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I am submitting herewith a dissertation written by Brian C. Bock entitled "Movement Patterns Relative to Nesting Site Locations in a Population of Green Iguanas (Iguana iguana) in Panama." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Psychology.

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MOVEMENT PATTERNS RELATIVE TO NESTING SITE LOCATIONS
IN A POPULATION OF GREEN IGUANAS
(IGUANA IGUANA) IN PANAMA

A Dissertation
Presented for the
Doctor of Philosophy
Degree
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Brian C. Bock

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To my family;
this degree is our accomplishment,
not mine.

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ABSTRACT

The green iguana (Iguana iguana) population located around Lake Gatun, Panama, faces a scarcity of nesting sites. Female iguanas from this population gather annually at the available sites to nest in aggregations and the hatchling iguanas emerge several months later to rapidly disperse away from these sites. This study investigated nesting site fidelity of the iguanas in this population over five nesting seasons and also studied the movements of female and hatchling iguanas from the nesting sites. Evidence for a genetic structuring of the population related to these movements was also gathered using allozyme analysis.

An intensive mark-recapture effort of female iguanas over five nesting seasons produced evidence of strong nesting site fidelity in these lizards. Some iguanas may have nested solitarily, however, and females also explored and occasionally nested in new sites that became available to them during this study. Thus, the site fidelity demonstrated was not absolute, although most female iguanas returned to the same nesting site year after year.

Investigations of female iguana nestings movements and hatchling dispersal demonstrated that both involved rapid movements of comparable distances away from the nesting sites. Females followed over two successive nesting seasons seemed to be returning to established home areas. Several female iguanas that had been marked as hatchling iguanas were recaptured as nesting females at the site near where they were first captured.

Electrophoretic analysis of blood and tissue samples obtained from female iguanas captured at the nesting sites revealed significant allele frequency differences among these iguanas at one of the two polymorphic loci inspected. The evidence suggests that female iguanas associated with the most isolated nesting aggregation may belong to a distinct local population that is somewhat reproductively isolated from the population associated with the remaining two nesting sites studied. The nesting site fidelity exhibited by female iguanas and the movement patterns documented for both female iguanas and dispersing hatchlings corroborate this electrophoretic evidence and suggest that limited dispersal and nesting site fidelity are producing a restriction of gene flow between these two local demes.

PREFACE

I remember . . . reading over the notes of all these encounters, and recalling Joseph Cambell, who wrote . . . that men do not discover their gods, they create them. So do they also, I thought, looking at the notes before me, create their animals.

Lopez, 1978

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CHAPTER I

INTRODUCTION

Movement, Gene Flow, and Population Structure

Gene flow is an important determinant of population structure. Theoretically, only low levels of gene flow are required to prevent the genetic differentiation of subdivided populations (Futuyma, 1979; Hartl, 1980). For this reason, gene flow has traditionally been assumed to have a significant effect on most natural populations (Mayr, 1963; Dobzhansky, 1970). Unfortunately, assessing the levels of gene flow in nature has proven difficult. Recent evidence, however, suggests that gene flow may be more restricted than previously thought (Ehrlich & Raven, 1969). Microgeographic differentiation between a number of seemingly contiguous animal populations also has been demonstrated (Burton & Feldman, 1981; Patton & Feder, 1981; Selander, 1970; Selander & Kaufman, 1975). And the traditional conception of gene flow has been questioned recently on theoretical grounds, as well. Endler (1973, 1977) has argued that gene flow may be ineffective in preventing the divergence of populations that are exposed to clinal variations in selective pressures. Similarly, Shields (1982, 1983) has recently attacked the traditional assumptions concerning the deleterious effects of inbreeding that can result from restricted gene flow.

Obviously, additional studies on the extent and consequences of gene flow are needed so that its significance to natural populations can be firmly assessed (Jackson & Pounds, 1979). Because even limited

gene flow may have a considerable effect on diverging populations, information on the extent of gene flow among populations in species that are not considered highly vagile will be of particular initial interest.

Reptile Movements

Reptiles are not noted for their movement abilities (Orr, 1970; Baker, 1978; Dingle, 1980). Presumably poikilothermy, low metabolic rates, and inefficient modes of locomotion combine to constrain most reptiles from ranging widely. Striking exceptions to this generalization are found, however, in certain aquatic reptiles. Crocodilians (Crocodylidae and Gavialidae) often move considerable distances within their riverine and estuary habitats (Bustard & Singh, 1983; Chabreck, 1965; Joanen & McNease, 1970, 1972; McNease & Joanen, 1974; Webb & Messel, 1978), and saltwater crocodiles (Crocodylus porosus) have been sighted far out to sea or in areas hundreds of kilometers from their nearest known breeding grounds (Bustard & Choudhury, 1980). The yellow-bellied sea snake (Pelamis platurus, Elapidae) is another reptile species often found in open ocean (Dunson & Ehlert, 1971; Kropach, 1971, 1975). It apparently floats passively in drift lines, carried by ocean currents, and presumably has thereby colonized most of the tropical Pacific (Minton, 1975). The most spectacular of all reptile movements, however, are those of the various species of marine turtles (Cheloniidae and Dermochelyidae). Their migrations between nesting beaches and feeding grounds frequently entail movements of

thousands of kilometers (Carr, 1975; Green, 1984; Parmenter, 1983; Pritchard, 1973, 1976).

Nevertheless, most terrestrial reptiles largely deserve their sedentary reputations. Terrestrial turtles (Testudinidae and certain Emydidae) typically have restricted home ranges (Auffenberg & Iverson, 1979), even though seasonal movements associated with shifting food resources or hibernation have been reported. These movements rarely exceed a few kilometers, however (Van Denburgh, 1914; Gibson & Hamilton, 1983; Swingland & Lessells, 1979; Woodbury & Hardy, 1948). Freshwater turtles (certain Emydidae, Chelydridae, Kinosternidae, and Trionychidae) also largely confine their activities to specific areas within their home rivers or ponds (Bury, 1979). Yet because of their nesting requirements, some female aquatic turtles must migrate kilometers along the shoreline to reach suitable terrestrial nesting habitat. They also will travel overland to nest as far as a kilometer from shore (Moll & Legler, 1971; Plummer & Shirer, 1975; Moll, 1978; Obbard & Brooks, 1980; Congdon et al., 1983). Terrestrial excursions by male and immature aquatic turtles also occur (Gibbons, 1970), but the extent of these movements is unknown.

Well-defined home ranges and restricted movements also have been demonstrated in many species of colubrid and viperid snakes, although home range shifts and movements of individuals out of their home ranges during mating and nesting season have been observed (Carpenter, 1952; Clark, 1970; Fitch & Shirer, 1971; Madsen, 1984; Parker & Brown, 1972; Platt, 1969; Stickel & Cope, 1947). Some communally hibernating

temperate snake species, however exhibit seasonal migrations to hibernacula each fall and dispersals as great as 18 kilometers from hibernacula have been documented (Aleksiuk, 1967; Brown & Parker, 1976; Brown et al., 1982; Hirth et al., 1969; Parker & Brown, 1980; Prestt, 1971; Reinert & Kodrich, 1982; Viitanen, 1967).

Most lizards also appear to be territorial or at least highly site specific. There is abundant information on the territoriality and home range sizes of lizards (see Stamps, 1977), but specific information on the actual movements of lizards is more limited. The homing abilities demonstrated by lizards that have been displaced are unimpressive (Krekorian, 1977; Mayhew, 1963; Noble, 1934; Spoecker, 1967; Weintraub, 1970). Mark-recapture studies of lizards frequently discount emigration and equate disappearance with mortality, and this assumption may often be well founded; immigration rates into these populations are typically quite low. Those investigations that have rigorously censused areas adjacent to the main study sites have found dispersal to be either negligible (Andrews & Rand, 1983; Blair, 1960; Lin & Lu, 1982; Mayhew, 1963; Tinkle, 1967a,b; Tinkle et al., 1962) or limited (Baharav, 1975; Case, 1982; Parker & Pianka, 1976; Spoecker, 1967; Van Devender, 1982a). Two estimates of neighborhood size calculated for two well-studied iguanid lizard populations (Kerster, 1964 for Sceloporus olivaceous; Tinkle, 1965 for Uta stansburiana) were quite small, with estimated genetically effective population sizes in these lizards being less than 300 individuals. Thus, the available evidence indicates that most lizard species have quite low vagilities.

This generalization is not without qualifications, however. Most populational studies of lizards do not focus specifically on dispersal, so some lizard populations that have been characterized as sedentary actually may have contained two types of individuals; those that dispersed little, and those that dispersed distances so great as to escape detection by the censusing techniques. Several lizard populations have been shown to lack well-defined home ranges, while others that have home ranges also contain certain transient individuals that apparently wander among the remainder of the resident population (Auffenberg, 1978, 1981; Baharav, 1975; Boag, 1973; Carpenter, 1959; Lin & Lu, 1982; MacKay, 1975; Tanner & Krogh, 1973). Movements by such lizards are difficult to monitor, but could be substantial.

Regular movements, however, that involve the return of individual lizards to their points of origin are easier to document. Davis and Ford (1983) noted a habitat shift in a population of western fence lizards, Sceloporus occidentalis (Iguanidae), in which many individuals left their breeding territories after the mating season and foraged in a nearby wooded area, but returned to their territories again before hibernation. In Caucasia, regular movements also occur in several species of rock lizards of the genus Lacerta (Lacertidae). Each year, populations of these lizards make seasonal migrations between summer habitat and rock outcrops which serve as winter hibernation sites, covering distances as great as 500 meters each way (Darevskii, 1978). Bradshaw (1971) also has described an interesting emigration-immigration cycle related to rock outcroppings in a population of

Amphibolurus ornatus (Agamidae) in Australia. Each year following the breeding season, a gradual exodus of juveniles occurs from the main outcrop of the population to outlying marginal habitat. Those lizards that survive to maturity eventually return to the main outcrop, however, and displaced the current cohort of juveniles, thereby continuing the cycle of "delayed recruitment" in this population.

Regular movements in lizards related to nesting also occur. Blair (1960) reported that most of the female rusty lizards, Sceloporus olivaceous (Iguanidae), in his study site made excursions out of their home ranges to nest. These nesting movements were only partially attributable to a lack of suitable nesting sites within the home ranges, however, because some females nested in home ranges of other females that had gone elsewhere to lay. Another instance of lizard nesting movements that is more clearly related to a scarcity of nesting sites was described by Parker and Pianka (1976) for a population of leopard lizards, Crotaphytus wislizeni (Iguanidae) in northern Utah. Females from this population made oviposition trips to an confined area of loose soil and nested in close proximity to one another, and also apparently returned to nest at this site over successive years, as well. Bustard (1968) also reported nesting migrations in the Australian gecko, Gehyra variegata, where gravid females would make excursions out of their home ranges to nest together, often laying their eggs in contact with one another under pieces of bark on the forest floor. Communal laying such as this also has been described in a number of other gecko species (Cagle, 1946; Chou, 1979; Greer, 1967;

Kushlan, 1981; Noble & Klingel, 1932; Oliver & Shaw, 1953; Taylor, 1963), and in other lizard families as well (Magnusson & Lima, 1984; Rand, 1967; Uzzell, 1966; Wells, 1981). These cases probably also involve movements by some of the nesting females out of their home ranges due to a scarcity of suitable nesting sites. Magnusson and Lima (1984) have recently described a case, however, in which female Kentropyx calcaratus (Teiidae) nest together despite an apparent abundance of available nesting sites, which suggests that there may be other benefits to communal laying as well.

Iguanine Nesting Migrations

The pinnacle of lizard communal nesting, however, and especially of lizard nesting migrations, is seen in several related species of iguanine lizards that inhabit various soil-poor islands in the Neotropics. In the Caribbean, female Mona Island ground iguanas, Cyclura stejnegeri, migrate up to 6.5 kilometers to reach the communal nesting areas that constitute only 1% of the surface of their island (Weiwandt, 1977). Elsewhere in the West Indies, Cyclura collei and Cyclura nubila also apparently face a scarcity of soils suitable for nesting, but the extent of their nesting migrations are not known (Weiwandt, 1982). Two other iguanine species in the genus Conolophus also migrate to communal nesting sites on islands in the Galapagos Archipelago. Christian and Tracy (1982) documented movements of 1.5 kilometers away from a nesting aggregation by female Conolophus pallidus, and Werner (1982) described the nesting migrations of Conolophus subcristatus on Isla Fernandina,

where females traveled up to 15 kilometers to nest in soils within the crater peak of this volcanic island.

Finally, one mainland iguanine species, the green iguana (Iguana iguana), also makes nesting migrations and nests communally when suitable soils are scarce. Rand (1968) first described aggregative nesting in this species in a population that inhabits a densely forested area in central Panama. Each year, female iguanas congregate in the few available clearings to nest together in high densities, some presumably having migrated considerable distances to do so. Prior to the present study, however, information on the extent of the movements of iguanas in this population with respect to the nesting site locations was limited (Burghardt et al., 1977; Drummond & Burghardt, 1982; Montgomery et al., 1973). It was known that some iguanas did nest at the same site over successive years and the impressive ability of so many female iguanas to converge upon the few inconspicuous and inaccessible nesting sites each year made it seem plausible that they might be imprinted on their natal nesting sites. For this reason, the following research objectives were adopted:

1. to determine the degree of site fidelity exhibited over successive nesting seasons by the nesting iguanas;
2. to obtain information on whether or not natal nesting site fidelity occurs;
3. to obtain specific information on the actual movements of nesting female iguanas through the use of radiotelemetry techniques;

4. to document the extent of hatchling iguana dispersal from the nesting sites;
5. to determine whether the movement patterns of the iguanas relative to their nesting site locations had produced any genetic structuring of the population.

CHAPTER II

BACKGROUND INFORMATION ON IGUANA

This chapter presents a synopsis of the available information on iguana behavior and ecology, as well as a description of the iguana population in Panama that is the subject of this investigation, including consideration of its habitat, nesting phenology, and recent history. Furthermore, because any adequate understanding of an organism requires some knowledge of its evolutionary past, the phylogenetic relationships and distribution of Iguana iguana are also briefly reviewed. Green iguanas belong to an apparently monophyletic group of iguanid lizards informally recognized as the iguanines (Avery & Tanner, 1971; Etheridge, 1982). Consideration of the characteristics of this group, including its presumed origin and current distribution, reveals that Iguana iguana is a highly derived iguanine that is unique in several respects.

Iguana Phylogeny and Distribution

The acceptance of continental drift and plate tectonics theory has produced a recent revolution in biogeographic thinking and the role vicariance events have had in determining the distributions of biotas is currently under reevaluation. Considerable disagreement exists, in fact, over what the important processes were in the shaping of the distribution of the Neotropical fauna. This is in part due to the geological complexity of the Neotropics, especially of Central America,

as well as to the different aspects of the distributional data that various biogeographers stress (Savage, 1982). Most biogeographers agree, however, that by the Eocene there must have been a fragmentation of a generalized Neotropical fauna into South American and Mesoamerican elements (Duellman, 1979; Rosen, 1976; Savage, 1966). Some degree of isolation between middle Central America and South America must have persisted from this time until the emergence of the current Panamanian isthmus sometime in the Pliocene, between six and three million years before present. During this isolation, the presumed iguanine stock developed as part of the Mesoamerican fauna (Savage, 1966). Based upon the habits of the modern iguanine genera, the ancestral iguanines were probably refuging, terrestrial lizards adapted to xeric conditions. They also probably could climb to some extent to forage in low vegetation (Burghardt & Rand, 1982).

By the Miocene, the eight modern iguanine genera presumably had initiated their differentiation (Gorman et al., 1971). The divergence of four of the iguanine genera was probably facilitated by their island endemism: Cyclura is restricted to islands in the West Indies, Amblyrhynchus and Conolophus are confined to the Galapagos Archipelago, and Brachylophus is found only on the Fiji and Tonga island groups of the South Pacific. The three Pacific genera presumably diverged after having colonized these areas via long-distance dispersals. Cyclura also may have rafted into the Caribbean, or it may have diverged in situ on a proto-Greater Antillean plate as it drifted from Central America to its current position. A vicariance event also has been

evoked as an explanation for the divergence of two other iguanine genera that are now considered mainland forms. Murphy (1983) has suggested recently that Dipsosaurus and Sauromalus may have diverged from Iguana and Ctenosaura stock, respectively, while isolated on lower Baja California as it rafted away from Mexico, and have only recently reinvaded Central America via a northern route.

Despite their apparent abilities as long distance colonists, however, none of the iguanine genera except Iguana have been successful in invading the South American continent, even though lower Central America has provided a dispersal corridor between the two continents for reptiles throughout the Pleistocene (Stuart, 1957). Perhaps the derived arboreal specializations of Iguana iguana contributed to its successful range expansion into areas that other iguanines have not colonized. Regardless, green iguanas have assumed one of the most widespread geographical distributions of all Neotropical reptiles (Figure 1). Iguana iguana occurs from central Mexico through Central America to Paraguay and southern Brazil on the mainland, and the genus has spread through the Lesser Antilles to the Virgin Islands in the Caribbean, as well as a number of other islands along the Caribbean and Pacific coasts.

Throughout this range, however, green iguanas only occur in lowland areas; altitudinal records for the species do not exceed 1000 meters (Etheridge, 1982). Because most areas below 1200 meters in Central and South America are tropical in climate, with high, relatively constant temperatures throughout the year (Duellman, 1966;



Figure 1. Approximate distribution of the genus Iguana.

Stuart, 1966), the altitudinal restriction of iguanas to the lowlands may well be primarily due to temperature constraints.

At lower elevations, however, moisture is the principle environmental factor influencing the distribution of tropical reptiles (Duellman, 1966), and the widespread occurrence of Iguana iguana in the lowlands can be attributed in part to its being one of the few tropical reptile species tolerant of great differences in moisture conditions. Green iguanas still occur in typical iguanine (xeric) habitats, yet they also thrive in more mesic, densely forested areas not exploited by other iguanines. Perhaps their arboreal specializations provide them with better thermoregulatory opportunities than are available to the other more terrestrial forms. In any case, Iguana iguana is certainly a highly derived iguanine species, unique in its adaptations to the arboreal folivore niche (Rand, 1978).

Given their arboreal specializations and herbivory, dense lowland tropical rain forests would seem to be the ideal green iguana habitat. Yet surprisingly, iguanas are not commonly found in the interiors of continuous forest (e.g., Dixon & Soini, 1975), although they are quite abundant in densely forested areas along rivers or near forest edge. Rand (1972) suggested that this distribution was related to the rather specific nesting requirements iguanas have. Iguanas lay a single clutch each year, and like all other iguanines studied to date, they seem to need to bury their eggs deep within burrows constructed in areas which receive direct sunlight. Iguana eggs have stringent incubation requirements. Artificially incubated iguana eggs must be

maintained at a fairly constant 30°C to insure hatching (Licht & Moberly, 1965), which closely matches temperature values recorded from within natural iguana nests (Rand, 1972). Iguana eggs also are sensitive to moisture conditions, with high humidities late in the developmental period often resulting in clutch failures (Bock & Rand, in press; Braunwalder, 1979). This may explain why iguanas throughout their range exhibit a synchronous, annual breeding cycle closely tied in its timing to local annual rainfall patterns (Rand & Greene, 1982). Even so, the incidence of clutch failure in natural iguana nests can be high (Rand & Dugan, 1980). Thus, the reputation green iguanas have for preferring broken forest, forest edge, and riparian habitats may result from their annual need for access to rather specific nesting habitat, including the need for open clearings. Living in such areas may have other benefits as well, but nesting ecology is probably the principle factor influencing the distribution of green iguanas within the lowland Neotropics. Incubation requirements also have been implicated as a critical factor in determining the geographic range of the desert iguana (Dipsosaurus dorsalis) (Muth, 1980). Thus, because green iguanas retain the ancestral, terrestrial iguanine mode of nesting, they have been unable to exploit dense rain forest habitats as fully as their arboreal specializations otherwise might allow.

Iguana Reproductive Phenology

Unlike most tropical lizards (Fitch, 1970), green iguanas exhibit a restricted, annual breeding cycle. Rand and Greene (1982) examined

latitudinal variation in the timing of the iguana breeding cycle over a transect of 36 populations from Mexico to Brazil. Emergence of the hatchling iguanas varied closely with the onset of the annual rainy season throughout this range, with mating, nesting, and incubation of the eggs generally occurring in the dry season. There are a number of reasons why such a synchronization of the breeding cycle might be adaptive. During the mating season, male iguanas establish mating territories which they defend vigorously from other males. They also engage in extended courtship with a number of females. Thus occupied, they rarely feed, and often appear emaciated by the end of the six week ordeal (Dugan, 1980, 1982). Similarly, gravid female iguanas also fast for the last few weeks before nesting (Müller, 1972; Pütz, 1982), presumably because of the expanding volume of eggs within their abdominal cavities. By confining mating and nesting activities to the late rainy season or dry season, reproductive adults can thereby fast during a time of relative food scarcity, while drawing upon fat reserves deposited over the course of the preceding rainy season. Still, it is probable that advantages to offspring are what primarily determine the timing of the iguana reproductive cycle. Clutches laid during the dry season might incubate more rapidly at higher, more stable temperatures and be at less risk of flooding. Emergence of the young during the beginning of the rainy season, at the time of maximum new leaf flush (Wolda, 1978), also may provide them with plentiful, high quality food resources (Coley, 1982; Milton, 1979). Young iguanas are presumably under strong selective pressures for rapid growth, since

the intensity of predation on iguanas decreases substantially as they become larger (Greene et al., 1978).

Green iguanas have a polygynous mating system (Dugan, 1980, 1982). In Panama, dominant males comprise less than half of the adult male population, but are responsible for a vast majority of the copulations. Female iguanas copulate a number of times during the nesting season, but often do so only with the same dominant male. Occasionally, female iguanas will breed in their second year, but most females postpone breeding until their third year or later. Clutches may vary in size from 12 to 70 eggs, with larger females producing larger clutches (Rand, 1984). Apparently, even the largest females deposit all of their eggs in a single mass when they nest. Depending on the local availability of suitable nesting sites, iguanas will nest either solitarily (Alvarez del Toro, 1960) or in aggregation (Rand, 1968).

A solitary nesting iguana typically begins by creating or locating a depression in the general nesting area it has selected. A burrow is then extended into the side of the depression at a downward angle. Iguanas also will burrow horizontally when they nest in exposed banks. Iguanas appear very wary when on the ground, especially during the initial stages of digging when the burrow is not yet deep enough to serve as a refuge. Digging is energetically expensive (Rand & Rand, 1978), so burrows are gradually extended over a series of digging bouts that may continue for several days. Once a burrow is long enough to accommodate the female's body and at a depth of 20 to 50 centimeters, the clutch is laid. The eggs are oviposited in an enlarged chamber at

the end of the burrow, which the iguana fills in as it emerges. Finally, the iguana scatters dirt and debris around the entrance to the burrow, presumably thereby concealing its exact location from clutch predators. Some solitarily nesting iguanas return to their nests for up to several weeks after laying and scatter more dirt over the area of their nest (Alvarez del Toro, 1972).

Where large open areas with relatively soft soils are available, iguanas exhibit little tendency to nest in close association with one another. Yet where clearings are scarce or where soils are particularly hard, iguanas will gather to nest together in groups at suitable sites (Rand, 1968). At these nesting aggregations, several modifications in the typical iguana nesting pattern are apparent.

Although nesting activity at an aggregation may continue for up to six weeks, any one iguana is usually only present at a site for a few weeks at the longest. Thus, there is considerable overlap among individuals at a nesting aggregation in terms of their stage of nesting. Each year, the first iguanas to arrive spend several days exploring the area before beginning to dig. Apparently, the initial, compacted surface layer of soil provides the most difficult digging (Rand & Dugan, 1983), for once the first burrows are initiated at a nesting site, they become highly desirable to new iguanas arriving to nest there. Iguanas that initiate burrows often spontaneously abandon them, presumably to rest. Unoccupied burrows typically are soon appropriated by other iguanas at the aggregation. Iguanas also will attempt to ^{steal} commandeer occupied burrows. Sometimes the resident iguana

readily abandons the burrow, but more commonly, disputes ensue (Rand & Rand, 1976), involving displays, and less frequently, actual fighting. Resident iguanas usually, but not always, retain possession of their burrow.

When not engaged in nesting disputes, iguanas occupying burrows continue to dig in intermittent bouts. The first iguanas to lay at a nesting site deposit their eggs at the end of the burrows and fill the burrows back in as they emerge. They then scatter dirt and debris about on the surface of the clearing, as do solitary nesting iguanas, and also attempt to fill in other partially completed burrows in the area, regardless of whether they are occupied or not. While filling, spent iguanas defend their nest burrows much more vigorously than do digging iguanas, but when the burrow is covered, this defense wanes. Spent iguanas usually remain at the nesting site for only a day or two after laying before departing.

While it may require several days of intermittent digging to complete a burrow, iguanas can reexcavate a filled burrow in a few short digging bouts. They often dig through the eggs at the end of the burrow, scattering them within the burrow and out onto the surface of the clearing, where eventually they desiccate or are eaten by scavenging black vultures (Coragyps atratus) or turkey vultures (Cathartes aura) (Sexton, 1975). However, iguanas that reexcavate a burrow usually continue digging and extend the burrow deeper. Iguanas within deeper burrows, especially if they have been buried inside by filling iguanas, often will dig separate emergence tunnels rather than exiting

via the burrow entrance. When they emerge, these iguanas usually fill the entrance to their burrow if it is still open, but are less thorough about filling their more vertically oriented exit holes. These holes are often used by subsequent iguanas to gain access underground. As the nesting season progresses, the burrows at a nesting site can become interconnected and quite complex. It is not uncommon to see several iguanas at a nesting site disappear underground and use the same burrow system simultaneously.

Rand and Dugan (1983) excavated a number of these complex burrow systems. Apparently iguanas in deep burrows tend to bury their clutches in side chambers off of the main passageways, thereby reducing the amount of clutch destruction caused by subsequent use of the system. Where soils are particularly hard, there is evidence that the burrow systems persist intact and are used repeatedly year after year. These burrow systems often extend deeper underground than do solitary iguana burrows, so clutches laid within complex burrow systems presumably are safer from clutch predation. It also has been suggested that repeated annual use of a nesting site helps maintain the area as a clearing (Rand, 1968), and may even improve the properties of the soil for incubation purposes (Rand & Dugan, 1980).

Hatching of the neonate iguanas is also highly synchronous, with emergence of the young usually confined to a short period of a few weeks early in the rainy season (Burghardt et al., 1977). All eggs of a clutch that hatch generally do so within a few days of one another. The hatchlings presumably cooperate in digging emergence tunnels to the

surface. They are particularly vulnerable to predation in the open, so they exit the emergence holes cautiously, often in small groups, and move off to the protection of the surrounding vegetation (Drummond & Burghardt, 1982). Although juvenile and adult iguanas are strictly diurnal, hatchling iguanas are known to emerge from their exit holes at night as well (Drummond & Burghardt, 1983). Most hatchlings emerge with an ample reserve of yolk, which they have reabsorbed into their abdominal cavities, presumably to be consumed while they disperse away from the nesting site in search of suitable habitat. The mass exodus from the vicinity of the nesting site may be related to predator avoidance, as predators soon learn of the local abundance of hatchlings at the nest sites. Troyer (1982a; 1982b) demonstrated that some hatchlings also briefly move into the more typical adult habitat in the canopy, associate briefly with the adults, and presumably acquire from them at this time the intestinal bacterial gut fauna required for their herbivorous diet. Hatchling iguanas are very gregarious during and after their dispersal (Burghardt et al., 1977), which may function to help spread this gut fauna amongst them (Troyer, 1982a; 1982b). Within a few weeks of emergence, the dispersal tendencies of the hatchling iguanas disappear and they become quite sedentary (Henderson, 1974), although still often associating together in small, ephemeral groups.

In summary, it is apparent that green iguanas are exceptionally social lizards. The young emerge and disperse in groups and remain gregarious thereafter; the adults exhibit a complex, territorial social system. Even nesting females, which admittedly gather together

primarily because of scarcity of suitable nesting sites, exhibit a number of behaviors unique to this social situation. Although they compete with one another while nesting, they do so using ritualized displays which serve to minimize energy expenditures and fighting (Rand & Rand, 1976). Their tendency to lay in side chambers of burrow systems also suggests that communal nesting is a well established part of the behavioral repertoire of this species. Rand (1968) characterized iguana communal nesting as being intermediate between solitary nesting and a more cooperative, colonial system. Even at this intermediate stage, the iguanas exhibit considerable behavioral sophistication to accommodate their nesting together in such high densities.

Another exceptional ability exhibited by female iguanas related to their communal nesting is their ability to locate the nesting sites in the first place. With widely scattered sites, some iguanas may have to navigate considerable distances from their home ranges to nest, which may entail use of some specialized orientation mechanisms. There is even the possibility that iguanas may be imprinted on their natal sites. Movement patterns also can influence population structure, so the nesting migrations of green iguanas are of interest from this perspective as well. If dispersal from the nesting sites is limited, populations could become subdivided through limited gene flow among the demes associated with each site. This, in turn, could have significant consequences on the demographic, social, and genetic characteristics of the population as a whole.

Study Site: The Barro Colorado Nature Monument

This investigation involved obtaining information on the movement patterns of iguanas with respect to nesting site locations in an iguana population which may well be limited by nesting site availability. The iguana population studied inhabits the Barro Colorado Nature Monument (BCNM), a biological reserve maintained by the Smithsonian Tropical Research Institute in central Panama. It was here that aggregative nesting in iguanas was first described by Rand (1968). Over the past 15 years, further studies by Rand, Burghardt and others have continued to expand knowledge of various aspects of the biology and behavior of these iguanas. This research on the movement patterns of iguanas relative to nesting site locations is part of a continuing, long-term investigation of the iguanas within the BCNM.

Barro Colorado Island (BCI) is a 1500 hectare island in Lake Gatun of the Panama Canal. BCI was formerly a hilltop in the Chagres river valley and became an island with the damming of the Chagres in 1913 during the construction of the Panama Canal. Biologists began visiting the island shortly thereafter and in 1923, the governor of the Canal Zone formally conferred upon it biological reserve status. The Smithsonian Institution was granted jurisdiction over the island in 1946. The remainder of the BCNM, that being the peninsulas of the mainland adjacent to BCI, did not come under Smithsonian stewardship until the 1970's. Even so, as part of the former Canal Zone, these areas did enjoy a certain amount of protection from human development prior to their becoming a part of the biological reserve.

The vegetation of the BCNM is semideciduous lowland tropical forest (Foster & Brokaw, 1982). The climate is characterized by stable temperatures throughout the year, ranging from 21°C to 32°C, and by a pronounced seasonality in rainfall. Barro Colorado Island receives approximately 2.5 meters of rainfall each year, with 90% of it occurring between the months of May and December (Deitrich et al., 1982). Thus there is a pronounced dry season during the remaining four months of the year. In Panama, iguanas establish mating territories at the onset of the dry season and copulate during an approximately six week period from early December through mid-January (Dugan, 1980, 1982). Gravid female iguanas can be seen nesting in aggregation around the BCNM from February to mid-March, and hatchling iguanas emerge there early in the rainy season, in May. Admittedly the aggregative nesting observed in the BCNM may be somewhat atypical; this area has undergone drastic environmental changes in recent years which may have influenced and be influencing the iguana population in a number of ways. Therefore, it is worthwhile to consider the history of central Panama with respect to the iguana population of the BCNM.

Pollen records indicate that lowland forest of the type currently seen in the Lake Gatun vicinity has probably persisted in this area for the past 35,000 years (Bartlett & Barghoorn, 1973; Foster & Brokaw, 1982). Prior to the formation of the lake, iguanas probably nested in sand bars and banks along the many small to moderate sized rivers of the region. Human activities, especially shifting agriculture, also could have provided the iguanas with a transient supply of nesting

clearings during this time. Records of maize pollen extend human agriculture in the area back at least several thousand years (Bartlett et al., 1969). The discovery of metate grinding stones and charcoal at various places on BCI supports the notion that portions of the island have been subjected to selective clearing prior to the arrival of Europeans to the area (Foster & Brokaw, 1982). In fact, human disturbances to the forest may have been quite pronounced in pre-Colombian Latin America. Heatwole (1966) and Bennett (1968) reported evidence that large portions of Panama were cleared and heavily populated at the time of European contact and that many of these areas became forested again after the decimation of the native American populations during the Spanish Conquest.

Effects of Europeans on the forests of central Panama were probably quite local until the industrialized assaults on the forest began in 1850 with the construction of the Panama Railroad across the isthmus. This railway passed quite close to BCI and even today iguanas can be seen nesting along the banks and roadcuts of the nearby relocation of its tracks. At the beginning of the French effort to construct a canal through the isthmus there were numerous scattered settlements around BCI and the French themselves cleared substantial areas of forest as part of their construction activities. Roughly half of the forest on BCI is young, regrowth forest which has been cleared at some time since the 1800's, largely by the French for agricultural purposes (Chapman, 1938). In contrast, the older forest on BCI is estimated to be at least 300 to 400 years old (Foster & Brokaw, 1982). Since the

completion of the canal in 1914, the area surrounding Lake Gatun has been largely protected from human development and most cleared areas have been allowed to grow back into forest. There has, however, been limited use of the forests of the former Canal Zone, including the peninsular portions of the current BCNM, for shifting agriculture. Also, a laboratory clearing and several smaller clearings have been maintained on BCI, and other areas near the laboratory clearing have been used from time to time for agricultural purposes, as well.

If Iguana iguana is in fact a species confined to forest edge, then the creation of Lake Gatun may have had a cataclysmic effect upon the iguana population of the area. At first glance, precisely the opposite effect might be expected. Lake Gatun inundated 420 square kilometers of swamp, river valley, and lowland forest, producing a correspondingly enormous amount of shoreline. For instance, although BCI is an island of only 5.5 kilometers maximum diameter, its flooded lower stream valleys give it a highly convoluted contour, with over 40 kilometers of shoreline. However, the shores along Lake Gatun differ considerably from the water's edge of a free-flowing lowland river. The Lake Gatun shoreline exposed to the canal typically has hard, steep banks which are continually being eroded by the wash from passing ships. Beaches are formed at the bases of these banks, but usually are inundated except during very long dry seasons. The remainder of the BCI shoreline either is bordered with marsh vegetation, or has forest growth up to and overhanging sharply defined banks (Croat, 1978; Kenoyer, 1929). Apparently the lack of current in the

reservoir, as well as the relative absence of seasonal variation in water levels, has prevented the formation of the types of banks and beaches in which iguanas can nest. So with the damming of the Chagres in 1913, the iguanas presumably were required to retreat with the advancing waters, leaving their former nesting sites behind them. There may have been substantial social disruption and wandering by these refugee iguanas during this several year period of lake rise. Within the BCNM, it is doubtful whether any areas have persisted which were used by iguanas as nesting sites prior to the creating of Lake Gatun.

In summary, prior to 1913, the iguana population in the vicinity of the BCNM was probably well established along the rivers, and iguanas also possibly had opportunities to live near and nest in clearings produced by human activities. With the formation of Lake Gatun, however, the traditional river nesting sites were lost, and since that time, the amount of deforestation in the area due to human disturbance has varied, but overall there has been a general decreasing trend. Currently iguanas within the BCNM nest at artificial clearings, usually in high densities.

Iguana Nesting Sites Within the BCNM

The three areas within the BCNM that have the most iguana nesting activity each year are all on small islands adjacent to either BCI or the mainland (Figure 2). Small islands are apparently better nesting areas for iguanas because they lack resident terrestrial predators

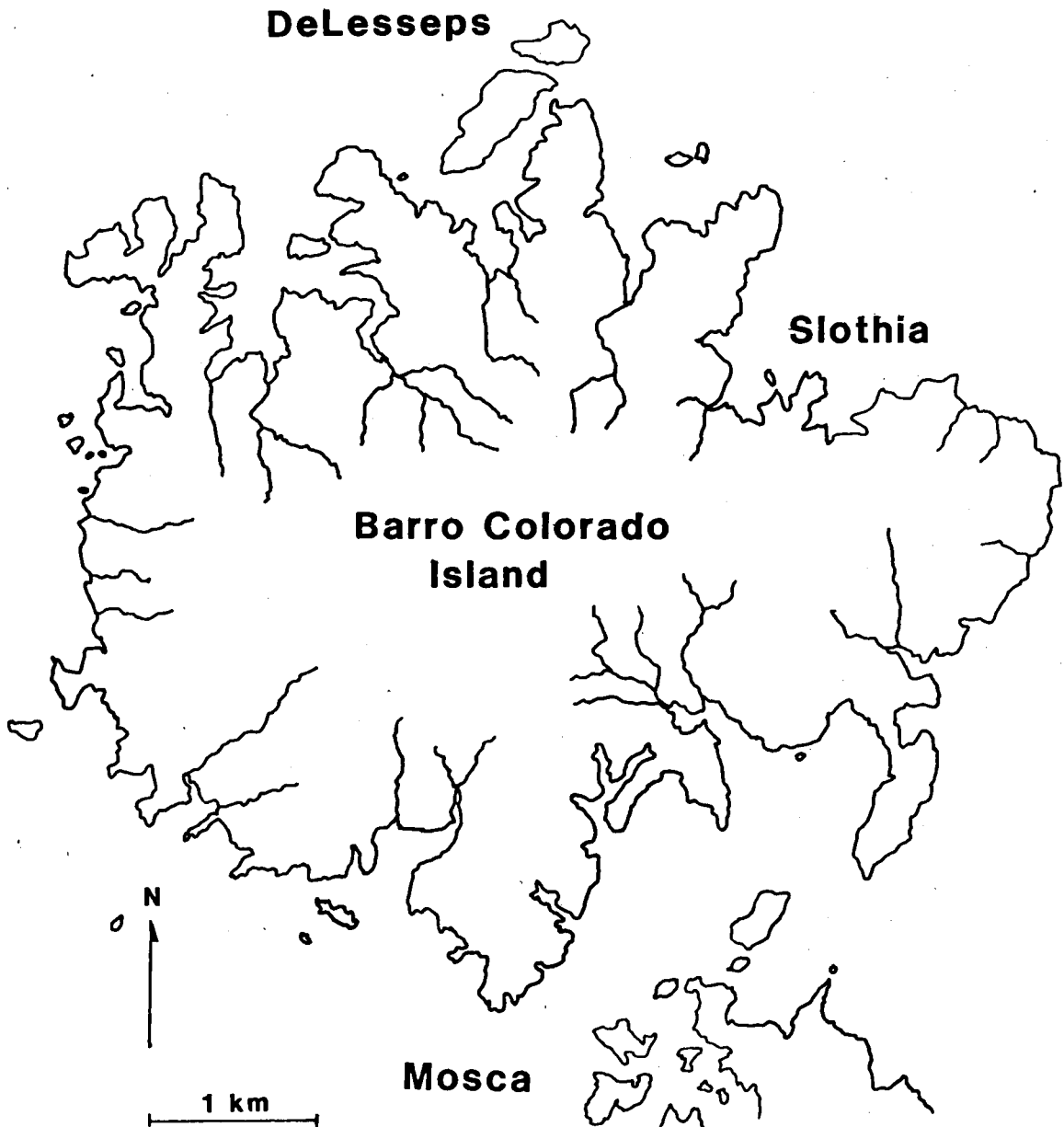


Figure 2. Barro Colorado Island and the locations of the three main nesting aggregations of DeLesseps, Slothia, and Mosca.

(Rand & Robinson, 1969; Drummond, 1983). However, iguanas frequently nest in association with the nests of American crocodiles (Crocodylus acutus), and the nest-guarding female crocodiles often disrupt and occasionally kill iguanas that are digging near their nests (Dugan et al., 1981). This nest-guarding behavior persists throughout the incubation period, however, so although iguanas nesting near crocodiles are at risk, their clutches may benefit from the defense of the nesting site the crocodile provides after the iguanas have departed. Even so, the nesting association of crocodiles and iguanas probably is primarily a result of their sharing similar nesting requirements and the scarcity of suitable sites around the BCNM. Both crocodile and iguana eggs are probably safer from clutch predation on smaller islands than are eggs laid in similar areas on large islands and the mainland.

The primary nesting site of this study was located on the 0.3 hectare islet of Slothia, adjacent to BCI in the Laboratory Bay. Slothia is separated from the closest point on BCI by a shallow channel of water which decreases in width during the dry season as the lake level drops. During especially severe dry seasons a land bridge may form, but Slothia is usually isolated from BCI by at least 15 to 20 meters of water.

Slothia was at one time entirely cleared and has been used intermittently in the past by the Smithsonian staff as a site for gardening, raising chickens, and various scientific studies. Iguanas may have been nesting on Slothia since the 1930's, but by the mid-1960's, when Rand discovered the nesting aggregation there, most of the island had

grown back up with second growth forest, so that the iguanas were confined to nesting in an approximately 5 by 10 meter area of flat, open ground. Rand (1968) initially estimated that between 100 to 200 female iguanas visited Slothia each nesting season and suggested that their annual activity there may have contributed to the persistence of this clearing. Iguanas have continued to nest in the clearing on Slothia every year since the aggregation was discovered, but in decreasing numbers. During this study, from 50 to 100 iguanas visited the clearing each year. The reason for this decline in numbers is not apparent, although disturbances from the human observers or the nesting crocodile on Slothia, as well as the development of alternate nesting areas nearby, may all have contributed.

A second iguana nesting aggregation is located on the island of DeLesseps, approximately 2 kilometers northwest of Slothia along the Panama Canal channel. DeLesseps was once continuous with the adjacent island of Orchid, but French construction activities and the later creation of Lake Gatun produced a narrow, deep cut between the two. Iguanas nest in exposed banks along this cut and in banks on the east end of DeLesseps. These banks are maintained in part by rainy season landslides and may have been used by iguanas as nesting sites for some time. Iguanas also nest in aggregation on the top of this island, which has been considerably altered in recent years. DeLesseps has been largely cleared and in 1974 a large portion of it was bulldozed level by the Panama Canal Commission. Very hard, mineral soils and bedrock were exposed, and the area is currently only sparsely colonized

by grasses. Iguanas nest in a number of restricted areas on the top of DeLesseps, presumably where soils are most suitable for digging. Although density estimates are difficult to obtain on DeLesseps, certainly far more iguanas nest there than on Slothia each year and DeLesseps currently may well be the largest nesting aggregation within the BCNM.

A more recently discovered area of iguana nesting activity is on two adjacent islands in the Gigante Bay area. This region only lately became a part of the BCNM, and both Mosca Island and the nearby island of Guindilla were recently cleared by the former resident of Guindilla. Tall grasses now cover most of these clearings, and iguanas nest on both islands in high numbers. This study focused primarily on the iguana nesting activity on Mosca island, so hereafter both areas will be referred to collectively as the Mosca nesting aggregation or site. Despite the seemingly uniform soil conditions within the clearings at this site, the iguanas still nest close together in confined areas, much as they do on DeLesseps. This is in contrast to the overdispersed distribution of nests frequently seen in other, less densely forested areas where iguanas occur (G. Rodda, pers. comm.). Perhaps when iguanas are required to nest within a limited area, benefits to nesting in even closer proximity to one another develop. A likely benefit is probably related to predator detection. Most of the areas on Mosca where iguanas nest are near the water's edge and the iguanas typically all flee to the lake when these areas are approached. Presumably a combined vigilance contributes to their effectiveness in detecting

approaching threats, which may be highly adaptive to iguanas nesting in restricted areas that predators can exploit once they locate. The iguanas on Mosca also nest in the same locations year after year, which also suggests that use of an area may condition the soil to make it more attractive in subsequent years (Rand & Dugan, 1983), thereby concentrating nesting activity for this reason, as well. Accurate estimates of iguana densities on Mosca and Guindilla are lacking, but they clearly have far more nesting activity each year than does *Slothia*, and they may rival DeLesseps as the largest nesting aggregation in the BCNM.

Two other nesting aggregations in the BCNM were not incorporated into this study because of their distant, peripheral locations. One is at a clearing on the Palenquilla Peninsula, which is separated from BCI by over a kilometer of Lake Gatun. During the dry season, the water between BCI and this peninsula is often extremely rough because of the north eastern trade winds that drive across this part of the lake. The second aggregation occurs at the Buena Vista lighthouse clearing, 2 kilometers distance from BCI. Both of these sites have nesting activity comparable to that seen on *Slothia* each year, and both, being mainland sites, experience clutch predation on occasion.

There also is limited iguana nesting activity at several minor nesting sites on and around BCI. Iguanas formerly have been reported to nest in the Laboratory Clearing on BCI, and did nest nearby in a small clearing at the lake edge in the years immediately preceding this study. This area has grown over with vegetation, however, and now no

nesting activity is known to occur anywhere within the Laboratory Clearing area.

In 1981, however, construction of a new growing house on BCI created a clearing just over 200 meters away from Slothia. During that nesting season, iguanas nested in a large mound of loose dirt at the construction site. Since completion of the growing house, iguanas have continued to nest in the surrounding areas that have not yet grown back with vegetation. A large, flat helicopter landing pad also was constructed between the growing house and the lake at about the same time, and iguanas also continue to attempt to nest there each year. For the purposes of this study, the initial mound of dirt, the open areas surrounding the completed growing house, and the helicopter landing pad area shall all be referred to collectively as the Growing House clearing or nesting site.

Iguanas also nest in a cleared area on the small island of Pepper, which lies next to BCI approximately midway between Slothia and DeLesseps. Given the types of areas where iguanas prefer to nest throughout the rest of the BCNM, it is surprising that this island is not the site of a major nesting aggregation. It is a small island in sheltered waters close to BCI with a clearing which receives direct sunlight and is not susceptible to flooding, yet very few iguanas visit this island each year and still fewer nest there. Perhaps some subtle differences in the soils on Pepper make this an unattractive site to the iguanas for nesting.

Finally, iguanas occasionally will nest in association with nests of leafcutter ants (Atta spp.). Although the areas surrounding such nests are typically devoid of vegetation, they are still usually shaded by the forest canopy. Temperatures within leafcutter ant nests may be elevated, however, possibly permitting iguanas to successfully nest under these conditions. Although leafcutter ants occur on BCI, the few documented instances of iguanas nesting association with these ants have all been in nests located on small islands around the BCNM. Iguanas also never have been encountered attempting to nest in treefall areas in the forests of BCI, despite the attention this forest has received from biologists over the years.

CHAPTER III

IGUANA NESTING SITE FIDELITY

Many of the nesting clearings around the BCNM are inconspicuous and relatively inaccessible and the ability of female iguanas to aggregate at these few sites is impressive. Since iguanas are potentially quite long-lived lizards (Müller, 1968), many of the iguanas present at a nesting aggregation each year are probably not nesting for the first time. Prior to this study, iguanas with distinctive physical characteristics or deformities had been seen over successive nesting seasons at the Slothia site. Whether the iguanas ever changed nesting sites over years or how they initially located a nesting site was not known, nor whether they might be returning to their natal sites upon first nesting. Therefore, an intensive mark-recapture effort was undertaken to investigate the nesting site fidelity of iguanas in the BCNM over successive nesting seasons.

Nesting Iguanas: Observation and Capture Methods

Previous studies of the Slothia nesting aggregation had primarily involved unobtrusive observation of nesting activity. Initial observations were made through a telescope from BCI and later from a blind constructed next to the nesting clearing on Slothia. In 1979, as part of a radiotelemetry investigation, Rand and Burghardt noosed several iguanas on Slothia from this blind and found that they returned to the clearing and continued nesting after their release. During the 1980

nesting season noosing efforts were intensified considerably and still the activities of the iguanas did not seem to be significantly disrupted. Most captured iguanas returned to the clearing shortly after their release and those present in the clearing during a noosing attempt soon resumed their activities. Furthermore, an American crocodile (Crocodylus acutus) that had nested on Slothia made numerous intermittent charges from the lake into the clearing which interrupted the nesting activities of the iguanas, but they soon returned to the clearing after the crocodile had departed. Since the iguanas appeared tolerant of such disturbances, intensive noosing was continued on Slothia during the 1981, 1982 and 1983 nesting seasons (but see below).

Iguanas at other nesting sites were captured in Havahart Tomahawk live-animal traps placed around the nesting clearings. In 1981 and 1982, the DeLesseps, Mosca, Pepper, and Growing House nesting areas were trapped. On DeLesseps, the exposed banks in which iguanas were known to nest were terraced each year so that the traps could be placed on the level areas created. At the other sites, the traps were set in and around areas where iguanas were found to nest. Because iguanas rapidly overheat when left in direct sunlight (McGinnis & Brown, 1966), the traps were covered with palm fronds or other large leaves. Iguanas entered the traps either because of the shade provided or as a result of their normal exploration of the nesting clearings. When the traps were not set for capture, they were left open so that the iguanas could habituate to passing through them.

During the 1983 nesting season, only the Growing House nesting site was trapped. The dry season had begun unusually early this year, however, which produced exceptionally low lake levels, so the remaining traps were set out on the beaches that had become exposed around the Laboratory Bay area.

Throughout this study, iguanas at the various nesting sites were occasionally encountered digging in shallow burrows and some of these were successfully captured by hand.

All iguanas captured during this study were weighed, measured for snout-vent length (SVL) and tail length, and marked and released at their site of capture. Permanent marks were given to each iguana by systematically clipping several dorsal crest scales in unique, individually characteristic patterns (see Appendix). No evidence of crest scale regeneration was observed during this study. Each iguana also was painted with a temporary field identification number before being released each year.

In 1981, 1982, and 1983, the nesting behavior of the iguanas on Slothia was observed from the blind located at the edge of the nesting clearing. For each day of the nesting season, observations began shortly after sunrise, before the iguanas became active, and ended at dusk when it became too dark to see (1290 person-hours of observation over three seasons). Those iguanas that laid while still visible within their burrows were classified as laying shallow; those that disappeared completely underground to later emerge spent were classified as laying deep. An iguana was considered to have experienced

nesting interference if it was interrupted while laying by the nest-guarding crocodile or if its clutch was disturbed by other digging iguanas.

Continuing research on iguanas in the BCNM has provided additional information on the nesting patterns of those iguanas marked between 1980 and 1983. In 1984, iguanas were again captured on Slothia, and other iguanas were tentatively identified there on the basis of their patterns of missing crest scales as observed from the blind. Iguanas also were trapped in 1984 at the DeLesseps and Growing House nesting sites.

Nesting Iguana Recapture Patterns

Return of nesting iguanas to the Slothia aggregation. During the 1980 nesting season, 65 iguanas were noosed at the Slothia nesting site, representing about two thirds of the iguanas that visited Slothia that year. From 1981 to 1983, a majority of the iguanas that visited Slothia were captured; all but two iguanas that nested on Slothia in these years were marked individuals. A majority of the iguanas that visited Slothia in 1984 were either captured or tentatively identified on the basis of their dorsal crest scale patterns, as well. Thus, the information obtained from the Slothia nesting site permits inspection of the degree of fidelity exhibited by the iguanas to this site over successive years.

A total of 165 individual iguanas were seen on Slothia during one or more of the five nesting seasons in which iguanas were intensively

noosed. However, only 20% to 45% of the iguanas seen on Slothia in a given nesting season returned again the following year. Disturbances to the iguanas from the capturing procedures may have contributed to these surprisingly low rates of return. Although most iguanas visited the clearing again following their release, some of these iguanas did not continue their nesting efforts, but instead apparently left Slothia within a day or two of their captures. Table 1 shows the proportion of marked iguanas that did and did not remain on Slothia during the three years with the most complete information, as well as the return rates for each group and whether they remained following their captures in the second year. Those iguanas that did not remain on Slothia for more than two days following their release exhibited lower rates of return to Slothia the following year than did those iguanas that remained. Also, of those iguanas that visited Slothia in two successive nesting seasons, those that did not remain on Slothia following their captures in the first year also tended to not remain following their release in the second. Although neither of these differences are statistically significant, they suggest that some iguanas may have been more sensitive to disturbances than others and thereby contributed more to the low rates of return to the Slothia nesting site over successive years.

Each year, however, a number of individually recognizable but unmarked iguanas left Slothia spontaneously before they could be noosed, which suggests that capturing activity was not the only factor which could have influenced iguanas to leave Slothia without nesting or

Table 1

Rates of Return to the Slothia Nesting Site Over Successive Years for Iguanas That Remained on Slothia and That Departed Slothia Following Their Release

Year	Number of iguanas released on Slothia	Number of these iguanas to return to Slothia the following year	Number of these iguanas to depart Slothia following their release
<u>1981</u>			
Remained on Slothia	54	25	5
Departed Slothia	8	3	2
<u>1982</u>			
Remained on Slothia	35	13	6
Departed Slothia	11	3	2
<u>1983</u>			
Remained on Slothia	28	7	0
Departed Slothia	11	1	0

to not return to Slothia the following nesting season. The nest-guarding crocodile was responsible for considerable disruption of the nesting activity on Slothia each year and the iguanas also interfered with one another to varying extents. Competition between iguanas for possession of the nest burrows was intense and not all of the iguanas that visited Slothia each nesting season laid there. Observations of nesting activity from 1981 to 1983 revealed that a higher proportion of those iguanas that did lay on Slothia returned the following year than did those that were unsuccessful in their attempt to nest on Slothia (three years pooled, Heterogeneity $G = 9.345$, $p < .005$). Also, many of the iguanas that returned to Slothia in 1983 and 1984 without having laid there the year before were iguanas that had successfully nested on Slothia in other earlier years. There were no significant differences in return rates between those iguanas that laid shallow versus laid deep, or between those that did versus did not experience nesting interference over these years.

Recaptures over nonconsecutive years. When so many of the iguanas marked on Slothia in 1980 failed to return the following year, it was suspected that the iguanas might be reproducing in alternate years. Since clutch size and female size are highly correlated in iguanas (Fitch & Henderson, 1977; Rand, 1984), it seemed possible that some of the iguanas might have been foregoing reproduction during a given year to invest more energy towards growth, so that larger clutches could be produced in subsequent nesting seasons.

A total of 143 individual iguanas were captured on Slothia between 1980 and 1983, and 47 of these iguanas were recaptured there one or more times over subsequent years (Figure 3). Of the 14 iguanas whose first and last captures spanned three years, ten were seen in all three years and four missed the intervening year. Of the 11 iguanas whose first and last captures spanned four years, seven were present on Slothia all four years, three skipped one year and one skipped two years. Finally, four iguanas were seen on Slothia in 1980 and 1984. One of these was present in each intervening year, one skipped just one nesting season and one was present only in the first and fifth year. The fourth iguana in this class visited Slothia in four of the nesting seasons, and was found nesting elsewhere in 1982 (see below).

The sizes of the iguanas that returned to Slothia over nonconsecutive nesting seasons did not differ significantly from the average size of Slothia iguanas ($t = -.84$, $p > .05$, mean SVL of the nine iguanas for the years preceding their absence = 378 mm versus mean last-capture SVL of all iguanas captured on Slothia = 370 mm). There also was no significant difference between the growth demonstrated by the eight iguanas that were absent for one year on Slothia and the growth seen in the 20 iguanas that were present on Slothia over three consecutive nesting seasons, although the iguanas that missed a year did grow slightly more ($t = .175$, $p > .05$, mean change in SVL of iguanas that skipped a year = 12.4 mm versus mean change in SVL of iguanas over their last three consecutive nesting seasons on Slothia = 11.7 mm).

Year					Number of Iguanas
1980	1981	1982	1983	1984	
X					42
X	X				7
X	X	X			5
X			X		1
X	X		X		1
X		X	X		1
X	X	X	X		4
X				X	1
X	X	X		X	1
X	X		X	X	1
X	X	X	X	X	1
65	X				24
	X	X			8
	X		X		2
	X	X	X		4
	X	X		X	1
	X	X	X	X	3
	62	X			13
		X	X		2
		X		X	2
		X	X	X	1
		45	X		16
			X	X	2
			39	X	22
				35	

X = Present on Slothia

Figure 3. Recapture results for female iguanas at the Slothia nesting site over five nesting seasons.

The low frequency with which iguanas were seen to skip nesting seasons on Slothia and the unspectacular growth demonstrated by those iguanas that missed an intervening year suggests that deferring reproduction to enhance growth is not a strategy regularly employed by female iguanas once they begin to reproduce. If iguanas do nest each year after attaining sexual maturity, however, the question still remains as to where those iguanas were nesting that did not return to Slothia.

Crossover between nesting sites. The most obvious alternate location where Slothia iguanas could have nested is the nearby Growing House clearing site on BCI. A total of 25 iguanas were trapped at the Growing House site from 1980 to 1984. Seven iguanas were captured either at this site or on Slothia in one year and on the other site in a subsequent year and six iguanas were seen on both sites during the same year. Given the close proximity of these two sites and the evidence of free movement between them, they will be considered hereafter as a single, collective nesting aggregation.

An additional 209 iguanas were trapped at the other nesting sites and beaches around the BCNM from 1981 to 1984. Most of these iguanas were captured at the nesting aggregations of DeLesseps and Mosca. Probably only a small fraction of the iguanas that visited these sites each year were captured. There also was limited nesting activity on the small island of Pepper in 1981, 1982, and 1984. In 1983, no iguanas nested on Pepper, but tail-tracks in the sand revealed that iguanas were exploring most of the newly exposed beaches that year, and

iguanas were captured at three of the six regularly trapped beach sites.

The recapture information obtained from these sites indicates that the movements between them by nesting females was extremely limited. In 1984, five *Slothia* iguanas were identified on the basis of their dorsal crest scale patterns as seen from the blind. Three had patterns of missing crest scales corresponding to iguanas marked on *Slothia* in previous years and two had crest scale patterns of iguanas that had been marked at the DeLesseps nesting site in 1981 and 1982. This is the only information obtained during this study which indicates that any of the nesting iguanas ever visited more than one of the major nesting sites. When only confirmed, "hands-on" recaptures are considered, only two cases of crossover between sites were documented, and both involved captures at minor nesting sites on Pepper and Salt islands, which lie midway between the *Slothia* and DeLesseps nesting aggregations. One iguanas noosed in 1980, 1981, 1983 and 1984 on *Slothia* was trapped in 1982 attempting to nest at the clearing on Pepper. Another iguana was initially captured in 1983 at an exposed beach on Salt Island. In 1984, this iguana was captured at the DeLesseps nesting aggregation. (A third iguana initially captured on an exposed beach in 1983 also was captured on DeLesseps in 1984, but the exceptional movements of this iguana, as determined by radiotelemetry, are discussed in detail in Chapter V).

The remaining 59 iguanas captured in two or more nesting seasons demonstrated fidelity to their site of original capture. Figure 4

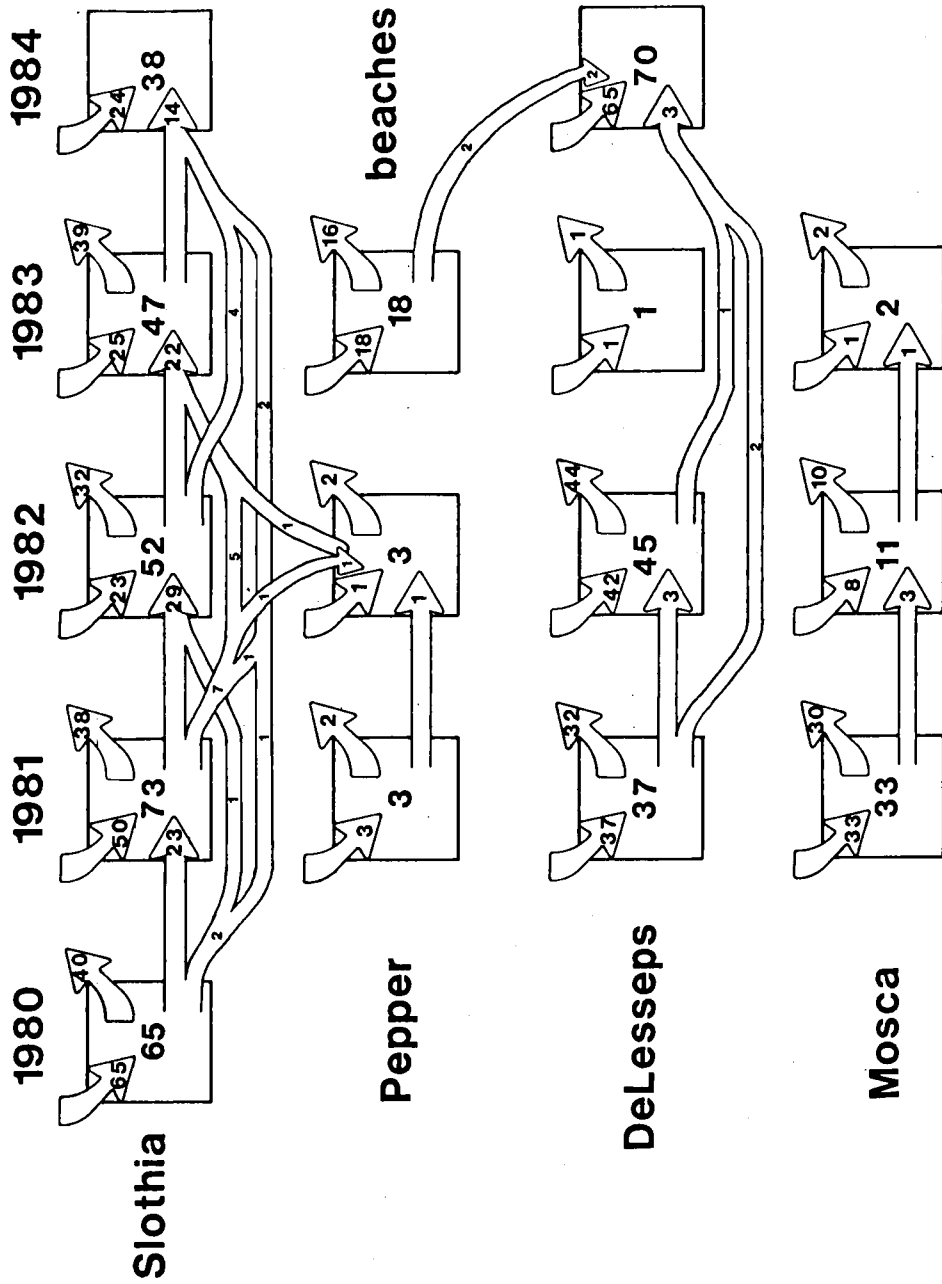


Figure 4. Recapture results for nesting iguanas within the BCNM over four nesting seasons. Arrows into cells indicate the number of new iguanas marked at a site that year, arrows out of cells indicate the number of iguanas that were captured at a site and not seen again, and arrows between cells represent recaptures over years.

summarizes the capture results for all nesting sites from 1980 to 1984. These results may actually underrepresent the degree of fidelity exhibited by these iguanas. Many iguanas trapped at the DeLesseps and Mosca nesting sites could have returned in later years but avoided the traps. This seems especially likely given that only three of the 161 trapped iguanas released in 1981, 1982, and 1983 were retrapped again during the same nesting season, despite the fact that painted iguanas were repeatedly seen fleeing the nesting areas when these areas were approached to check the traps. This learned avoidance of the traps probably contributed to the low recapture rates at the trapped sites over successive nesting seasons as well.

This bias would not have reduced the chances of detecting cross-over between the major nesting sites, however. If substantial numbers of iguanas had been changing sites from year to year, more of the trap-naïve *Slothia* iguanas should have been trapped while nesting elsewhere and any marked DeLesseps or Mosca iguanas would certainly have been noosed had they visited *Slothia*.

There is some indication that the iguanas were exhibiting natal nesting site fidelity. Between 1974 and 1978, over 700 newly hatched iguanas were toe-clipped on or near the *Slothia* nesting site (Burghardt, pers. comm.). At present, there is no evidence for any skew in the primary sex ratio of iguanas, so roughly half of these individuals could be expected to have been females. Yet only seven of the 396 nesting female iguanas captured during this study were individuals that had been toe-clipped as hatchlings. Despite intensive

trapping efforts at other sites, all seven of these individuals were captured on Slothia. Although these data are limited, they document that some iguanas do return to their natal site to nest, and provide no evidence of nesting by iguanas at sites other than the ones from which they hatched.

Nesting in new clearings. Despite the fidelity most iguanas exhibited over years, some iguanas did attempt to nest in new clearings that became available to them during this study. Three of the 65 iguanas marked on Slothia in 1980 were trapped while exploring the new Growing House construction site in 1981. Sixteen iguanas nested in the large mound of loose dirt present at this site this year and 14 clutches were destroyed by nest predators (Rand & Dugan, 1983). Iguanas also nested at two exposed beaches in 1983; one a mainland beach that also suffered heavy clutch predation and the other a beach on Salt Island, which experienced a successful hatch (see Chapter VI). Iguanas also were captured at a third beach where no nesting activity was apparent, and there were iguana tail-tracks in the sand of virtually every beach inspected. None of the iguanas captured on the beaches in 1983 were recaptures, but a number had worn dorsal crests. Burrowing appears to be the primary factor producing crest wear in iguanas, which suggests that at least some of the iguanas captured on the new nesting areas had nested elsewhere before.

The nesting site fidelity demonstrated by most of the female iguanas in this study suggests that they may have had a familiarity with the location of their nesting sites that they relied upon year

after year. However, because iguanas were seen to nest opportunistically in new clearings, it appears that at least some of the iguanas were exploring the shoreline and exercising some selectivity during their migrations as to where they nested.

Disappearance of marked iguanas. The fate of the numerous female iguanas that were captured and released but not recaptured is unclear. Certainly mortality was responsible for some of the disappearance of these marked iguanas. Adult iguanas are susceptible to predation (Greene et al., 1978) and female iguanas may be especially at risk while involved in their nesting migrations and activities. Many iguanas captured during this study had scars or other evidence of having survived a predation attempt and 37% of the iguanas had evidence of tail regeneration upon first capture. There are some inherent problems with attempting to make inferences about predator pressures based upon tail break frequencies, (i.e., tails are not always lost to predators, or at least to predators which still pose a threat to adult iguanas; see Schoener, 1979), but even so, 17 of the 64 iguanas recaptured during this study either had lost complete tails or had lost more of a regenerate tail from the time of their first capture, which suggests that adult female iguanas do experience some predation. In fact, two iguanas attempting to nest on *Slothia* from 1980 to 1983 were observed to fall prey to the nest-guarding crocodile and several more iguanas were found floating dead in the lake, also probably victims of crocodile attack. Unfortunately, not enough is known at present about iguana demographics to permit estimation of the amount of disappearance

of the female iguanas that can be attributed to mortality. Certainly mortality is not a trivial factor, but it also was probably only responsible for a portion of the marked iguanas not seen again.

Another unresolved question related to this disappearance of marked iguanas concerns where those iguanas went to lay that were unsuccessful at nesting on Slothia. A few were captured at the nearby Growing House site, but there was not indication that any moved to the other known nesting areas around the BCNM. Inspection of all known leafcutter ant nests in the Laboratory Bay area during the 1983 nesting season failed to produce any evidence that iguanas were nesting in these areas. There may have been scattered isolated nesting elsewhere that went undetected, but if so, it must have occurred in areas that would be considered at present as unsuitable for incubation purposes.

An observation from the 1983 nesting season may be pertinent to this question. An iguana on Slothia laid its clutch on the surface of the ground under a pile of leaves at the edge of the clearing. Surprisingly, this clutch was undisturbed when uncovered a month later, well after the end of the nesting season. The outermost eggs of the egg mass had desiccated, but 16 of the 32 eggs still looked potentially viable and five of these were artificially incubated to hatching.

Four other iguanas were observed to spontaneously oviposit on the surface of the clearing on Slothia from 1980 to 1983. These exposed clutches were quickly destroyed by vultures. There also was evidence to suggest that five other iguanas may have laid their eggs on the

surface before leaving Slothia in 1981. Each of these iguanas was seen gravid one day and spent the next without having been observed to lay in the clearing. Iguanas occasionally did lay overnight on Slothia, but they usually were seen the following morning filling and defending their nest burrows. These five iguanas simply passed through the clearing without stopping to fill and showed no signs of having been underground. A search of the leaf-litter on Slothia after this nesting season, however, failed to produce any signs of their eggs.

This curious behavior of laying on the surface is probably due to the inability of the iguanas to retain eggs indefinitely. Nesting is energetically taxing, especially when competition for the nest burrows is intense. Some females may just be unable to secure a suitable nest burrow in time. In a long-lived species such as the green iguana, aborting a clutch on occasion may be more adaptive than a continued attempt to nest in a year when competition is intense or the risk of predation is great.

Conclusions: Iguana Nesting Movements

The recapture results indicate that female iguanas tend to return to the same nesting sites year after year. There is some indication that the iguanas actively assess the quality of the sites they visit: some iguanas seemed more prone to abandon a site after having been captured than did others, and those iguanas that were successful in laying at a site were more likely to return to the site over subsequent years. The iguanas also explored and occasionally nested in new

clearings that became available to them over the course of this study. The evidence does not suggest that the few iguanas captured over nonconsecutive nesting seasons were only reproducing in alternate years. These iguanas probably nested during the intervening year at other locations near their original site of capture. Although the noosing and trapping disturbances of this study could have increased the tendencies of the iguanas to change nesting sites, the documented incidence of crossover between nesting sites was quite limited. The data available on recaptures of iguanas that had been marked as hatchlings suggests that the female iguanas may have been demonstrating fidelity to their natal nesting sites.

The two major unresolved questions arising from this investigation concern the low recapture rates of the marked iguanas and the possibility that scattered isolated nesting may have occurred undetected. Mortality no doubt accounted for some of the disappearance of marked iguanas; the remaining marked iguanas did not appear to be going to other aggregations to nest, but may have opted for solitary nesting following their capture. There is no reason to suspect, however, that solitary nesting, if it occurs, would involve movements greater than those made by females nesting at the traditional communal sites.

CHAPTER IV

GENETIC CHARACTERISTICS OF THE POPULATION

Nesting female iguanas in the BCNM were shown to exhibit strong nesting site fidelity, but they also explored and opportunistically nested in new clearings that became available, indicating that a strict imprinting mechanism was not in operation. High rates of return by female iguanas to the same nesting sites over years also might be expected, however, if the females simply remained near their sites throughout the year. With a scarcity of nesting sites, limited dispersal by hatchling iguanas also might be advantageous. Female hatchling iguanas remaining near their natal site would stand a better chance of relocating this proven site when they first nested and also would minimize the costs of their nesting migrations. Similarly, male hatchling iguanas remaining near their natal sites would insure access to such females when they reached breeding age. Thus, with widely separated nesting sites and limited dispersal from them by the iguanas, each nesting site could become a focal point for a semi-isolated deme or local population of iguanas associated with it. To inspect for evidence of such a genetic subdivision of the iguana population in the BCNM, samples obtained from female iguanas captured at the major nesting sites were examined electrophoretically.

Sampling Techniques and Electrophoretic Methods

Sacrificing breeding females from the BCNM for electrophoresis was not feasible. It also was deemed that biopsies for muscle samples and

cardiac or ocular sinus punctures for blood samples would be too traumatic to these already stressed iguanas. However, the crest-clipping marking technique (see Appendix) yielded a small amount of tissue at the base of each cut dorsal scale. This procedure rarely resulted in bleeding, however, so to obtain blood, the terminal 5 millimeters of tail of each iguana was clipped and a small amount (approximately 100 microliters) of blood was "milked" from the cut tail tip and collected in heparinized capillary tubes. This bleeding technique worked for many, but not all, of the iguanas captured. These sampling procedures did not appear to have any adverse effects on the iguanas.

Samples obtained in 1980 from nesting iguanas captured on Slothia were labeled and placed on ice until they could be transported to the laboratory on BCI, where they were stored in liquid nitrogen for the remainder of the field season. The samples were then packed in dry ice, transported to the University of Tennessee, Knoxville (UTK) and stored in an ultracold (-80°C) freezer. Each sample was thawed and prepared on the same day as electrophoresis. Tissue samples (crest scales and cut tail tips) were minced and ground in approximately equal weight to volume ratios of tissue to grinding buffer (Selander et al., 1971). The whole blood samples were diluted (1:1) with deionized water.

Horizontal starch gel electrophoresis techniques followed Selander et al. (1971). Gels consisted of 11.75% (47 gm starch/400 ml buffer) electrostarch (Otto Hiller Company, P.O. Box 1294, Madison WI 53701,

Lot 392). Gels were run under differing electrophoretic conditions and stained using recipes modified from Selander et al. (1971) and Harris and Hopkinton (1978). Alleles of presumptive genetic loci were labeled according to the relative mobilities of their protein products. Where multiple loci were demonstrated on a particular stain, each locus was designated numerically.

Analysis of the 1980 samples revealed that tissue samples from the bases of the crest scales were sufficient for a maximum of two electrophoretic runs per individual; the tail tips provided little or no additional tissue. The volume of blood collected from the cut tail tips usually was sufficient for several electrophoretic runs. Resolution of these whole blood samples was often poor, however, because they had not been separated into cellular and plasma fractions and analyzed separately.

In 1981 and 1982, samples were obtained from female iguanas captured at each of the three main nesting sites of Slothia, DeLesseps, and Mosca. The whole blood samples obtained from these iguanas were centrifuged and the cellular and plasma fractions were separated prior to their storage in liquid nitrogen. Again, the tissue and blood samples were transported to UTK, stored in the ultracold, and prepared for electrophoresis as in 1980, with the exception that cellular blood fractions were diluted (1:1) and mixed with deionized water before analysis and the plasma samples were analyzed without dilution.

Genetic diversity among conspecific populations is most often expressed as differences in allele frequencies at the polymorphic loci

(Avisé, 1974). Because of the limited quantities of tissue and blood samples obtained from the nesting iguanas, the electrophoretic survey focused on the identification of robustly polymorphic loci. Even so, only two segregating loci were identified in this population: a 6-Phosphogluconate dehydrogenase locus (6-PGD 2) on the Tris-Citrate pH 8.0 buffer system for tissue, and an esterase locus (Est) with an α -naphthyl acetate substrate on the Poulik buffer system for the cellular blood fractions. Samples obtained from the nesting female iguanas in 1981 and 1982 were subjected to electrophoresis on these two systems when sample volumes permitted, individuals were rerun to establish the reliability of the scorings of these loci. Expected genotype proportions under Hardy-Weinberg equilibrium were calculated for each locus using Levene's (1949) formula for small sample sizes. These were compared to the observed proportions by a G test for goodness of fit (Sokal & Rohlf, 1981). Allele frequencies at the three nesting sites were compared statistically using a Heterogeneity G test (Sokal & Rohlf, 1981). Wright's (1978) standardized variance in allele frequencies among these sites (F_{ST}) also was calculated for the common allele at each locus, following the procedures of Eanes and Koehn (1978). F_{ST} is an estimate of the variance in allele frequencies at a locus that occurs among population subdivisions and thus provides a measure of the genetic differentiation within a population.

In 1983, nesting female iguanas were not sampled, but hatchling iguanas were collected and killed to provide more substantial samples for electrophoretic survey. Because hatchlings from the BCNM could not

be collected for these purposes, hatchlings were obtained from three other sources. Twenty-five hatchling iguanas were collected from along an 800 meter transect along the Rio Duablo Abajo, west of Santo Tomas, Chiriqui Province, in western Panama (D. Werner, pers. comm.) and another 30 hatchling iguanas were obtained from Hato Masaguaral, Guarico Province, Venezuela. In addition, 28 hatchling iguanas were obtained from artificially incubated eggs that had been laid by females from central Panama. Some of the eggs were obtained from BCNM iguanas, but most were obtained from three females collected near Gamboa, approximately 15 kilometers southeast of the BCNM. Only four clutches contributed all but four of the 28 hatchlings obtained from the artificially incubated eggs. The hatchlings collected from western Panama and Venezuela, unlike those obtained from incubated eggs, probably were not clutch-mates, as they were collected away from the nesting sites at approximately one week of age.

Muscle samples (whole hind legs) obtained from the central Panama, western Panama, and Venezuela hatchlings were stored in liquid nitrogen until they could be transported to UTK and placed in the ultracold freezer. To prepare the samples for electrophoresis, they were thawed, minced, and mixed in a 1:1 ratio (gm/ml) of tissue to grinding buffer (Selander et al., 1971). This mixture was centrifuged at 15,000 X g for 20 minutes at 4°C; the supernatant was decanted and stored in the ultracold until analyzed.

These samples were subjected to electrophoretic analysis on all monomorphic and polymorphic loci that had been identified during the

previous electrophoretic surveys of the crest scale and blood samples. The esterase locus proved to be better resolvable for these muscle samples on the LiOH buffer system rather than on the Poulik buffer system that had been used with blood samples. Table 2 summarizes the electrophoretic conditions used for each of the 20 presumptive genetic loci stained in this analysis. Allele scoring and statistical analysis were as described above. The average proportion of loci heterozygous per individual was calculated for each population from direct counts of heterozygotes.

Results of the Electrophoretic Analysis

Crest scale tissue samples from the nesting iguanas occasionally were not sufficient for electrophoretic analysis and blood samples could not be obtained from every female, so the sample sizes for the allozyme comparisons are less than the actual number of iguanas captured in 1981 and 1982. Allele frequencies at each nesting site for the esterase and 6-PGD loci are summarized in Table 3. Observed genotype proportions for each locus at each site did not differ significantly from those expected under Hardy-Weinberg equilibrium.

No significant allelic differences among the female iguanas from the three nesting sites were demonstrated at the 6-PGD locus, but significant heterogeneity in allele frequencies among these females was demonstrated at the esterase locus (Heterogeneity G test, $p < .05$). F_{ST} values also indicated that significant allele frequency variation existed among females from the three sites at the esterase locus ($\chi^2 =$

Table 2

Electrophoretic Conditions for the Protein Loci Scored in the Analysis of Allozyme Variation in Iguana iguana Tissue Samples

Gel buffer systems ^a	Voltage (v)	Time of run (hrs)	Protein stains
Tris-Citrate 8.0	125	5	Glutamate oxalate transaminase (GOT) Glycerol-3-phosphate dehydrogenase (α -GPD 1) Glycerol-3-phosphate dehydrogenase (α -GPD 2) Isocitrate dehydrogenase (M-IDH 1) Isocitrate dehydrogenase (M-IDH 2) Malate dehydrogenase (S-MDH 1) Malate dehydrogenase (S-MDH 2) Phosphoglucumutase (PGM) 6-Phosphogluconate dehydrogenase (6-PGD 1) 6-Phosphogluconate dehydrogenase (6-PGD 2)
LiOH	325	4	Esterase (EST), α -naphthyl acetate substrate General protein (GP 1) General protein (GP 2) General protein (GP 3) General protein (GP 4) Leucine aminopeptidase (LAP) Malic enzyme (M-ME)
PGI/Phos	100	5	Octanol dehydrogenase (ODH 1) Octanol dehydrogenase (ODH 2) Superoxidase dismutase (SOD)

^aSource: Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, & J. B. Gentry. (1971). Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the Old-field mouse (Peromyscus polionotus). Studies in Genet. VI., Univ. Texas Publ., 7103, 49-90.

Table 3

Allele Frequencies from the 6-PGD and EST Loci in Iguanas Captured at Three Nesting Site Locations, With F_{ST} and G_H Values

Nesting site	6-PGD				EST			
	A	B	C	Sample size	A	B	C	Sample size
DeLesseps	.08	.77	.15	152	.24	.76	--	76
Slothia	.07	.72	.21	158	.27	.71	.02	104
Mosca	.06	.74	.20	80	.50	.50	--	32

$$F_{ST} = .0025$$

$$\chi^2 = 1.92, df = 2$$

$$p > .05$$

$$G_H = 2.02, df = 4$$

$$p > .05$$

$$F_{ST} = .0357$$

$$\chi^2 = 15.15, df = 2$$

$$p < .001$$

$$G_H = 7.14, df = 2$$

$$p < .05$$

15.15, $df = 2$, $p < .001$), but not for the 6-PGD locus (Table 3). The significant differences at the esterase locus were clearly the result of disparate allele frequencies in the female iguanas from the Mosca nesting site.

Table 4 summarizes the results of the electrophoretic analysis of the hatchling iguana samples that were collected from central Panama, western Panama, and Venezuela. The allele frequencies present in the central Panama hatchlings at the EST locus differed from those of the nesting females from the BCNM (Heterogeneity G test, $p < .005$). This is not surprising considering that many of the hatchlings sampled were offspring of females that were not residents of the BCNM and that these hatchlings also were not a random sample, because they had been obtained from only a few clutches. Even so, the estimates of average heterozygosity per individual calculated from these samples for central Panama is probably sound. Nei (1978) determined that average heterozygosity in a population can be accurately estimated from a small number of individuals, provided that a sufficiently large number of loci are studied and the average heterozygosity is low. The average heterozygosity estimate for the central Panama population, as well as those calculated for the other two populations that did not share this sampling bias, were all low, as were the proportions of polymorphic loci demonstrated for each population (Table 5).

Allele Frequency Differences Among the Nesting Sites

The evidence of allele frequency differences at the esterase locus between female iguanas captured at the Mosca nesting aggregation and

Table 4

Allele Frequencies at 20 Protein Loci for Three *Iguana iguana* Populations

Locus		Central Panama	Western Panama	Venezuela
6-PGD 2	a'	-	-	.05
	a	.125	-	-
	b	.768	.14	-
	c	.107	.86	.95
EST	a'	-	-	1.0
	a	.111	-	-
	b	.889	1.0	-
6-PGD 1	a	-	1.0	-
	b	1.0	-	1.0
PGM 2	a	-	-	.05
	b	1.0	1.0	.95
SOD	a	.04	-	-
	b	.96	1.0	1.0
S-MDH 2	a	-	.02	-
	b	1.0	.98	1.0
S-MDH 1		1.0	1.0	1.0
M-ME		1.0	1.0	1.0
ODH 1		1.0	1.0	1.0
ODH 2		1.0	1.0	1.0
M-IDH 1		1.0	1.0	1.0
M-IDH 2		1.0	1.0	1.0
α -GPD 1		1.0	1.0	1.0
α -GPD 2		1.0	1.0	1.0
GOT		1.0	1.0	1.0
LAP		1.0	1.0	1.0
GP 1		1.0	1.0	1.0
GP 2		1.0	1.0	1.0
GP 3		1.0	1.0	1.0
GP 4		1.0	1.0	1.0

Table 5

Levels of Genetic Variability in Three Green Iguana Populations

Population	Proportion of loci (n = 20)	
	Polymorphic per population	Heterozygous per individual
Central Panama	.15	.0304
Western Panama	.10	.012
Venezuela	.10	.010
Mean =	.12	.0175

females that were captured on Slothia and DeLesseps indicates that these iguanas may belong to two distinct, separate local populations. Iguanas from the Mosca nesting site probably do not often disperse far enough to encounter and mate with the iguanas from the other two sites. Strong selective pressures acting differently on iguanas near Mosca than on iguanas near Slothia and DeLesseps could maintain the observed differences at the esterase locus, even in the presence of gene flow between these demes, but pronounced selective differences over such short distances seem unlikely. There is, however, a north-south rainfall gradient across this portion of the isthmus of Panama (Rand & Rand, 1982) such that the Mosca nesting site should receive, on average, less rainfall. Even mild selective pressures related to such an environmental gradient could produce allelic differences between iguanas from Mosca and the other sites if gene flow between the iguanas from these two areas is restricted. Selection has been proposed as the force behind clinal single locus allelic variations along environmental gradients for a number of other species as well (Christiansen & Frydenberg, 1974; Johnson, 1976; Johnson, 1971; Koehn, 1969; McKenzie & Parsons, 1974; Merritt, 1972).

The genetic differences between the Mosca iguanas and those captured at the other two nesting sites also may be due to stochastic factors. With limited dispersal of male and female hatchling iguanas from the nesting sites and adult female nesting site fidelity, the iguanas in the BCNM might become distributed into somewhat reproductively isolated demes associated with the nesting sites. Also, each

deme may have experienced a founder effect at the time when the site became available for nesting purposes after the formation of Lake Gatun, and Mosca is probably a recently established nesting site (Rand, pers. comm.). With small deme sizes and restricted gene flow, drift also could have contributed to a continued random genetic divergence of the iguanas associated with these nesting sites. The polygynous mating system, variable female fecundity, and overlap of generations of iguanas (see Chapter II) all would have contributed to a reduction in their effective deme sizes (Futuyma, 1979) and the nesting site fidelity exhibited by the female iguanas further suggests that gene flow between the sites may be restricted. Other studies have demonstrated marked local genetic differentiation in animal populations that presumably originated from a structuring of these populations through low vagility or other behavioral factors (Burton & Feldman, 1981; Hedgecock, 1978; Patton & Feder, 1981; Patton & Yang, 1977; Selander, 1970; Selander & Kaufman, 1975; Taylor & Powell, 1977).

Only two polymorphic loci were demonstrated during the analysis of the samples obtained from the nesting female iguanas; one exhibited allele frequency differences among the nesting sites, the other did not. Thus, it is not clear whether the differences observed between the Mosca females and those from Slothia and DeLesseps were due to selective differences operating specifically on the EST locus, or to drift and founder effects that by chance were not evident with the 6-PGD locus. Had more polymorphic loci been available for inspection and the EST locus still proved to be the only one to show allelic

differences among the sites, then selective influences would have been more strongly suggested. Conversely, had a number of polymorphic loci been shown to exhibit allele frequency differences among the sites, then the operation of drift or founder effects would have been implicated. While the results of this analysis do not permit a confident resolution of this question, a restriction of gene flow between iguanas associated with the Mosca nesting site and those near Slothia and DeLesseps probably does function to help maintain the allele frequency differences between these iguanas at the esterase locus.

Levels of Genetic Variability in Green Iguanas

The more extensive electrophoretic analysis conducted on samples obtained from hatchlings show green iguanas to have very low levels of genetic variability relative to most other lizard species that have been studied. Gorman et al. (1977) have reviewed the available information on levels of heterozygosity in mainland lizard populations. They excluded insular populations from consideration because such populations exhibit varying degrees of reduction in genetic variability, presumably due to factors such as founder effects or small effective population sizes on small islands (Gorman et al., 1975; Soule & Yang, 1973). In mainland lizard populations, however, they found that levels of heterozygosity could be categorized into three distinct ranges of values: (1) around 2% for fossorial and nonvagile species, (2) around 5% for more typical, sit and wait iguanid lizards, and (3) over 9% for actively foraging predatory lizards.

Table 6 has been modified from Gorman et al. (1977) to include recently published information on levels of heterozygosity in sexually reproducing mainland lizard populations. Subsequent studies of genera already included in Gorman et al. (1977) have increased the ranges of heterozygosities initially reported, but without greatly altering the mean heterozygosity values for any genus. Also, information on six additional genera has increased by three the number of families considered, thereby broadening the basis for comparison.

All three of the Iguana iguana populations inspected in this study exhibited low levels of genetic variability as compared to most other mainland lizards, including other iguanids. Four other lizard genera exhibited comparably low levels of average heterozygosity: three fossorial forms (Bipes, Anniella and Typhlosaurus) and the genus Uma, an iguanid genus which is restricted to sand dune habitats (Norris, 1958; Stebbins, 1944). At the other end of the continuum, two presumably highly vagile, predatory lizard species, as well as several species of the lacertid genus Acanthodactylus, exhibit high levels of heterozygosity. Little is known about Acanthodactylus except that they apparently are territorial, yet exhibit heterozygosity levels among the highest recorded for any vertebrate (Blanc, 1980; Blanc & Cariou, 1980).

Gorman et al. (1977) noted an apparent correlation between increasing vagility and increasing heterozygosity in the lizard genera studied. They put forward two hypotheses that could explain this correlation; these being the same hypotheses that have been evoked to

Table 6

Levels of Genetic Heterozygosities in Mainland Lizard Populations^a

Habitat mode	Family Genus	# Populations (# Species)	Range of % heter.	Mean % heter. ^b	References
Fossorial	Amphisbaenidae ^c				
	Bipes	3(3)	0.0-3.2	1.1	Kim et al., 1976
	Anniellidae				
	Anniella	4(2)	0.0-2.2	1.1	Bezy et al., 1977
Terrestrial or arboreal and territorial sit and wait	Scincidae				
	Typhlosaurus	3(2)	0.6-1.8	1.1	Kim et al., 1978
	Iguanidae				
	Uma	5(5)	0.3-2.9	1.3	Adest, 1977
	Iguana	3(1)	1.0-3.0	1.7	This study
	Crotaphytus ^d	5(4)	2.1-4.6	3.2	Montanucci et al., 1975
	Uta	17(1)	0.0-10.0	4.8	McKinney et al., 1972
	Anolis	10(1)	1.8-6.8	5.1	Webster et al., 1972
	Callisaurus	4(1)	3.0-7.9	5.5	Wade et al., 1983
	Sceloporus	27(3) ^e	0.0-14.8	6.8	Adest, cited in Gorman et al., 1977
Terrestrial or arboreal and sit and wait	Gekkonidae				
	Phyllodactylus	2(1)	2.8-3.0	2.9	Murphy & Pappenfuss, 1980
	Hemidactylus	1(1)	-	5.2	Pasteur et al., 1978
	Agamidae				
Vagile searcher	Lacertidae	8(1)	5.3-8.7	6.5	Nevo & Alkalay, cited in Nevo, 1978
	Acanthodactylus	6(4)	14.0-25.0	18.0	Blanc & Cariou, 1980
	Lacerta	3(1)	5.9-12.9	9.1	Gorman et al., 1975
	Telidae				
	Cnemidophorus	1(1)	-	14.6	Gorman et al., 1977

^aModified from Gorman et al. (1977).^bEach population weighted equally, regardless of sample size.^cSome taxonomists consider amphisbaenians as a taxon of equal rank to lizards.^dCalculated for populations with 8 or more individuals. Sample sizes for individual loci sometimes less than 8. Montanucci et al. (1975) recognized two genera (Gambelia and Crotaphytus) that are closely related and are most often treated as Crotaphytus.^eIncludes four chromosomal races (possible species) of S. grammicus.

explain differences in heterozygosities observed across broader taxonomic groupings (Nevo, 1978). The first, referred to as the niche-width variation hypothesis (Hedrick et al., 1976; Levene, 1953), holds that higher levels of genetic variability should be maintained in populations exposed to more variable environments. However, Soule (1976) distinguished between three types of the niche-width theories: (1) environmental-grain variation theories, (2) environmental-amplitude variation theories, and (3) resource predictability variation theories. Proponents of these various theories either hold that (1) environmental variability and unpredictability produce low levels of heterozygosity (because individuals become fixed with "jack-of-all-trades" alleles), or that (2) environmental variability and unpredictability produce high levels of heterozygosity (because heterozygosity confers biochemical flexibility to individuals). Distinguishing what effects niche-width has on levels of heterozygosity is further complicated by the fact that the second major hypothesis related to levels of heterozygosity, the gene flow variation hypothesis, often leads to the same predictions as do the various niche-width theories. Presumably, many species with narrow-niches are also often rare, sedentary, or distributed in small, semi-isolated demes. As a result, such species would be more susceptible to the heterozygosity-eroding effects of bottlenecks and inbreeding. Soule (1976) has argued that unless effective population size and time since the last bottleneck are considered, species differences in heterozygosities cannot be used to test niche-width variation hypotheses. Unfortunately, information on these parameters

for naturally occurring populations are usually unobtainable. Intraspecific experimental studies attempting to control for population size effects have been equivocal. Powell (1971), McDonald and Ayala (1974), and Powell and Wistrand (1978) reported positive relationships between levels of genetic and environmental variability in Drosophila, whereas Minawa and Birley (1978) and Dawson and Riddle (1983) failed to find any relationship.

Thus, it is probably not wise to conclude why Iguana iguana exhibits such low levels of genetic variability. The niche of the green iguana could be described alternately as either wide (it is a long-lived species found in a variety of habitats) or narrow (it is a highly derived lizard, singularly specialized to the arboreal folivore niche). Iguana iguana also has a wide distribution and is apparently a good colonist, yet it often occurs in localized populations comprised of highly sedentary individuals. Regardless of which of these aspects of Iguana iguana biology prove to be important determinants of the levels of genetic variability it demonstrates, this analysis has documented that green iguanas maintain levels of genetic variability among the lowest known for a lizard species.

Conclusions: Green Iguana Allozyme Variation

An electrophoretic analysis of blood and tissue samples obtained from female iguanas captured at three nesting sites within the BCNM revealed evidence of a genetic structuring of this population. Significant allele frequency differences were demonstrated at an esterase

locus among the female iguanas captured at the Mosca nesting site and female iguanas captured at the other two nesting sites of Slothia and DeLesseps. Thus, the iguanas that inhabit the vicinity around the Mosca nesting site in the BCNM may comprise a local population somewhat distinct from the iguana population associated with the Slothia and DeLesseps sites on the other side of BCI. While the causes of the allelic differences among these local populations are not known, a restriction of gene flow between these demes is implicated. The overall levels of genetic variability demonstrated by the nesting female iguanas were quite low. A complete electrophoretic analysis of samples obtained from hatchling iguanas collected from three geographically separated iguana populations confirmed these results by demonstrating average levels of heterozygosity per individual among the lowest reported for a lizard species. The reasons for these low levels of genetic variability are not clear, but a number of hypotheses that have been advanced to account for differences in levels of genetic variability among various species typically make certain assumptions concerning the vagilities of the species under consideration and these assumptions are often unsubstantiated. The following two chapters, therefore, present information on the actual vagilities of hatchling and nesting female iguanas with respect to the nesting site locations within the BCNM, so that this information can be interpreted with respect to the electrophoretic results obtained from this investigation.

CHAPTER V

MOVEMENT PATTERNS OF NESTING FEMALE IGUANAS

Prior to this study, the postnesting movements of iguanas from the Slothia nesting site had been investigated twice, but the results obtained from these two studies were somewhat contradictory. Montgomery et al. (1973) captured four iguanas on Slothia, fitted them with harness-style transmitters, and intensively monitored their movements from the nesting site. Two of the iguanas moved more than 2 kilometers across the interior of BCI; the mean distance traveled by all four iguanas was 1600 meters (Figure 5). In 1979, Rand and Burghardt (unpubl.) force-fed temperature-sensitive transmitters to gravid iguanas on Slothia to investigate the effects of thermoregulatory factors on iguana nesting behavior. They also made occasional radiolocations after the iguanas had left Slothia and recovered five of the transmitters after they were passed by the iguanas. Each transmitter was recovered along the lake shoreline less than a kilometer from Slothia; the mean distance traveled by these iguanas up to the time they lost their transmitters was only 500 meters.

The contrasting pictures of iguana nesting migration obtained from these two studies may have been a result of the limited sample sizes upon which they were based or also may have been due to the different methodologies they employed. In 1979, some of the transmitters probably were passed by the iguanas before they had completed their migrations, so the movements documented represent only minimum

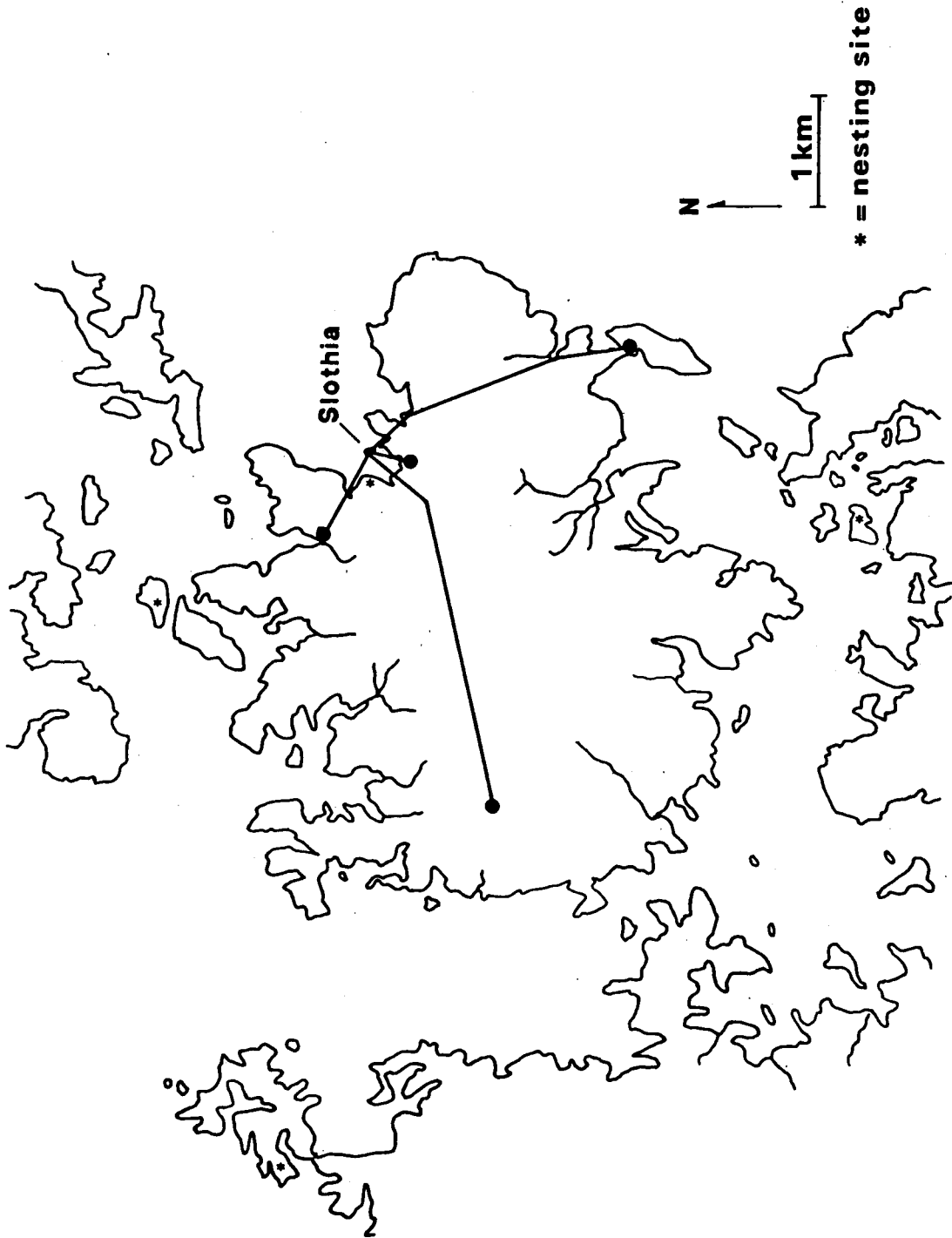


Figure 5. Postnesting movements of four female iguanas radiotracked from Slothia.

dispersal distances. Alternately, the iguanas radiotracked by Montgomery et al. (1973) could have gone inland and moved greater distances because they were disturbed by the more intensive tracking procedures and the harness-style transmitters to which they were subjected. Therefore, in 1982 and 1983 iguanas in the BCNM were radiotracked again in an attempt to obtain more information on iguana nesting movements and hopefully resolve the discrepancies between these earlier studies.

Radiotelemetry Methods

In 1982, transmitters similar to those used in 1979 by Rand and Burghardt were force-fed to the iguanas just prior to their release. The transmitters (Model HLPI-2165 LD, Wildlife Materials, Inc., Carbondale, Ill.) weighed approximately 10 gm and broadcast constant pulses at frequencies in the 150.7 to 151.27 MHz range. Movements of the iguanas were monitored until the transmitters were passed, in some cases up to several weeks later. In 1983, miniature two-stage whip-antenna transmitters (Model HLPI-2750 LD, Wildlife Materials, Inc., Carbondale, Ill.) were mounted upon acrylic saddles and glued to the dorsal pelvic regions of the iguanas with a structural adhesive (3M brand 3532 B/A). This required that each iguana be held overnight to allow the adhesive to set properly. The transmitter-saddle assemblies weighed approximately 15 gm and remained on the iguanas until they were shed or the adhesive failed to hold. The transmitters emitted constant pulses at frequencies in the 150.70 to 151.27 MHz range; several remained on the iguanas and operating for over a month.

A Model La-12 radiotelemetry receiver (AVM Instrument Co., Champagne, Ill.) and a Falcon V radiotelemetry receiver (Wildlife Materials, Inc., Carbondale, Ill.) were used interchangeably during this study. A three element hand-held yagi antenna was used with both receivers.

In 1982, four iguanas were successfully radiotracked from the Slothia nesting site and another transmitter was force-fed to a gravid iguana captured in the Laboratory Clearing on BCI. In addition, an iguana that had visited Slothia during the two previous nesting seasons was trapped on Pepper Island in 1982 (see Chapter III) and radiotracked away from this site. In 1983, five iguanas captured on Slothia were radiotracked, as were three iguanas trapped at a beach location approximately 800 meters east of Slothia on a peninsula of BCI. No nesting occurred on this beach, so the iguanas captured there provided an opportunity to obtain information on iguana prenesting movements.

The iguanas were released at their site of capture and transmitter locations were determined at least twice a day, more often when the iguanas were on the move. Approximate locations of the iguanas were determined by triangulation from a boat. Iguanas were occasionally sighted, but to reduce disturbance to them, the boat rarely approached closer than 50 meters to the signal source and attempts to visually confirm radiolocations were not made. The iguanas radiotracked in this study traveled rapidly, but intermittently, so the routes of their movements usually had to be inferred from a comparison of their radio-locations before and after a move. Whenever an iguana remained in the

same area for more than two days, it was considered to no longer be on the move. When noticeable changes in the signal characteristics occurred in the transmitters of such iguanas or there were no detectable movements by the iguanas over a number of days, inland radiolocations were made. Usually the transmitters were recovered on the ground or in the water along shore but occasionally they were still on the iguana. In these cases, the locations of the iguanas were confirmed from the ground and triangulations from offshore were resumed.

Movement Patterns of Radiotracked Females

Figure 6 illustrates the movements made by the three iguanas captured on the beach on BCI in 1983, as well as those of the iguana captured in the Laboratory Clearing in 1982. Three of these four gravid iguanas did not move to a nesting site during the two weeks or more that their transmitters were with them. Two remained near their points of release, while the third moved 800 meters along the BCI shoreline within four days of its release before coming to a stop. There was no evidence that any of these three iguanas had nested while they were being radiotracked. A fourth gravid iguana, however, demonstrated the longest movements of any iguana radiotracked in this study, passing by the Slothia, Growing House, and Pepper nesting areas before stopping and presumably at the DeLesseps nesting site, almost 3 kilometers away. After nesting, it moved a short distance off of DeLesseps and remained in the same area until disturbed by an inland radiolocation 11 days later. It then moved a kilometer away from DeLesseps

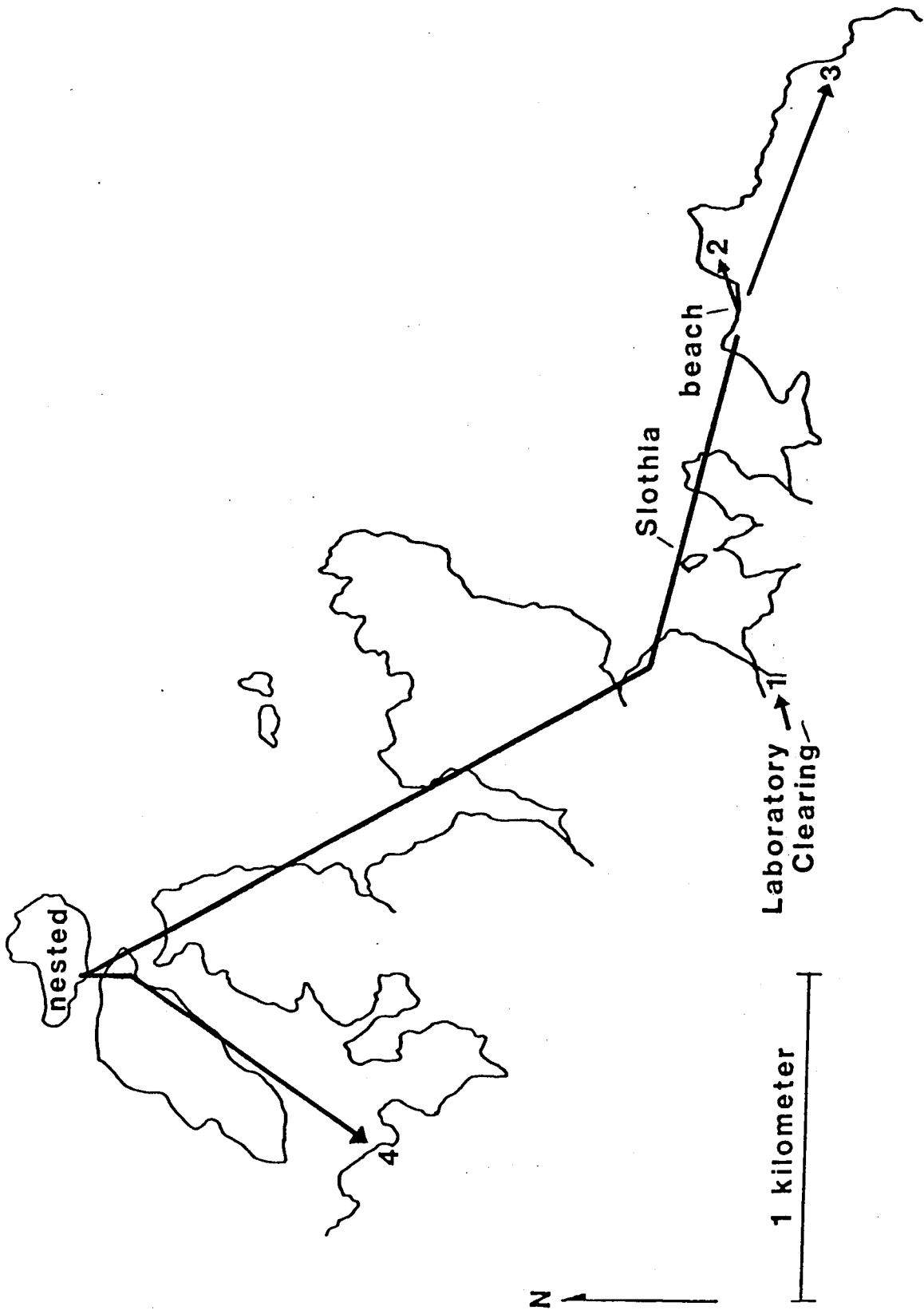


Figure 6. Prenesting movements of four iguanas captured before their arrival at a nesting site.

before stopping once more on BCI. This iguana was trapped attempting to nest again on DeLesseps in the following nesting season, as well.

In Table 7, the dispersal information obtained for each iguana radiotracked away from the Slothia nesting site is summarized. On four occasions, radiotracked iguanas departed Slothia without laying; one moved to the Growing House site, where it probably nested, but the movements of the other three gravid iguanas that left Slothia provided no clues as to where else they might have laid their eggs.

Each of the iguanas radiotracked from Slothia in this study had to swim in order to leave this nesting site, and many appeared to swim much of the remainder of their nesting migrations, as well, although several direct, overland crosses of peninsulas also were documented. Those iguanas that moved the greatest distances from Slothia did not exhibit continuous movements, but rather traveled by alternating rapid, direct movements with periods of relative immobility. Several of these iguanas exhibited displacements of as much as a kilometer in a single day. All of the iguanas radiotracked in this study, however, had ended their movements within a week after leaving Slothia, some having dispersed distances of as much as 1.5 kilometers away from Slothia. Two iguanas moved again, however, after apparently having been disturbed by inland radiolocations. Both moved distances less than in their previous dispersals and then adopted sedentary existences again.

Three iguanas were radiotracked away from Slothia in both 1982 and 1983 (Figure 7). One returned to the same general area of BCI each

Table 7

Dispersal Distances of Female Iguanas Radiotracked Away from the Slothia Nesting Site in 1982 and 1983

Iguana	Nesting status	Distance moved (m)	Days spent moving	Days iguana remained	Distance from Slothia (m)
<u>1982</u>					
No. 82	Departed gravid	575	2	11 ^b	475
No. 180	Departed gravid	140	1	--	140
No. 205	Departed gravid	2320	3	8	1520
No. 239	Laid after release	1100	5	2 ^a	
		605	2	5	1400
<u>1983</u>					
No. 33	Captured spent	190	2	14 ^a	150
No. 82	Captured spent	240	1	21 ^a	
		115	4	12	300
No. 180	Captured spent	380	3	69	190
No. 239	Departed gravid	270	1	2	
	Laid at growing hs.	215	1	-- ^b	455
No. 168	Departed gravid	1310	2	24	530

^aIguana disturbed by inland radiolocation.

^bTransmitter lost while iguana was on the move.

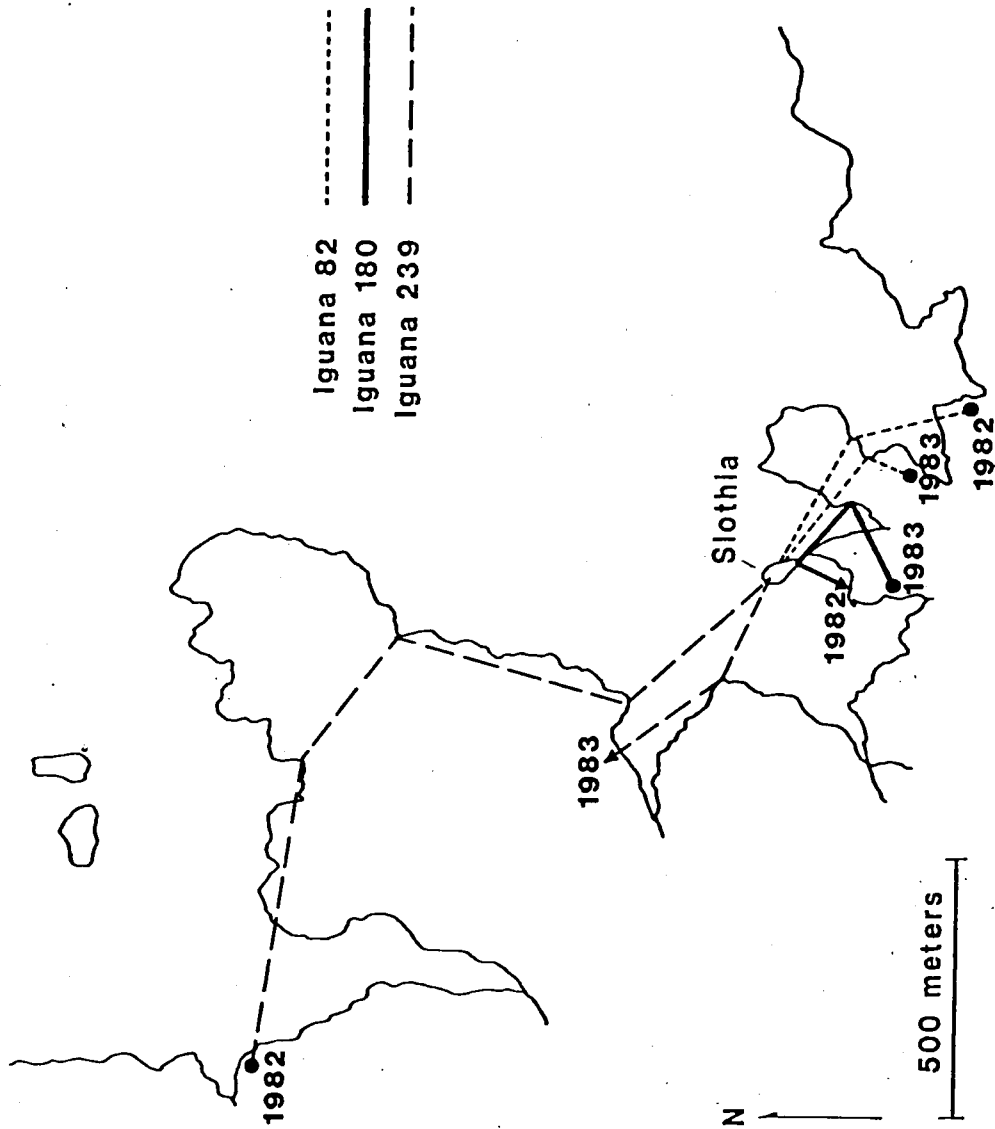


Figure 7. Movements away from Slothia of the three female iguanas radiotracked over two consecutive years (1982 and 1983).

year; the other two were radiotracked until their movements had ceased in one year, but apparently lost their transmitters while they were still actively dispersing in the other. Both of these iguanas, however, departed Slothia in the same direction in each year. Another iguana was radiotracked from Pepper Island in 1982, and it moved to within 400 meters of Slothia before its transmitter was lost. This iguana had nested on Slothia in 1980 and 1981 and was captured there again in 1983 and 1984. In 1983, it was radiotracked a second time and again moved only a short distance from Slothia to BCI before settling down.

The mean displacement distance of the seven Slothia iguanas that were radiotracked in 1982 and 1983 until their movements had ceased was 650 meters, similar to the mean distance value obtained in 1979 by Rand and Burghardt. Figure 8 illustrates the movements from Slothia of those iguanas radiotracked in 1979 along with those documented for iguanas radiotracked in only 1982 or 1983 (i.e., those iguanas not depicted in Figure 7).

Conclusions: Female Iguana Nesting Migration

The prenesting movements exhibited in 1982 and 1983 by the four gravid iguanas released away from the nesting sites were curious. Three failed to move to a nesting area after their release and the fourth demonstrated exceptional vagility, passing by a number of potential nesting sites before finally stopping to nest at a site 3 kilometers away. Both movement patterns may reflect responses of the

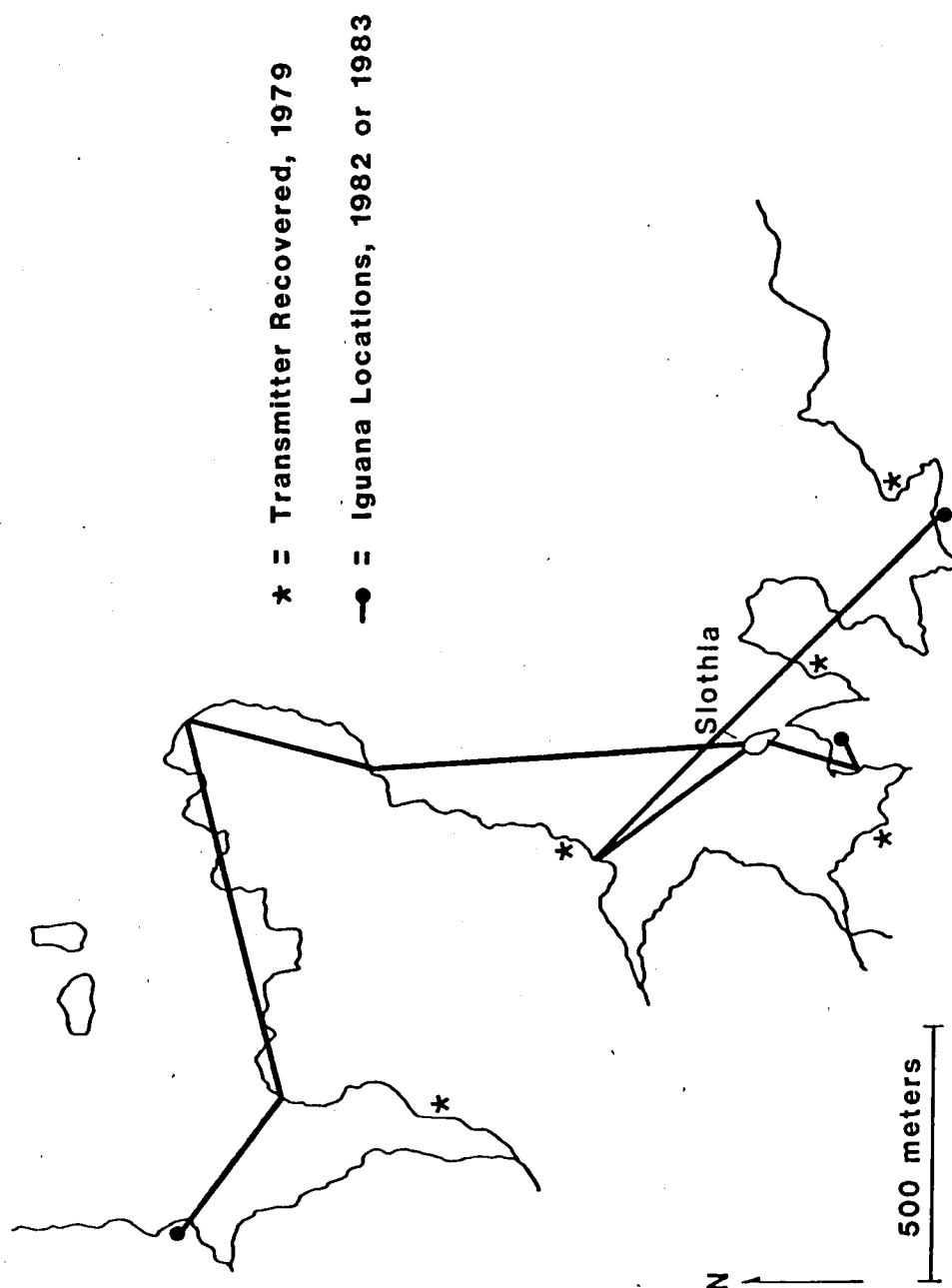


Figure 8. Movements away from Slothia of female iguanas radiotracked in only one year (1979, 1982 or 1983).

iguanas to the disturbance of being handled prior to their arrival at the nesting sites. The iguanas were apparently easily disturbed while at the nesting sites and after their departures, as well. A number of the iguanas released on Slothia from 1981 to 1983 (see Chapter III), including four of the radiotracked iguanas considered here, departed Slothia without having nested. Radiotracked iguanas also occasionally left areas on BCI where they had been residing when an observer approached too near. Thus, some of the movements demonstrated by iguanas radiotracked in this and the two earlier studies are probably more a result of the disturbances to the iguanas of their being handled and followed than they are representative of iguana nesting movements in general.

Even so, the results of this study are more in accord with the results obtained by the less obtrusive study of Rand and Burghardt in 1979 than they are with those of Montgomery et al. (1973). None of the 14 Slothia iguanas radiotracked from 1979 to 1983 ever ventured inland or continued moving for a period of more than a few days time, nor did any move as far as did two of the iguanas radiotracked by Montgomery et al. (1973). These two iguanas were probably driven inland by the disturbances to them of the harness-style transmitters they wore or the close inland radiolocation disturbances they experienced. Montgomery et al. (1973) found that, given the locations of the known nesting sites in the BCNM, the movements of these iguanas were difficult to interpret. Thus, the results obtained in 1979 and from this study are

probably far more representative of iguana postnesting movements than were those documented by Montgomery et al. (1973).

However, both Montgomery et al. (1973) and this study demonstrated that iguanas are capable of making sustained, long-distance movements. Despite having a great potential vagility, however, the actual distances traveled by most of the iguanas radiotracked away from Slothia in this study were quite limited. The directness of the routes they adopted and the abruptness with which their movements stopped suggests that the iguanas were familiar with their surroundings. Several migrated through areas where another iguana later settled, so it seems doubtful that they were simply moving off until they encountered suitable habitat. Rather, the movements of those iguanas radiotracked over two successive nesting seasons suggests that the iguanas may have been returning to established home areas. At this time, however, we know little about any navigational mechanisms they may have been using.

Finally, the female iguana nesting migrations documented through this radiotelemetry study are consistent with the results of the recapture studies discussed in Chapter III, as well as the electrophoretic results presented in Chapter IV. Several of the radiotracked iguanas returned to nest on Slothia in subsequent years, including one iguana whose postnesting movements in the initial year placed it in closer proximity to the DeLesseps nesting site than to Slothia. So in spite of the nesting site fidelity the iguanas exhibit, they also are obviously moving distances great enough to provide ample opportunity for gene flow between the Slothia and DeLesseps sites. Yet the iguanas

apparently restricted their movements to the shoreline, as well, which would thereby even more effectively isolate by distance the iguanas from the Mosca nesting aggregation, located on the far side of BCI, from those that nest at the Slothia and DeLesseps sites.

CHAPTER VI

DISPERSAL OF HATCHLING IGUANAS

No iguanas live on Slothia year-round. Like the females before them, the newly emerged neonate iguanas also depart Slothia to reside on BCI. Hatching of the clutches is highly synchronous, occurring within a short period of a few weeks at the beginning of the rainy season in late April and early May. Diurnal emergence of hatchling iguanas on Slothia and their departure from the nesting clearing has been studied in detail (Burghardt, 1977; Burghardt et al., 1977; Drummond & Burghardt, 1982) and nocturnal emergence also has been described recently (Drummond & Burghardt, 1983). Most diurnally emerging hatchlings leave their nest holes and move out of the clearing in small groups; this socially facilitated departure is thought to function to reduce predation on them at this vulnerable time and to promote orientation during their initial dispersal. Drummond and Burghardt (1982) demonstrated that hatchling iguanas emerging in groups were more likely than were solitarily emerging hatchlings to leave the clearing to the southeast, which is the most direct route to take towards BCI. Hatchling iguanas also occur in small groups once they settle on BCI, but because they are so cryptic and wary, it is difficult to directly observe their dispersal to BCI. Burghardt et al. (1977) and Drummond and Burghardt (1982) did observe some hatchlings moving in small groups across the narrow channel that separates Slothia from BCI and also found Slothia hatchlings together along the nearby

BCI shoreline. They cautioned, however, that other *Slothia* hatchlings were seen to move solitarily into the vegetation upon their arrival to BCI, while others departed *Slothia* alone, adopting overwater routes towards distant points of BCI. Recapture rates of *Slothia* hatchlings on BCI were low, so the overall extent of hatchling dispersal from *Slothia* could not be determined, although some evidence suggested that it might be considerable; each year *Slothia* hatchlings were found in the Laboratory Clearing on BCI, 500 meters away. Recently, however, a new marking technique has made it possible to relocate large numbers of *Slothia* hatchlings after they have reached BCI, thereby permitting the movements of dispersing hatchling iguanas to be more completely documented.

Capturing and Censusing Methods

In late April of 1981, 1982, and 1983, prior to the beginning of hatchling emergence, the areas in the clearing on *Slothia* where nesting had occurred were enclosed with a fence similar to that used in 1977 and 1978 by Drummond and Burghardt (1982). Once emergence began, the enclosure was checked frequently during the day so that hatchlings that had emerged within the fence could be collected before they were captured by diurnal predators such as basilisk lizards (*Basiliscus basiliscus*) or Greater Anis (*Crotaphaga major*). The enclosure also was checked at least once a night and early every morning so that nocturnally emerging hatchlings could be collected.

Most of the hatchlings captured on *Slothia* during the three hatching seasons were processed and released within 12 hours of their

collection. Each hatchling was weighed to the nearest .1 gm and measured for snout-vent length (SVL) and tail length to the nearest millimeter. Hatchlings captured in 1981 and 1982 were individually marked with unique combinations of toe-clips; in 1983, hatchlings were marked with unique color combinations of plastic beads (see Appendix for a description of these hatchling marking techniques). In all three years, each hatchling also was dabbed on each side with a spot of Scotchlite ® Reflective Liquid (3M Co., 7210 Silver or 7211 Yellow). This paint has a dull appearance in daylight, but reflects light intensely when illuminated at night. The marked *Slothia* hatchlings were released either singly or in groups, depending upon the time of day, weather conditions, and number of hatchlings to be released at a given time. They were released either at the south edge of the clearing or in the low vegetation to the south of the blind.

To minimize disturbance to the dispersing hatchlings, no attempts were made to observe their departure from *Slothia* or their movements on BCI during daylight hours. But because hatchling iguanas climb out to the ends of branches and grass blades to sleep, those painted with the reflective liquid were highly visible at night when illuminated. By searching along the BCI shoreline each evening with a spotlight from a boat, large numbers of the painted hatchlings could be located. Unmarked hatchlings also were located during these evening searches each year, and they were usually captured, held overnight, and processed and released early the next morning. Occasionally hatchling iguanas were captured in the Laboratory Clearing on BCI as well, and

these were often processed and released on the same night as their capture. All iguanas captured off of Slothia were released at their original points of capture.

In 1981, there was only a limited hatch on Slothia (see below), so only a few short evening searches of the BCI shoreline were made. In 1982, surveys of the shoreline were conducted nightly after emergence on Slothia began. For the first week, the surveys focused on the shoreline of BCI within sight of Slothia; the searches were expanded the following week to include up to 10 kilometers of shoreline. Because of the success in locating hatchlings in this fashion in 1982, the field season was extended the following year. Extended shoreline searches were conducted each night after emergence began in 1983, and systematic Laboratory Clearing searches were incorporated into the evening surveys as well once Slothia hatchlings began to appear. Shoreline surveys were conducted for 30 consecutive nights after the first hatchlings were released on Slothia, and for an additional 13 nights over the course of the following three weeks. Weather occasionally required that the surveys be cut short, but most were of the full 10 kilometers distance.

In 1981 and 1982, the locations of all paint-marked iguanas seen along the shoreline were mapped, and those hatchlings within reach from the boat were approached, captured, identified, and returned to their perches. In 1983, the locations of all paint-marked hatchlings were mapped again, but the bead-marking system used this year did not require that the hatchlings be captured for identification. By

cautiously approaching the sleeping iguanas and quickly noting their bead colors, they usually could be individually identified without being disturbed.

Results of Hatchling Iguana Recapture Efforts

Hatchling iguana marking and recapture success. Drummond and Burghardt (1982) had difficulties capturing hatchlings on Slothia using the fence technique because it was frequently disturbed by the nightly visits of an American crocodile (Crocodylus acutus) that also had nested in the clearing. This crocodile nested on Slothia in each year of this study as well, but in 1982 and 1983, it stopped visiting the clearing when its clutch hatched, prior to any observed iguana emergence, and in 1981, the crocodile nest and all but one of the iguana clutches failed to hatch because of the exceptionally heavy rains that fell in late April and May (Bock & Rand, in press). The single iguana clutch to hatch on Slothia in 1981 emerged within the fence on June 1, approximately one month late, and all emergence on Slothia in 1982 and 1983 occurred within the confines of the fence, so for all three years, the entire Slothia cohort was successfully captured and marked.

Table 8 summarizes the hatchling iguana marking and recapture results for 1981, 1982, and 1983. Because of the small number of hatchlings to emerge on Slothia in 1981, only a limited effort was made to relocate them on BCI in this year. Even so, non-Slothia hatchlings were seen along the shoreline near Slothia, indicating that other

Table 8

Hatchling Iguana Marking and Relocation Success from 1981 to 1983

Year	Number of Slothia hatchlings marked	Number of evening surveys conducted	Number of Slothia hatchlings relocated	Number of non-Slothia hatchlings encountered
1981	25	-- ^a	-- ^a	-- ^b
1982	350	14	141	19
1983	279	43	93	165

^aOnly limited evening searching was conducted.

^bRecords on non-Slothia hatchlings sighted were not quantified, but unmarked hatchlings were seen along the shoreline near BCI.

nesting sites had fared better than *Slothia* and that their hatchlings had dispersed far enough to come into contact with the few *Slothia* hatchlings that did emerge.

In 1982 and 1983, large numbers of *Slothia* hatchlings were relocated on BCI during the evening shoreline searches. A higher proportion of the *Slothia* hatchlings released in 1982 were relocated on BCI than in 1983, but most of the 1982 hatchlings were recaptured only once, and none were recaptured more than three times. In contrast, over half of the 1983 *Slothia* hatchlings relocated were resighted more than once and many were repeatedly seen on as many as 17 separate nights. This difference between the years was partly due to the longer field season in 1983, but also was related to the different marking techniques used in the two years. In 1983, the bead-marked hatchlings could be recognized when relocated without being handled, whereas the toe-clipped 1982 hatchlings had to be captured for identification. Many 1982 hatchlings disappeared following their release; others were seen in the same areas in subsequent nights, but higher up in the vegetation, out of reach for capture and definite identification.

There also were differences between the 1982 and 1983 hatching seasons in terms of the number of non-*Slothia* iguanas encountered. Although only 19 unmarked hatchlings were captured in 1982, they were abundant in 1983. One hundred and six non-*Slothia* hatchlings were captured, marked, and released on BCI in 1983, and an additional 59 hatchlings from the beach nesting site on Salt Island were marked as well.

Of the 813 hatchling iguanas that were individually marked and released within the BCNM in 1982 and 1983, only 38% were relocated again, and many of these were only recaptured or resighted one time. These figures exaggerate the extent of hatchling disappearance, however, for on each night of censusing, a number of paint-marked hatchlings were seen too high up in the vegetation to be identified and recorded. Some may have been hatchlings that were disturbed by having been censused a previous night (see above), but hatchlings also are known to spontaneously move up into the canopy during their first weeks to associate with adult iguanas and presumably acquire from them a microbial gut fauna (Troyer, 1982a, 1982b). Hatchling iguanas also may move into the canopy while dispersing in order to maintain a direct route, as in crossing peninsulas, for instance. But the forest canopy is not considered suitable hatchling habitat and hatchlings that move into the canopy presumably do not remain there long. Searches with a spotlight from a tower that extends above the canopy near the Laboratory Clearing on BCI in 1982 and 1983 failed to reveal any paint-marked hatchlings in the tree-tops of this area. Thus, it is doubtful that movements into the canopy can account for all of the disappearance of marked hatchling iguanas during this study.

There was not reason to suspect that hatchlings had moved into the low vegetation of the forest interior, either. The interior of BCI usually supports a high density of observant biologists, yet hatchling iguanas have never been sighted in the forest understory away from clearings, although reports of hatchlings in the Laboratory Clearing at

this time of year abound. In 1983, one scientist was conducting systematic night searches of the forest interior around the Laboratory Clearing, collected large, green orthoptera (which were approximately the same size and color of hatchling iguanas). Approximately 45 hours of night searching from 24 April to 26 May of 1983 revealed no hatchling iguanas, paint-marked or otherwise (J. Bellwood, pers. comm.), although 163 sightings of marked and unmarked hatchlings in the Laboratory Clearing were made over this same period of time.

It is likely, therefore, that the major cause of disappearance of the hatchling iguanas marked in this study was predation and that those hatchlings encountered during the evening searches made up the bulk of the remaining iguanas from that hatching season. Studies of survivorship in juvenile iguanas in other populations have reported tremendous losses to the cohort in the initial months following emergence (Harris, 1982; Van Devender, 1982b). The hatchlings in the BCNM may be even more prone to predation because of the postemergence dispersals from the nesting sites they are required to make. The paint and bead-marking procedures also may have increased their conspicuousness to predators, although recent studies on survivorship in two other lizard species have not shown markings to significantly influence mortality rates (Jones & Ferguson, 1980; Simon & Bissinger, 1983).

Extent of hatchling dispersal. The results of this study may underrepresent the extent of hatchling dispersal, as some of the hatchlings relocated on BCI probably were still actively dispersing. The 1982 data should be more affected by this bias, since the evening

shoreline searches were ended shortly after emergence had finished this year. Even so, the extent of hatchling dispersal documented in 1982 was surprising (Figure 9). Although many hatchlings were located along the BCI shoreline adjacent to Slothia, a number dispersed greater distances and some traveled over 1.5 kilometers in less than two weeks time. Many of those hatchlings that traveled the farthest had not been recaptured before, so the extent of their dispersal was not a result of their having been handled after they had left Slothia.

In 1983, even though most hatchling iguanas were not recaptured for identification and the evening surveys continued well after emergence had finished, the extent of dispersal documented was similar to that seen in 1982 (Figure 10). Again, the largest concentrations of hatchlings were on the points of the BCI shoreline nearest to Slothia, but a number of hatchlings also demonstrated more considerable displacements as well. The increased length of the field season this year did not result in more sightings of hatchlings farther away from Slothia; rather those hatchlings repeatedly resighted dispersed in a short time from Slothia and then remained relatively sedentary thereafter. Hatchlings continued to move into the Laboratory Clearing on BCI, however, as the season progressed.

Figure 11 shows the distribution of last-location dispersal distances of Slothia hatchlings for 1982 and 1983. Despite differences between the two years in terms of the numbers of Slothia and non-Slothia hatchlings to emerge, the censusing methods used, and the lengths of the field seasons, the dispersal distances exhibited were

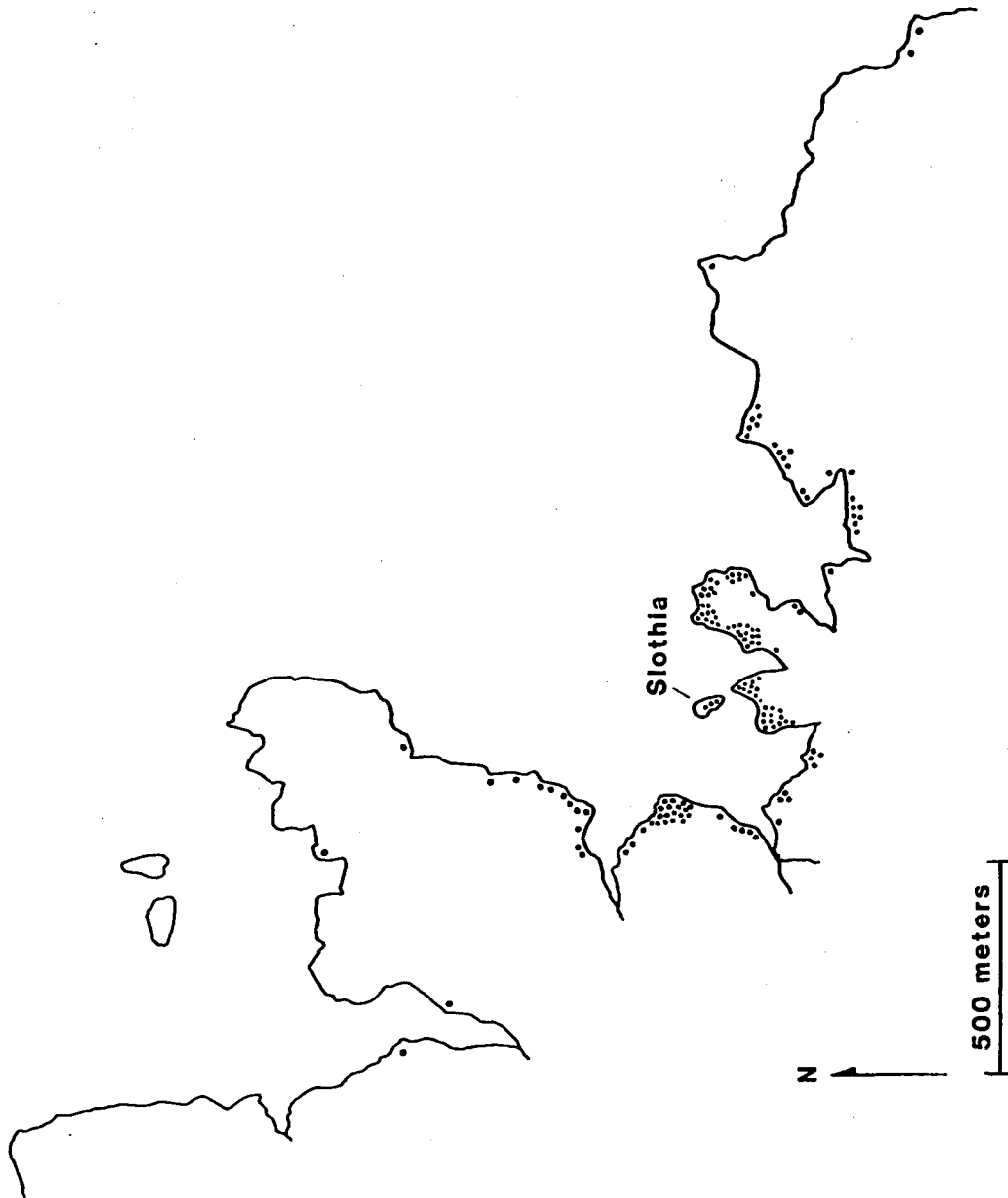


Figure 9. Slothia hatchling dispersal (1962). Each dot represents the location of last-recapture for each hatchling iguana seen after its release on Slothia.

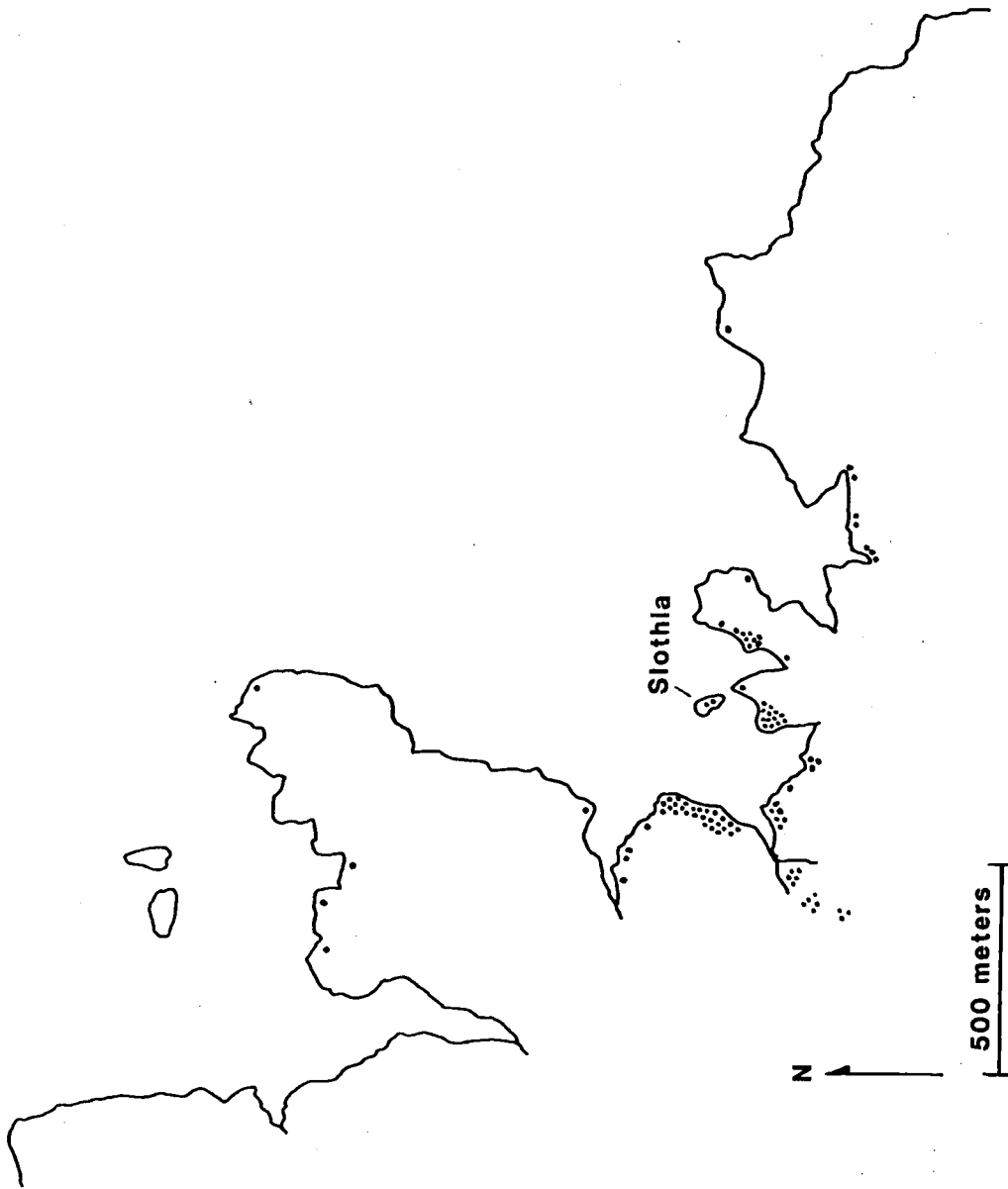


Figure 10. Slothia hatchling dispersal (1983). Each dot represents the location of last-resighting for each hatchling iguana seen after its release on Slothia.

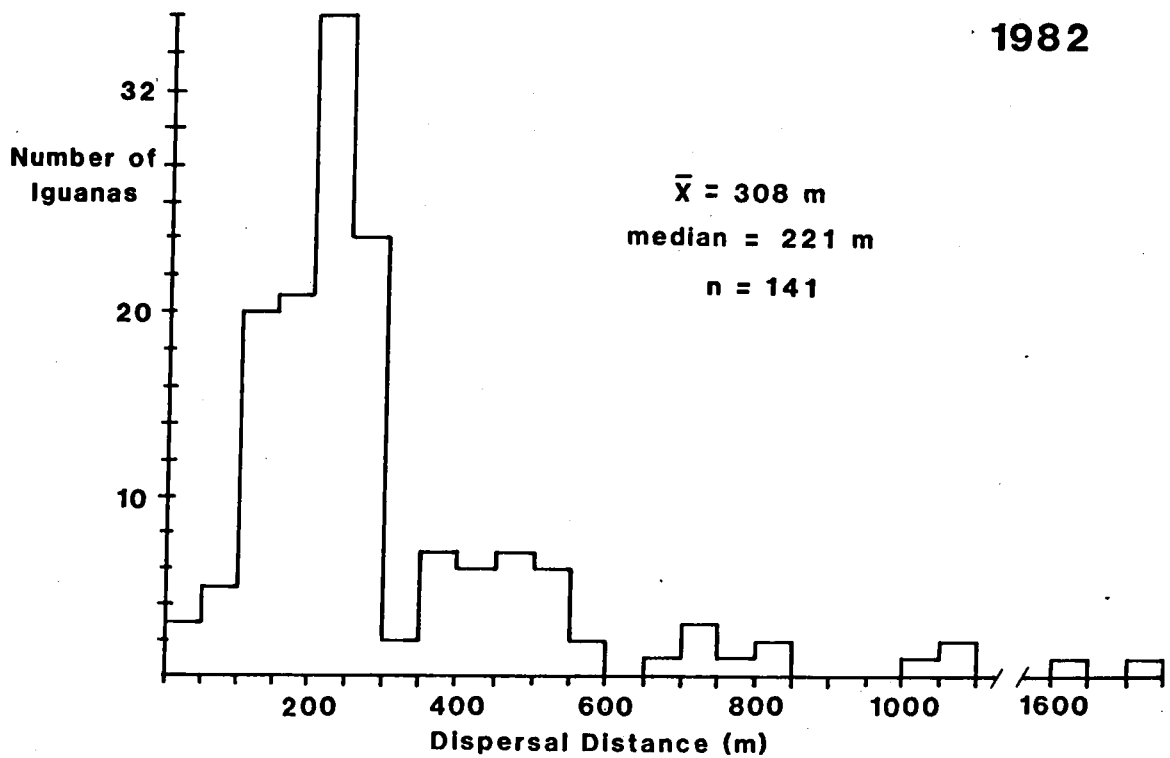
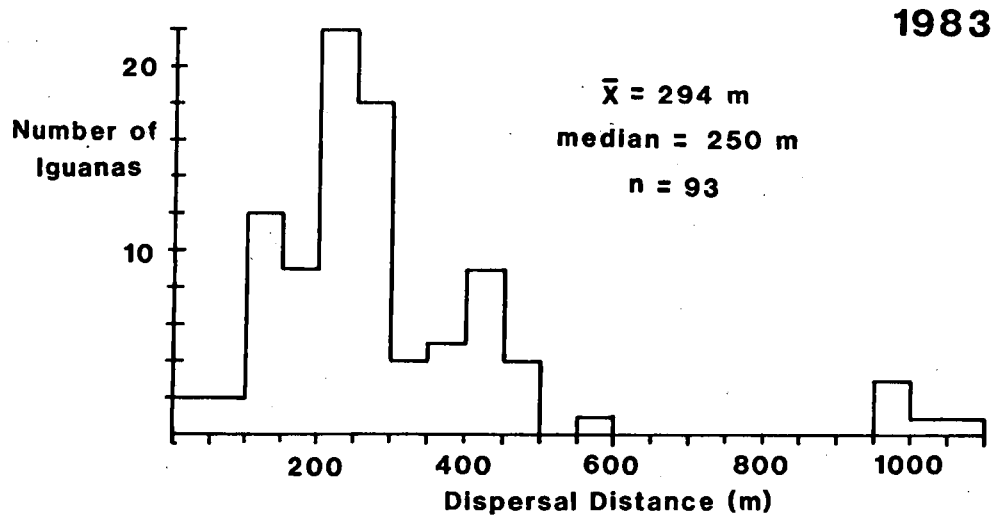


Figure 11. Distribution of dispersal distances of hatchling iguanas from the Slothia nesting site in 1982 and 1983.

not significantly different (Wilcoxon two-sample test, $Z = .81$, $p > .05$). The distribution of dispersal distances in both 1982 and 1983 were positively skewed, with dispersals of distances of 300 to 400 meters underrepresented in each year. This may reflect constraints that the topography of BCI placed on where the hatchlings could disperse; much of the area on BCI this distance from Slothia is forest interior rather than shoreline. Topographic factors may have significantly influenced the overall shape of the dispersal distribution as well, but they apparently did so in equivalent fashion over both years.

Each time a hatchling was relocated, its rate of movement could be calculated as the distance traveled since its release or last relocation divided by the number of days that had elapsed. Because so many hatchlings in 1983 were repeatedly seen in the same areas, the average rate of movement documented in this year was half of that seen in 1982, when most hatchlings were captured only once shortly after their release on Slothia. More relevant figures, however, are the maximum rates of movement exhibited, which were quite similar in each year. In both 1982 and 1983, over 93% of the recaptures or resightings involved movement rates of less than 200 meters per day. Of the 443 times Slothia hatchlings were relocated in these two years, only five hatchlings ever moved at rates of more than 300 meters per day and the maximum rate documented was a movement of 493 meters in one day.

Only nine of the 59 hatchlings released on Salt Island in 1983 were resighted, but several of these hatchlings also exhibited sizable displacements that brought them into contact with iguanas that had

dispersed from Slothia. There are several possible reasons why more of the Salt hatchlings were not resighted. Some of them may have dispersed to areas that were not a part of the regular evening surveys and greater number of them may have suffered predation during their longer swims to BCI. Also, there appeared to be less suitable hatchling habitat along the BCI shoreline adjacent to Salt. The low lake levels that enabled iguanas to nest on Salt in 1983 also had produced steep exposed mud banks around the canal side of BCI, especially near Salt where the wash from ships in the canal is pronounced. In 1982 hatchlings could ascend into the overhanging vegetation virtually anywhere along the edge of BCI, but in 1983 they were often found in low vegetation in clearings or in grasses and sedges that had grown up in the mud along certain parts of the shoreline. As these areas were scarce near Salt, hatchlings emerging there may have been required to disperse farther simply in order to arrive at suitable habitat.

Figure 12 illustrates the dispersal of those hatchlings in 1983 that exhibited the greatest movements, including several that were resighted over successive nights while dispersing. Although some may have followed the shoreline or crossed peninsulas, many apparently swam the greater portions of their journeys. There are several possible advantages to hatchling iguanas of swimming rather than dispersing along terrestrial routes. Hatchlings are vulnerable to both terrestrial and aquatic predators, but the time they are at risk is probably less if they migrate by swimming and their routes of movement also would be less predictable than if they all moved along the shoreline.

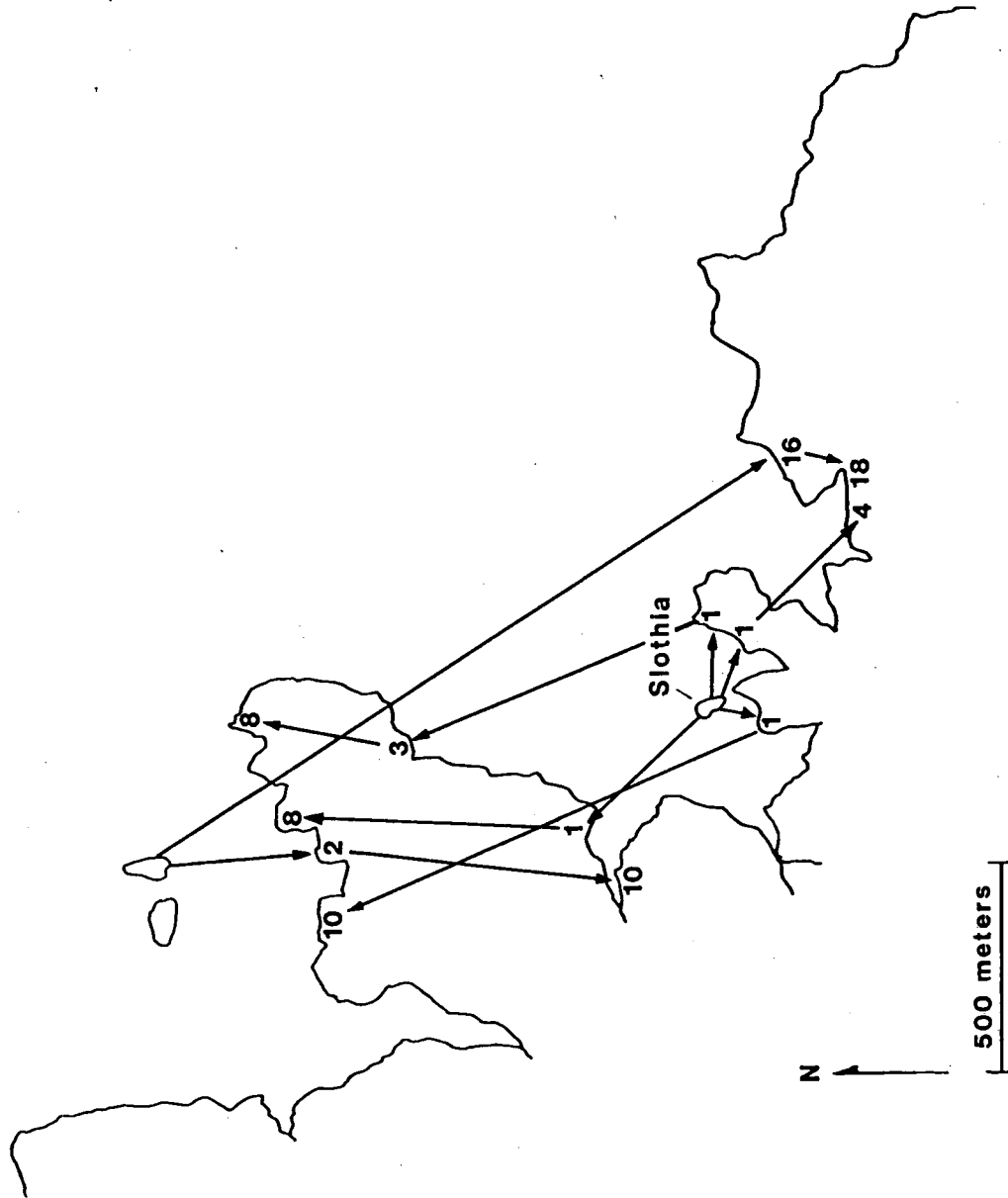


Figure 12. Locations of successive resightings of the farthest dispersing hatchlings (1983). Numbers indicate the days that had elapsed since their release at the nesting site.

Hatchling iguanas are adept swimmers and are frequently seen out in Lake Gatun during the hatching season. Swimming would provide the hatchlings with a more direct means of leaving the nesting sites and it is a far more energy efficient form of locomotion than terrestrial locomotion (Schmidt-Nielsen, 1972). This may be particularly important to hatchling iguanas, considering the distances some of these tiny (approximately 12 gm) lizards move. In general, the costs of locomotion per gram are inversely related to total body weight (Tucker, 1970), yet hatchling iguanas moved distances equal to those traveled by nesting female iguanas (see Chapter V) that are several orders of magnitude more massive.

Given the synchronous emergence and departure of hatchling iguanas from the nesting site and their gregariousness once dispersal has ended, one might expect social factors to influence their actual movements as well. One question of interest is how the hatchling iguanas dispersed relative to the movements of their clutch-mates. Unfortunately, the high density of nests on Slothia and the overlap of their hatching usually made it impossible to confidently assign iguanas found within the enclosure as clutch-mates. However, in 1982 one group of 40 hatchlings emerged from a single emergence hole in a short period of time, so that they could reasonably be assumed to belong to the same clutch. Figure 13 gives the location of those hatchlings from this clutch that were recaptured on BCI (numbers indicate the days elapsed since their release on Slothia). The hatchlings from this clutch did

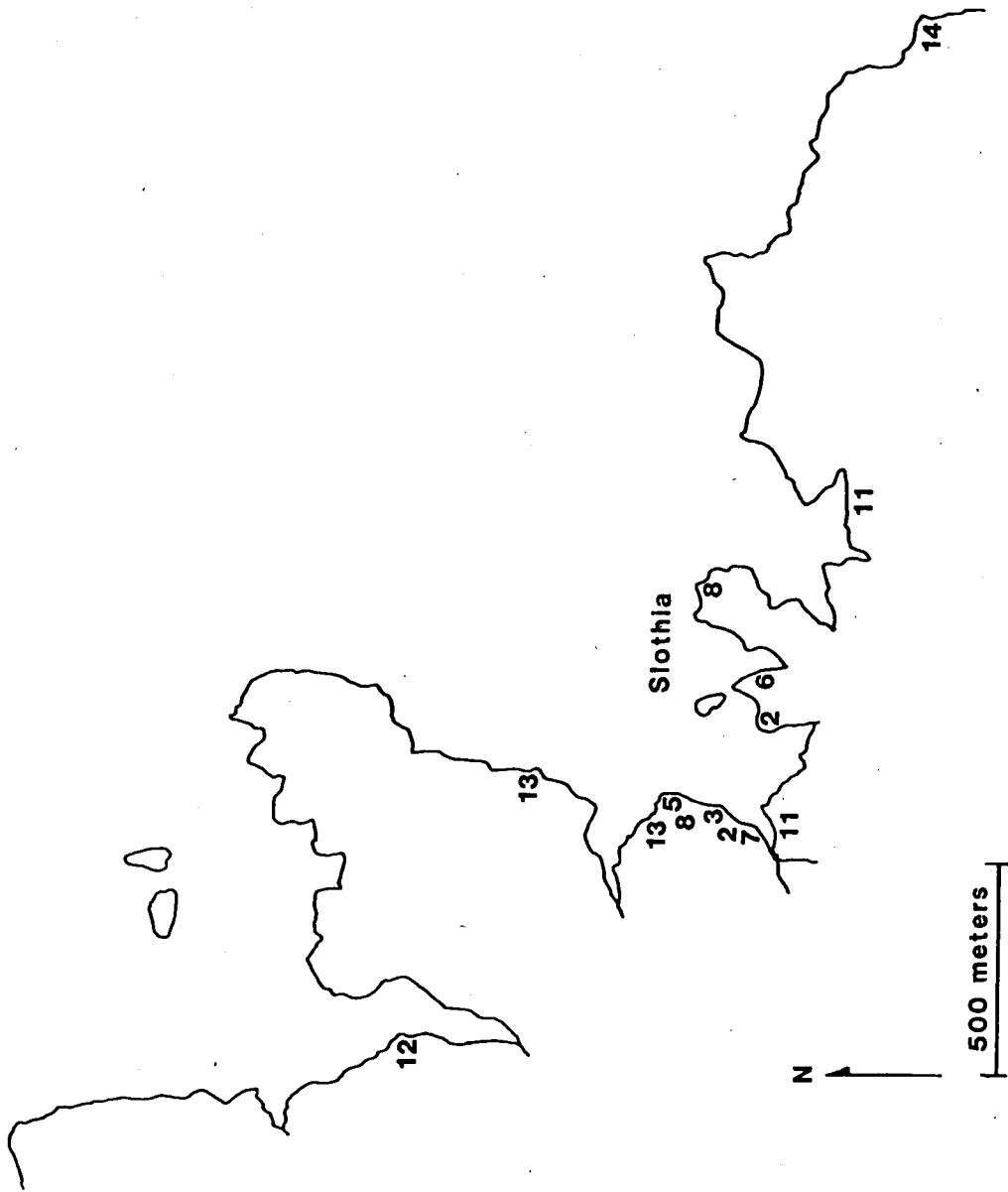


Figure 13. Locations of last-recapture of those hatchling iguanas from a clutch of 40 later seen on BCI (1982). Numbers indicate the days that had elapsed since their release on Slothia.

not appear to associate as they dispersed to BCI, nor did they all necessarily move in similar directions or for similar distances.

Iguanas emerging from different holes on Slothia, and therefore presumably from different clutches, are known to form groups when leaving the clearing (Burghardt et al., 1977). Thus, a more reasonable question may be one of how hatchling iguanas that emerge on the same day disperse relative to one another. Figure 14 shows the resighting locations of those hatchlings from a group of 52 released on the same day that were later seen on BCI. Again their dispersals were scattered. Similar results are obtained when the dispersals of hatchlings released in smaller groups are plotted, as well. While these data are limited, they do not seem to indicate that the social cohesiveness of iguanas hatching together on Slothia persists while they disperse to BCI.

The iguanas certainly associated together in groups once they settled on BCI, however. Part of this association may have been a result of microhabitat availability, but even within large patches of apparently suitable hatchling habitat, the iguanas were frequently seen together in small groups. In 1983, when the iguanas were not as disturbed by the censusing procedures, these associations would persist for days at a time. Slothia iguanas occasionally were seen together with hatchlings they had been released with, but they also were commonly seen in the company of other Slothia iguanas that had been released days before or after. In 1982, few non-Slothia hatchlings were located during the evening surveys, but in 1983, numerous unmarked

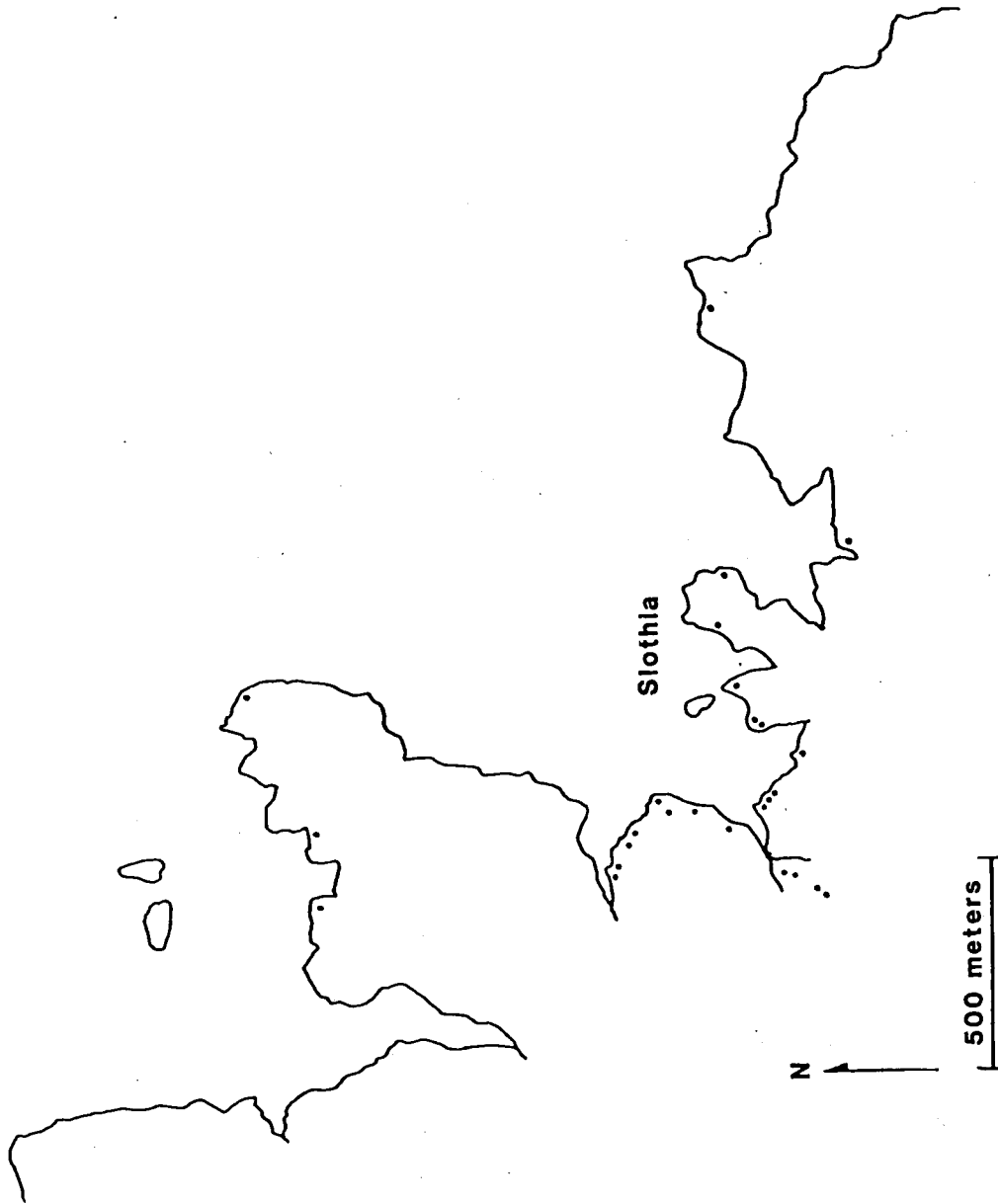


Figure 14. Locations of last-resighting of those hatchling iguanas from a group of 52 released on Slothia on the same day (1983). Each dot represents the location of last-resighting for each hatchling seen after its release on Slothia.

hatchlings were found along the shoreline freely associating with the *Slothia* iguanas. These non-*Slothia* hatchlings presumably emerged from nests located in the beaches that had formed around BCI in 1983 due to the exceptionally dry conditions this year. Marked hatchlings that had emerged on Salt Island were seen in association with *Slothia* hatchlings in this year, as well.

Preoccupation with the gregariousness of these lizards might obscure detection of the alternate possibility that spacing factors influence their dispersal. Hatchling iguanas presumably leave *Slothia* because their high densities there attract predators. Hatchlings might similarly benefit by not associating together in too high of densities once they reach BCI. This could conceivably influence hatchling dispersal in one of two ways. One expectation might be that the first hatchlings to emerge would be the ones to become established in the hatchling habitat on BCI closest to *Slothia*, so that later emerging hatchlings would be required to disperse further before settling down. An alternate, opposite expectation might be that the initial hatchlings to emerge might disperse the farthest because they would be subjected to a continual influx of later arriving hatchlings, whereas the last hatchlings to emerge could settle without experiencing any additional density increases.

To test for both of these possibilities, the extent of dispersal of the first 91 iguanas to emerge on *Slothia* in 1983 was compared to the dispersal of the last 98 hatchlings to be released in this year. The distributions of dispersal distances for these two groups did not

differ significantly (Wilcoxon two-sample test, $Z = .63$, $p > .05$), although the mean dispersal distance for hatchlings that emerged earlier in the season was slightly higher. Considering the amount of predation hatchling iguanas apparently experience, however, it is not surprising that crowding does not seem to play a major role in hatchling dispersal.

Conclusions: Hatchling Dispersal Movements

There was considerable variation in the three years of this study in terms of the proportions of hatchling iguanas seen on BCI that had been marked on Slothia. In 1981, non-Slothia hatchlings were seen on BCI in the vicinity of Slothia, but Slothia contributed almost no hatchlings to this year's cohort. In contrast, almost all of the hatchlings located along the BCI shoreline in the following year had emerged on Slothia. Finally, in 1983 numerous hatchlings from both Slothia and elsewhere were found associating together on BCI. Clearly hatchling iguanas do disperse far enough to bring themselves into contact with iguanas from other nesting areas, although factors such as hatching successes at the various sites can influence the amount of intermingling that actually occurs from year to year.

The increase in the number of non-Slothia hatchlings seen near Slothia in 1983 may have been due to the greater availability of nearby nesting sites this year; several marked hatchlings that emerged from Salt Island were seen on BCI near Slothia in 1983. However, in both 1982 and 1983, a number of Slothia hatchlings dispersed distances that

were great enough to have easily brought them into contact with iguanas from the major nesting aggregation of DeLesseps, assuming that DeLesseps hatchlings were capable of making comparable movements. Thus it appears that dispersing hatchling iguanas, like nesting female iguanas, move distances that provide ample opportunity for gene flow between the nesting sites of DeLesseps and Slothia. However, hatchling iguanas also like the nesting females, tended to confine their movements to the lake shoreline, which would decrease the possibility that hatchlings from Slothia or DeLesseps could contribute to gene flow between these sites and the nesting aggregation of Mosca, on the opposite side of BCI.

CHAPTER VII

SUMMARY AND CONCLUSIONS

Summary

The green iguana (Iguana iguana) population inhabiting the Barro Colorado Nature Monument (BCNM) in Panama may be limited by nesting site availability. This study investigated the movement patterns of iguanas in this population with respect to the nesting site locations and examined the possible consequences to the genetic structure of this population of these movements.

A mark-recapture study of nesting female iguanas at three main nesting aggregations within the BCNM was conducted from 1980 to 1983. It provided no evidence of actual crossover by the female iguanas between any of the major nesting sites over the years, although a few instances of crossover between the major sites and minor nesting areas were documented. Also, the iguanas readily explored and occasionally nested in new areas that became available to them during the course of this study. Overall, however, the female iguanas tended to show strong nesting site fidelity over successive nesting seasons. A few of the iguanas captured during this study had been marked as hatchlings and all were captured at the nesting site near where they had been marked. Although limited, this evidence is consistent with the possibility that the iguanas were exhibiting fidelity to their natal sites.

To investigate whether the nesting site fidelity was contributing to a genetic subdivision of this population, tissue and blood samples

obtained from nesting female iguanas at the three main nesting aggregations were analyzed electrophoretically. Two polymorphic enzyme-coding loci were identified; one locus showed no significant gene frequency differences among the iguanas from the three nesting sites, but the second locus showed significant genetic heterogeneity which was due to allele frequency differences between females from the Mosca nesting aggregation and females that had been captured at the Slothia or DeLesseps sites. This suggests that the iguanas near Mosca may be members of a separate local population distinct from the local population of iguanas associated with the Slothia and DeLesseps sites, and that gene flow between these two demes is limited.

A further electrophoretic analysis was conducted on samples obtained from three geographically separate iguana populations, including iguanas collected in central Panama. This analysis confirmed the low levels of genetic variability demonstrated by the nesting site comparison study and placed Iguana iguana in the company of only a few other lizard species in terms of the low levels of genetic variability they show.

The movements of nesting female iguanas from the Slothia nesting site were monitored in 1982 and 1983 through the use of radiotelemetry. Iguanas are apparently easily disturbed by radiotracking and some of the movements they exhibited, as well as some iguana movements reported in a previous investigation (Montgomery et al., 1973) are probably atypical. However, a number of female iguanas that were radiotracked away from the Slothia nesting site in 1982 and 1983 exhibited movements

that appeared to be more representative of iguana nesting movements. They all completed their movements away from Slothia within a few days time and followed routes which suggested that they were relying heavily on swimming during their major moves. Some crossed directly over peninsulas, however, but none ever ventured very far from the lake shoreline. The movements of three iguanas radiotracked over two successive nesting seasons suggested that they were returning to established home areas. The distances traveled by the female iguanas probably were sufficient to bring them into contact with iguanas from the DeLesseps nesting site, but not with iguanas from Mosca, especially considering the tendency of these lizards to move along the lake shoreline, and Mosca's location on the opposite side of Barro Colorado Island (BCI).

The dispersal of hatchling iguanas from the Slothia nesting site was also studied in 1981, 1982 and 1983. In 1981, Slothia experienced an almost total hatching failure, but large numbers of paint-marked hatchlings from Slothia were located at night along the BCI shoreline in 1982 and 1983. Like the female iguanas, the hatchlings also dispersed rapidly from Slothia and appeared to swim major portions of their dispersal distances. They frequently associated with each other while on BCI, apparently independently of sibship. In 1983, numerous Slothia hatchlings and hatchlings that had emerged on from other sites came into contact, and in both 1982 and 1983, Slothia hatchlings dispersed distances similar to those exhibited by nesting female iguanas. Thus it appears that hatchling iguanas, as well as nesting

female iguanas, exhibit movements with the potential to produce gene flow between the iguanas around the Slothia and DeLesseps nesting sites. However, because the hatchlings also tended to remain along the lake shoreline, the nesting aggregation of Mosca again appeared to be more isolated from the other two nesting sites than the direct-line distances between them would suggest.

Conclusions

The green iguana population around the BCNM in Panama probably was well established in the area before the creation of Lake Gatun, but may have experienced considerable disruption when the lake formed in 1913. There has been a gradual reduction in the amount of open clearings available for nesting ever since, so currently female iguanas must migrate to the existing sites each year to nest in aggregation. This scarcity of nesting sites may actually be limiting to the population, giving rise to a clustering of the iguanas within the BCNM around the available sites. A mark-recapture study of nesting female iguanas showed that they exhibited strong nesting site fidelity over successive years, and investigations of the movements of nesting female and dispersing hatchling iguanas away from the nesting sites showed that both moved rapidly along the lake's shoreline and then abruptly adopted sedentary existences at short to moderate distances away from their nesting sites. These results, therefore, all corroborate the electrophoretic evidence obtained from an analysis of samples collected from females at the nesting sites, which suggested that there may be a

restriction of gene flow between the most isolated nesting site studied, on the far side of Barro Colorado Island, and the other two major nesting sites of this study.

Although no information was obtained during this study on the movements of yearling iguanas or adult males, the electrophoretic results suggest that they may not venture far from their natal sites. Evidence obtained on the movements of adult female iguanas and dispersing hatchlings revealed that although their potential vagilities are great, their actual movements from the nesting sites are more modest. Both female and hatchling iguanas demonstrated movements of over 1.5 kilometers in roughly a one week period of time, but most moved much shorter distances, and both groups became quite sedentary after their dispersals had ended.

Animals moving outside of their home areas are generally considered to be more prone to predation, and the migrations of female and hatchling iguanas are probably energetically expensive as well. The movements they demonstrated during this study appeared sufficient to distribute them from the nesting sites without taking them too far to return. Their tendencies to remain along the lake margins also may be related to their need to return to the nesting sites; they could possibly use the shoreline as a navigational cue, and both hatchling and female iguanas appeared to rely heavily upon swimming when they moved. There may be other benefits to iguanas of living along the forest margins as well, but this study has demonstrated that green iguanas do remain near the forest edge and are capable of moving

directly and rapidly to and from the nesting sites, with females usually exhibiting fidelity to a particular nesting site over years.

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APPENDIX

IGUANA PROCESSING AND MARKING TECHNIQUES

Female Iguana Processing Techniques

Prior to going into the field, data forms were prepared with spaces for all of the information to be recorded. Whenever possible, iguanas were processed in areas where they could be easily cornered and recaptured if they escaped while being handled. Each iguana was weighed on a Salter suspended scale (Model 235, 5 kilogram $\pm$ 10 grams) to the nearest 5 grams. Snout-vent lengths and tail lengths of each iguana were measured to the nearest millimeter. If the tail was regenerate, tail length was recorded as two values (base length + regenerate length). If the tail was noticeably broken or deeply scarred, the distance of the deformity from the vent was recorded. The iguanas were inspected for other unusual characteristics such as scars or missing toes. If present, the whitish shoulder scars were either sketched or described. General condition of the dorsal crest also was noted. The pattern of missing crest scales was then inspected to see whether it corresponded to that of any iguanas marked in previous years. Iguanas often have naturally missing crest scales, but they seldom occurred in patterns that could be confused with those resulting from the crest clipping marking technique. If the iguana's crest did seem to be marked, its identity was confirmed by comparing the information just recorded with a copy of the data recorded for this iguana in previous years. If the iguana was a new individual, it was assigned the next number in the marking series and crest clipped as described below.

Female Iguana Crest-clipping Marking Technique

The iguana's crest is a series of long, single scales that arise posterior to the head and continue along the middorsal line across the iguana's back and onto the tail for some distance. To crest clip a new iguana with the next number in the marking series, an initial base scale was selected from among the first five or so long crest scales on the neck. If the iguana had naturally missing or aberrant scales along its back, the initial base scale was selected so that as many of those scales as possible were incorporated into the mark. If the iguana's crest was complete, selection of the initial base scale was essentially arbitrary.

Once cut, the initial base scale became the "Units Base," and defined the identity of all scales lying posterior to it. They are as follows:

UB 1 2 3 4 5 6 7 8 9 0 TB 1 2 3 4 5 6 7 8 9 0 HB 1 2 3 4 5 6 7 8 9 0

and so on, with UB = Units Base, TB = Tens Base, HB = Hundreds Base, etc. The UB, TB, and HB scales were clipped on all iguanas marked and the appropriate scales in the units, tens and hundreds series also were clipped. The constant spacing of the three units scales is what made the confident recognition of recaptured iguanas possible. Some iguana's crests were so tattered that not all of the missing or short scales could be incorporated into the pattern to be cut. Therefore, after crest clipping, the condition of all of the remaining crest

scales were noted. The recording convention was as follows: clipped scales were recorded, missing scales out of the pattern were recorded with an M, short scales were recorded with an S and normal scales were not mentioned. Thus a marked iguana with crest number 167 with a missing 5th scale in its tens series and a short 2nd scale in its hundreds series would have been recorded in the notes as follows: UB 7 TB 5M 6 HB 1 2S. Recording the condition of all of the iguana's crest scales allowed for more reliable identification of the iguana upon subsequent recapture. However, iguanas lost additional crest scales from one year to the next and other characteristics occasionally changed as well: scars faded, tails were lost and regenerate tails even appeared to have lost length (i.e., the iguana lost its tail again anterior to the previous break). But lost crest scales in adult iguanas did not appear to regenerate, nor did missing toes. Snout-vent length never changed more than 1 to 2 centimeters over a year (a snout-vent length 5 millimeters shorter was considered to be within measurement error). Usually the correspondence of pattern of missing crest scales and other characteristics between years was good and the iguanas were easily identified as recaptures, even when some characteristics had changed. But occasionally inspection of the other characteristics made it uncertain as to whether an iguana was really marked. In these cases, the uncertainty of the iguana's identity was noted and it was clipped to have a number 2000 greater (that is, the Base Thousands and 2 scales were cut).

Hatchling Iguana Toe-clipping Marking Technique

This technique involved clipping one toe from each foot of each hatchling iguana. All of the toes on the front feet were used and all but the last toe on the hind feet were used, so a total of 400 4-toe combinations were possible. Toes on each foot were numbered 1 to 5 starting from the "thumb" and counting out. The feet were toe clipped and recorded as one would read a page, from the iguana's left to right and top (anterior) to bottom (posterior). For example, an iguana number 4324, would have the following cut toes: the 4th toe out on the front left foot, the 3rd toe out on the front right foot, the 2nd toe out on the hind left foot and the 4th toe out on the hind right foot (= FL4, FR3, HL2, HR4). Since over 400 toe clipping combinations were to be used, the dewlaps of each hatchling marked in 1981 and 1982 also were cut in one of two ways. One involved cutting a V-shaped notch into the ventro-posterior margin of the dewlap; the other cut involved snipping off the small row of scales along the anterior margin of the dewlap, adjacent to the underlying extension of the hyoid apparatus. This allowed for 800 possible combinations of dewlap cuts and toe clipping marks to be made.

Hatchling Iguana Bead Marking Technique

This technique involved attaching colored beads to the iguanas by threading the beads onto a piece of plastic monofilament that was pierced through a flap of skin at the nape of the hatchling iguana's neck. In 1983, the iguanas from the Slothia nesting site and Laboratory Bay area were beaded with unique combinations of beads of

the colors red, yellow, white, green and blue. Each iguana was marked with four beads, so 625 possible unique combinations could be assigned. Hatchling iguanas captured on the nesting beach on Salt Island also were given unique bead marks using the above five colors, plus an orange bead, always in the first bead position. To bead mark an iguana, a piece of plastic monofilament was cut and one end was burned into a ball thick enough to prevent the beads from sliding off. The other end was cut at a sharp angle and the first two beads were threaded onto the filament in the proper order. The loose skin beneath the dorsal crest of the hatchling iguana's neck was then pinched into a fold and a hypodermic syringe needle was pierced through the fold. The needle was rotated several times while in the flap of skin, then withdrawn and the monofilament was carefully threaded through the pathway created. The final two beads of the pattern were then threaded onto the monofilament on the other side of the iguana. The excess monofilament was cut off and, taking care not to burn the iguana, the free end was burned into a ball as well. The four beads were thus firmly attached to the iguana, two to a side with the mark read from the iguana's left to right. The monofilament was cut off long enough to accommodate subsequent growth of the iguana. Before each iguana was released, its beads were checked to insure it had been correctly marked.

VITA

Brian Carl Bock was born in Cedar Rapids, Iowa on July 30, 1956. He attended elementary schools in this city and became an Eagle Scout and an average but enthusiastic wrestler while attending Washington High School. After graduating in May, 1974, he enrolled as a Biology major at Iowa State University in Ames, Iowa and became a member of Alpha Sigma Phi fraternity. In May, 1978, he graduated with Bachelor of Science degrees in Biology and Psychology and enrolled in September, 1978, in the Graduate School of The University of Tennessee, Knoxville. He received the Doctor of Philosophy degree with a major in Psychology in December, 1984. The author is a member of Sigma Xi and several professional societies.