into a territory (Figure 12), or by intercepting a female outside a territory. For the first half of the copulation season, females would occasionally leave a territory to feed, at which time they would be attacked by peripheral males. At least three times at Guacimos, a female who left her territory had to struggle to evade the three peripheral males that had simultaneously mounted her. Peripheral males displayed more often than the average small male (peripheral or pseudofemale), but not as often as an average territorial male (Figure 2). Many peripheral males were medium in size, but all sizes except the very largest were represented.

Territorial male behavior consisted primarily of territory patrolling, presumably in search of intruding males and receptive females. Territorial males reacted cautiously to most intruders, headbobbing and slowly approaching until near the intruder or until the intruder fled. However, territorial males seemed to recognize some individual iguanas at a distance; frequently a territorial male would move at near maximal speed toward an intruding male, which almost inevitably ran or jumped out of the tree. In contrast, the arrival of a resident female would ordinarily evoke no more than a headbob. In 2 of 5 territories, the dominant male circled the periphery of his territory on a regular basis, taking 45–90 min for a circuit. In another 2 of these 5 territories the territory lacked circumferential branches that would permit patrolling along a circuit. The intensively monitored male at Guacimos so often interrupted

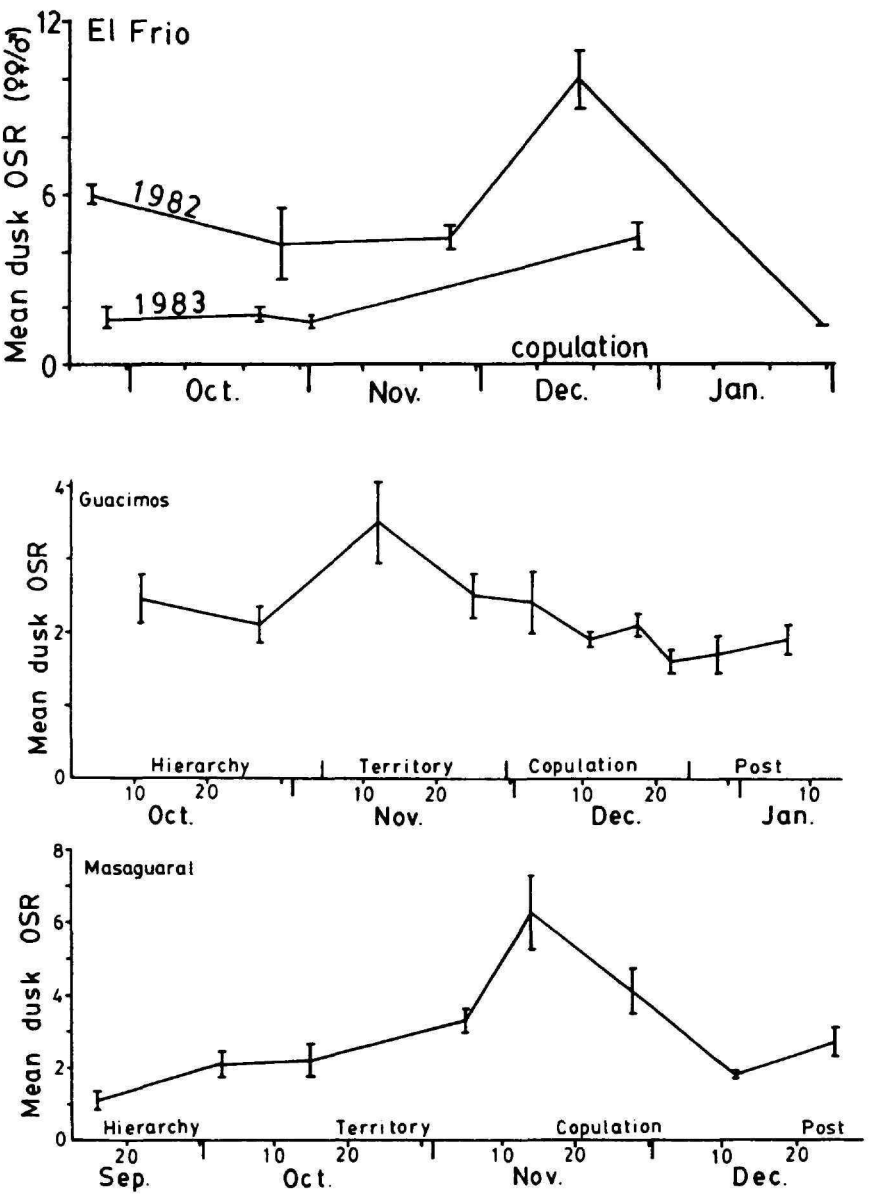

FIGURE 9.—Dusk OSR by season at three sites. The El Frio values are monthly means for each year separately, as they differed significantly (paired $t = 5.67$; df = 3; $P = 0.011$). The vertical bars are ± 1 SE, based on daily records.

his circuit to repel the frequent intrusions of peripheral males (Figure 12) that no regular circuit was apparent.

While patrolling, a territorial male would approach each of his females (Figure 13). The deliberate approach to females seemed to be the same as the deliberate approach given by territorial males to unfamiliar iguanas. In particular, I observed no distinctive headbob associated with courtship; the shudder bob associated with courtship described by Dugan (1982a) occurred in a wide variety of high intensity contexts. Males gave shudder bobs (= vibratory head nodding, Distel and Veazey, 1982; or low-frequency head bobbing, Müller, 1972) more often than did females, but both sexes gave them in high

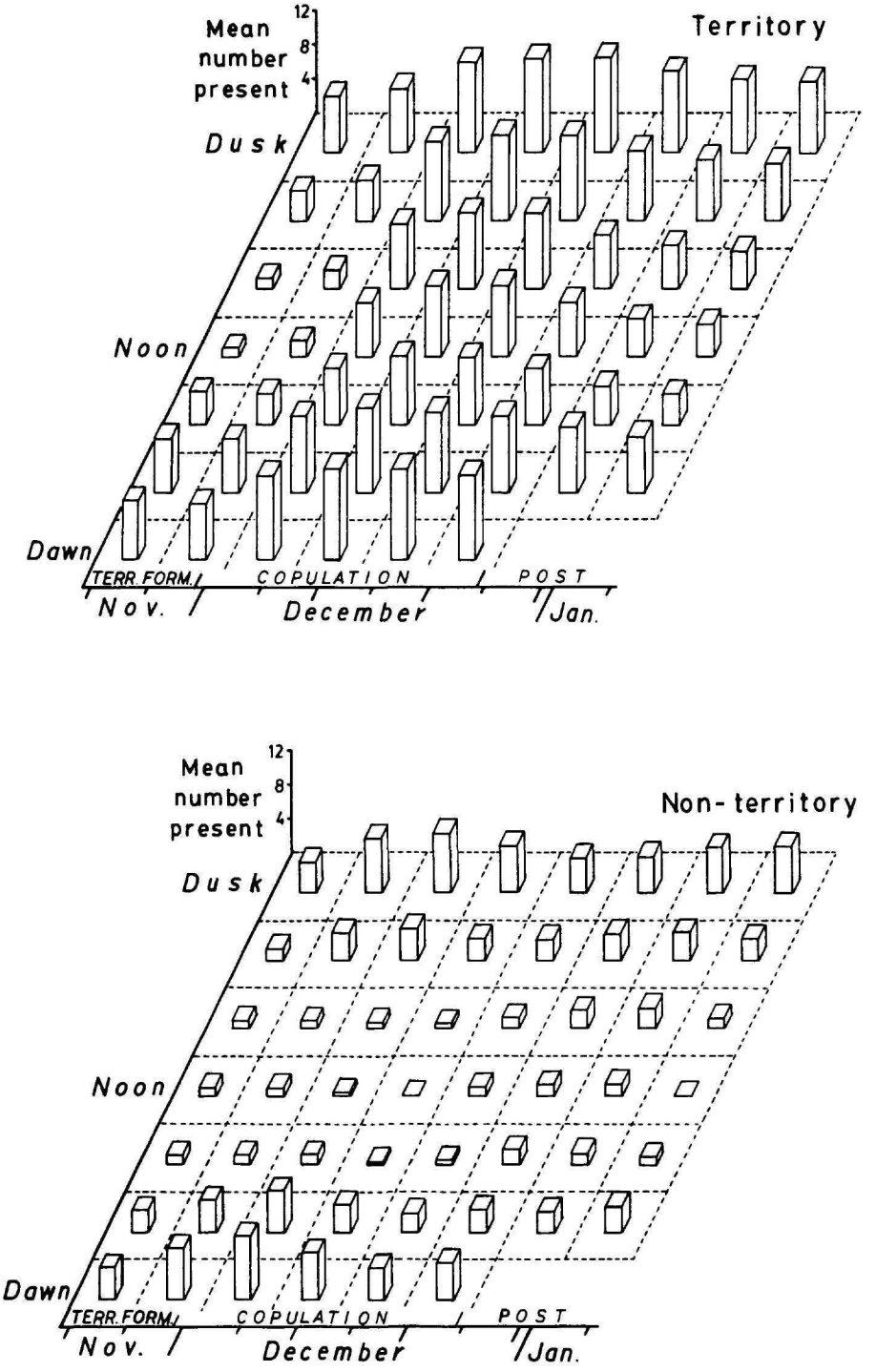

FIGURE 10.—Seasonal progression of daytime occupation of a mating territory and the adjacent nonterritorial tree at Guacimos. Usually only one male was among the territorial iguanas and few females were among the nonterritorial iguanas. The scant midday attendance in the "nonterritory" at the end of the copulation season was an abortive attempt by male CW to establish a late territory.

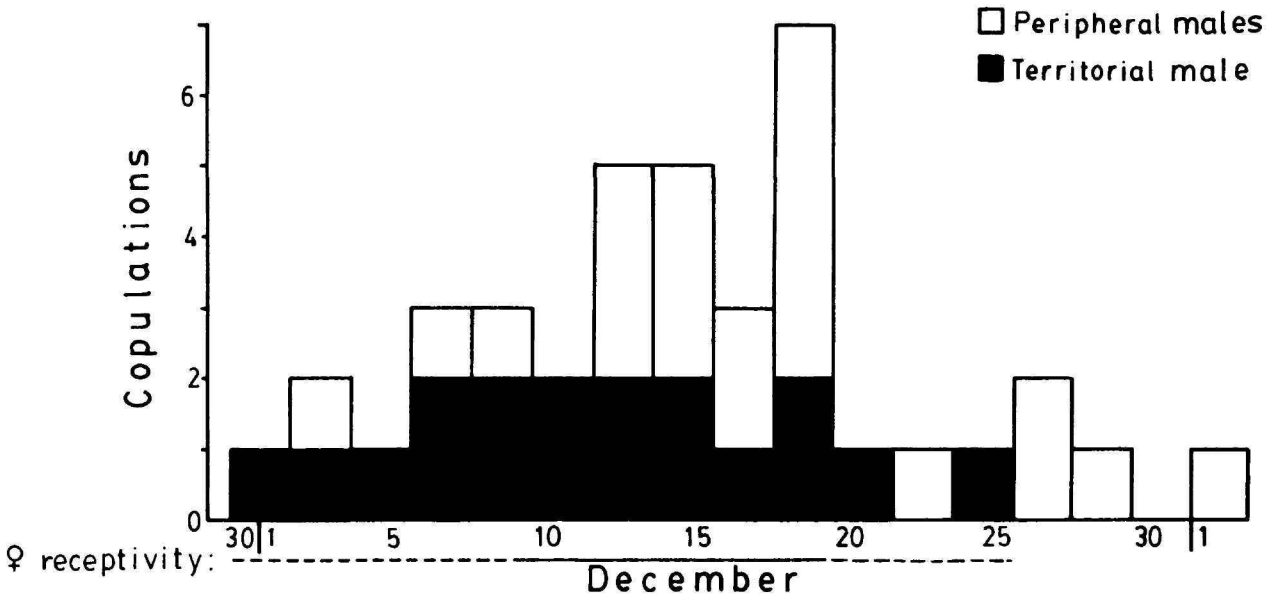

FIGURE 11.—Copulation activity by date for Guacimos. The dashed line below the abscissa indicates that a single unusual female was receptive on these dates (see text); the seven other resident females were receptive during the period marked by a solid line.

intensity interactions with both males and females.

Female responses to approaches ranged from no overt reaction to vigorous biting, fleeing, and headbobbing. The no-reaction option was rare and usually resulted in a copulation attempt. However, only 30 of 248 copulation attempts at Guacimos were preceded by the female responding passively to a male approach. A small but unquantified number of passive responses occurred that did not progress to a copulation attempt (usually interrupted by a simultaneous peripheral male intrusion). Nevertheless, the total number of passive responses was a tiny fraction of the 657 approaches recorded for resident females while intruding males were absent at Guacimos.

Female rejection behaviors included waving one leg while lying down, arching or lashing her tail (if approached from the rear), headbobbing, walking away, facing, running away, and biting the male, generally in the face. Interpreting the passive responses as evidence of behavioral receptivity, and the range of dates on which passively received copulation attempts occurred as the window of receptivity for the six nearly continuously observed females at Guacimos ($n = 25$ passive responses), the six were receptive for 27, 0, 8, 1, 5, and 1 days. The female that was receptive for 27 days, AH, was aberrant in every measure of female reproductive performance (see below); she accepted all males indescriminately (both territorial and peripheral) over a span of dates 50% longer than the receptive seasons of all the other females combined. Captive iguanas are receptive for periods of about 1 week (Braunwalder, 1979; Pütz, 1982). Excluding AH and including three other females that were quantifiably receptive, female receptivity was brief and relatively synchronous. Receptivity for all eight females occurred in the period from 30 November to 19 December; seven of these were receptive during only 11 days: 9–19 December. Four were receptive simultaneously on 11 December.

All of the copulations performed by H, the male in the intensively monitored territory, were observed. At the beginning (30 Nov–5 Dec) and end (20–24 Dec) of the copulation season, male H's copulations occurred on alternate days. During the middle of the copulation season (6–19 Dec, except 16 Dec), male H copulated once daily. On four of the five skipped days at the beginning and end of the season male H everted his hemipenes and exuded a white, viscous liquid. His choice of right or left hemipenis did not differ from a random sequence (Runs test: $r = 10$; $n = 7,9$; $0.05 < P < 0.95$). Comparable data are not available for any other site or male, although it is noteworthy that on one day at El Frio male P copulated shortly after dawn and then again shortly before dusk. This was the only observed exception (out of 55 copulations observed at all sites) to the generalization that iguanas copulate no more than once per day.

The dawn and dusk copulations of male P also were anomalous in their time of occurrence. Most territorial male copulations occurred around midday (Figure 14). Copulations by territorial males were more concentrated in time ($F = 3.90$;

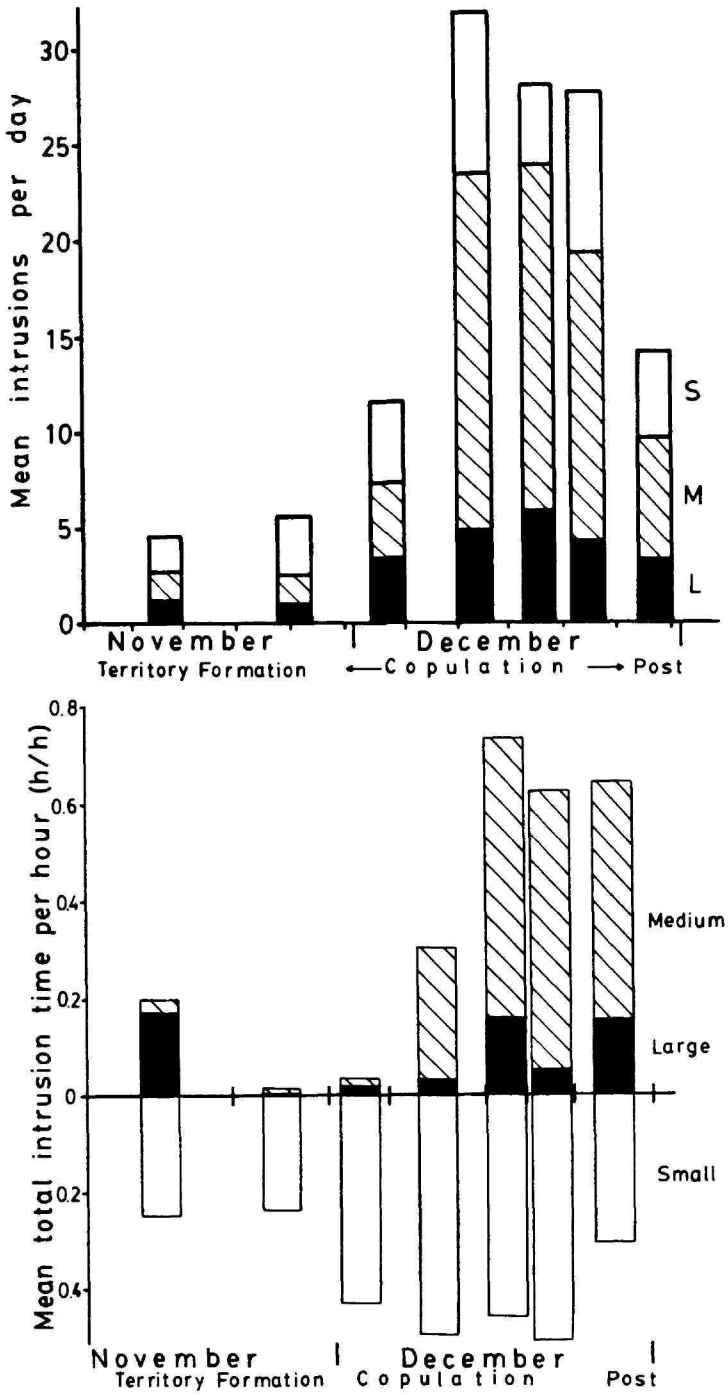

FIGURE 12.—Intrusions by peripheral males at Guacimos. The upper graph shows the numbers of intrusions per day; the lower shows the total time per day of peripheral male occupancy in the intensively monitored territory. In the lower graph the small male intrusions were graphed separately as the observed pattern differed. Moreover, the small male intrusions were of limited significance to the resident male, as small males did not obtain any copulations by intruding (see Table 4).

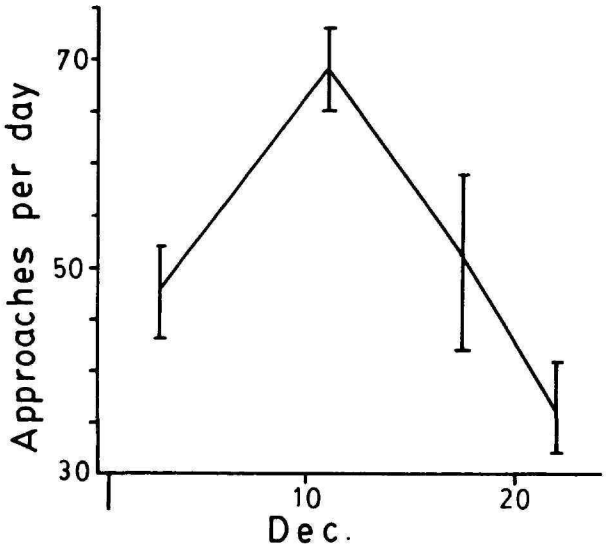

FIGURE 13 (opposite).—Total approaches per day of resident females by the territorial male at Guacimos when intruding males were absent. The vertical bars are ± 1 SE, based on daily totals.

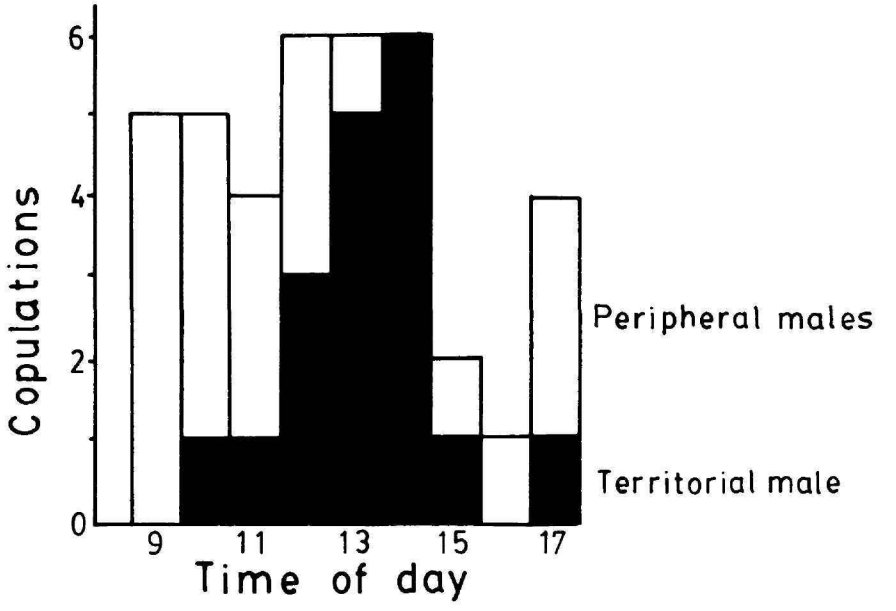

FIGURE 14.—Copulations at Guacimos by time of day. The territorial male was always present; the number of peripheral males varied from 3 to 8, although only 5 peripheral males obtained copulations.

df = 21,18; $P = 0.002$) than were those of the more opportunistic intruders. The difference is also significant for copulation attempts ($F = 2.57$; df = 202,43; $P < 0.0012$), indicating that the peripheral males were attempting and obtaining copulations at a wider range of times of day. This might be related to an apparent once-a-day limitation on copulations. If males stopped attempting to copulate after their first copulation of the day and if the territorial males were able to obtain a copulation after basking every day, their copulations would be relatively concentrated at midday.

Did territorial males stop attempting to copulate after their first success of a day? I identified 12 precopulatory intervals of about 2 h that could be paired with 12 identical but postcopulatory times-of-day for dates that were only one or a

few days earlier or later (dates and times were matched to control for seasonal or daily/temperature changes in ardor). For example, the number of a male's copulation attempts between 1000 h and 1200 h on a day when the male copulated at 1200 h would be compared to the number of his copulation attempts between 1000 h and 1200 h a few days later when he copulated at 1000 h. No copulation attempts occurred in the intervals after a success, whereas significantly more (mean 0.83 ± 0.21) occurred in the intervals that were not preceded by a copulation (Wilcoxon matched-pairs signed-rank $T = 0$; $n = 61$; $P = 0.025$). However, iguanas may be unavoidably refractory even after a failed copulation attempt. If this were so one would expect a similar reduction in copulation attempts by peripheral males. For the two peripheral males for whom adequate data exist, no evidence of a refractory period was detectable in terms of number of copulation attempts (Wilcoxon $T = 9.5$; $n = 6$; $P >> 0.05$), number of intrusions (Wilcoxon $T = 17.5$; $n = 8$; $P >> 0.05$), or latency to next copulation attempt (Mann Whitney $U = 12$; $n = 5,6$; $P = 0.33$). Unlike the territorial males, peripheral males attempted to copulate after a successful copulation. Although no peripheral males were observed to succeed in obtaining more than one copulation per day, the peripheral males very low success rate during any copulation attempt (see following section) would render two successes on a single day improbable. Although the territorial male stopped copulation attempts after a success, there was no reduction in his locomotor activity (mean increase = 1.9 m/h) or approaches to resident females (mean increase 0.015 approaches/h). This implies that the male may have been invigorated and was surely not exhausted by copulation, and that even if approaches to females are equivalent to "courtship," they are not necessarily a preliminary to copulation. Close approaches to females may be an unavoidable correlate of territorial patrolling.

The average copulation of the territorial male at Guacimos lasted 9.0 min, 2 min longer than that of the average peripheral male copulation ($t = 1.72$; df = 31; $P = 0.047$) (Table 3). This difference was significant even if comparing only the uninterrupted copulations of each male type ($t = 2.37$; df = 24; $P = 0.013$). The durations of copulations among all iguanas in my sample did not deviate significantly from those reported by Dugan (1980:79; 1982b) ($t = 1.32$; df = 64; $P = 0.19$), although my sample probably includes more peripheral male copulations, which bring the means closer together. Uninterrupted territorial male copulations at Guacimos were significantly longer than those in Dugan's sample ($t = 3.05$; df = 37; $P = 0.0042$).

During copulations, both territorial and peripheral males exhibited low-amplitude spasmodic head twitches that occurred synchronously with even lower amplitude tail base movements and abdominal contractions (cf. head movements reported by Braunwalder, 1979; Pütz, 1982). Twitch rates varied from 0 to 48 beats per minute (bpm), with the mean of 33 nonzero measurements on males being 21.9 (SD = 11.9). Three measured means for entire single copulations were 12.7, 20.7, and 20.8 bpm.

My impression is that the contractions represented sperm transfer contractions. For the 12 copulations for which adequate data exist, the contractions began within a few seconds of intromission and continued for an average of 75% of the total copulation time. On three occasions white viscous fluid was visibly emanating from a hemipenis when a copulation was broken up while the male was still contracting. Cessation of pulses was a good predictor that uncoupling was imminent.

Some females changed territories during the copulation season, but most females became extremely consistent in their choice of sleeping trees (Figure 6). Inconsistent females generally were (1) small, (2) harassed by the larger females, and (3) inclined to leave the tree early and return late (Figure 7). Most consistent females remained in the tree throughout the day. I termed the latter "residents." At Guacimos 11 females were residents in the intensively monitored territory for some or all of the copulation season. The territorial male copulated with eight of these, all of whom had been residents since the beginning or almost the beginning of the mating season. Of these eight, one of the two largest females in the territory left to become a resident in an adjacent territory during the copulation season. Her departure as a resident followed immediately after losing an encounter with the other largest female, with whom she had previously interacted amicably. She departed (as a

TABLE 3.—Copulation time (min) by male class and site.

Site and number of individuals sampled	Uninterrupted			Interrupted			Total		
	Mean	*n*	SD	Mean	*n*	SD	Mean	*n*	SD
Territorial males									
El Frio (1)	8.3	2	1.1		-		8.3	2	1.1
Guacimos (1)	10.4	13	3.4	5.2	5	2.7	9.0	18	3.9
Masaguaral (2)	7.4	5	3.3		-		7.4	5	3.3
Subtotal	9.5	20	3.4	5.2	5	2.7	9.5	20	3.4
Peripheral males									
Guacimos (5)	7.7	13	2.1	2.3	2	2.5	7.0	15	2.8
Total	8.8	33	3.1	4.4	7	2.5	8.0	40	3.4

resident) before being inseminated by the territorial male, but she returned for a brief daytime visit on the following day, copulated with the territorial male, and then left permanently (i.e., did not enter the tree again during the mating season).

Three females became residents after the beginning of the copulation season. Two of these had copulated elsewhere shortly before changing territories. One was the largest female seen at any site (of 166 total), and just before switching she had copulated with the largest male. The resident male in her new territory mounted this female five times, but each time she resisted violently and escaped. She left the territory as a resident after five days, but returned irregularly thereafter. My impression was that she moved to the intensively monitored territory and then left the territory to find a new refuge with less harassment by males. The other two late-arriving female residents were not mounted by the resident male.

Similar female behavior was seen at Masaguaral. A major difference was that five of the nine females that were residents in the clump of four study trees (two territories) at Masaguaral switched territories (but not clump) several times; one switched at least 12 times. The Masaguaral data established only a minimum number of switches for these five females, but the mean of these minima was 6.2. The female that switched at least 12 times copulated with both territorial males. In the female dominance hierarchy this female ranked third from the top (out of 14 (including all females in area)). However, high rank was not associated with switching, as the nonswitching females were ranked 1, 2, 4, and 8.

Twenty females were residents for at least part of the copulation season at Guacimos in 1983 ($n = 11$) or Masaguaral in 1982 ($n = 9$). Of these, seven were observed to copulate with at least two different males; seven more probably copulated with multiple males, based on the observed pattern of their territory switches; and five probably (two definitely) were not multiply mated.

For the six females at Guacimos whose mating behavior was completely monitored, the average number of copulations per female was 4.8 ± 4.7, but this value is grossly distorted by the one aberrant female, AH, that copulated 15 times. Excluding her, the average is much lower and less variable (3.0 ± 1.4).

All mating behaviors dropped abruptly in vigor and frequency around 18 December 1982 at Masaguaral and 19 December 1983 at Guacimos. Displays waned, locomotion dropped, male aggression decreased noticeably, female belligerence peaked (then apparently dropped sharply a few weeks later), male territory defense became irregular, and territorial males resumed feeding. Most importantly, the frequency of copulations at Guacimos dropped sharply from nine (17–19 Dec) to one (20–22 Dec), with that one involving the aberrant female AH. Excluding AH there was only one copulation after 19 Dec, and that was a forced copulation of a cripple (broken foreleg). Four females from a nearby area were inspected for reproductive condition 15–22 December 1983. Three were on the threshold of ovulating (follicles > 20 mm dia.) and the fourth had begun ovulating.

TABLE 4.—Average number of clutches fertilized by males of various classes at Guacimos, using three hypotheses for the nature of sperm competition.

	First precedence	Mix	Last precedence
Male size			
Small	0	0	0
Medium	0	1.2	1.3
Large	3.9	2.7	2.6
Male role			
Pseudofemale	0	0	0
Peripheral	0	0.9	0.8
Territorial	6.0	3.6	4.0

MATING SUCCESS.—To evaluate the relative reproductive success of males of different roles or sizes one would prefer representative observations of the entire male population. Unfortunately, it was extremely difficult to keep small males in view. They appeared to avoid reproductively active areas and none were seen to copulate. This is especially noteworthy as copulations were extremely conspicuous, owing to (1) the prominent perches usually occupied by copulating iguanas, (2) the violent physical grappling associated with most of the observed copulations, and (3) the relatively long duration of copulations. Thus, the successful males easily were identified and these individuals could be apportioned among the size classes and roles they represented.

The best size class data are for Guacimos. I based the proportions of the various size classes on the mix found among known size animals: 48% small, 26% medium, and 26% large. No pseudofemales were observed to attempt a copulation at Guacimos, so it is possible that pseudofemale behavior in this population served only to avoid the attacks of larger males. Of the males that slept in either the intensively monitored territory or an adjacent undefended area during the copulation season, an average of 1.0 (16%) per night was a territorial male, 2.6 (43%) were peripheral males, and 2.4 (40%) were the pseudofemales not seen to attempt mating (although of a size believed to be physiologically competent, based on dissection of 57 roadkills: Rodda, 1991).

Mating success is usually measured by the number of copulations obtained. However, because females under continuous observation copulated from 1 to 15 times, it seems reasonable to treat one female's sole copulation as being much more significant than would be one of another female's 15 copulations. In Table 4, reproductive success has been apportioned using three alternative hypotheses for the form that sperm competition might take. Under the mix hypothesis all matings were counted as fertilizing $1/n$ of each clutch, where n is the number of copulations each female received. Under the first-precedence hypothesis the first copulation was assumed to fertilize all of that female's eggs; under the last-precedence hypothesis the last fertilization before 23 December (a likely

ovulation date) was assumed to fertilize all eggs. For these computations it was necessary to know all of each female's copulations. Thus, only the six females under continuous observation were used. Based on these computations it would appear that there is an enormous advantage to being a large territorial male, and the discrepancy between classes is greatest if early inseminations take precedence in obtaining fertilizations.

Qualitatively, this finding was observed in every territory, but the total success of peripheral males was higher in some territories and lower or negligible in others. The two key variables were access to the territory and the density of females. Isolated palm trees were almost impossible for a peripheral male to invade, whereas territories with multiple entry points were less defensible. Interlocking canopies, multiple trunks, and multiple territories within a tree (e.g., Guacimos, C in Figure 1) promoted the success of peripheral males. At El Frio, the territory of male P had almost unlimited entrance routes, but the low density of females and the superb visibility in the nearly leafless territory made it difficult for an invading peripheral male to escape detection.

Discussion of General Mating Behavior

A major goal of behavioral ecology has been to identify the ecological factors that could be used to predict mating behavior (Dugan and Wiewandt, 1982). Are the mating behaviors described herein predictable from the ecology of green iguanas? Iguanas are the most arboreal and folivorous of the iguanines (Etheridge, 1982). Although the green iguana is thought to have only recently invaded its arboreal niche, it has done well there, having spread throughout the warm Neotropics (Rand, 1978).

I believe that much of the iguana's mating behavior can be traced to its arboreal folivory (Troyer, 1983). A large ectotherm with a catholic folivorous diet is in a very favorable position. Leaves are abundant and widespread, and an ectotherm's energy requirements are low enough that it can withstand long interruptions in its food supply (Pough, 1980). A large arboreal lizard is no more at risk when it has close neighbors. Iguanas are acutely aware of the predator avoidance reactions of their neighbors and seem to take advantage of the information gained. Thus, iguanas can afford to aggregate at high densities in the microhabitats that afford the highest protection from the few predators they cannot outclimb (monkeys, large raptors, small felids, and opossums). Given high densities, the absence of monopolizable resources, and the absence of parental care, male iguanas must compete directly with one another for access to mates, and females will have a large number of conveniently located males from which they can inexpensively select a male that has outlived, outfought, and outcourted his competitors. If these traits have a heritable component, the winning males have better genes, at least episodically (Borgia, 1979:45–71; Trivers, 1985:348–359).

The form of male:male competition is shaped by the complex three-dimensionality of the iguana's arboreal habitat and the large number of females that may reside in a single tree (in excess of 30 per tree in preferred habitat). If their habitat were two-dimensional, a male could perhaps herd a small harem of females, as in bison (Lott, 1981) or hamadryas baboons (Kummer, 1968:122–150), but most trees have numerous radiating escape routes and no circumferential pathway that a male could use to force females to remain. Thus, males must entice females to stay and be prepared to compete with sperm in case they don't.

I believe that a combination of the inability to monopolize resources or mates with the phylogenetic legacy associated with being a lizard (little or no parental care, ectothermy, etc.) explains the basic features of the iguana mating system. Foremost among these are intense male:male mate competition, small mating territories with a regional male dominance hierarchy, and female mate choice based on male quality. The details of iguana mating are not so easily predicted. The specifics may hinge on more subtle phenomena, such as individual recognition or a prior-residence advantage in obtaining a mating territory. However, the generalized hypothesis is consistent with (1) the aspects of iguana mating that have been the same wherever studied, and (2) the aspects that have differed between studies (Table 5).

In considering differences between the conclusions of the present study and of Dugan (1980, 1982a, 1982b; see Table 5), I believe it is parsimonious to first (1) evaluate the possibility that the differences are of interpretation rather than fact, and (2) search for evidence that the iguanas in both studies used the same "strategy" (Austad, 1984 found different tactical expression under slightly different conditions). For example, territorial behavior may shift to a dominance hierarchy at sufficiently high densities (Evans, 1951; Wilson, 1975:269–297). Iguana densities at the El Frio site were similar to the higher densities at Flamenco, and the behavior seen at El Frio was almost identical with that reported for Flamenco. The greatest differences between Flamenco and my sites occurred at my highest density site (Guacimos).

The only item from Table 5 that may be a difference in interpretation rather than fact is my finding of no specific courtship displays. I found that territorial males treated all unknown iguanas in a basically similar way: a slow approach with an elaborate headbob. If the approached iguana ran, mounted a female, flattened itself and postured laterally, or gave an elaborate headbob, the territorial male would probably attack. In the absence of these responses, the territorial male would probably headbob again (Fleishman, 1988, observed a similar reaction in *Anolis auratus*). The approach and headbobbing could be considered courtship if distinct in form when given to females. Dugan (1980:133–136) concluded that the headbob was distinct, in that her careful evaluation of filmed headbobs revealed that a shudder bob was most likely to occur in close distance heterosexual interactions. However, her male

TABLE 5.—Comparisons between this study and Dugan (1980, 1982a, 1982b). The statements under "Dissimilar" summarize the conditions observed in the present study (Venezuela).

Similar	Dissimilar
GENERAL	
Sex ratio	Density higher
Sexual size dimorphism	One-dimensionality of habitat
Daily activity pattern	Slightly earlier phenology
Sequence of mating behavior	Larger body sizes (both sexes)
	Lack of mandibular reddening
HIERARCHY FORMATION	
Display rate elevation	Intense fights sometimes seen
Locomotion increase	Fewer displays
Males jockey for female hot spots	
Male dominance hierarchy	
Injurious fights rare	
TERRITORY FORMATION	
Large male exclusion of small males	Higher OSRs
Males stopped eating during territory defense	Higher female numbers
Females remain in territory	No male following of foraging females
Males/females moved toward each other	Not all large males territorial
	Territories smaller
COPULATION	
Pseudofemale/territorial/peripheral roles	More forced copulations
Most reproductive success to large males	Greater synchrony
Ovulations coincided with collapse of mating	Receptivity rare
Few male:male interactions in some territories	Longer copulations
Never more than one copulation/male/day	Numerous intrusions
	Little or no "courtship"
	Females mated with multiple males

iguanas were sufficiently separated during the mating season that she had few or no opportunities to witness close male:male interactions. In my sites, close male:male interactions often involved shudder bobs. Müller (1972) also noted that all types of bobs were given in threat, courtship, and territorial defense contexts. Moreover, Dugan (1980:107) presented data showing that shudder bobs comprised 20% of all bobs in both Nov–Dec (mating season) and Jul–Sep (nonmating). Thus, there was no seasonal association between the occurrence of shudder bobs and mating. Shudder bobbing as an indicator of intensity rather than courtship also has been reported by Ruby (1977) for *Sceloporus jarrovi* and Rothblum and Jenssen (1978) for *Sceloporus undulatus*.

It is possible, however, that a real difference in courtship behavior occurred as well. In general, the Venezuelan male iguanas were less visual and more physical with females than were those in Panama. Forced copulation was attempted only by peripheral males in Panama. In Venezuela, both peripheral and territorial males frequently mounted or carried about violently reacting females (see "Forced Copulations"). Forced mounts overwhelmingly constituted the modal type (83%) seen in Venezuela, whereas they constituted only 22% at Flamenco. Although the Panamanian male iguanas less often used physical force, they more often used visual displays. In my sample of 10 15-min intervals for each of five large territorial males, no male displayed as often as the average given for Flamenco by Dugan (1980:74–75) ($t = 15.3$; $df = 267$; $P << 0.001$) and they did not show the bright red and yellow associated with breeding males in Central America. The only large arboreal lizard species in Venezuela is *Iguana iguana*. It is possible that colorful and distinctive visual "courtship" displays arose as a species isolating mechanism in Central America, where the similar black iguana, *Ctenosaura*, is present. In many parts of the green iguana's range that have no ctenosaurs, marked sexual dichromism is lacking (Hoogmoed, 1973; Lazell, 1973; Bakhuis, 1982; cf. Müller, 1972).

The three types of male behavior observed in this study (territorial, peripheral, pseudofemale) also were seen in Panama, although the relative mating success of the three types differed between the Venezuelan sites and between Venezuelan and Panamanian sites. Dugan (1982b) observed relatively greater mating success among the pseudofemale males in Panama than I did among pseudofemale males in Venezuela. In captive iguanas from Belize, Allison Alberts, Nancy Pratt, and John A. Phillips (pers. comm.) have found that pseudofemale males can be recognized not only behaviorally, but also by the

size of their gonads (proportionately larger) and absence of mandibular reddening. In their one pseudofemale male whose femoral pore secretions were analyzed, the secretion's chemical composition differed from that of other males and more closely resembled that of adult females. This may contribute to the territorial iguanas' apparent inability to recognize some pseudofemales as being adult males. Pseudofemales seemed to be abstaining from behavioral competition for dominance while continuing to feed and grow during the mating season. Occasionally in Panama and in Venezuela they engaged in sperm competition when the opportunity for an uncontested copulation arose.

The minor differences in the phenology of reproduction between this study and Dugan's are paralleled by the differences between the sites in the timing of rainfall (Rand and Greene, 1982; Sarmiento, 1984).

Most of the differences in social behavior between the llanos and Flamenco sites may follow from the microhabitat density differences. On Flamenco, territories of 1–4 females ($x = 2.6$) included at least one large tree. At Guacimos three territories occurred in a vertical stack in one small tree that nonetheless included over 25 females. With females in Venezuela concentrated in lines along water courses, the opportunity for mate monopolization would be enhanced, leading to higher OSRs (Figures 8, 9) and a greater number of peripheral males. Without a territory, a peripheral male can only obtain a copulation by guile or force. Both intrusions and forced copulations were more common in the Venezuela sites. Dugan (1982b) reported only 6% of total copulations were forced, whereas the majority of copulations at Guacimos (> 50%) were forced. With the nearly continuous threat of territorial intrusions or take-overs, it would not seem advantageous for a Venezuelan male to abandon his territory to court females foraging away from a territory, as Dugan (1982b) reported.

The ubiquity of intrusions and forced copulations at the Venezuelan sites produced a high frequency of multiple copulations and probably considerable sperm competition. If sperm competition occurs without specialized structures for sperm storage (none was evident in gross dissections performed by myself or Rand, unpub. data), the volume of sperm a male places in each female may be an important determinant of his reproductive success. The long copulation times (Table 3) and the protracted abdominal pumping suggest that a large quantity of material was being transferred during each copulation. Dissections of road-killed males indicated that large males have testes exceeding 1% of their body mass (wet mass). Although I am not aware of any compendium of this value for lizards, the range of values reported for the great apes is from 0.017% to 0.269% (Short, 1979). Thus, the notoriously huge-testicled chimpanzee has only about one-quarter the relative gonadal tissue of an iguana. This suggests that iguanas are producing large numbers of sperm. If ejaculates are costly (Dewsbury, 1982; Nakatsuru and Kramer, 1982), this could account for the apparent limitation of territorial male iguanas to one copulation per day. Why iguanas would produce only one large ejaculate per day rather than two or more smaller ones is unknown, but it may be an adaptation to female control of copulation frequency. As females almost always succeeded in avoiding unwanted copulations (see "Forced Copulation, Results") and were rarely receptive, it may be advantageous for a male to place as much sperm as possible into a female on the rare occasions when she allows herself to be mated. In light of the apparent pressure to maximize sperm output per ejaculation it is surprising that the iguanas did not avoid use of the most recently used testis and alternate hemipene use in the manner observed for anoline lizards (Crews, 1978; Tokarz, 1988).

Any explanation for the limitation of territorial male iguanas to copulating only once per day must address the absence of such a limit in peripheral male mating attempts. A sperm shortage might not result in a once-a-day limit on copulation attempts by peripheral males because (1) peripheral male copulations are routinely interrupted, and (2) peripheral males might benefit more from an incomplete sperm transfer than from conserving their sperm for an unlikely future copulation. Their shorter copulation times suggest that they do not transfer as much sperm in an average copulation.

Sexual selection might be expected to reward intermale combat, especially among smaller-size older males that had little probability of growing large enough to obtain a territory. Holders of territories gained many more copulations on average (Table 4); thus, acquisition of a territory might be worth a life-threatening struggle under certain circumstances. Yet few serious fights were observed by myself or by Dugan (cf. Alvarez del Toro, 1982:88). If vacant territories exist (as they did), and if females are free to switch territories at any time and prefer to reside in the territories of the largest males (as they appeared to), then a very large male would not need a particular territory and a smaller male would not necessarily gain mates by gaining a territory. After a large territorial male was temporarily removed by Dugan (1980:84), his medium-size successor was not able to entice the "widowed" females to remain, yet the females returned to the territory when the former resident male was released and he regained his territory. I observed females switching territories so as to remain with a large male that had changed territories. If this phenomenon is general, it would imply that intersexual selection for large male size puts a limit on the gains that could be made by an extraordinary intrasexual effort. If females are only attracted to the largest males there would be no advantage in a smaller male risking injury in a serious fight, nor any reason for a very large male to fight for a particular territory when adjacent space is unoccupied.

Forced Copulations

Definition of Forced Copulation

A "forced" copulation can be characterized as one in which the female struggles physically and violently (including jerky, unusual, rapid, or high amplitude movements) in an apparent

attempt to escape from a mounting male, as distinctly contrasted with an "ordinary" copulation in which the female rests passively or moves slowly without apparent attempt to escape when mounted. This definition of "forced" copulation includes cases in which the female struggles violently for part of the copulation time, but does not necessarily struggle throughout the entire duration of the copulation or attempt (cf. Stamps, 1983). Green iguanas probably do not possess the requisite metabolic physiology for violent physical struggle lasting the 5–15 min duration of a completed copulation (Bennett and Licht, 1972). Note that the proposed definition is based on the female's behavior, not on an assumed conflict of interest between the sexes. The male may be physically forcing the female to act against her own interests, or she may be furthering her interests by testing the strengths of various potential mates. These possibilities are not distinguished using this definition because they are not separable on the basis of field observations.

The Forced Copulations section includes (1) a description of the contexts of forced copulations, (2) an analysis of the variability among individuals in their participation in forced copulations, (3) a discussion of the ecological and evolutionary factors that may be responsible for the frequent occurrence of forced copulations in this species, and (4) a review of the literature pertinent to forced copulations, especially with regard to lizards. The latter is used to test, in a preliminary fashion, the generality of the evolutionary factors that I have hypothesized to promote forced copulations.

RESULTS

To avoid biases from incomplete observations, I have used in this section only observations from the continously observed territory at Guacimos.

OCCURRENCE OF FORCED COPULATIONS.—Initially, all resisted copulation attempts were categorized as "mild" or "violent." If an attempt was resisted for a sustained period of time (> ~20 sec) or if rapid, repeated, or unusual physical movements were involved (e.g., fast running, jumping from branch to branch while mounted, biting, etc.) the attempt was coded as "violent." Less dramatic responses were categorized as "mild." Of the 243 copulations attempts clearly seen, 29 (12%) were generally passive, 22 (9%) involved mild resistance, and the remainder (79%) were violently resisted. The unresisted attempts matched the behavior reported by Dugan (1982b) for territorial male copulations in Panama.

The territorial male under intensive observation at Guacimos attempted to copulate 43 times, and was successful (intromission achieved) 18 times (42%, Figure 15). In 19 (44%) of the attempts the females did not resist, on 3 occasions (7%) he was mildly resisted, and 21 (56%) times the females resisted violently. Comparable figures for five peripheral males were 21 successful copulations (10%) of 200 attempts; of these attempts, 10 (5%) were unresisted, 32 (12%) mildly resisted, and 178 (89%) violently resisted. If male status were unimportant to the females, the proportion of their behaviors in each of the resistance categories would not differ between

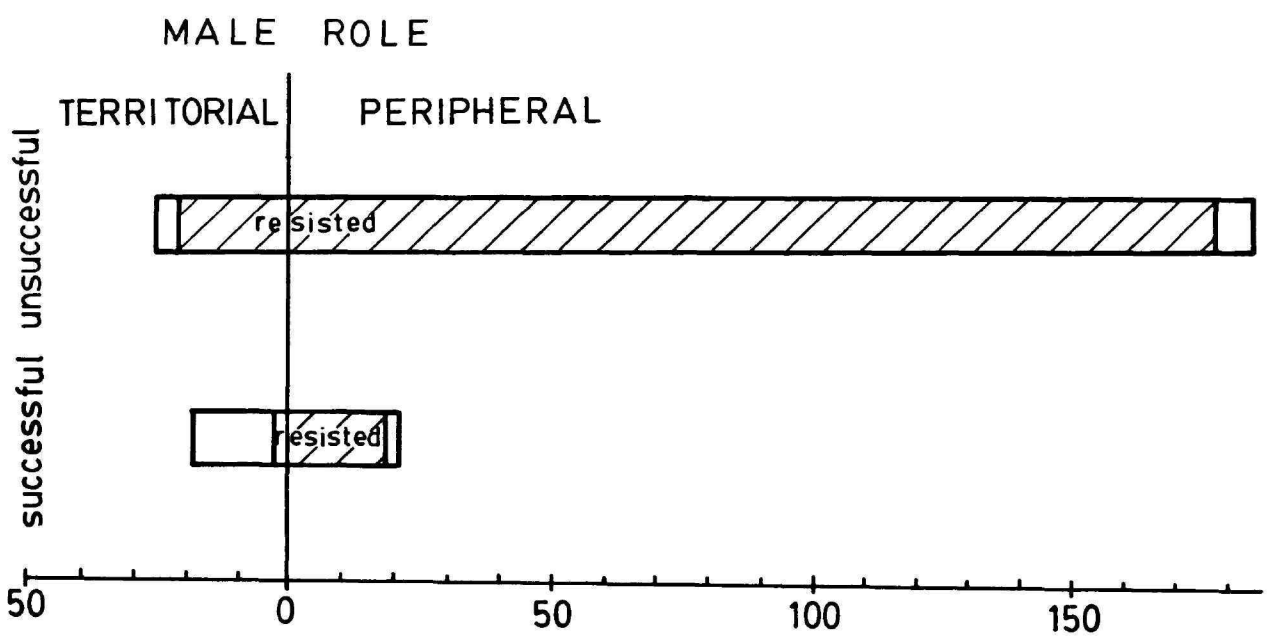

FIGURE 15.—The distribution of copulation attempts with reference to male role, success, and female resistance. In each of the four conditions, the open bars represent the unresisted copulation attempts, and the hashed bars represent resisted attempts.

territorial and nonterritorial males. However, the females were selective. There was a highly significant association between success and absence of resistance in the distribution of the territorial male's copulation attempts ($G = 20.1$; $P < 0.001$) but none in peripheral male attempts ($G = 1.3$; $P > 0.1$). There was also a significant association between male role (territorial vs peripheral male) and success ($G = 11.3$; $P < 0.001$) or resistance ($G = 19.2$; $P < 0.001$), with greater success and less resistance being associated with territorial males. This pattern was seen in all 11 territories observed. Male role (whether territorial or peripheral) was the only variable found to explain differences in the frequency or context of forced copulations among males.

These statistics imply that females selectively resisted peripheral males and the territorial male's success was influenced by the female's behavior. Territorial males seemed to modify their copulation efforts both by not mounting most of the females that signaled their rejection and by discontinuing most copulation attempts if the female tried to escape once mounted. In contrast, peripheral males did not appear to be sensitive to the female's reaction.

CONTEXT OF FORCED COPULATIONS.—Most forced copulations occurred when a peripheral male ran into a territory and mounted the first female encountered, or when a female left a territory and was mounted by a peripheral male, usually the first one encountered. Therefore, almost all extra-territorial copulations were forced (Table 6). Although location generally was not associated with success, forced copulation attempts initiated on the ground rarely (3%) were successful (Table 6), perhaps because female escape efforts were not vitiated by the concurrent requirement of climbing along a branch.

Peripheral males were opportunistic in the timing of their copulation attempts, with the result that the times of day of their attempts ($F = 2.567$; df = 200,43; $P < 0.0012$) and successes ($F = 3.905$; df = 211,8; $P = 0.0025$) were more variable than were those of the territorial male. Peripheral males' copulation attempts also spanned a longer season ($F = 12.67$; df = 200,43; $P < 0.0014$). Female resistance was not restricted to time-of-day or a particular season; time-of-day for attempts ($F = 1.135$; df = 212,28; $P = 0.36$), time-of-day for successes ($F = 1.880$; df = 18,18; $P = 0.10$), and date of attempts ($F = 0.786$; df = 212,28; $P = 0.83$). The time-of-day for successes comparison is grossly distorted by the results pertaining to one anomalous female (see "General Mating Behavior"). With this female removed, the resisted copulations were significantly more variable in timing than unresisted copulations, which tended to cluster around midday ($F = 4.85$; df = 10,10; $P = 0.009$).

Female iguanas stop eating during the mating season, presumably to provide more space for the developing ova. If the date of cessation of feeding is taken as a predictor of a female's physiological readiness for mating, one might expect an association between date of feeding cessation and behavioral receptivity as measured by first unresisted copulation attempt. This was observed for the 6 females for which both dates are known (Spearman $r = 0.986$; $P < 0.0013$). There was also a correlation between the dates of feeding cessation and first successful copulation by the territorial male (Spearman $r = 0.943$; $P = 0.0048$). Data are available for only 5 females for the same comparison with the first success date of

TABLE 6.—Distribution of copulation attempts by location, with regard to male role, female resistance, success of all attempts, and success of forced attempts. The statistics are tests for independence. Parenthetical values are percentages of totals at that location.

	Adjacent to territory			In territory	
	Ground	Bushes	Tree	Outer edge	Core
Male role ($G = 29.65$; $P < 0.001$)					
Peripheral	36(100)	23(96)	15(100)	87(76)	39(74)
Territorial	0	1	0	28	14
Female resistance ($G = 17.64$; $P = 0.001$)					
Forced	36(100)	23(96)	15(100)	98(85)	43(81)
Unforced	0	1	0	17	10
Success of all attempts ($G = 9.116$; $P = 0.058$)					
Successful	1(3)	3(13)	1(7)	17(15)	12(23)
Unsuccessful	35	21	14	98	41
Success of forced attempts ($G = 3.491$; $P = 0.479$)					
Successful	1(3)	2(9)	1(7)	8(8)	6(14)
Unsuccessful	35	21	14	90	37

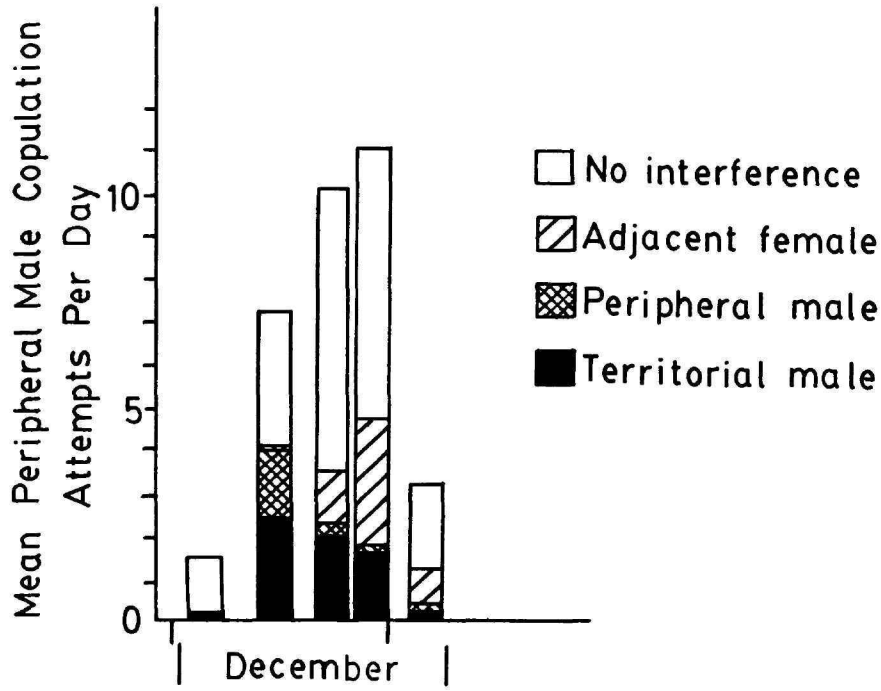

FIGURE 16.—The frequencies of third party interference in copulation attempts.

peripheral males, thus the correlation is nonsignificant though fairly strong (Spearman $r = 0.825$, NS). If this effect is real, it would imply that the females' resistance to the peripheral males was temporally selective, with lowered resistance correlating with physiological receptivity. An alternate possibility is that the males timed their attempts selectively with reference to female receptivity, but no evidence of this was found (dates of attempts by a territorial male Spearman $r = 0.64$; $P = 0.12$; peripheral males Spearman $r = 0.05$; $P = 0.92$).

A female's violent reaction when mounted might serve to draw the attention of other iguanas, possibly resulting in interference. On most occasions, the females escaped prior to the arrival of other iguanas, but there were noticeable seasonal changes in the amount and kind of assistance (Figure 16). For example, in late December adjacent females interfered with peripheral male copulation attempts more frequently than did the territorial male in whose territory the forced copulation attempt occurred (Figure 16). In contrast, in early December adjacent females did not participate as third parties in copulation attempts (Figure 16). Figure 16 tabulates only the actions occurring during forced copulation attempts. In many cases in which a peripheral male attempted a copulation within a territory and the territorial male was not tabulated as interfering, the territorial male was moving vigorously toward the mounted pair, but did not reach their vicinity before the female had escaped, apparently on her own.

VARIABILITY AMONG FEMALES.—Females varied conspicuously in the frequency of copulations attempts, and the frequency of resistance (Figure 17). However, the various females were visible for differing intervals and a spurious correlation between territorial and peripheral male attempts could be generated if the number of attempts on each female was simply a function of the amount of time observed. To avoid this problem, I considered the seven females for which the observations were essentially continuous and analyzed each female's scores in relation to (1) the number of attempts by peripheral males, (2) the success rates of peripheral males, (3) the number of attempts by the territorial male, and (4) the success rates of the territorial male. Attempts were separated from successes to distinguish between the effects of male versus female behavior. Presumably the male's motivation would play the pivotal role in a decision to initiate a copulation (an "attempt") whereas once begun, the female's behavior would be an important determinant of success.

ATTEMPTS BY PERIPHERAL MALES.—Two factors potentially contributing to the variability observed in the number of times each female was mounted were (1) the time females spent in vulnerable perches (those perches near the periphery of a territory where most peripheral male copulation attempts occurred), and (2) whether peripheral males directed attacks at

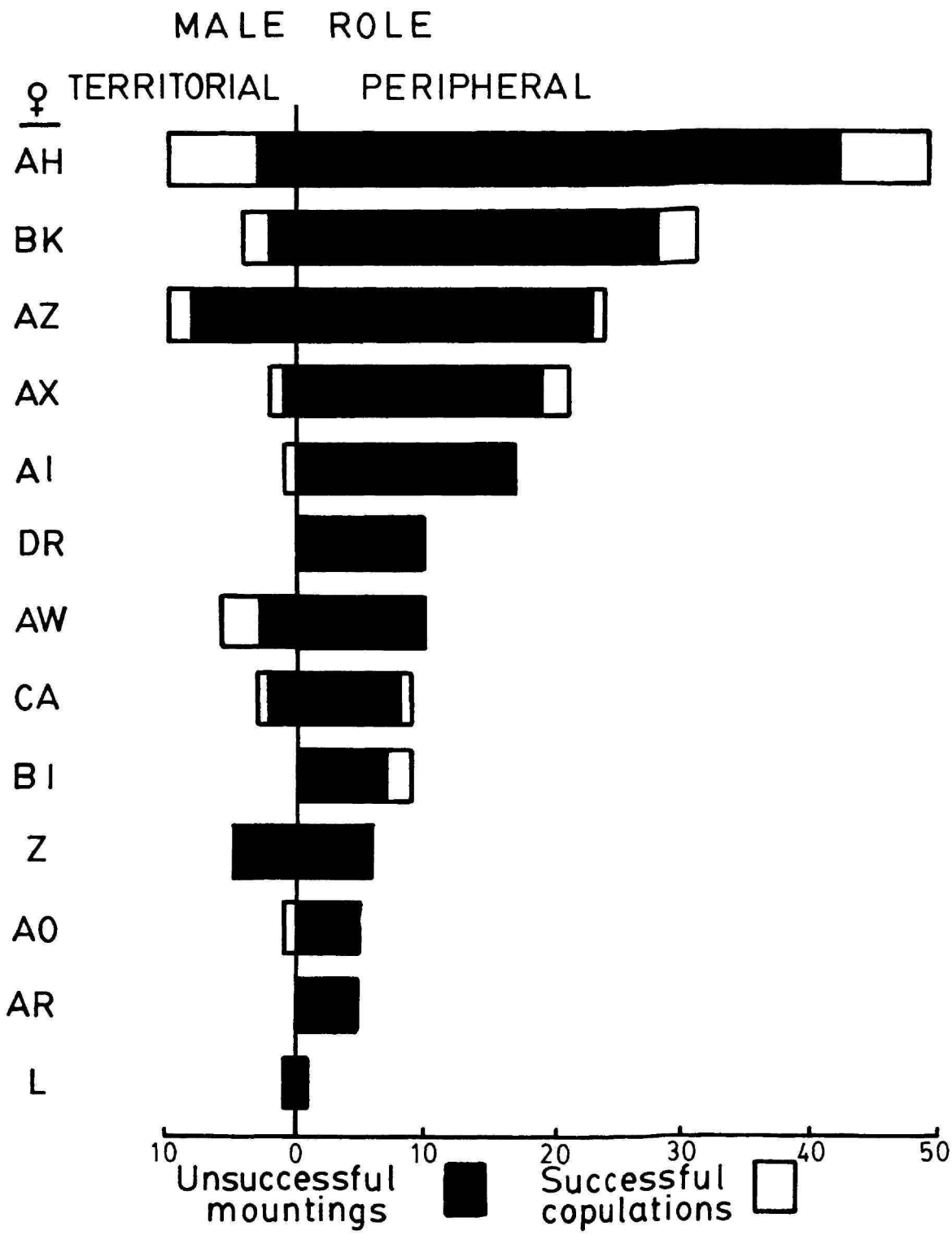

FIGURE 17.—Frequencies of copulation attempts on females divided by male role and success.

certain females. The vulnerable perches factor was addressed by subtracting each female's relative use of each perch during the mating season from that observed prior to the mating season (each female's perch use scores summed to 100% for each season). The difference was a relative score (negative values for perches avoided during the mating season; positive values for perches used more during the mating season) that was correlated with the rate of copulation attempts per iguana hour experienced by other females at that perch. Thus, a female that shifted her perch usage toward vulnerable perches would exhibit a positive correlation and a female that exhibited a negative correlation would be avoiding vulnerable perches. The possibility that peripheral males were directing their efforts toward specific individuals was tested by contrasting the rate of attempts at each perch when a specified female was present with that when other females occupied the perch. A paired t-test was used to compare attempt rates for each female, with each perch providing one comparison. A test statistic significantly greater than zero denotes a preferred female.

For most females, these tests indicated no significant change in perch use and no significant selectivity by peripheral males (Table 7). The significant values that were obtained suggest individual effects worthy of further study. All of the females except AX exhibited a nonsignificant change in perch usage, generally away from the more vulnerable perches used before the mating season toward less vulnerable perches used during the mating season. Interestingly, the exception was the female that occupied the lowest position in the dominance hierarchy among resident females (based on the outcome of interactions, see "Female Dominance Relations"). This raises the possibility that females might have been contesting among themselves for the use of less vulnerable perches. However, no direct evidence for this was observed, and there was no other evidence of an association with dominance status. For example, the female with the next to lowest rank (CA) shifted her perch usage away from vulnerable perches.

The peripheral males avoided females AI and CA significantly, but did not significantly prefer any (Table 7). However, the mean preference scores correlated with the sizes of the females (Spearman $r = 0.75$; $P < 0.05$), with the larger females preferred. An exception was female BK, who received a relatively large share of copulation attempts despite her modest size. At the times of the observations, BK had a freshly broken arm and had difficulty climbing through the trees. Males seemed to be directing their attempts toward this particularly defenseless female. With BK removed, there was a nearly perfect correlation between the peripheral males' female preference scores and female size (Spearman $r = 0.957$; $P < 0.01$).

SUCCESSES OF PERIPHERAL MALES.—I attempted to identify the factors contributing to variability in the success rates of peripheral males on individual females by building a multiple regression model based on these factors: (1) territorial male interference rate, and (2) the percent of peripheral male attempts resisted. Together they did not have a significant influence ($F = 3.29$; df = 2,6; $P = 0.14$). I attribute this lack of significance to the low variability in the measured traits to two factors: (1) the territorial males' actions rarely interrupted an attempt, and (2) the females almost always resisted vigorously.

ATTEMPTS BY THE TERRITORIAL MALE.—I repeated the analysis used for peripheral males attempts, with strikingly similar results for the territorial male (Table 8). I also tested the frequency with which the territorial male approached each female during the times of day when he copulated. A G-test for heterogeneity in the sample indicated that some females were approached significantly more often ($G = 30.8$; df = 6; $P < 0.001$). However, I found no evidence that the differences correlated with the number of times each female was mounted. Several multiple regressions were attempted, incorporating various mixtures of (1) the size of each female, (2) the activity level of each female (based on mean number of meters moved per hour; this was used because lethargy could be confused with consent in mating iguanas), (3) number of days receptive, (4) number of peripheral male copulations per female, and (5) number of territorial male approaches per female. None approached significance (all $P > 0.25$).

SUCCESSES OF THE TERRITORIAL MALE.—Four factors were considered as possibly contributing to the success of the

TABLE 7.—Results of statistical tests of individual female variability in number of peripheral male copulation attempts as outlined in the text.

Female	Vulnerable perches		Preference of male	
	Spearman r	P	t	P
AH	0.06	0.81	0.32	0.75
AI	-0.40	0.10	-2.42	0.027*
AW	-0.01	0.97	0.86	0.40
AX	0.60	0.008*	0.07	0.94
AZ	-0.40	0.10	-0.94	0.35
BK	-0.31	0.21	1.56	0.14
CA	-0.30	0.23	-3.09	0.007*

* $P < 0.05$

TABLE 8.—Results of statistical tests of individual female variability in number of territorial male copulation attempts, as outlined in the text.

Female	Vulnerable perches		Preference of male	
	Spearman r	P	t	P
AH	-0.36	0.14	1.01	0.33
AI	-0.07	0.78	-2.11	0.050*
AW	0.10	0.70	0.55	0.59
AX	-0.53	0.025*	-1.53	0.14
AZ	-0.01	0.97	1.19	0.25
BK	-0.31	0.21	-0.15	0.88
CA	0.22	0.39	-2.36	0.031*

* $P < 0.05$

TABLE 9.—Published observations reporting at least 10 copulations seen in a species of lizard.

Species	Study	Copulations observed	Percent forced	Herbivore	Insectivore
Iguana iguana	Dugan, 1982b	49	6	x	
	this study (all sites)	55	>50	x	
Conolophus sub-cristatus	Werner, 1982	19?	5-10	x	
Amblyrhynchus cristatus	Trillmich, 1983	117	0	x	
	Rauch, 1985	28?	0?	x	
Cyclura cornuta stejnegeri	Wiewandt, 1977, 1979	21	0	x	x
Tropidurus delanonis	Werner, 1978	"about 40"	10?		x
Sceloporus jarrovi	Ruby, 1976, 1981	12	0		x
Uta stansburiana	Tinkle, 1967	12	0		x
Anolis garmani	Trivers, 1976	88 partial	1?		x
A. vallencienni	Hicks & Trivers, 1983	75	1		x
A. lineatopus	Rand, 1967	12	0		x
A. polylepis	Andrews, 1971	13	0		x
A. carolinensis	Gordon, 1956	11	0		x
	Ruby, 1984	14 inc.	0		

territorial male, two reflecting the male motivation and two quantifying female reactions. Fecundity is closely associated with size in iguanas (Rand, 1984). Therefore, both female size and the number of times she was copulated by peripheral males might be associated with the male's motivation level (i.e., males might be more highly motivated to copulate with a female who would be likely to produce more offspring). The percent of the territorial male's attempts that were resisted and the mean vigor of her resistance probably reflects primarily the female's interests. The absolute number of the territorial male's successes produced a highly significant model ($R^2 = 0.99$; $F = 97.4$; df = 3,6; $P = 0.017$) with the factors vigor of resistance ($F = 34.5$; df = 1,6; $P = 0.010$), number of peripheral male copulations ($F = 36.5$; df = 1,6; $P = 0.009$), and size of females ($F = 36.3$; df = 1,6; $P = 0.009$) all making significant contributions. In this model, vigorous female resistance was associated with reduced success. Female size, and the number of times she had been copulated by peripheral males were associated with increased success.

VARIABILITY AMONG SITES.—The data reviewed above, which were obtained from one site that included several territories, can be qualitatively compared with observations from two other, less-intensively studied sites. Two differences among sites were apparent. One was that at the two other sites, which had lower densities of iguanas, far fewer peripheral male intrusions into a territory occurred. At the lowest density site, none were seen. Second, it was apparent at all sites that the architecture of a territory influenced the success of peripheral males. Solitary palms provided a territorial male with a nearly impregnable territory, whereas a tree with numerous entry paths was difficult for a territorial male to defend.

COMPARISONS AMONG LIZARD SPECIES.—Fourteen studies have reported viewing at least 10 copulations in the field (Table 9). Six passed the criterion by only 2–4 copulations. Trivers (1976) observed 88 copulations of *Anolis garmani*, but only one of these was observed in its entirety.

The utility of this list is marred by its geographic and taxonomic narrowness. Only eight genera are represented and all are in the Iguanidae. All occur in a region between the southern United States and the Galápagos Islands. Fortunately, the Iguanidae includes both herbivores and insectivores, allowing a comparison between iguanas and the more typical insectivorous lizards. Forced copulations varied from 0% to > 50% of the observed copulations in four herbivorous species, but occurred at a rate of 1% or less (with one exception, discussed below) in nine insectivorous species.

DISCUSSION OF FORCED COPULATIONS

In the intensively monitored area, forced copulations were the modal type of mating behavior, including 88% of the attempts and over 50% of the successful copulations. However, these values may not be typical for the green iguana in the llanos of Venezuela, in that a relatively high density site was chosen for observational ease and high densities could promote the forced copulation tactic in a variety of ways (see below). Nonetheless, the observed values are extraordinarily high compared to the 6% of copulations among iguanas in Panama (Dugan, 1982b) as well as the other lizard studies (all ≤ 10%; Table 9). Few taxa have been reviewed for the incidence of forced copulation, but among them are colonially nesting monogamous birds (Gladstone, 1979) and waterfowl (McKinney et al., 1983). The proportion of total matings that are forced in these groups are known for only a few species, but all values are substantially less than the 50% reported here for the green iguana. Among colonial species, only a few percent of total copulations have been reported as forced, even though forced copulations are frequently observed (Emlen and Wrege, 1986).

Afton (1985) reported the highest value among waterfowl: 19.6% for copulations among Lesser Scaup (*Aythya affinis*). However, most values for waterfowl are much lower (McKinney et al., 1983).

I am aware of only two well-studied vertebrate species for which physically violent copulations are the modal pattern: garter snakes *Thamnophis sirtalis* (Garstka et al., 1982) and elephant seals *Mirounga angustirostris* (Cox and Le Boeuf, 1977). Both species are somewhat unusual. Many garter snake males "mount" a female simultaneously when the female emerges from the hibernaculum and the female eventually copulates with the most persistent male. However, this does not satisfy my definition of a forced copulation, because all copulations in these populations are physically competitive. No separate class of forced copulations exists. Female elephant seals protest almost all attempts until the day or two before they leave the breeding area. Cox and Le Boeuf (1977) suggest that this is a tactic for inciting male:male competition, because protesting females often attracted the attention of adjacent males, resulting in the copulation being interrupted by an adjacent male 62% of the time. Cox and Le Boeuf reported that females never escaped by their own actions. Mounted female iguanas also attracted adjacent males during forced (and nonforced) copulation attempts, although it is not evident that the adjacent males approached the mounted pair in substantially greater numbers as a result of the females' resistance. It is evident that iguana females usually escaped prior to the arrival of an adjacent male. Only 25% of the resisted attempts were interrupted after the time of the arrival of an adjacent male. In 74% of the resisted attempts the female escaped without assistance from a male. Thus, the context for forced copulations in the iguana does not closely match either the garter snake or elephant seal situation.

The salient feature of female mating resistance in the iguana is that it was directed primarily toward peripheral males. The females resisted 95% of the peripheral male attempts but only 56% of the territorial male attempts. Had all copulation attempts been successful, the study females would have received 83% (205 out of 248) of their ejaculates from peripheral males. Largely as a result of the females' selective resistance, the actual value was 54% (21 out of 39).

If females resist peripheral males in order to preferentially obtain the sperm of territorial males, the 56% resistance rate for territorial male attempts seems paradoxical. Some degree of female rejection is associated with copulation attempts in almost all species. Prior and subsequent to a period of receptivity females of many species reject mating attempts. In addition, females of many species mate selectively during their period of receptivity. The 56% rate of rejection is not unusual. The mode of rejection is. Dugan (1982b) characterized the rejection postures of female iguanas in Panama as a distinctive arching of the tail. In many insectivorous lizards, the female simply runs away from unwanted suitors (Rand, 1967). I routinely observed one or both of these forms of rejection among the Venezuelan iguanas. But unlike the males in these other lizard populations, the Venezuelan iguana males did not always abort their copulation attempts just because a female signaled her unwillingness. On a proximate level, this male reluctance to heed the females' rejection signals seems to account for the extraordinary frequency of forced copulations in this population.

Why might a Venezuelan male iguana not take no for an answer? A peripheral male has nothing to lose by forcing a copulation unless females recognize individual copulators and discriminate against them at some later time when they become territorial males, as suggested by Dugan (1982b). For a territorial male, a more immediate penalty is possible: harassing a female may lead to her departure from the mating territory. Territorial switching occurred, although there may be a cost to switching. Cooper (1985) reported that unfamiliar females were subject to greater male harassment in a territorial iguanid, *Holbrookia propinqua*. I did not observe this. I did observe a decrease in a female's apparent rank in the female dominance hierarchy when she entered a new territory. This penalty took the form of chases and movement restrictions, and it seemed to have a greater effect on relatively small females. Large females deferred to smaller residents for 1–3 days after entering a new territory, but new small females often were chased until they left permanently. Thus, a female's reluctance to switch territories may provide the degree of site fidelity that permits a territorial male to attempt forced copulations on resident females without causing them to abandon his territory.

It is also possible that the females' preference for large mates causes them to tolerate some harassment in the territories of the largest males. If this is true, one would expect forced copulations to be more common in the territories of the largest males and to be more common at the sites in which females expressed greater unanimity in their preferences for specific males. Forced copulation attempts by territorial males were not observed in Panama, where the average territorial male attracted 2.6 females and no male attracted more than 4 (Dugan, 1982b). In the intensively monitored area in Venezuela, eight mating territories averaged about 7 females per male (range: 4–14), and the majority of copulation attempts by territorial males were forced.

Large male size and highly skewed operational sex ratios (OSR) may elevate the frequency of forced copulations by a more direct pathway as well. A large male iguana can carry a protesting female about in his mouth. Sexual size dimorphism may permit the larger sex to physically coerce members of the smaller sex. More highly skewed territorial OSRs should produce a larger pool of floater or peripheral males if the population sex ratio is otherwise unchanged. The relative rarity of forced copulations among insectivorous lizards (Table 9) may be attributable to the low OSRs in the territories of many insectivores (Stamps, 1977:301–303) and the attendant paucity of peripheral males.

Sexual size dimorphism, diet, and OSR are not independent

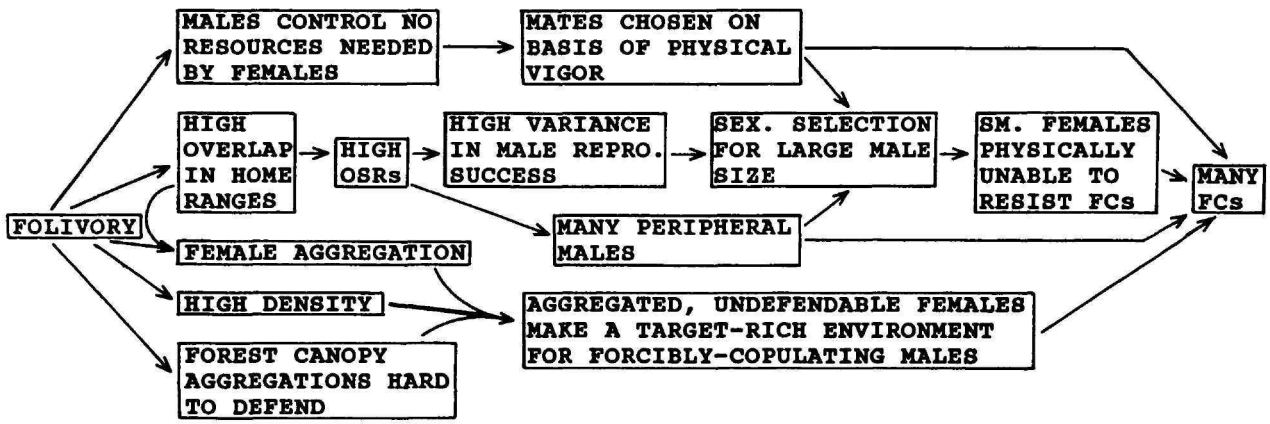

FIGURE 18.—Factors hypothesized to promote forced copulations (FCs) in *Iguana*.

of one another (Carothers, 1984). High overlap in home ranges is characteristic of herbivores (Stamps, 1977) and is associated with high variance in male reproductive success leading to sexual selection for large male size. In the herbivorous iguana, females do not need to maintain a feeding territory, as leaves are effectively superabundant. Instead, iguana females aggregate in the sites best suited for predator defense (trees bordering water courses).

From the peripheral male perspective, the high density of females provides many conveniently located targets for forced copulations. In the absence of defendable resources, a lek or harem-like mating system may develop. From the territorial male iguana perspective, the extreme aggregations of females necessitate an energetically costly defense of an arboreal "harem." Sexual selection for large male size may ensue, and reduce the females' physical ability to resist forced copulations. It is also possible that the absence of a male-controlled resource leads female iguanas to select a mate at least partially on the basis of a suitor's physical vigor, as evidenced by the ability to force copulations. All of these factors are directly or indirectly related to the iguana's folivory (Figure 18).

Do the available data from other lizard species support an association between folivory or herbivory and forced copulations (Table 9)? With the exception of *Tropidurus*, species exhibiting a substantial proportion of forced copulations are herbivores. *Tropidurus* is an unusual insectivore in that it occurs in very high densities in the Galápagos Islands (Werner, 1978). In this case, the unusual features of island living in the Galápagos have created conditions allowing the lizards to attain the high densities and extreme aggregations characteristic of most herbivores. The general association of forced copulations with dense aggregations has been noted for a variety of taxa. Emlen and Wrege (1986) termed forced copulation a "cost of coloniality" in their White-fronted Bee Eaters. Gladstone (1979) made the same association for a diverse group of monogamous birds. Swallows and elephant seals forcibly copulate in their dense aggregations. Thus, herbivory may not be the only situation that will lead to dense aggregations of females (and opportunities for forced copulations) in lizards, but it may be a common precursor.

The apparent absence of forced copulations in the herbivorous lizards *Cyclura* and *Amblyrhynchus* appears to be related to a physically unique aspect of saxicolous living. Although many herbivorous lizards are arboreal, these two species take refuge in rocky crevices in which the females scrape off unwanted suitors (Trillmich, 1983; Wiewandt, 1977:170). Thus, while herbivory may lead to greater male size and large numbers of peripheral males as in *Iguana* (Figure 18), these features do not lead to forced copulations in *Cyclura* and *Amblyrhynchus* because the females have an effective deterrent. In addition, the crevices are a defendable resource, which eliminates two of the factors that promote forced copulation in *Iguana* (Figure 18). Crevices are an essential resource and they are easy to defend. Thus, females seek mates with high quality burrows, rather than choosing males directly for their physical vigor (Rauch, 1985).

Female Dominance Relations

The existence of a dominance hierarchy implies that the participating individuals are competing for a limited resource (Brown, 1975:92-95). Dominant male iguanas obtain possession of the best mating territories, but the advantage of high rank among female iguanas is obscure. This section explores the factors that might generate a dominance hierarchy among female iguanas.

TABLE 10.—Interaction and dominance matrices for resident females at Masaguaral during the 1982 mating season. Values in the interaction matrix represent the iguana's number of "victories" over the corresponding animal (see text); values in the dominance matrix express the difference between the numbers of victories within each dyad: 1 (iguana "dominant" because it won more often than it lost to the corresponding animal), 0 (iguana "subordinate" for the converse reason) or 0.5 (interaction sums equal).

Interaction matrix

Winner	Loser					
	AP	AR	AD	BB	Q	AJ
AP	-	1.5	2	1	3	2
AR	0.5	-		1.5	2	
AD			-	1	1	2
BB		0.5		-	3	0
Q					-	2
AJ						-

Dominance matrix

Dominant	Subordinate					
	AP	AR	AD	BB	Q	AJ
AP	-	1	1	1	1	1
AR	0	-	0.5	1	1	0.5
AD	0	0.5	-	1	1	1
BB	0	0	0	-	1	0.5
Q	0	0	0	0	-	1
AJ	0	0.5	0	0.5	0	-

TABLE 11.—Interaction and dominance matrices for resident females at Guacimos during the 1983 mating season. Values as in Table 10.

Interaction matrix

Winner	Loser						
	AW	AH	AZ	BK	AI	CA	AX
AW	-	2	2	3	1	3	1
AH		-	3	2	4	2	1.5
AZ		1	-	0.5	2	3	2.5
BK			0.5	-	0.5	3	
AI				0.5	-	1	2
CA						-	1
AX		0.5	0.5				-

Dominance matrix

Dominant	Subordinate						
	AW	AH	AZ	BK	AI	CA	AX
AW	-	1	1	1	1	1	1
AH	0	-	1	1	1	1	1
AZ	0	0	-	0.5	1	1	1
BK	0	0	0.5	-	0.5	1	0.5
AI	0	0	0	0.5	-	1	1
CA	0	0	0	0	0	-	1
AX	0	0	0	0.5	0	0	-

METHOD OF TABULATING DOMINANCE RELATIONS

Most stationary females eventually retreat after being approached by another iguana, and if they do not do so, the approaching iguana may walk over the stationary one. Thus, an approach and withdrawal (outcomes 2–4, collectively "low intensity outcomes") were somewhat ambiguous for inferring female dominance relations. For each pair of animals I tabulated the sum of each iguana's number of victories indicated by their high intensity interactions (each victory = 1) and the consensus of the low intensity outcomes if there were at least three low intensity outcomes recorded for the dyad (maximum score of 1 for the aggregated low intensity outcomes). If the aggregated low intensity outcomes exhibited a clear asymmetry, I awarded the victorious animal a 1 and the loser a 0. If a dyad's low intensity outcomes were nearly or exactly equal, each participant was awarded 0.5 points. The summed high and low intensity outcome scores were arrayed in an interaction matrix. A dominance matrix was prepared on the basis of which animal in each dyad had the higher score in the matched cells of the interaction matrix. Thus, if the interaction matrix for the dyad of AH and AZ showed AH with 3 wins over AZ and AZ with 1 win over AH, AH would be treated as dominant to AZ. In the dominance matrix each iguana received a score of 0 (subordinate), 1 (dominant), or 0.5 (interaction matrix totals tied).

RESULTS

Because females are generally nonaggressive and inconsistent in their interaction outcomes outside of the mating season, interaction matrices for the nonmating period did not indicate a significant linear hierarchy for any site. Using Kendall's (1970:144–161) K index (0 = no relationship, 1 = totally linear hierarchy; see Appleby, 1983), the nonmating index for Masaguaral was 0.09 ($n = 6$ females; $P >> 0.1$) and that for Guacimos was 0.34 ($n = 6$; $P >> 0.1$). In contrast, females formed conspicuous dominance hierarchies at both sites during the mating season (Tables 10, 11). At Masaguaral, the small hierarchy size ($n = 6$ females) and lack of information on 6 of 15 pairwise comparisons preclude a statistically significant linear relationship, but the K index (0.72) and the absence of reversals suggest that the females were hierarchically organized. At Guacimos, the females were unequivocally organized into a linear dominance hierarchy during the breeding season (K = 0.86; $n = 7$; $P = 0.017$).

At Guacimos, the dominance ranks of females corresponded exactly with their relative sizes (due to ties in sizes: Spearman $r = 0.98$; $P < 0.05$), whereas the dominant female at Masaguaral was only the third largest. Nonetheless, most of the

variation in rank at Masaguaral was associated with variation in size (Spearman $r = 0.82$; $P = 0.05$).

The relatively large fraction of interactions involving females moving toward sleeping perches suggests that the females may have been contesting access to preferred sleeping sites. At Guacimos, the higher density site, many sleeping sites were occupied every night, and females tended to return to the same sleeping site regularly. The alpha female at Guacimos slept at one site 19 nights in a row. These results were not observed at Masaguaral, where there seemed to be a surplus of suitable sleeping sites, many of which were unoccupied on any given night. For example, the most consistent use of a perch at Masaguaral was that of low-ranking female Q, who returned to one site for eight nights in a row. The dominant female, however, rarely slept in the same site for more than two nights, and her longest run was four nights. The height, diameter, and inclination of each sleeping site at Masaguaral was estimated from photographs. I calculated that there were at least three times as many suitable perches as there were sleeping females. The number of perches that were used at least once by a sleeping iguana at Masaguaral was also about three times the number of iguanas that normally slept at that site.

At Guacimos, the tips of the branches overhanging the water were preferred for sleeping perches. Because the focal tree at Guacimos had been dead for many years prior to our observations, only thick limb stubs remained and there were approximately as many overwater limbs as there were sleeping iguanas at Guacimos. At Masaguaral a preference for branch ends was not observed, probably because the entire canopy of many small branches was over water during the rainy season, and the water quickly receded beyond the positions of all perches during the dry season. At the lowest density site, El Frio, there was no evidence of any competition for perches, probably because the number of perches vastly exceeded the number of iguanas and most perches were over water year round.

At Masaguaral, I compared the rank of breeding females to various measures of perch use in an effort to identify a resource that might be sought after. I considered perch height, perch diameter, perch inclination, perch use by the focal animal, perch use by the other female iguanas when the focal animal was absent, and the number of perches controlled by a perch (i.e., the number of perches that were more distal). The only significant association was perch control ($r = 0.39$; $P < 0.005$). Consistent with this positioning of dominant females at the base of limbs, there was a significant difference between dominant and subordinate females. Dominant females were more likely to block another's movements than attempt to pass a stationary female (Mann-Whitney $U = 7.5$; $P < 0.02$).

At Guacimos, the females expressed a clear preference for the ends of branches, irrespective of the heights, diameters, or inclinations of the branches. Thus, for almost all sleeping perches at Guacimos, the number of more distal perches was zero. The number of branch ends at Guacimos normally exceeded the number of females present. There was no evidence that the female dominance hierarchy existed to secure more suitable sleeping sites for the more dominant animals.

Another possible benefit of high rank might be the opportunity to bask with fewer interruptions. However, there was no significant correlation between rank and variance in basking interval length (Spearman $r = 0.29$; $P >> 0.1$).

The final hypothesis that I considered for the advantage of high rank was that high rank gave access to preferred mating territories during the copulation season. Among the observations that supported this was the correlation (reported above) between rank and use of perches that controlled access to other perches. On 18 December 1982 (late in the copulation season), there was a radical shift in mating territories at the Masaguaral site, with the most dominant territorial male shifting sleeping trees to that formerly occupied by a lower ranking male recently incapacitated by leg injuries. Coincident with this shift in male territorial ownership was a matching shift in female perch use. That is, the majority of the females shifted sleeping trees to remain with the dominant male ($G = 65.25$; $df = 1$; $P < 0.001$). This suggested that proximity to a dominant male was more important than the attributes of a particular sleeping site.

On numerous occasions at both Guacimos and Masaguaral, new females were harassed by repeated high intensity contests with resident females of all sizes. Most were immediately chased from the territory and did not return. A few remained by taking up positions on the periphery of the territory. Only the largest new females remained for more than one day. After the second day, these large newcomers were tolerated by all but the larger or more dominant resident females. Thus, small females rarely remained in preferred mating territories. The territorial males did not participate in this exclusion. On a few occasions, males approached new females and headbobbed. This could be interpreted as courtship or a challenge to determine the new animal's sex, but territorial males did not attack or harass new females, as did the resident females.

If high rank was associated with the opportunity to remain in a preferred mating territory, this privilege did not extend to the opportunity to copulate more often, or earlier, or later in the copulation season. There was no significant correlation between rank and these measures of copulation priority (all $P >> 0.05$).

Discussion of Female Dominance Relations

To understand female dominance relations in the green iguana, it is necessary to identify the privilege associated with high rank and to determine if the dominance hierarchy is based in part on past competitions. If the outcome of interactions is determined only by fighting ability, relative size, or some other rapidly measurable attribute (Jackson and Winnegrad, 1988), there would be little advantage to the larger females from their having established themselves as dominant, for they might

have to demonstrate their fighting ability any time a limiting resource was contested. On the other hand, the reduced fighting associated with a dominance hierarchy depends on each individual's ability to recognize and defer to individuals of higher rank (Brown, 1975:92–96). If iguanas cannot identify other iguanas individually, they cannot easily keep track of a challenger's status.

While the definitive experiments have not been conducted to test the ability of iguanas to recognize individuals, I observed a number of occasions in which an individual iguana seemed to be reacting differently to a newly arriving iguana than it did to familiar residents (see above "Results" and "Nonbreeding Behavior, Results"). In addition, there were numerous occasions in which an iguana initially reacted inappropriately to an approaching iguana, only to sharply alter its behavior when the iguanas came into closer proximity. Neither of these demonstrate individual recognition, for the iguanas might simply be classifying all other individuals into classes such as familiar versus stranger. However, the very widespread use of headbobs after an interaction, or when separated in time from any known interaction suggests that the displaying animal was facilitating future success by proclaiming its present status. This could be of survival value only if the displaying iguana was individually recognized by future competitors. Likewise, Dugan (1980:77) noted that male iguanas followed and courted females away from the mating territories. As the females in her study never mated away from territories, such courtship could not benefit the male unless there was individual recognition of suitors. Dugan (1982a) showed that various aspects of male headbob displays exhibit individual stereotypy, providing enough information that individual recognition could be based on the headbobs alone. Thus, it is plausible that the green iguana possesses the discriminating ability to take advantage of the fight-reducing attributes of a dominance hierarchy. This would help explain the scarcity of reversals in the dominance hierarchies (i.e., there are few values below the diagonals in Tables 10 and 11; see Landau, 1951).

What is the privilege associated with dominance? Of the three hypotheses considered, i.e., access to preferred sleeping perches, access to sites for undisturbed basking, and access to preferred males, only the latter was supported by the data. This is surprising, given the conspicuous and unequivocal competition among males for access to females. Although Darwin (1874:228–230) explicitly recognized the possibility of simultaneous sexual selection among both sexes, most studies of sexual selection have assumed that only one sex is limiting (Bateman, 1948). Altmann et al. (1977) coined the phrase "competitive mate choice" to describe female harem members competing among themselves for access to resources under the control of the harem master. Although the logic of their model could apply to the iguana situation, Altmann et al. explicitly sought to explain situations in which the harem master controls food or other resources needed by the females. No such resources are evident in iguanas.

Dominant male iguanas offer females only sperm and a degree of protection from some harassment by subordinate males. Is it possible that this protection from harassment is the resource being contested by the females? Three lines of evidence suggest otherwise. If a female were greatly concerned with harassment, her most effective action would be to enter an isolated mating territory having few or no other females. Numerous such territories exist, especially at the beginning of the mating season, yet they are rarely used. If there is some hidden physical feature of these territories that makes them undesirable, females could still minimize harassment by seeking out the most remote recess of their own mating territory, instead of chosing the perches that they used. In contrast, the higher ranking females at Masaguaral tended to use the perches that controlled the greatest number of other perches. By definition, these are the more accessible ones, rather than the more remote ones. Therefore, the high-ranking females were not choosing individual perches on the basis of escape from harassment. Finally, escape from harassment would not seem to be an objective for which the females would be competing. Their interests would be the same (evict the intruder male) and they might be expected to cooperate. Females often played a pivotal role in chasing intruder males out of territories (Figure 16). Whether independently pursuing their individual interests or actively cooperating, the effects of their actions were complementary rather than in opposition.

If the female dominance hierarchy did not exist for apportioning the privilege of escaping harassment, what resource was being apportioned? The answer to this question may become evident with an understanding of why male iguanas never mate more than once a day. As noted in "General Mating Behavior," the receptivity window for females is only a few days in length, and several females may be simultaneously receptive. If some nutritional, energetic, or physiological constraint on males limits them to one copulation per day, then there is a practical limit to the number of females that can occupy a territory and be guaranteed a timely and adequate supply of the resident's sperm. Based on the synchrony of females in the intensively monitored territories, this limit is roughly eight females per male. Therefore, it may be in each female's interest to guarantee that she does not have to share her male with more than about seven others.

As a practical matter, it might be unreasonable for selection to have operated in such a way that female iguanas would have evolved the ability to count their female competitors. Rather, selection would more likely have rewarded aggression that would tend to disperse females and minimize the chances that a single mating territory would house an excessive density of female competitors. Consistent with this expectation were the observations that (1) female belligerence rose sharply during the breeding season, (2) high female rank was associated with exclusion of other females from the mating territory, and (3) females switched mating territories to remain with a dominant male (rather than being tied to a particular sleeping perch). In

addition, the higher level of aggression directed at unfamiliar females would seem to be an appropriate mechanism for minimizing the pool of resident females in a territory while simultaneously reducing the severity of contests among the established residents.

This argument assumes that the sperm of preferred males is sufficiently superior that the costs of interfemale competition do not exceed the gain accrued through mating with a preferred male. In "General Mating Behavior," I presented evidence for strong female preferences for the largest territorial males. I was not able to estimate the costs of interfemale competition, but they are probably minute. I saw no evidence that any female was ever injured, forced into marginal habitat, or forced to forego copulation as a result of interfemale contests. Thus, the benefits of mating with a preferred male would not need to be great for interfemale competition to evolve.

The possibility that both sexes could be simultaneously competing for access to one another in the absence of any defendable resources is not one that has received much attention since the time of Darwin (1874:474–511). Bateman (1948) and Trivers (1972) assumed that an asymmetry between the sexes existed, and determined the direction of a unitary selective force. Recently, Hammerstein and Parker (1987) have argued that this is an oversimplification, that several conflicts of interest exist between the sexes in mating objectives, including the question of who searches for a mate, who agrees to mate first, who avoids inbreeding, whether to attempt additional matings, whether to desert, etc. With multiple parameters to be simultaneously maximized, a single compromise solution may leave the interests of both partners incompletely satisfied. In the case of iguanas, the timing or availability of sperm appears to be constrained in some way (i.e., sperm may be cheap but not free: Dewsbury, 1982; Nakatsuru and Kramer, 1982). The constraints on sperm delivery may create additional conflicts of interest, even in the absence of defendable resources. This may lead to mutual and simultaneous intrasexual selection pressures on both sexes.

RESUMEN

Rodda, Gordon H. The Mating Behavior of *Iguana iguana*. *Smithsonian Contributions to Zoology*, number 534, 40 pages, 18 figures, 11 tables, 1992.—El comportamiento de apareamiento de las iguanas verdes (*Iguana iguana*) fué observado en tres diferentes sitios durante diecinueve meses en los llanos de Venezuela. El comportamiento de las iguanas difiere durante el périodo de aparamiento en tres principales caraterísticas: (1) durante el tiempo de actividad de sobrevivencia fuera de la temporada de crianza, las iguanas adultas pasan la mayoria del tiempo inmoviles; (2) se supone que están descansando; (3) sus interacciones presentan menos actividades de alta intesidad y sus movimientos diarios fueron frecuentemente nomadas.

Durante la temporada de apareamiento, un sitio fué observado continuamente durante las horas del día (iguanas duermen durante la noche), pudiendose contar en su totalidad todas los intentos de copulaciones ocurridos (N = 250) y sus interaciones territoriales. En todos los sitios, los machos dominantes controlaron el acceso a pequeños territorios de apareamiento. Pero dentro de estos territorios no parece existir condiciones necesarias para las hembras o sus crías. De este modo, las hembras pudieron escoger directamente compañeros en base al fenotipo. Las hembras se agruparon en los territorios de apareamiento de los machos más grandes associandose preferiblemente con estos. Los machos dominante copularon una vez por día, aunque en varias ocasiones mas de una hembra fué receptiva a varios machos en el mismo día. Los machos menos dominantes (pequeños) exhibieron comportamiento seudofemeninos por ejemplo; algunos se abstubieron de competir sexualmente mientras que otros se ubicaron en la periferia de las zonas de apareamiento tratando de forzar copular con hembras mientras estas estubieran desprevenidas (comportamiento macho de periferia). Las hembras que no cooperaron fueron montantas simultaneamente hasta por tres machos. En el 95% de las 200 copulaciones observadas, las hembras resistieron el intento de apareamiento de los machos de las periferia, mientras que en el caso de los machos dominantes (N = 43) tan sólo resistieron el 56%. La selectividad de las hembras probablemente incrementa la representación genética de los machos dominates en las futuras generaciones. Durante el périodo de apareamiento las hembras mantienen una jerarquia dominante entre ellas. Las hembras de bajo rango tienden a ser excluidas de los territorios de apareamiento favoritos. En este sistema, ambos sexos pueden estar sujetos a la selección sexual. Se supone como hipótesis que los factores ecológicos resposables por el inusual sistema de apareamiento están relacionado a la falta de recursos de defenza, iguanas herbivoras (follaje), y a la alta densidad de iguanas presentes en las áreas de apareamiento favoritas.

Literature Cited

Afton, A.D.
1985. Forced Copulation as a Reproductive Strategy of Male Lesser Scaup: A Field Test of Some Predictions. *Behaviour*, 92:146–167.

Altmann, S.A., S.S. Wagner, and S. Lenington
1977. Two Models for the Evolution of Polygyny. *Behavioral Ecology and Sociobiology*, 2:397–410.

Alvarez del Toro, M.
1982. *Los Reptiles de Chiapas*. Third edition, 248 pages. Chiapas: Instituto del Historia Natural Tuxtla Gutiérrez.

Andrews, R.M.
1971. Structural Habitat and Time Budget of a Tropical *Anolis* Lizard. *Ecology*, 52:262–271.

Appleby, M.C.
1983. Probability of Linearity in Hierarchies. *Animal Behaviour*, 31:600–608.

Austad, S.N.
1984. A Classification of Alternative Reproductive Behaviors and Methods of Field Testing ESS Models. *American Zoologist*, 24:309–319.

Bakhuis, W.L.
1982. Size and Sexual Differentiation in the Lizard *Iguana iguana* on a Semi-arid Island. *Journal of Herpetology*, 16:322–325.

Bateman, A.J.
1948. Intra-sexual Selection in Drosophila. *Heredity*, 2:349–368.

Bennett, A.F., and P. Licht
1972. Anaerobic Metabolism during Activity in Lizards. *Journal of Comparative Physiology*, 81:277–288.

Beuchat, C.A.
1988. Temperature Effects during Gestation in a Viviparous Lizard. *Journal of Thermal Biology*, 13:135–142.

Borgia, G.
1979. Sexual Selection and Evolution of Mating Systems. *In* M.S. Blum and N.A. Blum, editors, *Sexual Selection and Reproductive Competition in Insects*, pages 19–80. New York: Academic Press.

Brattstrom, B.H.
1974. The Evolution of Reptilian Social Behavior. *American Zoologist*, 14:35–49.

Braunwalder, M.E.
1979. Über eine Erfolgreiche Zeitigung von Eiern des Grünen Leguans, *Iguana i. iguana*, und die damit Verbundene Problematik (Reptilia: Sauria: Iguanidae). *Salamandra*, 15:185–210.

Brown, J.L.
1975. *The Evolution of Behavior*. 761 pages. New York: W.W. Norton.

Carothers, J.H.
1984. Sexual Selection and Sexual Dimorphism in Some Herbivorous Lizards. *American Naturalist*, 124:244–254.

Clark, D.L., and J.C. Gillingham
1990. Sleep-site Fidelity in Two Puerto Rican Lizards. *Animal Behaviour*, 39:1138–1148.

Cooper, W.E., Jr.
1985. Female Residency and Courtship Intensity in a Territorial Lizard, *Holbrookia propinqua*. *Amphibia-Reptilia*, 6:63–69.

Cox, C.R., and B.J. Le Boeuf
1977. Female Incitation of Male Competition: A Mechanism in Sexual Selection. *American Naturalist*, 111:317–335.

Crews, D.
1978. Hemipenile Preference: Stimulus Control of Male Mounting Behavior in the Lizard *Anolis carolinensis*. *Science*, 199:195–196.

Darwin, C.
1874. *The Descent of Man and Selection in Relation to Sex*. Second edition, 688 pages. New York: A.L. Fowle.

Dewsbury, D.A.
1982. Ejaculate Cost and Mate Choice. *American Naturalist*, 119:601–610.

Distel, H., and J. Veazey
1982. The Behavioral Inventory of the Green Iguana, *Iguana iguana*. *In* G.M. Burghardt and A.S. Rand, editors, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pages 252–270. Park Ridge, New Jersey: Noyes Publications.

Dugan, B.A.
1980. A Field Study of the Social Structure, Mating System and Display Behavior of the Green Iguana (*Iguana iguana*). 171 pages. Unpublished doctoral dissertation, University of Tennessee, Knoxville, Tennessee.
1982a. A Field Study of Headbob Displays of Male Green Iguanas (*Iguana iguana*): Variation in Form and Context. *Animal Behaviour*, 30:327–338.
1982b. The Mating Behavior of the Green Iguana, *Iguana iguana*. *In* G.M. Burghardt and A.S. Rand, editors, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pages 320–341. Park Ridge, New Jersey: Noyes Publications.

Dugan, B.A., and T.A. Wiewandt
1982. Socioecological Determinants of Mating Strategies in Iguanine Lizards. *In* G.M. Burghardt and A.S. Rand, editors, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pages 303–319. Park Ridge, New Jersey: Noyes Publications.

Emlen, S.T., and L.W. Oring
1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science*, 197:215–223.

Emlen, S.T., and P. Wrege
1986. Forced Copulation and Intraspecific Parasitism: Two Costs of Social Living in the White-fronted Bee-eater. *Ethology*, 71:2–29.

Etheridge, R.E.
1982. Checklist of the Iguanine and Malagasy Iguanid Lizards. *In* G.M. Burghardt and A.S. Rand, editors, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pages 7–37. Park Ridge, New Jersey: Noyes Publications.

Evans, L.T.
1951. Field Study of the Social Behavior of the Black Lizards, *Ctenosaura pectinata*. *American Museum Novitates*, 1493:1–26.

Fitch, H.S., and R.W. Henderson
1977. Age and Sex Differences in the Ctenosaur (*Ctenosaura similis*). *Milwaukee Public Museum Contributions in Biology and Geology*, 11:1–11.

Flanigan, W.F.
1973. Sleep and Wakefulness in Iguanid Lizards, *Ctenosaura pectinata* and *Iguana iguana*. *Brain Behavior and Evolution*, 8:401–436.

Fleishman, L.J.
1988. The Social Behavior of *Anolis auratus*, a Grass Anole from Panama. *Journal of Herpetology*, 22:13–23.

Garstka, W.R., B. Camazine, and D. Crews
1982. Interactions of Behavior and Physiology during the Annual Reproductive Cycle of the Red-sided Garter Snake (*Thamnophis sirtalis parietalis*). *Herpetologica*, 38:104–123.

Gladstone, D.E.
1979. Promiscuity in Monogamous Colonial Birds. *American Naturalist*, 114:545–557.

Gordon, R.E.
1956. The Biology and Biodemography of *Anolis carolinensis carolinensis*

Voigt. 263 pages. Unpublished doctoral dissertation, Tulane University, New Orleans, Louisiana.

Hammerstein, P., and G.A. Parker
1987. Sexual Selection: Games between the Sexes. *In* J.W. Bradbury and M.B. Andersson, editors, *Sexual Selection: Testing the Alternatives*, pages 119–142. Chichester, England: John Wiley and Sons.

Harris, D.M.
1982. Preliminary Observations on the Ecology of *Iguana iguana* in Northern Columbia. *In* G.M. Burghardt and A.S. Rand, editors, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pages 150–161. Park Ridge, New Jersey: Noyes Publications.

Hicks, R.A., and R.L. Trivers
1983. The Social Behavior of *Anolis valencienni*. *In* A. Rhodin and K. Miyata, editors, *Advances in Herpetology and Evolution Biology*, pages 570–595. Cambridge, Massachusetts: Museum of Comparative Zoology.

Hoogmoed, M.S.
1973. The Lizards and Amphisbaenians of Surinam. In *Biogeographica: Notes on the Herpetofauna of Surinam, IV*, 4: 419 pages. The Hague: W. Junk, Pubs.

Howard, R.D.
1978. The Evolution of Mating Strategies in Bullfrogs, *Rana catesbeiana*. *Evolution*, 32:850–871.

Jackson, W.M., and R.L. Winnegrad
1988. Linearity in Dominance Hierarchies: A Second Look at the Individual Attributes Model. *Animal Behavior*, 36:1237–1240.

Kendall, M.G.
1970. *Rank Correlation Methods*. Fourth edition, 202 pages. London: Charles Griffin.

Kummer, H.
1968. *Social Organization of Hamadryas Baboons: A Field Study*. 189 pages. Chicago: University of Chicago Press.

Landau, H.G.
1951. On Dominance Relationships and Structure of Animal Societies. *Bulletin of Mathematical Biophysics*, 13:1–19.

Lazell, J.D.
1973. The Lizard Genus *Iguana* in the Lesser Antilles. *Bulletin of the Museum of Comparative Zoology*, 145:1–28.

Lott, D.F.
1981. Sexual Behavior and Intersexual Strategies in American Bison. *Zeitschrift für Tierpsychologie*, 56:97–114.

McKinney, F., S.R. Derrickson, and P. Mineau
1983. Forced Copulation in Waterfowl. *Behaviour*, 86:250–294.

Müller, H.
1968. Untersuchungen Über Wachstum und Altersverteilung Einer Population des Grünen Leguans *Iguana iguana iguana* L. (Reptilia: Iguanidae). *Mitteilungen aus dem Instituto Colombo-Alemán de Investigaciónes Cientificas*, 2:57–65.
1972. Ökologische und Ethologische Studien an *Iguana iguana* L. (Reptilia: Iguanidae) in Kolumbien. *Zoologische Beitrage N F*, 18:109–131.

Nakatsuru, K., and D.L. Kramer
1982. Is Sperm Cheap? Limited Male Fertility and Female Choice in the Lemon Tetra (Pisces, Characidae). *Science*, 216:753–755.

Neville, M.
1972. The Population Structure of Red Howler Monkeys (*Alouatta seniculus*) in Trinidad and Venezuela. *Folia Primatologica*, 17:56–86.

Peracca, M.G.
1891. Osservioni sulla Riproduzione della *Iguana tuberculata* Laur. *Bolletino Museo di Zoologia e Anatomia Comparativo Riproduzione Universita di Torino*, 110:1–8.

Pough, F.H.
1980. The Advantages of Ectothermy for Tetrapods. *American Naturalist*, 115:92–112.

Pütz, R.
1982. Erfahrungen bei der Haltung und Zucht des Grünen Leguans *Iguana iguana iguana*. *Herpetofauna*, 20:21–25.

Rand, A.S.
1967. Adaptive Significance of Territoriality in Iguanid Lizards. *In* W.M. Milstead, editor, *Symposium of Lizard Ecology*, pages 106–115. Columbia: University of Missouri Press.
1978. Reptilian Arboreal Folivores. *In* G.G. Montgomery, editor, *The Ecology of Arboreal Folivores*, pages 115–133. Washington, D.C.: Smithsonian Institution Press.
1984. Clutch Size in *Iguana iguana* in Central Panama. *In* R.A. Seigel, L.E. Hunt, J.L. Knight, L. Malaret, and N.L. Zuschlag, editors, *Vertebrate Ecology and Systematics—a Tribute to Henry S. Fitch*, pages 115–122. Lawrence: Museum of Natural History, University of Kansas.

Rand, A.S., and H.W. Greene
1982. Latitude and Climate in the Phenology of Reproduction in the Green Iguana, *Iguana iguana*. *In* G.M. Burghardt and A.S. Rand, editors, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pages 142–149. Park Ridge, New Jersey: Noyes Publications.

Rauch, N.
1985. Female Habitat Choice as a Determinant of the Reproductive Success of the Territorial Male Marine Iguana *Amblyrhynchus cristatus*. *Behavioral Ecology and Sociobiology*, 16:125–134.

Rodda, G.H.
1990. Highway Madness Revisited: Roadkilled *Iguana iguana* in the Llanos of Venezuela. *Journal of Herpetology*, 24:209–211.
1991. Sexing *Iguana iguana*. *Bulletin of the Chicago Herpetological Society*, 26:173–175.

Rodda, G.H., B.C. Bock, G.M. Burghardt, and A.S. Rand
1988. Techniques for Identifying Lizard Individuals at a Distance Reveal Influences of Handling. *Copeia*, 1988(4):905–913.

Rodda, G.H., and G.M. Burghardt
1985. *Iguana iguana* (Green Iguana) Terrestriality. *Herpetological Review*, 16:112.

Rodda, G.H., and A. Grajal
1990. The Nesting Behavior of the Green Iguana, *Iguana iguana*, in the Llanos of Venezuela. *Amphibia-Reptilia*, 11:31–39.

Rothblum, L., and T.A. Jenssen
1978. Display Repertoire Analysis of *Sceloporus undulatus hyacinthinus* (Sauria: Iguanidae) from South-western Virginia. *Animal Behavior*, 26:130–137.

Ruby, D.E.
1976. The Behavioral Ecology of the Viviparous Lizard *Sceloporus jarrovi*. 223 pages. Doctoral dissertation, University of Michigan, Ann Arbor, Michigan.
1977. The Function of Shudder Displays in the Lizard *Sceloporus jarrovi*. *Copeia*, 1977(1):110–114.
1981. Phenotypic Correlates of Male Reproductive Success in the Lizard *Sceloporus jarrovi*. *In* R.D. Alexander and D.W. Tinkle, editors, *Natural Selection and Social Behavior*, pages 96–107. New York: Chiron Press.
1984. Male Breeding Success and Differential Access to Females in *Anolis carolinensis*. *Herpetologica*, 40:272–280.

Ryan, M.J.
1985. *The Túngara Frog*. 230 pages. Chicago: University of Chicago Press.

Sarmiento, G.
1984. *The Ecology of Neotropical Savannas*. Cambridge, Massachusetts: Harvard University Press.

Short, R.V.
1979. Sexual Selection and Its Component Parts, Somatic and Genital Selection as Illustrated by Man and the Great Apes. *Advances in the Study of Behavior*, 9:131–158.

Stamps, J.A.
1977. Social Behavior and Spacing Patterns in Lizards. *In* C. Gans and D.W. Tinkle, editors, *Biology of the Reptilia, Volume 7: Ecology and Behaviour*, pages 265–334. London: Academic Press.
1983. Reptilian Herbivores, a Review of Iguanas of the World. *Science*, 220:1145–1146.

Swanson, P.L.
1950. The Iguana, *Iguana iguana iguana* (L.). *Herpetologica*, 6:187–193.

Tamayo, F.
1964. *Ensayo de Classificacion de Sabanas de Venezuela*. Caracas: Universidad Central de Venezuela, Facultad de Humanidades y Educacíon, Escuela de Geografia.

Tinkle, D.W.
1967. The Life and Demography of the Side-blotched Lizard, *Uta stansburiana*. *Miscellaneous Publications of the Museum of Zoology of the University of Michigan*, 132:1–182.

Tokarz, R.R.
1988. Copulatory Behaviour of the Lizard *Anolis sagrei:* Alternation of Hemipene Use. *Animal Behaviour*, 36:1518–1524.

Trillmich, K.G.K.
1983. The Mating System of the Marine Iguana (*Amblyrhynchus cristatus*). *Zeitschrift für Tierpsychologie*, 63:141–172.

Trivers, R.L.
1972. Parental Investment and Sexual Selection. *In* B. Campbell, editor, *Sexual Selection and the Descent of Man*, pages 136–179. Chicago: Aldine Publishing Co.
1976. Sexual Selection and Resource-accruing Abilities in *Anolis garmani*. *Evolution*, 30:253–269.
1985. *Social Evolution*. 462 pages. Menlo Park, California: Benjamin/ Cummings Publishing Co.

Troyer, K.
1983. Posthatching Yolk Energy in a Lizard: Utilization Pattern and Interclutch Variation. *Oecologia*, 58:340–344.

Van Devender, R.W.
1982. Growth and Ecology of Spiny-tailed and Green Iguanas in Costa Rica, with Comments on the Evolution of Herbivory and Large Body Size. *In* G.M. Burghardt and A.S. Rand, editors, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pages 162–182. Park Ridge, New Jersey: Noyes Publications.

Werner, D.I.
1978. On the Biology of *Tropidurus delanonis* Baur (Iguanidae). *Zeitschrift für Tierpsychologie*, 47:337–395.
1982. Social Organization and Ecology of Land Iguanas, *Conolophus subcristatus*, on Isla Fernandina, Galapagos. *In* G.M. Burghardt and A.S. Rand, editors, *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pages 342–365. Park Ridge, New Jersey: Noyes Publications.

Wiewandt, T.A.
1977. Ecology, Behavior, and Management of the Mona Island Ground Iguana, *Cyclura stejnegeri*. 338 pages. Unpublished doctoral dissertation, Cornell University, Ithica, New York.
1979. La Gran Iguana de Mona. *Natural History*, 88(10):56–65.

Wilson, E.O.
1975. *Sociobiology: The New Synthesis*. 697 pages. Cambridge, Massachusetts: Belknap Press.

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