AN ECOLOGY OF THE BAHAMIAN HUTIA
(Geocapromys ingrahami)

By

KEVIN CLARK JORDAN

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by

Kevin Clark Jordan

In tribute to my parents,
I offer this with fondness to the children
of the Bahamas.

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Abstract of Dissertation Presented to the Graduate School
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By

Kevin Clark Jordan

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A year-long field study of the Bahamian hutia
(Rodentia: Capromyidae: Geocapromys ingrahami) was conducted
in 1985 on a population introduced in 1973 from East Plana
Cay to Little Wax Cay, Exuma, Bahamas. Capture-recapture
and pellet count analyses indicated that the original cohort
of 11 animals (six males, five females) had grown to exceed
1200. Tracking of subjects dusted with fluorescent powder
showed the population to comprise adjacent non-overlapping
colonies denning in rock crevices or under leaf piles of the
silver thatch palm (Coccothrinax argentata). Colonial
territories were defended, and displaced animals returned
home within days. Habitats with fresh water were preferred
but not necessary. Laboratory studies revealed a basal
metabolism far below the Kleiber function without

modification of thermal conductance. Adult body size (900 g) and reproductive ability were achieved at one year, and annual survivorship was estimated at 78%.

Activity in the field was intermittent between 4:00 p.m. and 10:00 a.m. to avoid heat rather than predation. The animal has few defenses and has suffered a severe range reduction since the Amerindian invasion, and especially since the European discovery, due to predation by people and introduced cats and dogs. East Plana Cay remains the only known original population.

Geocapromys ingrahami is a semi-arboreal folivore with an appetite for bark, including phloem. Hutia depredation has extinguished four species of tracheophyte on Little Wax Cay since the introduction and threatens several more. The explosion of the Little Wax Cay population is due to release from nutritional constraint. Hutias on Little Wax Cay are larger and healthier than those on East Plana Cay, a larger, drier island with poorer forage. But the poor range quality of East Plana Cay may be due in part to chronic overbrowse by G. ingrahami itself. If so, Little Wax Cay is expected to converge on East Plana by a reduction in hutia density and body size, a reduction in the number of tracheophyte species, and a replacement of six-meter forests with unpalatable scrub. The Bahamian hutia can swim, and may disperse to neighboring islands.

CHAPTER I

INTRODUCTION

The hutias (Rodentia: Capromyidae) are endemic to the West Indies, and the Bahamian hutia (Geocapromys ingrahami) is the only non-volant mammal endemic to the Bahamas. Hutias are represented in the fossil record by six genera or subgenera (Varona 1974), to which a seventh has recently been added (Woods 1989), and of which only three survive. Each of those three has itself lost at least one species to extinction since the Pleistocene, one (G. thoracatus) as recently as 1960 (Clough 1976).

Known from pre-Columbian deposits throughout the West Indies, hutias were an important human food on many of the islands before their extirpation or the importation of domestic livestock (Fernandez 1555, Allen 1891, Duerden 1897, Miller 1916a, Miller 1916b, Lawrence 1934, Allen 1942, Koopman and Williams 1951, Wing 1969, Wing 1972, Mittermeier 1972, Morgan 1977, Morgan and Woods 1986). They also may have been carried between islands by early travelers for food (Allen 1891, Clough 1972). But with the development of the West Indies following the European discovery, hutia populations have dwindled under the combined pressure of predation and competition from humans and exotics.

Subsistence hunting, habitat losses to agriculture and development, and predation by cats (Felis catus), dogs (Canis familiaris), and possibly by the mongoose (Herpestes auropunctatus) all may have contributed to the reduction of hutia stocks to a few isolated populations (Clough 1972, Clough 1976, Morgan 1977, Oliver 1977, Morgan and Woods 1986).

Evolution of the Capromyidae

The earliest known hystricognath rodents appear in African deposits from the upper Eocene, followed in South America by Argentine and Bolivian formations from the Deseadan age of the Oligocene. That all four hystricognath superfamilies (Chinchilloidea, Erethizontoidea, Cavoidea, and Octodontoidea) are represented suddenly in Deseadan South America suggests either an invasion of South America from elsewhere, or a long unpreserved South American diversification from a single ancestral stock. By extrapolation of current rates of evolution, Sarich and Cronin (1981) believe in a Paleocene dispersal of hystricognaths from Africa to South America by rafting, and Landry (1957) agrees, asserting that hystricognaths were once worldwide. Lavocat (1973) and others suggest an African invasion by rafting, but later, during the Eocene. A.E. Wood (1981) believes that the invasion was from North America via a Central American migration, with similarities

between African and South American hystricognaths arising by parallel evolution.

The hystricognath family, Capromyidae, is unknown from South America (excluding Myocastor, sometimes classified with the hutias), occurring only in the West Indies (including the Cayman Islands and Little Swan Island) during the Pleistocene and Recent (Varona 1974, Woods and Howland 1979, Woods 1982). Nor is any rodent known from the Antilles before the Pleistocene, except possibly Proechimys corozalus, known only by a fossilized mandible from Puerto Rico (Hall 1981, Woods 1982), and recently renamed Puertoricomys corozalus by Woods (in press).

Echimyidae and Octodontidae are among the first hystricognath families to appear in Oligocene South America, persisting through the Recent, and occurring in the Indies during the Pleistocene and Recent, with echimyids also in Pleistocene and Recent Central America. Woods and Hermanson (1985) showed that the three living capromyid genera (Capromys in Cuba, Geocapromys in the Bahamas and Jamaica, and Plagiodontia in Hispaniola) were more closely related to Makalata (an echimyid), Octodon (an octodontid), and Myocastor than to Dasyprocta or three Old World genera: Atherurus, Petromys, and Thryonomys. Furthermore, capromyid proteins were found to be more derived than those of echimyids or octodontids, suggesting the origin of Capromyidae from an echimyid-octodontid ancestor, rather than vice versa (Woods and Hermanson 1985).

The three living genera of Capromyidae and the one of Myocastoridae resolve, according to Woods and Howland (1979), into two types of masticatory apparatus. Capromys and Geocapromys are orthognathous, whereas Plagiodontia and Myocastor are plagiognathous. In addition, Quemesia (from remains in Hispaniola) and Elasmodontomys (from remains in Puerto Rico) of the recently extinct family, Heptaxodontidae, were plagiognathous, whereas the extinct capromyid, Hexalobodon (from remains in Hispaniola), was orthognathous. But Heptaxodontidae may not be closely related to Plagiodontia (or to the extinct plagiodontine, Isolobodon, also from Hispaniola), due to differences in the fourth lower premolar.

Woods and Howland (1979) proposed four possible reconstructions of the capromyid radiation, favoring the following: An echimyid ancestor invaded the Antilles from Central or South America and radiated from Hispaniola, giving rise to the plagiognaths in a primitive radiation, and to capromyines later. Hexalobodon either invaded Cuba to spawn the capromyine radiation, or was an early Cuban capromyine that re-invaded Hispaniola. The hypothesis is supported by the age of the plagiodontines, the apparent recency of the Cuban Capromys radiation, the diversity of Hispaniolan capromyids, the great environmental heterogeneity of Hispaniola throughout the Tertiary, and the absence of pre-Pleistocene hystricognath remains from the Antillean record. The reconstruction has recently been more

fully elaborated (Woods 1989, in press) with respect to specific taxa and routes of dispersal, and accounting for the recent description by Woods (1989) of a new extinct genus of plagiodontine from remains in western Haiti: Rhizoplagiodontia, comprising a single species: R. lemkei.

Evolution of Geocapromys

The name Geocapromys was first used by Chapman (1901) as a subgenus of Capromys to distinguish three living species (one of which has since gone extinct) by their shorter tail and claws, the near absence of a pollex, and a wider ascending process of the maxilla than in other Capromys. G.M. Allen (1917) elevated the name to generic rank, noting that all Geocapromys had an additional anterior re-entrant fold on P_4 and a more severe anterior convergence of the upper tooth rows. Miller (1929) summarized the morphological differences between Geocapromys and Capromys, and Morgan (1977) tabulated cranial and mandibular differences in defense of a generic distinction. Woods (1982) supported the distinction on the basis of a blood protein analysis of living representatives of the two groups. However, Varona (1974) retains Geocapromys as a subgenus of Capromys. Here the generic status is recognized, not least because in that case Capromys is endemic to Cuba, whereas Geocapromys is not.

Anderson et al. (1983) recognized two living and four extinct species of Geocapromys. The two living species are G. ingrahami from East Plana Cay, Bahamas (Allen 1891), and G. brownii from Jamaica (Fischer 1830). Geocapromys columbianus (Chapman 1892), G. megas (Varona and Arredondo 1979), and G. pleistocenicus (Arredondo 1958) were all described from remains in Cuba, and Morgan (1977) described a separate extinct species endemic to the Cayman Islands. Geocapromys thoracatus, described from a population on Little Swan Island off the coast of Honduras (True 1888), was also reported by Miller (1916a) from Jamaica. Common on Little Swan Island through the first half of this century, no hutias were found there in 1960 when a U.S. Coast and Geodetic Survey expedition visited the island, and two scientific expeditions in 1974 confirmed their absence (Clough 1976). Clough (1976) suggested that the combination of a 1955 hurricane and a documented introduction of house cats to the island shortly afterward may have been responsible for the extinction of that population, the last of the species.

Three subspecies of G. ingrahami, all Bahamian, have been recognized since Ingraham collected the type specimen from East Plana Cay (Allen 1891). Lawrence (1934) described G. ingrahami irrectus from remains on Crooked Island, Eleuthera, and Long Island. She distinguished it from G. i. ingrahami on the basis of a longer premaxilla, tooth row, and individual tooth width, and shorter lower incisors. The

type specimen is from an Indian cave site on Crooked Island. In the same paper, Lawrence (1934) described G. i. abaconis from remains collected from caves on Great Abaco. According to her, G. i. abaconis had noticeably longer frontals than either other subspecies, with the orbital margin being a smooth ledge without a pointed postorbital process. G.M. Allen (1937) reported a large series of bones he referred to G. i. irrectus from a cave deposit on [Little] Exuma Island (insert by Hecht 1955) that he concluded to be pre-Columbian.

Geocapromys ingrahami remains also have been collected from late Pleistocene or Recent deposits on New Providence, Cat Island, Andros, Acklin's, and Great Exuma Island (Hecht 1955, Morgan 1977, Morgan in press), and from an Indian kitchen midden on San Salvador (Wing 1969). Two Geocapromys skins were reported to have been collected from a population on Samana Cay before 1929, but no live representatives were found there in 1934, possibly due to hurricanes in 1929 and 1932 (Barbour and Shreve 1935).

The Bahamian subspeciation of G. ingrahami probably corresponds to the Pleistocene fluctuation in sea level that first consolidated and then submerged great portions of the archipelago, segregating many of the islands by large expanses. A drop of 120 m from the present sea level at the height of the Wisconsinian glaciation about 17,000 years ago would have joined the 30 islands and approximately 660 cays into five large and several small islands, thus increasing

the exposed area from its current 11,406 km² to about 124,716 km². At that time, the Great Bahama Bank would have been separated from Cuba by only 15 km (Buden 1979, Olson 1982). Figure I-1 shows the known distribution of living and extinct G. ingrahami.

The intermediate size of fossil Bahamian Geocapromys between the extant Bahamian G. ingrahami and the larger extinct Cuban G. columbianus, the Pleistocene proximity of Cuba to the Great Bahama Bank, and the predominantly Cuban origin of Cayman mammals all cause Morgan (1977, in press) to favor a Cuban origin of the genus Geocapromys.

Morgan's hypothesis does not contradict the model of Woods and Howland (1979), as elaborated by Woods (1989, in press). If the ancestral Hispaniolan echimyid gave rise to a Cuban Geocapromys via Hexalobodon, Geocapromys may then have radiated north to the Bahamas and south to Jamaica and the Caymans during the Pleistocene reductions in sea level. The blue water southern route would have required some sweepstakes dispersal as well. The Cuban evolution of Capromys from Geocapromys may have produced a local radiation that outcompeted the ancestral line, leaving Capromys alone to represent the family.

Though people may have assisted in hutia dispersal by carrying them among the islands as livestock (see above), the Geocapromys radiation began before the first appearance of humans in the West Indies about 4000 years ago. Morgan (1977) has found Geocapromys remains predating human

habitation in the Cayman Islands. And recently, Morgan (in press) has obtained a radiocarbon date of 8000 years B.P. for G. ingrahami bones from Banana Hole, New Providence, Bahamas.

Ecology of the Capromyidae

The Genus Capromys

The genus Capromys is restricted to Cuba, where it comprises a variable number of living species, depending on the reference (Varona 1974, Oliver 1977, Eisenberg 1978, Woods 1984, Woods 1989, Woods in press). Eisenberg (1978) characterizes C. nana as a scansorial omnivore, C. pilorides as a semiarboreal frugivore/folivore, and both C. (Mysateles) melanurus and C. (Mysateles) prehensilis as arboreal folivore/frugivore. Descriptions and systematics are treated in detail by Mohr (1939), and distributions are given by Varona (1974). Life histories have been investigated by Bucher (1937), and Abreu et al. (1986) used fecal pellet counts to determine the size of a wild population of C. prehensilis.

But by far the Capromys species most studied has been the one most available for study, the 3-4 kg hutia conga (or banana rat), Capromys pilorides. A large but uncensused population survives today on the compound of the U.S. Navy base at Guantanamo Bay, where they are occasionally struck

by automobiles (L. Hurst pers. comm. 1984). The species climbs trees for fruits or leafy forages, but is not highly adapted to arboreal folivory, either with respect to skeleto-musculature or gastrointesinal morphology. Reproduction, growth, and behavior were studied by Taylor (1970), who reported a gestation period of 123 days, a nursing period of 153 days, and a mean litter size just greater than two, with a range of one to four. The estrous cycle averaged 16.3 days, and sexual maturity was achieved at about 10 months, before adult size. Canet and Alvarez (1984b) captured 63 individuals from assorted habitats and reported two litters per year, with a range of one to six. The sex ratio was 2:1 in favor of males, and feeding was significantly more nocturnal than diurnal. Genetic polymorphism has been addressed by Camacho et al. (1986), and Canet and Alvarez (1984a) found great interpopulational variation in gross morphology, pelage color, and diet.

Plagiodontia aedium

The Hispaniolan hutia (Plagiodontia aedium) is endemic to that island, where it persists in isolated pockets that Woods (1986) has hoped to protect in Haiti with the establishment of a national park system. Its status and distribution have been addressed in the Dominican Republic by Sullivan (1983) and J. A. Ottenwalder (pers. comm. 1988). Little work has been conducted in other aspects of its

biology (Radden 1968), and its life history remains largely unknown, though gestation lasts 119 days (Johnson et al. 1975), and one individual has been kept at the Florida Museum of Natural History Hutia Colony (unpublished records) in excess of eight years. Woods (1984) characterizes P. aedium as a semiarboreal herbivore, feeding on roots, stems, bark, and leaves.

Geocapromys brownii

The Jamaican hutia (Geocapromys brownii) may enjoy slightly greater numbers than P. aedium. However, its distribution is severely restricted, and populations reported but not censused by Oliver (1982) share almost immeasurably small densities (Jordan unpublished field notes, Wilkins 1987a, Wilkins 1987b, Wilkins et al. 1987). The animal is a semiarboreal herbivore, feeding on fruits, roots, and bark, in addition to leaves, and denning in rock crevices (Jordan unpublished field notes, Wilkins 1987a, Wilkins 1987b, Wilkins et al. 1987). Ottenwalder (1983) determined metabolic rates of G. brownii at various ambient temperatures, finding the basal rate to be 61% of the Kleiber (1961) prediction for a mammal of its size. A captive breeding program at the Jersey Wildlife Preservation Trust (Oliver 1976) revealed the K-strategy that Kleiman et al. (1979) found typical of caviomorphs, with subjects

producing litters of one to three after a gestation of about 123 days.

The Jersey project has culminated in a reintroduction of 41 animals to a private 74 ha release site in Jamaica (Copse Mountain, northeastern Westmoreland Parish) in March 1986, following a habitat survey by transect and quadrat (Oliver et al. 1986). Wilkins (1987a) of the Florida Museum of Natural History monitored the animals after release, and studied the vocalizations, movement patterns, and behavior of G. brownii in the wild. In addition, she has made the first attempt to evaluate the size of wild populations, censusing by several techniques in Hellshire Hills, Worthy Park, and the John Crow Mountains.

Geocapromys ingrahami

The Bahamian hutia (Geocapromys ingrahami) occurs naturally today only on East Plana Cay, the site of its discovery by the scientific community (Allen 1891). The island is located at 22° 36' N, 73° 30' W, with a total area of 465 ha, and a maximum elevation of 65 ft above mean sea level. It is uninhabited, and shows no sign of human settlement. The substrate is limestone, covered in places by thin sandy soil. The surface is rocky and loose, with many cracks, crevices, and small caves, and one large cave (Clough and Fulk 1971, Clough 1972). There is no fresh water except that found once in a shallow depression,

presumably left from precipitation. Clough and Fulk (1971) estimated the precipitation at 635 to 890 mm annually, and the mean annual temperature at 25.0 to 26.5°C. The vegetation is classified as semiarid, distributed in thickets of woody shrubs approximately one meter in height (Clough 1972). Clough and Fulk (1971) distinguished eight plant communitites, and reported three species of lizards, 37 species of birds, and 31 species of vascular plants. The only other mammal reported is the bat, Macrotus waterhousii, found in the large cave on the south face (L. Wilkins pers. comm. 1982).

Following is an excerpt (taken from Allen 1891) from the M.S. Notes of Mr. D.P. Ingraham, collector of the type specimen of Geocapromys ingrahami: "During my stay of two weeks, weather bound, under the lee of the island, I secured about twenty specimens of this animal, which at first I thought was gregarious in its habits, or inclined to live in colonies, but the occurrence of so many individuals at this point may have been due to the favorable conditions of the locality for affording it hiding places...Its food was the leaves, twigs, and bark of the bushes, especially the black buttonwood, and the succulent growth of the cactus plants. It seemed very fond of the fruit of the paw-paw, and even of the body of the tree itself, as I have seen the trunks of this tree, nearly as large as my body, eaten so nearly off that they would not sustain their own weight."

The Bahamian hutia is a rabbit-sized nocturnal herbivore. The average East Plana Cay adult weighs about 700 g and is either grayish-brown or, rarely, blackish-brown. It spends the daylight hours in surface crevices and forages at night. It moves slowly on all four legs and is a deliberate climber. According to Clough (1972) it neither swims, digs, nor builds nests. It communicates by two types of vocalization: one in free animals and the other in animals captured and held. It leaves urine markings in the form of a white precipitate on sand and rock, and along twigs and roots. Aggression is rare in the wild, and no scars have been noted on captured animals. Five adults held for four days in a 1 X 2 m wire pen on East Plana Cay did not fight, though each withdrew from the others to eat (Clough 1969, Howe 1971, Clough 1972, Clough 1973, Howe 1974).

In a laboratory at the University of Rhode Island, hutias were found to be gregarious allogroomers, developing loose linear social hierarchies with the dominant males most closely associated with the females. However, the animals showed no territoriality, and little agonistic behavior was demonstrated in established groups, except when females were in estrus. Urine marking by both sexes was frequent regardless of the estrous condition of the females. Males apparently could determine if a female was in estrus by sniffing her urine scent mark, and both marking and sniffing behavior intensified during estrus. Also, urine sniffing

was shown to induce marking behavior, and hutias preferred to mark urine-scented sticks than to mark odor-free controls. Both urine marking and a second type of behavior described as wrestling were concluded to be non-agonistic behaviors that promoted social organization and group cohesion (Howe 1971, Clough 1973, Howe 1974, Howe 1976, Howe 1982).

Rebach (1971) compared the gas exchange and water balance of G. ingrahami and another New World hystricognath, the nutria (Myocastor coypu). Not surprisingly, the island-dwelling hutia produced more concentrated urine and feces than the wetland-dwelling nutria. And whereas the hutia could regulate urine osmolality to a maximum of 2000 milliosmoles as a function of daily water allowance, the nutria had no such ability. Also, the basal metabolism of the nutria rose when its water allowance was restricted, but that of the hutia actually fell by two-thirds (from $0.820 \text{ ccO}_2\text{g}^{-1}\text{hr}^{-1}$ on fresh food and water to $0.274 \text{ ccO}_2\text{g}^{-1}\text{hr}^{-1}$ on pellets and no water). Furthermore, hutias given pellets but no fresh water suffered only mild weight losses, but nutrias denied fresh water lost 20% of body mass. And hutias given 0.25 M NaCl solution maintained body mass after initial losses, but all nutrias on the same treatment died within three days (Rebach 1971).

Clearly, the Bahamian hutia is well-adapted to its xeric habitats, and may have been common historically on small islands with no fresh water at all.

Six hutia forage species were identified in penned trials on East Plana Cay, and average daily food consumption and fecal production measured. Six test animals consumed 21.63 g dry weight of forage per kilogram body weight per day, and produced 83 pellets or 5.64 g dry weight of feces per kilogram body weight per day. Island vegetation condition was concluded to be similar to that noted there by Ingraham in 1891 (Clough 1972).

Before this study, population demography was largely unknown, though breeding was thought to occur throughout the year (Clough 1972, 1974), and recorded litter size had never exceeded one (Howe and Clough 1971, Clough 1972). The maximum reported lifespan of G. ingrahami in the wild was nine years (Clough 1985). Taylor (1970) determined the estrous cycle to average 10.1 days, with a range of nine to 11 days in one animal. The gestation period was unknown but estimated at 110 to 120 days, with two animals having had interbirth intervals of 210 and 325 days (Howe and Clough 1971).

Hutias are precocial at birth, and have been observed ambulatory with eyes open after just a few hours, and eating solid food by the third day (Howe and Clough 1971). Howe and Clough (1971) provided growth curves of four G. ingrahami in the laboratory from birth up to age seven months, showing average body weight increases from about 80 g at birth to about 500 g at the end of the period.

In 1967 and 1968, Clough (1972) censused hutias on a 0.47 ha plot spanning two community types on East Plana Cay. Hutia density was estimated by nocturnal sightings and diurnal pellet counts at 30 animals per ha over 400 ha of suitable habitat, for a total island population of 12,000. Average body weight of 98 hand-captured hutias of both sexes combined was 708.6 g, with males slightly larger than females. On a return trip in 1973, Clough (1974) noted no significant difference either in population density or in combined average body weight, and speculated that the population age structure was stable throughout the year. A brief reconnaissance in July 1983 by Woods and Jordan (unpublished field data) yielded a similar estimate of population density, and four animals captured by hand had a mean body weight of 719 g.

Six of 41 animals caught by hand on the island in 1968 had "mangy fur, scabby skin on the back and rump, were underweight" and had inflamed eyelids or cataracts (Clough 1972). However, the capture technique may have biased the sample in favor of weak animals. Both sick and healthy animals carried the louse, Giricola o'mahonyi (Clough 1972).

Predation of G. ingrahami has never been reported in the wild, the only vertebrate predators on East Plana Cay being ospreys (Pandion heliatus) and occasional small falcons (Falco sp.), as observed by Clough (1972).

On 14 January 1973, Clough (1974, 1985) removed 11 animals (six males and five females) from East Plana Cay to

Little Wax Cay in the Exuma Cays Land and Sea Park. In March of 1981, he released 13 animals to Warderick Wells Cay, also in the Exuma Park (Clough 1985). Both transplant sites were selected for their apparent lack of predators. On returning in 1983, Clough (1985) found an abundance of hutias on the first site, and scattered sign on the second. Interestingly, three animals of five captured on Little Wax Cay weighed over 1000 g, a weight that none of 122 captured on East Plana Cay had achieved (G. C. Clough pers. comm. 1983). Seven animals taken from Little Wax Cay to the Ardastra Gardens in Nassau in May and June, 1983, had a mean body weight of 946 g (unpublished zoo records, Ardastra Gardens).

The Bahamian hutia inhabits a harsh, isolated, and rarified system. According to Clough (1973), "A violent hurricane or the introduction of a predatory mammal could upset this balance so that hutias could suddenly become extinct. Their stable, high-density population is maintained only under very specific conditions and by definite adaptations and concessions in behavior, reproduction, and mortality."

This project was designed to address the nature of those adaptations, and to observe the dynamics of hutia population growth in an unexploited habitat. By assessing hutia habitat impacts, I have hoped to discern the nature of Bahamian ecosystems before hutia decimation, and thus to inform plans for Bahamian conservation.

Figure I-1. The Commonwealth of the Bahamas, showing the distribution of living and extinct Geocapromys ingrahami.

CHAPTER II

THE STUDY SITE

Of the three sites available for a field study of the Bahamian hutia, Little Wax Cay was the clear choice. East Plana Cay, the only remaining natural reservoir of the species and the source of the two transplanted populations, was too remote for an extended study. Warderick Wells had been inoculated with hutias in 1981, too recently to have grown a population of measurable size or impact. Little Wax Cay, the smallest of the three, had been inoculated in 1973, and samples since had indicated a thriving increase from the original cohort of six males and five females (Clough 1974, 1985).

A major advantage in studying Little Wax Cay over East Plana was that the date of inoculation and the size of the founder population were both known. The population was therefore closed with respect to time as well as space, obviating assumptions of demographic stasis. Instead the reintroduction provided a unique opportunity to determine, in terms of the Verhulst-Perl logistic growth model, the value of r for a K -selected species. The value of K might be taken as the density of the East Plana Cay population, characterized by its long isolation and lack of human

disturbance. Solution of the logistic equation for a species threatened with extinction could greatly benefit plans for its management.

Little Wax Cay is a 19.4 ha island of low-elevation limestone, located 60 km southeast of Nassau in the middle Exuma Cays. It is the second most northern island in the Exuma Cays Land and Sea Park, a rectangular preserve spanning 35 km from north to south and 13 km from east to west. The park was established in 1958 after a survey conducted by the New York Zoological Society and the Conservation Foundation (Ray 1961).

The island is characterized by rocky windward coasts to the north, east, and south, with cliffs reaching 12 m, contrasted by long sandy beaches on the low-energy west coast. In general the topography is crater-like, with a system of narrow ridges forming a perimeter rim about the lowland interior. The interior is dotted by seven ponds and a mangrove swamp, and is distinguished by a surprising variety of habitats. The following six of eight Bahamian community types described by Correll and Correll (1982) are represented on Little Wax Cay: coastal rock community, sand strand formation, coastal coppice, whiteland community, fresh water formation, and mangrove community.

I dropped anchor off the northwest coast of Little Wax Cay at 10:00 AM on Tuesday, 12 March 1985, in the nineteen-foot sloop, Fawn. The vessel was a shoal-draft, full-keel, fiberglass structure designed by Carl Alberg and

manufactured by Cape Dory Yachts of East Taunton, Massachusetts. The next five weeks were spent establishing a camp, cutting trails, and mapping the island.

Camp was erected at the top of a hill above the anchorage, behind a small dune. The beach below was a narrow strip deposited on slab limestone and shifted by a strong tidal surge between Little Wax Cay and Bush Hill, a smaller island to the north. I named the beach Thom's Landing after Mr. Thom Goodwin, a good friend and seaplane pilot who had flown me to the island on reconnaissance the previous year.

A map of the island was constructed from an outline enlarged from U.S. Defense Mapping Agency Hydrographic/Topographic Center Chart number 26257 and surveyed by hand-held compass (Fig. II-1). The chart provided 20 ft (6 m) and maximum elevations. All other elevations were estimated to the nearest five feet (1.5 m) above mean sea level. The trails were cut by machete to connect important features by transecting habitat gradients. The trails were designed both to allow passage through the dense interior brush and to facilitate habitat sampling.

From March through August of 1985, I worked on the island during the daytime, and slept on the boat at night to avoid mosquitoes and to minimize my effect on the hutia distribution. During that time, there was only one tent in Camp, which I used for the storage of materials and supplies. During September, the boat was anchored off

Pyfrom Cay, in the Norman's Cay lagoon, for protection from storms while I returned to Gainesville for supplies and an assistant for the population studies that followed. During October, November, and December, I slept in a small tent opening to a wire pen constructed for the observation of hutia behavior. My assistant, Mr. Donnie May of Gainesville, camped in the original main tent, and the supplies were moved to a third tent erected nearby.

Figure II-1. Little Wax Cay, Exuma, showing trails cut by the author. Elevations are estimated in feet above mean sea level.

CHAPTER III

STUDIES OF THE HABITAT

Materials and Methods

Vegetation sampling was designed for correlation with hutia distribution, and for assessment of hutia browse impact. The various community types present on Little Wax Cay were resolved for sampling into two general types: dunes and woodlands. The dunes were sampled by line transect, and the woodlands were sampled by rectangular quadrat.

Dune communities occupied one of the small western beaches and Moon Beach, the latter by far the larger. Three transects were laid across Moon Beach, approximately 40 m apart along radii of its crescent shape from high water line to western-most dune (Fig. III-1). Plants within 0.5 m of the transect line on either side were recorded by species name, and cover was measured within the 1 m band to the nearest centimeter. In addition, the following measurements were taken from patches within the band showing hutia browse: largest and smallest diameter (± 0.5 mm) of shoots browsed, percent of shoot length affected by browse, percent of shoot length girdled, and percent of shoots killed

(estimates). Woody dicots were noted also for deepest tissue layer affected (cork, cork cambium, phloem, vascular cambium, or xylem).

Optimum woodland plot size and shape were selected by laying out a 5 X 16 m rectangular plot in each of three different inland habitat types: rocky upland (Dilly Lane), rocky lowland (Burma Road), and sandy lowland (Shortcut). Each plot was delineated at 1 m intervals. The plant species present in each 1 m² subplot were tallied and summed to yield totals over larger plots of different sizes and shapes (Table III-1).

The smallest plot that contained at least 95% of the total species present in each of the three sampling areas was 3 X 9 m. A 3:1 ratio of length to width supports the recommendation of Gauch (1982) for sampling xeric shrub and woodlands.

Twenty rectangular vegetation sampling plots 3 X 9 m were allocated among the inland habitats as follows: coppice, 16, mangrove swamp, 2, pond banks, 2 (Fig. III-1). The 16 coppice plots were placed randomly along the trails. The two mangrove plots were placed along the southern and western edges of Mangrovia, the interior being inaccessible in wet weather. One pond bank plot was placed on the eastern bank of Loch Ness. The other was placed on the eastern bank of Great Lake.

Within each vegetation plot, several observations were recorded. A shoot arising from the ground separately or

splitting from another shoot within 10 cm of ground level was regarded as an individual shoot. The clear bole of a shoot was denoted the "primary shoot". That part continuing along the main axis of the shoot above the first branch point was denoted the "secondary shoot". All other branches, including all leaf-bearing branches were denoted "tertiary shoots". Such nomenclature is not established in the literature, but was developed here to evaluate the effects of hutia browse. For each primary shoot the following data were recorded: species name, basal diameter (± 0.5 mm), growth form (tree, shrub, or vine), height class (<1 m, 1-3 m, >3 m), and presence or absence of damage due to the following causes: disease, fire, hutia browse, invertebrates, or unknown causes. In addition, a note was made of hutia damage to exposed roots. Naturally, dead individuals were so noted.

The following additional measurements were recorded from plants browsed by hutias: minimum and maximum diameter (± 0.5 mm) of browsed shoots, minimum and maximum height (± 0.5 dm) above ground of browsed shoots, and the innermost tissue layer affected by browse (cork, cork cambium, phloem, vascular cambium, xylem). Within each of the three shoot designations (primary, secondary, and tertiary) two subjective estimates were made: the percentage of total shoot length affected by hutia browse, and the percentage of total shoot length girdled by hutia browse. Finally, an estimate was made of the percentage of the leaf-bearing

shoots that had been killed by visible injuries. Damage to the primary shoot was always the most critical, and in many cases, high mortality was associated with little or no browsing of the leaf-bearing shoots.

All diameter measurements were made with a vernier caliper. All height measurements were made with a retractable fiberglass tape measure, by climbing trees when necessary. Voucher specimens were collected of all vascular plant species found on Little Wax Cay over the course of the study. Leafy shoots and flowers were pressed and stored on edge in a tent exposed to full sunlight. Smaller flowers and fruits were preserved in 70% ethanol in plastic vials. All vouchers were identified by W.S. Judd and K.D. Perkins of the Florida Museum of Natural History, University of Florida, Gainesville, where all specimens were deposited.

Unless otherwise specified, all statistical operations were performed using the Personal Computer version of the Statistical Analysis System (SAS Institute Inc. 1985). I am obliged to caution that functional relationships within the data are speculative, as the data are not the results of controlled experiments.

Results

Table III-2 is a comprehensive list for 1985 of the vascular plants of Little Wax Cay.

To enable parametric analysis of the data pertaining to community structure, a series of data transformations were necessary. Values of basal diameter were converted to basal area assuming a circular cross-section. To test each plant species for a normal distribution over the 20 vegetation plots, the following three quantities were computed for each species on each plot: (a) the sum of the individual basal areas, (b) the square root of (a), and (c) the base-ten logarithm of (a). The best transformation was (c), for which 18 of 30 species tested were distributed normally ($p > 0.05$) according to Shapiro and Wilk's W-test (Shapiro and Wilk 1965, Royston 1982), as computed by SAS-PC Procedure Univariate (SAS Institute Inc. 1985).

A correlation matrix of the log transformed total basal areas showed a high degree of correlation among the 30 species. Proxies were eliminated as follows: the species with the greatest number of significant ($p < 0.05$) correlates was retained first, and the correlates dropped in decreasing order of R^2 value to a threshold of 0.65. Then the species with the second greatest number of significant correlates among the remaining species was retained, dropping the correlates in order, and so on. The threshold R^2 value of 0.65 eliminated 11 of the 30 species, leaving 19, the maximum permissible for ordination of 20 plots. Of the 19 species selected for ordination (Table III-2), 15 had normal distributions of the log transform of summed basal area.

Ordination was performed on the log transforms by two different methods (see Gauch 1982): principal components analysis (PCA) and detrended correspondence analysis (DCA). PCA was conducted using SAS-PC Procedure Factor, Method Principal, Rotation Varimax, with four factors retained (SAS Institute Inc. 1985). DCA (Hill and Gauch 1980, Gauch 1982) was conducted using the personal computer version of program DECORANA (Hill 1979), using the default options of four iterations for rescaling and 26 segments for detrending.

Results of PCA and DCA differed only in detail. Notwithstanding Wartenberg et al. (1987), the results of DCA in this study were judged the more ecologically correct (Fig. III-2). The first axis of ordination provided a strong representation of increasing soil moisture or decreasing elevation. The second axis appeared to represent a gradient from sandy to rocky substrate, but the representation was not as strong. Note the similarity of the two mangrove plots (number 7 and number 8), the two pond bank plots (number 3 and number 11), and the two sandy hillside plots (number 2 and number 16). The uniqueness of plot number 20 may have been due to the presence of a species there that was absent elsewhere: Sophora tomentosa. Two other species unique to plot number 20 were eliminated from the ordination as proxies of S. tomentosa: Rubiaceae [unknown] and one species represented by only two individuals, thus neither collected nor identified. All three species were rare within the plot and heavily browsed

by hutias. The latter two were represented by only eight individuals combined. Plot number 20 was located on the southeast shore, the closest point of Little Wax Cay to Shroud Cay, only 60 m to the south.

A total of 2497 individual trees, shrubs, and vines of 30 different species were inspected in the 20 vegetation plots. Of those, 1157 individuals had been browsed by hutias, including representatives of all 30 species sampled. Many of the browsed trees, including some with extensive tissue mortality, showed little or no hutia damage to the secondary and tertiary shoots. On the other hand, only 80 browsed individuals showed no damage to the primary shoots. For those reasons, primary shoot browse was taken to be the best index of hutia impact.

For parametric statistical analysis the estimates of percent of primary shoot browsed, percent of primary shoot girdled, and percent mortality were transformed by taking the arcsine (in radians) of the square root of the percentage (Sokal and Rohlf 1981).

The following variables were tested for variation from a normal distribution over all individuals within each of the 15 most numerous plant species: basal diameter, maximum diameter browsed, minimum diameter browsed, minimum height browsed, maximum height browsed, and the arcsine transforms of percent of primary shoot browsed, percent of primary shoot girdled, and percent mortality. Normality was tested by evaluating Shapiro and Wilk's W-statistic at a decision

level of 0.05. Only three of the eight variables were distributed normally, and those only for five of the 15 species tested. Since all of the distributions were skewed in favor of small values, two transforms of the same eight variables were tested for normality by species. Best fits (for 13 of 15 species) of basal diameter and maximum diameter browsed were given by the base-ten logarithm. Best fits (for 10 of 15 species) of all other variables were given by the square root. All subsequent statistical operations were performed on the appropriate transform.

Significant correlations ($R^2 > 0.45$, $p < 0.0001$) were found over all species between the following three variables: basal diameter, maximum diameter browsed, and minimum diameter browsed; and also between the following three variables: percent of primary shoot browsed, percent of primary shoot girdled, and percent mortality.

Chi-square tests of association were performed on the entire plant sample to examine the relationship between the presence or absence of hutia shoot browse and the condition of each of the other categorical variables (Table III-3). Hutias appeared to prefer live, tall, woody individuals to all other combinations. However, vines may have been under-represented in the browsed population due to their more fragile structure and the possibility that they may have been eliminated by partial browse or consumed entirely. Also, there was no relationship between the presence of hutia browse damage and the presence of damage by fire or

invertebrates. The possible role of browse in introducing disease was only marginally significant ($p = 0.069$). Occasional root browse was noted in high association with shoot browse.

Of the 1150 woody dicots that were browsed, 92.5% (1064) had been chewed to the xylem, 4.0% (46) had been chewed to the vascular cambium, 2.7% (31) had been chewed to the phloem, and 0.8% (9) had been chewed at the cork layer only. A chi-square test of association showed no significant variation ($p = 0.890$) in that ratio among the 25 woody dicot species.

A chi-square test over all plots showed a highly significant association ($p < 0.001$) between the presence of hutia shoot browse and the identity of the plant. Barring differential effects of browse on mortality, the ratio of browsed to unbrowsed individuals of a species over all plots may be interpreted as a ratio of hutia selectivity (Table III-4). For each species, a chi-square test for difference from a 50% ratio of browsed to unbrowsed plants was also performed. Coccoloba diversifolia and Manilkara bahamensis were clear favorites, whereas Smilax havanensis (a vine) and Metopium toxiferum (the poisonwood) were avoided. Although the leaves of Coccothrinax argentata were seen being browsed by hutias in the pen, the species was not shoot browsed, probably by virtue of being a monocot, and thus lacking a band of phloem beneath a layer of bark.

The logarithm of basal diameter was subjected to a two-way analysis of variance by plant species and the presence or absence of shoot browse. The ANOVA was performed by the General Linear Models Procedure of SAS-PC (SAS institute Inc. 1985). The three-factor model (the two fixed main effects plus an interaction term) accounted for most of the variance and was significant ($R^2 = 0.67$, $p = 0.0001$). The Type III sums of squares for plant species and the interaction term showed that both were significant ($p = 0.0001$), but the Type III sums of squares for browse presence showed that it was not ($p = 0.1483$). Not surprisingly, size differences among vascular species were explained by species identity and not by hutia preference, even though preference and species were related. However Student's t-test of the difference in mean basal diameter of browsed versus unbrowsed plants across all species showed that hutias did prefer the larger individuals ($p < 0.05$). The summary indication is that hutias preferred species achieving larger size, and not that they were cuing on size itself.

For browsed individuals, each continuous variable was subjected to a two-way ANOVA by species and height class, with the interaction term included (Table III-5). Variables that can be used as indicators of hutia feeding preference include minimum diameter browsed, maximum height browsed (smaller, higher shoots being less accessible than larger, lower ones), percent of primary shoot affected, percent of

primary shoot girdled, and percent shoot mortality. For each of those latter variables, the ANOVA model was significant ($p = 0.0001$) but it never accounted for much of the variance ($R^2 \leq 0.57$). The most ecologically important index of feeding preference, percent shoot mortality, had only 33% of its variance explained by species and height class, although both effects and their interaction were significant ($p = 0.01$). The combination of low R^2 value and low p value is probably due to the power conferred by large sample size ($N = 1155$). Thus, although plant species identity was important in eliciting shoot browse, something else was of prime importance (see Chapter V).

Pairwise comparisons by species of transformed percent shoot mortality were made by t -tests, using Fisher's Least Significant Difference at a comparisonwise error rate of 0.05, the experimentwise error rate having been controlled by the ANOVA (Ott 1984). The greatest mortality was suffered by Manilkara bahamensis, Coccoloba diversifolia, and the two unidentified species from plot number 20: one collected and referred to the family Rubiaceae, and one represented by only two plants, not collected (Table III-6). Manilkara bahamensis and C. diversifolia were widespread on the island. Manilkara bahamensis, also called the "wild dilly," is a congener of the popular sapodilla (M. zapota), whose latex is used in the production of chicle. Coccoloba diversifolia is a congener of the seagrape (C. uvifera) whose edible purple fruit is succulent and sweet. Less

damage was suffered by Sophora tomentosa, although it was represented by only six individuals, again restricted to plot number 20. Due to the severity of browse impact on those five species, combined with low numbers in three of them, they must be regarded as being at risk of extinction on Little Wax Cay.

The possibility of extinction by hutia browse draws support from the historical record. Table III-2 lists the plants collected from the Thom's Landing area of Little Wax Cay by Oris Russell in 1958 during the original survey for the establishment of the Exuma Cays Land and Sea Park (Russell 1961). Due to the limited nature of the 1958 collection (one day's effort on a small part of the island), no inferences can be made regarding species present in 1985 but absent from the 1958 list. However, four species listed in 1958 were absent in 1985, and must have been eradicated during the 27 years between. The only biological change known to have occurred during that period was the introduction of the eleven founder hutias by the Bahamas National Trust in 1973.

One of the missing plant species was the seagrape itself (Coccoloba uvifera). Although Russell (1961) found it common on the western dunes in 1958, I found but one individual in 1985, and that was dead and weathered at the south end of Moon Beach. Captive feeding experiments (Chapter IV) showed it to be a preferred hutia forage.

A second missing species was the "hog-cabbage palm", "buccaneer palm", or "Sargent's palm" (Pseudophoenix sargentii). Due to its current rarity everywhere (it is legally protected in the United States) it was never tested for hutia preference. Nonetheless, the tender shoot tip has a history of use as a favored food for domestic hogs (Correll and Correll 1982). Furthermore, Correll and Correll (1982) mention that wild hogs have severely reduced its numbers. Among the many decomposing palm snags I found on Little Wax Cay in 1985, there were several 1-2 m in height that may have been P. sargentii. But no live representatives could be found.

The last two species missing in 1985 were Picrodendron baccatum and Solanum bahamense. The first is commonly called "black wood", although Russell (1961) referred to it as "white wood", a name Correll and Correll (1982) apply to the unrelated Schoepfia chrysophylloides. Picrodendron baccatum produces an orange-yellow to light brown drupe of 2 to 2.5 cm diameter. Solanum bahamense, called the "canker-berry", produces a red berry of 6 to 8 mm diameter.

A fifth species, Bumelia americana, appears in the 1958 list, but in 1985 the only member of that genus on Little Wax Cay was B. glomerata. Since the two are easily confused, no conclusions are drawn from the difference.

The three dune transects of Moon Beach (Fig. III-1) showed minimal hutia browse. Percent ground cover by species is shown in Table III-7 for a band extending 0.5 m

to either side of the transect line. Of eight species present, only four showed signs of bark browse, which was limited to five percent of the combined shoot length within any cluster. No plant mortality was suffered as a result of hutia browse. I conclude that hutia browse in the sand strand habitat was incidental, and impact minimal.

Table III-1. Plant species totals by plot size and shape at three locations.

<u>Plot Shape</u> (ratio)	<u>Plot Size</u> (m)	<u>Area</u> (m ²)	<u>Number of Species</u>		
			<u>site 1</u>	<u>site 2</u>	<u>site 3</u>
1:1	1 X 1	1	5	5	3
	2 X 2	4	8	7	7
	3 X 3	9	8	10	11
	4 X 4	16	14	12	13
	5 X 5	25	14	14	14
1:2	1 X 2	2	5	5	4
	2 X 4	8	9	9	10
	3 X 6	18	12	13	14
	4 X 8	32	15	14	15
	5 X 10	50	15	14	15
1:3 (optimum)	1 X 3	3	5	6	7
	2 X 6	12	11	11	13
	3 X 9	18	15	14	15
	4 X 12	48	15	14	15
	5 X 15	75	16	15	15
1:4	1 X 4	4	5	7	7
	2 X 8	16	13	13	13
	3 X 12	36	15	14	15
	4 X 16	64	15	15	15
1:5	1 X 5	5	6	7	8
	2 X 10	20	13	13	13
	3 X 15	45	15	15	15
1:6	1 X 6	6	7	7	9
	2 X 12	24	15	13	13

Note: The optimum plot was selected as the smallest one containing 95% of total species at each of the three sites.

Table III-2. The vascular plants of Little Wax Cay.

Cyperaceae

- + Cladium jamaicense Crantz

Palmae

- * + Coccothrinax argentata (Jacq.) L.H. Bailey
- Pseudophoenix sargentii H. Wendl.
- + Sabal palmetto (Walt.) Lodd. ex Roem. & Schult.

Smilacaceae

- Smilax havanensis Jacq.

Amaryllidaceae

- Hymenocallis arenicola Northrop

Casuaraceae

- Casuarina equisetifolia L.

Picrodendraceae

- Picrodendron baccatum

Polygonaceae

- * + Coccoloba diversifolia Jacq.
- [Note: Coccoloba uvifera (L.) L. was represented by but one individual, dead, on the northeast dunes, and so is mentioned here but not considered in the living flora.]

Amaranthaceae

- Iresine flavesens H. & B. ex Willd.

Nyctaginaceae

- + Guapira discolor (Spreng.) Little
- Guapira obtusata (Jacq.) Little
- ? Commicarpus scandens (L.) Standl.

Portulacaceae

- Portulaca rubricaulis Knuth

Capparaceae

- Capparis flexuosa (L.) L.

Leguminosae

- * Cassia lineata Sw.
- Galactia sp.
- * + Pithecellobium keyense Britt. ex Britt. & Rose
- * + Sophora tomentosa L.

Rutaceae

- * Zanthoxylum coriaceum A. Rich.
- Zanthoxylum flavum Vahl

Table III-2. (continued)

Surianaceae

- + Suriana maritima L.

Malpighiaceae

- Byrsonima lucida (Mill.) DC.
- Malpighia polytricha A. Juss.

Euphorbiaceae

- Argythamnia lucayana Millsp.
- * Ateramnus lucidus (Sw.) Rothm.
- * Drypetes diversifolia Krug & Urb.

Anacardiaceae

- * Metopium toxiferum (L.) Krug & Urb.

Rhamnaceae

- * + Reynosia septentrionalis Urb.

Rhizophoraceae

- * Rhizophora mangle L.

Combretaceae

- * + Conocarpus erectus L.

Myrtaceae

- + Eugenia axillaris (Sw.) Willd.
- * Eugenia foetida Pers.

Theophrastaceae

- * + Jacquinia keyensis Mez

Sapotaceae

- Bumelia americana (Mill.) Stearn
- * Bumelia glomerata Griseb.
- * + Manilkara bahamensis (Baker) Lam. & Meeuse

Asclepiadaceae

- Cynanchum sp.

Convolvulaceae

- Ipomoea violacea L. (= macrantha Roem. & Sch.)

Boraginaceae

- * + Bourreria ovata Miers

Avicenniaceae

- Avicennia germinans (L.) L.

Solanaceae

- Solanum bahamense L.

Table III-2. (continued)

Bignoniaceae

Tabebuia bahamensis (Northrop) Britt.

Rubiaceae

- + Casasia clusiifolia (Jacq.) Urb.
- * Catesbaea parviflora Sw.
- + Erithalis fruticosa L.
- * Randia aculeata L.
- + Rhachicallis americana (Jacq.) O. Ktze.
- + Strumpfia maritima Jacq.
- [unknown]

Goodeniaceae

- + Scaevola plumieri (L.) Vahl

Asteraceae

- Ambrosia hispida Pursh
- + Borrichia arborescens (L.) DC.
- Salmea petrobioides Griseb.

*Used in ordination

†Present in 1985 and identified by Russell (1961) in 1958

-Identified by Russell (1961) in 1958 but absent in 1985

Note: One additional species was found near the southeast coast, represented by only two individuals, both less than one meter in height and well-browsed by hutias. For the sake of their conservation they were not collected, thus not available for identification.

Table III-3. Results of chi-square tests of association between the presence of shoot browse and selected categorical variables of all plants.

<u>Category</u>	<u>Status</u>		<u>x²</u>	<u>df</u>	<u>p</u>
growth form	vine	<u>shrub</u> <u>tree</u>	339	2	<0.001
plant height	<1m	<u>1-3m</u> <u>>3m</u>	406	2	<0.001
damage due to:					
disease	yes	no	3.31	1	0.069
fire	yes	no	2.13	1	0.145
invertebrates	yes	no	0.02	1	0.894
unknown causes	yes	no	2.20	1	0.138
roots browsed	<u>yes</u>	no	10.3	1	0.001
status	<u>alive</u>	dead*	19.6	1	<0.001

*Snags were sampled in the same way as live plants.

Note: Forms associated with browse are underlined.
(N = 2435)

Table III-4. Selectivity ratios (number browsed/number observed) of 30 plant species.

<u>Species Name</u>	<u>Selectivity</u> (0<x<100)	<u>N</u>	<u>p*</u>
<u>Sophora tomentosa</u>	100.00	6	<0.025
<u>Zanthoxylum coriaceum</u>	100.00	4	<0.05
<u>Coccoloba diversifolia</u>	89.29	28	<0.005
<u>Manilkara bahamensis</u>	88.80	125	<0.001
<u>Guapira discolor</u>	76.92	221	<0.001
<u>Eugenia axillaris</u>	76.43	140	<0.001
<u>Bourreria ovata</u>	75.82	91	<0.001
<u>Ateramnus lucidus</u>	71.48	270	<0.001
<u>Pithecellobium keyense</u>	71.00	100	<0.005
<u>Erithalis fruticosa</u>	61.62	99	<0.025
<u>Randia aculeata</u>	39.19	347	<0.005
<u>Jacquinia keyensis</u>	28.57	42	<0.01
<u>Rhizophora mangle</u>	26.09	69	<0.005
<u>Conocarpus erectus</u>	22.00	50	<0.005
<u>Eugenia foetida</u>	20.13	159	<0.001
<u>Catesbaea parviflora</u>	16.67	12	<0.025
<u>Metopium toxiferum</u>	15.63	32	<0.005
<u>Smilax havanensis</u>	0.00	281	<0.001
<u>Coccothrinax argentata</u>	0.00	175	<0.001
<u>Argythamnia lucayana</u>	0.00	4	<0.05
<hr/>			
[unknown]	100.00	2	>0.1
<u>Malpighia polytricha</u>	100.00	1	>0.1
<u>Rubiaceae [unknown]</u>	85.71	7	>0.05
<u>Cassia lineata</u>	80.00	5	>0.1
<u>Bumelia glomerata</u>	75.00	8	>0.1
<u>Drypetes diversifolia</u>	50.30	167	>0.1
<u>Tabebuia bahamensis</u>	42.86	7	>0.1
<u>Reynosia septentrionalis</u>	41.86	43	>0.1
<u>Cynanchum sp.</u>	0.00	1	>0.1
<u>Zanthoxylum flavum</u>	0.00	1	>0.1

*P-values are given for individual chi-square tests of departure from a 50% ratio.

Note: A chi-square test of association between species identity and the presence of shoot browse, over all species and all 20 plots, was highly significant. (N = 2497, $p < 0.001$)

Table III-5. Results of a two-way analysis of variance, by species and height class, of selected continuous variables of browsed plants.

<u>Dependent</u> <u>Variable</u>	<u>Model</u>		<u>Type III p-value</u>		
	<u>R²</u>	<u>p</u>	<u>species</u>	<u>height</u>	<u>interaction</u>
basal diameter	0.69	0.0001	0.0001	0.0001	0.0032
maximum diameter					
browsed	0.69	0.0001	0.0001	0.0001	0.0032
minimum diameter					
browsed	0.57	0.0001	0.0001	0.0001	0.0001
minimum height					
browsed	0.20	0.0001	0.0001	0.5277	0.5254
maximum height					
browsed	0.47	0.0001	0.0001	0.0001	0.0001
% primary shoots*					
browsed	0.24	0.0001	0.0001	0.0021	0.0001
% primary shoots*					
girdled	0.22	0.0001	0.0001	0.4516	0.0001
% leaf-bearing					
shoots killed	0.33	0.0001	0.0001	0.0057	0.0002

*The "primary shoot" is the clear bole.

Note: N = 1155

Table III-6. Pairwise comparisons by species of transformed percent shoot mortality.

<u>Species Name</u>	<u>Mean</u>	<u>N</u>	<u>T Group</u>		
[unknown]	1.253	2	A		
Rubiaceae [unknown]	1.215	6	A		
<u>Manilkara bahamensis</u>	0.875	111	A	B	
<u>Coccoloba diversifolia</u>	0.873	25	A	B	
<u>Sophora tomentosa</u>	0.596	6	C	B	
<u>Pithecellobium keyense</u>	0.585	71	C	B	
<u>Ateramnus lucidus</u>	0.498	193	C	B	D
<u>Tabebuia bahamensis</u>	0.424	3	C	E	D
<u>Bumelia glomerata</u>	0.393	6	C	E	D
<u>Bourreria ovata</u>	0.314	69	C	E	D
<u>Randia aculeata</u>	0.308	135	C	E	D
<u>Guapira discolor</u>	0.223	170	C	E	D
<u>Metopium toxiferum</u>	0.185	5	C	E	D
<u>Drypetes diversifolia</u>	0.177	84	C	E	D
<u>Eugenia axillaris</u>	0.158	107		E	D
<u>Erithalis fruticosa</u>	0.153	61		E	D
<u>Jacquinia keyensis</u>	0.146	12		E	D
<u>Reynosia septentrionalis</u>	0.112	18		E	D
<u>Rhizophora mangle</u>	0.086	18		E	D
<u>Eugenia foetida</u>	0.010	32		E	
<u>Zanthoxylum coriaceum</u>	0.010	4		E	
<u>Malpighia polytricha</u>	0.010	1		E	
<u>Cassia lineata</u>	0.010	4		E	
<u>Conocarpus erectus</u>	0.010	11		E	

Note: Means of the same T group are not significantly different at an alpha level of 0.05. The experimentwise error rate was controlled at 0.05 by ANOVA. (N = 1155)

Table III-7. Sand strand plant community analysis by three transects of Moon Beach.

<u>Species Name</u>	<u>Percent Ground Cover</u>		
	<u>transect 1</u>	<u>transect 2</u>	<u>transect 3</u>
<u>Scaevola plumieri</u>	25.6*	13.2*	33.6*
<u>Ambrosia hispida</u>	21.5	15.5	0.0
<u>Surlana maritima</u>	9.9*	10.5*	5.9*
<u>Erithalis fruticosa</u>	7.6*	0.0	9.8*
<u>Hymenocallis arenicola</u>	11.9	0.0	3.7
<u>Coccothrinax argentata</u>	1.6**	1.8	2.2
<u>Cassia lineata</u>	0.4	2.3*	1.6*
<u>Sophora tomentosa</u>	0.0	0.0	1.1
barren sand	21.5	56.7	42.1

*Indicates species showing signs of bark browse. No cluster was browsed for more than 5% of the combined length of its shoots, and no mortality was suffered from hutia browse.

**Leaves of one tree were chewed for a loss of 10% of area.

Figure III-1. Little Wax Cay, showing the 20 vegetation sampling plots (boxed) and the three dune transects (circled).

Figure III-2. Detrended correspondence analysis of the 20 vegetation sampling sites: axis 2 as a function of axis 1.

CHAPTER IV
STUDIES OF THE INDIVIDUAL

Age and Growth

Materials and Methods

A principal tool of demographic analysis in populations sampled by capture-recapture is an index for aging live animals. Most commonly used is body mass (Zullinger et al. 1984), although variations within any age class may be great. Tooth characteristics are used commonly in aging wildlife species (see review by Larson and Taber 1980). Most encouraging to this study is an index developed by Ruckel et al. (1977), who used simple linear regression to model the relationship between eye lens weight in muskrats (Ondatra zibethicus) and the combined width of the upper incisors, measured at the tip ($R = 0.77$, $p < 0.0001$).

In the interest of developing an index for aging live specimens of G. ingrahami, several measurements were taken biweekly from birth of three animals born in the Florida Museum of Natural History Hutia Colony, University of Florida, Gainesville. Body mass (± 10 g) was taken with a 500 g Pesola spring scale while the animal was contained in

a lightweight capture sac. Body length (± 0.5 mm) and total length (± 0.5 mm) were taken with a cotton cord transferred to a millimeter rule. Right hind foot lengths with and without claw (± 0.5 mm), and right ear length (± 0.5 mm) were measured directly with a millimeter rule. Paired incisor widths (± 0.01 mm) were measured with a Mitutoyo dial caliper at four points: upper incisors at the gumline and tip, and lower incisors at the gumline and tip. Also noted were the pelage color and texture, any marks or deformities, and the status of the reproductive organs (testes: palpable or not, vagina: perforate or not, teats: shorter or longer than 1 mm).

All measurements were taken after anesthesia with five to ten drops of Metofane on a cotton ball in a brown glass jar placed over the animal's muzzle. Anesthesia was controlled by adjusting the distance between the jar and the animal's nose. A moderate-to-shallow plane of anesthesia was maintained by keeping respirations deep and regular, and by maintaining the blinking reflex.

Because Bahamian hutias had only recently been added to the FMNH colony, only three animals were born there during the course of this study. Those three were the only ones of known age that could be used as standards for the development of an aging index. The male was born on 1 December 1986, eartagged K1136, and named Donnie. A twin female, born on the same day, was eartagged K1137 and named Laurie. Another female, born on 3 May 1987, was eartagged

K1139, and named Barbara. Since high quality forages had appeared to be present in excess on Little Wax Cay (see Chapter III), the use of animals fed ad libitum in the lab was deemed appropriate to the development of age and growth criteria, but only for Little Wax Cay hutias. Body size differences and forage differences between Little Wax and East Plana Cay are discussed at length in Chapter VI.

Results

Two of the three known-age animals, Donnie and Laurie, were traced for six months, beginning at age two weeks. Barbara was measured at one, 14, and 28 days of age but died of natural causes in the fifth week.

After plotting each metric as a function of age, body mass (BMAS) and upper incisor width at the gumline (UGUM) were selected for being easy to measure and for having limited variation at each value of age. Since both plots were curved, non-linear least-squares regression was performed using SAS-PC Procedure NLIN (SAS Institute Inc. 1985). The MARQUARDT method was specified because sequential observations were not independent. As both curves were monotonically asymptotic from below, the following model was tested:

$$y = a + B_0(1 - e^{B_1x})$$

where y was the body metric, a was the y -intercept, x was age, and B_0 and B_1 were the parameters being estimated. Ricker (1979) referred to the model as Putter's Growth Curve No. 1.

For BMAS, the birth weight (a) was visually estimated from the plot as 90 g, Barbara's weight at one day having been 95 g. Pooling all three individuals, the least-squares estimate of B_0 was 911 g and that of B_1 was $-0.0039 \text{ days}^{-1}$. For UGUM the y -intercept was visually estimated from the plot as 2.35 mm, Barbara's value at one day having been 2.38 mm. Again pooling subjects, the least-squares estimate of B_0 was 1.84 mm and that of B_1 was $-0.0124 \text{ days}^{-1}$.

To develop models spanning the older ages, the two juvenile models were used to age two hutias captured on Little Wax Cay as juveniles and raised to adult size in the FMNH colony. The male had been eartagged K1132 and named Theodore. The female had been eartagged K1106 and named Bunny. Both had been weighed and measured regularly since capture on 20 November 1985. For Theodore, the BMAS model was used to estimate age on 20 November (75 days) and on 14 December 1985 (79 days), the date of next measurement. Adding 24 days to the 20 November estimate gave a second estimate of the 14 December age (99 days). The same was done with the UGUM model, yielding two more estimates of age on 14 December (84 days, 94 days). Averaging the four estimates gave a combined estimate of 89 days on 14 December, for an estimated birth date of 16 September 1985.

Age at all subsequent measurements was estimated by counting forward from the birth date. The same procedure was applied to Bunny, yielding an estimated birth date of 7 September 1985. Theodore's estimated age at last measurement was 619 days, and Bunny's was 663 days, both fully adult. Pooling data for those two animals with the three known-age juveniles increased the number of observations for any metric from 27 to 37 (40 for BMAS).

Again separate models were developed for BMAS and UGUM. For each metric Putter's Curve No. 1 was fitted using two models: (1) a one-parameter model, with B_0 specified and B_1 estimated by the model, and (2) a two-parameter model, with both B_0 and B_1 estimated by the model. In all cases, the y-intercept values were the same as those used in the juvenile models. The reason for testing a one-parameter model was to constrain the asymptote to a value obtained from wild adults, instead of allowing the model to fit itself too specifically to the lab-reared animals.

Analysis of data obtained on first capture of 111 hutias on Little Wax Cay (65 males and 46 females) showed bimodal frequency distributions of both BMAS and UGUM, as well as several other metrics. All metrics were heavily skewed toward the higher values. Shapiro and Wilk's W-test rejected normality for all metrics at a decision level of 0.05. Separating the data by sex reduced neither the bimodality nor the skew. For the females, BMAS showed a first peak at approximately 320 g and a second, larger peak

between 800 and 960 g. UGUM showed a first peak at about 3.60 mm and a second, larger peak just above 4.50 mm. For the males, BMAS showed a very small first peak at approximately 320 g, and a much larger second peak just below 960 g. UGUM showed a small first peak at about 3.60 mm and a large second peak between 4.50 and 4.80 mm.

In each case, the first peak was taken to represent the distribution of juveniles, and the second that of adults. To separate the juvenile and adult distributions, adulthood was defined as the attainment of reproductive age. It was assumed that, as in most species exhibiting determinate growth, size measurements would begin to stabilize at the age of first reproduction. The smallest Little Wax Cay animals known to have reproduced were Theodore at 670 g and Bunny at 710 g, both in captivity at FMNH. Theodore's age was 396 days and Bunny's was 405 days, as estimated by the juvenile models. Thus, a body mass of 690 g (the average of 670 and 710 g) was selected as the threshold for adults.

Analysis of Little Wax Cay first-capture data for females of BMAS greater than or equal to 690 g indicated normal distributions ($N = 30$, $p > 0.05$) of all metrics. Means ($\pm$ one standard deviation) of BMAS and UGUM were 890 (± 118) g and 4.60 (± 0.21) mm, respectively. Analysis of data for males of 690 g or more ($N = 55$) yielded normal distributions ($p > 0.05$) of all but two metrics, including BMAS. Means ($\pm$ one standard deviation) of BMAS and UGUM were 949 (± 139) g and 4.68 (± 0.23) mm, respectively.

Student's t-test showed no difference in adult UGUM means between the sexes ($p > 0.10$). Student's t-test for a difference in adult BMAS between the sexes yielded a t-value of 1.965, marginally rejecting the null hypothesis at a decision level of 0.05. Since the distribution of BMAS in adult males had been marginally non-normal ($p = 0.044$), a Wilcoxon Rank Sum test was performed and narrowly failed to reject a null hypothesis of no difference in adult BMAS by sex ($p = 0.052$).

Having determined the threshold body mass of wild adults as 690 g, two models of UGUM versus age in weeks (AGEW) were tested using the data pooled from the five captive animals. In the one-parameter model, an asymptote of 4.64 mm (the average of 4.60 and 4.68 mm) was specified in the form of a B_0 value of 2.29 mm (4.64 mm minus the y-intercept value of 2.35 mm). The estimate (and 95% confidence interval) of B_1 was -0.054 (-0.050, -0.058) weeks⁻¹. The model was both accurate and significant ($R^2 = 0.9980$, $p < 0.01$). A two-parameter model estimating both B_0 and B_1 provided a slightly better fit to the laboratory data ($R^2 = 0.9989$, $p < 0.01$), but did not allow UGUM to reach the average value obtained from wild animals exceeding 690 g.

Likewise, two models of BMAS versus AGEW were tested using the data pooled from the five captive animals. In the one-parameter model, an asymptote of 918 g (the average of the male and female median values, since the male distribution had been non-normal) was specified in the form

of a B_0 value of 828 g (918 g minus the y-intercept value of 90 g). The estimate (and 95% C.I.) of B_1 was -0.030 (-0.027, -0.032) weeks⁻¹. The model was both accurate and significant ($R^2 = 0.9881$, $p < 0.01$). Again, a two-parameter model estimating both B_0 and B_1 provided a slightly better fit to the laboratory data ($R^2 = 0.9889$), but did not allow BMAS to reach the average value obtained from wild animals exceeding 690 g.

For the sake of comparison with published growth models (Zullinger et al. 1984), the relationship of BMAS to age was also modeled according to three sigmoid growth equations: the von Bertalanffy, the Gompertz, and the Logistic (Table IV-1). In each case the asymptote was specified as 918 g. Results are shown in Table IV-1. Although all models were significant and the fits consistently good ($R^2 \geq 0.98$, $p < 0.01$), the data were not sigmoid. Predicted values of body mass were lower than observed for juveniles and higher than observed for adults. Thus the best model of body mass versus age of Geocapromys ingrahami on Little Wax Cay is considered here to be the one-parameter version of Putter's Curve No. 1.

But the best regression model overall for the ontogenetic growth of G. ingrahami on Little Wax Cay is the one-parameter version of Putter's Curve No. 1, using paired upper incisor width as measured at the gumline:

$$UGUM = 2.35 + 2.29 (1 - e^{-0.054 (AGEW)})$$

For that reason it was the one used in Chapter V to age the animals live-trapped on Little Wax Cay. Observed and predicted values of UGUM are shown in Figure IV-1 for the five subjects used in model derivation.

A one-sided Kolmogorov-Smirnov comparison by sex of the UGUM values obtained on first capture of all 65 males and 46 females caught on Little Wax Cay indicated distinct distributions ($p < 0.05$), with the male distribution centered on a greater value. Thus, despite a similar growth pattern in known-age animals younger than 12 weeks, a sexual divergence in older known-age animals and in the field data recommends the eventual development of separate growth models by sex. Due to small sample size, that was not possible in this study.

Furthermore, all models assuming determinate growth become useless in distinguishing ages for which the index approaches constancy. In G. ingrahami, the models developed here cannot distinguish between ages over one year, when UGUM and BMAS values approach within one standard deviation of the mean value for adults. Since the predictive capability of all models discussed here is restricted to the yearling classes, recommendations of their use are appropriately qualified.

Table IV-1. Parameter values from three sigmoid models of body mass (Y) versus age in weeks (X).

<u>Model</u>	$\frac{K}{(\text{weeks}^{-1})}$	$\frac{I}{(\text{weeks})}$	$\underline{R^2}$	$\underline{P}$
von Bertalanffy Y = A(1 - (exp/3)) ³	0.0399	8.4703	0.9844	<0.01
Gompertz Y = Ae ^{-exp}	0.0456	12.7232	0.9823	<0.01
Logistic Y = A / (1 + exp)	0.0654	21.3353	0.9760	<0.01

defined: exp = e^{-K(X - I)}

Note: The value of the asymptote (A) was specified as 918 g in all cases.

Figure IV-1. Paired upper incisor width at the gumline (UGUM) as a function of age in weeks (AGEW): observed and predicted values using Putter's Growth Curve No. 1.

Metabolic Rates

Materials and Methods

Metabolic rates of four Bahamian hutias were determined at 11 different temperatures by measuring oxygen consumption. Being crepuscular-nocturnal, the subjects were fed in the evening and tested in the late morning or early afternoon to help ensure their being post-absorptive and at rest. Each subject was placed in a six-sided rectilinear basket measuring 10 X 10 X 20 cm, made of sheet tin and hardware cloth. The basket was placed in an airtight steel ammunition box measuring 18 X 36 X 43 cm. The gasketed box top was fitted with two brass jets for air hoses and a rubber fitting for a 50°C mercury thermometer. Room air was pumped into the chamber through one of the jets to exit by the other through a column of soda lime to remove carbon dioxide and a column of calcium chloride to remove water. The air then passed by a thermometer, through a Brooks R215-A Rotameter flow meter, and into an Applied Electrochemistry oxygen sensor and S-3A oxygen analyzer, with output recorded on a strip chart. The chamber was ballasted with lead and submerged in a water bath for temperature control. Paper towels were placed between the basket and the lead to prevent conduction.

Body mass (± 1 g) was recorded at the beginning and end of each trial on an Ohaus triple-beam balance. Rectal

temperature ($\pm 0.1^{\circ}\text{C}$) was taken at the beginning and end of each trial with a digital Bailey Bat-8 Telethermometer inserted to a depth of 10 cm. The following measurements were taken every 15 minutes: chamber temperature, air flow rate, air flow temperature, and barometric pressure. Resting oxygen consumption was taken as the minimum plateau during any two-to-three-hour session, and corrected to standard temperature and pressure. Metabolic rates were determined at ambient temperatures ranging from 9 to 37°C .

The four subjects used were selected to represent both sexes and a range of body sizes. After the first trial, the juvenile male (Theodore) weighed 541 g, the juvenile female (Bunny) weighed 666 g, the adult male (Ron) weighed 832 g, and the adult female (Helen) weighed 1061 g. The two juveniles had been caught on Little Wax Cay and kept for six months in the FMNH Hutia Colony. The two adults had been caught on East Plana Cay and kept for four years in the FMNH colony.

Results

Body temperature averaged 37.0°C over both ages and sexes, and was independent of ambient temperature below 32°C (Fig. IV-2). Student's t-test and the Wilcoxon Rank Sum test both found a significant ($p < 0.05$) difference in metabolic rate over all temperatures between the juveniles

and the adults (Fig. IV-3), but the number of points above the median was not different ($p = 0.23$).

The thermoneutral zone was estimated visually from Figure IV-3 and confirmed by performing simple linear regressions of mass-specific metabolic rate (R) against ambient temperature (T_a). A simple linear regression performed on the pooled data from 9.0 to 26.6°C explained most of the variance and was significant ($R^2 = 0.68$, $p < 0.0001$):

$$R = 1.135 - 0.030(T_a)$$

where R is in units of $\text{ccO}_2\text{g}^{-1}\text{hr}^{-1}$ and T_a is in degrees centigrade. The slope of the regression may be interpreted as minimal thermal conductance (McNab and Morrison 1963). Both explanation and significance fell when the domain was extended to the next higher temperature, indicating a change of slope associated with thermoneutrality.

A simple linear regression on the pooled data from 26.2 to 34.3°C was neither accurate nor significant ($R^2 = 0.03$, $p = 0.51$), indicating no relationship between the two variables on that domain, and substantiating it as a fair estimate of the thermoneutral zone. Separate regressions performed on the juvenile data alone and on the adult data alone were not substantially different from those performed on the pooled data.

Sixteen measurements within the thermoneutral zone yielded an average ($\pm$ standard error) basal metabolic rate of $0.3432 (\pm 0.666) \text{ ccO}_2\text{g}^{-1}\text{hr}^{-1}$. Rebach (1971) found it to vary between 0.274 and $0.820 \text{ ccO}_2\text{g}^{-1}\text{hr}^{-1}$ depending on diet.

Student's t-test, the Wilcoxon Rank Sum test, and the number of points above the median all showed a difference ($p < 0.05$) in mass-specific metabolic rate between juveniles and adults within the thermoneutral zone. The opportunity was taken to test the well-known Kleiber (1961) relation:

$$R = A(M^B)$$

where R is the basal metabolic rate ($\text{ccO}_2\text{g}^{-1}\text{hr}^{-1}$), M is body mass (g), and A and B are parameters having values of 3.42, and -0.25, respectively. In this study, non-linear least-squares regression was performed on the data pooled from all four subjects within the thermoneutral zone, by using the NLIN procedure of SAS (SAS Institute Inc. 1985) to estimate the two parameters. The MARQUARDT method was specified because sequential values were not independent. The model, which was both accurate and significant ($R^2 = 0.98$, $p < 0.01$), estimated the value of A as 11.94 and that of B as -0.54.

The equation discovered here places G. ingrahami below the Kleiber function at all realistic values of body mass, according to the following ratio:

$$R_J/R_K = 3.49M^{-0.29}$$

where R_J is the mass-specific basal metabolic rate predicted by the model derived in this study, and R_K is that predicted by the Kleiber equation. For a body mass of 500 g the ratio is 0.58, and for a body mass of 1000 g the ratio is 0.47. Ottenwalder (1983) found the mass-specific basal metabolic rate of Geocapromys brownii ($M = 2456$ g) to be 0.61 times that predicted by Kleiber, and McNab (1978) found the rate of Capromys pilorides ($M = 2630$ g) to be only 0.48 times that predicted. Obviously, the increasing departure with increasing mass of G. ingrahami is due to a capromyid exaggeration of the very principle explained by Kleiber, that mass-specific metabolism is inversely related to mass.

That the hutias as a family run lower than other mammals may be an adaptation to a folivorous diet. The association of low metabolism with folivory has been discussed at length by McNab (1978, 1986). Since Geocapromys suffers the further disadvantage of a semi-desert habitat, selection for metabolic economy in that genus may be stronger than in other capromyids.

A series of minimal thermal conductance (C) values were computed for each subject according to McNab and Morrison (1963) as follows:

$$C = R / (T_b - T_a)$$

where T_b is the body temperature ($^{\circ}\text{C}$) at each value of ambient temperature (T_a) below the thermoneutral zone. Minimal conductance values were found to differ significantly ($p < 0.05$) between the juveniles and adults by Student's t-test, the Wilcoxon Rank Sum test, and the number of points above the median. The relationship between minimal conductance and body mass was modeled by the equation of McNab and Morrison (1963):

$$C = A(M^B)$$

where the value of A was 1.00 and that of B was estimated as -0.50. In this study, non-linear least-squares regression was performed on the data pooled from all four subjects below the thermoneutral zone, by using the NLIN procedure of SAS (SAS Institute Inc. 1985) to estimate the two parameters. The MARQUARDT method was specified because sequential values were not independent. The model, which was both accurate and significant ($R^2 = 0.99$, $p < 0.01$), estimated the value of A as 1.43 and that of B as -0.58.

The discrepancy between the two models is only slight, as expressed by the following ratio:

$$C_J/C_M = 1.43M^{-0.08}$$

where C_J is the minimal conductance predicted by the model derived in this study, and C_M is that predicted by McNab and

Morrison (1963). For a body mass of 500 g the ratio is 0.87, and for a body mass of 1000 g the ratio is 0.82. Ottenwalder (1983) found the minimum conductance of Geocapromys brownii (M = 2456 g) to be 0.97 times that predicted by McNab and Morrison (1963), and McNab (1978) found that of Capromys pilorides (M = 2630 g) to be exactly as predicted. Apparently the hutias have depressed basal metabolic rates without unusual thermal conductances.

No sweating or urine bathing, and little panting or licking behavior were noted in any of the subjects of this study, even at an ambient temperature of 37°C and a body temperature hovering over 40°C, three degrees above normal. Ottenwalder's (1983) experience with G. brownii was similar, and Quay (1965) found no sudoriferous glands about the mouth of Capromys pilorides.

With Rebach's (1971) findings of extreme urine concentrating ability in G. ingrahami, these observations may help explain its dietary water economy, and its resultant success in dry habitats. Concessions must have been made to achieve that economy, and in a species of small-to-medium body size evolved in the warmth of the oceanic tropics and subtropics, evaporative cooling may have been surrendered early. The only liability is a risk of overheating, to which the animal has adjusted by avoiding the midday sun.

The combination of depressed metabolism, reduced evaporation, renal sophistication, and a crepuscular-to-

nocturnal activity pattern clearly forms a complex of adaptations to the rigors of life on small dry tropical islands.

Even folivory itself, discussed above as a cause of low metabolism, may be an effect of natural selection on those islands. Herbivores in general enjoy direct access to primary productivity, whereas higher trophic levels depend on the surpluses of intermediates, thermodynamically constrained to decrease at every level. Thus carnivores would not be generously supported by a plant community under water stress. The fact that G. ingrahami has few natural predators suggests that just such a trophic simplicity does obtain in the Bahama Archipelago.

Figure IV-2. Body temperatures of four subjects as functions of ambient temperature.

Figure IV-3. Mass-specific metabolic rates of four subjects as functions of ambient temperature.

Food Preferences

Materials and Methods

Food preferences were determined on Little Wax Cay by cafeteria-type feeding trials using animals kept individually in a portable plastic air kennel. Each animal was kept for three to five days, then replaced by another for the next trial. For each trial several leafy shoots of six-to-ten different species were cut fresh and separated into leaves and shoots. The two organ types were weighed separately by species on an Ohaus triple-beam balance and placed inside the air kennel with the subject. A comparable amount of each forage type was weighed and stored in an open plastic bag to provide a control for evaporative loss. Water was provided to the animal ad libitum in a steel can wired to the kennel door.

After 24 hours, all vegetative and fecal material was removed from the kennel. Fecal pellets were used in the calibration of a population estimator (Chapter V). The vegetative material was sorted by species and organ type (leaf or shoot) and weighed. Likewise, the controls were weighed and an evaporative loss rate computed as a percentage of original mass. The starting mass of each test forage was then devalued for evaporation according to the control data, and the ending mass subtracted from that figure to yield the mass consumed by the animal. A

consumption rate was computed by dividing the mass consumed by the mass presented.

It should be noted that conditions on the island prevented the use of large replicate samples, as are normally associated with food preference studies. Specifically, animals could not be withdrawn from the wild population in any number without affecting the population study, on which the project was concentrated. Thus several different animals were used at different times without giving any two the same forages, and individual feeding preferences may have influenced the data. But rankings based on consumption rate here need only be approximate, as they were computed solely for the sake of comparison with Clough's (1972) data from East Plana Cay, in which forages were simply assigned to three classes: high, medium, and low preference.

Results

Of the forty species browsed on Little Wax Cay, only two were listed by Clough (1972) as being hutia browse on East Plana Cay (Table IV-2). Obviously, the discrepancy is due in part to differences in the flora of the two islands. Of the 31 higher plant species listed for East Plana Cay by Clough and Fulk (1971), only six were among the 51 terrestrial species listed in this study for Little Wax Cay. And although the two browsed species in common were of

medium or high preference on East Plana Cay, they were near the bottom of the preference list on Little Wax Cay.

Of the 31 plant species on East Plana Cay, Clough (1972) listed only six as hutia browse. The list was restricted to species that the author had actually seen being browsed by non-captive hutias. But 40 species were browsed on Little Wax Cay, including many that were barely sampled by hutias. Slight consumption may or may not have been detected in the feeding trials, and leaf predation could not have been detected during the plant community analysis (Chapter III). But even the slightest bark injuries were detected in the community analysis. This is not to call those species "browse" in the sense of Clough (1972), but since they were browsed they could not be ignored here.

Instead I believe that hutias may seek a variety of forages in their diet, as much as any one favorite. Also, the individual animal may rely on an initial sampling of a forage in order merely to identify it. The decision of whether or not to continue eating would follow, but the sign would remain regardless.

The flora of East Plana Cay is restricted almost entirely to low-growing coastal herbs and shrubs. As a group, that type of species gave scattered results in the Little Wax Cay feeding trials. The only species that Clough and Fulk (1971) listed as "trees" were the silver thatch palm (Coccothrinax argentata) and the buttonwood (Conocarpus

erectus). Coccothrinax leaves were eaten, but not preferred by hutias in the Little Wax feeding trials and in the observation pen (see Chapter V and APPENDIX A). The only Coccothrinax leaves on East Plana Cay were at the top of a few trees 7-10 m tall in a single grove at the west end of the island. Neither Clough (1972) nor the hutias on that island could have suspected that they might be food. As for Conocarpus, its leaves and stems were medium-preference forages on East Plana Cay, but were shunned on Little Wax.

Clearly, the hutias of Little Wax Cay have both a more preferable and a more diversified diet than do their counterparts on East Plana Cay, and this despite the much greater size of East Plana. No doubt, some of the floral poverty of East Plana Cay is due to a drier climate than that of the Exuma Cays (Chapter VI). But the shortage of favored species there is probably due in part to the hutias themselves. Evidence is presented elsewhere in this study (Chapter III) that overbrowse by G. ingrahami has already extinguished four plant species on Little Wax Cay, and that it threatens to eliminate several more within the next few years.

Table IV-2. Results of captive forage preference trials.

<u>Species Name</u>	Consumption Rate			<u>Clough Rank</u>
	<u>leaves</u> (0<x<1)	<u>shoots</u> (0<x<1)	<u>sum</u> (0<x<2)	
<u>Randia aculeata</u>	0.885	0.487	1.372	
<u>Ateramnus lucidus</u>	0.815	0.427	1.242	
<u>Casasia clusiifolia</u>	0.229	1.000	1.229	
<u>Rhizophora mangle</u>	0.661	0.567	1.228	
<u>Drypetes diversifolia</u>	0.967	0.162	1.129	
<u>Coccoloba uvifera</u>	0.612	0.493	1.105	
<u>Bourreria ovata</u>	0.897	0.196	1.093	
<u>Suriana maritima</u>	0.717	0.191	0.908	
<u>Guapira discolor</u>	0.744	0.106	0.850	
<u>Zanthoxylum flavum</u>	0.511	0.271	0.782	
<u>Scaevola plumieri</u>	0.640	0.103	0.743	
<u>Reynosia septentrionalis</u>	0.638	0.089	0.727	
<u>Manilkara bahamensis</u>	0.721	0.000	0.721	
<u>Eugenia axillaris</u>	0.379	0.291	0.670	
<u>Rhachicallis americana</u>	0.467	0.203	0.670	
<u>Salmea petroboides</u>	0.255	0.363	0.618	
<u>Erithalis fruticosa</u>	0.487	0.092	0.579	
<u>Sophora tomentosa</u>	0.369	0.153	0.522	
<u>Argythamnia lucayana</u>	0.432	0.087	0.519	
<u>Catesbaea parviflora</u>	0.469	0.028	0.497	
<u>Bumelia glomerata</u>	0.458	0.000	0.458	
<u>Pithecellobium keyense</u>	0.041	0.369	0.410	
<u>Zanthoxylum coriaceum</u>	0.242	0.098	0.340	
<u>Ambrosia hispida</u>		(0.329)	0.329	
<u>Smilax havanensis</u>	0.151	0.163	0.314	
<u>Tabebuia bahamensis</u>	0.133	0.146	0.279	
<u>Coccoloba diversifolia</u>	0.139	0.095	0.234	
<u>Cassia lineata</u>	0.225	0.000	0.225	
<u>Jacquinia keyensis</u>	0.142	0.066	0.208	
<u>Coccothrinax argentata</u>	0.207	-----	0.207	
<u>Borrchia arborescens</u>	0.144	0.019	0.163	
<u>Strumpfia maritima</u>	0.096	0.062	0.158	High
<u>Eugenia foetida</u>	0.105	0.000	0.105	
<u>Sargassum sp.</u>		(0.071)	0.071	
<u>Hymenocallis arenicola</u>		(0.006)	0.006	
<u>Conocarpus erectus</u>	0.000	0.000	0.000	Medium

The following species were tested on East Plana Cay by Clough (1972), but were not present on Little Wax Cay:

<u>Forestiera segregata</u>	Medium
<u>Phyllanthus epiphyllanthus</u>	Medium
<u>Croton lucidus</u>	Medium
<u>Tournefortia gnaphalodes</u>	Low

Note: Species are ranked by combined consumption rate of leaves and shoots (separated unless in parentheses). Included are the preference ranks of Clough (1972).

CHAPTER V
STUDIES OF THE POPULATION

Materials and Methods

Population size and distribution were estimated by several methods. The first was fecal pellet production. Pellet sampling trays were made on site from asphalt-impregnated roofing felt salvaged from a dump on nearby Norman's Cay. Three rolls of the roofing felt were unrolled on Beryl's Beach and painted with green latex paint mixed with sand to provide a natural color and texture. The 36-inch-width (91 cm) rolls were then cut into 127 cm lengths. A 3.7 cm lip was folded upward on all four sides of each section and reinforced with poultry wire to hold the shape in sun and rain. The resulting rectangle was 83.6 cm wide and 119.6 cm long, providing a horizontal sampling area of 1 m². A grid of 374 holes (17 rows and 22 columns), each 2 mm in diameter was then punched in each tray to allow water to pass without carrying away pellets.

Two trays were placed just outside each of the 20 vegetation plots. The trays were situated to sample whatever range of microhabitats existed in each plot, for

example: one tray on rock and the other on sand, one in sunlight and the other in shade. In addition, four trays were placed randomly among the dunes of Moon Beach. Finally, one tray was placed on the barren rock of each of the four corners of the island (Fig. V-1). Each week for 13 weeks the pellets on each tray were counted and removed, so as not to be included in subsequent counts. On one occasion the count was delayed by one day, resulting in an eight-day count followed by a six-day count. Those two counts were added and divided equally, yielding two seven-day approximations for consistency of data analysis. Rarely were individual tray counts disqualified due to upset by storms. As a precaution, exposed trays were weighted with rocks. (On one occasion the two trays near Camp were blown into the trees by a government helicopter conducting routine low-altitude surveillance.)

In order to convert weekly counts of pellets removed from 1 m² trays into estimates of hutia density, the rate of pellet production per animal had to be measured. Pellets were collected from animals used during the food preference study. Each animal used was kept individually for three to five days in a plastic air kennel and given water and assorted forages ad libitum. All pellets produced were collected and counted at 24-hour intervals.

Also necessary to the calibration of pellet counts was the computation of a sampling bias factor, in case the trays were either preferred or avoided by hutias in the field.

Urine-marking behavior of Bahamian hutias is well-documented (Howe 1971, Clough 1972, Clough 1973, Howe 1974, Howe 1976, Howe 1982, Clough 1985, and Chapter IV Additional Notes), and several of the pellet trays became regular marking posts. The bias factor was computed by placing a tray of 0.25 m^2 area inside the observation pen (see Chapter IV) with a known number of captive hutias. Pellets were counted and removed from the pen tray each week.

Population size, structure, and distribution were also examined by trapping and tracking. Ten live-traps were constructed on site using half-by-one-inch (1.27 X 2.54 cm) welded wire mesh cut into 1.2 m squares. Each square was cut and folded into a five-sided box 0.6 m long, 0.6 m wide, and 0.3 m high, open on the bottom. A square floor 0.6 m on a side was hinged to the rear bottom edge and the box raised from the floor at the front edge on a hinged aluminum peg 0.3 m high. A copper trip-wire was strung from the peg to both rear corners and the bait suspended three to four inches from the box roof. The first bait used was parrot seed mix in a gauze bag. Though effective, it was discontinued after the first week in favor of coconut shell, discarded after each use.

Nine of the ten traps were deployed near the trails, each between consecutive pairs of the twenty vegetation plots (Chapter III). One box trap was placed in Camp, between the main tent and the observation tent. In addition, four Tomahawk folding live traps, 15 cm X 15 cm X

60 cm, were deployed between Camp and a rocky hill to the north, known to be a hutia denning site (Fig. V-1). Traps were run for six weeks, being set on Saturday, Sunday, Tuesday, and Wednesday between 5:00 and 7:00 p.m., and cleared the following morning between 8:00 a.m. and noon. Occasional exceptions were made for foul weather. Empty traps were closed and the bait removed. Animals trapped were transferred by a wand net into a linen sack with a drawstring opening.

Body weight was obtained by hanging the sack on a two-kilogram Pesola spring scale, and subtracting sack weight afterward. To the sack was added a small brown glass jar containing a cotton ball wetted with 10 to 15 drops of Metofane (methoxyfluorane) as anesthetic. I worked the mouth of the jar over the animal's muzzle by feeling through the sack. When the animal stopped struggling, I removed it and laid it on its side on the outside of the sack. Anesthesia was controlled by adjusting the distance between the jar and the animal's muzzle. A moderate-to-shallow plane of anesthesia was maintained by keeping respirations deep and regular, and by maintaining the blinking reflex. Whenever possible all measurements were taken in the shade to avoid heat stress and eye injury. Body length (± 0.5 mm) and total length (± 0.5 mm) were taken with a cotton cord transferred to a millimeter rule. Right hind foot lengths with and without claw (± 0.5 mm) and right ear length (± 0.5 mm) were measured directly with a millimeter rule. To apply

the live-animal aging index developed in Chapter III, paired incisor widths (± 0.01 mm) were measured with a Mitutoyo dial caliper at four points: upper incisors at the gumline and tip, and lower incisors at the gumline and tip. Rectal temperature was taken with a mercury thermometer lubricated with vegetable oil and inserted to a depth of 2-3 cm for the duration of the session. Also noted were sex, status of the reproductive organs (testes: palpable or not, vagina: perforate or not, teats: shorter or longer than 1 mm), pelage color and texture, and any distinguishing marks or deformities, especially of the ears, tail, or feet. In addition, two animals were bathed in warm soapy water for the collection of ectoparasites, which were stored in vials of 70% ethanol under a thin film of kerosene to preserve color. All animals captured for the first time were tagged through the left ear with a monel ear tag, size 1, purchased from the National Band and Tag Co., 721 York St., P.O. Box 430, Newport, Kentucky. 41072. Tags were numbered consecutively with a four-digit number having a "K" prefix.

On each Sunday or Wednesday morning, one animal at each trap site, selected by its sex and size, was then dusted with fluorescent powder purchased from Radiant Color, Inc., 2800 Radiant Ave., Richmond, California. A 35 mm film cannister full of powder was placed in a zip-lock plastic sandwich bag along with the reviving hutia. The bag was closed and gently rolled for five to ten seconds until the animal was thoroughly coated. On release it staggered into

the brush and was allowed to recover and have one night of normal activity before being tracked some 36 hours later on a Monday or Thursday night. Animals were tracked beginning an hour after dusk, with a battery-operated 12-volt flashlight equipped with a General Electric ultraviolet fluorescent light bulb (model F6T5). Enough powder was transferred to the substrate that a full night's activity could be traced. Each animal was tracked until the trail ended at a den site without emerging again, or in five cases, until the subject itself was spotted in the flashlight beam.

Data were recorded as follows: my assistant, Donnie May, carried the flashlight, beginning at the trap site and moving along the track until it changed direction. At that point I called "Mark" to stop him. I took a compass bearing on him by sighting on his light, and we both estimated the distance between us. I recorded the bearing and took the range as the average of our two estimates. Then I moved to him, and he set out again. Tracking sessions lasted from one to three hours. Special notations were made of powder residues on leaves or shoots indicating browsing or climbing, or of extensive residues on the ground indicating a lengthy stay due to social activity or sleeping. Individual tracks are mapped in Figures V-3 to V-11.

It was fully expected that dusted hutias might transmit the powder to other animals during normal activity.

Therefore only the first animal dusted at each trap site (the "seed" animal) was tracked, and all animals trapped were scanned with the UV lamp for powder traces. After testing several colors, only two were used on hutias. To identify the source of powder to secondarily-powdered animals, chartreuse powder was used at traps A, C, E, G, and I, and green powder at traps B, D, F, H, and J. Whenever a dusted animal was captured, no matter the source of the powder, it was recharged to promote its labelling of animals with which it associated. The intent was to determine whether or not the population had a colonial structure. If the population were colonial, the number of animals labelled by any seed animal would reach a constant and be geographically confined. If the population were not colonial, new animals would continue to be labelled, and color mixtures might appear on animals at neighboring trap sites.

Over the next several weeks of trapping and tracking, no color mixtures occurred. Also, only one animal was captured away from its home site, being caught once at the neighboring site and back at its home site the next week. I therefore concluded the existence of non-overlapping colonies. Having found that secondarily labelled animals could deposit trace on the substrate, I determined the home range of each colony by waiting at the trap while Mr. May worked away from it in one direction to the farthest powder trace. We then took polar coordinates as before, and he

turned to his left and moved ahead, always keeping the outermost trace to his left. I followed at intervals, recording as before, the two of us proceeding counterclockwise until we had closed the loop at the original outer trace. We thereby enclosed all traces within an exact boundary. Colonial home ranges are mapped in Figures V-2 to V-6.

The first night of trapping yielded the rats reported by Clough (1985) as well as hutias. I identified them as (Rattus rattus) and decided to treat them exactly as the hutias regarding body measurements, dusting, and tracking. To prevent confusion with hutia tracks, orange powder was used at traps A, C, E, G, and I, and magenta powder on rats at traps B, D, F, H, and J. Tracking the individual rats was more difficult than tracking the hutias. Their sparse hair carried and distributed less powder, leaving trails that were shorter and more broken. An attempt was made to determine home ranges about several trap sites, but results were poor.

As a further test of territoriality, the last week of the trapping study was devoted to an experiment ("Operation Pinball") in which trapped animals were relocated around the island. Use of fluorescent powder was discontinued. An animal trapped at site A was released at site B and vice versa. The same was done for sites C and D, and for sites E and F. For sites G, H, and I a three-way exchange was made: the animal at site G was released at site H, the animal at

site H released at site I, and that at site I released at site G. Since time was limited trap site J was excluded so I could use the trap to increase the effort at the other sites. Three experimental traps developed in the summer were pressed into service with the four Tomahawk traps used in Camp and a fifth that had been held in reserve. The nine available traps were used to double the number at sites A through I. The animals were relocated on Wednesday, 4 December, and the traps set on the evening of Friday, 6 December, allowing two full days for the animals to orient and return without being influenced by baited traps. The traps were set and cleared four times in the following week.

Even though the trap effort had been increased, I still risked having displaced animals return to their home sites without being detected. In Operation Pinball II, eight animals were captured by hand in Camp over bait by candlelight on Wednesday, 4 December. One of the eight was released at each of trap sites B through I. On subsequent nights, hutias were netted while foraging in Camp. A mosquito net was laid on the ground and the four corners gathered to leave an effective net area 1 m^2 . Each corner was tied with nylon twist and the four lines bent to a length of dacron braid running through a block to a chair 3 m away under the canopy. Each evening at sunset, the net was baited with parrot mix, coconut scraps, and bits of rice left from supper. As soon as six to eight animals were on the net (ten to fifteen minutes), I hoisted it like a purse

seine. Tagged animals were noted and transferred to a 20 l plastic bucket with a punctured lid. Untagged animals were measured, tagged, and kept separately until recovered from anesthesia. The net was reset and the process repeated until an hour after the last animal had been caught, whereupon all were released. By so doing I believe to have sampled the Camp Colony as completely as possible in any single evening. Netting was conducted each night from 5 December through 12 December.

Results

Shapiro and Wilk's W-test of normality showed the 13 weekly pellet counts to be normally distributed ($p > 0.05$) for only 26 of the 48 collecting trays. When the trays were grouped by location (two at each of the 20 vegetation plots, the four dune trays grouped into two pairs, and the four barren rock trays in two pairs), only eight of the 24 locations showed normality. By contrast, a square-root transformation of the data yielded normality for 42 of the 48 trays and 21 of the 24 locations. In separate one-way analyses of variance, F-tests of the transforms showed significant differences among both the trays ($R^2 = 0.69$, $p < 0.0001$) and the locations ($R^2 = 0.50$, $p < 0.0001$). When the tray was modeled as a nested effect of location, explanation was not improved ($R^2 = 0.69$), although both effects were significant ($p < 0.0001$). The significance of the tray

effect is taken to indicate a microhabitat influence. In the nested model, pairwise comparisons by location of the transformed counts were made by t-tests using Fisher's Least Significant Difference at a comparisonwise error rate of 0.05, the experimentwise error rate having been controlled by the ANOVA (Table V-1).

Hutia density estimates were computed from the means of the pellet count transforms (Table V-1). Six individual captives were used to compile a mean daily production figure of 86 pellets per animal. In addition, a family group of two adults and one small juvenile kept in an 11.3 m^2 wire enclosure constructed on site deposited 249, 203, and 222 pellets in a 0.25 m^2 tray over three consecutive seven-day intervals. The pellets were of two clearly different sizes, with subtotals as follows: 166 large and 83 small, 150 large and 53 small, 126 large and 96 small. The average figure of 75 pellets per individual per week per 0.25 m^2 converts to 43 pellets per individual per day per 1 m^2 . Assuming a total production of 86 pellets per individual per day per 11.3 m^2 , the trays had sampled with a bias of 5.6 times random. Estimates of hutia density per ha were computed by squaring the means of the square-root transforms of the field data (Table V-1) and dividing each result by 0.34 (the product of 7 days per week, 86 pellets per individual per day, $0.0001 \text{ ha per m}^2$, and 5.6).

It should be noted that among the six individual captives, there appeared to be an inverse relationship

between body mass and mean daily pellet production. A one-way analysis of variance marginally rejected that hypothesis at an alpha level of 0.05 ($R^2 = 0.54$, $p = 0.06$). Also, because the trays collected pellets along a continuous range of sizes, and because many pellets were broken or crushed in the deposit, no attempt was made to sort them for possible inferences of population age structure. Instead, such inferences were restricted to analyses of the livetrapp data.

Obviously, hutia distribution was not uniform. In an attempt to explain the distribution in terms of the island's vegetation, pellet count means, by vegetation plot, of the untransformed weekly pellet counts were regressed (recalling the Central Limit Theorem) against the log transform of the within-plot sum of each plant species' basal area (Chapter III). Iterative regressions were performed using SAS-PC, Procedure REG, option MAXR, to build a linear model one-variable at a time, maximizing the value of R^2 at each step (SAS Institute Inc. 1985). For the one-factor model, Conocarpus erectus (the buttonwood) was selected as the best single index of hutia density ($R^2 = 0.21$, $p = 0.04$). The regression was positive, even though C. erectus was utterly avoided as a browse species in the field (Chapter III). Either the relationship was spurious or both were responding to some other factor. The low value of R^2 placed the buttonwood in further doubt as a hutia density predictor. The regressions worsened with the addition of each plant species, none contributing significantly ($\alpha = 0.05$), and

R^2 reaching a ceiling of 0.55 with ten species in the model. Apparently, individual forage species did not determine hutia distribution.

Another series of linear regressions was tested, this time between the pellet counts and the first two axes of plant community ordination, as determined by detrended correspondence analysis (Chapter III). In the first model, the square-root transforms of the weekly counts were regressed, by location, against the vegetation plot values occurring along the first axis of ordination. Although the model was significant ($p < 0.0001$), it was quite poor ($R^2 = 0.09$). The second axis of ordination was added as an independent variable, it having been constructed orthogonal to the first axis (Gauch 1982). The second axis was not significant ($p = 0.94$), and model R^2 was not materially improved. When the means, by vegetation plot, of the untransformed weekly pellet counts were regressed (again recalling the Central Limit Theorem) against the first two axes of ordination, the model was not significant ($p = 0.19$). The loss of significance may have been due to a loss of statistical power in going from a sample size of 520 observations to only 20, although apparently no great predictive power was at stake. Thus, no combination of vegetative information could provide a useful predictor of hutia distribution on Little Wax Cay.

To test for possible effects of substrate characteristics, I scored the twenty vegetation plots

subjectively according to three physical criteria: availability of rock crevices ("Crevice"), protection from wind and rain ("Shelter"), and proximity to fresh (or brackish) water ("Water"). Conocarpus erectus characteristically grows near fresh or brackish water, and had been the dominant plant at all seven of the ponds and the edge of the mangrove swamp, points where the pellet counts had been highest. For each of the three variables, whole number values from one to three were assigned, with one as the low score. Significant correlations were found between Crevice and Shelter ($R = -0.59$, $p = 0.0059$), and between Water and Shelter ($R = 0.55$, $p = 0.0130$). An analysis of variance with fixed effects was performed by using the General Linear Models Procedure of SAS-PC (SAS Institute Inc. 1985) on the three main effects and two of the four possible interaction effects (Crevice by Water, and Crevice by Water by Shelter). When the square-root transforms of the weekly pellet counts were analyzed, the five-way ANOVA yielded a weak model ($R^2 = 0.37$, $p = 0.0001$). The Type III Sums of Squares of all five effects were significant ($p < 0.05$), perhaps by dint of sample size ($N = 520$). When the means, by vegetation plot, of the untransformed weekly pellet counts were analyzed (again recalling the Central Limit Theorem), the result was a highly predictive model ($R^2 = 0.86$, $p = 0.0198$), significant despite small sample size ($N = 20$). The Type III Sums of Squares for the individual main effects had mixed p -values.

Water had the most significant effect ($p = 0.0275$), followed by Crevice ($p = 0.0607$), and Shelter ($p = 0.0937$).

Interaction effects were not significant.

In conclusion, the distribution of hutias on Little Wax Cay was best explained by the proximity of fresh water and rocky cover, without reference to the distribution of plants. Apparently the hutias had distributed themselves according to the substrate, and then fed on whatever was there, exercising forage preferences only after substrate preferences.

The total number of hutias on Little Wax Cay was estimated by establishing zones of hutia density, as estimated from the pellet counts in Table V-1. Four density zones were distinguished (Fig. V-12): Very High Density (164 to 203 hutias per ha), High Density (72 to 158 hutias per ha), Medium Density (13 to 53 hutias per ha), and Low Density (fewer than 13 hutias per ha). The area of each density zone was multiplied by the average of the density estimates within that zone, and the total population taken as the sum of the zone estimates. The resultant figure was 1265 hutias, for an average density of 65.3 per ha (26.4/acre) over the entire island.

Given an initial population of 11 in January of 1973, the intrinsic rate of population growth (r) may be computed using the exponential growth equation (the obvious model choice):

$$N_t = N_0 e^{rt}$$

Setting N_0 and N_t equal to 11 and 1265, respectively, and t equal to 12.5 years, the value of r is 0.3796 per year. The annual population growth factor ($\lambda = e^r$) thus has a value of 1.4617.

Hutia distribution was conspicuously associated with ponds and rocks. The Very High Density belts were the pond banks themselves. The High Density zone included all seven ponds and the mangrove swamp, and extended up the interior slopes wherever the substrate was rocky. The zone of Medium Density was exposed coastal slope where the substrate was rocky, extending to the interior where the substrate was sandy. The Low Density zone was restricted to the narrow belt of barren beach and coastal rock.

Population age and sex structure were determined by analysis of the livetrapped data. One hundred and twelve different hutias were examined in a total of 342 different captures, for an average of 3.05 captures per animal. In addition, 23 rats (Rattus rattus) were captured, but none more than once.

Of the 112 hutias captured, 65 were males and 46 were females, the first having escaped without measurement. Ages were estimated by the incisor-width regression developed in Chapter III. Of the 65 males, 21 were aged 12 months or less, leaving 44 of reproductive age. Of the 46 females, 22 were aged 12 months or less, leaving 24 of reproductive age.

Thus, although the juvenile classes comprised almost exactly the same number of males and females, the adult classes were biased by almost two-to-one in favor of males. Although the incisor regression may have slightly underaged some females (see Chapter III), a heavy sexual bias remained among the adults. Either the population sex ratio was uneven, or the adult females were under-represented in the traps. Figure V-13 shows age distribution by month among the juveniles.

No animals were trapped under two months of age (Fig. V-13). Two months was also the age at weaning of the two animals raised in captivity from birth at the FMNH colony. Naturally, juveniles dependent on maternal nutrition would not be expected to appear in baited traps. Assuming constant monthly juvenile survivorship, the 43 juveniles captured from ages two to 12 months represent another nine hutias aged less than two months. Measurements on first capture of the 24 adult females showed that five were lactating and two others were gravid. One of the pregnancies was confirmed on recapture 11 days later, when the subject had lost 140 g and was lactating. (The youngest reproductive female was aged 50.5 weeks by the incisor-width regression.) Assuming a litter size of one, five lactating females would indicate only five nursing young. Averaging with the prior estimate of nine yields a final estimate of seven nursing young undetected by the traps. The total juvenile cohort represented would thus have numbered 50.

A population age ratio of 68 adults to 50 juveniles in a long-lived species suggests two possible conditions: a stable population with a Type I survivorship curve (high juvenile survivorship followed by low adult survivorship), or a more equitable survivorship schedule in a population of increasing size. The pellet count census certainly favors the latter.

If a hutia fetus can be palpated only during the last two weeks of a 17-week pregnancy, then the two pregnancies detected may represent 17 total. With the five lactating females, the total number of adult females breeding would have been 22 of the 24 captured, or 92%. Such a high breeding percentage is entirely consistent with an expanding population. But given that gestation lasts twice as long as lactation, the five lactating females may represent only 10 pregnancies. The number of adult females breeding would then have been only 15 of 24, or 63%.

As a check, the 50 juveniles in 1985 must have been produced by the adult females of 1984, who would have numbered 16 ($24/1.46$). (Lest demographers be offended, the author is aware that the growth rates of the individual age classes may not be assumed equal to the population growth rate unless the age distribution is stable. But without good estimates of age-specific life-table parameters, that is not possible to determine. In this case it was not even possible to divide the population into uniform age intervals, but only to distinguish juveniles from adults.

Thus within each of those two unequal intervals, the population growth rate is applied as a best estimate.) Assuming 63% of adult females breeding, a litter size of one, and one litter per female per year, 16 females could produce only 10 young. With 92% of adult females breeding and three litters per female per year, the same 16 females could produce 44 young. But a cohort of 50 young would require continuous impregnation for an unlikely four litters in the same year. It is more likely that the adult females were simply under-represented in the traps, as suggested by the biased adult sex ratio.

Averaging the estimates (and recalling from Chapter I the known interbirth intervals of 210 and 325 days), an average of 1.5 litters per female per year, a breeding ratio of 90%, a litter size of one, and a cohort of 50 young in 1985 implies an adult female population in 1984 of 37. With λ equal to 1.46, those 37 would have become 54 in 1985, bringing the adult sex ratio for that year much closer to parity.

Assuming one young per litter, 1.5 litters per year, a female contingent of 50%, and 90% of adult females bred, the annual per capita birth rate over all adults would be 0.68. Without mortality, the adult class would increase by a factor of 1.68 each year. Since the value of λ is approximately 1.46, the difference must be due to an annual mortality of approximately 0.22, for an annual survivorship of 0.78.

During the last week of trapping, an adult male was captured at trap site G, a few meters from the site where the 11 founder hutias had been released in 1973. The animal had patches of white hair on its back, and an eartag in its right ear that was not one of mine. The number indicated, however, that it was not one of the original 11, but one of the five animals tagged by Clough on a return visit to Little Wax Cay in June of 1983 (see Chapter I). The longevity record thus stands at nine years, achieved by a hutia on East Plana Cay (Clough 1985). With an annual survivorship of 0.78, that age would be reached by about one animal in ten.

The reason for the under-representation of adult females in the traps is unclear. One possibility is that the range of adult females was restricted by the presence of young in a den. Another is simply that adult males dominated the traps as a matter of territoriality.

Population spatial patterns in general were investigated by tracking dusted animals and by recapturing tagged animals. In all, ten subjects (four males and six females) were tracked individually at as many different trap sites. Subjects were tracked during the second night after their release, allowing approximately 36 hours of free movement. At trap sites C, D, E, F, and H, the tracking session ended when the animal itself was sighted. At the other five sites, the session ended when no more powder traces could be detected.

In each case specific areas were found where large amounts of powder had been deposited on the substrate. Such areas were taken to indicate lengthy stays, and at least one in each case must have been a sleeping or denning site. At trap sites A, G, I, and J, the heaviest deposits were found about rock crevices. But at trap sites B, C, D, E, F, and H, where the substrate was sandy, the heaviest deposits were found under leaves of the silver thatch palm (Coccothrinax argentata). The senescent lower leaves of that species hang down along the trunk, and in shorter trees may touch the ground to form natural thatch huts that shed the rain. (Often when caught away from Camp in a squall I could crouch in a Coccothrinax thicket and write my notes in comfort until the weather passed.) Apparently the hutias had substituted Coccothrinax thatch piles for rock crevices where the latter were not to be found. That all five of the animals sighted during tracking were located in sandy areas is evidence of the inferiority of thatch to rocks as cover.

In addition to the tracks of individuals, the geographic limits of whole colonies were measured by locating the outermost signs of secondarily labelled subjects. Colonial home range measurements varied. At trap sites C, D, and F, where the numbers of animals dusted were 6, 4, and 5, respectively, the values were centered closely around 0.1 ha. But at sites A and I, where 17 and 5 animals were dusted, the values were three to four times as large.

Of some interest is that sites C, D, and F were sandy but sites A and I were rocky, suggesting a substrate effect on colony range size. However, the only animal ever to have been captured at a trap site other than its home site was tag number K1028, an adult male who, unfortunately, had been used as the seed animal at trap site I. Also, that animal's individual 36-hour track was many times as long as any of the other nine individual tracks. Thus, the unusual ranginess of that subject may have inflated the measured range size of its colony, producing only the appearance of a substrate effect. Ignoring trap site I, measured colony range size was an almost linear function of the number of animals dusted, and the average dusted area per dusted animal at the remaining four sites was 0.0189 ha. Over the entire area of the island, that estimate yields a population estimate of 1024 hutias. Given the crudity of that estimation procedure, its result is regarded as supportive of the more precise pellet count estimate of 1265 hutias, which is strongly preferred.

Operation Pinball I, in which individuals at adjacent trap sites were exchanged, resulted in a further indication of territorial fidelity. Of nine animals (four males and five females) removed from their home sites on 4 December, four (one male and three females) were recaptured at their home sites by 12 December. The subject recaptured at site H on 12 December after having been moved from site H to site I on 4 December was actually making a second return home. The

first was during Hurricane Kate, which passed through the Ragged Islands 160 km to the south of Little Wax Cay on 18 November. I had first removed the animal (an adult female, tag number K1009) from trap site H on 4 November to place her with a male (tag number K1008) from site I in the large behavior observation pen erected in Camp. On the morning of 19 November, I awoke to find that the wind had caused several Drypetes trees supporting the pen's roof to stretch large holes in the wire. The male remained but the female was gone. She was recaptured back at site H on 1 December.

In Operation Pinball II, of eight animals (four males and four females) removed from trap site A to sites B through I (recall the exclusion of site J), all but one were recaptured at the home site by 12 December. The single exception was a juvenile male (tag number K1027) aged 30 weeks by upper incisor width. All of the other subjects were fully adult. I sighted number K1027 still alone near the release point some six hours after release. By contrast, the animal removed from site A to site B, an adult female, was recaptured at site A by hand only three hours later. The subject farthest removed from home also was an adult female (tag number K1034) released at site I. She was recaptured at trap site H on 10 December, six days after release, and finally back at site A on 12 December, the last day of the study. Trap site I was approximatey 340 m from site A.

Clearly, G. ingrahami is territorial. Not only are home territories sought by displaced individuals, but those animals may be helped along by individuals enforcing their own territories against trespass. I released male number K1008 from the observation pen on the evening of 19 November, the day after the hurricane. The next night I saw him being chased around my tent (adjacent to the pen) by a large untagged hutia carrying chartreuse powder. The powder identified the chaser as a native of the Camp Colony, within whose range the Camp had been erected. Male number K1008 was never seen again, not even with the intensive capture effort later staged at site A on the Camp Colony. I concluded that if he had not returned home to site I, he at least had left or been expelled from the area of site A without being adopted by the Camp Colony.

Since both eartags and fluorescent powder traces had indicated no voluntary movement of hutias among the different trap sites (except during the perturbation of Operation Pinball), each site was determined to have sampled a separate subpopulation. Trap sites B through J had been monitored with single traps for 18 sessions, and trap site A had carried 5 traps (one box and four Tomahawk traps) for 18 sessions. Four more sessions were conducted during the week of Operation Pinball, in which animals were relocated and traps were reshuffled.

The local subpopulations about the ten trap sites were estimated by several computations (Table V-2). Minimum

known alive figures are listed both on the basis of 18 trap sessions and on the basis of 22 trap sessions. In addition, program CAPTURE (Otis et al. 1978, White et al. 1982) was used to estimate, with a 95% confidence interval, the subpopulation size about each trap site on the basis of only the 18 sessions when trap effort was constant at each site. For site A, CAPTURE was used to compute two estimates (with confidence intervals): one using the data from all five traps located there, and one using the data from the box trap alone. Finally, CAPTURE estimated the total number of hutias on Little Wax Cay from the pooled single-trap data (excluding the Tomahawk captures at site A) as if the island were supporting a single, free-ranging population that was either non-colonial or comprising colonies that were non-territorial.

Several different models were used within Program CAPTURE, each making different assumptions of the data. Model M_h allowed heterogeneity of capture probability among hutias, model M_b allowed capture probability to change as a behavioral response to the first capture, and model M_t allowed capture probabilities to vary with time. Model M_0 was the default option, assuming constant capture probability. At each site, Program CAPTURE selected the preferred model, by a chi-square comparison of fit, and each selection is indicated in Table V-2. Also indicated for each subpopulation is Program CAPTURE's determination by z-test ($\alpha = 0.05$) of population closure.

Subpopulation estimates by model M_0 and M_h were similar in eight of the ten cases, with M_0 being the preferred model in six. Models M_b and M_t were never preferred. The two trap sites where models M_0 and M_h differed strongly (sites D and J) were the two most exposed sites of the ten. Trap site D was on Moon Beach, an exposed sandy site, and trap site J was on the southeast coast, an exposed rocky site. In each case, model M_h produced a much higher estimate of subpopulation size.

Four sites failed a test of population closure. All four were located on sand or sandy soil, without rocky crevices. Trap site C, which tested as closed, was also fairly sandy, but was located in the north central part of the island, in desirable habitat between and near the two largest inland bodies of water. Given that the island population was geographically closed and that the subpopulations were behaviorally closed, two interpretations of a statistical rejection of closure are possible for each such site: (1) it supported a colony so large that few animals were caught more than once, or (2) it was intercolonial and traversed by animals from several different colonies. The former interpretation suggests prime habitat. The latter suggests marginal habitat. The analysis of fecal pellet distribution, which showed a clear preference for rocky substrates near fresh water, strongly supports a conclusion that the sites failing the closure test were located on marginal habitat.

Interestingly, when the single trap data from all ten sites were combined, program CAPTURE estimated an island-wide population of only 88 hutias, and called the population open. The contrast of such an estimate with the more thorough and much larger pellet count estimate indicates clearly that the trapped animals had been arranged in local groupings separated by large interstitial areas that had not been sampled by the traps.

The colony whose range and demography were investigated most intensively was the Camp Colony. With five traps operating for five weeks, 16 different hutias were captured and tagged. Of those, thirteen eventually carried powder and two others were seen frequently around Camp in the company of dusted subjects. The remaining one was probably extracolony. Seven more animals were captured during the intensive netting operation of the final week. Of those seven, four carried powder, but one of the four was always seen alone on the dunes of Thom's Landing or in the brush to the south, outside the measured range of the Camp Colony. I conclude that the Camp Colony comprised a total of 18 hutias.

Nine of the colony were males and seven were females, with two having escaped capture without being sexed. Ages of the 16 measured were determined by upper incisor width and standardized to 1 December 1985. Age structure was as follows: juveniles (one year or less), three males and four

females; adults (over one year), six males and three females.

A ratio of seven juveniles to nine adults in a long-lived species without delayed maturation indicates rapid population growth. That the juveniles must have been produced by only two adult females (3/1.46) is impressive, though aided by the possibility that one of the two escapees might have been a breeding female. Due to the intensity of the trap effort at that site, I am confident that all hutias ranging from that colony were identified. However, it may be possible that one or two females remained in the den with nursing young. That the captured adults numbered two to one in favor of males further suggests the presence of hidden adult females.

Thus, the trends seen earlier over the entire island population were almost exactly represented by the Camp Colony alone. Such would be expected in a population comprising discrete colonies, and further substantiates the conclusion that the hutias of Little Wax Cay are not a single panmictic mass.

Additional Notes

Here I offer some casual observations made during the execution of the investigations that precede.

Throughout this study, the hutias of Camp Colony were regular visitors to Camp. Each afternoon at a little after four o'clock, the first foragers would arrive sniffing the ground and pausing by stages to nibble at the vegetation. My impression was that they were very near-sighted, and that they oriented primarily by scent. I noticed that if I stood or sat still, they would move freely around me, sometimes even approaching to sniff my boots. If I moved my arms slightly they would not react, but if I moved them greatly or moved my feet at all, the hutias would squeak and run away.

There were two types of vocalization that I could distinguish. Though I made no attempt to record them, I assume them to be the same two that Clough (1972) recorded on East Plana Cay. One was a quiet "chortle" that was emitted casually during the normal movements of sniffing and foraging. It was common but not frequent, and was not associated with the presence of other hutias. As such, it seemed almost contemplative, as of a person talking to himself.

The other vocalization was a shrill squeak that always accompanied alarm and usually preceded a pounding retreat through the brush. The signal had a tendency to chain

reaction, the first hutia alerting others who relayed the alarm abroad as the animals retreated in waves. Such was the population density in Camp at dusk that I often precipitated a rout of a dozen or more. The brush came alive at such moments, alerting me to whose island it truly was.

In the evenings I sometimes ran along the narrow trails in darkness to surprise them, and could hear them dropping from the trees. The sound of fifteen or twenty fat rodents thumping and squeaking through the brush on an island in the moonlight is not to be forgotten.

The playful wrestling behavior noted by Howe (1971) I observed only once, but it was just as he described, and not unlike the play of two young dogs.

Likewise, the marking behavior studied by Howe (1971, 1974, 1976, 1982) was practiced liberally by Little Wax Cay hutias. Everything I brought ashore and left exposed was marked with distinctive brown streaks. Even objects placed on the driftwood shelves in Camp were routinely knocked off by curious hutias climbing, then marked by others on the ground. Books, papers, clothes, and instruments were stored in the tents, but on occasion hutias slipped in and left their marks inside.

They were incorrigible explorers. Every corner of every tent eventually saw a hutia. One evening after supper, Donnie looked up to see the impressions of one's feet as it walked across the rainfly overhead. And climbing

into his sleeping bag one night, Donnie once had one scramble out to meet him.

To observe the behavioral interaction of hutias with the only other mammals on the island (R. rattus), two of each were placed in a 13-foot Boston Whaler runabout, 50 m off Thom's Landing on 4 November. Following are my notes of the event:

So at 1245 after weighing only one of the rats (K1010 = 120 g) because the other two had jumped overboard and gotten wet, K1010 and an untagged rat were released into the Whaler's forward locker, covered tightly by a plank, while the air kennel holding two hutias was placed far aft. They were opened simultaneously. K1010 quickly moved up into a loose coil of 1/2" nylon twist while the other rat stayed put. After 20 minutes the hutias were still inside the kennel, so I shook them out. The male (K1008) ran forward. On seeing it, the untagged rat jumped overboard for Donnie to recover, while hutia K1008 continued overboard for me to recover. Both swam with the seas toward shore: the rat smoothly and with diving to escape Donnie's hand, the hutia with labored, deliberate strokes and no diving. Both were returned to the Whaler after observed swimming about 30 seconds: hutia to the stern, where he hunched in the port corner while K1009 hunched in the starboard. No huddling. Over the next 15 minutes the rats groomed themselves and huddled in the bowlines while the hutias merely hunched in separate corners, no movement but some shivering by K1008 whose hair was almost dry.

Finally a box trap was placed aboard, amidships, upside down between the thwart. K1008 was introduced, then the untagged rat. K1008 had chosen a corner into which it faced, hunching. The rat approached, touching, turned to go, and K1008 lightly nipped its tail. A few more minutes of exploration by rat and it returned to K1008, still hunching into the corner, face to wire, butt along one side. Rat huddled against K1008, back to front, still very wet from its swim. K1008 made no more to repel the rat at any time afterward.

After 10 minutes, female hutia K1009 was introduced, approached K1008 and rat, was repulsed by a frontal spring by rat. K1009 retired to a different corner, face to wire. K1010 was then introduced, ran

about more energetically than other rat, approached K1009 who recoiled as if expecting attack. Finally K1010 huddled against K1009 while untagged rat remained huddled to K1008. Unbelievable.

Another 10 minutes and I carried trap to Camp. Perturbations made rats scamper about but not the hutias. Placed trap on ground near Camp, weighted with rocks, covered with tarp. After 30 minutes, uncovered to see two hutias huddled in one rear corner, two rats in other. Again perturbation caused rats to scramble, often to the hutia huddle, from which they were never repulsed.

Several other checks through the afternoon, all as above. Administered about one pint of parrot mix to center of trap (loose on ground beneath) and a jar lid of fresh water, as drip-bottle nozzle proved defective. Intermittent rain through evening. Will check for survivors in the morning.

In the morning I awoke to find all four animals huddled together with no wounds nor other signs of antagonism.

Further interactions with R. rattus were noted regularly over the baited net in Camp. They were always uneventful, except for the occasional poke of a hutia's nose toward an overly intrusive rat (one within 10 cm). But the rat always jumped clear to return later. I could find no way to say that the two were antagonistic species, at least not behaviorally. And since R. rattus is primarily a seed-eater, however indiscriminate, I doubt a competition for food with the folivorous hutia. On the possibility of competition for cover, Donnie one morning saw a rat run directly into a known hutia hole (Figure V-23). I would guess that the nocturnal hutias were probably inside, but after waiting several minutes, Donnie did not see any animal exit by any route. I must conclude a peaceful coexistence, at least for now.

It may be noted here that hutias themselves later proved to be quite thigmotactic, at least among concolonials. On the first night of the intensive netting of the Camp Colony, I put those captured each time into a 20 l plastic bucket with a perforated lid, so as to keep them separate from those still at large. Each time I opened the lid to add the next bunch of three or four, the ones piled within just looked up quietly as if a single resting organism. Some were not even visible. The heat they generated was enough to warm one's hands from the outside of the bucket, but the animals never squeaked or suffered that I could tell. When the last had been captured, I removed the lid and stood back thinking that they would come popping out, but they did nothing at all. I finally had to overturn the bucket, and even then several of them lay squatting on the ground for some seconds before ambling off into the brush.

It is important to note that in the Rattus encounter described above, G. ingrahami had proved to be a capable swimmer. This is in contradiction to Clough (1972), and important to realizing the true dispersal ability of the species. No doubt the effort is aided by a noticeably water-resistant coat and dense dry underfur. Thus, though certainly not a preferable avenue of travel, the sea is no permanent barrier to their movement. Given sufficient cause, such as overpopulation or habitat destruction, they

may, with a cooperative tide, disperse to colonize neighboring islands.

Several evenings each week of November and December I stayed up until midnight photographing hutias in the observation pen. I began by sitting in the observation tent and shooting through a hatch in the pen. As the animals acclimated to me I was able to enter the pen myself with camera in hand. The camera was a Nikon Nikkormat Ftn with a Nikon SB10 strobe and one of two lenses: a Nikon 55 mm macro and a Vivitar 70 X 210 mm macro zoom.

For the first three weeks of November two adults were kept in the pen: Ralph (K1008), the male captured at trap site I, and Alice (K1009), the female captured at trap site H. On the morning of 7 November I awoke to see Ralph mounting Alice inside the rocky cave constructed in the pen. Alice crouched facing me while Ralph mounted her from her left rear, clutching her haunches with his forepaws. There was little visible motion except for periodic shuddering by Ralph, after which he shifted his weight on his hind feet and renewed his grasp with his forefeet. After three such cycles, one every two-to-three minutes, they separated. He ambled off, and she licked at her groin and remained.

On 15 November I awoke at 7:45 and spent the next 24 hours observing Ralph and Alice from the observation tent. My notes are reproduced in Appendix A.

After Hurricane Kate passed by on 18 November, allowing Alice to escape through a hole in the pen roof, I released

Ralph and replaced them with three new hutias on 20 November: an adult female (June) and juvenile male (Theodore) captured together at trap site G, and an adult male (Ward) captured at trap site E. The adults remained somewhat wary of me in the pen, as had the previous adults. But Theodore became so accustomed to me as to allow close-ups of him sniffing the camera. He provided hundreds of photographs and later contributed to the captive age-and-growth study (Chapter IV) used retroactively to age live-trapped subjects. He also has reproduced successfully (with June) in the FMNH colony.

All subjects were capable, if deliberate, climbers, moving much like little bears. They climbed vertical members by hugging them alternately with forepaws and hindpaws, flexing and extending the spine in between. Horizontal members were handled more tentatively, by walking atop stout ones or by hanging from slender ones. I did occasionally see a hutia nibbling at the season's growth while hanging from a 5 mm twig 2 m off the ground. It is important to note that Theodore climbed much more readily than any of the adults. Being smaller and lighter, he was more agile than the adults and more able to reach the leaf-bearing shoots. However, none of the hutias under captive observation climbed much while fresh cuttings of desirable species were available on the ground. I fed the animals in the observation pen by providing freshly cut leafy shoots each afternoon at about five o'clock. To get photographs of

hutias climbing, I had to reduce the ration of fresh cuttings, sometimes to none at all. Bark-chewing was routine on fresh cuttings, but aloft was limited to a few shoots of Drypetes diversifolia by an adult male (Ralph), again only when fresh cuttings were exhausted. Apparently hutias do not climb trees unless they have to, and then the juveniles climb first. A bowl of fresh water replaced each day was rarely visited, as noted in the observations of 15 November (Appendix A).

Bathing of two hutias to collect ectoparasites revealed only a single species: the louse, Gliricicola o'mahonyi. Specimens were mounted by Eric Milstrey of the University of Florida and identified by K. C. Emerson of Sanibel, Florida. This is the same species collected by Clough (1972) from G. ingrahami on East Plana Cay, and was probably transplanted with the hutias in 1973.

Data on hutia predators is provocatively scarce. Domestic cats and dogs are the two most listed species, as well as the barn owl (Tyto alba), and of course, man. Until December I had never, in all my crawling about on the ground, found any bones or other remains of G. ingrahami, nor any sign whatever that any hutia had ever died on Little Wax Cay. Finally, while climbing along a cliff on the north shore on 6 December, I spotted the fused innominate bones of an adult in thin sand 2 m beneath a large rock where I had seen an osprey perch several times before. The sacrum was found a meter away and, most notably, the cranium. The

latter was intact, but for a hole extending the width of the occipital bone and communicating with the foramen magnum. Also the right parietal bone was excavated from its right margin to the midline, and from the post-orbital process forward. The right nasal bone was absent and the left severely damaged. Both zygomatic arches were missing, as well as the lateral member of the left orbit. The only missing tooth was the right incisor, preventing the use of the incisor-width formula for the determination of age. Nonetheless, ossification of the cranial sutures and the pelvic members indicated an individual fully adult.

It is hard to imagine how a bird like an osprey, designed to plunge its feet through water after fish, could pluck a rodent from the land. Add to that the fact that one is diurnal and the other chiefly nocturnal (although their activity periods do overlap for several hours) and osprey predation seems unlikely. However, while clearing traps one morning, Donnie and I both saw an osprey flying north along Moon Beach with a rat in its claws, the tail hanging aft. Although that particular evidence is strictly circumstantial, I think the possibility of the osprey as an incidental coastal predator merits further inquiry.

On the afternoon of 12 December, just a few days before leaving the island, I found in the middle of Burma Road, just a few meters from trap site eight, the skin and skeleton of a male hutia recently killed. Following is an excerpt of my notes:

Walking south on Burma Road, clearing traps for the last time, found remains of a hutia in the middle of the trail, exactly opposite pellet mat 16b. Carcass consists of almost complete skeleton, with head dismembered and remaining attached to skin, which, with appendicular members likewise attached distally, has been entirely removed from axial skeleton and turned completely inside-out. Everted hide with head and pectoral girdle remains attached to axial frame by tibiae. Mandibles are separate from all and occipital region has been broken away. Obviously some powerful predator has killed and skinned the subject or found it dead and then skinned it.

Estimate death within the last 48 hours.

Saved all remains.

A few ribs distributed in 1/3 m oval extending one meter south along trail.

Following measurements taken at 1345: upper incisors at gumline, 4.05 mm; at tip, 3.46. Right lower incisor at gumline, 1.92; at tip, 1.51. Left mandible missing.

The incisor-width regression showed the animal to be fully adult. The left pinna was severely torn and no eartag was present.

The cranial damage and eversion of the skin and skeleton are typical of raptor predation. The location of the carcass in an inland wood seems to vindicate any seabird scavenger as well as any predator adapted to hunting in the open, unless the animal had been obtained elsewhere and only dropped there. Barn owls (Tyto alba) had been sighted by yachtsmen on Shroud Cay, just 60 m to the south of Little Wax. In any case, the historical importance of T. alba as a capromyid predator can be expected to continue wherever the two might coincide.

One May morning, a well-intended yachtsman let his dog ashore to run before I could stop him. In only 10 minutes the dog was back with tail wagging, and smartly dropped an

adult female dead at our feet. My dissection notes are reproduced in Appendix B. The dog's facility showed me graphically what the impact of its species must have been historically on hutia populations.

Twice I glimpsed snakes on Little Wax Cay, once in the rocks of Rocky Road, and once in the rocks of the western shore. Both were small, having a diameter of about one centimeter, and since they lost themselves immediately in the rocks, I could only tentatively identify them as the brown racer (Alsophis vudii vudii), a species well-established in the Exuma Cays (Bahamas National Trust 1983). Admittedly, most species of Bahamian snake are small and probably not important hutia predators: the brown racer, the golden or pygmy boa (Tropidophus canus), and the blind snake (Typhlops biminensis). I remind myself, however, that G. ingrahami is not born weighing 1 kg, and that at a birth weight of 80 g, it might offer fair prey to the likes of A. v. vudii. But even that allowance need not be granted to establish a squamatan predator of G. ingrahami.

As General Curator in 1984 of the Ardastra Gardens, a zoological and botanical park in Nassau, I had the opportunity to obtain and handle many live specimens of the Bahamian boa (Epicrates striatus strigulatus). The animal commonly reaches a length of 2 m or more, and I have no doubt that even a moderately sized individual would have no trouble taking a Bahamian hutia. Denis Knowles (pers. comm. 1984), an accomplished amateur naturalist in Nassau, tells

with regret a story of how one of his Bahamian boas escaped its cage one night and ingested his Mexican yellow-headed Amazon (Amazona ochrocephala oratrix). And C. A. Woods (pers. comm. 1989) had several Haitian villagers lead him to a Hispaniolan boa that they had just killed after watching it swallow a Hispaniolan hutia (Plagiodontia aedium). Dissection revealed the hutia, a species that typically weighs one-and-a-half times as much as G. ingrahami.

A final note: one afternoon while baiting a box-trap with coconut in Camp, I noticed a hutia crouching in the brush, watching me. After setting the trap, I stepped back to watch the animal succumb to my cleverness. But rather than trip the wire by accident while reaching for the bait, the animal reached deliberately to the side and pulled the tripwire directly, trapping itself in the box and dropping the bait within easy reach. I was reminded of something Donnie May had said when we discovered that displaced hutias were returning to their home colonies: "These little guys seem to have it all figured out."

Table V-1. Results of the pellet census.

<u>Plot Number</u>	<u>Mean of the Transformed Weekly Pellet Counts</u>	<u>T Group</u>	<u>Estimated Number of Hutias per Hectare</u>
14	8.306	A	203
5	7.471	A B	164
9	7.335	C B D	158
4	6.626	C B D	129
13	6.523	C D	125
16	6.509	C E D	125
17	6.388	E D	120
7	6.062	F E D	108
8	5.882	F E D	102
6	5.870	F E D	101
20	5.667	F E G	94
15	5.457	F G	88
19	5.274	F G	82
1	4.951	H G	72
north Moon Beach	4.232	H I	53
south Moon Beach	4.206	H I	52
2	3.676	J I	40
12	3.493	J I	36
18	3.158	J	29
3	3.071	J	28
11	3.004	J	27
10	2.081	K	13
north rocks	1.636	K	8
south rocks	1.343	K	5

Note: Plots of the same T group were not significantly different at an alpha level of 0.05. The experimentwise error rate was controlled at 0.05 by ANOVA in which the two pellet trays at each plot were treated as a nested effect of plot location. (N = 24 to 26 in all cases)

Table V-2. Capture-recapture estimates of the populations about each trap site.

Trap Site	Closure	MK_1^*	MK_2	M_0	M_h	M_p
A (5 traps)	closed	17	17	16(17)18	15(<u>18</u>)20	15(17)19
A	closed	6	17	4(<u>6</u>) 8	4(<u>8</u>) 12	3(<u>6</u>) 9
B	closed	8	10	4(<u>12</u>)20	6(11) 1	
C	closed	8	8	5(<u>11</u>)17	6(<u>11</u>)16	4(<u>9</u>) 14
D	open	7	12	4(<u>7</u>) 10	9(<u>31</u>)53	0(<u>9</u>) 19
E	open	8	12	5(<u>9</u>)13	7(<u>8</u>) 9	
F	open	5	6	3(<u>5</u>) 7	5(<u>5</u>) 6	1(<u>6</u>) 11
G	closed	10	13	7(13)19	8(<u>11</u>)14	-1(13)28
H	open	6	9	2(<u>7</u>) 13	5(<u>6</u>) 8	4(<u>6</u>) 8
I	closed	9	11	6(<u>12</u>)18	8(<u>17</u>)27	
J	closed	6		0(<u>11</u>)22	8(29)50	
all combined	open	73		74(<u>88</u>)102	86(105)124	

* MK_1 is the minimum known alive during the first 22 trap sessions, excluding Operation Pinball. MK_2 is the minimum known alive over all trap sessions, including Operation Pinball, during which two traps were placed at each site except site J, where trapping was discontinued.

Note: Each estimate is shown in parentheses surrounded by lower and upper bounds of its 95% confidence interval. The preferred estimates, as selected by program CAPTURE, are underlined. Blanks indicate impossible models.

Figure V-1. Little Wax Cay, showing the locations of the ten live-traps (circled).

Figure V-2. The area marked by hutias about trap site A (Camp Colony). Powder was distributed over 0.29 ha.

Figure V-3. The area marked by hutias about trap site C. Powder was distributed by six animals over 0.12 ha. Faint dash represents 36-hour track of K1014, a juvenile female.

Figure V-4. The area marked by hutias about trap site D. Powder was distributed by four animals over 0.10 ha. Faint dash represents 36-hour track of K1042, an adult male.

Figure V-5. The area marked by hutias about trap site F. Powder was distributed by five animals over 0.10 ha. Faint dash represents 36-hour track of K1032, an adult female.

Figure V-6. The area marked by hutias about trap site I. Powder was distributed by five animals over 0.38 ha. Faint dash represents 36-hour track of K1028, an adult male.

Figure V-7. The 36-hour track of K1041, a juvenile female, from trap site B.

Figure V-8. The 36-hour track of K1016, a juvenile female, from trap site E.

Figure V-9. The 36-hour track of K1024, an adult female, from trap site G.

Figure V-10. The 36-hour track of K1017, a juvenile female, from trap site H.

Figure V-11. The 36-hour track of K1069, an adult male, from trap site J.

Figure V-12. Little Wax Cay, showing the distribution of hutias. Average density on the pond banks: 184 per ha, in the lowlands: 109 per ha, in the uplands: 35 per ha, on the coasts: 6 per ha.

Figure V-13. Demography of 111 live-trapped hutias.

Figure V-14. A juvenile male eats aloft in a whitewood tree (Drypetes diversifolia)

Figure V-15. The adults prefer to stay on the ground.

Figure V-16. A rat is tolerated over bait on a mosquito net purse seine.

Figure V-17. An anesthetized adult hutia models the capture kit.

Figure V-18. From Moon Beach northward the habitat changes from marginal to barren.

Figure V-19. The cliffs of the eastern ridge are creviced but exposed. Shroud Cay lies in the center background.

Figure V-20. The banks of Loch Ness, as those of the other ponds, are sites of great activity.

Figure V-21. Sandy inland habitat supports a meter-high termite nest.

Figure V-22. The view northeast down Dilly Lane shows the rocky limestone substrate that hutias find ideal.

Figure V-23. One of those formations provides a known hutia den.

Figure V-24. Hutia browse is extinguishing the highly preferred wild dilly (Manilkara bahamensis).

Figure V-25. Of high preference but greater regenerative ability is the crabwood (Ateramnus lucidus).

Figure V-26. A friend reviews the work of the day.

Figure V-27. Fawn awaits September on three anchors at Pyfrom Cay, Exuma.

CHAPTER VI

DISCUSSION

The evolution of capromyid rodents has been studied at some length (see Chapter I). Observations of live subjects, however, have been fewer, and ecological studies only recently attempted. The bias of research in favor of the historical is due, no doubt, to the greater availability of bony specimens than live. In the single case of G. ingrahami, itself richly represented in deposits, that bias is brought closer to parity.

The most complete study of hutia ecology has been Clough's (1972), and limited by atrocious logistic hostility, even that attempt was brief. It was, however, all the more remarkable for its yield of welcome information from only three weeks' research over a ten-year period. And Clough himself is to thank for making this study possible. His introduction of 11 G. ingrahami to Little Wax Cay in 1973 has enabled a protracted study in greater detail than had ever been possible on a capromyid population.

Of course the presentation of such an ideal population for study is due to the animals themselves. An explosion from 11 to more than 1200 individuals in only 12 years is quite remarkable in view of the current wisdom in hutia

biology. Capromyids generally have been relegated to the category of K-strategists, the biotically sluggish end of the over-used r-K continuum of the Verhulst-Perl logistic growth model. The hutias of Little Wax Cay are a graphic example of what a so-called K-selected species can accomplish in the absence of predation, and in the near absence of mortality itself. A long life, in combination with an almost total removal of superior trophic levels, has allowed a species of modest reproductive output to achieve a population density (65/ha) in excess of the parent population (26/ha) on East Plana Cay.

In terms of the logistic model, when environmental resistance is relieved, population growth is enhanced. The reason why G. ingrahami is the only capromyid alive in measureable densities is certainly that its few surviving populations are the only capromyid populations safe from predation. All other populations of all other species of hutia are subject to some combination of cat, dog, mongoose, and man. And those that have not been extinguished have been severely rarified.

Since the two studied populations of Bahamian hutia are both virtually predator-free, the difference in density between them must be due to some other source of environmental resistance. One possibility is the availability of fresh water. While G. ingrahami requires very little (Rebach 1971, Appendix A of this study), it certainly prefers it in its habitat (Chapter III). Little

Wax Cay has seven inland ponds and a mangrove swamp. All are filled by rain and closed to the sea, and most hold water through the dry season. Annual rainfall in the north Exumas has not been measured, but Nassau averages 1360 mm, and Georgetown, Exuma, averages 1046 mm (Bahamas Meteorological Department records). Annual rainfall in the southeastern Bahamas has been estimated at 762 mm (Clough and Fulk 1971), with Inagua getting only 643 mm (Bahamas Meteorological Department records). Also, Clough (1972) found only one fresh water pond on East Plana, and that near the eastern end of that long, narrow island. A low water allowance can affect hutias in two ways: by reducing the animal's metabolism (Rebach 1971), and by dictating a xerophytic community.

The plant community of Little Wax Cay is different from that of East Plana. Although 23 times as big, the latter hosts 19 fewer species of tracheophyte. Only eight species in as many genera are shared, those being the silver palm (Coccothrinax argentata), the buttonwood (Conocarpus erectus), and the following coastal herbs and shrubs: Hymenocallis sp., Sophora tomentosa, Suriana maritima, Ipomea sp., Strumpfia maritima, and Ambrosia hispida.

Part of the floristic difference is no doubt due to the great difference in rainfall budget between the two islands, with Little Wax Cay getting perhaps twice as much rain annually as East Plana. The difference in rainfall between the northern and southern Bahamas is great enough for Buden

(1979) to have assigned them to different classifications in the Holdridge Life Zone system: tropical dry versus tropical very dry. Such a pronounced environmental gradient is not to be underestimated in its effect on floral distributions.

But part of the difference in forage base is due to the hutias themselves. Strongest evidence of plant extinction by hutia browse is given by comparison of my 1985 Little Wax Cay list with the list of plant species noted there during the 1958 Exuma survey (Chapter III). Exhaustive search in 1985 could not discover one species noticed immediately in 1958: the hog-cabbage palm (Pseudophoenix sargentii). A second extinguished species, the seagrape (Coccoloba uvifera) was found only in the form of a single snag at the south end of Moon Beach. Though not tested, the first is probably a desired hutia forage, it having a history of use as a livestock food (Correll and Correll 1982). The second was found in this study to be a highly preferred hutia forage. Two other plant species listed in the 1958 survey were absent in 1985. The introduction of 11 Bahamian hutias in 1973 is the only biological perturbation known to have occurred on Little Wax Cay between 1958 and 1985. Thus, while circumstantial, the evidence is strong that G. ingrahami has eradicated at least four plant species from Little Wax Cay by way of overbrowse.

Further sign of hutia impact is the shoot damage to extant species sampled in this study (Chapter III). Although results of this study show that G. ingrahami should

properly be regarded a folivore, its habitat impact was more obviously due to bark-chewing. Never were plants found to have been chewed all the way through, however, as is common with the North American beaver (Castor canadensis) or the North American porcupine (Erethizon dorsatum). Rather, destruction of tissues down to and including the phloem was the norm, and girdling was common. Shoot browse was severe enough to cause extensive mortality in the wild dilly (Manilkara bahamensis), the pigeon-plum (Coccoloba diversifolia), and two species whose rarity prevented identification. Those species must be regarded as being at risk of extinction from Little Wax Cay.

A chi-square test of association over all species and plots showed hutia browse to be species-specific. But species found to have been shoot-browsed most severely in the field were not necessarily the most preferred in captive feeding trials. Reconciling the difference is the conclusion drawn in Chapter IV that the hutias of Little Wax Cay have distributed themselves according to substrate preferences first, exercising forage preferences second. Plant ordination by both detrended correspondence analysis and principal components analysis (Chapter III) pointed to a substrate influence on plant distribution (Axis 2, Figure III-2). Captive trials did show that, whereas some plant species were desirable for leaves but not for bark and others vice versa, most of those tested were preferred in either both aspects or neither.

Of particular interest is a comparison of feeding preferences between Little Wax Cay hutias and their counterparts on East Plana Cay. Of those plant species growing on both islands, the one that Clough (1972) found to be of "high" preference (Strumpfia maritima) was found in this study to be of low preference on Little Wax. The high preference Little Wax species were simply not present on East Plana. Another case is that of the buttonwood (Conocarpus erectus), which Clough (1972) found to be of "medium" preference on East Plana, but which on Little Wax Cay was utterly avoided. I doubt that G. ingrahami had changed so radically its feeding preferences in only 12 years. Rather, the indication is that the older East Plana Cay population is simply making do with inferior forages. The question remaining is whether the better forage species have been excluded by climate or edaphic factors, uninvestigated here, or by a history of hutia browse. Certainly a superior forage base on Little Wax Cay would help account for a superior hutia density there. The swift extinction on Little Wax Cay of four species already, and the severe depredation of several others, forbodes an accelerated reduction in range quality with continued population expansion.

Observations of penned hutias on Little Wax Cay showed them to climb after forage primarily when fresh leaves and bark were not available on the ground. Of course in nature leaves do not fall until they are senescent and a large

measure of their nutrients reabsorbed by the shoot for circulation to active organs (Barbour et al. 1980, Campbell 1987). And Opler (1978) asserts that generalist folivores (including mammals) tend to feed on young leaves. On the other hand, Dixon (1966) found that senescent leaves were more digestible to aphids (Drepanosiphum platanoides) than mature leaves. In any case, after many months of observation, I am compelled to describe G. ingrahami as a terrestrial folivore with arboreal capability, or an arboreal folivore that would rather be on the ground, and I find myself rediscovering the term "semiarboreal".

While the evidence of bark-chewing is ubiquitous on Little Wax Cay, I never saw free-ranging hutias in the act of barking trees. In captive trials, hutias ate much less bark of a given species than leafy material in most cases. I conclude that bark constitutes an important but secondary part of the hutia diet. Thus I characterize G. ingrahami as a semiarboreal herbivore, in the sense of Eisenberg (1978).

On Eisenberg's (1978) scale of arboreality, G. ingrahami rates as Class 2: having little anatomical specialization for climbing, and spending less than 50 % of its time aloft. On his (1978) scale of herbivory, it rates as Class 4: having a greatly enlarged stomach or cecum (the latter in this case), with leaves constituting at least 40% of the diet, and the remainder comprising "other plant parts."

Among forages, leaves are usually more digestible than bark, but lower in total caloric content. The reason is that digestibility is a function of protein and water content, high in leaves and fruits, whereas total energy derives from low-digestibility fiber content, high in bark and wood (R. Kirkpatrick pers. comm. 1982). Thus, the importance of bark to hutias may be simply to balance the diet. Servello (1981) found that pine voles (Microtus pinetorum) avoided restriction in total energy intake during Virginia winters by simply switching from apple fruit to bark. Dissection of an adult female G. ingrahami killed by a yachtsman's dog (Chapter IV, Appendix B) revealed an intestinal tract of approximately 6.5 m in length, with a caecum 180 mm long by 60 mm wide. The stomach contained assorted small chunks of bark in addition to leaf fragments. Clearly G. ingrahami is well-equipped to digest fibrous foods, and probably has relied on them for some time.

A folivorous diet is entirely consistent with a low metabolic rate (McNab 1978). A basal rate ($\pm$ SE) of $0.343 (\pm 0.067) \text{ ccO}_2\text{g}^{-1}\text{hr}^{-1}$ for G. ingrahami is well below the Kleiber (1961) prediction for an animal of its size. In fact the whole family Capromyidae (if G. ingrahami, G. brownii, and Capromys pilorides are any indication) departs progressively from the Kleiber function with increasing body mass, and does so without appreciable modification to thermal conductance. Of the three capromyids for which conductance values are known, G. ingrahami has the one that

falls farthest below the value predicted by McNab and Morrison (1963), achieving about 85% of the prediction. And G. ingrahami inhabits the driest habitats.

The relation between conductance and metabolism on warm dry islands is discussed in Chapter IV, as well as the possibility that folivory itself may enjoy a trophic advantage in such systems. Where water is limited, conductance, metabolism, urine volume, and primary productivity must all be sharply budgeted, and the hutias have survived by dint of adaptive complex.

Part of the low metabolism complex is low reproductive output (McNab 1980b). If, as McNab (1980b) suggests, "all species are as r-selected as possible," then the life history strategy of hutias is further indication of a penurious habitat. And their dominance of native systems signals that the strategy is keen enough.

That some wet forest mammalian arboreal herbivores are nocturnal (for example the two-toed sloth, Choloepus sp.) is probably more an adaptation to predation than to thermoregulation. In fact, most mammals highly adapted to folivory have to conserve what little heat they produce from their restrictive diet, simply for the sake of homeothermy. McNab (1978) cites the example of the three-toed sloth (Bradypus griseus), which has all but surrendered to poikilothermy despite a dense woolly coat providing very low conductivity. Opler (1978) points out that "almost all mammalian arboreal herbivores are tropical denizens" since

they need a year-round supply of young leaves. Certainly the maintenance of homeothermy provides additional cause for a primarily tropical distribution.

But not all tropical forests are wet. The Bahamian hutia has, since its appearance, been confined to small oceanic islands known for their lack of fresh water. In such habitats, the problem of heat conservation has been replaced by one quite the opposite. And one must recall that endotherms are generally even more harmed by high temperatures than low. Obviously, a crepuscular-nocturnal activity pattern is adaptive to hot dry habitats where heat loading places high metabolic demands on diurnal species to cool the body. The almost spherical hutia does not have the anatomical cooling devices of desert leporids or heteromyids, and has compensated behaviorally instead. Nightly activity is certainly not a strategy to avoid predation, as the chief reported predator of G. ingrahami, in the absence of man and his pets, is an owl (Tyto alba).

Given its nearsightedness and waddling gait, G. ingrahami is easy prey for any half-hearted predator. The yachtman's dog (above) took only 10 minutes to dispatch an adult female. The vulnerability of hutias is further indicated by the fact that wherever predators (including man) are present, hutias are not. As oft-cited is the owl, and as odd the possibility of osprey predation, the Bahamian boa (Epicrates striatus strigulatus) seems best suited to the niche of hutia predator. Given the preference of G.

ingrahami for rock crevices as dens, avian predation must be wholly incidental, occurring while hutias are abroad. But the snake is at home in the same rocky dens, and may prey at will. I suggest that the genus Epicrates, itself well-radiated in the Antilles (Buden 1975), may have been as important as T. alba to the history of hutias, and possibly moreso.

The rats (Rattus rattus) that Clough (1985) had thought "numerous" on Little Wax Cay in 1973, seemed to have "nearly disappeared" by his return in 1983. But for his report of them, I would not have noticed them in 1985 until they showed up in my traps. I don't know if that is a sign of their competitive displacement or my poor eyesight, but it was provocative enough for me to address by forcing hutias and rats into captive contact (Chapter V, Additional Notes). There was no evidence of antagonism, much less injury, and the two species huddled as if one. The only sign of an imperfect coexistence was the occasional nip of a hutia toward a rat approaching too close over the baited net in Camp. But the response threshold was only about 10 cm (Figure V-16), and the rats always escaped to return within a few minutes and forage freely, if perhaps nervously. The bait was parrot seed, taken as eagerly by both species, and both craved chunks of the coconuts I brought from neighboring islands. The rats did den in rocks, and one was seen scampering in daylight into a known hutia hole (Figure V-23). Hence a competition is possible, but not proven, and

I consider the resources of the island so generous as not to press it, at least not yet.

What limits hutia populations, as any, depends on where they are. In established populations where only endemic predators are present (East Plana Cay, Little Wax Cay) hutias abound. Everywhere else (Hispaniola, Jamaica, Cuba, and all of the settled Bahamian islands) populations have been reduced since the Amerindian invasion, and especially since the European discovery, by both humans and exotic predators. The only exception is Capromys pilorides, reported to be doing well in Cuba, especially on the compound of the U.S. Naval Base at Guantanamo Bay.

The effect of habitat destruction is illustrated in the extreme by the case of Plagiodontia aedium in Haiti. J. A. Ottenwalder (pers. comm. 1984) has found that the case of P. aedium in the Dominican Republic is not far behind. And L. Wilkins (pers. comm. 1986) has said the same of Geocapromys brownii in Jamaica. The effect of exotic predators is illustrated by the case of the Swan Island Hutia (Geocapromys thoracatus), extinguished after a combination of hurricane and house cat introduction (Clough 1976).

Leibig's (1840) law of the minimum, as restated by Taylor (1934), stipulates that populations are limited by whatever resource of time or space is in short supply. In all other populations of hutia but the East Plana and Little Wax Cay populations of G. ingrahami, predation and habitat destruction have kept densities so low that other factors

have not been limiting. And in the new population of G. ingrahami on Little Wax, apparently nothing has been limiting. Naturally, that trend cannot continue, and one must ask what shall limit it first and to what level.

Clough (1972, 1974) at length has described adult hutias on East Plana Cay as weighing only 600 to 800 g. And he caught several with mangy coats and inflammations of the skin and eyes. By contrast, the same species on Little Wax Cay in 1985 was characterized by much larger adults (700 to 1100 g) that appeared to be disease-free. Clough (1985 and unpublished field notes) found that five animals captured on Little Wax in 1983 all outweighed any East Plana adult, even those fed ad libitum in his lab.

As mentioned above, the inferior forage base on East Plana Cay supports a hutia density four-tenths that of Little Wax. The reduced size and vitality of East Plana Cay hutias may be caused by the same nutritional inferiority. If so, and if hutia depredation is even part of the cause of the low forage quality, it bodes ill for the hutias on Little Wax Cay. They may multiply until food becomes limiting, in which case the Little Wax Cay ecosystem shall converge on that of East Plana, stabilizing at a lower hutia density sustained by a poorer forage base, and characterized by smaller animals of poorer health.

On the subject of body size variation among the populations of G. ingrahami, I am reminded of Lawrence's (1934) work with skeletal remains from East Plana Cay,

Crooked Island, Long Island, Abaco, and Eleuthera. No taxonomist, I think that her assertion of three distinct subspecies of G. ingrahami may have been premature. Rather, the cranial differences, which were restricted primarily to variations in size, might have been due simply to differential nutrition. However, even if the three populations were in the process of speciation, that process is one of differential selection, which may well have been driven by differences in the quality of the forage base.

Another discrepancy between the Little Wax and East Plana Cay populations is in regard to the partitioning of space. The hutias of Little Wax Cay have arranged themselves in colonies with non-overlapping territories. When translocated among colonies, subjects returned home within hours to days, depending on the distance. Observations suggest that intercolonial antagonism may enforce colonial boundaries and discourage wayward individuals from trespass. On East Plana Cay, Clough (1972) observed no antagonism among five hutias contained in a single 2 m² wire pen for four days. Nor, in two cases, were animals captured from different colonies of Little Wax Cay antagonistic when housed in a large wire pen in a territory alien to all. It seems that intercolonial antagonism simply breaks down away from the home colony, as when mixed subjects are caged. The cage is home to none, so none defend it.

Clough (1969, 1972, 1973) was left with the impression that G. ingrahami is simply non-territorial, and that "They have responded to high density by developing great social tolerance, managed in part by elaboration of a system of social communication built on scent marking" (Clough 1973).

But when six hutias were transported from East Plana Cay to the University of Florida in 1981, something unexpected happened. The animals had been transported from East Plana to Nassau in three wood-and-wire cages lashed to the deck of the barkentine Regina Maris. The animals were flown by a commercial airline from Nassau to Gainesville, and installed in two adjoining wood-and-wire cages at the Florida Museum of Natural History Hutia Colony. Several weeks later, after acclimation to the facility and a daily diet of lab chow and fresh produce, the partition separating the two cages was removed. Over the next several days, injuries were noted on several of the animals, and after just a few weeks, three of them were dead. All three had died of injuries sustained from fighting, and all three had shared the same cage since leaving East Plana Cay. The three survivors had shared the other. I believe that the period of transportation had been long enough that the two groups of animals, together at the time of capture, had formed separate fidelities once divided. When exposed to each other in close quarters, the two groups fought to the death. Since then, the Florida Museum of Natural History

has transported each set of captured animals as a single group, and never recombined animals once separated.

Thus, the tendency to group structure of G. ingrahami on Little Wax Cay may exist also in East Plana Cay hutias, however oblivious they appear. Before I censused the Little Wax Cay population, I had assumed that the population of East Plana was greater, and that perhaps the territoriality observed at the Florida Museum of Natural History and on Little Wax Cay was something that broke down at high densities. But knowing that the hutia density of Little Wax was in fact 2.5 times that of East Plana, I speculate that the behavior does just the opposite, intensifying at high density and all but disappearing at low. I find that idea easier to live with, especially if the function of the territoriality is, as is usually the case, resource partitioning. The idea gains strength as I recall that the small groups (no more than four) studied by Howe (1971, 1974, 1976) were housed in a room-sized enclosure that was many times the size of the cages used for similar groups in Gainesville.

Also, I point out the presence of ear scars on a hutia photographed by Clough on East Plana Cay (Howe 1982). Few hutias live-trapped on Little Wax Cay did not have similar tears in the dorsal or caudal margin of at least one ear, narrow as a hutia's incisor, and exactly as described from the adult female killed by the yachtsman's dog (Appendix B). I was left with the strong impression after handling over a

hundred G. ingrahami and seeing a few agonistic nips among mixed hutias in captivity, that torn ears may be very much a sign of antagonism if not combat, however brief.

Social structure in the Capromyidae is not well-known, despite captive studies touching some aspects of it (Radden 1968, Taylor 1970, Oliver 1977). J. F. Eisenberg has suggested (pers. comm. 1987) that a study be conducted on the Guantanamo Bay population of the conspicuous 4 kg Cuban banana rat or hutia conga (Capromys pilorides). It would certainly be a contribution to the biology of the family, and could draw from the preliminary work of Taylor (1970) and Canet and Alvarez (1984b).

Even at this point, comparisons may be made to the genus Kerodon (Caviidae), which occupies rock piles for shelter in the arid Caatinga of northeastern Brazil (Lacher 1981). Food and shelter are extremely clumped, and an entire outcrop may be controlled by a single male. Since polygyny is the rule, the dominant male commands resources for a harem of females and some subordinate males in addition to itself. Lacher (1981) argues that the behavior of Kerodon is more complex than that of any other caviid, involving patterns to defend the rock pile from outsiders, as well as patterns to promote group cohesion with minimal injury to females and young.

A similar habitat and social structure have been extensively studied by Hoeck (1975, 1982, et al. 1982) in the African rock hyraxes, Procavia and Heterohyrax, in the

Serengeti National Park of Tanzania. Both genera (monotypic) inhabit rock outcrops or kopjes surrounded by a "sea of grass" that isolates the kopjes as habitat islands. Both are folivorous and strongly convergent on Kerodon (Eisenberg 1981). C. A. Woods (pers. comm. 1983) has noted an anatomical convergence of the entire order Hyracoidea on the Capromyidae, each having radiated folivory into both arboreal and rock-dwelling niches. Procavia and Heterohyrax correspond to Geocapromys, whereas Dendrohyrax compares to Plagiodontia and the more or less arboreal Capromys.

The capromyids of the Caribbean provide a pattern of radiation, speciation, and extinction involving a complex of K-selected adaptations to folivory on oceanic islands. But the family is not unique even in that pattern. Eisenberg (1978) and L. Wilkins (pers. comm. 1986) point to a similar one among the murid "cloud rats" (Phloeomyinae: Phloeomys and Crateromys) of the Phillipines. Eisenberg (1978) provides a full discussion of the evolution of arboreal herbivory in mammals, with special attention to a convergence of the phloeomyines and the capromyids. The similarities are thorough enough to extend from body size and morphology to reproductive output. The hystricognath radiation of the West Indies may thus parallel a small part of the extravagant myomorph radiation of the East Indies. I saw a photograph over Wilkins' desk in the Florida Museum of Natural History almost daily for several months before I asked her how she had gotten such a good close-up of a young

Plagiodontia aedium in the wild. I was embarrassed and amazed to hear her say it had been taken half a world away, of an unrelated species. In one respect at least, I am in the company of Cabrera, who, given the first skin of Phloeomys before its location, temporarily identified it as Capromys (Eisenberg 1978).

Nor is this the first report of a rodent's going from rare to destructive in a short period of time. Twenty nutria (Myocastor coypu) were imported to Louisiana in 1938 to establish a fur farm in response to a demand dating to the early 1800's. By the late 1950's, the feral population numbered approximately 20 million, and by 1962 the species had replaced the muskrat (Ondatra zibethicus) as the state's number one furbearer. Though native to South America, where it burrows and forages along river banks, it has grown to pest status in parts of North America, Europe, and Asia by way of crop damage, irrigational disruption, and displacement of native fur-bearers (Nowak and Paradiso 1983).

B. K. McNab (pers. comm. 1986) speculates that the low reproductive output of capromyids may be due in part to relief from the pressure of competition with species of a similar niche. If so, and there is every reason to agree, then one of the major forces of ecology has been suspended in those systems, and it may be said that the hutias have evolved more in response to the physical environment than the biological. In the case of G. ingrahami, the only other

vertebrate folivores in its habitat have been the iguanas of the genus Cyclura. The Recent range of G. ingrahami overlaps that of the iguanas, which number three species and seven subspecies in the Bahamas alone, with an eighth in the Turks and Caicos (Auffenberg 1976).

As reptiles, of course, the iguanas represent a metabolic extreme that hutias could not approach without compromising homeothermy. In fact hutia metabolism, though low for mammals, may be high for vertebrates on desert islands. Cyclura iguanas are capable arboreal feeders, often climbing 5-10 m in search of leafy forage, and leaping to the ground from 5 m if disturbed (Auffenberg 1976, Iverson 1979). However, most of their feeding is terrestrial, like Geocapromys. In the most liberal sense, there might be an odd convergence there, greatly limited by occurring at the class level. Some competition for food must have existed historically, and there is no proof that hutias and iguanas did not displace each other locally. But the idea of tree-climbing in a three-foot lizard is only slightly more ridiculous than that in a flat-footed, fat, myopic rodent, and may be further evidence that any competition is decidedly low-key. And because ectothermy obligates the iguana to a diurnal activity pattern for the maintenance of body temperature (Iverson 1979), the Geocapromys niche does not seem seriously courted.

Instead, I see the system as one in which an array of ancestral species, historically marooned, has dwindled to a

handful that are struggling to get as much lifeblood as possible from the same rock. It should be no surprise that they occasionally bump into each other, but the question of competition remains open.

The motive for introducing (reintroducing?) G. ingrahami to two new islands from the sole remaining population on East Plana Cay was to ensure the species against the kind of catastrophic extinction suffered by G. thoracatus on Swan Island. In the absence of predation, disease, and nutritional constraint, the population of Little Wax Cay has exploded to a density greater than the founding population on East Plana. Data from this study indicate that four species of tracheophyte have already been extinguished since the introduction, and that several more are soon to follow. That East Plana Cay, an island of 465 ha supports only 31 vascular plant species while Little Wax Cay, an island of 19.4 ha, supports 51 may be due to climatic differences. Or it may be due to the location of Little Wax Cay in a long chain of large and small islands, as opposed to the isolation of the Plana Cays, a pair located 25 km from the nearest neighbor. But the possibility remains that the depauperate structure of the East Plana Cay plant community is due, at least in part, to overbrowse by G. ingrahami. In 1968, Clough (1972) noted that hutias there had all but eliminated the paw-paw (Carica papaya) that Ingraham himself saw being ravaged by hutias in 1891 (Allen 1891).

Also, the kind of vegetation on East Plana is typically xeric scrub, a type avoided by Little Wax Cay hutias, who prefer the more delicate and palatable leaves of the taller tree species that characterize that island. The indication is that, given time, the more palatable inland species of Little Wax Cay will be exchanged for an inland expansion of the coastal scrub. Mitigating against that is the geography of Little Wax Cay, which, while of the same coral limestone as East Plana, has a different topography. East Plana has a central longitudinal ridge, falling away to the sea on all sides. Little Wax has a broken perimeter ridge, falling away to the sea on one side, and to a series of interior ponds on the other. Protection from dessicating winds and provision with a year-round fresh water source may help preserve the original community from complete destruction. Among the highly selected forages, species of high regenerative capability, such as the crabwood (Ateramnus lucidus), shall enjoy an advantage over the slower-growing species, such as the wild dilly (Manilkara bahamensis), and may displace them under pressure of hutia browse. In any case, I expect a reduction of the inland growth from tree to shrub, and a severe rarification of the more palatable species.

However it is important to recognize, as noted by Correll and Correll (1982), that much of the flora of the Bahama Archipelago is not native. Thus, alteration of that flora by an animal that is native should not be disparaged.

There is no doubt that G. ingrahami is native, having colonized the Bahamas at least 8000 years B.P., some 4000 years before the arrival of man (Morgan in press). In fact, if G. ingrahami was present historically in the north Exumas, as it was in the south (Allen 1937, Hecht 1955) then Little Wax Cay may actually be returning to its native state via hutia browsing. The dense, lovely communities of the Exuma Cays and elsewhere may actually be the result of an ecological release from hutia browse by the predatory activities of man and his pets. What is native and what is good must be reconciled by the Bahamian people, and sought by their government agencies in the light of this and other scientific appraisals (Jordan in press).

An eventual drop in the population of G. ingrahami on Little Wax Cay is anticipated in response to its own habitat impact, and the ecosystem is expected to converge on that of East Plana Cay.

The plant-herbivore interaction has been addressed much more from one side than the other. The impact of herbivores on plant communities is well-documented (for small mammals see reviews by Batzli 1975, Golley et al. 1975, Naumov 1975, Chew 1978, and Potter 1978). The most analytical studies have used fenced exclosures paired with unfenced test plots, as in a study of white-tailed deer (Odocoileus virginianus) in northwestern Pennsylvania by Jordan (1967).

However, though a numerical response of herbivores to their forage base is almost tautologically taken for

granted, it has rarely been addressed directly (Pease et al. 1979, Vaughan and Keith 1981, Mezhzherin and Mikhalevich 1983, Swenson 1985, Servello and Kirkpatrick 1987), and continues to frustrate animal demographers. "That wildlife population sizes are a function of habitat adequacy is commonly accepted in wildlife management. In a majority of cases it would appear that habitats are important primarily from the standpoint of nutrition" (Kirkpatrick 1980). Students of the nutritional effect have concentrated on captive manipulations of diet, assessing specific physiological impacts analytically in pursuit of mechanism. The next step, which is not an easy one, is to translate those impacts into life table parameters, as in the construction of population simulators (Tipton 1980) such as that developed by Jordan (1982) for the pine vole (Microtus pinetorum) in Virginia.

Unfortunately, demographic responses of wild populations to their own growth would seem best observed in transplants. The reason is, of course, that existing populations have already achieved equilibrium, or their specific version of it. And the best transplants to observe would be those to habitat islands prohibiting migration, where browse impact would resultantly be most severe. But ecological transplantation is at least controversial and at worst catastrophic, and only at best in the service of nature. The controversy has not been helped by the participation of sporting privateers and the fanatic

uninformed. Where a given animal species is absent, there is usually some good reason, and it should not be introduced. But where it has been extinguished by the intrusion of man, it may be restocked in good conscience, and probably should be.

Furthermore, it is imperative that such reintroductions be allowed to seek their own demographic destiny, be it equilibrium, cyclicity, or boom and crash. For if people intercede to "rescue" a crashing ecosystem, the experiment goes for naught, and the science degenerates to zookeeping. Knowing what makes a system fail can help explain how it works, and seeing what replaces it is to indulge the natural mechanism. As long as the subjects are endemic, that can be done with confidence, and some measure of duty. Again, if it is a true reintroduction, then the system is returning to a prior state that is arguably more natural than the one perturbed.

Of course the experiment must be contained to a predetermined area. The ability of G. ingrahami to swim at least short distances may permit spontaneous dispersal to neighboring islands in the Exuma Cays. Uncontrolled, that could lead to a stepping-stone depredation of valued habitat. Hutia sign has been reported on Shroud Cay and, if confirmed, is proof of their dispersal capability, and a portent of impacts that were not the intention of the original Little Wax Cay introduction.

I have received the endorsement of the Bahamas National Trust to lead a research team to the Exuma Cays Land and Sea Park in the summer of 1990, for the purpose of taking an inventory of terrestrial vertebrates, both living and extinct. If we confirm the reports of living hutias on Shroud Cay, I shall recommend that the opportunity be taken to test the effects of native predators on hutia population dynamics. If native hutia predators (barn owls and Bahamian boas) are present, then any hutia population establishing on Shroud Cay may be held in check without severe habitat impact. But if those predators are absent (especially the boa) I shall consider recommending their transplantation to Shroud Cay. Both the barn owl and the boa are distributed widely in the Exuma Cays, on islands of all sizes. But no action will be taken without assessing all possible environmental impacts, and all recommendations will be cleared through the other scientific advisors to the Bahamas National Trust. Regardless of what action is taken, follow-up studies will be conducted annually to monitor habitat impacts of hutias on Little Wax Cay, Shroud Cay, and Warderick Wells.

Warderick Wells Cay, Clough's second hutia transplantation site, is perfect for testing the effects of native predators on hutia dynamics. I saw a female adult on an interior sandy slope on the afternoon of 24 August 1989. If the cohort of 13 dropped there in March of 1981 had grown at the same rate as the 11 placed on Little Wax Cay in 1973,

then there should have been approximately 324 on Warderick Wells at the time of the sighting. Warderick Wells is in many ways the gem of the Exuma Cays Park, and a number of prominent Bahamians have expressed concern that it will be adversely affected by hutia browse. Warderick Wells provides an ideal opportunity to recreate a pre-human Bahamian ecosystem, with hutias under the control of endemic predators, rather than over-controlled by exotic predators, or out of control with none at all.

But it remains imperative that Little Wax Cay be left alone. I specifically recommend that the Bahamas National Trust and the Ministry of Agriculture prohibit any activities that may influence the destiny of that island, and that interested parties trust it to the agents of its nature.

CHAPTER VII

CONCLUSION

The Bahamian hutia is a low-metabolism, folivorous rodent with arboreal capability and an adult body mass ranging from 600 to 1200 g. It suckles for eight weeks, reaches reproductive maturity at one year, and produces one to three litters per year of one or, rarely, two young. Animals den in rock crevices or, in their absence, under leaf piles of the silver thatch palm. The population on Little Wax Cay is divided into colonies that control adjacent non-overlapping territories. Colonial fidelity is high, but mixed animals on neutral ground may form a group bond. The animal is crepuscular to nocturnal to avoid heat stress, it orients by olfaction, and prefers but does not need fresh water in the diet.

Extensive removal of bark in addition to leaves poses a significant threat to favored plant species. Four tracheophyte species have been eliminated since the 1973 introduction of a founder cohort of 11 animals from East Plana Cay. The population currently numbers over 1200, and several forage species of high preference are suffering severe depredation. The current density of 65 hutias per ha exceeds that of the parent population, which subsists on a

range of poorer quality in a drier habitat. The depauperate community of East Plana Cay may be due in part to hutia browse pressure, and the population of Little Wax Cay is expected to decline.

All hutias are vulnerable to predation. Woods and McKeen (1989) have compared them anatomically to the North American porcupine (Erethizon dorsatum), and I think of Geocapromys ingrahami ecologically as a porcupine without quills. Having radiated in the Antilles in the absence of cats, dogs, mongoose, and people, capromyid populations were historically controlled by a combination of the barn owl (Tyto alba), the quality of local forages, and I think, the Caribbean boa (Epicrates striatus). With the invasion of man, and especially since the European discovery, capromyid populations have been decimated throughout the family's range, and that range severely reduced by the extinction of many whole populations, one of which has been listed as a separate species (G. thoracatus).

The survival in high density of G. ingrahami on East Plana Cay is imputed to its extreme remoteness, which has discouraged permanent settlement and the introduction of new predators. The explosion of the Little Wax Cay population is due to a similar absence of people and exotics, a plentiful supply of fresh water, and a temporary excess of palatable forages. The Bahamian hutia can swim and may spread to neighboring islands in the Exuma Cays Land and Sea Park.

Geocapromys ingrahami has been relieved of the risk of extinction by Clough's (1974, 1985) transplantations to Little Wax Cay and Warderick Wells Cay. It is imperative that those two systems be allowed to follow their own ecological course. Current studies by the author are monitoring their progress.

APPENDIX A
BEHAVIORAL OBSERVATIONS OF TWO CAPTIVE ADULTS

Slept in to 0745 when awakened by Donnie bearing three peanut butter and jelly sandwiches and 1/2 gallon instant tea. Wonderful. Breakfasted in photo tent on this my first 24-hour stakeout of the pen. Both hutias approached from cave to the hatch, sniffing my breakfast (0750). Some casual browsing on yesterday's fresh cuts of wild dilly, Eugenia axillaris, Randia aculeata, and then Ralph retired to cave (0820) while Alice crouched on rocks between cave and east wire, in the waxing sunlight. So until 0945 when Ralph joined Alice on east rocks, crouching rear-to-rear. Are they raising body temperature from a nightly low, or using the sun to keep a minimum as they rest? (Ralph has always been more shy and skittish than Alice, concentrating his activity on searching the wire for escape routes, climbing it extensively and checking all the joints, while Alice contents herself with browsing: on ground if fresh cuts are available, aloft if not. Ralph's muzzle is abraded dorsally from pushing it through the wire. I have seen both drink freely from their bowl, both Norman's Cay fresh water and water from Camp Pond, and Norman's Cay water two days old and full of sand and litter. Note: Ralph is noticeably larger than Alice, therefore more thermally inert?) At 1045 Ralph approached hatch in dappled sun, sniffed about, licked his flanks, crouching amid Drypetes trunks at center, scratched. Alice still on east rocks. At 1050 Ralph returned to cave mouth, facing outward from the dark, retreated to groom. Alice stationary, resting in the sun, Ralph grooming intermittently in cave.

- 1122: Ralph joined Alice on E. rocks.
- 1134: Alice passes out through cave; Ralph remains on E. rocks.
- 1135: Alice back into cave.
- 1155: Both in cave.
- 1215: Ralph in sight in cave, Alice out of sight.
- 1230: Both out of sight.
- 1243: Alice resting in full sun on E. rocks.
- 1300: Alice retires to cave, both out of sight.
- 1310: Alice stationary on E. rocks in full sun. With the sun rising in SE, that area is the brightest (warmest) in the pen from dawn 'til afternoon.
- 1330: Both out of sight in cave.
- 1407: Alice crouching on E rocks in full sun.
- 1415: Ralph joins Alice on E rocks, sun now past zenith, E

- rocks in semi-shade, W half of pen exposed.
- 1430: Both spooked into cave by my movements.
- 1435: Alice returns to E rocks, crouching still.
- 1437: Alice comes to gate, sniffing and squeaking, and looking at me.
- 1440: Ralph approaches center pen from cave, Alice still investigating me.
- 1442: Ralph joins Alice, sniffs through hatch.
- 1447: Both foraging on dead leaves of Drypetes and dilly in shade by hatch.
- 1455: Alice drinks fresh water from pond for 35 seconds, then Ralph does same for 2 minutes, 40 seconds, then both return to leaf-eating in sunlight of W. side (where I placed the cuttings yesterday). So until
- 1510: Ralph to cave, then joined by Alice.
- 1513: Ralph to E rocks, there joined by Alice, both inactive.
- 1533: Alice browses leaves in W pen.
- 1538: Both to leaves at S pen, autogrooming.
- 1540: Both to leaves at W pen.
- 1544: Ralph to leaves at center, then licks groin 3 minutes, then forages.
- 1550: Ralph to E rocks, patrolling wire, then foraged about, as Alice. Both in continuous activity while I ate supper, returning with fresh cuts of dilly and Bourreria ovata and Drypetes at
- 1800: Started generator with full gas tank, put in fresh food (see above), began charging 4 "D" cell Ni-Cd batteries, brand new. Pen illuminated by one 60 watt 120 v light bulb in spun aluminum shade, covered by dark green plastic filter = good effect: pen looks as if under a bright moon. Both subjects foraging among fresh cuts, except when I stepped in to separate the food so they couldn't hide in it, and for 5 minutes afterward, which they spent hiding in the cave.
- 1835: Both emerge from cave and forage freely among the cuts. I am in total darkness in my tent, invisible to subjects except while writing under glow of red-filtered caving light.
- 1900: Continuous activity since last entry: foraging, patrolling wire. Ralph just squeaked from wire by hatch; Alice came quickly to him from cave where she'd been briefly.
- 1915: Ralph has been patrolling wire; Alice in cave or on E rocks now emerges to forage. Movements of both since 1800 have been quicker than during daylight hours.
- 1925: Ralph drank for 5 seconds, still on patrol; both foraging.
- 1953: Alice has been in cave since 1945, now emerges. Ralph still patrolling, foraging, occasionally climbing NE corner Drypetes by hugging it with forelegs, then hindlegs, then forelegs, etc., and descending head first.
- 2115: Both still active, foraging freely.

- 2130: Ralph drank H₂O for 20 seconds.
 2155: Both to cave, out of sight.
 2220: Alice emerges, followed by Ralph. Both forage.
 2255: Ralph drinks 15 seconds, but I notice that he contacts H₂O only once in 5 seconds, and barely enough to ripple it.
 2305: Ralph to cave.
 2310: Alice joins Ralph, both out of sight.
 2325: Ralph emerges, patrolling, followed by Alice, foraging.
 2358: Ralph drinks 85 seconds and retires to cave, then to patrol. Thrice hutias have approached wire from outside; one and Ralph sniffed each other for 2 to 3 minutes around 2145. Alice continues to forage; Ralph does so intermittently.
 0003: Alice to cave.
 0015: Alice emerges to forage on Bourreria ovata.
 0022: Alice to cave.
 0030: Ralph to cave, grooms, then Alice emerges to forage on dilly leaves. Note: Both like to remove leaves at the pulvinus and hold them while chewing. Dilly leaves exude sap from petiole; many are lying on the ground, entire, removed from cuttings, many extensively chewed. Both seem to show this leaf preference: Manilkara bahamensis > Bourreria ovata > Drypetes diversifolia > Eugenia axillaris. I've not seen them chew bark tonight.
 0035: Ralph climbs a Drypetes on patrol, then descends.
 0038: Alice to cave; Ralph takes a sip, then eats Drypetes leaves. Joins Alice at 0040, both out of sight.
 0050: Both emerge to forage or forage and patrol.
 0115: Alice to cave; brief visit from Ralph at 0129; she emerges at 0120.
 0125: Ralph does some serious climbing: upward by shinnying as described earlier, hugging the trunk with forelegs, then hindlegs, then forelegs, etc., sometimes in rapid succession; downward in same motion only inverted and more swiftly, as a kind of controlled slide. Investigates the roof, munches live Drypetes leaves. On returning with one, is approached by Alice, sniffing; he turns from her, keeping his leaf. On smaller trunks (< 5 cm) he walks down, just as he walks on lateral shoots, alternating limbs, so: left front and right rear together, right front and left rear together, or almost together. On the ground it's a waddle; in trees it's a deliberate bear-like motion: strong but short-limbed and ungraceful. Passes among shoots laboriously with more muscle than balance, swiveling wildly on small (< 1 cm) shoots, or snapping them under weight. Can traverse a gap equal to his body length by grasping with forepaws before releasing hindpaws. Note: on descent forepaws point downward but hindpaws point parallel to the ground plane and not upward as those of tree squirrels. On

- ascent, both forepaws and hindpaws point roughly parallel to ground, with palms gripping trunk between them.
- 0150: Ralph back on ground patrol, Alice foraging among cuttings.
- 0205: Ralph drinks, joined by Alice.
- 0215: Ralph to cave.
- 0218: Alice joins him.
- 0242: Ralph emerges scratching, then Alice. Former patrols and forages, latter forages.
- 0300: Ralphs drinks briefly.
- 0312: Alice drinks briefly.
- 0340: Alice into cave with Ralph, but Ralph out again.
- 0345: Alice out to forage.
- 0403: Generator out of fuel after precisely 10 hours 3 minutes on a full tank (about 3 gallons). Refilled it to complete this stakeout. No oil burned, but may need a change.
- 0415: Alice drinks 45 seconds.
- 0500: Both in cave, out of sight.
- 0520: Ralph emerges to forage, followed by Alice.
- 0530: Both to cave.
- 0540: Both emerge to forage.
- 0550: Alice to cave.
- 0600: Ralph to cave.
- 0615: Dawn illuminates the pen; I turn off generator, secure flood lamp in tent. No sign of subjects.
- 0625: Alice on E rocks.
- 0630: Alice to cave.
- 0720: Alice emerges to forage in S pen.
- 0730: Ralph joins Alice, now foraging in center pen.
- 0735: Alice to E rocks, Ralph also.
- 0745: Ralph to cave, Alice on E rocks.

APPENDIX B
DISSECTION OF AN ADULT FEMALE KILLED BY A DOG

Geocapromys ingrahami Necropsy #1 KCJ A101
Female adult hutia killed 26 May 1985 at 1700 hrs on Little
Wax Cay by potcake hound of visiting yachtsman. Subject
placed on ice in cooler overnight, withdrawn cold, air dried
and dissected 27 May by K.C. Jordan

Body Length: 336 mm
Total Length: 497 mm
Body Mass: 1070 - 150 = 920 g (spring), 922 g (balance)
Right Ear: 25 mm
Right Hind Foot: 52 mm with claw: 57 mm
Paired Incisor Width at gumline at tip
 Upper: 4.74 mm 3.85 mm
 Lower: 4.38 mm 3.54 mm

Sex: female, vagina perforate
Reproductive Status: 2 pairs mammae = 1 pair lateral
thoracic, 1 pair later abdominal. Subject lactating on
right thoracic, not on left side. Right abdominal nipple
undeveloped from areola.

Appearance: Appears plump, healthy, no external lesions or
abnormalities at time of death. Left ear torn and healed
long ago, wound made by animal with small narrow teeth,
probably another hutia. Right ear torn badly in two places
and healed long ago, one wound appears made by incisors of
hutia size. All wounds located on the caudal margin of the
pinna, as if attacked from the rear. Eyes clear at the time
of death, nares oozing fresh (arterial) blood. Cause of
death probably concussion or cervical dislocation by dog,
who returned with the carcass after only ten minutes on the
island. I believe I felt the animal's last breath on
removing it from the dog's (gentle) grip. Old wound on
dorsal tail, 1/3rd from end.

Dissection: Dissected GI tract and photographed it. Fully
dissected, but not stretched, small intestine = 4350 mm;
cecum = 180 mm along straight line, 235 mm along curved
longitudinal ligament (cecum quite curved), average width =
60 mm; colon = 1940 mm; stomach = 80 mm across (max) X 55 mm
cranial to caudal (max). Removed urinary and reproductive
tracts together, photographed and preserved in 10% formalin.
Noted 1 swelling with increased vascularization in each
uterine horn, right one larger than left one, no other
abnormalities. (right swelling = 9 mm across, left swelling

= 6 mm across) Wrapped eviscerated carcass in 1" chicken wire for burial maceration. Dissection performed outdoors; flies may appear in photos. Photographs taken with Nikkormat Ftn, Ektachrome 400, outdoors. Placed 4 fecal pellets in each of 2 vials of 10% neutral buffered formalin.

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BIOGRAPHICAL SKETCH

Kevin was born in Springfield, Illinois, and grew up in Warren, Pennsylvania. His mother is the former Elizabeth Mae McLaughlin of Forest Hills, New York, and his father is Dr. James Schuyler Jordan, a biologist retired from the U.S. Forest Service, Allegheny National Forest. Kevin has a B.A. in biology from Cornell University, and an M.S. in fisheries and wildlife sciences from Virginia Tech. He lives on the coast in New Smyrna Beach, Florida, where he teaches and writes, and does pretty much whatever he wants.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Charles A. Woods, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg
Katharine Ordway Professor
of Ecosystem Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John E. Robinson
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Larry D. Harris
Professor of Forest Resources
and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Francis E. Putz
Associate Professor of Botany

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Dean, Graduate School