

# THE MATING BEHAVIOR OF IGUANA IGUANA (PART 2)

A CONDENSED VERSION OF A STUDY BY GORDON H. RODDA

## 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 2).

In considering differences between the conclusions of the present study and of Dugan (1980, 1982a, 1982b; see Table 2), 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 sim-

ilar 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 2 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 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 (non-mating). 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 Janssen (1978) for *Sceloporus undulatus*.

It is possible, however, that a real difference in

**Table 2.** — Comparisons between this study and Dugan (1980, 1982A, 1982b). The statements under "Dissimilar" summarize the conditions observed in the present study (Venezuela).

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

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) ( $t = 15.3$ ;  $df = 267$ ;  $P \ll 0.001$ ) 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 sex-

ual 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



Adult male, *Iguana iguana*, Greg Scott residence. Photograph: R.W. Ehrig

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 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 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; 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 continuously 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%). 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 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 ( $G = 20.1$ ;

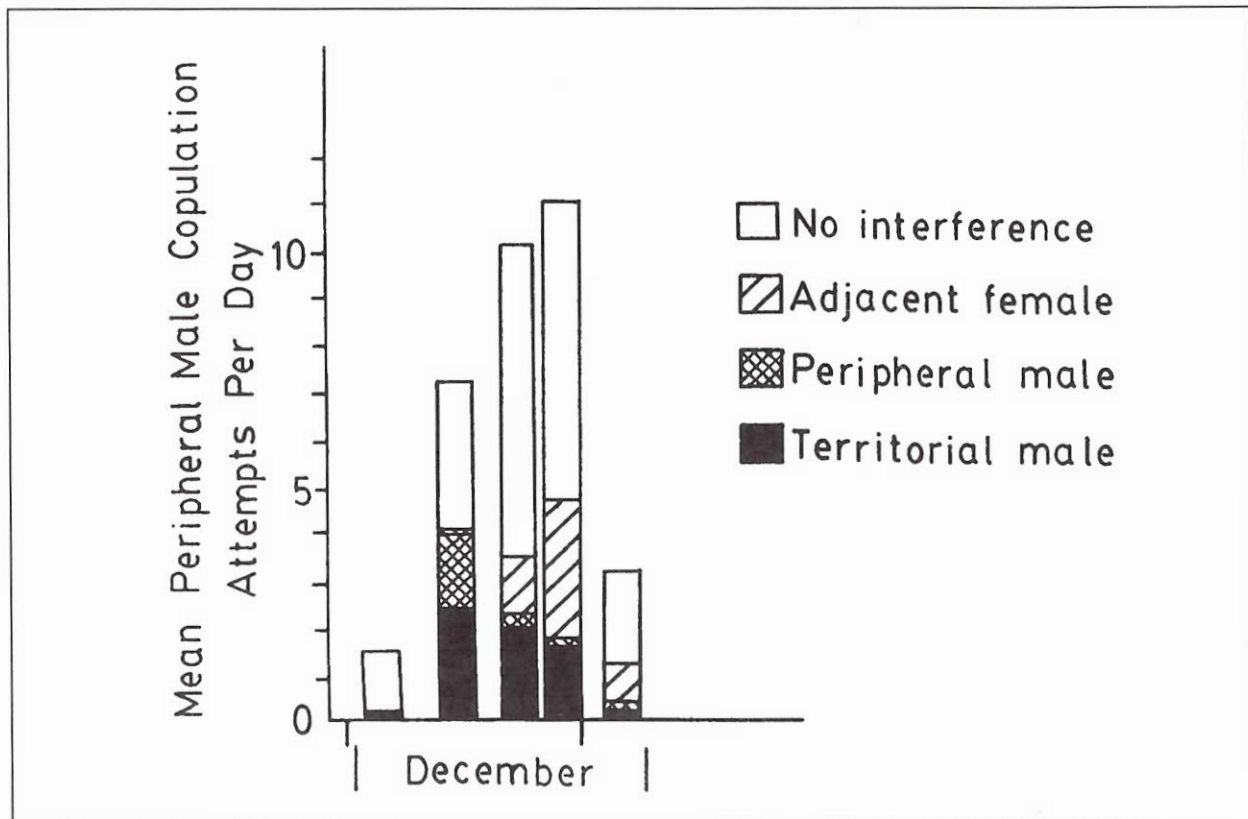


FIGURE 3. The frequencies of third party interference in copulation attempts.

$P < 0.001$ ) 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. Although location generally was not associated with success, forced copulation attempts initiated on the ground rarely (3%) were successful, 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 mid-day ( $F = 4.85$ ;  $df = 10, 10$ ;  $P = 0.009$ ).

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 S females for the same comparison with the first success date of 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 3). 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 3). In contrast, in early December adjacent females did not participate as third parties in copulation attempts (Figure 3). Figure 3 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 4). 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 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.

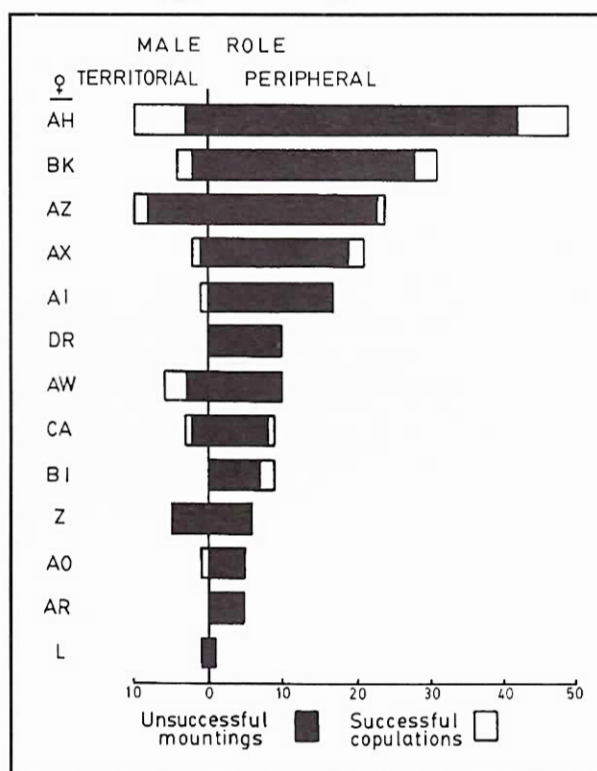
For most females, these tests indicated no significant change in perch use and no significant selectivity by peripheral males. The significant values that were obtained suggest individual effects worthy of further study. All of the females except AX exhibited a nonsignificant change in perch usage, generally 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. 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  $r = 0.957$ ;  $P < 0.01$ ).

**SUCCESSSES 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 male attempts, with strikingly similar results for the territorial male. 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



**FIGURE 4.** Frequencies of copulation attempts on females divided by male role and success.



**Table 3.** — Published observations reporting at least 10 copulations seen in a species of lizard.

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

(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 were significant (all  $P > 0.25$ ).

**SUCCESSSES OF THE TERRITORIAL MALE.** — Four factors were considered as possibly contributing to the success of the 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 3). 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 Galapagos Islands. Fortunately, the Iguanidae includes both herbivores and insectivores, allowing a comparison between iguanas and the more typical insectivorous lizards. Forced cop-

ulations 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 3). 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) sug-



Free ranging Florida Keys, *Iguana iguana*, female. Photograph: R.W. Ehrig

gest 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 3) 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 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 energetical-

ly 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 5).

Do the available data from other lizard species support an association between folivory or herbivory and forced copulations (Table 3)? 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 Galapagos Islands (Werner, 1978). In this case, the unusual features of island living in the Galapagos 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

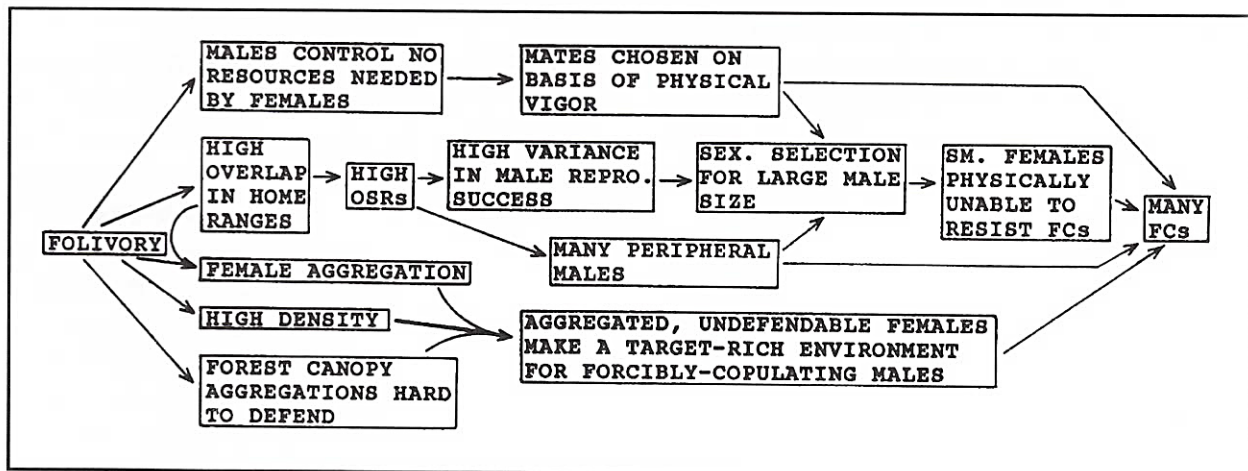


FIGURE 5. Factors hypothesized to promote forced copulations (FCs) in Iguana.

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 5), 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 5). 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.

#### 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), 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;  $P \gg 0.1$ ) and that for Guacimos was 0.34 ( $n = 6$ ;  $P \gg 0.1$ ). In contrast, females formed conspicuous dominance hierarchies at both sites during the mating season (Tables 4, 5). 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 tend-

**Table 4.** — 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	—		

ed 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,

**Table 5.** — Interaction and dominance matrices for resident females at Guacimos during the 1983 mating season. Values as in Table 4.

		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	—	

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

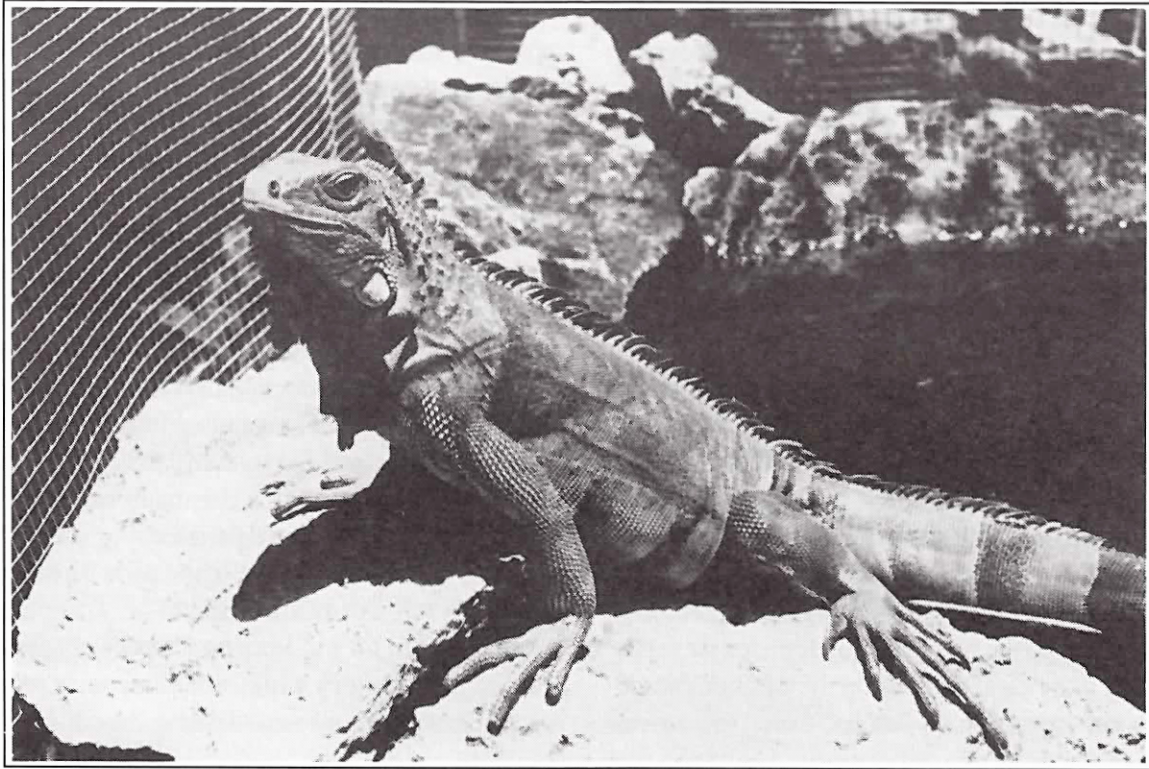
than one day. After the second day, these large newcomers were tolerated by all but the larger or more dominant resident females. Thus, small females rarely remained in preferred mating territories. The territorial males did not participate in this exclusion. On a few occasions, males approached new 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



Adult female *Iguana iguana*, Scott residence, Big Pine Key. Photograph: R.W. Ehrig

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 diago-

nals in Tables 4 and 5; 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 choosing 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 3). 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.

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