

To the Graduate Council:

I am submitting herewith a dissertation written by Beverly A. Dugan entitled "A Field Study of the Social Structure, Mating System, and Display Behavior of the Green Iguana." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Psychology.

Gordon M. Burghardt
Gordon Burghardt, Major Professor

We have read this dissertation
and recommend its acceptance:

Cheryl B. Travis

Will Dwyer

John C. Peltzman

Arthur Stanley Rand

Accepted for the Council:

LEvans Roth
Vice Chancellor
Graduate Studies and Research

A FIELD STUDY OF THE SOCIAL STRUCTURE, MATING
SYSTEM, AND DISPLAY BEHAVIOR OF
THE GREEN IGUANA

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Beverly A. Dugan

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DEDICATED TO
Herman W. and Odessa Dugan

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LIZARD

A lizard ran out on a rock and looked up, listening
no doubt to the sounding of the spheres.
And what a dandy fellow! the right toss of a chin for you
and a swirl of a tail!

If men were as much men as lizards are lizards
they'd be worth looking at.

D. H. Lawrence (1928)

ABSTRACT

The social behavior of Iguana iguana (Sauria, Iguanidae), a large, arboreal lizard, was studied for 16 months on Flamenco Island, Panama. This 13.5 ha island at the Pacific entrance to the Panama Canal supports between 500 and 700 adult iguanas. The vegetation consists of lowland dry forest. The annual climate is marked by distinct wet (May through November) and dry (December through April) seasons.

During the non-breeding season, the iguanas were sporadically active. They ate leaves, flowers, and fruits, and movements were determined in part by patterns of food availability. The iguanas maintained overlapping home ranges. The largest males tended to avoid one another; rarely did 2 large males remain in the same location for more than a few hours. Large males confined their movements to an area that was roughly 1/3 the size of the home ranges of other members of the population.

Mating activity began in the last half of October, with increasing rates of display by large males. Male-female encounter rates were high in November. By late November, large males had established mating territories containing 1 - 4 females. Copulation occurred during the first 6 weeks of the dry season, from December through mid-January.

Male breeding strategies were related to size and the development of secondary sex characteristics. Small reproductively mature males, indistinguishable from females at a distance, moved into territories and mated opportunistically. Most medium males remained on the edge of territories, and assumed ownership of vacated territories. Large males maintained their status in a circumscribed area year-round, and thus

insured priority of access to suitable mating territories in November. Large males, 38% of total males, performed significantly more copulations (90% of observed) than did small or medium males.

Females mated preferentially with large males, ignored medium males, and violently protested copulation attempts by small males. Extensive courtship with several males before females established residence in a territory, and immediately prior to copulation, suggests that courtship is an important factor in female mate choice, in cementing bonds of familiarity between mates, and in facilitating female receptivity. Females mated several times during a single breeding period, usually with a single male. The adaptive significance of male and female mating strategies is discussed.

Agonistic encounters among males were rare. Spacing was mediated primarily by visual displays. Large males displayed more frequently than other members of the population; display rates were highest between mid-October and mid-January. The conspicuous nature of the headbob displays was enhanced by the intensified color of territorial males, and by the selection of highly visible display posts. Headbob displays play an important role in both territory establishment and mate acquisition.

Four headbob displays were identified, and the variability and contextual use of each were analyzed. The roll, high amplitude vertical and lateral (head rotation) head movements, was performed most frequently when the male was solitary or greater than 3 m from a female. The shudder, a series of shallow rapid vertical bobs, was performed most frequently when females were within 3 m of a male, and during male-female interactions throughout the year. The roll-shudder, rapid

alternations of rolls and shudders in variable sequences, occurred during transitions between social contexts, and between sequences of rolls and sequences of shudders. The signature bob, the most frequently occurring display, was used in a wide variety of contexts; this bob punctuated all other activity.

The temporal variability of each display is related to its contextual use. The roll is less variable than the shudder or roll-shudder, but much more variable than the signature bob. The roll is a conspicuous advertisement display; it may function to call attention to the signature bob that invariably follows. The shudder is the most variable of the 4 displays. Shudder duration was significantly longer during male-female interactions. This display may communicate the male's lack of aggressiveness, and its duration appears to reflect level of arousal. The roll-shudder is intermediate between the roll and shudder in its form, variability and use. The signature bob, the most stereotyped display, encodes species identity, and possibly population and individual identity. Interindividual variability was significantly greater than intraindividual variability in 12 analyzed components of this display. The variability in form and use of the headbob displays was interpreted in terms of the problems that an iguana displaying to wide-ranging conspecifics in a forest environment must solve.

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CHAPTER I

INTRODUCTION

Recent investigations have focused on identifying the selective pressures that have produced the variety of social behavior seen in the natural environment. Consistent correlations between a particular type of social organization and a limited set of environmental conditions provide evidence for the selective pressures responsible for the evolution of that social organization. Thus, an understanding of an organism's social behavior requires not only a description and classification of that behavior, but also a consideration of the environmental conditions responsible for its development and evolution. In addition, the constraints imposed by the organism's sensory and neural capacities effect the manner in which adaptation proceeds. Wilson (1975) proposed the terms "ecological pressure" and "phylogenetic inertia" to describe environmental and sensory constraints on social evolution.

Lizards are ideally suited for evolutionary studies of behavior for several reasons. Reptiles occupy a critical position in vertebrate evolution; the behavior of birds and mammals is deeply rooted in that of reptiles. Lizards are easily observed; many species are diurnally active and appear to be little effected by a human observer. Appreciable variation in social behavior appears to exist among lizards; however, most studies have focused on small, insectivorous members of the family Iguanidae (Stamps, 1977). The large herbivorous lizards in the subfamily Iguaninae are of particular interest from a comparative point of view,

since they differ from all other iguanids and most other lizards in their life history characteristics and ecological role. In this investigation, I have analyzed the social behavior of 1 member of the subfamily Iguaninae, Iguana iguana, in terms of the social and ecological environment in which the behavior occurs. In order to place the present study into the appropriate context, I begin with a general discussion of iguanid social behavior. In the following chapters, a description of the methods used in this study, and details of the green iguana's social behavior, mating behavior, and display behavior, are presented.

Before proceeding further, 4 terms commonly used by behavioral ecologists and which appear throughout this paper should be defined and elaborated: social structure, territory, mating system, and mating strategy. A SOCIAL STRUCTURE is the manner in which members of a population regulate their interactions during the non-breeding season. Typically, social structures are initially classified as territorial systems or dominance hierarchies. The term TERRITORY denotes a fixed area that is used exclusively by an individual or a group of individuals, and is defended from at least some members of the same species by advertisement, threat or attack (Brown, 1964). A MATING SYSTEM is the manner in which the reproductive members of a population apportion their energy and/or activity for mate acquisition. Mating systems have traditionally been classified as monogamous, promiscuous, or polygamous. Mating systems may consist of 1 or more MATING STRATEGIES, behavior employed by the individual in obtaining mates. The word strategy does not imply that a conscious decision is made by the individual who employs it. The mating system is usually classified on the basis of the most common mating strategy (Howard, 1978).

Clearly, the 4 terms are closely related. For example, in continuously breeding species, the social structure and mating system may describe the same aspects of the social organization. However, since Iguana iguana is a seasonally breeding species, the 2 terms will be used to refer to patterns of social interaction during the non-breeding season and breeding season, respectively.

Documentation of space usage and patterns of aggressive behavior are critical for the identification of a population's social structure. The distribution of resources in space and time will influence both of these parameters. If a critical resource is dispersed evenly in both space and time, and is in short supply relative to the number of individuals that exploit it, one would expect the area containing the resource to be defended. In contrast, if resource availability shifts in both time and space, animals will be forced to range over large areas. In such situations, a guaranteed resource supply is not likely to be attained by the aggressive defense of a fixed location (see Brown, 1964). For example, group size and social behavior have been related to foraging ecology and habitat in antelope (Jarman, 1974; Geist, 1974). Where antelope specialize in food items that are evenly distributed, small groups move through a limited area that contains sufficient food for group members. The small groups are usually male-female pairs or small family units, and frequently the foraging area is defended. Sexual dimorphism is slight. Where food is patchily distributed in space and time, the resource attracts many individuals and large groups move over large areas to locate seasonally abundant food. Marked competition between males and females attends the increase in group size. Where bulls and cows

maintain separate herds, competition among males for control of migratory female herds, or for control of locations in which stationary herds of females are feeding, increases markedly prior to the breeding season. Among mixed-sex herds of antelope, the reproductively mature males establish dominance hierarchies, with the dominant male having priority of access to receptive females. Greater sexual dimorphism is related to the intensity of intrasexual competition for mates. The development of sexual dimorphism continues after the age of sexual maturity, and is related to the bull's status in the dominance hierarchy (Jarman, 1974).

Mating systems are influenced by patterns of parental investment, as well as ecological variables. If 1 sex invests more in the production and care of offspring than the other, the sex that makes the greater investment becomes a limiting resource (a resource in short supply) for members of the opposite sex. Disparate parental investment leads to competition for mates among members of the limited sex (Bateman, 1948; Fisher, 1958; Trivers, 1972). This situation often results in polygamous mating systems. Among mammals, the female assumes most of the parental care, and polygyny is common. In birds, on the other hand, feeding and defense of the young often require both parents, and monogamy is most common. (For further discussion of factors favoring polygamy, see Orians, 1969; Williams, 1975; Wilson, 1975).

Other than nest construction, egg-laying, and in a few cases nest-guarding, parental care is lacking among iguanids. Since females invest more in gamete production than do males, polygyny is expected to be widespread in this group. Among polygynous species, an individual male's reproductive success ultimately depends on how many females he can mate

with. How this is achieved depends in turn on the ecological and social environment of the population. The form of intermale competition for mates reflects the nature and distribution of resources attracting females relative to the numbers of competing males. Competition may center on any number of resources, such as food and/or shelter used by females, a location within which to court and mate undisturbed, or the females directly (e.g., harem defense). In order to understand the mating system, major factor(s) governing intermale competition must be identified. Thus, the investigation of a mating system requires information about the ecology and social structure of the population.

Iguanid Social Behavior - Insectivorous Species

The social behavior of iguanid lizards has been more thoroughly studied than that of any other lizard family. The majority of these studies have been conducted on small, insectivorous members of the subfamilies Anolinae and Sceloporinae. The general account that follows is meant to represent the "typical" pattern of social behavior in these lizards. There are of course exceptions to this pattern, but the exceptions are few (Stamps, 1977), and are not germane to the comparison with the subfamily Iguaninae that follows.

Most of the insectivorous lizards are sit-and-wait predators. They are pursuers rather than active searchers, and much of their time is spent waiting for prey to appear (Andrews, 1971; Stamps, 1977). The visual orientation of iguanids is probably related to their feeding ecology and diurnal habits. Visual cues seem to be more important than chemical cues in foraging (Evans, 1961), and although chemical cues

probably play some role in communication (Cole, 1966; Defazio et al., 1977; Duvall, 1979), the signals used in social communication appear to be mainly visual (Ferguson, 1977).

The most thoroughly studied displays among iguanid lizards are the headbob displays, vertical movements of the head, legs, and/or trunk, usually accompanied by extension of the dewlap, a flap of skin under the throat. These displays are most often given by adult males. A widespread display among iguanids, termed the "signature bob" by Stamps and Barlow (1973), has often been shown to be highly stereotyped within a population, but to differ between species and geographic races (Carpenter, 1967; Ferguson, 1971). Signature bobs may occur independently of social encounters as the lizard moves through its activity range (assertion context), during agonistic encounters, and in courtship interactions. At least 1 other headbob display performed during courtship occurs in most species (Ferguson, 1977).

Among insectivorous iguanids, aggression and territory size appear related to food availability and intraspecific competition for food (Simon, 1975; Stamps, 1977). In the typical iguanid social structure, males maintain territories that overlap the activity ranges of several females. Female activities center around resources essential for survival (food, shelter, basking sites); male activities center around access to females and other resources. Although detailed observations on mate acquisition are lacking, it appears that females mate with the male that controls the area. Thus, most iguanid mating systems fall broadly under the category of "resource defense polygyny," defined by Emlen and Oring (1977) as a system where males acquire multiple mates indirectly, by defending resources essential to females.

As Stamps (1977) has pointed out, the combination of a sit-and-wait foraging strategy and heavy reliance on the visual modality is conducive to successful territorial defense. The raised lookout posts typically used by iguanid lizards are advantageous for spotting prey, other lizards, and for advertising one's location.

Iguanine Social Behavior

The subfamily Iguaninae consists of 7 genera and approximately 25 species. Most species are found in the Neotropics and Mexico. One genus (Brachylophus) occurs in the Old World tropics on Fiji and Tonga Islands (Avery and Tanner, 1971; Gibbons, in press); the genera Sauromalus and Dipsosaurus are found in desert regions of the Southwestern United States.

Until recently, iguanine social behavior was very poorly known (see Burghardt and Rand, in press). Since they differ from all other iguanids in their large size, longevity, and diet, one might expect deviations from the typical iguanid pattern of social behavior among the Iguaninae.

Iguanines are among the longest-lived lizards. Estimates of longevity range from a minimum of 10 years for I. iguana (Müller, 1968) to more than 40 years for Cyclura pinguis and C. cornuta stejnegeri (Carey, 1975; Wiewandt, 1977). In addition, the iguanines are among the largest of lizards. Dipsosaurus dorsalis, 1 of the smallest iguanines, averages 12.5 cm body length (Mayhew, 1971); average body length among members of the genus Cyclura may exceed 50 cm (Iverson, 1979).

Iguanines are primarily herbivorous. They are, however, opportunistic, and most species take animal matter when and where it can easily

be obtained. The correlation between large body size and herbivory has been recognized for some time (Ostrom, 1963; Sokol, 1967; Rand, 1978). Physiological relationships between diet and lizard body size have been examined by Pough (1973) and Wilson and Lee (1974). Presumably, herbivory is energetically more efficient for larger lizards, since energy requirement per gram of body weight decreases with increasing size, while activity (more needed with carnivory) requires more total energy for a large than a small lizard.

Among insectivorous iguanids, aggression and territory size appear related to food availability and intraspecific competition for food (Simon, 1975; Stamps, 1977). Turner et al. (1969) found a strong relationship between the home range size and body size in lizards. The same relationship exists in birds and mammals, and it has been suggested that larger animals need larger home ranges to meet their energy requirements (Schoener, 1968, 1977; McNab, 1963). Data from iguanines do not always conform to this prediction, however. In a year of food shortage, home range sizes did not differ significantly between female and larger male chuckawallas, Sauromaulus obesus (Nagy, 1973). Nagy suggested that since home range size did not increase as vegetation became less available, home range size in this population was not related to food availability and energy requirements. Alternate explanations are possible. For example, the energetic cost of longer distance movements might have outweighed the benefits to be gained from additional food. However, Nagy's observation contradicts the postulated relationship between home range size and body size in lizards.

The relationship between social structure and distribution and abundance of food is poorly understood for lizards of this subfamily. Because plant foods often differ appreciably in quality, in quantity, and in local, seasonal, and annual availability, one would expect iguanine movements and social behavior to be patterned accordingly. An iguanine may shift its center of activity for several days or weeks to follow seasonal fruiting and flowering patterns. Mona Island Cyclura cornuta stejnegeri usually forage in areas adjacent to retreats; however, longer-term shifts in location sometimes occur when preferred fruits are available elsewhere (Wiewandt, 1977). Where preferred food items are concentrated and superabundant, or patchy and shifting with time, their defense is not feasible (see Brown, 1964). Energetic feasibility of defending food supply also diminishes in densely vegetated habitats where surveillance is difficult.

Absence of food-based territorial defense does in fact appear to be a common pattern within the Iguaninae. Lizards may congregate near a food source and make short-term forays away from centers of activity (basking sites and retreats) to feed. Evans (1951) described a high density colony of Ctenosaura pectinata in Mexico that lived in a rock wall adjacent to a cultivated field where they fed on newly planted beans. Individuals defended areas of the rock wall, but did not defend foraging sites. Boersma (in press) found marine iguanas patchily distributed along the coast of Isla Fernandina, the concentration of iguanas varying with water depth, bottom gradient, and algal production. Feeding aggregations of dozens of desert iguanas (Dipsosaurus) were seen in flowering Cresote bushes (Larrea divaricata) by Cowles (1946). In a review of

social structure in the genus Sauromalus, Ryan (in press) concluded that food defense is not a primary function of territoriality in this genus.

Thus, while food distribution often influences patterns of movement, only infrequently is it an object of territorial defense in iguanine lizards. It is apparently seldom profitable for male iguanines to seek access to females via control over food resources. Nevertheless, proximity to the best food and water throughout the year may be an important determinant of male reproductive success. Even if the resource is not defended, frequent contact with females passing nearby may significantly enhance a male's breeding potential. This appears to be true of Cyclura cornuta stejnegeri (Wiewandt, 1977), and to a lesser extent, Conolophus subcristatus (Werner, in press).

The activities of most iguanines are retreat-centered. Retreats may be centers of social activity, may provide shelter from climatic extremes and escape from the sun, predators and conspecifics. Retreats also provide nesting sites for Cyclura carinata (Iverson, 1979). Locations near food and water seem to be important. In areas where rock cavities, tree holes, or animal burrows are not available, the lizards may dig their own, substrate permitting.

Although few detailed data on the distribution and use patterns of retreats are available, it appears that females select retreats for their comfort, safety and proximity to food and water (Wiewandt, 1977, 1979). In many populations of iguanine lizards, choice retreats appear to be the proximate object of male-male competition. In Conolophus, males must provide retreats for themselves and prospective mates during the breeding season. Territorial males dig 1 or more holes that they

share with females. Availability of existing holes and loose soil for excavation of new burrows, plus proximity to vegetation that provides food and shade, appear to be important components of a male's territory (Werner, in press). Similarly, territorial male Cyclura carinata defend a burrow which is also used by females. Natural crevices were scarce on Caicos Island where this species was studied, and the iguanas were forced to dig their own. Juveniles and subordinate males frequently shifted burrow locations, but territorial males defended a home burrow year-round (Iverson, 1979).

Retreats are of minimal or no importance to most populations of adult Amblyrhynchus, Iguana, and Brachylophus. Large aggregations of the Galapagos marine iguana, A. cristatus, are found on lava boulders adjacent to reef foraging areas. Resources critical to females are not economically defensible. A mating site is the proximate object of male-male competition during the breeding season. Males of this species defend a small area on the lava rocks during the breeding season (Carpenter, 1966; Eibl-Eibesfeldt, 1961; Boersma, in press; Trillmich, 1979). Territories are separate from aggregations of females and bachelor males, and do not contain food. A mating territory provides a place within which to court and mate undisturbed.

Data on the form, variability and use of displays among iguanines are lacking compared to that available for other iguanids (see Carpenter, in press). All iguanines seem to employ typical iguanid challenge displays (lateral presentation, side-flattening), but the form and use of headbob displays appears to be highly variable. In general, it appears that headbob displays among mainland iguanines serve much the same function as in other

iguanid lizards. Species characteristic headbobs are used during advertisement and agonistic encounters (Berry, 1974). In some insular species, on the other hand, headbob displays are much more variable in form and contextual use (Wiewandt, 1977; Iverson, 1979). It has been suggested that different selective pressures in the 2 environments may have produced differences in display variation and use between mainland and insular iguanines (Wiewandt, 1977; Dugan and Wiewandt, in press). Where there is geographic isolation and no possibility for ambiguity in species recognition, greater display variability in the population is more likely to occur. A test of this hypothesis must await more careful studies of a larger number of species.

In summary, it appears that the iguanines differ from other iguanids in that food-based territorial defense is rare. However, most iguanines are crevice and/or burrow-dwelling lizards, and among these species, male territories center around retreats. Territoriality is usually limited to the breeding season, but year-round defense of retreats has been reported. Presumably, the duration of territorial defense is related to the availability of retreats used by females relative to the number of competing males (Dugan and Wiewandt, in press). Few detailed investigations of headbob displays exist for members of the subfamily. Based on the limited data available, it appears that the importance of this display is less among insular iguanines than among other iguanids.

The Study Animal

Iguana iguana is large, long-lived and folivorous. The genus is found in the Caribbean islands, and from Mexico to southern Brazil and Paraguay. Iguana iguana is found in both xeric and mesic habitats

habitats throughout the Neotropics, but always at elevations below 1000 m (Peters and Donoso-Barros, 1970). The species is primarily aboreal, but in Islas Los Roques off the coast of Venezuela, iguanas have been observed living among rocks (Roze', 1956, cited in Rand, 1978).

General accounts of the green iguana's habitat and behavior can be found in Swanson (1950) and Alvarez del Toro (1972). The ecology and thermal behavior of the species have been investigated by Henderson (1974), Hirth (1963), and McGinnis and Brown (1966). Laboratory investigations of metabolic rates were conducted by Moberly (1968a, b). Growth and sexual dimorphism have been studied in NE Columbia (Müller, 1968) and western Nicaragua (Fitch and Henderson, 1977). Greene et al. (1978) discussed predation and anti-predator defenses. More recently, accounts of juvenile growth rates and general ecology (Harris, in press; Van Devender, in press), human predation (Fitch et al., in press), behavior and breeding in captivity (Distel and Veazey, in press; Mendelsohn, in press), reproductive schedules (Greene and Rand, in press)*, have been presented.

Various aspects of the reproductive biology of the green iguana have been rather thoroughly described. In Panama, the site of this study, egg laying occurs in February and March. Female iguanas lay a single clutch of between 2 and 6 dozen eggs annually, depending on the female's size (see Rand, 1968; Rand and Rand, 1976, for detailed accounts of communal nesting). Females may migrate as much as 3 km to find suitable nest sites (Montgomery et al., 1973). Egg laying is timed so that eggs incubate under optimal conditions and hatchlings emerge at a

*and hatchling orientation and migration (Drummond and Burghardt, in press).

time when food is abundant (Rand, 1972). The young hatch in early May at the start of the rainy season, and rapidly disperse from the nest site (Burghardt et al., 1977; Drummond and Burghardt, in press). In contrast to the information available on egg laying, incubation, and hatching, detailed observations of social structure and mating behavior are lacking. At the start of my study, it was known that iguanas mate sometime between October and February, at the end of the rainy season or early in the dry season, although a few May matings have also been suggested in some populations (Greene and Rand, in press). Peracca (1891) first described mating in captive iguanas. Müller (1972) presented a general account of green iguana social and mating behavior in NE Columbia.

Iguanas have been observed to perform visual displays in both the field (Müller, 1972) and the laboratory (Distel and Veazey, in press). Müller identified 2 types of headbob displays. The most common bob observed, "low frequency nodding (NFN)," was performed by both males and females. This bob was most frequently performed by males during the mating season in 3 contexts: territory advertisement, threat, and courtship. "High frequency nodding (HFN)," was described as a headshaking movement performed by territorial males during both threat and courtship. Distel and Veazey recognized 3 different headbob displays: "stereotyped head-nodding" similar in form and use to NFN; "rotatory head-nodding," similar in form to HFN but not observed during courtship; and "vibratory head nodding," classified as a courtship display. Lazell (1973) observed both "headbobbing" and "dewlap shaking," although detailed descriptions were not given.

Iguana iguana is unusual among iguanines in the extent to which it is aboreal and herbivorous. Many other iguanines do climb trees and bushes

to forage, and Enyaliosaurus (= Ctenosaura) and Ctenosaura utilize cavities in the tree trunks as retreats, but few remain in the canopy for extended periods of time. The only other predominantly arboreal iguanines, Brachylophus sp., are much smaller than the green iguana, and are apparently more omnivorous (Cahill, 1970; Gibbons, in press). In addition, female Brachylophus may breed several times per year, and it has been suggested that males maintain territories year-round (Dugan and Wiewandt, in press). Like Amblyrhynchus cristatus, most populations of Iguana iguana use burrows mainly for nesting. One would expect, therefore, that as observed in the marine iguana, territory defense in Iguana iguana males occurs only during the mating season (reported by Müller, 1972), and that rather than defending resources critical to females (food, retreats), Iguana iguana defends a mating territory. Constraints imposed by the arboreal habitat should also influence the green iguana's behavior. Unlike the marine iguana, Iguana iguana spends much of its time in a very complex habitat in which visibility is much reduced.

CHAPTER II

THE STUDY AREA AND METHODS

The Study Area

Flamenco Island is a 13.5 ha island (maximum elevation 75 m) at the Pacific entrance to the Panama Canal (Fig. 1). Flamenco is 3 km offshore; the Fort Amador Causeway connects this island and 2 others, Perico and Naos, to the mainland. The surface area consists of either rocky cliffs or a thin layer of rocky topsoil, depending upon the slope of the particular location. The vegetation consists of lowland dry forest according to Stuart's (1966) classification system. Scrubby second growth covers the island. The dominant tree species include Cecropia peltata, Spondias mombin, Bursera simaruba, and Sapium sp. Vines belonging mainly to the families Convolvulaceae and Sapindaceae are abundant. Trees occur in clumps along the grassy slopes.

Distinct wet (May through November) and dry (December through April) seasons occur in Panama. Total monthly rainfall between October, 1977 and March, 1979, is presented in Fig. 2. Monthly rainfall during the wet season months averaged 21.6 cm, and during the dry season months averaged 5.3 cm. Ambient air temperature tends to be higher during the dry season (Fig. 3). Daily temperatures averaged 29.1⁰ C in the dry season (avg. daily range, 23.6 - 32.2) and 27.8⁰ C in the wet season (avg. daily range, 24.0 - 30.6). However, strong northerly winds between December and March exert a general cooling effect. Temperature and rainfall data were recorded in Balboa, Canal Zone, approximately 5 km from Flamenco. The temperature data probably accurately reflect

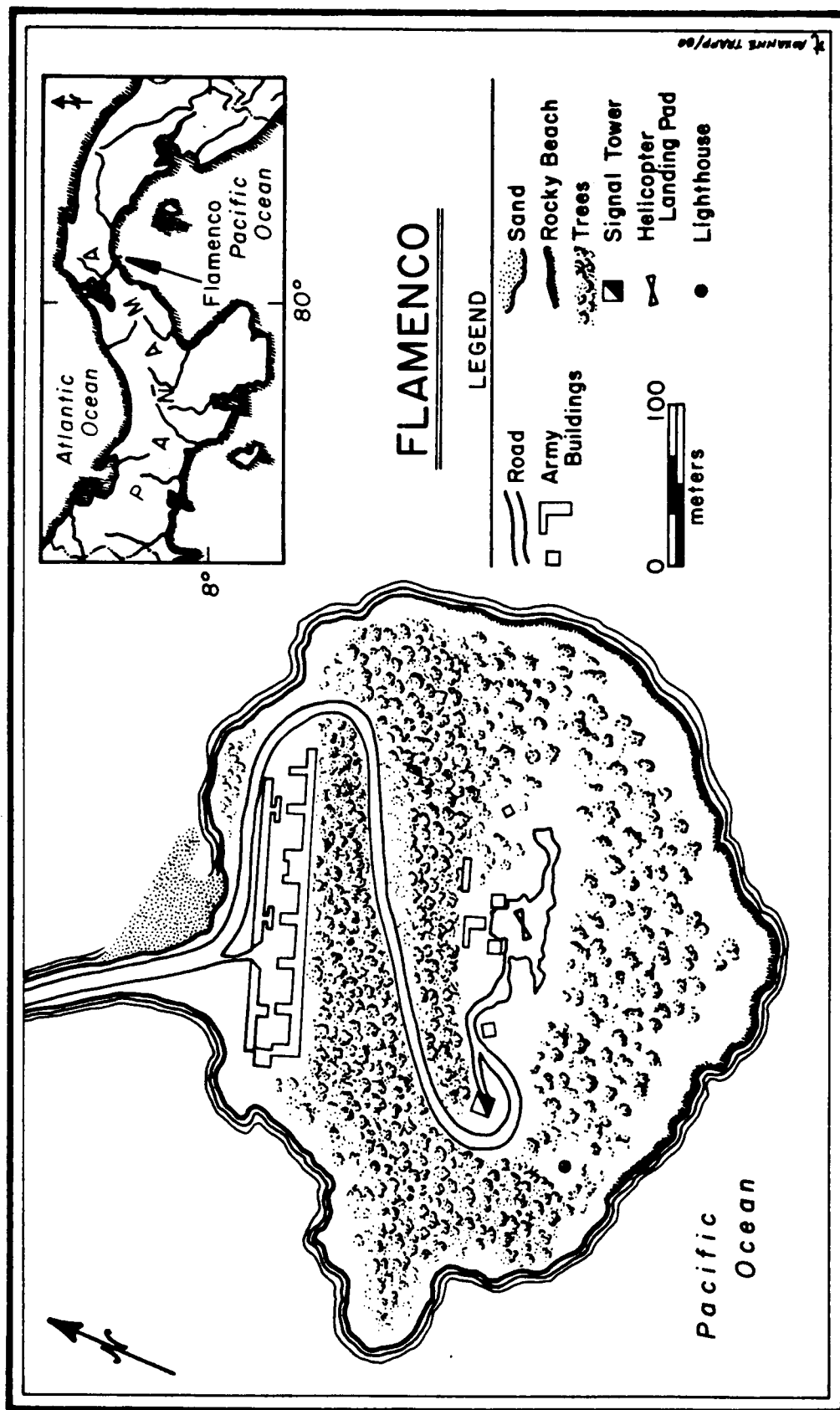


Figure 1. Map of Flamenco Island.

Inset above shows Flamenco's location with respect to mainland Panama.

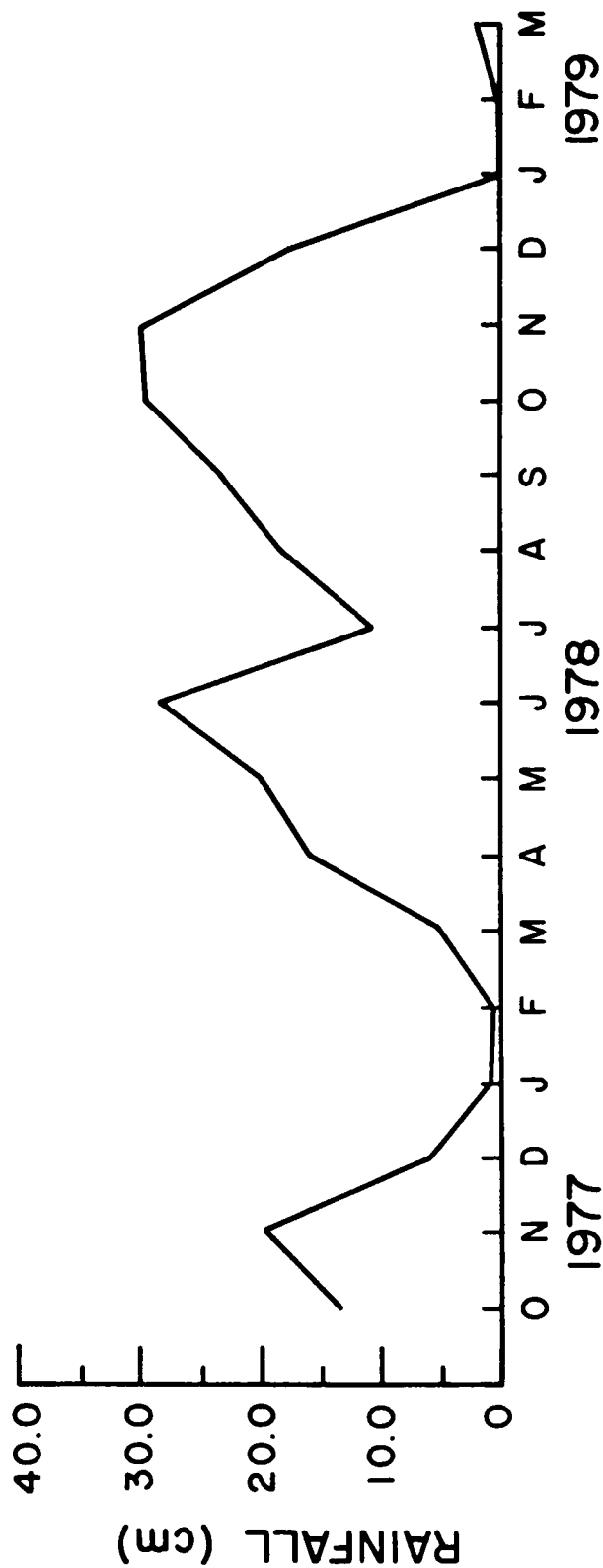


Figure 2. Total monthly rainfall in cm from October, 1977 to March, 1979.

Data are from the Panama Canal Co. Engineering and Construction Bureau, Meteorological and Hydrographic Branch, Balboa, Canal Zone.

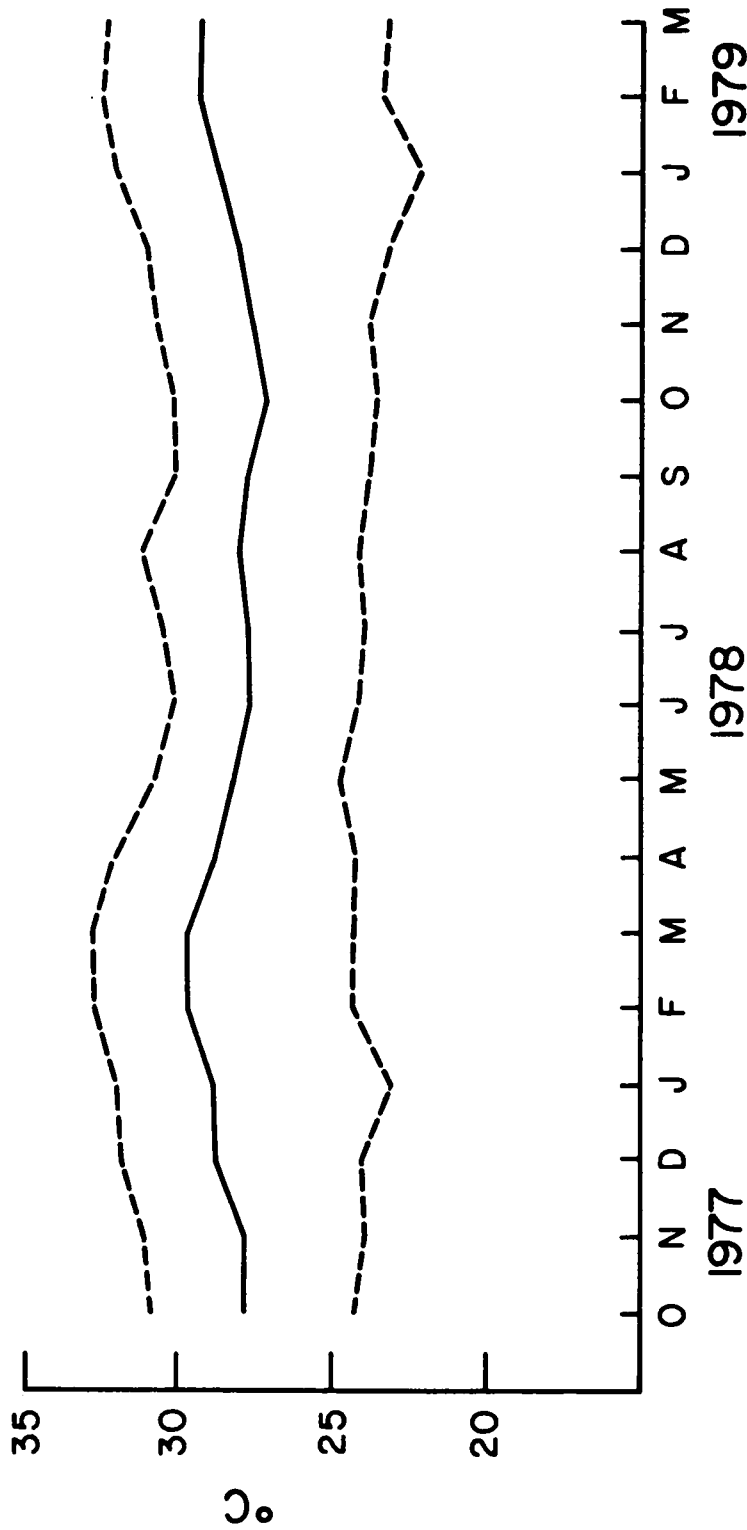


Figure 3. Average daily temperatures (solid line), and average daily minimum and maximum temperatures (dashed lines) between October, 1977 and March, 1979.

Data are from the Panama Canal Co., Engineering and Construction Bureau, Meteorological and Hydrographic Branch, Balboa, Canal Zone.

conditions on Flamenco; however, it was my impression that rainfall was slightly less on the island than on the mainland.

A road leading from the causeway to the top of the hill winds up the northwest side of Flamenco. Observations were confined to a 5.5 ha area on this side of the island. Flamenco's slope on the NW side allows an observer to watch the iguanas at or above the level at which they occur in the trees.

Other than the iguanas, the most conspicuous vertebrates on the island were as follows: reptiles--a small tree gecko (Gonatodes albugularis), the grass anole (Anolis limifrons), and a teiid lizard (Ameiva ameiva); birds--black vultures (Coragyps atratus), brown pelicans (Pelecanus occidentalis), cormorants (Phalacrocorax olivaceus), blue-gray tanagers (Thraupis episcopus), and during the dry season, the broad-winged hawk (Buteo platypterus); mammals--the crab-eating raccoon (Procyon cancrivorus), the Nine-banded armadillo (Dasypus novemcinctus), and the feral domestic cat (Felis domesticus).

Iguanas frequently perched in close proximity to the vultures, cormorants, broad-winged hawks, and pelicans. Blue-gray tanagers fed on Cecropia flowers, a favorite food of the iguanas. Although predation was never observed on Flamenco, potential predators on juveniles and small adults include the broad-winged hawk, domestic cats, and raccoons. A raccoon was observed to attack a large male iguana on the ground at Naos Island, 1 km from Flamenco. The raccoon was tentatively identified as P. cancrivorus. I never observed a Boa constrictor on the island; however, this snake is an iguana predator (Greene et al., 1978) and does occur on Flamenco (Rand, personal communication).

Data Collection

The general methods used throughout the study are presented in the following section. Procedures specific to a particular phase of the investigation will be described in the appropriate chapter.

Capturing and marking. Iguanas were captured with the aid of Panamanian field assistants and their hunting dogs. After spotting an iguana(s), 1 individual climbed the tree. The other 2 - 4 individuals stationed themselves below to catch the iguana as it leapt to the ground. If the iguana was not captured in mid-air, it immediately ran for the nearest burrow or rock cavity. The dogs captured fleeing iguanas, usually by grasping the iguana at the back of the neck.

One hundred and fifty-one animals were captured between April and December, 1978. Each iguana was weighed to the nearest gram, measured (snout to vent = SV, and total length), marked, and released at or near the point of capture. All lengths are reported as SV length in centimeters. Animals were marked by toe-clipping, freeze-branding or painting, and with colored vinyl tags attached with monofilament to both sides of the neck and tail base.

Capturing and marking seem to effect neither the iguanas' movements nor their behavior. This method of capturing did, however, have 2 major drawbacks. First, some iguanas were killed when the dog's teeth punctured the body wall. Twelve of the 151 captured animals died in this manner. Second, tail breaks occurred when the dogs grabbed the iguana by the tail. Seventeen of the captured iguanas had fresh tail breaks. Several of the iguanas that escaped were observed to lose tails as a result of an

encounter with the dogs. However, initial attempts to capture animals in snares tied to trees, and in baited traps placed both on the ground and in the trees, were completely unsuccessful. A marking pistol that shot encapsulated paint balls also proved to be an ineffective marking technique because of the limited accuracy of the pistol and the small size of the targets. In addition, the few animals that were marked in this manner proved to be more wary of a human observer than those that were captured with dogs. Attempts to immobilize iguanas with tranquilizer darts were beset with the same problems as were attempts with the marking pistol.

It is well-known that iguanas escape danger by diving into water. Although there is no fresh water on Flamenco, the iguanas did flee from a human tree-climber by leaping to the ground from as high as 10 - 15 m, sometimes landing on sharp rocks below. The most serious injury observed to result from such a dive was a scratched snout. Injuries do probably result from such dives, however. Two large males had broken bones some time before capture. These breaks, 1 a jawbone, the other a foreleg, were noticeable because of improper fusion of the bones. The actual number of iguanas that had sustained earlier injuries could not be determined. Many healed foreleg breaks were apparent in iguana skeletons examined at The Smithsonian Tropical Research Institute (STRI) (Rand, personal communication). A fall from a tree is the most likely explanation for such observations.

Radio telemetry. Radio transmitters were attached to 2 males and 3 females in November, 1978, and 2 males and 3 females in December, 1978. The transmitter package consisted of the transmitter (Model RM-1; AVM

Instrument Co., Champaign, Ill.), a mercury battery (Model RM-630; Mallory Battery Co., Tarrytown, N.Y.), and a 9 cm long antenna made of rubber-covered test-lead wire. The transmitter and battery were coated with beeswax. The entire transmitter package was 10 cm long, 1.8 cm wide, and 1 cm deep, and weighed 11 g. The transmitter was attached to the iguana's tail base with surgical adhesive tape.

Each transmitter broadcast a pulsed tone at 1 frequency in the 150 MHz range. Thus, each iguana was identified by the frequency broadcast by its transmitter. A receiver (Model LA-11-S; AVM Inst. Co.) was used with a 3-element yagi antenna for directionally receiving the signal. The direction of the iguana was determined from pulse intensity.

Observations and filming. A single animal was selected for continuous observation. The 12 daylight hours were blocked into 1 hour segments, and a running count was kept of the number of males and females observed during each block. In selecting a focal animal (Altmann, 1974), I attempted to ensure that the number of males and females observed in each time period remained roughly proportional, and that identifiable individuals were not observed repeatedly at the same time of day. With the exception of these 2 constraints, focal animals were chosen on the basis of visibility. Attempts were made to divide observation hours equally throughout the daylight hours for both males and females. Verbal accounts of the focal animal's behavior were recorded with a cassette tape recorder. Frequencies and durations of acts were extracted from the transcribed notes. Ambient air temperature (1 m above the ground, bulb shaded) was recorded at the start of each observation period.

Although observations were conducted in the same general fashion throughout the study, the details of the method changed as I learned more about the behavior of the iguanas, and as the number of marked animals in the population increased. Between October and November, 1977, behavioral data were collected in 1 hour focal animal samples. At the start of the first mating activity in December, 1977, I concentrated less on making systematic observations. In an attempt to learn as much as possible about iguana mating behavior, observations concentrated on 6 easily observed mating territories; observation periods ranged from 15 minutes to 6 hours. In both the 1977 and 1978 mating season, breeding groups rather than focal animals were sampled. Observations concentrated on the interactions among members of a breeding group, rather than on a particular individual.

One hour focal animal samples were again used between March and September, 1978. Each observation period was divided into four 15-minute intervals. At the start of each of the 4 intervals, I recorded the number of other iguanas visible in the tree occupied by the focal animal. In order to obtain frequent observations throughout the day for a large number of animals, 15 minute observation periods per animal were employed between October, 1978 and January, 1979. Unless otherwise indicated, behavioral data are reported as rates, or number of acts per 15 minute interval.

The iguanas were filmed with a Super-8 mm movie camera (Nizo S-80). A total of 885 m of film were exposed, 735 m between October and February, 1977 - 1978, and 150 m between October and January, 1978 - 1979. Camera-to-subject distance ranged from 50 to 100 m. Occasionally, it was

possible to film and conduct focal animal samples simultaneously. However, during periods of intense activity, simultaneous filming and recording behavioral observations were not possible. During all filming sessions individual identity and time of day were recorded for each exposure. The information was later transcribed onto a film log.

Census data. The study area was censused on an irregular basis between October, 1977 and September, 1978. Starting in October, 1978, after an appreciable number of animals had been marked, the study area was censused 24 times each month. A spotting scope placed at the entrance to the island was used to systematically scan parts of the study area that could not be seen from the side of the hill. After completing this scan, I walked along the road to the top of Flamenco, scanning the area with binoculars. During each census, the locations of sighted iguanas, both marked and unmarked, were plotted on an aerial photograph of the island. The individual's size, sex, activity, and exposure to the sun (sun, shade, sun-shade) were also recorded. Ambient air temperature (1 m above the ground, bulb shaded), light intensity, presence or absence of precipitation, and the time of day were recorded at the beginning and end of the census. Each map was completed in 1 - 1.5 hours, depending on the number of animals sighted. Each month's censuses were equally distributed throughout the day.

Determination of reproductive condition. Between August, 1978 and January, 1979, 53 animals (25 males, 27 females) were examined to assess reproductive condition. The following data were recorded for each animal: SV length, body weight, diameter of ovarian follicles or testes

length, ovarian or testes weight, and fat body weight. Outside of the mating season, animals were obtained from a variety of sources within 50 km of Flamenco. During the mating season (October - January), only iguanas (19 females, 15 males) from Perico Island, approximately .5 km from Flamenco and similar in topography and vegetation, were used.

CHAPTER III

CHARACTERISTICS OF THE POPULATION

Animals less than 17 cm SV length were rarely seen on Flamenco. Juvenile and adult iguanas are found in different microhabitats (Henderson, 1974; Greene et al., 1978). Juveniles remain in low bushes, and no attempt was made to locate, capture, and mark young iguanas. Thus, data on the iguana population of Flamenco apply to adults and immatures only.

Demographic characteristics were based on the size-frequency distribution of captured iguanas (Fig. 4). In using capture data, I assume that iguanas in all sex and size classes are equally likely to be captured. This assumption is difficult to validate. There was no indication that older/larger iguanas were more wary than younger/smaller animals. However, different responses to capture attempts were apparent. Smaller animals were initially more difficult to catch for 2 reasons: 1) They were usually the first to alert and escape from the tree by leaping to other trees or to the ground. Small animals frequently escaped before members of the capture team had positioned themselves below the tree. Larger animals, particularly large males, seemed more reluctant to leave the tree. 2) By virtue of their size, smaller animals were able to utilize more of the escape tunnels under the trees, and thus were more difficult to capture on the ground. Although an initial bias against small animals existed, this bias should be minimized when total records are considered. As the capture team gained familiarity with Flamenco and the escape responses of the iguanas, capture efficiency improved. Measures were taken not to excite the iguanas before obtaining strategic

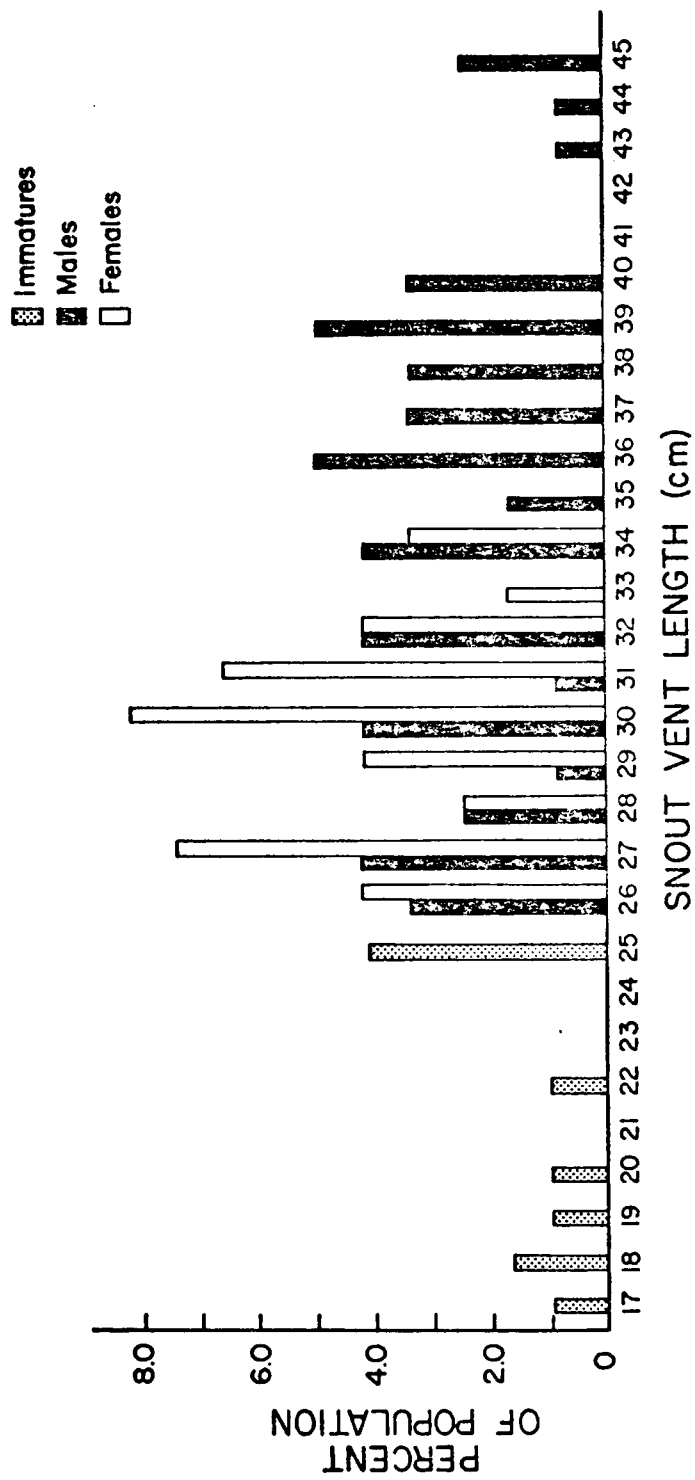


Figure 4. Snout-vent lengths in 1 cm size categories of male, female, and immature iguanas, expressed as a proportion of total iguanas captured ($N = 151$).

positions under the tree, and the most commonly used escape tunnels were known. The average number of iguanas taken per capture day was 7.8 for the first 6 capture sessions, and 17.3 for the last 6. Large males comprised 32% of total animals captured on the first 6 capture days, and 13% on the last 6 capture days. Thus, an estimate based on capture records probably overestimates the proportion of large males in the population. However, since capture efficiency improved steadily (fewer small iguanas escaped and a larger number of iguanas were captured each day), I assume that the bias is minimal.

Sex Ratio and Sexual Dimorphism

Of 151 animals captured, 64 were females, 76 were males, and 11 were immature (sex unknown). The adult sex ratio did not differ significantly from 1:1 ($\chi^2 = 1.2$, $df = 1$, $p > .20$).

Three classes of males, differing in size, behavior (see Chapters IV - VI), and in the development of secondary sex characteristics (see below), were recognized. Small males (26 - 31 cm) comprised 35% of the male population, medium males (32 - 36 cm) comprised 27% of total males, and large males (37 - 45 cm) comprised 38% of total males. Since the range in size of female iguanas was restricted (26 - 34 cm, see Fig. 4), and since no size related physical and/or behavioral characteristics were apparent, this sex class was not subdivided into size classes.

Body weight is plotted as a function of SV length in Fig. 5. The relationship between body weight and SV length does not differ between males and females (analysis of covariance, $F = .02$, $df = 1$, 79, $p > .05$). Males averaged 32.9 cm (s.d. = 5.1) and 1.53 kg (s.d. = 1.04); females averaged 29.7 cm (s.d. = 2.6) and 1.14 kg (s.d. = .34).

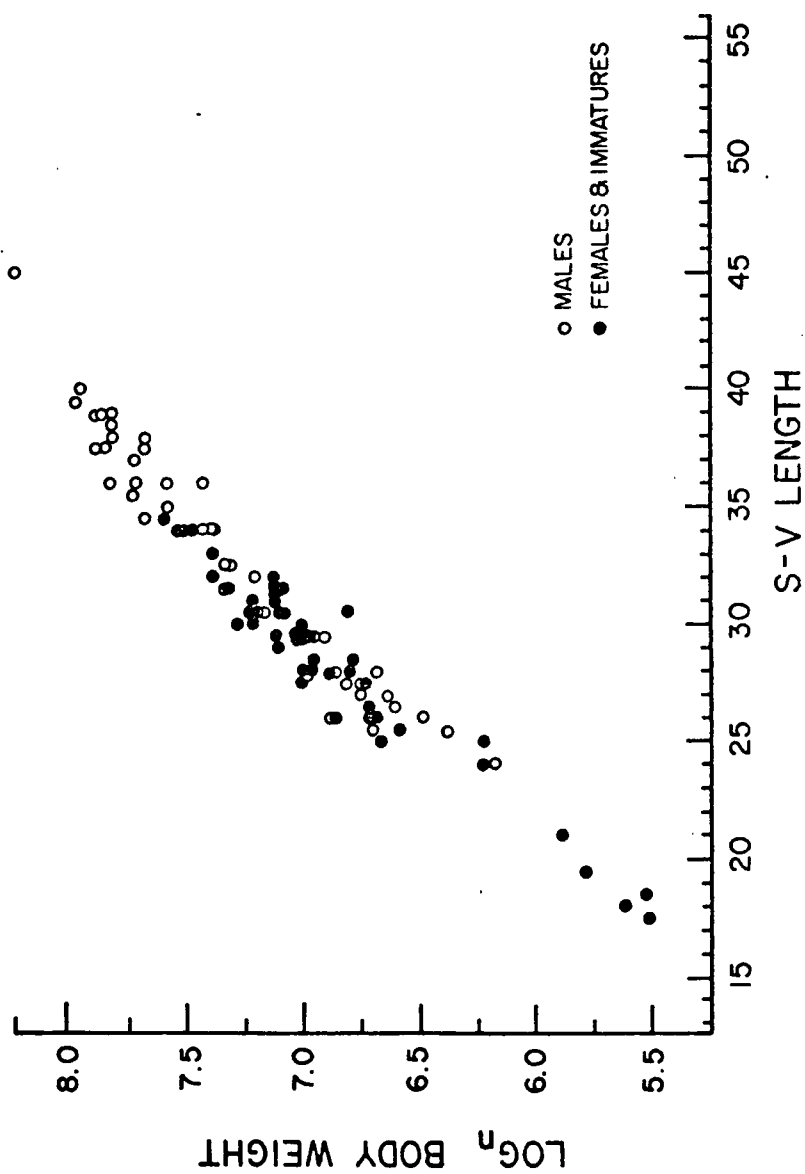


Figure 5. Body weight (natural logarithm) as a function of SV length.

Males grow to a larger size than females. The largest male captured (45 cm, 3.78 kg) was 11 cm longer and 1.91 kg heavier than the largest female (34 cm, 1.87 kg). The mean female weight was 75% of the mean male weight. In addition, males have larger heads, longer spines on the dorsal crest, larger femoral pores, and a larger dewlap (morphometrics in Fitch and Henderson, 1977; Müller, 1968). Males and females also differ in color. Females and small males, vary from bright green to dull, dark green. Larger males are dull gray, gold or tan. The male's color intensifies during the breeding season, at which time most large males vary from bright gold to red-orange. Breeding coloration is at least partly related to social factors. One territorial male changed from bright orange to dull brown within a few hours after having been deposed by a larger male. Two days later he regained both his territory and his bright coloration.

Secondary sexual characteristics develop slowly in mature males. Enlargement of the femoral pores coincides with the onset of reproductive maturity (see below). The distribution of immatures in Fig. 4 indicates the stage at which femoral pore enlargement occurs. In all other respects, small males are indistinguishable from females. At 31 or 32 cm (in the 4th or 5th year), other secondary sex characteristics, such as size of the head and dorsal crest, begin to be evident. Rates of color change are highly variable, but all males greater than 36 cm are predominantly gold or tan.

Reproductive Maturity

Animals smaller than 26 cm were considered to be immature. The smallest males with enlarged testes and the smallest females with yolking follicles measured 27 cm. Although few animals below this size were collected, 3 small females (20, 21 and 24 cm) collected during the breeding season had undeveloped ovaries. These data, plus juvenile growth records from Barro Colorado Island, indicate that iguanas in Panama reach reproductive maturity in the third year (at approximately 30 months), between 25 and 27 cm.

This finding is in accordance with investigations in Nicaragua and Western Costa Rica (Fitch and Henderson, 1977), Columbia (Müller, 1968), and Panama (Rand, personal communication), in which the smallest females found to contain oviducal eggs were between 24 and 27 cm. Harris (in press) found extremely rapid juvenile growth rates in an area of northern Columbia. Although iguanas in this population reached reproductive maturity at 26 cm, individuals attained this size in 1.5 years. Although probably rare, recent evidence indicates that a few female iguanas in Panama may be reproductively mature in their second year (Rand, personal communication). Of 60 gravid females captured on Slothia (a small island near Barro Colorado Island in Gatun Lake, Panama) in February, 1980, 1 of these had been marked after hatching in May, 1978.

Population Density

Population density is usually estimated from mark-recapture records. In its simplest form, the mark-recapture method involves capturing a random sample from the population, and marking and releasing the individuals. Sometime later a second sample is taken. The population

size (N) is then estimated from the ratio of marked to unmarked animals in the second sample. This estimate, termed the Lincoln index, is computed as follows:

$$N = nT/t$$

where n = number of animals captured in the second sample, T = number of animals marked in the first sample, and t = number of animals captured in the second sample that were marked in the first. When several samples are taken, a population estimate is computed for each day and the Jolly multiple recapture method employed (Poole, 1974). In addition to meeting the restrictions of assumptions common to both methods, the reliability of both the Lincoln index and the Jolly multiple recapture method depends heavily on large representative samples (Poole, 1974). One hundred and fifty-one iguanas were captured on Flamenco on 12 sample days. Due to the small number of captures and recaptures per sample (see Appendix A), neither of the above methods was used to estimate the population density on Flamenco. Rather, 2 estimates were computed; Estimate I from the census data, and Estimate II from the proportion of large males in the population. A modified form of the Lincoln index was employed in both estimates, and thus the assumptions of the Lincoln index apply. These assumptions will be stated and discussed in the Discussion section at the end of this chapter.

Estimate I. A population estimate was computed for each of the 72 censuses using the formula for the Lincoln index (presented above) with the following modifications: n = total number of animals sighted in the census (marked + unmarked); T = total number of animals marked prior to the census date; and t = number of marked animals sighted in

the census. Thus, 24 estimates were computed in October, 25 in November, and 23 in December (Table 1). Population estimates for each month were averaged. Although the range of the 3 estimates was relatively slight (310 - 371), the standard deviations were quite large (Table 1). Since the population contained a larger proportion of marked animals during December (the last capture date was 15 December), and since the animals were more conspicuous at this time (see "Mating Season Activity"), and thus more likely to be sighted, only the December census data were used for Estimate I. According to Estimate I, the study area contains about 300 iguanas, or 55 iguanas per ha.

In order to assess the validity of the first estimate, the number of animals in a well-known portion of the study area (.4 ha) was compared to the number of individuals expected in an area of this size, with expected density being based on Estimate I. The test area was selected because a large portion of individuals in the area were marked, and visibility was excellent. Between 21 and 26 animals were sighted in the .4 ha area during each observation period in December. The original estimate predicted 22 iguanas in an area of this size. Not all areas in the study area are equally habitable, and thus one would not expect the iguanas to be evenly distributed. Uninhabitable areas include grassy slopes, the road, and an abandoned military installation. Therefore, in any particular location of suitable habitat, the actual number of iguanas should be greater than expected.

Table 1. Mean, standard deviation, and range of estimates of population density within the study area, based on census data for October, November, and December, 1978.*

	Month		
	October	November	December
$\bar{X}$ no. of iguanas	371	319	310
S. D.	170	125	48
Range	116-639	198-671	213-442
N. of censuses	24	25	23

*December data were used for Estimate I. See text for explanation.

Estimate II. In this second method, the number of large males in study was estimated from the census data. Again, a modified form of the Lincoln index was used: n = total number of large males observed in the census; T = total number of large males marked prior to the census; t = number of large males sighted in the census that were marked; and N_i = estimated number of large males in the study area per census. The average N_i over all censuses provided the final estimate (N) of the number of large males in the study area. Large males comprise 19% of the total captured animals in the iguana population. Thus, the total number of animals in the study area can be computed by dividing the estimated number of large males (N , from census data) by their proportion in the population (.19, from capture data).

I assume that the number of large males in the population can be approximated from the census data more accurately than the size of other sex and size classes for the following reasons: 1) Large males are less likely to lose plastic tags than are females or smaller males. Tags were lost when the monofilament tore the skin. The skin of large males, particularly that on the side of the neck, is much tougher than the skin of smaller animals. Tag loss in most females occurred 1.5 - 4 months after being marked. Large males retained their tags for a longer period of time than did most smaller animals (minimum of 6 months). 2) The home ranges of large males were smaller than those of other males and females (see "Home Range Size"). Thus, movement into and out of the study area was less likely for large males than for other members of the population. 3) Because of their size, color and behavior, large males were more conspicuous than other members of the population (see

"Sex Ratio and Sexual Dimorphism"). Therefore, large males were more likely to be sighted than were smaller males and females.

The number of large males (N) in the study area estimated from the ratio of marked to unmarked large males sighted in the 72 censuses was 37 (s.d. = 6). Assuming that large males were captured in proportion to their numbers in the population (see "Discussion"), then the total number of iguanas in the study area is approximately $37/.19$, or 195 (36 iguanas per ha).

Discussion

In other parts of their range, iguanas may grow to a much larger size than those on Flamenco. For example, Fitch and Henderson (1977) found that males in Costa Rica and western Nicaragua averaged 36.1 cm (25.5 - 55.0), females averaged 32.7 cm (23.6 - 41.1). It was my impression that the iguanas on Flamenco were much smaller than those on Barro Colorado Island (BCI), approximately 50 km north of Flamenco. An adult male captured on BCI measured 46.5 cm, larger than any male captured on Flamenco. The females I observed nesting on Slothia were on the average much larger than those on Flamenco. The average SV length of 65 females captured on Slothia during the 1980 nesting season was 36.8 cm (Rand, personal communication), 2.8 cm longer than the largest female captured on Flamenco. Similarly, Müller (1968) found large size differences in 2 populations of iguanas in Northern Columbia. In xeric habitat, the largest size-class measured 34.5 cm SV. A few miles away in a humid banana zone, the iguanas grew more rapidly and were larger. Of 4 animals captured from the banana zone, 1 male measured 42 cm SV. Müller attributed the difference in growth rates and size to

dry season food shortages in the xeric habitat. Although there never appeared to be a shortage of food on Flamenco, it may be that the available plants are low quality food items that do not permit rapid and sustained growth. BCI is a much more humid habitat, and contains more tree species. Perhaps the tropical moist forest on BCI provides a more nutritious diet for the iguana.

The 2 density estimates suggest that the study area supports between 200 and 300 iguanas, or 36 - 50 individuals per ha (45 - 70 kg/ha). The validity of both estimates depends on the extent to which the assumptions of the Lincoln index were violated. These assumptions are: 1) mortality and recruitment, and emigration and immigration, are minimal during the sample period, or can be accounted for, 2) all animals are equally likely to be captured (or sighted) on each sample day, 3) animals neither die nor emigrate after having been marked and released, but are distributed randomly throughout the population, and 4) animals do not lose marks.

Since iguanas are long-lived and slow to mature, mortality and recruitment are presumed to be low. Only 3 dead animals were found during the course of the study, and very few juveniles and yearlings were seen. Flamenco is an island, and iguanas were never observed on the causeway or in the water surrounding the island. Emigration and immigration are thus presumed to be minimal. Movements into and out of the study area probably occurred but could not be accounted for. Estimate II, based on sightings of large males, was probably less influenced by such movements than was Estimate I. The extent to which capturing and marking influenced the movements of smaller iguanas could

not be determined. Some females were sighted a few days after being captured in the area in which they were captured, but the movements and locations of others were unknown. Large males and some medium males, on the other hand, were regularly seen in the same location before and after being captured. Animals with brightly colored tags are more easily sighted than are unmarked animals. Although the study area was scanned carefully during censuses, it is probable that more unmarked than marked animals were overlooked. Since large males are exceedingly conspicuous without tags, this bias was probably minimized in Estimate II.

Estimate II depends to a large extent on the accuracy of estimates of population composition. As stated previously (see "Population Composition"), the estimate of population composition based on capture records may inflate the estimated number of large males in the population. Such a bias would produce a low estimate of population density. However, due to the rates of tag loss in smaller iguanas, it is likely that method II is more reliable than method I. The first animals were marked in April; most were marked between July and September. It is likely that some sighted iguanas had lost their tags and were recorded in error as being unmarked. Such a bias would tend to inflate the population estimate, and is more likely to have occurred with method I than II.

These figures are of necessity only rough approximations. However, it is obvious to an observer that Flamenco contains a large number of iguanas. Since hunting is presumably less common on Flamenco than in many other parts of the iguana's range, it would be of interest to know whether the island supports an unusually large population of iguanas. Müller (1972) reported 50 - 70 iguanas at "institute rock," (Punta de

Bet¹in, Santa Marta, Columbia). Unfortunately, he did not report the size of the area. Swanson's (1950) descriptive account of the natural history of Iguana iguana in Panama suggests that iguanas were extremely abundant along the roadsides during his travels in the 1940's. Rand (1978) noted that in areas where iguanas are not hunted by man, they can reach high densities. Iguanas are common enough in certain parts of the llanos of South America to be an important danger to the cotton crop (Rand, 1978). Although the data are too few to allow a firm conclusion to be drawn, there is no evidence that iguana density on Flamenco is unusually high. Iguanine lizards typically maintain population biomasses much higher than most lizard species, an observation that is probably related to their role as primary consumers (Iverson, 1979). Thus, it may be that under favorable conditions, Iguana iguana maintains population densities much greater than that on Flamenco.

CHAPTER IV

ACTIVITY AND SOCIAL STRUCTURE DURING
THE NON-BREEDING SEASON

Daily and Seasonal Activity

Activity budget. The cost of any activity may be expressed in terms of time and/or energy. The construction of an activity budget is one of the first steps in assessing the costs of activity. However, the main purpose of my investigation of iguana activity was not to assess the actual cost of various activities, but rather to detect relative differences among the various sex and size classes in daily and seasonal activity, and in the types of activities engaged in. Such differences presumably reflect different allocations of energy among individuals in different sex and size classes.

In order to quantify activity time, the durations of 4 acts were recorded during each observation period: Feeding bouts, perch changes, headbob displays, and social interactions. The duration of a feeding bout includes the time spent manipulating (biting, pulling with tongue or forelegs) and swallowing a plant item. A perch change was scored if the animal moved 4 feet in the process of changing its position and/or location. The headbob category includes the 4 types of headbob displays identified (see Chapter VI). Social interactions include act-response-act sequences between animals, as well as "avoidance interactions," 1 individual retreating at the approach of another. Perch changes and headbobs include only those instances that occurred outside

the context of a social interaction. Thus, all of the categories except social interaction include time engaged in physical activity. During a social interaction, an animal might be motionless.

Durations of acts were timed with a stopwatch or by vocally recording the onset and offset of a particular act. In the latter case, a stopwatch was used to transcribe durations from the taped records. Since it was often difficult to catch the onset of headbob displays, rather than attempting to record duration, each display was arbitrarily assigned 3 seconds duration. The duration of some displays may have been slightly overestimated. However, since shuffling of the forelegs before displaying, and short pauses between sequences of 2 different displays occurred, overestimation of duration is probably minimal.

In 79% of the observation periods (269 of 341), the iguanas spent less than 5% of the time engaged in any activity, and were active less than 10% of the observation period in 91% (310 of 341) of observations. Thus, activity data are expressed as the median percent time active, the appropriate statistic for highly skewed distributions. The measure of dispersion, the interquartile range (median $\pm$ 25% of observations) is less sensitive to extreme values, and more accurately reflects the shape of the distribution than do the mean and standard deviation. The percent time engaged in each activity, and overall percent time active, were cast into a frequency distribution with a class interval size of 1%.

The short duration of each act recorded, and the individual variability in activity, make detailed comparisons of percent time engaged in each act across sex and size classes difficult. These data are

summarized in Appendix B. Feeding activity will be discussed below. Comparisons of rates of headbob displays and social interactions across sex and size classes will be made in Chapters V and VI.

When overall time active across seasons is examined, however, certain trends become apparent (Fig. 6). The interquartile ranges indicate that females and large males were more likely to be observed active in October and November, 1977, and medium males were more likely to be observed active in March and April, 1978. The only significant difference found in activity level across seasons was for females ($\chi^2 = 10.9$, d.f. = 3, $p < .02$, Median test, Siegel, 1956). The increase in the activity level of females was primarily due to a greater amount of time engaged in social interaction (Appendix B).

Due to low within-cell frequencies, the Kolmogorov-Smirnov test was used to test differences in activity level among females and large and medium males in October and November of both years. The hypothesis tested was that one-half of the observations for each sex-size class fall above the common median percent time active computed from data collapsed across the 3 groups (see Siegel, 1956). In October and November, 1977, large males and females were significantly ($p < .02$) more likely to be observed active than were medium males. The same difference was not found to be significant in October and November, 1978.

Mating season activity begins in mid-October, roughly 6 weeks before copulation. The reduced activity of medium males relative to large males and females is related to his role in the mating system (see Chapter V). Medium males headbob less frequently than do large Males (Chapter VI and Appendix B), and are less likely to engage in

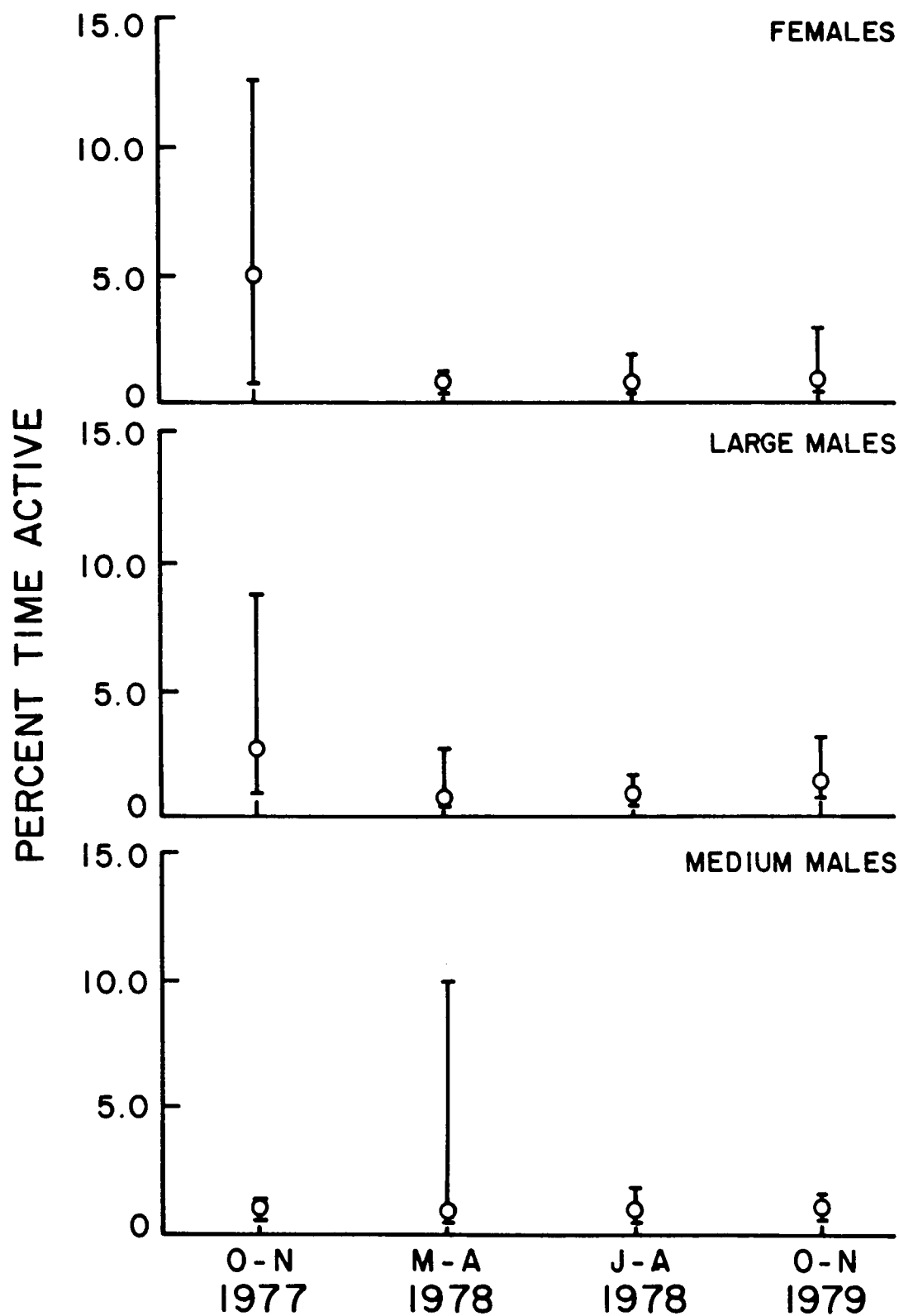


Figure 6. Median percentage of observation periods (N = 341) that iguanas were active during early mating season (October - November), dry season months (March - April), and the middle of the rainy season (July - August), 1977 - 1978.

Bars denote interquartile range.

courtship interactions than are large males or females (Chapter V and Appendix B). The greater activity observed among medium males in March and April may be an artifact of the small number of observations for this sex-size class during all periods.

The late wet season increase in activity among large males and females in 1977 was not observed during the same 2 months in 1978. Iguanas are less active during heavy rains (see below) and total rainfall was higher in October and November, 1978 than in 1977 (Fig. 2, page 18). The influence of physical factors on mating behavior in the 2 years will be discussed more fully in Chapter V.

The iguana's daily activity pattern was characterized by short periods of activity alternating with periods of inactivity. Regularities in this pattern were closely tied to the time of day and temperature.

Thermoregulation. The first activity period was the scramble for basking sites. Shortly before sunlight hit the tree, the iguanas began to move from their sleeping perches to exposed locations in the tops of the trees. During this movement into the sun, if the tree was crowded, iguanas encountered other iguanas and social interactions were relatively frequent. Once each individual was settled on an exposed branch, however, social interactions were rare. The exact time of onset of the basking period depended on the location of the tree. Iguanas in trees on the east side of Flamenco began basking earlier than iguanas on the west side. However, within any 1 tree, movement into the sun was highly synchronous.

After moving to an exposed perch between 0630 and 0800 hours, the iguanas spent the next 1 - 1 1/2 hours basking. The typical basking

posture consisted of sitting perpendicular to the sun, with forelegs and dewlap maximally extended. As the amount of time exposed to the sun increased, the iguanas went through a series of postural adjustments, presumably to avoid overheating. Individuals on foliated perches either sank slowly into the leaves, thus reducing the amount of body surface exposed to the sun's rays, or moved a few steps into the shade of an overhanging branch. Iguanas that perched on bare branches usually faced the sun and lifted much of the ventral body surface from the substrate by turning perpendicularly to the branch and balancing on 4 feet and the base of the tail. Panting invariably occurred in this posture, and preceded movement into the shade or sun/shade.

After basking for 1 or 2 hours, the iguanas moved to the shade to rest or begin feeding. The iguanas' mid-day activity was much less synchronous than early morning activity. During the mid-day heat, most of the iguanas rested in the shade, and fewer iguanas were visible than at other times of the day (Fig. 7). During the mid to late afternoon, many iguanas were again observed on exposed perches on the west side of the tree. After a late afternoon period and basking and/or feeding, the iguanas began moving to sleeping perches. Adult iguanas usually slept in a clump of leaves at or near the end of a branch, facing away from the trunk of the tree. Larger animals were occasionally found on the main part of a branch. Insofar as could be determined, the same parts of the tree were regularly used as sleeping and basking perches. A significant inverse relationship was found between the ambient air temperature and the number of iguanas visible during census periods ($r = -.66$, $df = 70$, $p < .01$), reflecting the general pattern of daily activity (Fig. 7).

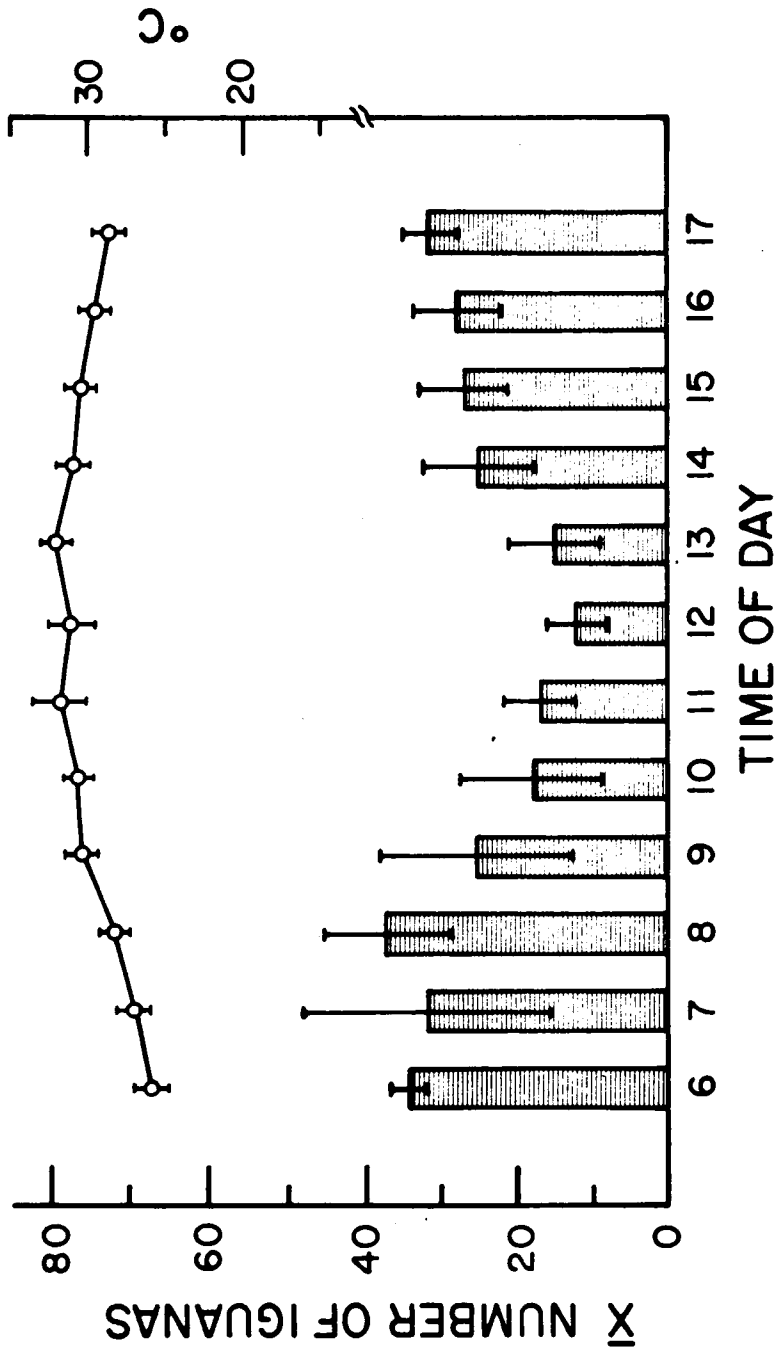


Figure 7. Bottom graph: Mean number of iguanas sighted at each hour of the day during 72 censuses conducted in October, November and December, 1978 (6 censuses were begun at each hour). Top graph: Average hourly temperatures recorded at the start and finish of each census.

Vertical lines indicate ± 1 standard deviation.

The schedule outlined above was affected by conditions of temperature, light intensity, and rainfall on any particular day. Although light rainfall interfered minimally with iguana activity, during a heavy prolonged rainfall, virtually all activity ceased. Iguanas were at times observed to continue a feeding bout that had begun before the onset of a heavy rain, but were rarely observed to initiate activity during a heavy downpour. Rather, they usually moved to sleeping perches and assumed a sleeping posture. If the rain occurred during late afternoon and stopped 1 to 2 hours before sunset, the iguanas rarely resumed activity. If a heavy rain occurred earlier in the day, the iguanas moved to exposed branches soon after the sun came out and resumed basking.

Feeding behavior. Iguanas spend very little time feeding. Seventeen bouts totaling 45 minutes of feeding activity were observed during 218 hours of focal animal sampling (February - August, 1978). In order to obtain more information on feeding behavior, focal animal sampling was interrupted to record the feeding activity of other animals. If an iguana in the same tree with the focal animal began to feed, the food item and if possible the duration of the feeding bout were recorded. The number of feeding bouts observed in each 1 hour time block was divided by the total number of iguanas visible during that time block, yielding an estimate of the number of feeding bouts per iguana hour.

With the exception of 0600 - 0700 hours, iguanas were observed feeding at all hours of the day (Fig. 8). Feeding bouts were least frequent in the early morning hours, when most of the animals were basking. The majority of observed feeding bouts occurred between mid-morning and

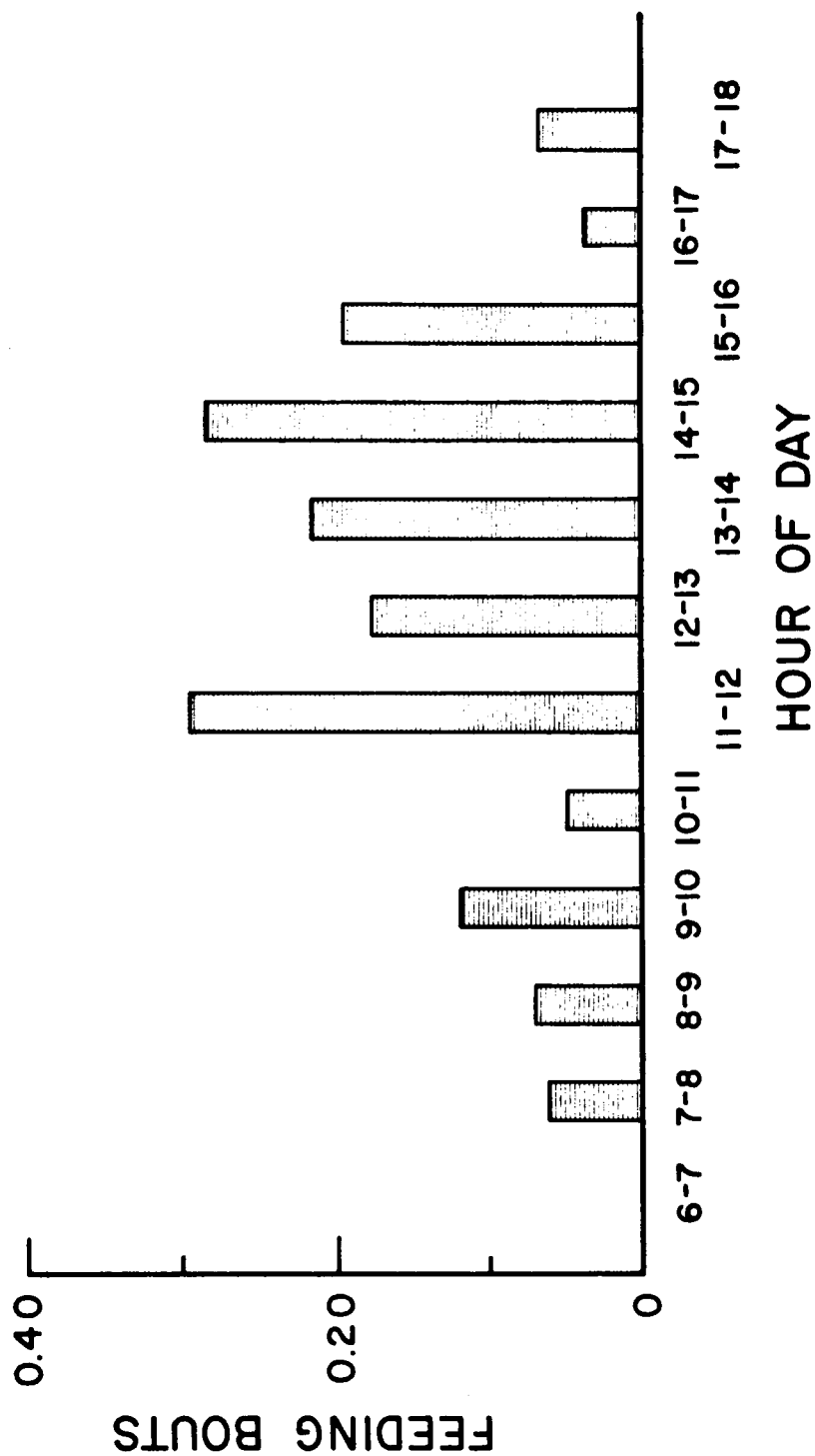


Figure 8. Distribution of observed feeding bouts throughout the day. Data are from both dry and wet seasons. Data based on 375 iguana hours, February through August, 1978.

mid-afternoon. On those few wet season days that were cool and overcast with intermittent showers, no iguanas were observed to feed. Thus, it appears that body temperature is 1 constraint on the iguana's foraging activity. Although detailed data on the feeding behavior of individuals are not available, I suspect that during periods of prolonged rain in the wet season, an iguana may not feed for a day or more. However, it was my impression that on favorable days, an iguana fed at least once, probably more. The durations of timed feeding bouts varied from 3 sec to 17 min. The majority (22 of 38) lasted from 1 to 5 min. Of the 11 feeding bouts that lasted longer than 5 min, 7 involved animals eating seasonally available "preferred" foods--Cecropia flowers and new leaves, and new Sapium leaves. Three of the remaining 4 involved animals eating new Genipa leaves.

Although the iguanas were observed to feed on all of the most common plants on Flamenco, they appeared to feed selectively on certain plant parts (Table 2). Leaves of the vine Paullinia, and new leaves of Genipa americanus, were eaten throughout the year. During the dry season, these were the most abundant and frequently eaten food items at the bottom of Flamenco. Various vines of the family Convolvulaceae were more common at the top of the study area, and both the leaves and flowers of these plants were eaten. At the end of the dry season, new Sapium leaves began to appear. New Sapium leaves and new Cecropia leaves and flowers became a significant addition to the iguanas' diet in the early part of the wet season. The next major shift in diet occurred between August and September at the onset of the Spondias fruiting season. Although the heavy foliage made observations difficult,

Table 2. Plants and plant parts eaten by iguanas on Flamenco.¹

	Plant Part		
	Leaves	Flower	Fruit
Trees			
<u>Genipa americanus</u>	* (mature) *** (new)		*
<u>Cecropia peltata</u>	* (mature) *** (new)	*** (in-florescences)	
<u>Sapium</u> sp.	*** (new)		
<u>Spondias mombin</u>	*		***
<u>Ficus</u> sp.	*		
<u>Tacoma stans</u>	*	*	
Vines			
<u>Paullinia</u> sp.	***		
<u>Ipomoea</u> sp.	**	**	
<u>Cissus sicyoides</u>	**	**	

¹Stars represent subjective ranking by quantity eaten: *** = eaten in great quantities when available; ** = eaten in moderate quantity; * = rarely eaten.

2 lines of evidence indicate that Spondias fruit was eaten in quantity at this time: 1) virtually all of the iguanas captured in August through October were flushed from Spondias trees; 2) the majority of iguanas examined during this period had Spondias leaves and/or fruit in the gut.

Movements

Except for occasional descents to the ground for basking, for tree-to-tree movement, for escape from disturbance, and (for females) for travel to nest sites, iguanas remained in the tree tops. Although the iguanas were rarely observed on the ground, they were quite familiar with rock cavities and underground retreats at the base of the tree. Inevitably, if an iguana was not captured before hitting the ground, it ran directly towards the nearest retreat. Indeed, most of the iguanas that were flushed from the trees were not captured. Thus, it appears that part of the time on the ground was spent in learning the locations of escape routes.

An iguana might stay in the same tree from 1 day to several weeks. A single tree could meet all of an iguana's short-term requirements--food, thermoregulatory sites, and sleeping perches. Long-range movements were prompted at least in part by local changes in food availability. Two trees in particular were observed to contain large numbers of iguanas during the dry season, when many of the trees were leafless. One, a large Sapium tree, contained between 9 and 13 iguanas between February and April. The most frequently eaten food item in this part of the study area was the vine Paullinia. The Sapium was leafless, but contained abundant vine cover. During this same period, between 6 and 9

iguanas were regularly observed in a Genipa americanus in another part of the study area. Both the Genipa and Paullinia leaves were eaten by the iguanas in this tree. Both trees contained a few recognizable animals, and it appeared that the composition of the 2 groups changed little during this period.

Field observations were interrupted in May and June. However, it was apparent that the large groups observed in the dry season dispersed early in the rainy season when a variety of new leaves became available. In July and August, no more than 3 iguanas were sighted simultaneously in the Sapium and no more than 2 in the Genipa. That at least some of the iguanas on Flamenco were moving to new food resources is evidenced by the fact that in these same months, 2 Sapium trees that had been unoccupied since January regularly contained between 1 and 3 animals. Residents of both trees were observed to eat new leaves.

Large congregations of iguanas were again found during the Spondias fruiting season. Spondias mombin fruits asynchronously during August and September. Some trees bearing this fruit contained 10 - 15 animals for the duration of the fruiting period, after which the iguanas moved to other locations.

Home Range Size

Home range size was estimated from the locations of marked iguanas plotted on an aerial photograph of the island. Locations were recorded during censuses, focal animal sampling, and while radio-tracking. Parts of trees or groups of trees that the animals were known to have used were circled, and the outer perimeters of the circles were connected. In 3 cases (2 females, 1 medium male), animals were sighted

in 2 different groups of trees that were some distance apart. In these cases, the width of the path connecting the 2 tree groups was arbitrarily designated as $1/2$ the diameter of the circle enclosing the smallest tree group. No attempt was made to estimate home range volume. Home range size was computed by 2 methods: 1) by weighing cut-outs of each home range, and 2) by counting the number of squares on a piece of graph paper each home range enclosed. Measurements were then compared to the appropriate 1 ha scale. The 2 methods gave results within 3 m^2 in all but 2 cases. The 2 measures were averaged for the final estimate.

The movements of all sex and size classes overlapped in both space and time (Fig. 9). The home range sizes of 8 females, 9 small and medium males, and 10 large males (Table 3), were compared using a one-way analysis of variance. A significant difference in home range size was found among the 3 groups ($F = 4.69$, $df = 224$, $p < .02$). The Student-Newman-Keuls test revealed that the home ranges of large males were significantly ($p < .05$) smaller than those of females and other males. This result is opposite the relationship usually observed between home range size and body size in lizards (Turner et al., 1969). This finding does not reflect sample size bias, since more sightings over longer periods of time were obtained for large males than for other members of the population. Although the home ranges of large males were smaller than those of other iguanas, each large male's home range contained at least 2 seasonally preferred food resources, plus a year-round supply of food.

LARGE MALES
 MEDIUM & SMALL MALES
 FEMALES

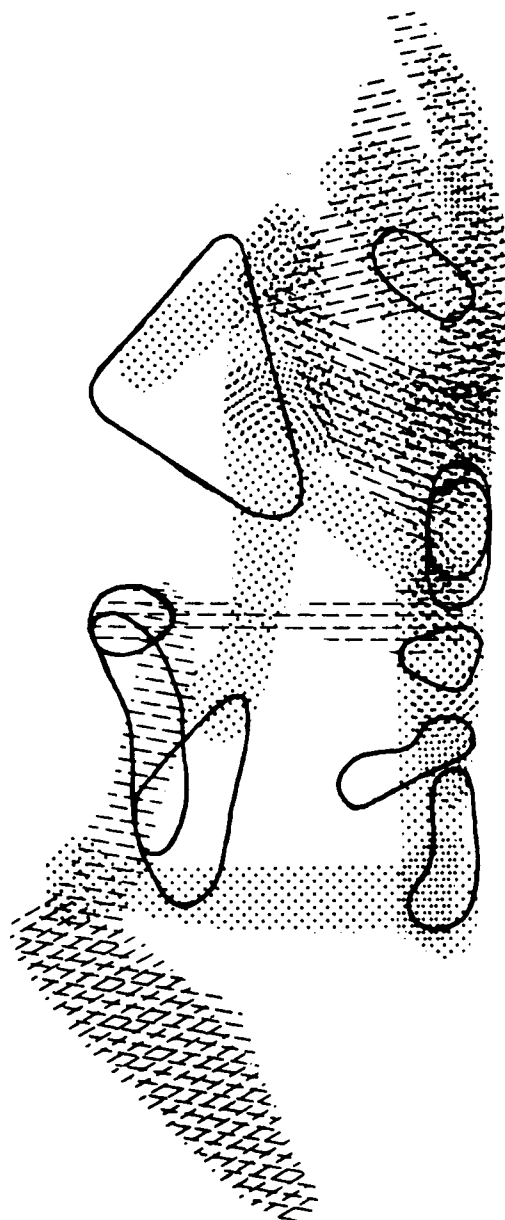


Figure 9. Home ranges of 10 large males, 9 medium and small males, and 8 females.
 This sample is only a small portion of the iguanas in the study area, and thus
 under-represents home range overlap.

Table 3. Mean home range size of iguanas for which at least 3 recordings per animal were made over a minimum of 2 months.

Group	Home Range Size (ha)		Number of Sightings per Animal	
	Mean	S.D.	Mean	Range
Large Males (N = 10)	.080	.073	41	21-71
Medium and Small Males (N = 9)	.220	.113	9	3-28
Females (N = 8)	.245	.181	9	3-22

Social Interactions

Iguanas were found singly or in groups throughout the year. However, I concentrated on larger groups in order to maximize the amount of information obtained from observations. Large congregations usually consisted of 1 large male, 1 - 3 medium males, 1 - 3 small males (when recognized) and 4 - 6 females.

It was not unusual to observe 2 large males in the same tree at the same time, although they never remained in the same location for more than a day. Only 2 agonistic encounters between large males were observed outside of mating season. In 1 of these, the males alternated signature bobs (see Chapter VI), accompanied by lateral body compression; in the other, a face-to-face pushing battle also occurred. Medium males also avoided one another; 2 or more medium males in the same tree used different parts of the tree.

Interactions between large and medium males were rarely observed. The differences in their behavior were striking. Medium males avoided large males at all times. Large males displayed more than medium males throughout the year (see Chapter VI). Only large males had access to conspicuous perches that were used as display posts. Conspicuous perches were also preferred as basking sites by females, and large males and females basked in close proximity.

As indicated previously, the iguanas were quite tolerant of each other during the basking period. However, the largest male excluded other males from "preferred" basking sites (i.e., basking sites used by large numbers of iguanas), and at times denied subordinates access to any basking sites. This exclusion was usually accomplished without

any overt interaction between the dominant and subordinate. For example, the large Sapium tree contained 9 - 13 iguanas during the 1978 dry season. During each of 3 morning observation sessions at this location, the large male basked in close proximity to 4 or 5 females. The medium male, rather than basking elsewhere in the tree, remained crouched on a shaded, vine-covered perch 1 m below the basking group. Similarly, in the Genipa tree containing 6 - 9 individuals in the 1978 dry season, the resident medium male was rarely observed basking. On 1 occasion, this medium male was observed on an exposed perch in mid-morning. The large male passed nearby on his way to the top of the tree, lunged at the medium male, and the medium male retreated to his usual perch in a clump of leaves. Medium males observed in trees that were not occupied by a large male did bask in the early morning and late afternoon, sometimes in the company of females. Although the animals were not marked, my description indicates that the same individuals were observed in both large trees throughout the dry season.

At all times of the day during the dry season, large males were more likely to be found close to 1 or more females than were medium males. Distance to the nearest female was recorded in 23 scan samples (March 24 - April 6) during the dry season when visibility was best (Fig. 10). Distance estimates were classified into 1 of 4 categories: 0 - 1.5 m, 1.5 - 3 m, > 3 m, and solo. Large males were less likely to be solitary and more likely to be near 1 or more females than were medium males ($\chi^2 = 30$, $df = 3$, $p < .001$). Although heavy foliage sometimes interfered with observations during the wet season, my impression is that this finding would generalize to the rainy season.

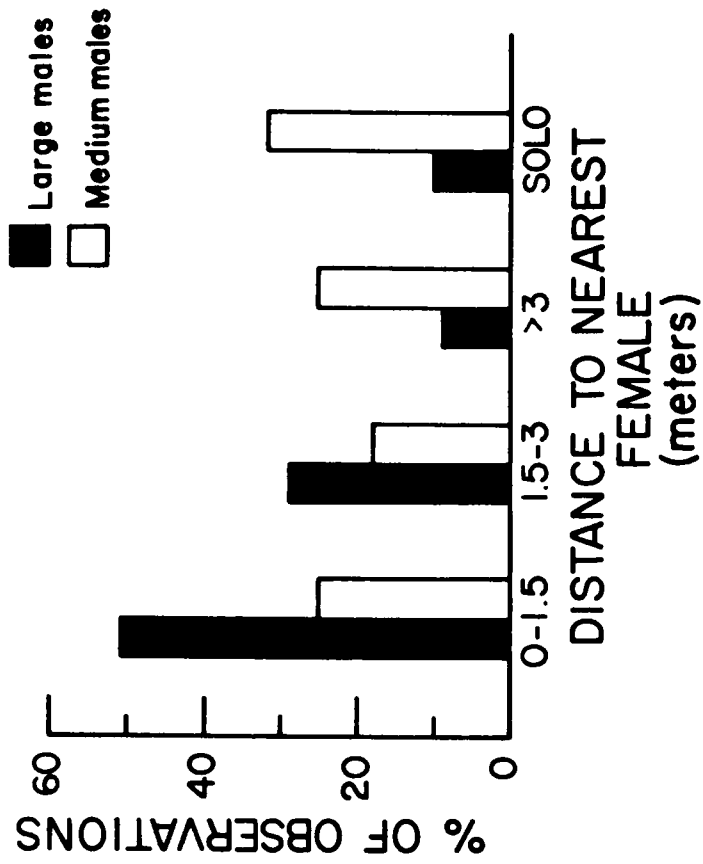


Figure 10. Proportion of observations in which large and medium males were recorded at varying distances from a female.

> 3 m = female in same tree but greater than 3 m from male. Based on 23 scan samples.

Encounters among smaller iguanas were brief (consisting of lunges and chases), and usually occurred during changes in location (moving from sleeping perches to basking sites, basking to feeding locations, to sleeping perches, etc.). These encounters may have functioned to establish dominance hierarchies in transient groups. Some mechanism for regulating interactions in such high density situations would be advantageous. However, the dense foliage and large number of unmarked animals prevented the determination of relationships between individuals.

Discussion

Moberly (1968a) estimated that iguanas spend 90% of their waking hours inactive. Overall, my observations are in accord with Moberly's estimate. The amount of time an iguana spends active, however, depends on seasonal and daily variations in the weather, as well as the animal's sex, size and social status. Energy requirements may exert a strong influence on the iguana's activity during the non-breeding season. Minimization of energy expenditures should be important to a large bodied reptile existing on energy-poor plant food (Pough, 1973). However, as Rand (1978) pointed out, very little is known about the quality of the iguana's diet, nor about the iguana's ability to utilize plant food.

The iguana's movements and the tendency to aggregate are related to patterns of food availability. Large groups of iguanas were observed during the last half of the dry season. These aggregations occurred in locations that contained abundant dry season food. However, why the iguanas were clumped in a few of the many vine-bearing trees is unclear. Certainly, the Genipa tree contained food in addition to Paullinia, but

another Genipa less than 100 m away was never occupied at this time, although it was at other times of the year. Perhaps exploitation of a known resource is more efficient than searching for new food items (see Auffenberg, in press), particularly at a time of potential food shortage. Social facilitation of feeding (Greenberg, 1976) may also have occurred; groups of iguanas frequently fed simultaneously. In addition, the iguanas may have been able to "predict" the location of future resources. New Sapium leaves began to appear in early April. The iguanas in the Sapium tree fed on the new leaves as they appeared. The Genipa was adjacent to a Sapium tree, and although the iguanas were never observed to do so, it is highly likely that they moved into the Sapium to forage.

Large congregations of iguanas were only observed at the bottom of the island during the dry season. There were no large Genipa trees on the top of Flamenco, and Sapium and Cissus were much less common. Most of the trees and bushes in this part of the study area were covered with vines (Convolvulaceae). Solitary iguanas at the top of the study area were observed feeding on the vines, but group foraging was never observed. The large aggregations at the bottom of Flamenco dispersed in the rainy season, when new leaves occurred in scattered areas throughout the island. Large congregations were again observed during the Spondias fruiting season.

Thus, with the exception of most large males, the iguanas moved over relatively large areas to follow seasonal patterns of food availability. A food-based territory is not theoretically feasible with such a pattern of resource distribution (Brown, 1964). In addition, the difficulty of surveillance in the densely vegetated habitat would increase the cost of year-round territoriality.

Avoidance behavior was more commonly observed than overt aggression. However, agonistic encounters did occur. The question of the function of aggression during the non-breeding season is a difficult one that may be elucidated by considering which individuals are avoided and/or challenged. Except during basking, smaller iguanas defended an individual distance (1.0 - 1.5 m) from others in the same size class. Although movements of large males overlapped spatially, temporal overlap appeared to be carefully regulated. Displays and perch sites communicated the large male's location, and possibly his status. Agonistic encounters were rare, but 1 battle proved to be rather revealing. A large male moved into a Cecropia that had been occupied by another large male for 3 weeks. More than 1 1/2 hours of challenge displays culminated in 2 pushing battles, after which the smaller resident retreated. The victor remained in the Cecropia for 2 days, and then returned to his usual Spondias tree, less than 50 m distance. Within a day, the previous resident returned to the Cecropia. Dominance relations among males may be established and maintained by such intermittent contact. By maintaining his status in a circumscribed area, the large male obtains priority of access to display posts, basking sites shared with females, and choice mating territory in November (see Chapter V). It is not clear why medium males remained in trees that contained large males. Both the Genipa and Sapium attracted large numbers of iguanas, presumably because of their food supplies. Perhaps it was more advantageous for these males to remain in an area with a rich food supply than to go elsewhere, even though this entailed avoiding a large male, and at times basking and feeding opportunistically. Remaining in a tree with a large male

might also place the medium male in a good position to take over the "sphere of influence" should the large male disappear. In addition, if familiarity breeds attractiveness, then remaining in a location that contains several females might increase the medium male's long-term prospects of obtaining a mate. Potential costs to the medium male include reduced growth rates, since avoiding the large male involved basking and feeding opportunistically.

Correlational studies suggest that home range size is influenced by energy requirements. Four interrelated factors are thought to affect home range size: metabolic rate, body weight, trophic level, and food distribution. McNab (1963) found that both basal metabolic rates and body weight are directly proportional to home range size in mammals, and concluded that home range size is determined by energy needs. In contrast, Schoener (1968) found that home range size among birds is proportional to body weight, but increases more rapidly than basal metabolic rate. Schoener suggested that the difference between birds and mammals could be explained if species were classified according to diet. Basal metabolic rates were higher in omnivorous than herbivorous birds. He argued that predators have larger home ranges than omnivores or herbivores of the same weight because of the relatively denser food of the latter.

Turner et al. (1969) pointed out that small sample sizes in the surveys of mammals and birds do not allow firm conclusions to be drawn regarding the influence of diet on activity range. Turner et al. reviewed home range size in 13 lizard species and found that, as in birds, a one-to-one relationship exists between body weight and home range

size, but home range size increases more rapidly than metabolic rates. Data on predatory and herbivorous lizards were too few to assess Schoener's hypotheses about diet and home range size. However, they did report that Dipsosaurus, a small herbivore, has about the same home range size relative to body weight as do insectivorous lizards. In view of this discussion, it is interesting to compare the home range size of Iguana iguana, a strict herbivore, with that predicted from the regression computed by Turner et al. The regression of home range (A) on body weight (W) showed that the relationship is best expressed by the following formula: $A = 171.4 W^{.95}$. This equation predicts that the home range size of an 1100 g lizard (a 30 cm SV iguana) should measure 13.3 ha, an area of approximately the same size as Flamenco, and 54.3 times the average home range size computed for female iguanas. This finding is in accordance with Schoener's (1968) prediction. Certainly female iguanas on Flamenco and elsewhere range over much larger areas during the nesting season (Montgomery et al., 1973), but this seasonal movement is not related to energy requirements. Iguanas on the mainland or on larger islands may move over larger areas to locate patchily distributed food resources. Whether or not home range size in Iguana iguana ever reaches or surpasses 13 ha cannot be answered with available data.

The regressions of lizard home range size and body weight did not differ significantly between males and females (Turner et al., 1969). Since overall energy requirements increase with body weight (Pough, 1973), if home range size is related to energy requirements, then among species in which sexual size dimorphism is pronounced, larger lizards should have larger home ranges than smaller lizards. Simon (1975) found that male

Sceloporus jarrovi maintained larger territories than females, although her study animals did not differ in size. She concluded that factors in addition to food availability may influence territory size. Males of many species have larger home ranges and/or territories than do smaller females, and social factors (mate acquisition) as well as food requirements are thought to contribute to differences between the sexes (Stamps, 1977; Schoener, 1977).

To my knowledge, it has never been demonstrated that the largest lizards in a population maintain the smallest home ranges as do the iguanas on Flamenco. This finding contradicts the postulated relationship between home range size and body size in lizards. The possible benefits to a large male of confining his movements to a limited area include priority of access to display posts, females, and a mating territory in November. One would not expect these factors to influence the movements of females and small and medium males. Access to males by females is not achieved by social status and territory establishment. By virtue of their size, small and medium males do not compete effectively with larger males. The island habitat may not permit dispersal by these males to less congested areas, but few benefits are likely to be reaped by adopting the "large male strategy." In short, the selective pressure for confined movements and maintenance of dominance status is different for large males and other members of the population. It may be advantageous for females and medium and small males to move through the home ranges of several large males. Familiarity with several large males established during the non-breeding season may decrease the time and energy a female must invest in selecting a mate in November.

A medium male might benefit from monitoring the activity of several large males if doing so increases the probability of establishing dominance in an abandoned home range (e.g., from the death or movement of a large male). The advantage of extensive movements for small males may be related to their role in the mating system. By virtue of their similarity to females, small males are able to invade mating territories and breed opportunistically (see Chapter V). If repeated contact increases the probability that a large male detects the sexual identity of a small male, and if individual recognition at some future date is possible, then it would be to the small male's advantage to avoid extended contact with large males. In addition, knowledge of the movements and activities of several large males, gained during the non-breeding season, might provide information on which the small male bases his "decision" of which territories to invade in December.

Presumably, the social environment of the iguanas on Flamenco influences the pattern of space usage to the extent that the usual relationship between home range size and body size in lizards is overshadowed. The effect of the social environment may not be large enough to mask interspecific differences in home range size, body size, and diet. However, these results suggest that social demands, as well as energy demands, should be considered in attempts to identify cause-effect relationships.

CHAPTER V

MATING SEASON ACTIVITY

Reproductive Phenology

The major physiological and behavioral changes between mid-October and late January are presented in Fig. 11. Testes growth begins in the last 2 weeks of October and increases at a steady rate until early November, at which time a plateau is reached. Follicular growth and yolk deposition also begin in mid-October, but growth is slow relative to that of the testes. The result is that males reach reproductive readiness before females.

Greater activity on the part of males in securing mates relative to that of females is expected in polygynous mating systems (Trivers, 1972). The depletion of fat stores by males in mid-December reflects the cost of this activity. The fat reserves of females decrease as ovarian weight increases, but fat reserves are not depleted until shortly before egg laying in February or March, reflecting the female's greater investment in gamete production (see Derickson, 1976, for a discussion of lipid utilization and reproductive activity in reptiles).

After the first week in November, variance in female ovarian weight is greater than variance in male testes weight. Part of the variation among females is related to size (Fitch and Henderson, 1977). Part of the scatter however, is attributable to a 2 - 3 week variation in reproductive development among females. Stigmata appear in the ovaries immediately prior to ovulation, and were first noticed in 1 or 2 females examined on 4 January. Stigmata were present in 3 of 4 females examined

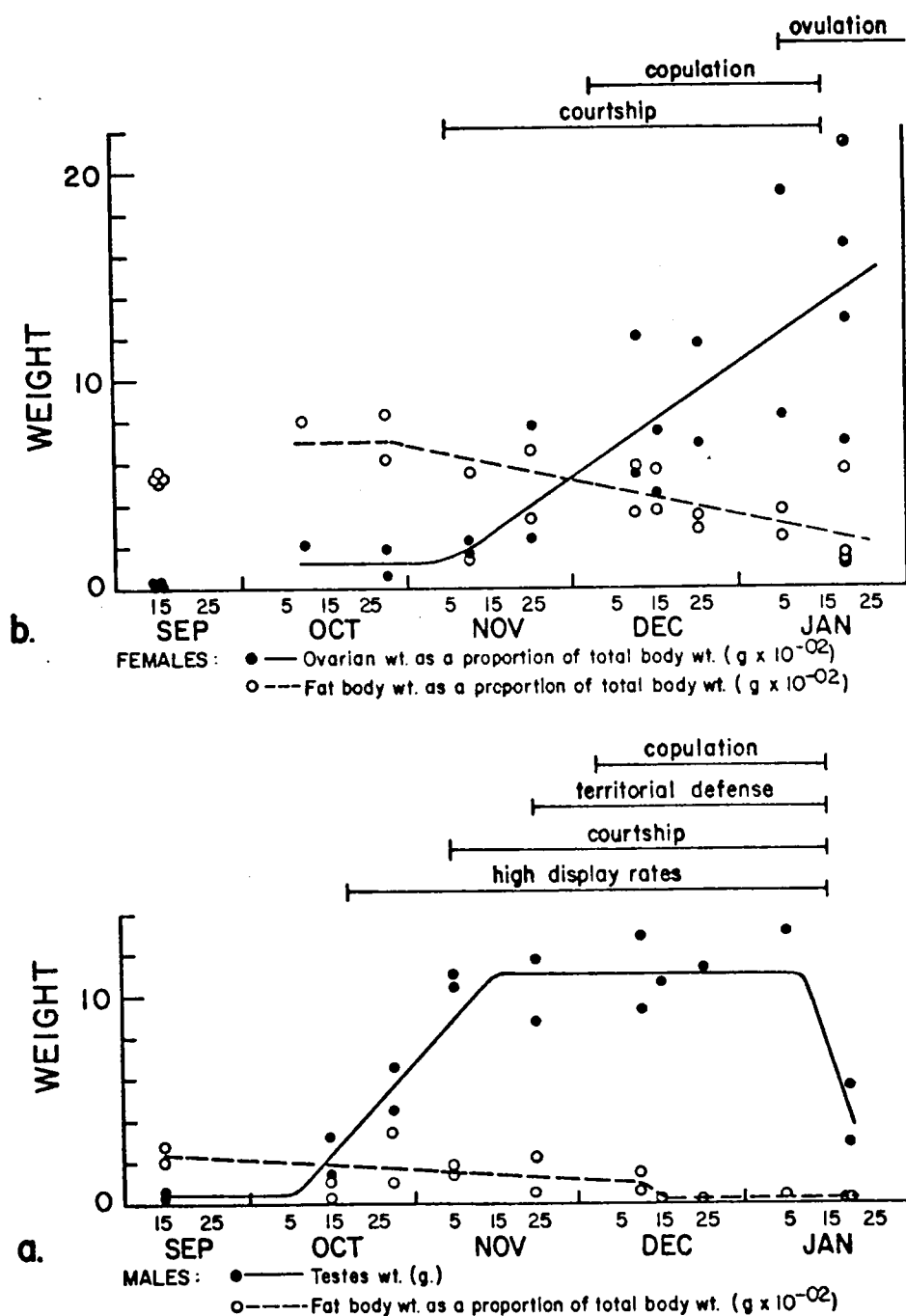


Figure 11. Changes in gonad and fat body weights from September through January, 1978 - 1979.

Curves were fitted by eye. Solid bars above each graph denote the period during which the specified behavior occurred. ● = female with oviducal egg.

on 20 January; the fourth female contained oviducal eggs. Ovulation begins in early January after ovarian follicles exceed 20 mm in diameter, and continues through January. In 1978 - 1979, ovulation began 5 weeks after the first observed copulation, and 3 - 4 weeks before the onset of nesting.

Ovulation and a sharp drop off in testes size in late January coincide with the breakdown of territories. Termination of female receptivity and reduced testosterone levels in males are the physiological events that underlie the change in social structure. However, the cues that elicit this rather rapid and drastic change are not obvious.

The general pattern of physiological and behavioral changes does not reflect the diversity in mating behavior observed in Iguana iguana. Due to the number of factors influencing mating behavior, I will first discuss environmental correlates of mating activity. Territory establishment by large males, interactions between females and territorial males, and the behavior of medium and small males will then be discussed.

Mating Behavior and Climatic Factors

The transition from the wet to the dry season in Panama typically occurs in late November or early December. The onset of the dry season is characterized by a sharp decrease in rainfall (Fig. 2, page 18) and a slight (1° C) increase in average daily temperature (Fig. 3, page 19). Although average daily temperature is slightly higher during the dry season, strong northerly winds exert a striking cooling effect. Data on relative humidity are not available; however, my perception of the weather in the dry season indicated that the relative humidity was much lower in the dry than in the wet season. One would expect strong winds to remove moisture.

In addition, one would expect strong winds to facilitate convective and evaporative heat loss from the iguanas and other animals. Thus, constraints imposed by physical factors on the daily activity of iguanas should be reduced during the dry season.

In 1977, rainfall began to decrease (Fig. 12) and the first northerly winds were recorded in late November. By the first week in December, northerly winds were strong and constant throughout the day. In 1978, although the increase in temperature occurred as in the previous year, rainfall was greater in the first 2 weeks of December than in any bi-weekly period in October or November. Although wind velocity was not recorded, the difference between the 2 years was obvious. Wind intensity and constancy was reduced in 1978. The first strong breeze was recorded on December 26, 1978. After this date, strong winds occurred on an irregular basis, and never continued for an entire day. Higher relative humidity than the previous year was associated with the greater rainfall and decreased wind. Again, data are not available, but my experience in the field indicated a striking difference between the 2 years.

The contrast in courtship activity observed in the 2 seasons may be related to the variance in weather conditions. Courtship occurs in the mating territory, which is an exposed tree that may be leafless (see next section). During extended courtship, the female retreats as the male approaches, and thus the pair moves throughout the tree, remaining exposed to the sun for long periods of time. Courtship begins in early November, but in 1977 was most intense in December. Male-female interactions were significantly more frequent in the 1977 than the 1978 mating season. The median number of courship bouts observed per 15 min

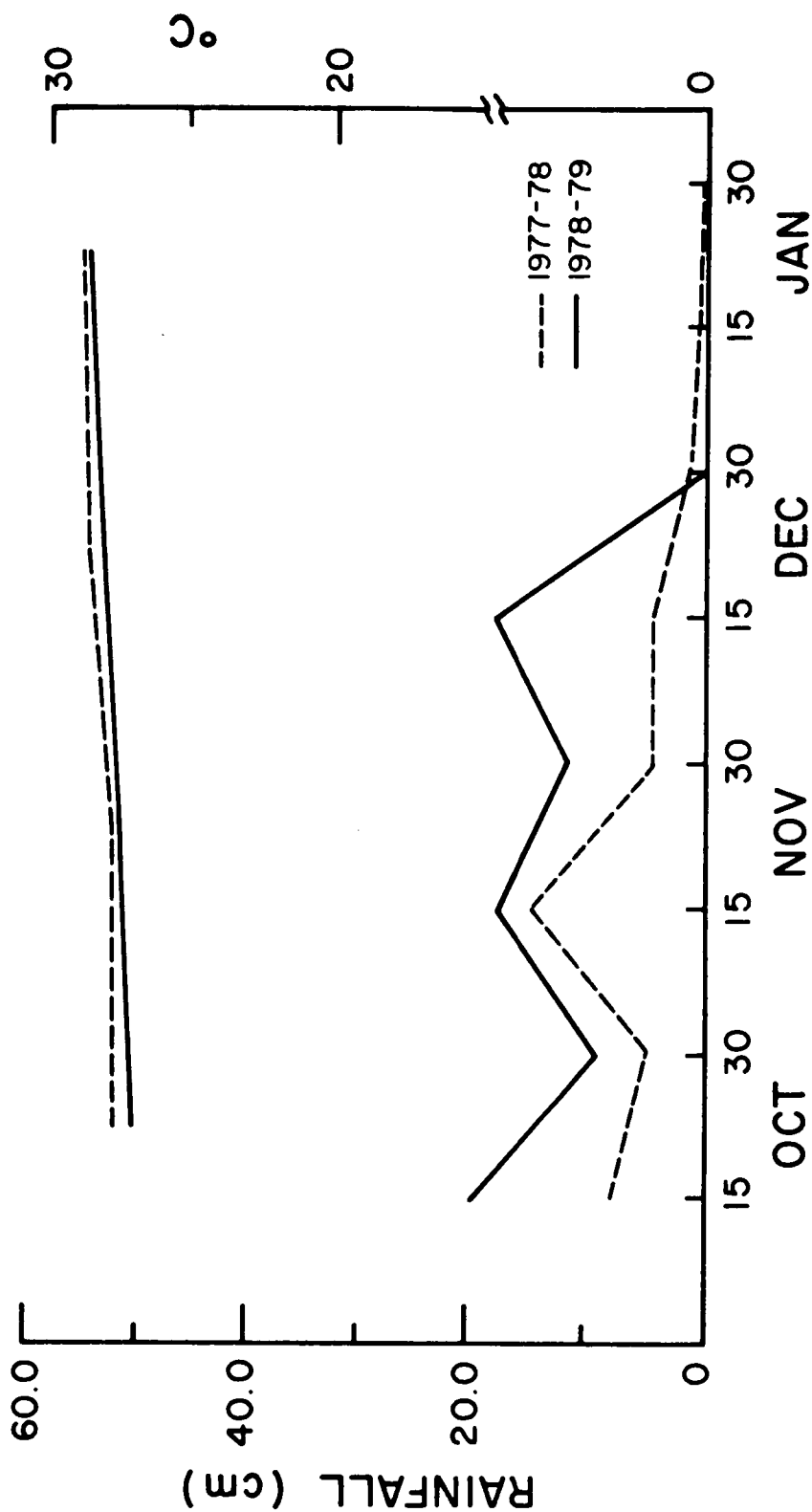


Figure 12. Bottom graph: Total bi-weekly rainfall, October through January. Top graph: Average monthly temperatures, October through January.

Solid lines are 1977 - 1978; dashed lines are 1978 - 1979.

interval was 1.7 in the 1977 mating season and .7 in the 1978 mating season ($\chi^2 = 20$, $df = 3$, $p < .001$, Median test; Siegel, 1956). Courtship bouts occurred infrequently throughout the day in 1978. In 1977, daily activity followed the same general pattern observed in the non-breeding season, but much of the mid-morning and mid- to late afternoon was spent in courtship (Fig. 13). Presumably, weather conditions in 1977 were more conducive to sustained activity in exposed locations than in 1978.

Differences in observational method may account for part of the differences in activity observed in the 2 years. In 1977, breeding groups were selected for observation on the basis of visibility and, in part, on the intensity of breeding activity. More hours were spent observing highly active groups than less active groups. In 1978, observations were systematically rotated among the visible groups in the study area, irrespective of courtship intensity. However, 2 observations suggest that procedural differences had minimal influence. First, activity levels were higher in October and November, 1977, than in the same months of 1978. These activity levels are inversely related to amount of rainfall (Fig. 6, page 44, and Fig. 12). Systematic observations were made during these months in both years. Second, informal observations made while walking through the study area indicated a strong difference in activity level between the 2 years. The 1977 mating season was marked by almost continual activity; several males could be observed courting, displaying or patrolling at any time of the day. In contrast long periods of inactivity through the study area characterized the 1978 mating season.

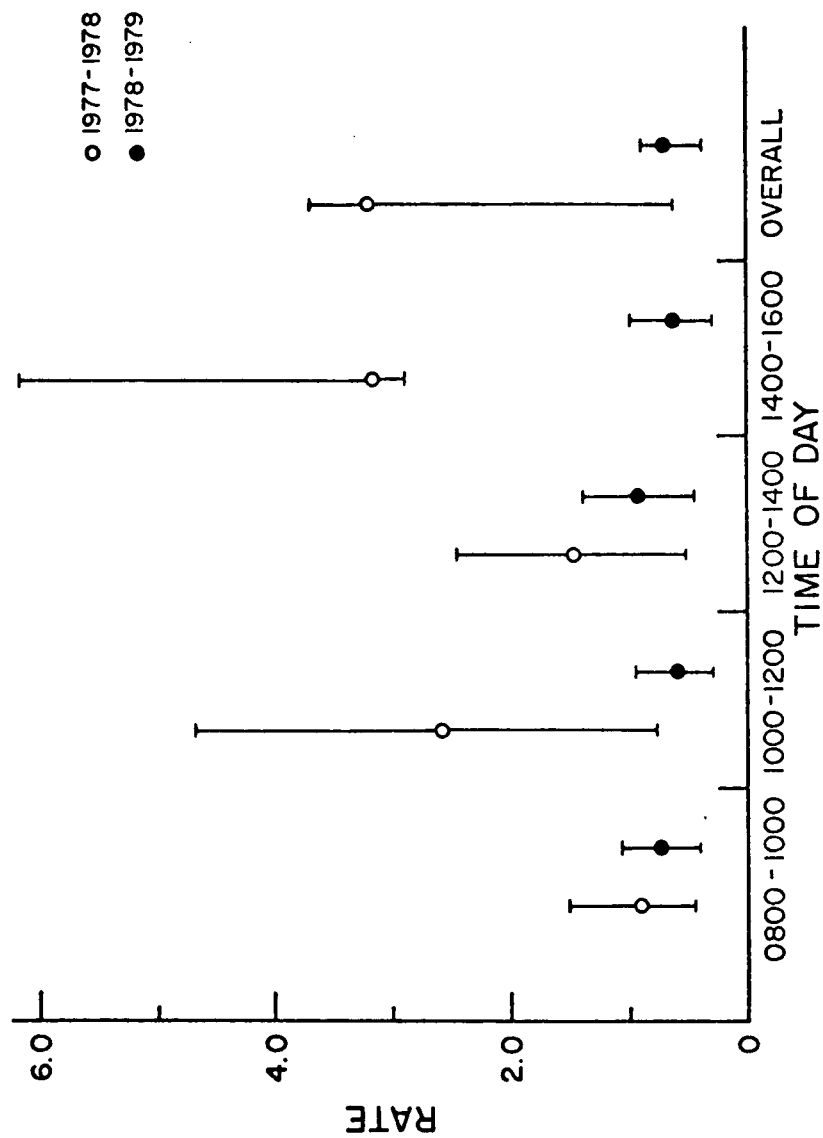


Figure 13. Median number of courtship bouts observed per 15 min interval in December and January, 1977 - 1978 (162 intervals; open circles) and 1978 - 1979 (117 intervals; closed circles).

Vertical bars indicate the interquartile range.

Territory Establishment

Increasing display rates by large males, rather than an increase in agonistic encounters, marked the onset of breeding activity. Only 2 agonistic encounters between large males were observed at this time. Large males tended to be well-spaced and conspicuous at all times. Display rates increased in mid-October, and were maintained at a high level till late January. Significant differences in display rates between months can be determined by inspection of Fig. 14. The vertical lines represent $\pm \text{s.d.} \times \sqrt{2/N}$, where N equals the number of observation intervals. Non-overlapping lines indicate a significant difference ($p = .05$) between any 2 pairs (see Burghardt, 1969). Significant increases in display rates were observed between October and November and other months during the non-breeding season, and between October and November, and December and January, when mating activity is most intense.

Most large males had established territories by later November. Medium males were no longer observed in the same tree with large males. Territorial males alternated periods of rest with display bouts, courtship bouts, and territorial patrols. Patrolling consisted of a series of short perch changes through the tree, each perch change being followed by a signature bob (described in Chapter VI). After late November, large males were rarely observed to feed. By late December, many of them appeared to be emaciated.

Observations in 1977 suggested that large conspicuous trees were preferred mating territories. In order to assess territory characteristics, the following measurements were made on all trees ($N = 76$) of adequate size to be used by adult iguanas in a .7 ha area: diameter at breast

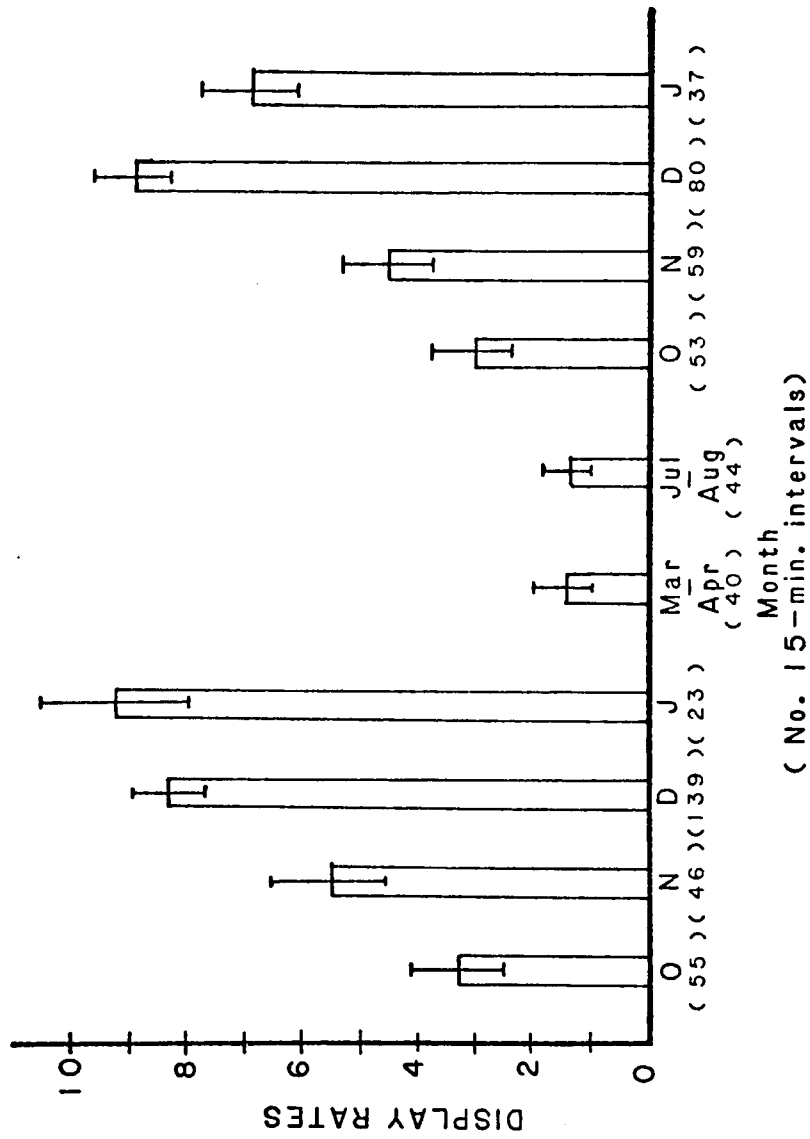


Figure 14. Number of headbob displays observed per 15 min observation interval. Large males only, 1977 - 1979. Vertical lines represent $\pm$ s.d. $\times \sqrt{2/N}$, where N = number of intervals. See text for explanation.

height (DBH), estimated height, estimated canopy volume, estimated percent canopy interlock with other trees, and estimated percent vine cover. Significant differences between trees that were used as territories in at least 1 of 2 seasons ($N = 9$) and those that were not were found for only 2 of the variables, DBH ($t = 6.55$, $df = 74$, $p < .001$) and canopy volume ($t = 4.04$, $df = 74$, $p < .001$). Due to different growth patterns, tall trees may have small canopies, and trees with large canopies may be relatively short. Trees used as territories tended to be taller ($\bar{X} = 17.0$, $s.d. = 3.28$) than other trees ($\bar{X} = 10.95$, $s.d. = 5.26$) but the difference was not significant. Tree species was also recorded. There was no apparent tendency for certain tree species to be preferred over others.

In other parts of the study area that contained fewer trees, the canopies of mating territories interlocked little or not at all with neighboring trees. Mating territories, then, provided conspicuous perches, a good vantage point from which to survey the surrounding area, and those trees with few access routes (little canopy interlock) were easily defended from intruding males. Food was not an essential component of a mating territory. Of 19 territories observed closely in both years, 6 did not contain food. The average of daily recordings of the number of females per male were compared for territories with and without food. The mean number of females per male in trees with food was 2.5, and 2.7 in trees without food. Males in the latter were no less successful in attracting females. Females in territories lacking food moved singly or in groups to nearby areas to feed in late morning. Males followed receptive females to feeding areas and stayed within a

few meters of the female(s), displaying frequently. Territorial males were rarely observed to feed during these excursions.

Mate Acquisition

Beginning in early November, large males were regularly observed with 1 or more females. At this time, males moved to trees that contained females, and females visited displaying males. It would be misleading to say either that males responded to the presence of females, or that females responded to the presence of males. Rather, both situations fit the patterns of movement in November. Pair formation occurred in 1 of (at least) 3 ways.

1. Males moved into trees already containing females, and established territories there. A solitary female was joined by a male in late October, 1978. The 2 remained together for the duration of the breeding period and were observed copulating on 20 December. A second female resided in the territory from early December until the end of the breeding period.

2. Males left their territories to court females in nearby trees. One female was courted by 2 different males for the last 2 weeks in November, 1978. At the end of November, she moved to the territory of 1 of these males, remained there throughout the breeding period, and copulated with him at least 3 times between 29 December and 11 January.

3. Individual females visited several males before taking up residence in a territory. Two females that were observed closely, 1 in 1977, the other in 1978, visited and were courted by 3 different males. The female observed in 1977 was courted by each male at least

twice. She moved into the territory of 1 of these on 13 December, and copulated at least twice with him between 3 January and 18 January. The second female copulated with the territorial male at least twice between 26 December and 11 January, 3 weeks after having settled into the territory.

These and other observations indicate that individual females were courted for at least 4 weeks by 1 or several males before becoming receptive (i.e., copulating), and females were receptive for at least 15 days, possibly longer.

Courtship and Copulation

In the most common courtship sequence (recorded as 1 courtship bout), the male approached the female from behind, performing a shudder bob (rapid, low amplitude vertical head movements) before, during or after the approach. The female then moved the posterior two-thirds of her tail to one side (tail arch). After the tail arch, the male stopped and performed a signature bob. This sequence was repeated from 1 to more than a dozen times, with pauses between each approach. Females did not tail arch when the courting pair were face to face. Rather, the female remained prone while the male repeatedly shuddered and bobbed before her. Although receptive females did not always headbob in response to the male, it appeared that receptive females were more likely than non-receptive females to perform shudder bobs and signature bobs in response to the male's shudder approach. Receptive females neither retreated nor tail arched as the male approached. The male moved up on the female from behind and secured a neck grip. At this point, the pair

sometimes walked slowly together, possibly a maneuver to find a secure position on what often appeared to be precarious perches. The male then twisted his tail under that of the female, and inserted a hemipenes. Copulation lasted from 2.5 to 12 min ($\bar{X} = 7.4$, s.d. = 2.6, $N = 26$). Males were never observed to mate more than once per day. Individual females were observed copulating from 1 to 5 times each during the receptive period, usually with the same male.

As noted previously, a minimum of 4 weeks of courtship preceded copulation. At least the last 2 weeks of the courtship period were spent with the male with whom the female mated. After copulating 2 or 3 times, the amount of courtship immediately prior to copulation decreased dramatically. Interactions between 1 pair observed in 1977 illustrate this point (Fig. 15). The proportion of 15 min observation intervals prior to copulation in which courtship occurred decreased from 7 December, when the first mating was observed, until 12 December, the last day this pair was observed. The mean number of courtship bouts in those intervals that courtship did occur follows a similar trend.

Each mating territory contained from 1 to 4 females. In addition to display, territorial patrol and defense, courtship made a significant demand on the male's time. It is therefore of interest to know how a male apportioned his time among the resident females. Data from 2 territories in which more or less continuous observations were available, and that contained at least 2 females during observation periods, are presented in Fig. 16. It can be seen that the males engaged in more courtship bouts with non-receptive females than receptive females. Thus, it appears that the amount of time that the territorial male spent with

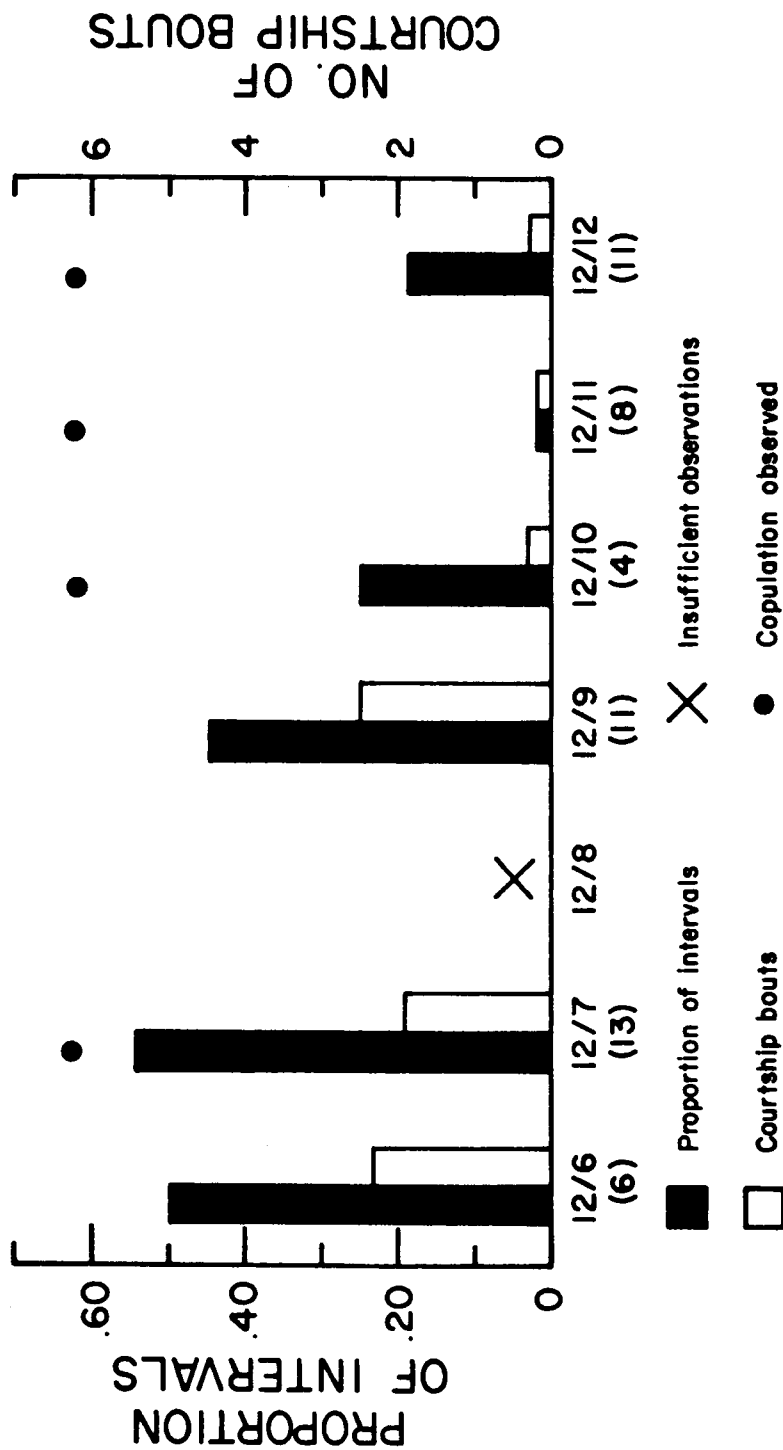


Figure 15. Mean number of courtship bouts and proportion of 15 min observation intervals in which courtship occurred.

Dot above bars indicates that a copulation was observed on that date. Data from a male-female pair observed in December, 1977. Number of intervals are in parentheses below date.

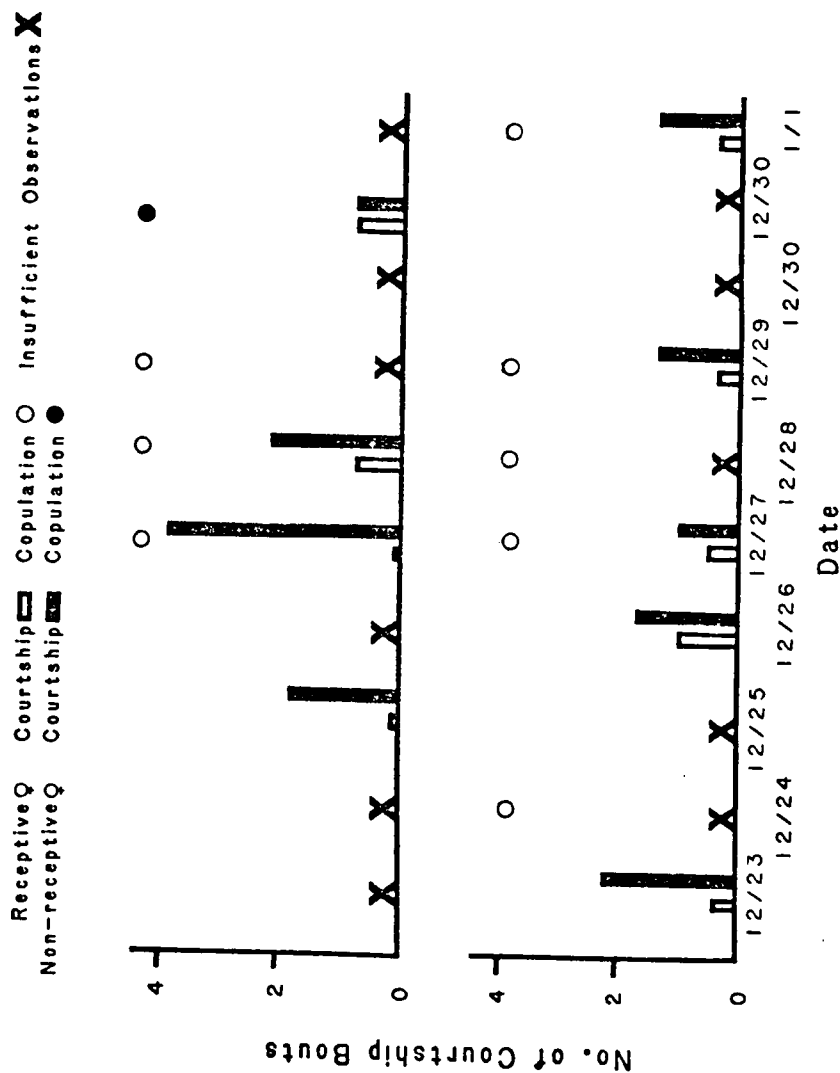


Figure 16. Mean number of courtship bouts per 15 min observation interval observed between a territorial male and each of 2 females.

The 2 graphs represent data from 2 territories (top male is Y-Shoulder, bottom male is Pig) observed in 1977. Circle above bars indicates copulation on that date.

each female depended in part on her reproductive state. Periods of receptivity among females in a single territory did overlap. In these cases, males courted each female daily, but mated with each on alternate days.

Although the pattern described above was typical, males varied in their courtship behavior. One male in particular (Macho) never persisted in courting any 1 female for very long. Rather than forming a "bond" with each female in succession, he alternated vigorous courtship bouts among his 4 females. Table 4 compares the number of matings per observation hour for the 2 males whose courtship patterns are presented in Fig. 16 (Pig and Y-Shoulder) and Macho. Presumably, Macho inseminated each resident female before the mating season ended, but he probably did not copulate as many times with each resident female as did Pig and Y-Shoulder with females in their territories.

The Behavior of Medium Males

One 36 cm male in 1978 did show intensified color, displayed, and patrolled a tree that had been a territory in 1977. However, other iguanas were never observed in the tree with him. Another 36 cm male also exhibited territorial behavior, and was observed to copulate with 2 females in his territory. All other medium males observed in both years remained on the periphery of a mating territory for periods of time varying from 1 week to the duration of the breeding period. They were rarely observed displaying, feeding, and were never observed patrolling. If a medium male ventured close to a territory, the large male displayed, then chased the medium male if the latter did not retreat. Peripheral

Table 4. Records of no. of females in territory and no. of copulations from 3 territories observed in 1977.

Summary of Observations	Male		
	Pig	Y-Shoulder	Macho
Hours Observed ¹	20	9	11
Period	12/6-1/3	12/23-12/31	12/12-1/9
$\bar{X}$ no. Females Observed in Tree	3	2	3
No. of Females Mated	4	2	1
No. of Copulations per Observation Hour	.70	.44	.09

¹Since 24 of 25 observed copulations occurred between 1000 and 1500 hours, only observations made during those hours are included.

males did court females moving into and out of territory. However, copulations never resulted from the observed courtship bouts.

In order to determine whether a medium male would take over a vacated territory, a large male (38 cm) was removed from his tree on 15 December, 1978. Within 2 days, the medium male (34 cm) that had been observed in the area for 2 weeks prior to the manipulation had moved into the territory, displayed from the post used by the previous owner, and patrolled the tree daily. However, the medium male was never observed with either of the 2 females that had accompanied the previous resident. After 2 weeks the large male was released in the area. He regained his territory within 24 hours, and the medium male was not seen again. One of the females seen in this tree before the manipulation was observed basking with the large male after his return.

The Behavior of Small Males

Because of their "discrete" habits and similarity to females, small males could move into and out of territories without being challenged. Some small males remained in territories for just a few hours, others for several days at a time.

Small males entered territories at a distance from, but within sight of, a large male without eliciting a response from the large male. They then typically moved to a clump of leaves at the end of a branch and remained motionless. Small males did not, to my knowledge, enter a leafless tree while the territory owner was present. If a patrolling male moved to within 2 m of a small male, the small male immediately dropped from the tree. However, if a small male was caught unaware by

the patrolling male and the owner approached within 1 m, he immediately lunged and head-butted the interloper from the tree.

Small males attempted to copulate with females in the territory when the territorial male was occupied elsewhere. In such attempts, the small male ran toward the female, leapt on her back, and tried to secure a bite, presumably on the neck, usually wherever he landed. In all 15 attempts observed, the female thrashed violently, threatened with mouth open, turned toward and attempted to bit her suitor. Large males were nearby and rushed to the female's defense in 5 of 15 observed attacks. Of the remaining 10, small males copulated successfully 3 times.

Size, Status and Mating Success

A total of 69 attempted copulations (i.e., male secured bit on neck or dorsum) were observed in both years. I assume that these observations are an adequate sample of copulatory activity in the study area for the following reasons: 1) most observed copulation attempts occurred on conspicuous perches, 2) copulations that occurred in less noticeable locations were easily sited because of the conspicuous nature of the copulatory posture, 3) the struggle that accompanied copulation attempts by small males was quite conspicuous, 4) most copulations exceeded 5 min in duration (see "Courtship and Copulation"), 5) activity in at least 2 territories could be monitored from any observation post in the study area.

Small males comprise 35% of the male population (Fig. 17) and performed 6% of observed copulations. Medium males, 27% of total males, performed 4% of the observed copulations, and large males, 38% of total

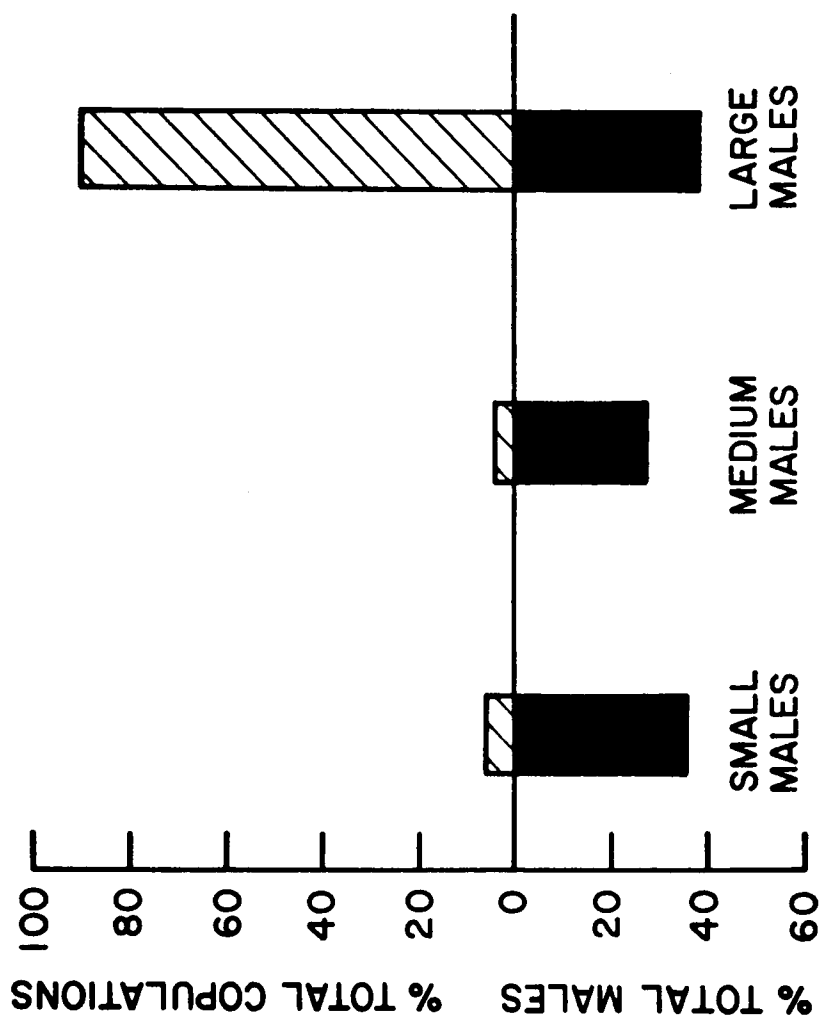


Figure 17. Top: percentage of observed successful copulations that were performed by small, medium and large males. Bottom: percentage of total males on Flamenco that were small, medium and large.

males, performed 90% of the observed copulations. The distribution of observed unsuccessful and successful copulation attempts among males in the 3 size classes differed significantly from the expected distribution (Table 5). This variance in male mating success is due in part to interference by territorial males, the reaction of females to small males, and differential access to females. Small males were significantly more likely to attempt copulation than were medium males (Kolmogorov-Smirnov test, $p < .01$). It appears that this difference in copulatory encounters is due to a higher frequency of unsuccessful encounters by small males, rather than a difference in frequency of successful encounters (Table 5). It should be noted, however, that the medium male that held a territory in 1978 performed both copulations observed for medium males.

Discussion

Large males. Large males are distinguished from medium and small males, and all females, by their relatively confined movements during the nonbreeding season. A large male's home range includes at least 1 Spondias tree, 1 other important seasonal food source, and a year-round supply of food (various vines). By virtue of their age, size and social rank, large males are able to establish themselves in an area where their own foraging efficiency can be optimized, and where a supply of females passing through the area is assured. In addition, a large male's home range contains 1 or more suitable mating trees. Since virtually all courtship and copulation occur in a territory, territory ownership is critical to a male's reproductive success.

Table 5. Observed (O) and expected (E) number of attempted and successful copulations.*

Observations		Males			P
		Small	Medium	Large	
Unsuccessful Attempts	O	12	0	8	<.01
	E	7	5.4	7.6	
Successful Attempts	O	3	2	44	<.01
	E	17.2	13.2	18.6	
Total Attempts	O	15	2	52	<.01
	E	24.2	18.6	26.2	

*Expected values are based on percent total males in each size class. Probability values (P) are results of Kolmogorov-Smirnov tests.

Confined movements, plus maintenance and communication of dominance status (selecting conspicuous perches, high display rates) outside the breeding season define the large male's long-term strategy. This strategy allows him: 1) close contact with females passing through his area (possibly important in mate acquisition at a later date), 2) insures his access to a mating territory in November, and 3) reduces the frequency of encounters and dominance struggles with other large males (by advertising one's location, mutual avoidance is facilitated). It may be of particular importance to a large, herbivorous lizard to avoid aggressive encounters and thereby minimize energy expenditures (see Dugan and Wiewandt, in press).

During the breeding season, large males defend not only the territory but also females resident within the territory. Territorial males were observed to defend females from attempted copulations by small males, to follow receptive females from the territory to feed, and to attempt to herd females from territories that were invaded by larger males. The time lag between copulation and ovulation, and the fact that female iguanas mate several times, suggest that sperm competition may occur in this species (Dugan and Wiewandt, in press). If so, the direct defense of females may be interpreted as post-copulatory guarding (see Parker, 1974).

Medium males. Because of their interactions with large males, medium males cannot move into territories and mate opportunistically as do small males. Nor have medium males achieved the size and status that is related to large male success. By remaining on the boundaries of

mating territories, medium males could monitor the activity of the breeding group. Observations indicated that medium males were occasionally successful in territorial establishment, and did take over vacated territories. However, this strategy brings minimal returns because: 1) the rate of the territory turn-over is quite low, and 2) females may not remain in territories that medium males do take over. In addition, copulatory attempts by medium males appear to be less frequent than such attempts by small and large males. Thus, mating success is relatively low for males in this size class.

Females did move close to peripheral males, and medium males did court females outside territories. Why did medium males not try to improve their mating success by copulating "by force" as did small males? At least 2 explanations are possible. 1) The risk of attack from a large male did not outweigh the benefits to be gained from such attempts. This explanation is only a partial one, since large males were never observed to interrupt courtship bouts that occurred between medium males and females outside territories; attacks from a large male would only be likely if a large male followed a female from the territory. 2) A medium male may gain a territory within the lifetime of those females with whom he interacts, and it may not be in the medium male's interest to "alienate" females. Learning influences long-term foraging movements in Cyclura carinata, a related iguanine (see Auffenberg, in press), and it seems likely that experience also plays a role in social relationships among lizards (Burghardt, 1977a, reviewed learning in reptiles).

Small males. The interactions observed between large and small males indicate that a small male was tolerated in the territory only until his sexual identity was discovered by the territory owner. Large males did not appear to recognize small males as males from a distance. Close range recognition may have been based on subtle visual cues, or a difference in responses between small males and females. Femoral pore secretions may have also provided chemical cues regarding sexual identity. Chemical cues communicate sexual identity in Sceloporus (Duvall, 1979), and although the function of the femoral pores is unknown, it has been suggested that they do function in chemical communication (see Cole, 1966; Wiewandt, 1977). The small male's strategy, then, involves not only morphological similarity to females, but also behavioral patterns that permit him to avoid large males, and thus remain in the territory and breed opportunistically.

The contribution of such a strategy to a male's fitness may be of particular importance in a long-lived species such as Iguana iguana. Observations of 2 males dating from July, 1976, indicate that a male does not reach 37 cm SV before its 7th year, and that large males may maintain a "sphere of influence" for at least 2 1/2 years. The low mating success in medium males, the number of years between reaching reproductive maturity and achieving large male status, and the possibility of death during the non-reproductive years, provide an explanation for why small male strategy occurs in green iguanas. However, the mechanisms underlying small male mating behavior are not known. The differences in the mating behavior of small, medium, and large males may be due to ontogenetic changes. It would certainly be to a male's advantage to mate as frequently as

possible in early adulthood. Alternatively, certain males may stop growing at an early age, in which case small male behavior would be related to size, but would be independent of age. Such genetically determined mating strategies have been reported in other vertebrates (e.g., red deer, Cervus elaphus--Darling, 1937; ruffs, Philomachus pugnax--Hogan-Warburg, 1966; Van Rhijn, 1973). Unfortunately, sufficient growth data to assess the latter hypothesis were not available.

Female breeding strategies. The pattern of female movements and the nature of interactions observed between small males and females indicate that female iguanas are selective in mate acquisition. Females mate preferentially with large males. The factor(s) influencing female mate preferences have not been identified; however, a complex of attributes probably convey the large male's suitability as a mate. His large size reflects his age, and therefore his ability to survive to old age. His size also gives him a competitive advantage over other males. Territory ownership not only reflects this superiority, but also offers the female a place to court and mate with minimal disturbance. In short, a male's age, size and territory may all communicate his genetic quality (see Howard, 1978). However, since a female's home range overlaps that of a number of large males, she encounters a number of suitable mates, but usually mates with only 1. Courtship behavior may provide additional evidence of a male's fitness as a mate (see "The Role of Courtship").

Females violently protested all copulation attempts by small males, but only rarely protested attempts by large males. Unlike large males, small males have neither proved their ability to survive to an

old age nor their ability to hold a mating territory. Nor do they provide the morphological and behavioral (courtship) stimuli that large males provide. Cox and LeBoeuf (1977) suggested that female protest during mounts is a mechanism of female mate choice. The female elephant seal's violent reaction to being mounted attracts other males in the vicinity, male competition for the female ensues, and the female thereby maximizes the probability of mating with a high-ranking male. Similarly, female iguanas protest mounts by small males and the territorial male interrupts the copulation attempt if he is nearby. If the large male is not in the vicinity (as is usually the case), the small male's ability to hold on to the female during the struggle may be an additional "test" to which small males are subjected. If the ability to capture and hold on to females can be passed on to the offspring, then it may be to the female's advantage to copulate with a persistent small male.

The role of courtship. Courtship may function in species and sex identification (e.g., Morris, 1956). Ctenosaura similis is sympatric with Iguana iguana over much of its range, and may share the iguana's arboreal habitat (personal observation). However, the 2 species differ morphologically have very different headbob displays (pers. obs.; Carpenter, in press). Both characteristics may be cues for species recognition (e.g., Jenssen, 1970b, 1977; Williams and Rand, 1977; Rand and Williams, 1970). It is doubtful, therefore, that proper species identification requires such a lengthy courtship period. The large male's rapid response to intruding males argues against the need for a long courtship period to insure proper sex identification.

Courtship prior to pair formation may provide a female with a portion of the information on which she bases her choice of mate. In November, before stable relationships are established, male-female encounter rates are high. Females are exposed to the display and courtship of several males, either because they visit males, males visit them, or because displaying males are conspicuous. The components of male display affect female mate selection in other iguanid lizards. Females given a choice between males performing either normal bob patterns or altered bob patterns showed significant preferences for "normal" males (Anolis nebulosus, Jensen, 1970b; A. carolinensis, Crews, 1975a). Male display rates have been shown to be an important correlate of male mating success in ruffs (Shepard, 1975) and of male sexual competence (number of spermatophores produced) in newts (Halliday, 1976).

The long courtship period may be important in facilitating receptivity in female iguanas. This has been shown to be the case in Anolis carolinensis (Crews, 1974). That the amount of courtship was reduced after females became receptive suggests that this same phenomenon may occur in Iguana iguana. If so, then "low" receptivity might be advantageous to a female in that a lengthy courtship period will give her the opportunity to review several males before being inseminated. Not all mating territories contain food, and males do not participate in egg laying. Aside from providing a location within which to mate, the male's primary contribution to the production of offspring is his genes. The male's genetic quality should be an important consideration in mate selection by females. Since male iguanas have minimal control (either direct or indirect, through resource control) over females, the importance

of courtship in assessing the male's genetic quality can be expected to increase (see Williams, 1966; Trivers, 1972). A similar function has been suggested for extended courtship among grouse (Wiley, 1974), the iguanine lizard Conolophus subcristatus (Werner, in press), and various other species (see review in Trivers, 1972).

After a female has established residence in a male's territory, the pair engages in courtship for at least 2 weeks before copulating. Extended precopulatory interactions after mate selection has presumably occurred may cement bonds of familiarity between mates, a mechanism that may be advantageous to both males and females. The establishment of such a bond should benefit the female if continuous attention from a male confirms her earlier choice of a fit mate. This would decrease the likelihood that a female will mate with a male who pretends to be highly fit but is not (Fisher, 1958; Williams, 1966). If bonds of familiarity are a prerequisite to copulation, this should benefit the male if the probability of desertion by a receptive female is reduced. Only 1 female iguana in both breeding periods was observed to switch mates after becoming receptive. Thus, desertion appears to be uncommon in receptive females. If a bond of familiarity must be established before copulation occurs, and if the receptive period is the optimum time for insemination, then it would be disadvantageous for a female that is receptive or near receptivity to seek another partner. Guarding against female desertion should be particularly important in species where females mate several times during a single breeding period, and where sperm competition may occur (Parker, 1974) as has been suggested for Iguana iguana (Dugan and Wiewandt, in press).

The cost of courtship persistence to the male, in terms of time that could be spent obtaining other mates, depends on the number of other receptive females available to him. The breeding synchrony among females in part determines the degree of polygyny (Elmen and Oring, 1977; Trivers, 1972). If courtship and copulation time is large relative to the total amount of time that mates are available, then the potential for monopolizing several females is low. The moderate asynchrony among female iguanas permits males successful in territorial establishment to mate with several females. The temporary consort relationships between a male and several successive females reflect this asynchrony. Whether males contribute to asynchrony by their selective attention to certain females, or whether females vary in their responsiveness to stimuli that induce receptivity and males consort more with females soon to be receptive, is unclear. However, in view of the length of the courtship period prior to copulation, staggered periods of receptivity are of benefit to males in that several mates can be obtained in the 6 week breeding period. Females mate preferentially with large males who comprise approximately 38% of the male population. Staggered breeding should be of benefit to females if it allows several females to have access to the same "preferred" male. The degree of asynchrony should primarily be constrained by the duration of the optimal nesting and hatching period, a source of potential cost to both males and females.

The relationship observed between courtship intensity and female receptivity suggests that a successful male should optimize the amount of time spent courting each female, depending on her reproductive state. This prediction is borne out by the comparison of 3 males in Table 4

(page 83). Pig and Y-Shoulder courted non-receptive females more than receptive females. They were observed to copulate more often than Macho, whose courtship bouts were briefer and more evenly distributed among his females on a daily basis. The female with whom Macho was observed mating had copulated 5 times with Pig, and once with a small male. Since sperm competition is a possibility in Iguana iguana (Dugan and Wiewandt, in press), the number of times a male copulates with each female, and when he copulates with her, may be important components of his reproductive success.

If a long period of courtship and frequent copulation are important to females, one might expect several female residents to compete for the male's attention. Females were observed to interrupt courting pairs, and dominance relationship among females were observed in some territories. Unfortunately, the data are too few to determine whether or not female aggression is related to competition for males.

CHAPTER VI

THE USE OF THE HEADBOB DISPLAYS

Prior to 1960, few researchers investigated the stereotypy of the Fixed Action Pattern (Barlow, 1968). Recently, the variability of these behavioral patterns has been examined more closely (e.g., Schleidt, 1970). The realization that FAP's can be quite variable led Barlow (1968) to propose that the term "Modal Action Pattern" (MAP) replace the term "Fixed Action Pattern." In the past 2 decades, many researchers have focused on quantifying the variability of MAP's in an attempt to understand the functions of relative differences in variability (e.g., Cullen, 1966; Marler, 1973; Wiley, 1973). The objective of the present investigation was to apply this approach in a field study of the headbob displays of Iguana iguana.

Three general approaches have been employed to investigate the variability in form and the communicative function of iguanid headbob displays. Investigators using what I term the releaser approach ask the questions: "What stimuli release the display?" and "What responses does the display release from a recipient?" (e.g., Hunsaker, 1962; Jenssen, 1970b; Stamps and Barlow, 1973; Crews, 1975a; Hover and Jenssen, 1976). The second approach looks at display variability. Comparative studies of display variability have provided evidence for character displacement among closely related species (e.g., Anolis sp.--Ruibal, 1967), the evolutionary development of display patterns within genera (Uta--Ferguson, 1971), and the divergence of display pattern in different populations

of the same species (e.g., A. nebulosus--Jenssen, 1971; U. stansburiana--Ferguson, 1971). Investigations of individual variability indicate that headbob displays may communicate individual identity in some species (e.g., A. carolinensis--Crews, 1975b; A. aeneus--Stamps and Barlow, 1973; A. nebulosus--Jenssen, 1971; Sauromalus obesus--Berry, 1974).

The third approach involves field observation to determine in what contexts the various displays occur (e.g., Ruby, 1977; Iverson, 1979; Wiewandt, 1977; Berry, 1974). The 3 approaches must be integrated to address questions concerning the biological role of the display and the adaptive significance of its form and variation. The specific objectives of this investigation were: 1) to describe the (headbob) display repertoire of Iguana iguana, 2) to quantify the variability of each display, 3) to identify the situations in which the displays are performed in the field, and 4) to relate the variation in form and context of each display to the iguana's natural history.

Many researchers in communication agree that before a behavioral pattern can be judged to serve a communicative function, it should be demonstrated that the performance of the behavior changes the probability of behavior in a recipient (e.g., Smith, 1968, 1977; Wilson, 1975). Iguanid headbobs are common during aggressive or courtship interactions, and during pauses in locomotion while moving through the home range or territory. Neither the recipient, nor the recipient's response, are always obvious in the latter case. However, a communicative function has been suggested in some iguanids studied (e.g., Hunsaker, 1962; Hover and Jenssen, 1976; Jenssen, 1970b; Cooper, 1972, cited in Ferguson, 1977; Ruby, 1977). Although this investigation is restricted to the

analysis of display form and contextual use, I assume that as inferred for other iguanids (see Ferguson, 1977), the headbob displays of the green iguana may serve a communicative function.

Methods

Carpenter and Grubitz (1961) introduced the display-action-pattern (DAP) graph. DAP graphs are generated from a frame-by-frame analysis of filmed headbobs. The head position in each frame is plotted on graph paper; I used the tip of the snout as the reference point for head position. Time in seconds is plotted on the X-axis. The Y-axis represents the amplitude of each vertical head movement.

All analyzed film was shot in the field at 18 fps. Camera speed was calibrated by filming a running stopwatch. The number of frames per second was counted in 10 randomly selected segments of the footage (15 m). In 8 of the 10 segments, camera speed was 18 fps; the camera ran at 17 and 19 fps in the remaining 2. This source of measurement error was considered to be acceptable. Although displays were given by all animals, large males displayed much more frequently than other members of the population. Thus, this analysis is based on observations of large males only. Displays were filmed between October and January, a period during which display rates are high (Fig. 14, page 75).

Since camera-to-subject distance varied, it was not possible to measure absolute amplitude. Therefore, a measure of relative amplitude was used; the high and low points were expressed as a proportion of the highest amplitude in each display. Only those displays in which the animal was roughly lateral to the camera, and in which snout

position could be clearly seen in each frame, were graphed.

In addition to measures of duration and amplitude, 2 measures of context were recorded for each display. Distance context refers to the distance between a displaying male and the nearest female(s). Estimates of distance were classified into 1 of 4 categories: 1) 0 - .5 m, 2) .5 - 1.5 m, 3) 1.5 - 3 m, 4) greater than 3 m. Social context categories were as follows: 1) Solo, the male was the only occupant of the tree; 2) Not directed, other iguanas were present in the same tree, but at a distance of greater than 1 m, and the displaying iguana was not interacting with another individual; 3) General social, a male and female(s) were within 1 m of one another, but no obvious interaction was occurring; 4) Male-female (M-F) interaction, and act-response-act sequence occurred between an initiator of the interaction and the respondent.

Head Movements

Five types of head movement were identified: the head jerk, the roll, the shudder, the roll-shudder, and the signature bob (Figs. 18 and 19). The head jerk consists of a variable number of abrupt up and down movements of the head. Occurrence of the head jerk appeared to be independent of social context, and thus this movement was not considered to be a display. It was performed by individuals in exposed locations (nesting females, animals basking on the ground), and in response to the approach of a human or (less frequently) another iguana. The number of filmed head jerks were too few to permit analysis of form. Further discussion of this bob will be delayed until the final section. In performing the roll, the animal lifts its head at approximately a 45°

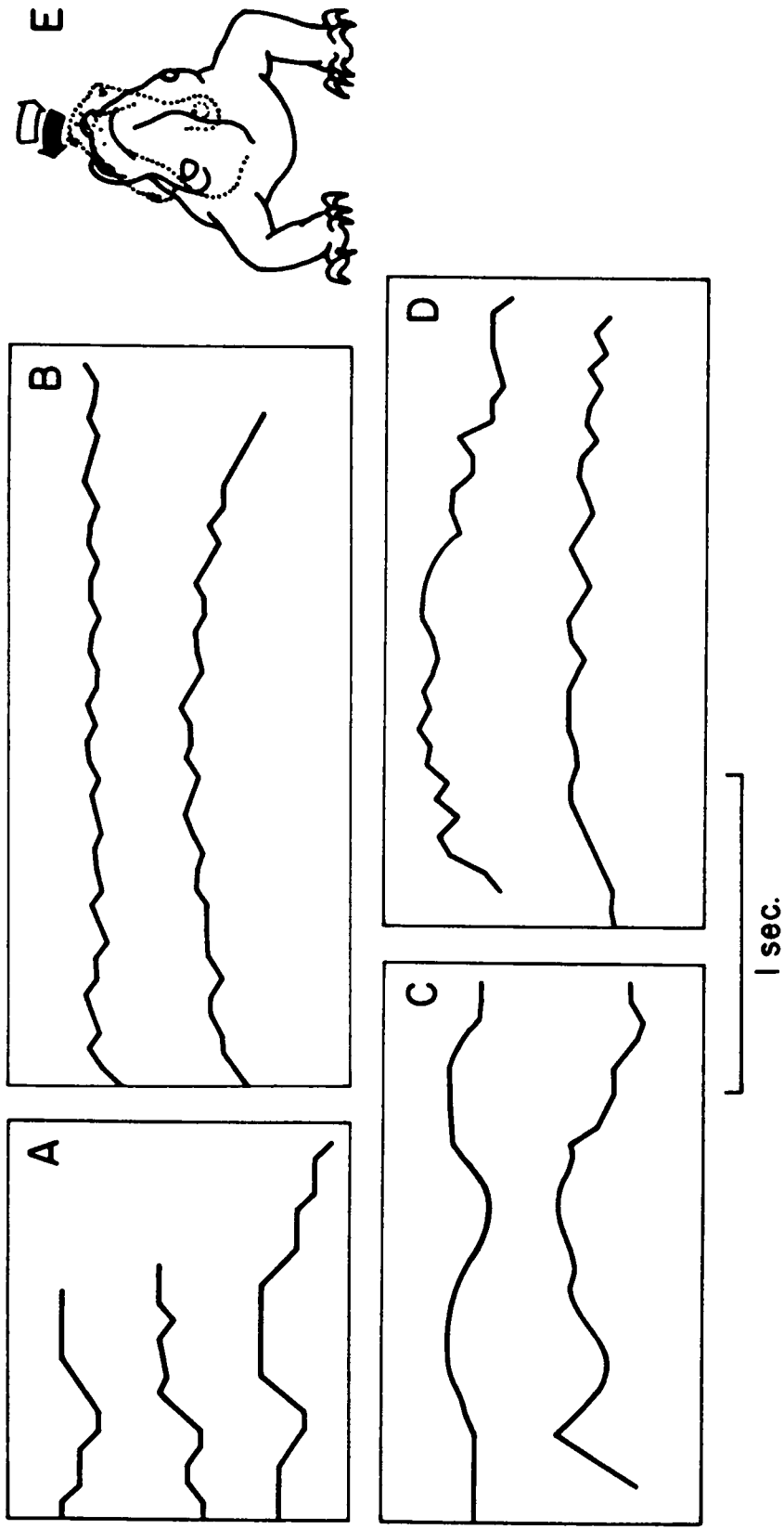


Figure 18. Patterns of iguana head movements: a) Head jerks from 3 individuals, b) Shudders from 2 individuals, c) Two rolls performed by the same individual, d) Roll-shudders from 2 individuals, e) Rotatory head movements performed during the roll.

Top graph (of d) is a shudder-roll-shudder sequence; bottom graph is a roll-shudder sequence.

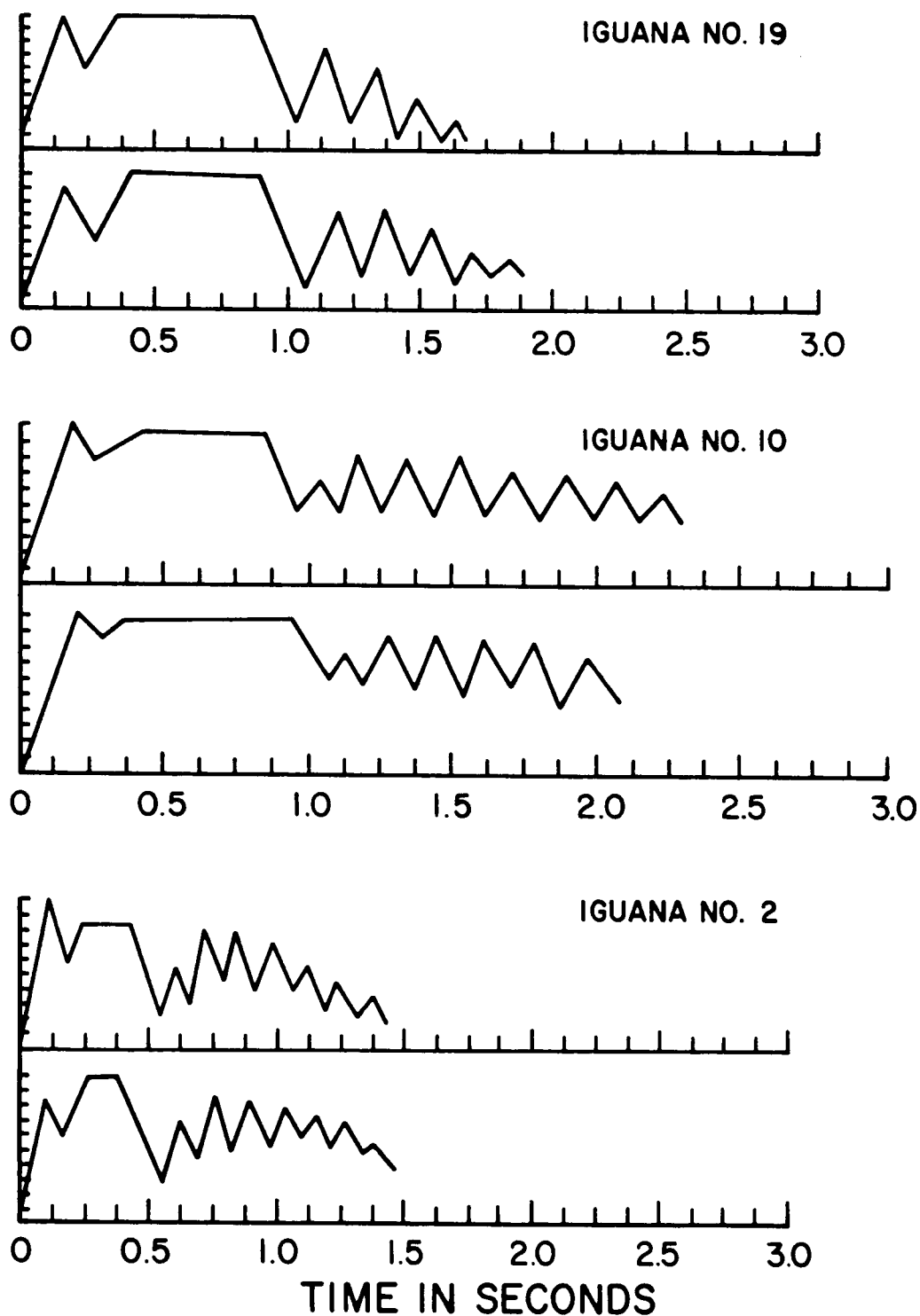


Figure 19. Samples of 2 DAP graphs of signature bobs from each of 3 different male iguanas.

Displays for each iguana were filmed on the same day.

angle to the substrate, and then rotates the head along the horizontal axis. The roll corresponds to Müller's (1972) "high frequency nodding," and to Distel and Veazey's (in press) "rotatory head-nodding." The shudder consists of rapid, low amplitude vertical head movements. Head position is variable, but the head is most often parallel to the substrate. Neck movement is more reduced in this bob than in the others. Occasionally, the animal raised the head or swung it from side to side while performing the shudder. More commonly, the neck was motionless and only the head moved vertically, producing a jiggling appearance. The shudder corresponds to Distel and Veazey's (in press) "vibratory head-nodding." The roll-shudder consists of rapid alternations of rolls and shudders highly variable sequences. The signature bob is a high amplitude vertical head movement, during which the head is elevated at a 60 - 90° angle, followed by a second high amplitude movement of longer duration (the plateau). A series of shorter, low amplitude bobs follows. During the plateau, the head is held up for about 1 sec, and head rotations occur. These head rotations are much reduced compared to those of the roll. The signature bob corresponds to Distel's "stereotyped head-nodding," and to Müller's "low frequency nodding."

The dewlap is maximally extended during all headbob displays. The signature bob was performed from both lying (entire ventral surface in contact with the substrate) and sitting (forelegs extended) positions. The forelegs were 1/2 to maximally extended during the roll, shudder, and roll-shudder. The roll and the signature bob were never performed while the animal was moving. Twenty-eight percent of filmed shudder bobs, and 11.8% of filmed roll-shudders, were performed while the iguana

was walking. During the roll-shudder, locomotion occurred simultaneously with the shudder, never with the roll component of this display.

Display rates varied with the season (Fig. 14, page 75) and with the sex and size class of the individual (Fig. 20). However, the proportion of total displays observed that were rolls, shudders, roll-shudders and signature bobs remained relatively constant throughout the year, except for the month of October (Fig. 21).

The signature bob was divided into segments (see below) and the variation in form and duration of each segment, as well as contextual use, were analyzed. Because the vertical and lateral head movements of the roll, shudder, and roll-shudder are of such low amplitude, subject-to-camera distance did not permit analysis of the form of these bobs. Only overall durations and contextual use of the 3 bobs will be discussed. The roll, shudder, and roll-shudder appear very similar in the field; the 3 bobs are less easily distinguished from each other than from the signature bob. Thus, the roll, shudder, and roll-shudder were analyzed as a group. Since the signature bob is the most unique of the headbob displays, I will discuss the variation in its form, duration, and contextual use separately.

The Roll, Shudder and Roll-Shudder

Temporal variation. A 3-way analysis of variance was used to assess differences in duration among display types, individuals, and distances between the displaying male and female(s). Since all displays were filmed in the field, it was not possible to have equal numbers of observations in each cell. Therefore, the data were analyzed using the

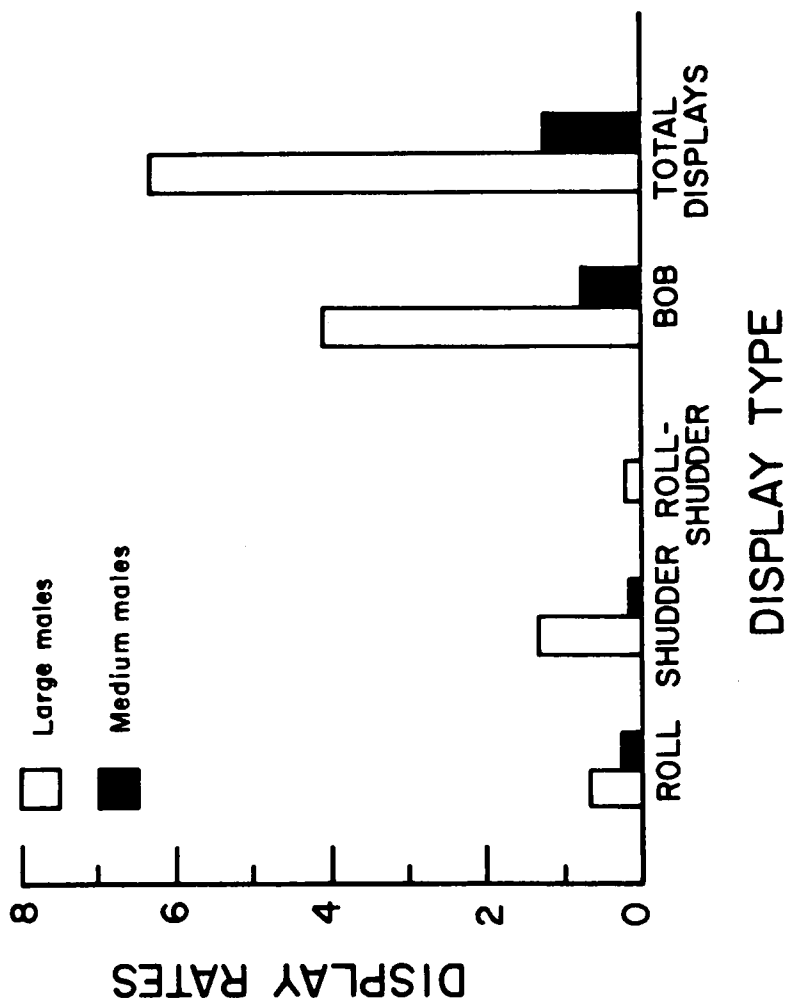


Figure 20. Mean number of headbob displays observed per 15 min observation interval for large males (543 intervals) and medium males (149 intervals).

Bob = signature bob. Based on observations during both the breeding and non-breeding season.

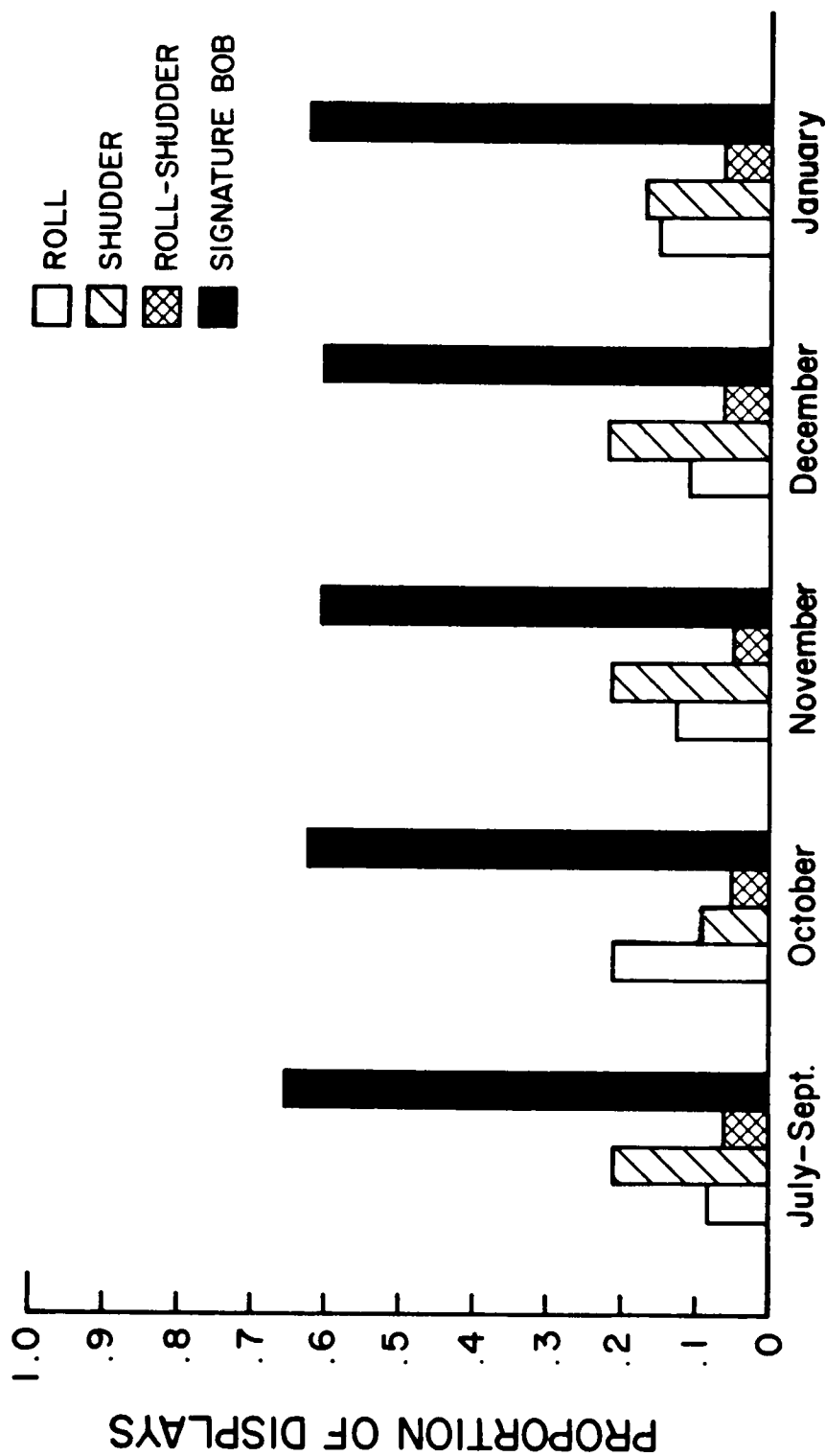


Figure 21. Proportion of total displays observed that were rolls, shudders, roll-shudders, and signature bobs, July through January, 1978 - 1979.

General Linear Models Procedure (Statistical Analysis System) for unbalanced designs (Barr et al., 1976). Three hundred and twelve bobs from 19 individuals were included in the analysis.

The only significant effect found was the display type by individual interaction ($F = 1.72$, $df = 18, 238$, $p < .05$), indicating that the duration of the display depended upon the type of display and the individual performing it. Although interindividual variation in display duration occurred, the relative duration and variability of the roll and shudder followed the same trend across individuals. The duration of the roll was shorter and less variable than that of the shudder (Fig. 22). Since roll-shudders occurred infrequently, individual differences in the performance of this display are difficult to interpret.

The comparison of overall means indicated that the roll tended to be shorter than either the shudder or roll-shudder; however, the variability of the latter 2 was larger than that of the roll (Fig. 23). The shudder and roll-shudder are almost identical in their duration and variability. The durations of the roll and shudder were normally distributed, and thus it was possible to test for significant differences in variability between the 2. The variability of the shudder was found to be significantly greater than that of the roll ($F = 3.05$, $df = 228, 48$, $p < .001$).

Although the distance by bob type interaction was not significant, an examination of bob durations at each distance revealed an interesting trend (Fig. 24). The shudder decreased both in duration and variability as distance from female increased. The roll-shudder increased slightly in duration at distance 2, but otherwise followed the same general trend as the shudder. The roll was little affected by distance from a female.

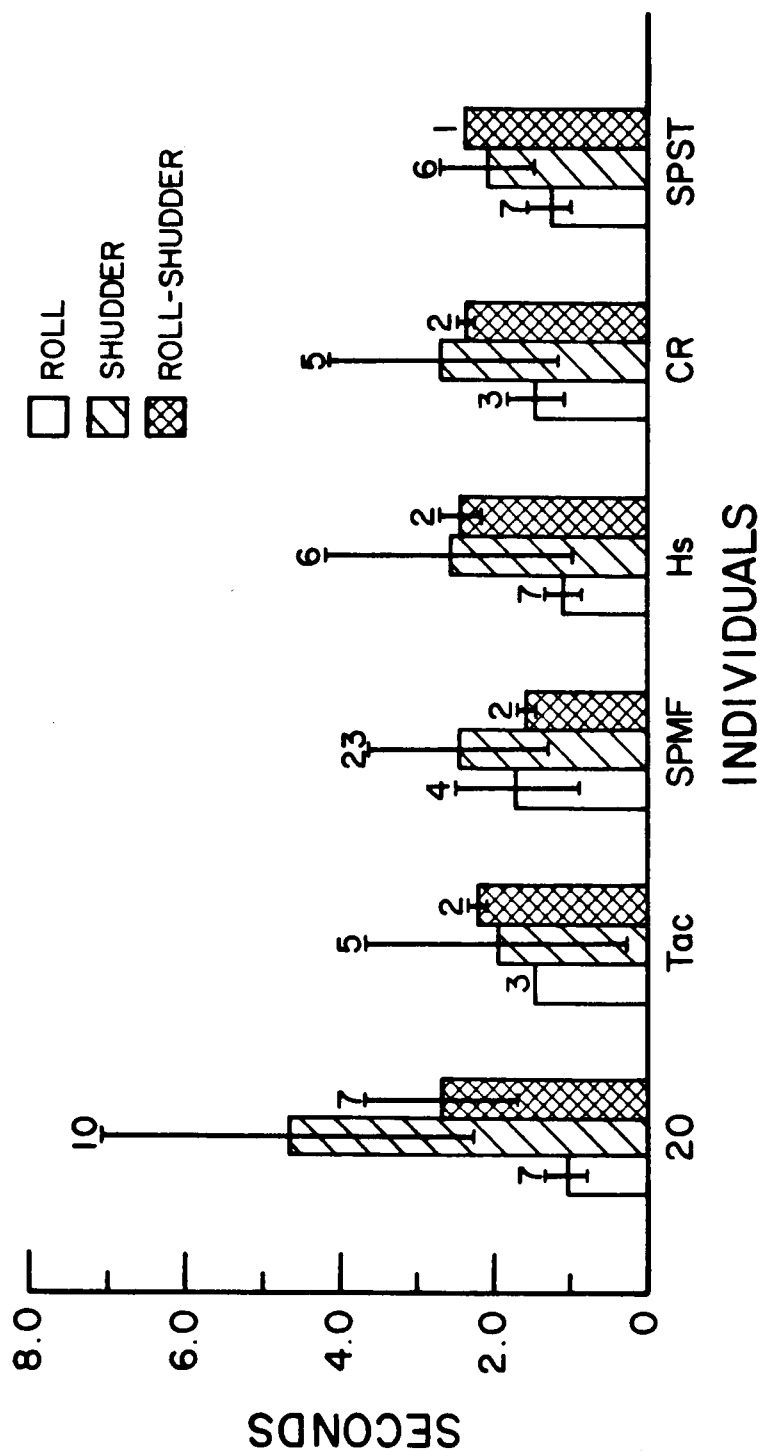


Figure 22. Mean duration $\pm$ 1 standard deviation of rolls, shudders, and roll-shudders performed by 6 individuals.

No. of each bob type is above the vertical line.

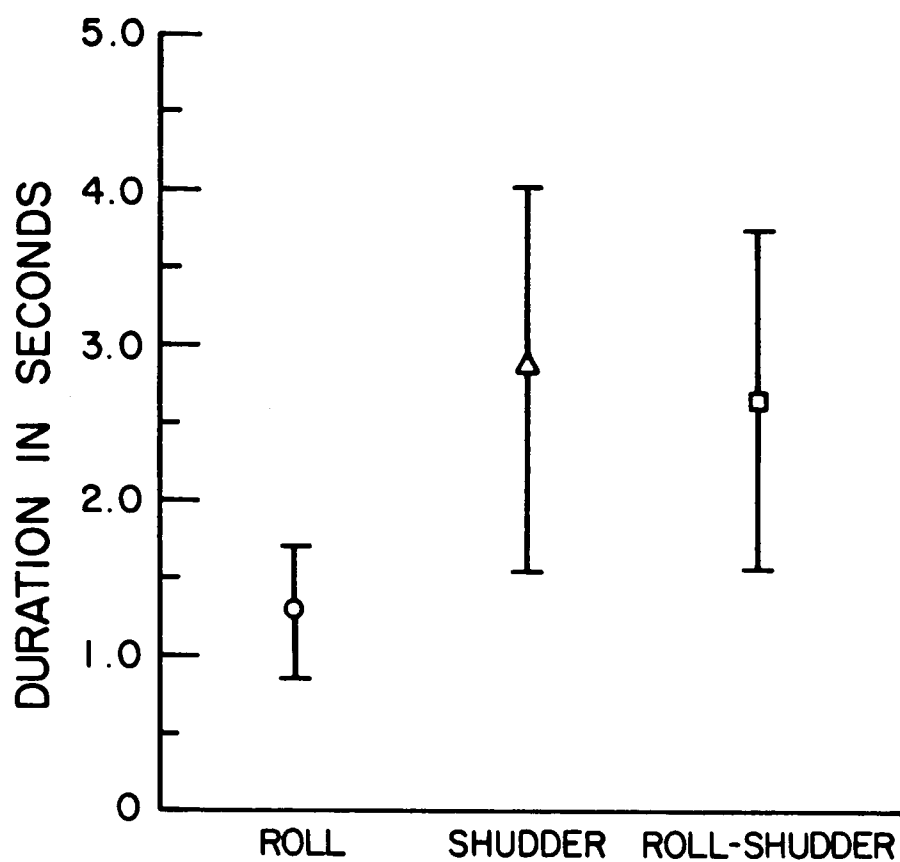


Figure 23. The mean duration $\pm$ 1 standard deviation of 312 filmed displays for 19 individuals.

Roll: 12 individuals, 49 displays; Shudder: 16 individuals, 229 displays; Roll-shudder: 14 individuals, 34 displays.

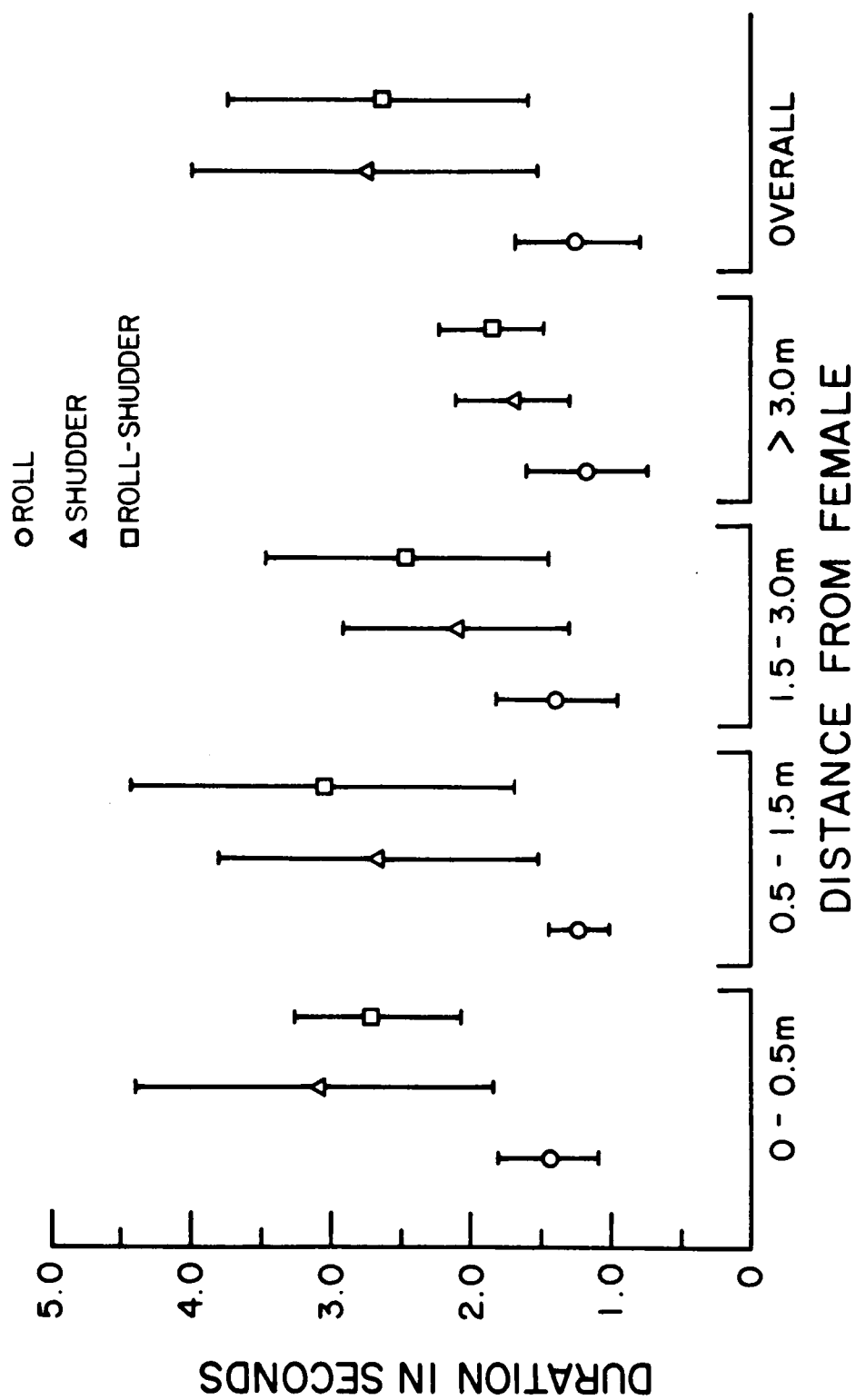


Figure 24. Mean durations ± 1 standard deviation of displays performed by male iguanas at varying distances from females.

Although a male and female at close distances are not necessarily interacting, 112 of 113 shudders performed during interactions occurred within distances of 1.5 m. Distance categories, therefore, do not contain information about the nature of the momentary relationship between the male and female. Since the shudder tended to decrease in duration as distance from female increased, it was of interest to ask whether or not significant differences in the duration of this display might be found among the social context categories. A 2-way analysis of variance was used to assess differences in duration of the shudder among individuals in 3 of the social context categories (shudders did not occur when the male was solo, see below). Individual differences in bob performance were found, as well as significant differences among contexts (Table 6). The context by individual interaction was not significant, indicating that bob duration in each social context varied in the same fashion across individuals. Duncan's multiple range test showed that the duration of the shudder was significantly ($p < .05$) greater during interactions ($\bar{X} = 3.19$ sec) than in the general social ($\bar{X} = 2.56$ sec) and not directed ($\bar{X} = 2.23$ sec) categories. The general social and not directed categories are distinguished only by the distance between the male and female. Thus, it appears that shudder duration is more influenced by the occurrence/non-occurrence of an interaction than by the distance between male and female.

Contextual use. The shudder was most likely to occur at close distances (0 - 1.5 m). Display performance was much more variable at intermediate distances. When the distance between male and female was

Table 6. Summary table of results from analysis of variance test for shudder duration showing main and interaction effects of context and individual.

Test	Mean Square	F	df	p
Context (C)	25.51	10.03	2,017	<.001
Individual (I)	70.19	4.12	15,194	<.001
I x C	21.64	1.12	17,194	n.s.

greater than 3 m, the roll tended to be more frequent than either the shudder or the roll-shudder (Fig. 25). Kruskal-Wallis 1-way analyses of variance by ranks revealed that the frequency of the 3 bobs differed significantly in distance categories 1 and 2 (Table 7).

Bob performance also varied according to the social context. Only rolls were performed when the male was solo; over 95% of observed displays were shudders during male-female interactions (Fig. 26). It should be noted that solitary males were observed to perform shudders or roll-shudders. However, this was a rare event that never occurred during filming sessions. The frequency of the 3 bobs differed significantly in all but the not directed category (Table 7).

These results indicate that the duration of the roll is independent of context, and that this display is more likely to occur in "non-social" situations. The shudder is a more variable display, its duration is related to the social situation, and this display is more likely to occur in social contexts. The use of the roll-shudder is a more perplexing problem. This display is clearly a composite headbob. The roll-shudder combines the movements of both the roll and the shudder. It most closely resembles the shudder in its duration and variability. Although low in frequency in all contexts, the roll-shudder tends to occur most frequently just outside the individual distance, which observation indicated is between 1 and 1.5 m, and in the intermediate social contexts, not directed and general social. It is at these distances and in these contexts that the apparent social nature of the large male's behavior may change (between not directed and general social, or general social and M-F interaction). In order to determine whether the

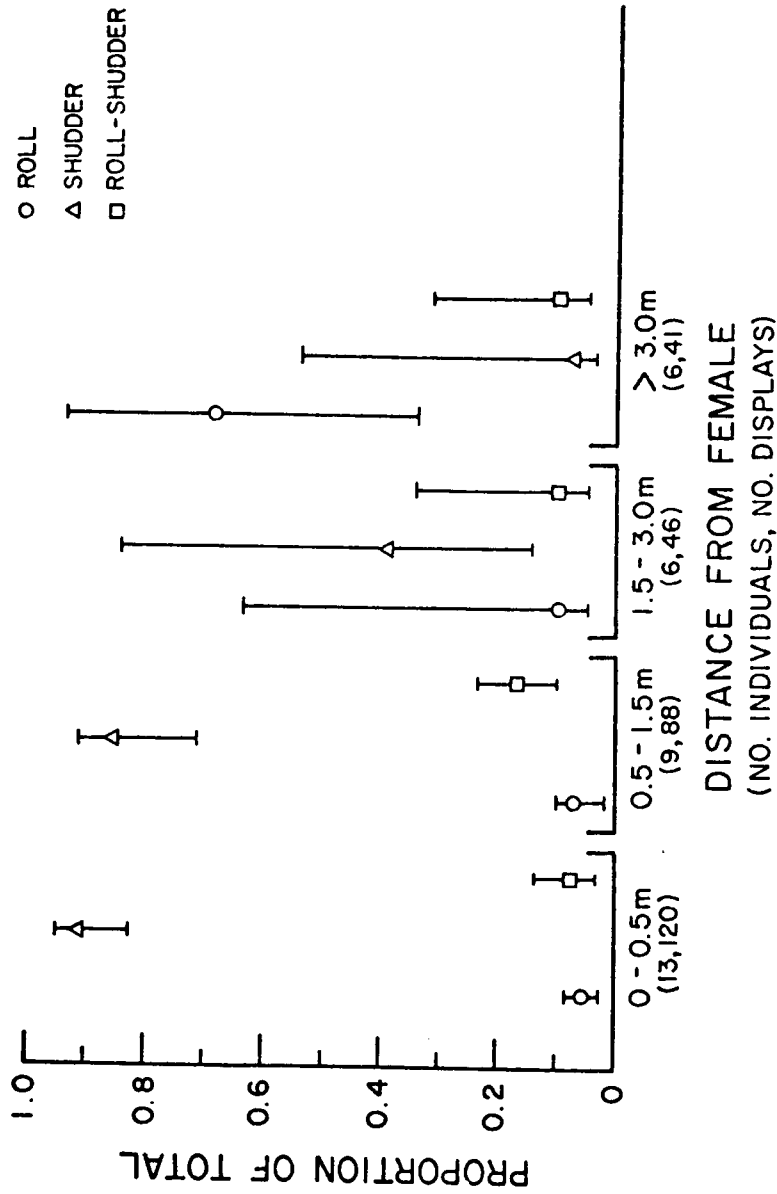


Figure 25. Median proportion of total roll, shudder, and roll-shudder displays given by males at varying distances from females.

Line denotes interquartile range; numbers in parentheses refer to the number of individuals and number of displays, respectively.

Table 7. Results of Kruskal-Wallis 1-way analyses of variance tests for display type by distance and social contexts.

	Distance Categories			
	0 - .5 m	.5 - 1.5 m	1.5 - 3 m	GT 3m
Chi	41.9	22.45	.16	4.92
Degrees of freedom	2	2	2	2
Probability	.001	.001	n.s.	.05<p<.10
	Context Categories			
	Solo	Not Directed	Gen. Social	M-F Interaction
Chi Squire	8.0	1.67	26.15	26.71
Degrees of Freedom	2	2	2	2
Probability	.02	n.s.	.001	.001

The hypotheses tested were that the roll, shudder, and roll-shudder are equally likely to occur in each distance category (top) and in each context category (bottom).

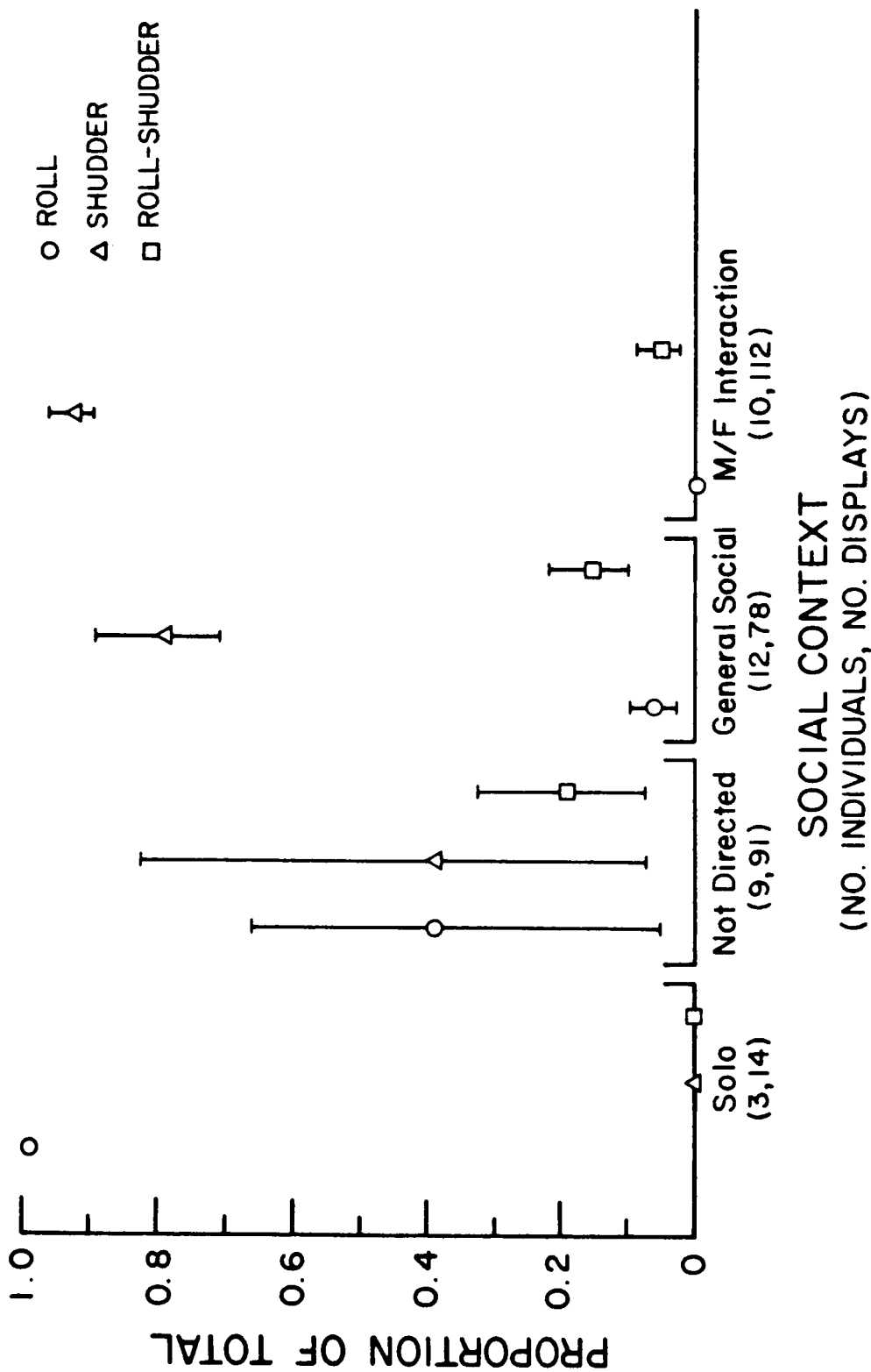


Figure 26. Median proportion of total roll, shudder, and roll-shudder displays given by males in different social contexts.

Line denotes interquartile range; numbers in parentheses refer to the number of individuals and number of displays, respectively.

roll-shudder occurs during transitions between social contexts, the situations in which the roll-shudder occurred were further subdivided into the following categories: 1) roll-shudders performed during transitions between sequences of rolls and sequences of shudders, between social contexts, and between patrols and social contexts; 2) roll-shudders interspersed among sequences of shudders; 3) roll-shudders interspersed among sequences of rolls; and 4) indeterminant contexts, in which activity preceding and/or following the display was not observed (Table 8). Roll-shudders were less likely to occur during sequences of rolls than sequences of shudders, but were never mixed with shudders in the course of a social interaction. Roll-shudders were significantly more like to occur in transitional situations than non-transitional situations ($\chi^2 = 5.45$, $df = 1$, $p < .02$).

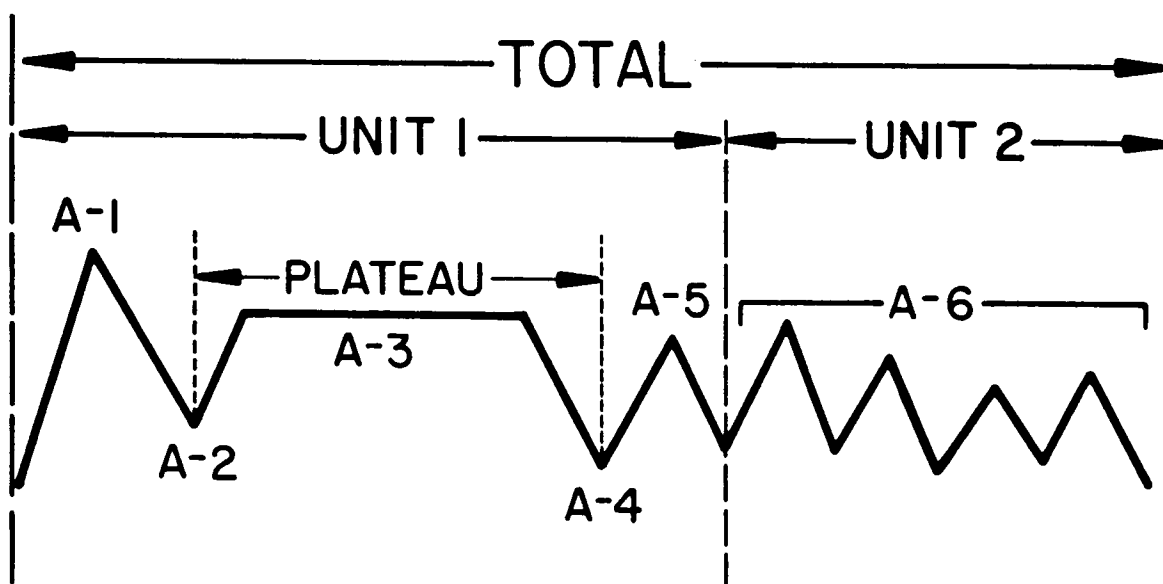
The Signature Bob

Variation of duration and amplitude. The variability of 12 components of the signature bob was analyzed (Fig. 27). Unit 1 (the pre-plateau bob, the plateau, and the post-plateau bob) occurred in all signature bobs and was considered to be the species typical component of this display. Unit 2 was more variable; any number of Unit 2 bobs might follow Unit 1. One of the 259 bobs analyzed stopped after Unit 1. Duration measures included the duration of Unit 1, Unit 2, the plateau, the total duration, and Unit 1 percent of total. Amplitude measures included the pre-plateau peak (A-1) and dip (A-2), the plateau peak (A-3), the post-plateau dip (A-4) and peak (A-5), and the mean amplitude of Unit 2 bobs (A-6). The number of Unit 2 bobs was also

Table 8. Specific situations in which roll-shudders were observed according to social context.

Situation	Social Context			Total
	Not Directed	General Social	Male-Female Interaction	
Transitions				
Between display types	1			1
Between social contexts ¹	4	9	4	17
Between patrols and social contexts	4			4
Total	9	9	4	22
Among rolls	1			
Among Shudders	5	3		8
Total	6	3		8
Indeterminant	2	1		3

¹Not Directed = from General Social. General Social = from Not Directed (6 cases) or from Male-Female Interaction (3 cases). Male-Female Interaction = from General Social.



RELATIVE AMPLITUDES

A-1 : Pre-plateau Peak

A-4 : Post-plateau Dip

A-2 : Pre-plateau Dip

A-5 : Post-plateau Peak

A-3 : Plateau Peak.

A-6 : $\bar{X}$ amplitude of Unit 2
bobs

Figure 27. Components of the signature bob used in analysis.

See text for explanation.

measured. The mean and standard deviations of each component, based on 259 bobs from 13 individuals, are presented in Table 9.

A 3-way multivariate analysis of variance was used to test the effects of individual, distance from female, and preceding behavior (roll, shudder, roll-shudder, locomotion, other, or unidentified) on the variability of the 12 bob components. Overall differences among the classification variables were tested using the Wilk's Λ , a multivariate statistic that may be converted to an Equivalent F value (Tatsuoka, 1971). The only significant effect was the main effect for individuals ($\Lambda = .008$, $F = 7.65$, $df = 144, 1456$, $p < .0001$), indicating that individuals differ on at least 1 of the measures of bob performance.

Discriminant analysis was used to explore individual differences in bob performance. This method is commonly employed to determine how to best use a set of variables to classify individuals into predetermined groups. In this investigation, discriminant analysis was used to identify the components of the signature bob that distinguished an individual's displays from those of other individuals. Thus, in the discussion of discriminant analysis that follows, the term group may be taken to mean individuals.

In discriminant analysis, the values of discriminating variables are weighted and combined to form a discriminant function(s) that maximizes the variance between groups while minimizing that within groups:

$$D_i = d_{i1}Z_1 + d_{i2}Z_2 + \dots + d_{ip}Z_p$$

where D_i is the score on the discriminant function i , the d_i 's are weighting coefficients, and the Z 's are the standardized values of the p discriminating variables used in the analysis. The coefficient reflects

Table 9. Overall means and standard deviations (S.D.) of 5 duration measures (D), 6 amplitude measures (A), and the number of Unit 2 bobs.*

Bob Component	Mean	S.D.
D - Unit 1	1.78	.14
D - Unit 2	1.24	.36
D - Total	3.01	.41
D - Plateau	1.06	.11
D - 1--% Total	60.33	6.81
A - 1	98.04	3.54
A - 2	56.31	10.35
A - 3	92.75	5.77
A - 4	28.91	12.07
A - 5	69.86	13.15
A - 6	62.12	12.19
No. Unit 2 bobs	4.72	1.09

*Durations are seconds, amplitudes are percentage of highest.

the relative contribution of its associated variable to that function. Each discriminant function yields a unique dimension describing the location of that group in multi-dimensional space with respect to other groups (Tatsuoka, 1971). A stepwise discriminant analysis selects independent variables for entry into the analysis on the basis of their discriminating power. In many cases, the full set of variables contains excess information about group differences. The stepwise procedure sequentially selects the "next best" discriminator at each step, and thus may produce a reduced set of variables that discriminates as well as, or better than, the original set (Nie et al., 1975).

All variables were found to differ significantly among individuals (univariate F-values, Table 10). The stepwise procedure used all of the variables except Unit 2 duration in forming the discriminant functions. The 11 functions significantly discriminated among individuals (Wilk's $\Lambda = .0006$, $F = 21.41$, $df = 132, 1940$, $p < .001$). Thus, given the variability accounted for by the 11 variables, Unit 2 duration does not significantly improve the discrimination among individuals.

The relative strengths of the variables as predictors can be assessed by examining the conditional F-values (Table 10). Dependencies among variables are written into the model; the stepwise procedure enters a variable into the analysis only if it adds a significant ($p = .05$) amount to the discrimination after its overlap with other variables has been parceled out. Thus, conditional F-values for each variable reflect the relative amount of information that variable adds to the discrimination after its overlap with other variables in the model have been taken into consideration. It can be seen from Table 10 that Unit 1 duration is

Table 10. Conditional and univariate F-values of signature bob components ranked according to conditional F's.*

Bob Component	Stepwise Conditional F-Value df = 12, 234	Univariate F-Value df = 12, 245
D - Unit 1	114.17	114.17
A - 2	34.12	34.26
A - 4	29.58	25.37
No. Unit 2 bobs	27.50	51.91
A - 5	22.33	29.41
A - 3	12.22	15.12
Plateau	9.41	104.38
D - 1--% Total	8.71	56.70
A - 6	6.37	13.51
A - 1	5.50	8.90
D - Total	4.92	14.56
D - Unit 2	1.80	25.56

*All values are significant at $p < .001$ except for the conditional F for Unit 2 duration, which is not significant.

by far the best predictor of an individual's bob performance, followed by the amplitude of the pre-plateau dip and the post-plateau dip, respectively.

Eleven discriminant functions were formed; the first 4 accounted for 89.3% of the variation among individuals (Table 11). The first discriminant function (DF1) accounted for 52.6% of the variability among individuals. Examination of the weighting coefficients indicates that the duration of Unit 1 and of the plateau contribute most of the separation among individuals along this dimension. DF2 accounts for 17.8% of the variability, and is primarily due to plateau duration, total duration, and Unit 1 duration. The relatively greater contribution of these 3 variables is repeated in DF3 (10.8% of variability) and DF4 (8.1% of variability). Thus, although Unit 1 percent of total, number of Unit 2 bobs, and the amplitude measures contribute to the separation of individuals, the first 4 discriminant functions are primarily due to durations, particularly those of Unit 1 and the plateau. The locations of the centroids for all individuals on the first 2 discriminant functions are shown in Fig. 28.

The validity of a discriminant analysis can be assessed by comparing the classification generated by the discriminant functions with that expected by chance. The expected percentage of correct classifications based on chance (determined from the proportional distribution of total sample displays among individuals) was 9.1. The percentage of signature bobs correctly classified was 88.4. In a more exacting test, the jack-knife classification, a single bob is classified using coefficients generated from all other bobs in the sample. The jack-knife procedure classified 83.7% of the displays correctly.

Table 11. Standardized discriminant function coefficients (d_i 's) showing the relative contribution of the variables to each discriminant function.

Bob Components	d_i			
	DF 1	DF 2	DF 3	DF 4
D - Unit 1	-4.404	-3.075	-2.852	-2.650
D - Total	-0.539	3.383	0.357	1.040
D - Plateau	-2.425	-6.597	0.482	1.511
D - 1--% Total	-0.043	0.168	0.022	0.153
A - 1	-0.031	0.031	-0.065	0.135
A - 2	0.007	-0.074	0.036	-0.026
A - 3	-0.034	0.027	0.082	0.013
A - 4	-0.034	-0.022	-0.087	0.008
A - 5	0.001	0.028	0.024	-0.049
A - 6	0.035	0.007	-0.020	-0.007
No. Unit 2 bobs	0.351	-0.358	-0.236	0.530
Percentage of variance among individuals	52.6	17.8	10.8	8.1
Cumulative Percentage	52.6	70.4	81.2	89.3

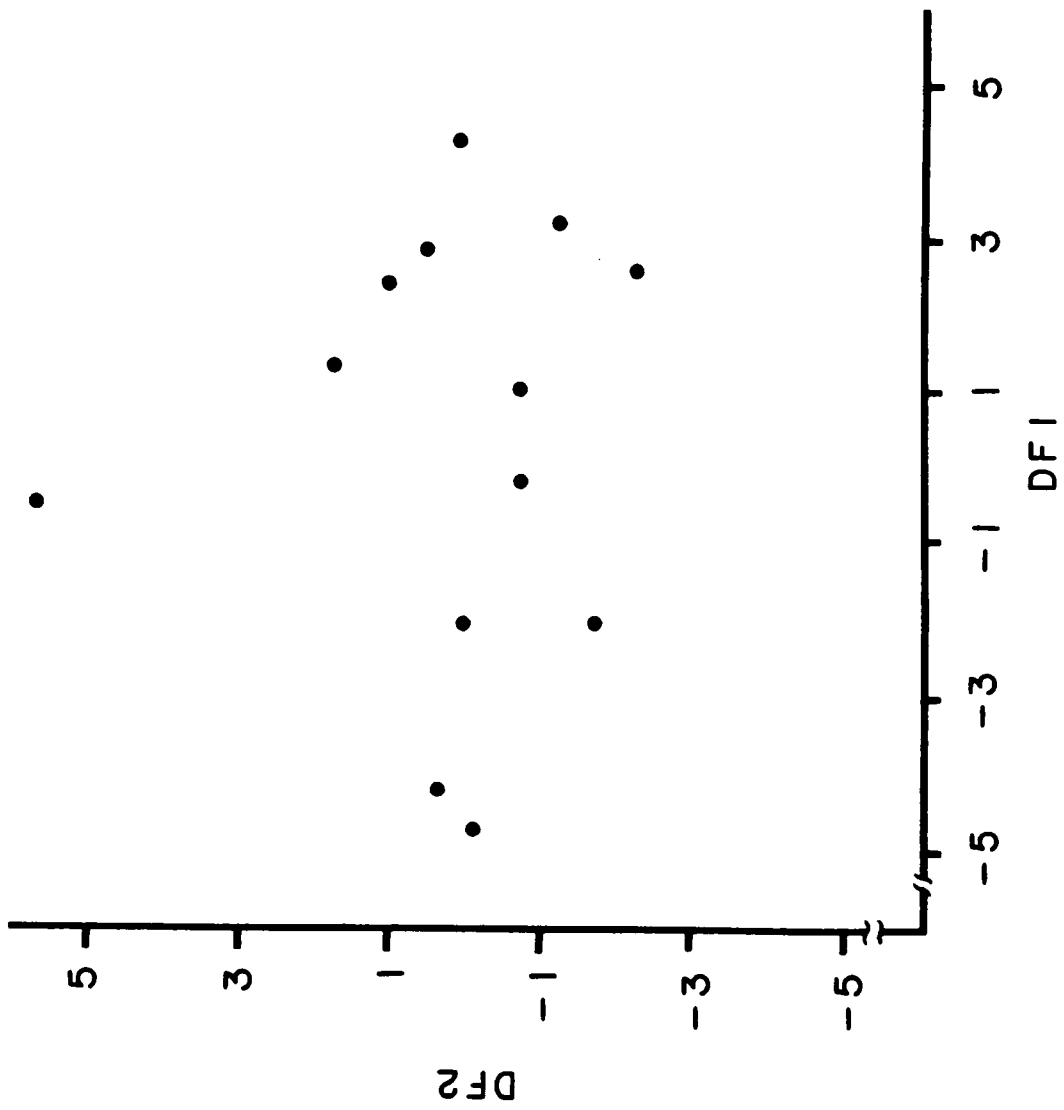


Figure 28. Centroids of individuals on the first 2 discriminant axes.

Contextual use. Although it is the most stereotyped of the 4 headbob displays, the signature bob is the most varied in contextual use. The signature bob always occurs after activity. Table 12 shows the proportion of over 1,000 observed bobs that occurred after specific acts that I have placed in 3 general classes. This display occurs during pauses in and at the termination of almost any activity in which a large male engages, and in any context, be it social or non-social. After performing a signature bob, an individual may continue the same activity, change to another activity, or cease activity.

Discussion

Table 13 summarizes the relationship between context and variability among the 4 headbobs, and proposes a signal function for each. According to differences in contextual use, it appears that the roll is used to transmit information over long distances, the shudder is used in close-range communication, and the roll-shudder occurs in intermediate situations. The relative proportions of the 3 display types observed across seasons supports these interpretations. The roll exceeds the shudder in proportion of total displays given only in October (Fig. 21, page 107). Increasing display rates in mid-October are the first sign of the onset of the breeding season, and at this time many large males are solitary. By early November, most large males are accompanied by 1 or more females. Relative differences in stereotypy are associated with differences in contextual use. In order to understand the varying degrees of stereotypy, it is helpful to consider the 4 displays, as well as possible selective factors influencing stereotypy.

Table 12. Proportion of total signature bobs observed that immediately followed 3 categories of events (N = 1,133).

Event	Proportion of Displays	Category Total
Other Displays		
Roll	.124	
Shudder	.179	.325
Roll-Shudder	.021	
Locomotion		
Position change	.092	
Perch change	.388	.480
Other		
Response to other	.054	
Preceding event not identified	.048	.195
Other	.093	

Table 13. Summary of characteristics of iguana headbob displays.

Display Type	Coefficient of Variation (Duration)	Contextual Use	Proposed Signal Function
Roll	32.38	Specific	Signal trans- mission over long distances
Shudder	44.46	Specific	Signal trans- mission over short distances
Roll-Shudder	40.80	Widespread but infrequent	Signal trans- mission at intermediate distances
Signature bob			
(Unit 1)	7.60	Widespread	Signal trans- mission at all distances
(Unit 2)	29.10		
(Total)	13.90		

The roll. Based on its contextual correlates, the roll may be considered an advertisement display. This bob may communicate a large male's presence to other males, who should avoid him, and/or to females, who should visit him. The roll may also introduce the signature bob that invariably follows. Stamps and Barlow (1973) reported that in Anolis aeneus, introductory head movements were more likely to precede a signature bob when another lizard was at a distance, as opposed to another lizard located close to the displaying individual. They suggested that introductory movements function to call attention to the signature bob. The roll may serve a similar function in Iguana iguana. An observer and photographer of iguana behavior quickly learns that it is very difficult to catch the onset of a roll, but virtually impossible to miss seeing the signature bob that follows.

Iguana iguana is a wide-ranging species that exists in a highly complex, low visibility habitat. Both distance and habitat complexity contribute to environmental noise. The degree of environmental noise can be expected to influence the evolution of signal characteristics (Marler, 1977).

As distance between communicator and recipient increases, variance in signal performance should decrease, thereby facilitating accurate detection of the signal from the background. Marler (1977) noted that among forest dwelling primates in which intertroop communication is important, discrete signals are relatively more common than among primates in which signals mainly function in intratroop communication. The roll appears to be a long-distance signal, and as predicted, is more stereotyped than the shudder or roll-shudder. The roll falls within the typical

range of variability of MAPS that have been quantified for a large number of species representing different taxonomic groups [coefficients of variation (C.V.'s) = 15 to 35, summarized in Barlow, 1977]; the shudder and roll-shudder exceed these values. That the variability in duration of the roll is significantly less than that of the shudder, a display used primarily in interactions, is consistent with this interpretation.

There is evidence that habitat complexity may influence the form of the headbob display in Uta stansburiana. Ferguson (1971) found a correlation between grassy habitat and display complexity among populations of this species, and argued that the difficulty of distinguishing conspecifics from moving grass accounts for the relationship. Similar obstacles to vision may have influenced the evolution of the form of the roll in Iguana iguana. During the high amplitude head rotation of the roll, the extended dewlap moves in a direction opposite that of the head. Since the dewlap is not a rigid structure, undulations occur simultaneously with the side-to-side movement. As a result, the roll is exceedingly conspicuous. Other environmental "noise," for example, leaves swaying in the breeze, recedes into the background. It may be significant in this regard that the dewlap of males is proportionately larger than that of females (Müller, 1968; Fitch and Henderson, 1977). The dewlap figures prominently in all displays, but is most noticeable during the roll and the signature bob. Sexual dimorphism in dewlap size may be related to the greater importance of display behavior in males, and the necessity of overcoming obstacles to display visibility.

The shudder. Shallow, rapid headbobbing has been reported in a variety of iguanid lizards, and has variously been termed "jiggling," the "shudder bob" or "shudder," and the "courtship nod" or "courtship bob" (Jenssen, 1977). In some anoline lizards, shuddering has only been observed in courtship interactions (Crews, 1975b; Stamps and Barlow, 1973; Jenssen, 1970a). In Sceloporus jarrovi this bob occurs during non-courtship encounters between conspecifics of either sex, and presumably reflects increasing arousal (Ruby, 1977). In Iguana iguana, the shudder occurs in male-female interactions both during and outside of the mating season, and thus is not considered to be a courtship bob. Outside of the mating season, shudders were most commonly observed when a male and female moved close to one another while basking. Male-female interactions were more frequent starting early to mid-November.

It has been suggested that the shudder evolved to allow close contact between males and females (Barlow, 1977; Stamps and Barlow, 1973). In Anolis aeneus, the courtship bob is most similar to the "multibob," display that is performed in the presence of a potentially threatening stimulus. Stamps and Barlow (1973) suggest that the courtship bob's resemblance to the multibob underlines the courting male's lack of aggressiveness. Similarly, the "courtship nod" of A. carolinensis is similar to the "head nod," a submissive display performed at the approach of another lizard (Greenberg and Noble, 1944; Crews, 1975b). In Iguana iguana, the reduced amplitude and neck movement of the shudder resembles the head jerk, a movement performed in a potentially threatening situation. The rapidity of the movements in the shudder seems to be the main feature distinguishing the 2 bobs; head jerks filmed at 18 fps and projected at

36 fps appear very similar to shudders. As observed in other iguanids (Jenssen, 1977), locomotion may occur simultaneously with shudder movements, never with the roll or signature bob. In 61 of 68 filmed cases in which locomotion and shudders occurred together, the displaying animal was approaching a female. If the shudder indicates a male's lack of aggressiveness, thereby decreasing the probability that the female will retreat at his approach, the ability to display and approach simultaneously would have an obvious advantage.

In addition to differences in form, the shudder differs from the roll in its greater variability in duration, and differs from both the roll and roll-shudder in contextual use. The shudder is more likely to occur in the general social context and during male-female interactions. Two factors that might favor lessened stereotypy among displays used in close-range communication have been proposed. Barlow (1977) noted that due to the tendency of the nervous system to filter out redundant input, lessened stereotypy should be favored for displays used in prolonged interactions. Particularly in courtship, mating pairs must be able to hold one another's attention. The prominence of the shudder in extended interactions between male and female iguanas is consistent with Barlow's hypothesis. Marler (1977) suggested that greater variability provides the potential to communicate more refined information over short distances, and adapt to feedback from a respondent. Such variability contrasts the observation that some displays remain relatively unchanged in a variety of circumstances that are presumably associated with different levels of motivation or arousal. Morris (1957) suggested that since a constant, unambiguous stimulus is more easily recognized, the evolution of a

display involves the development of "typical intensity," constancy of performance regardless of arousal level. Since the interactions between male and female iguanas were not analyzed, Marler's hypothesis cannot be evaluated. However, it is clear that the duration of the shudder is not constant across contexts. Shudder duration is significantly greater during male-female interactions than in non-interactional contexts. Assuming that the male's level of arousal is greater during courtship than while resting near a female, then the duration of the shudder may provide information about the male's level of arousal.

The difference in level of arousal may be the mechanism underlying the relationship between shudder duration and social context. The adaptive significance of the relationship may be related to the reduction in ambiguity regarding the male's intent. This hypothesis, suggested by A. S. Rand (pers. commun.), is consistent with the nature of male-female relationships during the breeding season. In general, males spent more time courting non-receptive females. Extended courtship before a female becomes receptive may be important in facilitating female receptivity, and/or in cementing bonds of familiarity between mates (see "The Role of Courtship"). Since pre-copulatory interactions seem to be important in synchronizing mating activity in iguanas, it should be of benefit to both males and females that courtship proceed in an orderly fashion. Since the male initiates most courtship sequences, this would involve recognition on the part of a female of: 1) the male's lack of aggressive intent, 2) the male's initiation of an interaction, and 3) that she is to be the recipient of the male's attention. As discussed previously, the shudder may communicate lack of aggressive intent regardless of the

social context. The similarities between the general social and M-F interaction contexts suggest potential sources of ambiguity in female recognition of points 2 and 3. In both contexts, the shudder was the most frequently occurring display. Most mating territories contained 2 or 3 females (see "Territory Establishment"), and in both contexts, the male was often close to more than 1 female. Furthermore, a male's approach cannot be an unambiguous signal of his initiation of courtship activity, since approaches occurred in a variety of contexts. For example, while moving to a basking site, or while moving throughout the territory, a male often moved close to 1 or more females. The most consistent difference observed in a large male's behavior in the general social and M-F interaction contexts was the duration of the shudder. In effect, the greater duration of the shudder may be equivalent to the male's saying: "I am talking to you." This message, along with other contextual cues (e.g., distance from male, male's orientation to female, male approaches female) may facilitate the female's recognition that she is the object of the male's attention.

The roll-shudder. Since the roll-shudder is a highly variable intergradation between the roll and the shudder, one might ask whether it should be classified as a separate display. Graded displays present problems for ethologists attempting to describe a species' repertoire and to determine the number of displays (Hinde and Rowell, 1962). Invariant combinations of separate display units in some cases seem to function as displays, as noted by McKinney (1961) in his study of the European eider. In contrast, the vocalizations of the South American

titi monkey (Moynihan, 1966) and the songs of the eastern phoebe (Smith, 1970) consist of shifting sequences of vocal display units, but the number of sequential patterns seem to be limited and to correlate with context and with the behavior of the displaying individual.

Smith (1977) recognizes 2 major categories of display sequences: fixed and variable. The former consist of invariant sequences of unit displays which Smith classifies as compound displays. The combination of display units in the variable category is limited by a set of rules relating pattern to context. Smith argues that in this case, rules rather than temporal patterns have been formalized, and thus variable sequences should not be classified as displays.

The roll-shudder combines 2 unit displays, the roll and the shudder, in variable sequences. Due to the low frequency of this display, it could not be determined whether the roll-shudder actually consists of a very few fixed sequences, or represents a range of variable combinations that are limited in number and are each related to a specific context. Based on the few available data, the form(s) of the roll-shudder appear to be analagous to the variable sequencing reported by Smith (1970) and Moynihan (1966), and would thus fit Smith's (1977) category of variable display sequencing.

The signature bob. The signature bob contains information about species identity, and possibly about individual and population identity. Based on the bob's pattern of occurrence, it fits the message category that Smith (1977) termed "general set alternatives." These displays occur before and/or after some definable activity, but give no information

about the activities that are being changed or the alternatives replacing them. They occur in a wide variety of circumstances, and information concerning the probability of future behavior is derived from the context. Signature bobs in Iguana iguana, as in other iguanids, are associated with other activities; they occur in a variety of circumstances, such as aggressive and courtship encounters, territory advertisement or assertion, and after locomotion. It may be significant that Distel (1978) found that he could elicit many behavioral patterns in green iguanas with electrical stimulation of various parts of the brain. The signature bob, however, was never performed in response to the onset of stimulation, but frequently occurred at stimulation offset, and before escape attempts. Distel noted that this display occurs during changes in level of excitation (i.e., stimulation), and suggested that it functions as a displacement behavior. Greenberg (1978) suggested that the signature bob reflects a general state of arousal, an hypothesis that is compatible with my observations of Iguana iguana, with Smith's classification, and Distel's findings.

The signature bob is much more stereotyped than most MAPS (C.V. of Unit 1 = 7.6). The C.V.'s listed in Table 13 (page 130) are based on data pooled from all individuals; the C.V. for each individual would be much smaller. Presumably, the variability of this display is influenced by factors in addition to the detection of the signal from the background, factors that may be related to species identification. Rand and Williams (1970) predicted that display redundancy should increase with habitat complexity, thereby multiplying species recognition information. Today, partial habitat overlap occasionally occurs between Iguana iguana and

2 other large-bodied lizards, Ctenosaura similis and Basiliscus basiliscus. It should be noted that factors in addition to display form may provide cues for species recognition (Rand and Williams, 1970; Williams and Rand, 1977). However, if Iguana and other similar lizards existed sympatrically in the past, one would expect species unique displays to evolve, and habitat complexity might increase the pressure for signal stereotypy. Where accurate communication of species recognition is important, one would also expect the species unique display to occur more frequently than more variable displays, as observed in Iguana iguana.

Performance of the signature bob, as well as the roll, shudder, and possibly roll-shudder, is more stereotyped within than between individuals. Individual differences in the signature bob were particularly striking, perhaps in part because components of this display were amenable to a more thorough analysis. Eleven of the 12 components examined contained enough unique information to contribute a significant amount of individual differences in display performance.

Individual differences in display performance may be related to individual differences in physical characteristics such as size and weight. The optimal duration and amplitude of a particular movement will be influenced by the mass and proportion of the appendages moved. Such mechanical factors are thought to influence the development of species-typical motor displays (Barlow, 1977), and may also influence performance of the display by a particular individual. Sufficient data were not available to correlate size and weight with measures of bob performance. Examination of the durations and amplitudes of the various measures of

bob performance for 6 males for whom size and weight data were available revealed no obvious relationship between size and weight and the various measures of bob performance. In the post hoc tests (Duncan's), there was no obvious tendency for males similar in size or weight to be consistently grouped together on any measures of bob performance. However, the small sample size and the slight range in lizard sizes may have obscured possible relationships. Although experimental support is lacking, signature bobs may communicate individual as well as species identity. Individual recognition should evolve if advantages are derived from discrimination between comparably detected signals. Jenssen (1978) argued that individual recognition would be of benefit among species inhabiting stable territories year-round, particularly in long-lived species, by decreasing aggressive interactions with nearest neighbors. Iguana iguana is territorial only during the breeding season, and nearest neighbors are 25 - 100 m distant. Although movements of large males overlap spatially at other times of the year, temporal overlap is rare. Individual recognition might allow a male to avoid a larger, dominant animal, and thereby avoid a potentially costly encounter. Individual recognition might also facilitate mate acquisition. Where males are spread apart and females pass through several males' territories before mating, the female presumably must be able to remember and compare displays from several males (Brander, 1967; Shepard, 1975). Since much early courtship between iguanas occurs in locations other than those selected for territories in late November, remembering the male's

identity, rather than the location of early courtship interactions, would aid the female in her final choice of mate.

Additional sources of information. Display modifiers are postures or movements which are not always associated with a particular display pattern, but which when present, may modify the message of the display (Jenssen and Hover, 1976; Jenssen, 1977, 1978). Lateral body compression (side-flattening) and lateral presentation to an opponent are 2 display modifiers that are performed during the challenge phase of an agonistic encounter, and that are common throughout the Iguanidae. As Jenssen (1977) pointed out, the visual apparatus has probably influenced the ubiquity of these modifiers in this family. With the exception of Anolis, which has a secondary fovea for binocular vision (Polyak, 1957), iguanids have a single central fovea; objects at or near a right angle to the head presumably yield maximal visual acuity.

During extended encounters, iguanas exhibited side-flattening which was enhanced by stiffening all 4 legs. The enlarged dorsal crest, in males is probably related to their greater emphasis on threat displays relative to other members of the population. Although agonistic encounters were more common among smaller than among larger individuals, they were of short duration. Smaller iguanas occasionally flattened the sides and exchanged signature bobs, but these threat displays rarely continued for an extended period of time as they did during encounters between large males. The dorsal crest spines of medium and large males are more prominent than those of smaller iguanas, and may function to enhance the male's apparent size during threat.

The occurrence of lateral presentation in Iguana iguana seemed to depend upon the relative positions of the branches on which the combatants were perched. The head rotations during the roll and the plateau phase of the signature bob may compensate for obstacles to full lateral presentation. The 3-dimensional head movements permit a partial lateral head presentation, and the sizeable subtympenic plate and enlarged jowl musculature are prominently displayed. Presumably, these structural features communicate information about a rival's strength in pushing battles involving the head. Similarly, the size of a male's jowl musculature should be related to the strength of his bite. Although biting was not observed in agonistic encounters, biting and jaw interlocking seem to be primitive fighting techniques among iguanids (Carpenter, 1967). Biting occurs during fights between nesting female iguanas (Rand and Rand, 1976). The skin on the large male's neck is much thicker than that of smaller iguanas, and may serve as a protective defense against a biting attack. Biting may produce rather long-lasting scars, as evidenced by those commonly seen on the necks of females where the male secures a neck grip during copulation. Similar scars on large males, as well as torn dewlaps, indicate that ritualized tests of strength between males do sometimes lapse into biting. Three-dimensional headbob displays involving both vertical and lateral head movements have been reported for 1 other iguanid, Cyclura cornuta stejnegeri (Wiewandt, 1977). Wiewandt also suggested that head rotations function to display the enlarged jowl muscles present in both sexes of this species, and communicate something about the individual's fighting "ability." It should be noted that C. c. stejnegeri is a ground-dwelling species that

does orient laterally during threat. The benefits, if any, derived from partial lateral presentation during head rotations in Iguana iguana may thus be only secondary.

The use of labile color patterns in territorial display is much reduced in iguanids as compared to agamid lizards (see review in Stamps, 1977). Some iguanids do show color lightening or intensification associated with dominance status (e.g., Anolis carolinensis, Greenberg, personal communication). Intensified color appears to be a permanent and conspicuous signal of territory ownership in Iguana iguana. Two lines of evidence lend strong support to this idea: 1) the rapid darkening of color after defeat (see "Size and Sexual Dimorphism"); and 2) the characteristics of the iguana's visual receptors. Iguanas have blue, green and red-sensitive systems in the lateral eye (Hamasaki, 1968; Hamasaki and Peregrin, 1970). Electroretinograms (ERG's) indicate that the green and red systems differ from the blue in several important respects. Stimuli from the blue spectrum elicit ERG's of significantly lower amplitude and longer latency. Blue receptors also have a longer refractory period than do receptors. In the red and green systems, ERG amplitude rises sharply as wavelength intensity increases; in the blue system, wave amplitude is unaffected by increasing stimulus intensity. Given these characteristics of the visual system, the bright orange color of territorial males should be easily detected and distinguished from the color of other iguanas. Long-distance vision appears to be well-developed; on several occasions iguanas were observed to orient towards a person entering Flamenco's gate, a moving stimulus some 150 m distant. The relationship between color intensification and status,

and the spectral sensitivity of the visual apparatus, suggest that the color "badge" (Smith, 1977) is an effective status signal in Iguana iguana. Where movement cues are reduced over long distances, a permanent display of color would allow transmission of information regarding location and status to continue.

In summary, signal transmission in Iguana iguana is accomplished with a highly redundant system of visual signals. The redundancy in the system may be viewed as an adaptation to a very complex habitat, where both distance and obstacles to vision contribute to habitat complexity. Among forest birds and monkeys that require signals to maintain inter-group spacing, auditory exchange is common since it is less hindered by obstacles than is vision. The importance of visual signals and the variability of the signals tend to increase in close-range, intragroup communication (Marler, 1977). Iguanid lizards do not have the option of using auditory signals. They must depend for the most part on visual communication, particularly for long-distance signalling. However, it appears that patterns of variation in visually communicating iguanas parallel such patterns in species living in similar environments, but employing other sensory modalities for communication.

CHAPTER VII

SUMMARY AND CONCLUSIONS

Summary

The social behavior of Iguana iguana was studied on Flamenco Island, a 13.5 ha island on the Pacific Coast of Panama. Between 200 and 300 animals inhabited the study area, a 5.5 ha area on the NW side of the island. The results are based on field observations conducted between October, 1977 and January, 1979. The methods included capturing and marking individuals, systematic observations of focal animals and breeding groups, filming, censuses of the study area, and radio-tracking. Iguanas from nearby areas were examined to assess reproductive condition throughout the year.

Iguanas in Panama reach reproductive maturity at approximately 26 cm SV length. Sexual dimorphism in body size, head size, length of the spines on the dorsal crest, femoral pore diameter, and coloration exist, but secondary sex characteristics develop slowly in adult males. Small reproductively mature males (26 - 31 cm) have enlarged femoral pores but are otherwise indistinguishable from females. All secondary sex characteristics except coloration are well developed in medium males (32 - 36 cm). Rates of color change are variable, but all large males (≥ 37 cm) are predominantly gold or tan.

The iguana's daily activity pattern begins with a morning basking period. Mid-day activity is variable; iguanas may feed, but usually spend the mid-day period resting in the shade or sun-shade. Afternoon activity consists of a basking period followed by movement to sleeping perches about 1 hour before sunset.

During the non-breeding season (February - October) the iguanas moved through overlapping home ranges. An iguana might remain in the same location for as long as 2 months. Long-distance movements were related to patterns of food availability. Iguanas eat leaves, flowers and fruits, and long-term shifts in location were found to follow patterns of food availability. During the non-breeding season (February - October), home ranges overlapped in both space and time. Large males confined their movements to an area that was roughly $1/3$ (.08 ha) the average home range size of other members of the population. Although smaller in size, the home range of all large males contained at least 2 seasonally preferred food resources, as well as a year-round supply of food.

Large groups of iguanas were observed in trees that contained abundant seasonally available food in the wet season. During the dry season, large congregations were observed in or near trees that would produce new leaves early in the wet season. These large groups typically consisted of 1 large male, 1 to 3 medium males, and 4 to 8 smaller iguanas.

Interactions among smaller iguanas in a single tree were brief and infrequent. Agonistic encounters typically occurred when 1 or both iguanas were changing location, for example, while moving from basking sites to sleeping perches. Smaller iguanas appeared to defend an individual distance. Overt interactions between medium and large males were rare. The largest male in the tree had priority of access to preferred basking and display sites. Large males were more likely to be observed close to 1 or more females, and performed headbob displays more frequently than medium males. Although the movements of large males overlapped in space, temporal overlap was infrequent. Large males were

rarely observed in the same tree for more than a few hours. Only 2 agonistic encounters were observed between large males during the non-breeding season. These observations suggest that large males tend to avoid one another, and that infrequent, intermittent contact may establish and/or maintain dominance relations among males in this size-class.

This pattern of social behavior began to change with the onset of mating activity. Color intensification and an increase in display rates among large males coincided with increasing testes size in mid-October. Courtship between large males and females began in early November, coinciding with increasing ovarian weight. During November, females were visited and were courted by several males, and males shifted location to court females in several nearby trees. By late November, most large males established a territory in a tall tree or group of trees. Medium males were no longer tolerated in the tree(s), and large males patrolled the territory several times daily. Mating territories contained from 1 to 4 females. Food was not an essential component of a territory. Males in bare trees were no less successful in obtaining mates than males in trees with food.

An individual female was courted for a minimum of 4 weeks before becoming receptive (i.e., copulating). Copulation was first observed in early December, coinciding with the start of the dry season. The period of female receptivity lasted for 2 to 3 weeks, and females copulated several times, usually with the same male, during the receptive period.

Small and medium males did not establish territories, and courted and displayed less frequently than did large males. By virtue of their

appearance, small males could move into a territory without being detected by the large male. Small males were observed to remain in territories and attempt to copulate with resident females when the large male was occupied elsewhere. Females always reacted violently to copulatory attempts by small males. Most medium males remained on the periphery of mating territories. Medium males were observed to court females moving into and out of territories, but females ignored most of these courtship advances. After removing a large male from his territory, the peripheral medium male was observed to move into the territory, display and patrol the tree. However, he was never observed with the females that had accompanied the previous territory owner. Two 36 cm males were observed to establish territories, and 1 of these males was successful in attracting and copulating with 2 females. Both methods of mate acquisition and mating success are related to the males' size and appearance. Large males copulated significantly more often (90% of observed) than did small or medium males.

Large males displayed more frequently than other members of the population. These males displayed throughout the year, but display rates were higher during the breeding season. Thus, the analysis of iguana headbob displays was based on filmed displays performed by large males between October and January.

Four types of headbob displays were identified. The shudder, a series of rapid low-amplitude vertical head movements, was performed most frequently when the male was within 1 m of a female. The roll, a high amplitude head movement during which the head is rotated was performed most frequently when the male was solitary or greater than 3 m

from a female. The roll-shudder, alternating rolls and shudders in variable sequences, occurred most frequently in transitions between long-distance and close-range signaling. The most distinctive display, the signature bob, consists of a high amplitude vertical head movement, followed by a similar movement of longer duration (the plateau). A variable number of more rapid, low amplitude bobs followed the plateau. The signature bob occurred in a variety of situations; this bob punctuated any activity in which a large male engaged.

Patterns of variability were related to differences in contextual use among the 4 displays. The temporal duration of the shudder was more variable than that of the other displays. The greater variability of this display may allow the male to keep the female's attention during courtship, and may also reflect adjustments to feedback from a responding female. The duration of the shudder was significantly greater when the male was interacting with a female. The increase in duration during interactions may reflect an increase in arousal level, and may also communicate that the male is directing the display to a particular female.

The variability in duration of the roll-shudder did not differ significantly from that of the shudder. The distinctiveness of the roll-shudder lies in its combination of movements, its performance in transitional social contexts and at intermediate distances from females, and in its low frequency of occurrence. The roll-shudder may reflect conflicting tendencies before entering or leaving a social situation.

The temporal variation of the roll was significantly less than that of the shudder, but much greater than that of the signature bob. The roll is a highly conspicuous advertisement display that may function

to call attention to the signature bob that invariably follows. The conspicuous nature and relatively greater stereotypy of this display presumably facilitate signal transmission over long distances in a complex habitat.

The signature bob is the most invariant of the displays. The signature bob encodes species identity, and possibly population and individual identity. Interindividual variability was significantly greater than intraindividual variability in the 12 components selected for analysis. In addition, 11 of the 12 elements analyzed contained enough unique information to reliably discriminate among individuals after overlap with other components had been accounted for.

Conclusions

Differences in the social behavior of iguanas in different sex and size class reflect the individual iguana's adaptation to its social and ecological environment. Year-round defense of food resources is not energetically feasible. Basking sites, shade and sleeping perches are abundant and widely distributed. The patchy distribution and seasonal availability of food resources, plus the structural complexity of and poor visibility in a tree or group of trees, make food defense impossible (see Brown, 1964). Thus, during the non-breeding season, the movements of all iguanas overlap in both space and time. During this period, however, the large male maintains his status in a confined area, and thus gains priority of access to females, display posts, and a suitable territory in November.

Territory ownership was critical to a male's mating success, and during the breeding season large males defended locations from which to

display, court and mate. Male iguanas, however, do not control resources that are critical to females, and male quality, rather than territory quality, seems to be the primary consideration in female mate selection. Characteristics that may reflect the male's suitability as a mate include territory ownership, survival ability as indicated by his size and age, and his courtship performance. The home range of a female iguana overlapped that of several male iguanas during the non-breeding season. Starting in early November, many females traveled from territory to territory and engaged in courtship with several males. The pattern of courtship interactions between female and large male iguanas is a prime example of what Williams (1966) termed "male salesmanship" and "female sales resistance."

The energy expenditure required of the large male strategy would not pay off for small and medium males because: 1) large males, by virtue of their size, have priority of access to choice mating territories, and 2) females mate preferentially with large males. However, males are more likely to encounter receptive females near breeding groups than elsewhere. In such a situation, males excluded from the breeding population can be expected to develop alternate strategies (Gadgil, 1972). Peripheral males have been observed in a wide variety of species (e.g., fish, Warner et al., 1975; amphibians, Wells, 1977; Howard, 1978; birds, Wiley, 1974; mammals, LeBoeuf, 1974). It is not always clear whether subordinate males remain near breeding groups to intercept and copulate with females or to take over vacated territories (Perrill et al., 1978; Wells, 1977). In Iguana iguana, which of the 2 subordinate strategies is more feasible depends on the size and appearance of the individual.

Headbob displays play an important role in communicating the large male's status and territory ownership. The evolution of the form and variability of the headbob displays can be explained in terms of the problems that an iguana displaying in a forest habitat must solve. The wide ranging movements of all sex and size classes require that the large male transmits long-distance signals that convey an agonistic message to other males and/or attract females. These long-distance signals must also overcome obstacles to vision and other environmental noise, such as leaves swaying in the breeze. The roll seems to fulfill the requirements for such a signal.

Since iguanas are territorial during only 2 weeks of the year, a male's identity cannot be determined by his association with a particular location. However, individual recognition should facilitate mate acquisition by females, and allow males to avoid agonistic interactions with other more dominant animals. The signature bob is another highly conspicuous signal that functions in both long-distance and close-range communication. In long-distance communication, the roll may communicate "I am here and am going to perform a signature bob," the signature bob may then communicate the male's identity.

In close-range interactions with females, the iguana must communicate his lack of aggressiveness, and thus be able to invade the individual distance of those females with which he interacts. The shudder seems to fulfill this function. The close temporal relationship between the shudder and the signature bob may convey 2 messages: lack of aggressive intent and identity.

In conclusion, the complexity of the social behavior of Iguana iguana reflects adaptations to an arboreal, herbivorous life-style. Patterns of movement during the non-breeding season follow shifting patterns of food availability. The distribution of food in time and space, plus the complexity of the arboreal habitat, make defense of a fixed location impossible. Similarly, mate acquisition by males cannot be accomplished by defending resources critical to females. Females, therefore, play an active role in mate selection, and exert pressure on those males successful in territory establishment to act out their role in the mating system. The most successful males are those who establish a territory and maintain high display rates, more or less continuously communicating both location and identity. Again, distance and habitat complexity influence the form of the displays and the manner in which they are performed. Signal transmission is accomplished in a highly redundant manner, involving selection of conspicuous trees and conspicuous perches in those trees, frequent performance of conspicuous displays, and color intensification.

Iguana iguana is widespread geographically. The species occurs in a variety of habitats and at varying densities. One would not expect all elements of the social structure and mating system to be identical under different environmental circumstances. Whether the behavior observed on Flamenco is typical can only be determined by comparative studies of Iguana iguana under different environmental circumstances.

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APPENDICES

APPENDIX A

Table A-1. Capture-recapture summary for 12 sample days on Flamenco. Number of unmarked iguanas (New), number of marked iguanas (Recaps.), and total number of iguanas (Total) captured by sex and size class.

Date		Males			Females			Immatures		Total
		≥37 cm	32-36 cm	25-31 cm	32-34 cm	29-31 cm	25-28 cm	Immatures		
								17-25 cm		
8 Apr.	New	2	2	3	0	1	2	0	10	
	Recaps.	0	0	0	0	0	0	0	0	
	Total	2	2	3	0	1	2	0	10	
14 Apr.	New	0	0	0	0	0	0	1	1	
	Recaps.	0	0	0	0	0	0	0	0	
	Total	0	0	0	0	0	0	1	1	
13 May	New	1	1	1	0	0	0	3	3	
	Recaps.	0	0	0	0	0	0	0	0	
	Total	1	1	1	0	0	0	3	3	
22 July	New	3*	0	0	2	3	0	0	8	
	Recaps.	1	0	1	0	0	0	0	2	
	Total	4	0	1	2	3	0	0	10	
29 July	New	5*	0	1	0	1	1	0	8	
	Recaps.	0	0	0	0	1	0	0	1	
	Total	5	0	1	0	2	1	0	9	

Table A-1. (continued)

Date	Males				Females			Immatures	
	≥37 cm	32-36 cm	25-31 cm	32-34 cm	29-31 cm	25-28 cm	17-25 cm	Total	
8 Aug.	New	3*	1	4	0	2	1	14	
	Recaps.	0	0	0	0	0	0	0	
	Total	3	1	4	0	2	1	14	
2 Sept.	New	0	4*	0	2*	3	1	12	
	Recaps.	1	0	0	0	2	0	5	
	Total	1	4	0	2	5	1	17	
9 Sept.	New	4	3	4*	0	2*	1	15	
	Recaps.	1	0	0	0	0	0	1	
	Total	5	3	4	0	2	1	16	
15 Sept.	New	0	2	1	1*	0	1	6	
	Recaps.	2	0	0	0	0	0	2	
	Total	2	2	1	1	0	1	8	
23 Sept.	New	2	2	3	2	5*	1	16	
	Recaps.	1	0	0	0	0	0	1	
	Total	3	2	3	2	5	1	17	
31 Oct.	New	1	1	1	0	3	1	9	
	Recaps.	0	1	2	0	1	0	6	
	Total	1	2	3	0	4	1	15	
15 Dec.	New	3*	1	4	4	5*	1	22	
	Recaps.	2	2	1	2	2	0	9	
	Total	5	3	5	6	6	1	31	

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*One animal included died.

APPENDIX B

Table B-1. Summary of activity budget data: Median percent time active and actual range of percent time active, across all observations.

	Feed	Perch Change	Headbob	Interaction
	Females			
Oct. - Nov., 1977	Median	.68		
Obs. hrs. = 25.7	Quartile Range	.34 - .75	0	.86
No. iguanas = 27	Actual Range	0 - 7.50	0 - .40	.42 - 13.75 0 - 100.00
Jan. - Apr., 1978	Median	.53	0	.64
Obs. hrs. = 39.2	Quartile Range	.26 - .79	0	.32 - .96
No. iguanas = 41	Actual Range	0 - 24.40	0 - .10	0 - 11.70
July - Aug., 1978	Median	.55	0	.68
Obs. hrs. = 40.7	Quartile Range	.28 - .83	0	.34 - 1.00
No. iguanas = 42	Actual Range	0 - 13.9	0 - .10	0 - 55.5
Oct. - Nov., 1978	Median	.58	0	.65
Obs. hrs. = 5.2	Quartile Range	.29 - .87	0	.32 - .97
No. iguanas = 22	Actual Range	0 - 15.40	0 - .10	0 - 66.70
	Large Males			
Oct. - Nov., 1977	Median	.52	.94	.71
Obs. hrs. = 25.3	Quartile Range	.26 - .78	.68 - 1.90	.36 - 3.75
No. iguanas = 27	Actual Range	0 - 1.90	0 - 6.10	0 - 100.00
Mar. - Apr., 1978	Median	0	.69	.69
Obs. hrs. = 10.0	Quartile Range	0	.34 - .75	.34 - .75
No. iguanas = 11	Actual Range	0	0 - 1.50	0 - 15.6

Table B-1. (continued)

	Feed	Perch Change	Headbob	Interaction
July - Aug., 1978 Obs. hrs. = 11.0 No. iguanas = 11	.55 .25 - .75 0 - 2.20	.55 .25 - .75 0 - 1.30	.61 .31 - .92 0 - 1.30	.61 .31 - .92 0 - 8.30
Oct. - Nov., 1978 Obs. hrs. = 28.0 No. iguanas = 112	0 0 0 - 6.10	.57 .29 - .86 0 - 9.80	.85 .57 - 2.20 0 - 7.00	.56 .27 - .82 0 - 100.00
Oct. - Nov., 1977 Obs. hrs. = 7.1 No. iguanas = 8	0 0 0	Medium Males .80 .40 - .83 0 - 1.30	0 0 0 - .30	0 0 0
Mar. - Apr., 1978 Obs. Hrs. = 13.8 No. iguanas = 14	.64 .32 - .95 0 - 28.30	.64 .32 - .95 0 - 2.20	0 0 0	.59 .29 - .88 0 - 16.70
July - Aug., 1978 Obs. hrs. = 6.5 No. iguanas = 7	.70 .36 - .75 0 - 10.60	.58 .26 - .88 0 - 1.00	.58 .26 - .88 0 - 2.30	.58 .26 - .88 0 - 13.30
Oct. - Nov., 1978 Obs. hrs. = 5.0 No. iguanas = 20	0 0 0	.56 .28 - .83 0 - 1.10	.91 .45 - 1.00 0 - 5.80	0 0 0 - 5.00

VITA

Beverly Ann Dugan was born in Asheville, North Carolina, on April 15, 1950. She attended elementary school in Asheville, and in 1968 was graduated from St. Genevieve-of-the-Pines Academy, Asheville, North Carolina. In the fall of 1971, she was inducted into Phi Beta Kappa, and in June of 1972 she received a Bachelor of Arts degree in Psychology from the University of North Carolina at Greensboro. In September, 1974, Ms. Dugan began graduate studies in Psychology, with a specialty in Animal Behavior, at The University of Tennessee, Knoxville. In September 1979, she accepted a temporary appointment as Instructor of Psychology at East Tennessee State University in Johnson City, and taught both undergraduate and graduate courses in several areas of Psychology.

Ms. Dugan is a member of various behavioral, herpetological, and scientific societies. In addition to animals and research, the author likes jazz, horseback riding, sunsets, and dry season winds.