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Analyses of the Effects of an Exotic Lizard (*Anolis sagrei*) on a Native Lizard (*Anolis carolinensis*) in Florida, Using Islands as Experimental Units

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To the Graduate Council:

I am submitting herewith a dissertation written by Todd S. Campbell entitled "Analyses of the Effects of an Exotic Lizard (*Anolis sagrei*) on a Native Lizard (*Anolis carolinensis*) in Florida, Using Islands as Experimental Units." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Arthur C. Echternacht, Thomas G. Hallam, Major Professor

We have read this dissertation and recommend its acceptance:

Jim Drake, Sally Horn, Susan Riechert

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Thomas G. Hallam, Department Head

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and recommend its acceptance:

Susan E. Riechert

Sally P. Horn

Accepted for the council:

Associate Vice Chancellor and
Dean of The Graduate School

Analyses of the effects of an exotic lizard (*Anolis sagrei*) on a native lizard (*Anolis carolinensis*) in Florida, using islands as experimental units

A Dissertation
Presented for the
Doctor of Philosophy Degree
The University of Tennessee, Knoxville

By Todd S. Campbell
May 2000

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DEDICATION

This dissertation is dedicated to my brother

Scott Campbell

who sparked my enthusiasm for life,

to my father

Carl Campbell

who inspired me to aim high at everything,

to my brother

Clark Campbell

who ignited my interest in the natural world,

to my mother

Bettie Campbell

who provided me the chance to do good things,

and to my wife

Kym Rouse Campbell

who supported me unconditionally through it all

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ABSTRACT

The green anole, *Anolis carolinensis* (Sauria: Polychrotidae), North America's only native anole, was abundant in even the most disturbed urban environs of Florida until recently. The Cuban brown anole, *A. sagrei*, was introduced to six Florida ports in the 1940s. Since then, it has become the most abundant lizard in peninsular Florida, has spread into Georgia and two other southeastern states, and has been blamed for the decline of *A. carolinensis*. Because *A. carolinensis* declines soon after the arrival of *A. sagrei*, it has been difficult to identify the mechanisms involved. I studied the effect of *A. sagrei* on *A. carolinensis* on dredge-spoil islands along the east coast of Florida. By introducing small numbers of *A. sagrei* to two very different islands, I contrasted their colonizing abilities, densities, and body conditions in two different habitat types. Stomach content analyses of the two species in sympatry indicated that they consume very similar proportions and taxa of arthropods, and that they consume each other's hatchlings in natural situations. In 1995, I introduced *A. sagrei* onto three islands occupied by *A. carolinensis*, and used three islands containing native *A. carolinensis* as controls. Over four summers, I monitored populations using capture-mark-recapture techniques, and collected body, microhabitat, and spatial data. Green anole densities and habitat parameters were similar over time on the controls. On the treatment islands, *A. sagrei* became dense in all habitat types, *A. carolinensis* declined as *A. sagrei* expanded, and survivors shifted their perch heights and utilized different habitats than they did prior to the introductions of *A. sagrei*. The decline was due to a lack of recruitment in subsequent years, suggesting that asymmetric intra-guild predation was involved in the rapid decline of green anoles. Sympatric green anole populations remained viable only in habitat patches containing dense understory vegetation, which may have provided more food and ameliorated the effects of hatchling predation. Green anoles might remain viable in urban or disturbed environs where *A. sagrei* attains very high densities, as long as sufficient understory vegetation is present to ensure successful recruitment of hatchling green anoles to adulthood.

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CHAPTER 1

Anolis lizards as model organisms for studying the outcome of interactions between native and exotic species

Yet, if we wield the sword of extermination as we advance,
we have no reason to repine the havoc committed.

-Charles Lyell, *Principles of Geology* (1932)

"They are of a most glorious green, and very tame.
They resort to the walls of houses in the summer season,
and stand gazing on a man, without any concern or fear."

-J. Lawson, *A New Voyage to Carolina* (1709)

BACKGROUND

The Threat of Biological Invasions

In his seminal book, C. S. Elton (1958) commented that "we must make no mistake; we are seeing one of the greatest convolutions of the world's flora and fauna." He was speaking of the human-mediated biological invasions which have dramatically altered human history (Crosby 1986) and global biodiversity (Vitousek et al. 1997). In fact, biological invasions are considered second only to habitat destruction in their effects on native biota and even entire landscapes (Wilson 1992). Habitat disturbance often makes system more invasible (Orians 1986, Hobbs 1989, Hobbs and Huenneke 1992), and in turn, invaders alter disturbance regimes in natural systems (Mack and D'Antonio 1998). This powerful synergism has led to substantial changes in whole ecosystems (Vitousek 1986), particularly in south Florida (Ewel 1986, Simberloff et al. 1997) and Hawaii (Moulton and Pimm 1986). Arms races between natives and invaders continue to balance in favor of invaders, to the extent that we may be facing a global homogenization of our planetary biota in the near future (McKinney and Lockwood 1999).

An "invader" is a species that easily crosses a barrier with or without the direct aid of humans, and establishes itself and expands its range on the other side (Ehrlich 1986). In fact, the most successful invaders are ones that are able to cross major barriers *because of* their relationship with man (Elton 1958). After arriving in new locations, invader populations often expand rapidly due to ecological release (Wilson 1961), and enter habitats beyond that of their native habitat (MacArthur and Wilson 1967) resulting from a lack of predators, a paucity of competitors, an overabundance of dietary or spatial resources, more favorable abiotic conditions, or a combination of these and other factors (Orians 1986, Shigesada and Kawasaki 1997). Organisms that are good natural colonizers also tend to be good invaders, but the genetic, morphological, physiological, behavioral, and ecological attributes that make particular species good colonizers are elusive (Ehrlich 1986, Pimm 1989, Williamson 1996). Caribbean lizards of the genus *Anolis* have long been considered good colonizers (Williams 1969, but see Spiller et al. 1998), and have been studied with regards to dispersal (Schoener and Schoener 1983, 1984), their ability to colonize new islands (Losos and Spiller 1999), and evolutionary diversification after colonization (Roughgarden 1995, Losos et al. 1997).

Although invasive species affect native species, natural patterns, and ecological processes through a variety of direct and indirect mechanisms occurring at genetic, individual, species, population, community, and ecosystem levels, the concept of environmental "impact" remains furtive with regards to invaders (Parker et al. 1999). Extremely prolific, obviously detrimental species such as the zebra mussel (*Dreissena polymorpha*) win by attrition, causing extinctions of native species and completely altering the systems which they invade (Riccardi et al. 1998). Exotic predators are often unequivocal in their effect, as in the brown tree snake (*Boiga irregularis*), which has nearly eliminated the avifauna of Guam (Rodda et al. 1999), and the brown trout (*Salmo trutta*), which has caused local extirpation and fragmentation of native fish populations (Townsend 1996). Plants often embody the concept of "habitat," so the effects of prolific exotic plant species are very often far-reaching. In Florida, whole ecosystems have been replaced by near monocultures of Brazilian pepper (*Schinus terebinthifolius*) and melaleuca (*Melaleuca quinquenervia*), which alter hydrology, microclimates, and fire regimes (Simberloff et al. 1997). Although the role of competition in the extirpation of native species can sometimes be important (e.g. Riccardi et al. 1998), it is most often minimal (Simberloff and Boecklen 1991), depending on the identity of the species involved. Invaders often compete with natives through subtle, more indirect pathways that are difficult to follow, but the effects of competition between invaders and surviving natives are often measurable, especially if background information is available on the native species or system (e.g. Moulton and Pimm 1983).

Of competition, Charles Darwin (1858) postulated that "the struggle will almost invariably be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers." In his work on Darwin's finches, Lack (1947) made an important argument for competition as a force in the evolution of animals. Even today, competition remains one of the most studied, but most elusive and controversial concepts in ecology (Connell 1983, Hairston 1989, Schoener 1983, Sih et al. 1985, Underwood 1986, 1997). Competition occurs when animals of the same or different species utilize common, limited resources (Tilman 1982), or if not limited, harm one another in seeking those resources (Birch 1957). In other words, competitors harm each other by controlling access to limited resources such as food or space (Keddy 1989). Harm can occur directly to individuals as a result of fighting for resources (interference competition), or indirectly via exploitation of limited resources (exploitative competition). Whatever the mechanism, the result is an alteration of one or more population parameters, such as a decline in birth rate or an increase in death rate (Tilman 1982), leading to a decline in fitness in one or both of the competitors (Schoener 1977), and ultimately leading to evolutionary consequences, especially if the interaction is asymmetric (Law et al. 1997).

The negative effects of competition may be minimized by coevolutionary forces such as resource partitioning (Schoener 1974, Toft 1985), competitive exclusion (Hardin 1960, Park 1948), and character displacement (Lack 1947, Brown and Wilson 1956), sometimes resulting in the evolution of different overall body sizes (Huxley 1942). By measuring differences in the feeding apparatus of sympatric and allopatric island birds and mammals, Hutchinson (1959) provided the first quantitative framework for assessing whether or not two species might partition their utilization of food resources, and thus, coexist. He stated that, to effectively minimize the effects of resource competition and coexist, the ratio of these features in sympatric species should be at least 1.28. This historical paper led to the theory of "limiting similarity" (MacArthur and Levins 1967), theoretical studies of species coexistence in ecological communities (Abrams 1983, 1998, Lawlor 1979), and the concepts of niche (Root 1967), niche width (Levins 1968), niche overlap (Colwell and Futuyma 1971, May and MacArthur 1972) and species packing (Roughgarden 1974).

The central paradigm of Hutchinson's historical study has been tested with a number of worldwide data sets and is generally accepted today (but see Simberloff and Boecklen 1981). On islands of the Lesser Antilles containing one species of *Anolis* lizard, sexual differences in body size exceed Hutchinsonian ratios in every case (Roughgarden 1995). This indicates that the two sexes diverged in body size to minimize intraspecific competition for food, but one must be careful in attributing cause and effect with this type of data, because sexual selection on male body size could also explain the pattern (Stamps 1983). On islands with two or more species, sexual dimorphism occurs to the same degree, but in every case, the species pairs differ from each other in body size by a ratio of over 1.28. Again, the fact that these species pairs co-occur, and exceed Hutchinsonian ratios, is suggestive of competition, but does not prove that competition-mediated evolutionary divergence was the cause of the pattern observed: the ratio simply indicates that species pairs with differences of more than 1.28 are able to coexist. In fact, a suitable combination of lizards, with respect to the size ratio, might have colonized the islands naturally, and successfully inserted themselves into the fauna at just the right time, rendering pattern and process difficult to distinguish (Losos 1994a).

Invasive species, if they are similar enough to native species in one or more of their niche parameters, may initiate competition-mediated evolutionary shifts in the behavior, morphology, or ecology of native species, ultimately leading to changes in community structure (Taper and Case 1992). The application of the above concepts to the study of community assembly (Case and Sidell 1983, Drake 1990) and resistance to invasion (Pimm 1989) were logical next-steps. In short, habitats containing natural, undisturbed communities of plants and animals and their various emergent properties are thought to be more resistant to invasion than are disturbed habitats. Thus, the sequence of arrival is important, and natural colonizers and invasive species must be able to fit into the physical landscape and biotic regime defined by natives in order to permanently insert themselves into a new biota. *Anolis* lizards are good colonizers and have been used as models for studying all of the above concepts (e.g. Roughgarden 1995).

To invoke competition as an explanation for present-day patterns, ecologists must often rely solely on inferential reasoning, as in the *Anolis* example above. However, such reasoning is haunted by the "ghost of competition past" (Connell 1980), in which the inability to demonstrate competition between two or more coexisting species is a result of past coevolutionary divergences that have eliminated or sufficiently reduced their level of competition. As a result, competition's ghosts can only be exorcized through rigorous experimentation. Unfortunately, competition is often invoked as an explanation in studies that do not warrant such conclusions, due to rampant pseudoreplication (Hurlburt 1984), statistical testing on improper sampling units, poor replication, or a combination of these and other fatal design flaws (Underwood 1986, 1997). Competition is elusive and expensive to study, so robust demonstrations of the mechanisms of competition and the factors that affect the outcome of species interactions are difficult to obtain (Gurevitch et al. 1992, Underwood 1997). Despite this, experimental evidence of competition has been compiled for many groups of organisms (Connell 1983, Gurevitch et al. 1992, Hairston 1989, Schoener 1983, Underwood 1986), and significant studies have been performed on lizards (e.g. Dunham 1980, Petren and Case 1996, Roughgarden 1995, Smith 1981).

Excellent opportunities exist for studying competition "ghost-free," by examining interactions between recent invaders and natives using experimental techniques. For example, manipulative studies have been performed on geckos using aircraft hangars in the south Pacific (Case et al. 1994, Petren and Case 1996, 1998, Petren et al. 1993). Moreover, if we have long-term background data on natural systems prior to invasion by exotics, they may be particularly good "natural experiments" for studying the mechanisms of competition. Invasions are, however, often caused, or at least exacerbated by, habitat alteration (Ewel 1986, Hobbs 1989), confounding the interpretation of cause and effect in studies of environmental impact. So, as much as it is crucial to understand the details of how invading organisms affect communities of native species *per se*, the proliferation of invaders and the magnitude of their impact on natives should more often be studied in the light of habitat alteration.

Habitat Alteration and Invasibility

As human population increases and development continues unfettered, loss of habitat and fragmentation of remaining habitat will continue to be the primary causes of the world-wide biodiversity crisis (Wilson 1992). Fragmentation results in a patchwork of native habitat "islands" embedded in a matrix of variously disturbed sites. Diamond (1975) applied the theory of island biogeography (MacArthur and Wilson 1967) to the concept of fragmentation, pitting the merits of a single large nature reserve against the pitfalls of several small nature reserves as two ends of a continuum, spawning the "SLOSS debate" (Simberloff and Abele 1976, 1982). Whereas large reserves are clearly more beneficial when a species require extensive core habitat, metapopulation theory predicts that for many species, several small reserves are no less viable than are large uninterrupted tracts of land (Hanski 1999). In fact, in many studies of fragmentation, habitat *subdivision* is confounded with habitat *loss*, the latter obviously having much greater influence on species diversity than the former (Fahrig 1997). So, while the biogeographical aspects of this problem have been debated energetically, the physical changes that occur in edge-rich remnant patches have been underappreciated (Saunders et al. 1991).

A decrease in habitat patch size brings an increase in the edge-to-interior ratio and increases the relative influence of edge-effects (Ranney et al. 1981), such as increases in the variability of abiotic factors (Murica 1995) and significantly increased vulnerability to biological invasions (Ewel 1986, Hobbs 1989). So, although intermediate levels of disturbance have long been thought to maximize species richness and benefit community stability (Connell 1978), with fragmentation, habitats often become so small as to be composed mainly (sometimes entirely) of edge, and doomed to harsher conditions and continued invasions (Hobbs and Huenneke 1992).

Just as habitat disturbance may open systems to invasions, in turn, invaders alter disturbance regimes, exacerbate the effects of fragmentation, and even dominate whole systems (Mack and D'Antonio 1998). Synergism between these processes often initiates a vicious cycle of invasion, habitat decline, more invasions, and so on. Exotic agricultural species are particularly devastating because humans manage whole landscapes for their optimal production. Habitat loss and fragmentation, proliferation of additional exotic species, and decline of native species often occur as a result of poor agricultural practices such as overgrazing (Hobbs and Huenneke 1992). Even native, managed species can become "pests" and devastate habitat when, despite their need for control, they are allowed to proliferate unchecked as would exotics, as white-tailed deer have been allowed to do in many areas because of public sentiment for animal rights (Anderson 1997). But unintentional invaders can be just as damaging when they occur in concert with habitat alteration and fragmentation. A noteworthy example is cheatgrass (*Bromus tectorum*) in the western United States, for which a positive feedback loop has been established where fragmentation occurs, cheatgrass invades and alters the fire regime, which exacerbates fragmentation, increasing cheatgrass dominance, and so on (Knick and Rotenberry 1997). In another study, the outcome of competition between native and exotic ants in California was influenced by proximity to an urban area, and thus, the degree of fragmentation (Suarez et al. 1998). Studies of these types of synergisms only arrived in the literature in about the last 10 years, but appear to be increasing in number.

There are many examples of the negative and positive effects of various levels of habitat alteration on the demographics, spatial structure, and community dynamics of native herpetofauna, and the success of exotic herpetofauna, especially lizards. In Puerto Rico, Turner and Gist (1970) demonstrated the influx of new lizard species into tropical rainforest areas where vegetation was disturbed by a low-level gamma radiation source. In the leaf-litter herpetofauna of a disturbed area in Costa Rica, Lieberman (1986) associated a decrease in species richness with fewer niches and greater variability of abiotic factors, and found that specialists were at a disadvantage, but he also found a large number of litter-dwelling species in a cacao plantation. In the Brazilian Amazon, Vitt et al. (1998) demonstrated that even the harvesting of individual trees in a tropical rainforest could effect the thermal regime and in turn, the lizard community. In the Dominican Republic, Lenart et al. (1997) found entirely different communities of *Anolis* lizards on sites subjected to different degrees of disturbance, and that the niche breadths of their stomach contents were directly correlated with the level of disturbance.

Herpetofaunal studies incorporating both habitat alteration *and* exotic species as agents of impact are rarer. Following the eradication of rabbits (*Oryctolagus cuniculus*) on Round Island, Mauritius, North et al. (1994) demonstrated significant increases in a number of lizard and snake species, which they attributed to the marked changes in vegetation structure. Likewise, Newman (1994) attributed the decline in McGregor's skink (*Cyclodina macgregori*) and the gecko, *Hemidactylus maculatus*, on Mana Island, New Zealand, to an increase in predation by the house mouse (*Mus musculus*), which was brought on by an increase in mouse populations caused by habitat changes resulting from the removal of cattle from the island. The lizards recovered after a mouse eradication program was implemented. Likewise, Ballinger and Watts (1995) demonstrated declines in native lizard populations after cattle were removed and vegetation increased in density on a prairie site in Nebraska, but attributed this solely to increases in vegetation density, which presumably rose above that observed in the past when bison were the agent of prairie disturbance. Finally, in yet another interesting manipulative experiment using aircraft hangars on Oahu, Hawaii, Petren and Case (1998) showed that the addition of habitat structure (aluminum baffles) reduced the intensity of interspecific resource competition between native and exotic geckos.

Lizards in general, and anoles in particular, are good colonizers (Williams 1969), and exotic anoles often ride the coat-tails of development, as did *Anolis sagrei* in Grand Cayman (A. C. Echternacht pers. comm.), *Anolis cristatellus* in the Dominican Republic (Fitch et al. 1989) and Florida (Salzburg 1984), *Anolis porcatus* in the Dominican Republic (Powell et al. 1990), three species on Bermuda (Losos 1996), and many other species (reviewed in Losos et al. 1993). Exotic anoles are valuable subjects for studying interspecific competition, community dynamics, and evolutionary processes (Losos 1994b), especially when more than one exotic anole species is present on a given site, as occurs in Florida (Butterfield et al. 1997). In addition, other exotics, such as the curly-tail lizard, *Leiocephalus carinatus*, are present in Florida, and may be negatively affecting native lizards and other species through predation, providing another possible level of analysis (J. Losos pers. comm.). But in areas highly disturbed by human habitation, such as south Florida, it is difficult to discern between habitat destruction and invasive species as causes of declines in native species because the effects are at least confounded and, more likely, synergistic (Hobbs and Huenneke 1992). Regions that are subjected to high levels of development and regular invasions, such as south Florida, provide great opportunities for studying synergisms between habitat alteration or fragmentation and the success and negative effects of exotic species.

The South Florida Problem

South Florida contains more introduced plants and animals than anywhere in the continental United States (Ewel 1986, Simberloff et al. 1997). Whole regions are now dominated by highly allelopathic invasive plants such as Australian pine (*Casuarina* sp.), Brazilian pepper, and melaleuca, which render habitat inhospitable for most native species, and the cycle continues. In fact, the complete take-over of a site by invasive plants is often as damaging as direct alteration by development since, not only has native habitat essentially disappeared, but the novel habitat represents a significant source of the invasive species in question. As a result, in Florida, biomass and food web relationships of whole ecosystems are built upon foundations of exotic species. One often finds non-native or feral predators consuming exotic prey species in habitats composed largely of exotic plants. This level of disruption occurs mainly on developed or otherwise highly disturbed sites (e.g. road corridors, canal banks, and residential sites), but many seemingly "natural" habitats are being invaded as a result of less obvious human influences (e.g. hydrological alterations which assist in the spread of exotics in the Everglades).

Along with an incessant battery of new plant and invertebrate invasions, south

Florida continues to be subjected to introductions of new species of reptiles and amphibians. As of the writing of Butterfield et al. (1997), the total was 36 species, including four amphibians, one turtle, 28 lizards (10 more than the native lizard fauna), two snakes, and even one crocodilian, and the number has increased since then (Meshaka et al. 1997). Many of these species are thought to be fairly innocuous, but some, including cane toads (*Bufo marinus*), Cuban tree frogs (*Osteopilus septentrionalis*), and curly-tail lizards, have long been known to have negative effects on native species (Wilson and Porras 1983). That the brown tree snake might become established is horrifying.

Nine species of Caribbean *Anolis* lizards have become established around the Miami area (Butterfield et al. 1997, Meshaka et al. 1997). That so many Caribbean island species have invaded the mainland seems contrary to the notion that mainland areas are resistant to invasion by island species, but is probably explained by increased invasibility of severely altered habitats throughout Florida. However, only the brown anole (*Anolis sagrei*) appears to be expanding its range (Godley et al. 1981, Campbell 1996, Campbell and Echternacht in prep.). Because our only native anole, the green anole, *Anolis carolinensis*, appears to be declining, the potential competitive interaction between these two has received considerable attention in popular literature but, despite regular pleas for studies since Collette (1961), the interaction has rarely been studied in detail, and became my impetus for pursuing this dissertation topic. To set the stage for defining the purpose and objectives of this research, a basic understanding of *Anolis* evolution, natural history, and ecology is warranted.

Background on Anolis Lizards

Anoles are small to medium-sized lizards in the family Polychrotidae (Frost and Etheridge 1989). Over 300 species of *Anolis* lizards are currently recognized (Frank and Ramus 1995), making this one of the most extensive vertebrate radiations on earth. This statement holds regardless of whether one presents the genus *Anolis* as monophyletic (Etheridge 1960) or as a polyphyletic assemblage of four genera (Guyer and Savage 1986). The group continues to be a source of turmoil for systematists (see Crother 1999 for a detailed coverage of the arguments), but studies of these lizards have resulted in some of the most detailed natural history treatises (e.g. Rand 1964), some of the finest manipulative experiments (e.g. Schoener and Spiller 1999), and some of the most intriguing (and controversial) evolutionary analyses of our time (e.g. Losos et al. 1997). Studies of these "model organisms" have contributed much to broader disciplines including community ecology and evolutionary biology. Their value is evident in the studies cited in Schwartz and Henderson (1991), the 400 studies cited in Roughgarden (1995), the prevalence of *Anolis* in Crother (1999), and contributions of *Anolis* researchers in ecological and evolutionary literature over the last 30 years (e.g. Roughgarden 1974, Schoener 1974, Losos 1994b, Spiller and Schoener 1994).

These mostly arboreal lizards are native to all the islands of the Caribbean (Schwartz and Henderson 1991) and are widespread in mainland South and Central America (Etheridge and DeQuiroz 1988), but only one species, *Anolis carolinensis*, is native to North America north of Mexico. Adult sizes range from 30 to over 200 mm snout-to-vent length (SVL), and the two sexes are often highly dimorphic in their morphology and behavior, whether due to resource partitioning, the nature of their mating system, or both (Stamps et al. 1997). Their mating systems are various iterations of male resource-defense polygyny without parental care (e.g. Jenssen et al. 2000). Females generally deposit a single egg in leaf litter about every week or two during their reproductive season, which is year-round in many tropical locations, or if seasonal, is often triggered by temperature or precipitation (Fitch 1982). Adults of both sexes vigorously defend three-dimensional territories against conspecific intruders (Evans 1938), and two or more female territories are generally nested in the territory of one male (Stamps 1983). Anole diets consist mainly of small arthropods, annelids, and molluscs (Schoener 1968, Schoener and Gorman 1968), but they also cannibalize their young and prey on hatchlings of other anoles and other small vertebrates (Gerber and Echternacht, in press).

Anoles are found in all types of habitats, xerophilic scrub to tropical rainforest. Early on, it was recognized that Caribbean anoles in complex habitats segregated themselves vertically (Oliver 1948) and by temperature (Ruibal 1961). The relationship between ecology and morphology was first mentioned by Collette (1961), refined by Rand (1964), and later attributed to the outcome of competitive interactions which led to the evolution of distinct ecologically-influenced morphologies, or "ecomorphs" (Williams 1969, 1972, 1983). That recurring combinations of ecomorphs occur in unrelated species on each large island of the Greater Antilles is a classic example of convergent evolution (Losos 1992, Losos et al. 1998, Beuttell and Losos 1999). The large numbers and wide ranges of ecomorphs present in local areas (e.g. 11 species at a single site in Cuba; J. Losos, pers. comm.) give testament to the influence of competitive interactions on habitat partitioning of sympatric species, and the ultimate organization of lizard communities (Losos 1992). Because *Anolis* lizards are good dispersers (Schoener 1983) and colonizers (Williams 1969), opportunities for new relationships have been numerous. One particular North American invasion has captured the attention of many.

Background on the Green Anole - Brown Anole Interaction

The green anole, *Anolis carolinensis* Voigt 1832, is found throughout the southeastern United States and is the sole *Anolis* lizard native to North America north of Mexico (Conant and Collins 1991). It is but one of 12 "alpha anoles" (Etheridge 1960) in the "*carolinensis* complex," a group of medium sized, slender, greenish trunk-crown anoles (Williams 1969). Some consider the complex to be a single species throughout the Caribbean (e.g. publications by T. Schoener, D. Spiller, and J. Losos). Others recognize different green anole species on different Caribbean islands (e.g. Schwartz and Henderson 1991), including the green anole on Cuba, *A. porcatus*, considered the progenitor of the entire *carolinensis* group (Williams 1969, Buth et al. 1980, Crother 1999), and two Bahamian green anoles, *A. smaragdinus* and *A. brunneus* (Schwartz and Henderson 1991). Taxonomy aside, a moderately sized, greenish alpha anole representing the trunk-crown ecomorph occurs on all the large Caribbean islands but Jamaica (Williams 1972, Beuttell and Losos 1999).

After colonizing North America some time during the Pleistocene, well over 20,000 years ago (Holman 1995), the ancestors of *A. carolinensis* probably experienced ecological release due to an absence of their Caribbean competitors (Williams 1969, Echternacht and Harris 1993), a phenomenon well known in their Caribbean relatives (Lister 1976b, Losos and de Quiroz 1997). Collette (1961) indicated that the green anole "...occupies both terrestrial or arboreal habitats though perhaps prefers the latter." With no sympatric trunk-ground congeners, it eventually utilized the entire vertical range of forested habitat, and was able to succeed in non-forested and highly disturbed urban environs (Echternacht and Harris 1993). Duellman and Schwartz (1958) considered green anoles abundant throughout the Florida Keys and southern Florida in the 1950's, but sporadic in the Everglades. They characterized optimum habitat for green anoles as "mesophytic hammock," but mentioned that they were also abundant in gardens and in shrubs around houses. Green anoles have long been associated with landscaping, screened porches, and pool sides of backyard Florida. Thus, despite rapid residential and urban development of peninsular Florida, green anoles remained abundant even in the most disturbed areas. That is, until recently.

The brown anole, *Anolis sagrei* Dumeril and Bibron 1837, is native to Cuba, the Bahamas, and their satellites (Schwartz and Henderson 1991), where it is considered a classic trunk-ground species (Williams 1969, 1972, 1983). This medium-sized "beta anole" (Etheridge 1960), arguably *Norops sagrei* (Guyer and Savage 1986), was first recorded in North America in the Florida Keys by Garman (1887), but was not documented from the mainland until over 50 years later, possibly because it did not become firmly established until after 1940 (Lee 1985). Since then, it has spread throughout Florida and into three additional southeastern states (Godley et al. 1981, Campbell 1996, Campbell and Echternacht in prep.).

The basic natural history of both species is fairly well known in the Caribbean (e.g. Rand 1964, Schwartz and Henderson 1991, Schoener 1968, 1969b, Williams 1969), and the green anole has been studied extensively in the United States (e.g. Jenssen et al. 2000 and references therein). Other than three very detailed morphometric analyses (Lee 1985, 1987, 1992) a study of reproductive cycle (Lee et al. 1989), and a number of studies of mating behavior (e.g. Tokarz 1998), the basic natural history of the brown anole in North America has gone largely undocumented (W. Meshaka, pers. comm.). To formulate questions about competition, a comparative analysis of published information on the life histories, reproductive biologies, and habitat affinities of these species is warranted.

Adults of both species breed during the summer months, becoming sexually active and establishing territories in March or April, and defending territories through August or September (Gordon 1956, Jenssen et al. 1995, Lee et al. 1989). Females are reproductively active for a slightly longer period than males, possibly because they store sperm (Tokarz 1998, T. Jenssen, pers. comm.). Females of both species lay eggs singly on an approximately weekly basis for the entire summer by alternating the use of their left and right ovaries (Gordon 1956), but brown anoles exhibited shorter oviposition intervals during a cage-study employing Florida animals in Tennessee (Vincent 1999).

Egg incubation is approximately 29 days for green anoles (A. C. Echternacht, pers. comm.), but varies depending on substrate temperature and moisture, and presumably, habitat type. In Florida, green anole hatchlings start life at 19 to 22 mm SVL (King 1966), and newly emerged brown anole hatchlings range from about 15 to 18 mm SVL (Duellman and Schwartz 1958). Hatchlings of both species are first seen in early June in central Florida (about 29^0 north latitude). Although brown anole hatchlings are usually seen first, this is probably because they are more numerous and conspicuous than are green anole hatchlings. Hatchlings of both species grow very fast, reaching adult size prior to their second summer of life (their first reproductive summer), and mortality appears to be highest in the winter thereafter (Lee et al. 1989, Gordon 1956). Each cohort undergoes a nearly complete replacement in the following year, so both species probably have a maximum average life span of less than 18 months in Florida (Oliver 1955, Gordon 1956, King 1966, Lee et al. 1989).

Green anoles occupy home ranges within one or a few large bushes or small trees, where they slowly creep along branches looking for food and defending a territory extending from the ground to high in vegetation, encompassing about 80 m^3 in Louisiana (Gordon 1956) and between 69 m^3 (Jenssen and Nunez 1998) and 173 m^3 (Jenssen et al. 1995) in South Carolina. However, their Caribbean counterparts perch higher in vegetation when brown anoles or other trunk-ground anoles are present (Schoener 1968, 1975) and are thus considered classic trunk-crown anoles (Williams 1969, 1972, 1983).

Evans (1938) studied the territorial behavior of brown anoles in an arboretum at Soledad, Cuba, and reported the territory size of this species to be 37.2 m^2, the ground surface occupied by a large bush or hedge. This habitat generalist generally prefers fairly open vegetation of disturbed sites, where it adopts a head-down, sit-and-wait posture, and perches low on large trunks or fence-posts (Schoener 1968, 1975, Lister 1976a, 1976b, Moremond 1979a, 1979b): a classic trunk-ground anole (Williams 1969, 1972, 1983).

Early Caribbean naturalists often remarked that the brown anole was either very abundant, or was the most abundant lizard that they had ever seen (Barbour 1904 for the Bahamas and Oliver 1948 for Bimini). Grant (1940) remarked that on Little Cayman, it "fairly swarms and interferes with *A. maynardi* by eating its food". Ruibal (1964) stated it was "extremely abundant" throughout most of Cuba, and mentioned that it was the most successful species in edificarian habitats it occupied with *A. porcatus* and *A. allisoni*. King and Krakauer (1966) stated that it was "...one of the most successful reptiles in south Florida," and Wilson and Porras (1983) reiterated that it occurred "almost everywhere." While living in the Orlando area between 1989 and 1993, I found brown anoles to be the most abundant terrestrial vertebrate that I had ever observed, in Florida or elsewhere.

Actual densities reported for *A. sagrei* vary widely, but are generally high compared to most terrestrial vertebrates. Oliver (1948) marked 17 brown anoles in a 112 m^2 area on Bimini, and had an 82 percent recapture rate, giving a population estimate of around 20 lizards, which translates to about 1,700 individuals per hectare (0.17 per m^2). Lister (1976a) reported over 2000 per hectare on Cuba. At 9,700 lizards per hectare, Schoener and Schoener (1980) reported their densities on Bahamian islands as "...the highest densities of any *Anolis* species, and possibly the highest recorded for any lizard species." I documented densities of up to 12,000 lizards per hectare on a small island on the coast of Florida (Chapter 2). However, brown anoles are overshadowed in density by at least a *Sphaerodactyllus* species (Gekkonidae) in the Caribbean (G. Rodda, pers. comm.), and a *Hemidactylus* species (Gekkonidae) in the south Pacific (E. Campbell, pers. comm.), both of which reach densities of over 50,000 lizards per hectare.

In Florida, brown anoles do not seem to reach high densities in the interiors of uninterrupted, "native" forested habitats, but do become abundant along their edges (personal obs.). As a result, green anoles and brown anoles often co-occur in these habitats. However, in altered habitats, the former is usually displaced or even replaced by the latter within a few years of its arrival. The replacement process is generally well underway or complete by the time biologists document brown anoles on a given site (Echternacht and Harris 1993), so many questions remain unanswered.

As the invasion of brown anoles proceeded, naturalists noted the reestablishment of the vertical distribution of these two species observed in the Caribbean. Oliver (1950) was actually the first to note that green anoles, which were abundant at that time throughout the Tampa area, tended to perch higher in vegetation than did brown anoles when the two occurred together. Although green anoles were found in close association with brown anoles in Key West, the former tended to perch in trees and shrubs while the latter perched mainly on the ground (Bell 1953). The effect of the vertical shift might seem trivial, since the two species evolved together in the Caribbean, and should be able to coexist in North America on some level (Echternacht and Harris 1993). In fact, the apparent decline of green anoles in Florida might simply be due to an upward shift when in the presence of brown anoles, rendering them less visible to humans not searching for them specifically. However, the brown anole is a new element in the North American biota, and laws of thermodynamics and food web theories predict that the insertion of a new faunal element requires *some* shift or accommodation, if only slight, in one or more trophic components, especially in disturbed habitats. Whether this is indeed occurring is unknown, as research on this potential problem has not yet been conducted. Instead, anecdotes about the North American interaction predominate, some having been perpetuated for many years.

The first written statements suggesting that the brown anole might negatively affect the native green anole in Florida via interference competition were made by Collette (1961), who suggested that "..the more aggressive, terrestrial *sagrei* should tend to drive the more generalized *carolinensis* out of the terrestrial part of its habitat." He also recognized that the physical organization and biological complexity of a site had important ramifications to this interaction, and showed that, on Cuba, *A. porcatus* and *A. sagrei* adjusted their perch height relationships based on the amount of vegetation present. King and Krakauer (1966) offered a vague statement that "native *Bufo* and *Anolis* are being adversely affected by competition with *Bufo marinus* and the introduced anoles," and called for a halt to the introductions before a population explosion occurred. King (1966) studied the effects of *A. distichus* on *A. carolinensis* in south Florida, and determined that they were competing, but his methods were barely mentioned, his data (when reported), appear to have been improperly analyzed, and his claims about competition were spurious at best.

In what was probably the most important *Anolis* paper ever written, Williams (1969) stated that the limitation of *A. sagrei* to coastal areas in Mexico and British Honduras (= Belize) coincided with the total exclusion of *A. carolinensis*, and attributed this to ecological release by the brown anole, resulting in it utilizing a broader niche than it would normally have occupied. Corn (1971) compared the thermal preferenda of these two species (and *A. distichus*), and briefly mentioned that *A. sagrei* "replaces *carolinensis* as it spreads." Brach (1977) indicated that *A. cristatellus*, an exotic anole which is very similar in size and habitat use to *A. sagrei*, might displace *A. sagrei*, and that *A. carolinensis* might be displaced by introduced exotics, especially *A. sagrei*. After observing the gray-throated morph of *A. carolinensis* at a number of sites in southwestern Florida, Christman (1980) noticed that green anoles became rare or were absent at these sites within a few years of the arrival of *A. sagrei*. Crews (1980) stated that green anoles were being excluded from coastal areas of south Florida, and attributed this to a lack of "preferred habitat of green anoles" (citing Schoener 1974), and competitive exclusion by brown anoles. He discussed their ecomorphs, perch height distributions, foraging habits, and the fact that brown anoles fare better in dry, open, disturbed areas. However, he avoided implicating population-level phenomena in favor of a detailed but unsupported claim that brown anoles were highly aggressive towards green anoles.

Hammer (1984) observed a male green anole breeding with a female brown anole, but despite never having observed signs of hybridization, postulated that hybridization might further threaten green anoles in Florida. In fact, only one further instance of interspecific mating has been documented (S. Porter, pers. comm.), no hybrids have ever been found (A. C. Echternacht, pers. comm.) and hybridization between two species seems highly unlikely, given that their lineages differ widely (Etheridge 1960), possibly at the generic level (Guyer and Savage 1986).

In keeping with the anecdotal trend, Hammer (1984) also injected a confident, yet totally unsupported statement that brown anoles had displaced green anoles through "heavy competition for food and habitat." The Florida interaction was even utilized as the main example of competition-mediated niche shift (fundamental vs. realized niche) in a biology textbook (Solomon et al. 1993): a good example, given Schoener (1975), but of course, no citations were provided, as no research had been done on the problem in Florida. Probably the most daring leap onto the anecdotal bandwagon was made in a picture-book by Carmichael and Williams (1991, but *not* E. E. Williams), where abundant brown anoles were postulated to present domestic cats with many learning opportunities for lizard-catching, thereby "turning their predatory attention to greens that had previously eluded cats because of their effective camouflage." Although ridiculous, this statement embodies the concept of "apparent competition" (Holt 1977), where the addition of a superior competitor also causes an increase in a common predator, thereby increasing predation on the inferior competitor, making it *appear* as though the former is the direct cause of the latter's decline. At best, high densities of brown anoles might be the cause of a perceived (but undocumented) recent increase in black racers (*Coluber constrictor*) and other semi-arboreal snakes in some urban areas (pers. obs. and T. Ferrell, pers. comm.).

Salzburg (1984) concluded that slight shifts in the spatial distribution of *A. sagrei* after removal of *A. cristatellus* at a study site in Miami were strong evidence of competition between the two, despite a lack of replication and improper analyses of repeated measurements. Lee (1985, 1987) studied morphometrics on numerous Florida *A. sagrei* populations, but Tokarz and Beck (1987) were the first to study the green anole - brown anole interaction in Florida. They approached the problem from the standpoint of interference competition, and concluded that intraspecific male-male aggression overshadowed interspecific aggressive interactions. However, their study was performed on lizards housed separately in small aquaria (0.04 - 0.10 m^3), and the green anoles were obtained from a commercial supplier in Louisiana. Brown (1988) confirmed the results of Tokarz and Beck (1987) in another cage-study using wild-captured lizards from the area of sympatry, and Gerber (in prep.) confirmed them in the field in Florida, using tethered individuals placed in the territories of conspecifics and heterospecifics. Brown and Echternacht (1991) demonstrated that interspecific behavioral interactions occurred in free-ranging individuals in Florida. They found green anoles to be the aggressors in male-male encounters, and suggest that such aggression has not been the cause of green anoles declines (Echternacht 1999). Conclusions from all these studies are at odds with the perch height shift observed in green anoles. That the shift occurs is not doubted, but the mechanism remains a mystery.

In a review of the effects of introduced species on native reptiles, Case and Bolger (1991) called for a detailed, manipulative, island-based study of the interaction. Gerber (unpublished manuscript) suggested hatchling competition and predation of hatchlings by adults might be important, demonstrated that these two competitors also consumed each other's hatchlings (Gerber and Echternacht, in press), termed "intraguild predation" (Polis et al. 1998), and showed that vegetation density affected the outcome of the interaction (G. Gerber, pers. comm.). Predation of green anole hatchlings by brown anole adults was confirmed in the field by stomach content analyses and behavioral observations (Campbell and Gerber 1996). Green anole recruitment to adulthood may also be lower in the presence of brown anoles in Florida (T. Vincent, pers. comm.). In a study using Florida lizards transported to large outdoor enclosures in Tennessee, Vincent (1999) demonstrated that brown anoles outproduce green anoles in terms of eggs, but the applicability of these results to field situations in Florida remains to be seen. Porter and Campbell (in prep.) performed a field study on spoil islands that addressed the effects of food availability on the interaction, but those results are pending. To my knowledge, the above-mentioned studies are the only attempts to study the interaction in North America.

Some detailed natural history studies and interesting colonization experiments have been conducted using the Bahamian populations of these two species (Schoener 1968, 1975, Spiller and Schoener 1998, Losos et al. 1997, Losos and Spiller 1999, and references therein). If, as Schoener and his associates hold, all the Caribbean green anoles are truly *A. carolinensis*, then a large amount of literature applicable to the Florida interaction has been amassed. However, if one considers green anoles in the Bahamas to be *A. smaragdinus* and *A. brunneus* (e.g. Schwartz and Henderson 1991, Crother 1999), then the results of the studies by Schoener's group are, at best, applicable only to a green anole *analog* in different habitats than are available in North America. In fact, even if the Bahamian population is viewed as conspecific with *A. carolinensis*, North American populations have been separated from them and all other *Anolis* species by thousands of years, and have been finely tuned to North American habitats, predators and competitors (or lack thereof) for thousands of generations. Furthermore, the Cuban subspecies of the brown anole (*A. s. sagrei*), rather than the Bahamian subspecies (*A. s. ordinatus*) appears to be the one taking over Florida (Campbell and Echternacht, in prep.). Lastly, island populations are thought to be prey-limited, while mainland populations are thought to be predator-limited (Andrews 1979). Despite these issues, the results of the Bahamian studies contribute to the study of the North American situation in at least a heuristic sense, and should be utilized to generate questions and guide further research.

Could these two species really compete for resources in North America? A logical consideration of the main factors required to invoke competition between two animal species, suggested by Schoener (1975) and Jenssen et al. (1984) indicate they might (Figure 1.1: all figures are in the Appendix). First and foremost, the daily activity periods of these diurnal species are highly overlapping: both exhibit a morning activity period, followed by retreat to shade in mid-afternoon, followed by a second activity period lasting nearly to sun-down. Second, they overlap extensively in their climatic niche in Cuba (Rand 1964) and the Bahamas (Schoener 1975), and basking individuals in Florida overlap considerably in their thermal preferences (Gerber, pers. comm., Campbell, unpubl. manuscript). Third, these habitat generalists overlap considerably in their structural niches: although green anoles prefer forested edge and brown anoles prefer more open, disturbed habitats, both are abundant in edge-rich habitats. The distinction lies in core habitats of uninterrupted, native forests, where brown anoles are much less abundant than they are in urban areas. At the microhabitat level, and in allopatry, the preferred vertical distributions of the two species overlap considerably because of the downward shift exhibited by green anoles due to ecological release (Echternacht and Harris 1993).

Morphology is also an important consideration in determining whether or not competition might be occurring (Figure 1.1). Body size is of major import in aggressive interactions, although apparently not an important factor in the interaction between *A. carolinensis* and *A. sagrei*. However, the size of the feeding apparatus, best defined as head size and shape parameters such as length, width and depth (Schoener 1968, Pianka 1986), may be important in assessing resource competition. Anoles often exhibit intersexual differences that exceed Hutchinsonian ratios (Stamps 1983, Roughgarden 1995). However, these two species are very similar in body and head size when compared within the sexes, but shift their body sizes when sympatric (Schoener 1969b). In fact, they exhibit more disparate body size and head shape parameters across sex within species than across species within the same sex (Chapter 3). So, sexual differences of adults are consistently greater than are species differences, as measured by Hutchinsonian ratios.

Another important test that must be met for competition to be plausible is an overlap in limited dietary resources by size and type (Figure 1.1). Studies of sympatric, Bahamian analogs of these species indicate that they consume very similar types and sizes of arthropod prey (Schoener and Gorman 1968). However, results from oceanic islands might not be applicable to mainland North America, where arthropods may not be limiting for anoles (Andrews 1979, but see Guyer 1988). On the other hand, habitat destruction and fragmentation has rendered Florida a patchwork of disturbed, invaded habitats among a matrix of human habitation, and it is highly likely that arthropod prey diversity has been depressed significantly in these situations.

Sharing of parasites can also lead to a different type of competition between invaders and natives, termed “parasite-mediated competition” (Schall 1992). This phenomenon has been demonstrated in other anoles (Schall and Staats 1997, Schall and Vogt 1993), and brown anoles in Florida species have been shown to share blood parasites (*Plasmodium*) with green anoles (Wozniak et al. 1996).

Predation is a powerful form of interaction, especially when it occurs among competitors. When competitors also eat each other (Polis et al. 1989), the superior competitor benefits from successfully garnering limited resources needed by the inferior competitor, but also consumes the inferior competitor, gaining energy from it, and removing it from the competitive interaction as well. That these species consume each other's hatchlings (Campbell and Gerber 1996, Campbell in prep.) led Gerber and Echternacht (in press) to believe that IGP might be important in this interaction.

In summary, past research indicates that these species might be competing for dietary and/or spatial resources, sharing parasites, and eating each other, but they are probably not engaged in aggressive interference to any great extent. Regardless of whether or not they compete, these two species (or their analogs) evolved together in Cuba and the Bahamas, and there is good reason to expect they can coexist in North America. In fact, there are many sites where both have been present for many years. Since brown anoles prefer open, disturbed habitats, and green anoles are forest and forest-edge dwellers, the negative aspects of the interaction may only be realized in urban settings, disturbed habitats, or along edges of native habitat, and relatively unimportant in contiguous, forest core habitats where green anoles are less abundant and have plenty of room to shift upward. However, as habitats of the southeast become fragmented by development and infiltrated by exotic vegetation, the brown anole could become the dominant anole, or lizard, or even vertebrate species present in the Florida landscape. It has already achieved this distinction at many locations.

PROJECT RATIONALE AND OBJECTIVES

Human-mediated biological invasions are inevitable and require continued study because of their threat to native species, biotic communities, and even whole ecosystems. Habitat alteration and biological invaders should be considered as potentially synergistic phenomena or, at least, considered as potentially confounding factors in field experiments employing native and exotic species. Florida is being rapidly developed and is particularly vulnerable to invasions by nearly any taxa (Simberloff et al. 1997), including reptiles in general and *Anolis* lizards in particular (Butterfield et al. 1997).

That the green anole is declining in Florida is rarely argued, but based purely on anecdotal evidence. This is at odds with the fact that green anoles have been abundant in disturbed, urban, and otherwise edge-rich, fragmented habitats throughout the southeast for many years. So, although this species is probably not threatened with extinction *per se*, they may be experiencing local extirpation because of habitat destruction, interactions with brown anoles, or a synergism between these factors. Results from the Caribbean studies may provide essential background for describing the North American interaction. However, research must be conducted in Florida in order to make statements about the effects of brown anoles on native populations of green anoles in the habitats where they evolved. That is the purpose of the research in this dissertation: to provide answers specific to the interaction between these two species in Florida.

Biological invasions provide unique opportunities for empirically testing the assumptions of many ecological theories (Williamson 1996). However, invaders usually become established and confer negative effects on native species before anyone has had the opportunity to study the dynamics of the invasion process, or the temporal development of negative interactions. At that point, only removal studies can provide empirical answers (e.g. Leal et al. 1998). By definition, removal studies are performed from the exact opposite viewpoint of that which occurs in invasions, by measuring the "recovery" of already negatively affected populations of natives. The magnitude of their recovery is then used as a surrogate to estimate the negative effect of the invader. This is a valid approach, and is clearly the only option in most cases. However, the surviving native populations probably contain a preponderance of individuals that have successfully adapted to their new situation, thereby representing "ghosts of invasions past." In a removal experiment, recovery of the native might occur *because* the native population is actually more resilient than were their unencumbered ancestors and, in turn, making the magnitude of the original impact seem much larger than was really the case. I circumvented this potential problem by performing experimental introductions of whole populations of invaders onto islands occupied by natives. Thus, I was able to approach questions about this interaction from a more "natural" viewpoint. Moreover, a detailed study on large populations of both species in the field seemed necessary to address the notion that plant architecture might influence the vulnerability of hatchlings to adult anoles. So, with the above facts in mind, I set out to empirically address five questions regarding the interaction between brown anoles and green anoles in Florida:

1. Are brown anole populations capable of negatively affecting whole populations of green anoles in Florida?

2. If brown anoles do have a negative effect, how quickly and to what extent are green anole populations affected?
3. Given a negative effect, what are some of the mechanisms operating in this interaction (e.g. predation, competition, or intraguild predation)?
4. Could habitat type, size, or configuration influence one or more of these mechanisms, thereby affecting the outcome of the interaction?
5. Which habitat features enables green anole populations to remain viable in the face of inevitable invasions by brown anoles?

In the dissertation that follows, I address these questions in three chapters. In the un-replicated pilot study in Chapter 2, I use two dredge-spoil islands with very different habitats (forested and non-forested) to show that as few as 18 donors can give rise to large populations of brown anoles within two years, and demonstrate intraspecific density-dependent effects on body size and condition as brown anoles fill the islands. In the gut-content analyses in Chapter 3, I describe diet niche breadth and overlap between green anoles and brown anoles collected from sympatric populations on three dredge-spoil islands. In the experiment in Chapter 4, I invade dredge-spoil islands with populations of brown anoles, demonstrate the numerical and spatial extent of the green anole decline, suggest some of the potential mechanisms operating in the interaction, and illustrate the potential effect of habitat type and vegetation architecture on the outcome of the interaction. But most importantly, I make recommendations regarding the environmental conditions that must be present for green anoles to persist on a given site in the face of an inevitable takeover by its brown congener.

CHAPTER 2

Rapid population expansion and body size changes of brown anoles, *Anolis sagrei* (Sauria: Polychrotidae) introduced to two small islands in Florida

INTRODUCTION

The brown anole, *Anolis sagrei* (Sauria: Polychrotidae), a native of Cuba and the Bahamas, was present in the Florida Keys as early as the late 1800s and was introduced in at least six separate ports in Florida in the 1940s (Lee 1985). It has spread throughout Florida and into Georgia, Louisiana, and Texas since that time (Campbell 1996, Echternacht and Harris 1993). Although many scientists have documented isolated instances of range expansion and establishment of populations via jump-dispersal (see Campbell and Echternacht in prep., for an exhaustive review), no studies have modeled the capabilities for range expansion for this species, determined its potential geographical limits in North America, nor collected baseline information that could be used in such analyses. This study reports baseline information on the capability of this species to expand numerically and geographically over very short periods of time.

Of all the *Anolis* lizards found in the Caribbean, the brown anole is among the best at colonizing new islands (Williams 1969, Lee et al. 1989, Losos et al. 1993). The natural history (Rand 1964, Schoener 1968), habitat affinities (Lister 1976a, Schoener 1975), reproduction (Lee et al. 1989, Tokarz 1998), and growth and demographics (Schoener and Schoener 1978) of this species are well-documented, but the underlying reasons for its extraordinary colonizing abilities are only just beginning to be fully understood. Since female brown anoles are also thought to store sperm (Tokarz 1998), a single female may be able to establish an entire population. Once established, *Anolis sagrei* is rather prolific: in Florida, females lay a single egg about every six days (Tokarz 1998) between mid-March and mid-September (Lee et al. 1989). *Anolis sagrei* defends fairly small areas (Evans 1938), so becomes quite dense. Densities reported for this species vary, but most estimates for Bahamian islands fall around $1/m^2$ (Schoener 1968, 1975), which is high for any terrestrial vertebrate. No accurate estimates have been generated from mark-recapture studies in North America.

Morphological, demographic, and habitat data has been collected for this species in the Caribbean (Lister 1976a, Schoener 1975, Schoener and Schoener 1978) and the Miami area (Lee 1985, 1987, Lee et al. 1989), but a comprehensive life history still needs to be generated for Florida populations (W. Meshaka, pers. comm.), especially north of the Miami area. Such information is needed for modeling the numerical and geographical expansion of this species in North America. Also, a number of experimental manipulations of whole populations of brown anoles on Bahamian islands have documented colonization ability, survival on small islands, and survival during hurricanes (Losos et al. 1993, Losos et al. 1997, Losos and Spiller 1999, Spiller et al. 1998). Although these studies gathered valuable information about the colonizing ability of this species, the results may or may not apply directly to the North American mainland situation, where different vegetation, different prey taxa, different guilds of predators and competitors, and different abiotic factors may be operating.

In early 1994, I initiated a study of the potential effects of expanding brown anole populations on native green anole populations. The focus of this paper is on the pilot study I conducted to merely determine whether or not small numbers of brown anoles could successfully colonize small dredge-spoil islands, and if so, to document the rate of population increase and densities attained. The four main objectives of this study were: **1)** to determine the colonization success of small numbers of adult brown anoles placed on two dredge spoil islands, **2)** to measure the numerical and spatial expansion of this species on two islands which support very different habitats (forested and non-forested), and **3)** to determine whether or not brown anoles could reach island carrying capacity on either island within a few years.

This study was designed to contrast the population expansion abilities and demographics of brown anoles on two completely different islands: one containing "high quality" green anole habitat (forest), and one containing "low quality" green anole habitat (low shrubs). The islands were not replicated, so this study was not an experiment *per se*, but the results helped me design experiments to test the effect of habitat type on the outcome of the interaction between these two species (Chapter 4). This pilot study was necessary to obtain preliminary data on brown anole populations prior to May 1995, when the experiment in Chapter 4 of this dissertation was slated to begin.

STUDY AREA

Early in 1994, I obtained permits to release a small number of brown anoles on two U. S. Army Corps of Engineers (ACOE) dredge spoil islands in Mosquito Lagoon, Brevard and Volusia Counties, Florida (Figure 2.1; all figures are in the Appendix), hereafter designated Island P1 and Island P2. Approval to release brown anoles was given because brown anoles were abundant in the area around Mosquito Lagoon and on many of the spoil islands in the lagoon (Campbell 1996), were known to be regularly transported to the spoil islands by recreational boaters and island campers, were already abundant on nearly every ACOE spoil island south of the Haulover Canal (Figure 2.1; R. Ashton, pers. comm.) and were expected to reach the remaining spoil islands of Mosquito Lagoon within a few years.

The two islands were picked for their small size and because they represented two ends of a continuum of habitat types (forested versus non-forested). Moreover, Island P1 (non-forested) was thought to be sub-optimal for green anoles and Island P2 (forested) was thought to be ideal for green anoles, a distinction of importance to the design of the experiments on which this pilot study would be based. Green anoles also occur on most of the ACOE spoil islands along the coast of Florida, including those in Mosquito Lagoon.

Island P1 (Figure 2.2) is about 0.048 ha in area above mean high water, and contains a vegetated area of about 0.020 ha, including six cabbage palms (*Sabal palmetto*) between 4 m and 6 m in height, a small patch of low, shrubby vegetation (2 - 3 m in height) dominated by Brazilian pepper (*Schinus teribinthifolius*), wild olive (*Vaccinium* sp.), marsh elder (*Iva* sp.), a narrow band of sea ox-eye daisy (*Borrhichia frutescens*), and sea blights (*Batis* sp.) along the southwestern cove. Soil is absent outside of the dense shrub areas, but cabbage palm fronds litter the island. The east shoreline is eroded to the point that the palms are leaning toward the water, but the southwestern cove is a low-energy shoreline and generally contains a thick mat of beach wrack.

Island P2 (Figure 2.3) is about 0.150 ha in area above mean high water, and consists of a distinct 0.030 ha eastern forested area bordered on the north, west, and south by a 0.120 ha high salt marsh zone that is drawn out into two “tails” to the west. The donut-shaped forest supports 69 cabbage palms ranging in size from 4 m to 7 m in height, two small wild olive bushes (*Vaccinium* sp.) and a large Brazilian pepper bush on the southern edge. The soil in the forested area is very well developed, and dead cabbage palm fronds form a spatially complex litter layer that is often over 30 cm deep. A centrally located depression collects fresh water after large rain events, but the water persists for only a few days (it is dry in Figure 2.3). The edge of the forest is nearly vertical and forms an abrupt edge between it and the marsh zone, but salt bush (*Baccharis* sp.) and *Iva imbricata* (2 - 3 m high) form a nearly impenetrable area immediately south of the forest. The high-marsh is dominated by *Borrichia* between 0.5 and 1.5 m in height, and borders on narrow beaches on the north and south edges and a cove to the west which consists of *Batis* marsh and mud-flat habitat which is regularly inundated and unsuitable for anoles.

METHODS

On June 5 and 6, 1994, a total of 37 adult brown anoles (24 females and 12 males, plus an extra female to account for potential mortality) were captured from large rocks on the shoreline of Lake Okeechobee at Pahokee Recreation Area, Palm Beach County, Florida, and held individually in waxed paper cups. On June 10, 1994, 12 females and six males were picked randomly from the cups, marked with exclusive numbers by toe-clipping, measured and weighed (see below), and released on each island. The 2:1 female-to-male ratio was chosen because brown anole males are known to defend territories that include the territories of at least two reproductive females (Evans 1938). The extra female was placed on island P2. Ten of the females placed on island P1, and all of those placed on island P2, were gravid. I returned to the islands in August 1994 to briefly search for surviving donors and any hatchlings they may have produced.

I monitored the donor's progeny with basic capture-mark-recapture (CMR) techniques during the summers of 1995 through 1997. I established regular search routes and made slow methodical searches around each island during daylight hours (between about 0700 and 2000). Each capture session, or "CMR session" consisted of making one full trip around an island while capturing, marking, measuring, and releasing lizards. At least three CMR sessions are required to accurately estimate adult lizard population sizes (see below). Between 1995 and 1997, I conducted sessions both in the early summer (May-June) and again in late summer (July-August). I returned to each island for a single day in 1998 to collect body parameters from a small sample of lizards.

Adult lizards were captured by hand or noose, permanently marked with exclusive numbers by toe-clipping, and temporarily marked on both lateral surfaces with their number for rapid sight-identification with a black Sanford Sharpie® fine point permanent marker. I measured SVL, tail length, and tail regeneration to 1 mm with a clear plastic ruler, and weight to 0.1g with a Precision® spring scale, and noted any significant external injuries, parasites, and deformities. Because these lizards defend small territories, they were always released within 1 m of their point of capture.

I chose to study only mature adult anoles for two reasons. First, I could only travel to the islands during the summer (May - August) when only large adults and very small hatchling were present. Second, upon hatching, brown anoles are only about 16 mm in snout-to-vent length (SVL), and are extremely difficult to toe-clip and measure without harming them and potentially affecting survival rates of an already vulnerable stage. Thus, I attempted to capture only reproductively mature lizards. In Miami, female brown anoles reach reproductive maturity at about 34 mm SVL, and males at about 39 mm SVL (Lee et al. 1989), so lizards visually estimated to be smaller than 35 mm SVL and 40 mm SVL, respectively, were not captured. When smaller lizards were accidentally captured, they were marked, measured, and weighed in the chance they might provide data on growth rates of young individuals, but were excluded *a priori* from all analyses other than growth and population estimates. In order to meet the assumptions of statistical independence, lizards captured more than once were included only once in all analyses other than those requiring that all observations of the same lizard be included (e.g. population estimation and growth analyses). I used only the first observation in statistical analyses, and for growth analyses, when two or more periods of growth were involved, I considered only the first measurement period.

Despite all of the above restrictions, population estimation techniques required a fairly large proportion of the lizard population to be sampled. However, modern statistical tests were only designed to distinguish differences between two or more populations based on samples comprising less than 5 percent of a given population (B. Muenchen, pers. comm.). At the other extreme lies a complete census, in which the entire population is measured, population parameters are known, and statistics are not required to test for differences. Between these two extremes lies relatively uncharted territory, with regards to statistics. In this study, none of the samples are true censuses, however, in order to accurately estimate lizard population sizes on the two islands, the samples were expected to be larger than 10 percent of the population on a given spoil island. I simply utilized common statistical techniques, with the knowledge that my results would be somewhat conservative with regards to rejecting a given null hypothesis.

Population Estimates

The program CAPTURE (Otis et al. 1978) was used to estimate the size of the brown anole population present on each island during the summer of each year. Accurate estimation of the size of closed populations from CMR data generally requires that the following assumptions be met: 1) the population is demographically and geographically closed, 2) marks are permanent, 3) marks are unaltered during the experiment and are noted correctly, and 4) all animals have an equal probability of being captured and their marks do not affect capture probabilities (Pollock et al. 1990).

The first three assumptions are absolutely required by all the models and their estimators provided in the program CAPTURE (Otis at al. 1978). Closure was met in this study, as each year the CMR sessions were conducted over a short enough time period to assume demographic closure (negligible birth and death), and both spoil islands are completely surrounded by water (negligible immigration and emigration). Toe-clipping is a permanent marking method for lizards, and although a small percentage of the lizards lose toes in territorial squabbles, errors resulting from lost toes can nearly always be resolved by looking at other body parameters (e.g. sex, size, tail loss, distinguishing marks, or injuries) combined with lizard location.

The fourth assumption can often be relaxed by using one of seven additional models and their estimators available in the program CAPTURE. In general, these models allow for unequal capture probabilities resulting from: 1) variability of environmental factors over time (Model Mt), 2) variability in behavioral responses of animals to fixed traps (Model Mb), and 3) heterogeneity inherent among individuals (Model Mh), or 4) a combination of any two of the above (Mtb, Mth, Mbh) or all three together (Mtbh). Thus, eight different models are available for estimating the sizes of populations for which the fourth assumption must be relaxed. Moreover, the program CAPTURE contains an algorithm for picking the best model based on the data itself, goodness-of-fit tests on each model, and tests between the different models. However, these tests are not independent, and thus have low power, so biological information is considered better for reducing the number of models from which to choose on an *a priori* basis (Pollock et al. 1990). Rather than using the estimate for the best model picked by CAPTURE, which might have resulted in different models being picked for each population estimate, I relied on five summers of experience, thousands of lizards in-hand, a knowledge of the literature on the behavioral ecology of anoles in general and *Anolis sagrei* in particular, and a realization of the potential influences of my sampling techniques on those lizards to pick the "best model" *a priori*. I chose Model Mth as the estimator in this study. Population estimates were not subjected to statistical testing in this study.

Individual Growth and Asymptotic Size

To visualize the growth of individual lizards, growth trajectories were plotted against time in days (e.g. Dunham 1978, Schoener and Schoener 1978, Stamps and Tanaka 1981, Van Devender 1978). The time line for this project was presented as a running total of the approximately 1,700 "project days" elapsed during this project, beginning on January 1, 1994 and ending on August 25, 1998. A line connecting the beginning and ending SVL of each recaptured lizard was plotted against project day, and all the trajectories for males and females were plotted together for each island. The range of growth data was restricted by *a priori* sampling dates and noosing protocols to that of adults, so growth models such as Von Bertalanffy or logistic-by-weight (Dunham 1978, Schoener and Schoener 1978) were not fit to these data. Despite the "restriction of range" in my growth data, growth can also be described indirectly by assessing asymptotic size: the end-result of growth throughout the life of a lizard. I tested for differences in this parameter between the two islands, and over the four summers of the study, using four different methods.

First, I plotted lizard growth (mm/day) as a function of SVL (e.g. Schoener and Schoener 1978, VanDevender 1978). Such plots illustrate the decline in growth rate that occurs as body size increases, and a growth model fit to the data should intersect with the abscissa at the SVL at which the lizards exhibit zero growth. I used the *ending SVL* for the abscissa, rather than the mean SVL recorded during the measurement period (presented in most studies), because asymptotic size should be best approximated in these plots by the final SVL measurement of a lizard. I chose to keep negative growth values in these data sets for three reasons: to keep sample sizes as large as possible (Schoener and Schoener (1978), to avoid selectively removing data that resulted from measurement errors which could occur in *either* positive or negative directions, and because of recent findings that lizards might actually shrink in size during harsh periods (Wikelski and Thom 2000). I fit simple linear regression lines to the data for each sex on each island so the x-intercept could be used as an estimator of asymptotic size, since the restriction of range problem would clearly prevent me from fitting a lifetime growth model to the data.

Second, I utilized only the individuals exhibiting little or no growth during the measurement period to estimate asymptotic size (e.g. Dunham 1978). However, in this study, I defined "zero-growth lizards" (ZG lizards), as lizards exhibiting negative growth (negative measuring error), no growth, or growth of less than 0.01 mm/day. The latter value is equivalent to only 1 mm of SVL growth over an entire summer, possibly a result of positive measuring errors of 1 mm SVL. This method is similar to that in other studies (e.g. Dunham 1978), but does not restrict the data to include only zero-growth and negative-growth measurement errors. I used only the lizards meeting these *a priori* criterion to estimate the mean asymptotic size of the zero growth lizards (hereafter Mean SVL_{ZG}), then tested for differences between the lizards from each island-sex-year sample using ANOVA.

Third, because I measured mostly year-old adult lizards, it is likely that many were already at or near their maximum size. Asymptotic size is presumably a variable trait that can be described and tested statistically, as can other morphological traits, such as limb length. To avoid missing the natural variation inherent in maximum body sizes that individuals can attain by simply picking the largest lizard in each sample as the asymptotic size of the population (Stamps and Andrews 1992), I analyzed the data from a subset of only the largest lizards in each sample. I chose the subset in an unbiased, *a priori* manner using data describing zero-growth lizards, by calculating the percentage of the recaptured lizards that were at or near zero-growth, then using this value as the cut-off above which all lizards in a given sample were presumed to be at or near their maximum size (hereafter $SVL_{Max\%}$). I calculated Mean $SVL_{Max\%}$ by first placing all the lizards from each sample in order by SVL, then eliminating all individuals smaller than the cut-off. To make certain that all the samples could be used in statistical tests, I included the largest three lizards if the reduced sample would have consisted of less than three. The SVL data from the reduced data set (including donor lizards) were cast into a three-way ANOVA using island (2 levels), sex (2 levels), and year (5 levels) as factors.

Finally, I estimated the asymptotic size of lizards of each sex on each island using an elegantly simple method proposed by Stamps and Andrews (1992), where the largest lizard in a sample is thought to represent the absolute asymptotic size (hereafter SVL_{Max})

of the lizards in a sample. To be valid, this method requires three assumptions to be true: 1) that asymptotic sized, zero-growth individuals existed in the population when the samples were taken, 2) that the sampling methods were sufficient to capture at least one such individual in each sample, and 3) that the coefficients of variation in samples of ZG lizards are small (thus, the standard deviations of SVL_{ZG} values are small relative to mean SVL_{ZG} values). I tested each assumption with my data. The above growth analyses addressed the first assumption by indicating the time of year when ZG lizards are present, and results from the Mean SVL_{ZG} analyses addressed the third assumption. To determine whether or not I was actually *capturing* ZG lizards in my samples (assumption two), I plotted lizard SVL against the order in which lizards were captured (e.g. lizard number) for each of the CMR sessions. Plots that reach an asymptote during the sampling session indicate that enough lizards have been captured to include at least one asymptotic individual, similar to the reasoning of constructing a species-area curve to determine the appropriate quadrat size or transect length for species diversity studies. I reported SVL_{Max} for each of the 20 island-sex-year samples, but since the value for each sample is just a maximum, and has no variance, statistical testing by year was not possible. Instead, I pooled the yearly values by sex and island, and tested for differences between the two islands for each sex, using the Tukey-Kramer paired t-test.

The Distribution of Body Sizes

Although growth trajectories, growth rate models, and asymptotic sizes are valuable parameters for demographic studies, much can be learned about how population structure varies over space and time by constructing distributions of individual SVL values, then testing for differences between mean SVL over time and space using basic statistics. For example, histograms of SVL frequencies in a sample at a given point in time can illustrate whether or not the population is continuously breeding (wide distribution) or exists as individual cohorts (tight distribution), and if the latter is true, when hatchling first appear and when they recruit into the adult population. I constructed separate SVL histograms for each of the 20 possible island-sex-year combinations, then lined them up vertically by SVL category to reveal any changes in the distributions over time. To test for statistical differences in mean SVL over space and time, I cast the SVL data into a three-way ANOVA using island (2 levels), sex (2 levels), and year (5 levels) as factors.

Body Condition

Body condition was represented as a "condition index" (CI) relating SVL to body weight using a formula modified from the one presented by Andrews et al. (1983):

$$CI = (\text{mass}^{0.333} / SVL) * 100$$

where the mass exponent is calculated by taking the reciprocal of the slope of the regression of log10 weight against log10 SVL. The slope of the log-log regression is near three for many small lizards (R. M. Andrews pers. comm.). However, the 0.333 mass exponent in their formula was generated from data taken on *Anolis limifrons*, a slender grass anole from Panama. I derived a mass exponent specific to the lizards in this study, rather than using 0.333, because it would have resulted in an index that was biased by lizard size. This was preferable to using the "coefficient of condition" [(mass/SVL)*100] of Floyd and Jenssen (1983). Although the latter index can be presented in interpretable units (a "weight percent"), it is by definition a size-biased index, which limits its utility in studies employing lizards of different sizes, such as the sexually dimorphic brown anole. I used only the adult lizards marked during this study to derive the mass exponent. To analyze body condition data, I cast the CI values for the adult lizards into a three-way ANOVA using island (2 levels), sex (2 levels), and year (5 levels) as factors.

RESULTS

A total of 916 exclusive lizards (465 females and 451 males) were captured, marked, measured, and released on the two islands during the five summers of this study, 643 on Island P1 (Table 2.1; all tables are in the Appendix) and 273 on Island P2 (Table 2.2). Four male anoles between 35 and 39 mm SVL were excluded from body size-related analyses because they fell below the minimum adult size established by *a priori* criteria. These males were likely mistaken for small females when they were captured, but had been marked and measured in the hopes that growth data might be retrieved. Thus, a total of 912 exclusive lizards were used in body size-related analyses, 465 females and 447 males.

Population Growth and Range Expansion

The population on Island P1 grew very rapidly (Table 2.1). Five adult males (3 captured), eight adult females (one captured), and 40 hatchlings from two distinct size classes were seen during a 102-minute search during the morning of August 19, 1994, indicating the introduction was successful. I searched the island for one hour on April 12, 1995 and captured six males, all but one of which were 60 mm SVL or larger, missed two more males, and observed 15 females. I found large numbers of large adult lizards of both sexes in early May 1995, less than 11 months after the initial colonization. The lizards had spread across the entire island, but were concentrated mainly in the vegetation patches and were rare in the open, rocky beach areas. By 1996, the lizards were abundant in all areas of the island, many were found high in vegetation, and many appeared smaller in size. Over 200 were marked, and the density of lizards was near $1/m^2$ (Table 2.1). In 1997, the P1 population was estimated at over 550 individuals, a density of over one lizard per square meter, and the lizards were visually smaller in size and weight. They were abundant from the splash zone to the highest, thinnest branches, and it was very difficult to walk more than a few meters without disturbing numerous lizards and causing a cascade of territorial squabbles. Never before, and never since, have I observed lizards in such high densities. The island was only briefly visited in 1998, so the population size could not be estimated, but the average time between captures was similar to that of 1997 (under three minutes, including data collection).

During the same period of time, the P2 population reached only about half the size and 10 percent of the density observed on Island P1 (Table 2.2). No adults or hatchlings were observed during the afternoon of August 19, 1994, but this survey was limited to less than 10 minutes by a bad storm and 20-knot winds. I returned in late April - early May, 1995, less than 11 months after the initial colonization, and found large numbers of large adult lizards of both sexes. Most the lizards were found in the cabbage palm forest where the donors were released. Although some were found in the marsh, none were over 5 m away from the forest edge. By 1996, the P2 population had doubled (Table 2.2), and lizards were abundant in the marsh around the forested area and had spread to the northwest and southwest along the beaches to the far reaches of the marsh "tails," but were very sparse in these habitats. It appeared that at least one male and a few females occupied every cabbage palm in the forest at this time, and lizards were often seen fighting in the canopy above 5 m. In 1997, the population expanded by only about 25 percent (Table 2.2). Lizards were not noticeably more dense in the palm forest, but they occupied a slightly wider geographic area than they did in 1996, and occurred in greater densities throughout the marsh. The island was only briefly visited in 1998, so accurate population estimates were not made, but times between captures were similar to that observed in 1997 (about nine minutes, including data collection).

One emaciated male green anole was captured from high in a shrub on Island P1 in July 1996, but no others were ever seen on that island. Conversely, 14 green anoles were found on Island P2 during the study (6 in 1995, 4 in 1996, 3 in 1997, and 1 in 1998). Regular recaptures of these lizards indicate that the population was very small in 1995, and may have declined during the study. None were found during very brief surveys in 1994, but green anoles were likely present in at least small numbers prior to the brown anole releases. Green anole data were not analyzed to test for negative effects resulting from the brown anole invasion because of small sample sizes, a lack of background (pre-invasion) data, and the fact that a more comprehensive experimental study was being conducted concurrent with this one to test for effects on green anoles.

Individual Growth and Asymptotic Body Size

A total of 168 lizards were measured two or more times in this study: 136 on Island P1, and 32 on Island P2. Growth trajectories for 136 lizards on Island Pl (51 females and 85 males) indicate that between-year growth rates of both male and female lizards declined over the study period on this island, and that the trend was more evident in males (Figure 2.4). Four of the 18 donor lizards (2F, 2M) were found again in 1995. All had grown in length by at least 2 mm, but remained smaller than many of their progeny, despite being their elders by at least one year. Flatter growth curves were exhibited by smaller lizards in each successive year. Moreover, the maximum size of the recaptured lizards declined substantially for males between 1996 and 1997, and again between 1997 and 1998. This was evident, but less dramatic, for females. Thus, over time, smaller lizards were represented in the pool of recaptured lizards.

When the 32 growth trajectories for Island P2 are partitioned by sex and year, sample sizes become small, but the trajectories suggest that growth rates and asymptotic sizes remained fairly stable throughout the study on this island (Figure 2.5). Five of the 19 donor lizards (3F, 2M) were found again in 1995. Four had grown 4 mm in length, and one already large male grew 2 mm in length, but as observed on Island P1, many of their progeny had surpassed them in size in 1995 (see following sections). Fairly large lizards (males over 62 mm and females over 47 mm SVL) continued to grow larger during every year of the study.

Growth trajectories revealed several demographic patterns in these lizards, despite the fact that they were constructed from adult lizards during only summer months. First, the trajectories for two male lizards from Island P1 (Figure 2.4) and three male lizards from Island P2 (Figure 2.5) show that small adult males (40 - 50 mm SVL) in mid-June or even as late as August of one year are capable of growing to full size by June of the next summer. This is consistent with growth rates exhibited in first year progeny measured in 1995, on which initial measurements were not made, but for which hatching dates could not have preceded July 1994. Also, the longest growth trajectories span less than 16 months: from the early sampling sessions of one year (May - June) to the late sampling sessions of the following year (July - August). Finally, most of the growth trajectories have their terminus in the late sampling sessions (July - August), indicating that mortality occurred more often between one year and the next than during the summer, but this could also have occurred because there were more opportunities for mortality to occur in the longer period between summers. The above facts suggest that the lizards on these islands hatched in summer months, grew to reproductive size by the beginning of the next summer, reproduced throughout their second summer but grew relatively little during that time, then perished at the end of their first and only reproductive season.

Plots of growth rate against the ending SVL for 136 lizards on Island P1 (Figure 2.6) and 32 lizards on Island P2 (Figure 2.7) provide an indication of asymptotic size, but a regression line could not be reliably fit to the data because of the substantial variability along the abscissa (SVL), combined with the restriction of range problem. The regression lines were often flat or positive, and the R^2 values were all very low, and are not shown on the plots. A clustering of data points representing minimal growth, zero-growth, and negative growth around the presumed asymptotic size of the lizards of a given population suggest that the lizards for which growth was measured were larger on Island P2 than on Island P1, but without the benefit of being able to fit an unbiased line to the data, asymptotic size must be estimated using other methods.

The plots discussed above include only 56 lizards which exhibited growth rates of 0.01 mm/day or less (ZG lizards). A 3-way ANOVA testing for differences in Mean SVL_{ZG} by island, sex, and year was inappropriate because data sets already partitioned by island, sex, and year were substantially reduced when only these 56 ZG lizards were included (Tables 2.3 and 2.4). Thus, the variability of data along the abscissa (SVL) in the growth plots could not be statistically explained by yearly differences in Mean SVL_{ZG} in females or males. Mean SVL_{ZG} values for each island-sex-year group were simply assessed for consistency with other asymptotic size estimations for the same groups.

Although I was not able to compare the ZG lizards by year, sample sizes pooled over the five years were suitable to compare Mean SVL_{ZG} between the two islands using the Tukey-Kramer paired t-test for each sex. The Mean SVL_{ZG} of females on Island P1 was 46.08 mm (s.e. = 0.36; range = 44 - 50; n = 24), whereas the Mean SVL_{ZG} of P2 females was 49.40 mm (s.e.= 0.40; range = 48 - 50; n = 5), and the 3.32 mm difference was highly significant (n = 29; t = 4.047; df = 27 ; P = 0.0004). The Mean SVL_{ZG} of males on Island P1 was 59.37 mm (s.e. = 0.59; range = 55 - 66; n = 19), whereas the Mean SVL_{ZG} of P2 males was 64.50 mm (s.e.= 0.63; range = 62 - 67; n = 8), and the 5.13 mm difference was also highly significant (n = 27; t = 5.101 ; df = 25 ; P = 0.0001).

Regarding $SVL_{Max\%}$, a total of 56 lizards, or exactly one-third of the 168 lizards for which growth data was available, were at or near zero growth as defined above, so any sample including the largest third of the lizards by SVL (hence, SVL_{Max33}) was assumed to include most of the asymptotic sized lizards in that sample. I sorted the lizards in each sample by SVL and culled from the largest third of the lizards in each. The mean of each reduced sample (Mean SVL_{Max33}) was considered a valid estimator of mean asymptotic size of the lizards in each population. The three-way ANOVA testing the effect of island, sex, and year on SVL_{Max33} returned highly significant values for all main effects and all interactions (Table 2.5). Despite small sample sizes in some cases, the residuals approximated a normal distribution, the analysis was deemed appropriate, and *post hoc* testing was done for individual samples by year and island.

First, I tested for significant patterns in Mean SVL_{Max33} over time for each sex within each island. The Mean SVL_{Max33} of females on Island P1 (n = 108) differed significantly over the five year study ($F_{4,103}$ = 3.0096; P = 0.0215), gradually increasing to the largest value in 1996, followed by a gradual decline in subsequent years (Table 2.3). Females on Island P2 (n = 42) showed a similar and significant pattern ($F_{4,37}$ = 18.5693; P < 0.0001): Mean SVL_{Max33} increased to a high of nearly 50 mm in 1996, followed by a gradual decline in subsequent years (Table 2.3). Males on Island P1 (n = 108) exhibited significant changes in Mean SVL_{Max33} ($F_{4,103}$ = 32.5606; P < 0.0001): they increased to a high of more than 61 mm SVL in 1995, followed by a steady decline to less than 58 mm in 1998 (Table 2.4). Island P2 males (n = 49) also exhibited a statistically significant pattern ($F_{4,44}$ = 13.8984; P < 0.0001), however, Mean SVL_{Max33} increased throughout the study, a pattern completely opposite of that observed on Island P1 (Table 2.4).

Differences between Mean SVL_{Max33} values on the two islands were substantial for both sexes, and increased in magnitude over time (Tables 3 and 4). Mean SVL_{Max33} of females were not significantly different on the two islands in 1994 ($t = 0.522$; $df = 6$; $P = 0.6202$), but were larger on Island P2 than on Island P1 in 1995 ($t = 5.213$; $df = 20$; $P < 0.0001$), 1996 ($t = 9.737$; $df = 51$; $P < 0.0001$), 1997 ($t = 10.797$; $df = 57$; $P < 0.0001$), and 1998 ($t = 2.919$; $df = 6$; $P = 0.0267$). Mean SVL_{Max33} of males were significantly larger on island P2 than on Island P1 during 1994 ($t = 3.182$; $df = 4$; $P = 0.0335$), 1995 ($t = 4.673$; $df = 28$; $P < 0.0001$), 1996 ($t = 10.580$; $df = 48$; $P < 0.0001$), 1997 ($t = 18.096$; $df = 54$; $P < 0.0001$), and 1998 ($t = 12.519$; $df = 13$; $P < 0.0001$).

The data in this study met the three assumptions required for analyses of absolute asymptotic sizes (SVL_{Max}) suggested by Stamps and Andrews (1992). First, the growth data indicate that on each island and in each year, sampling sessions were conducted when at least some ZG lizards were present (July and August). Second, regressions of lizard SVL against lizard number during each of the 30 CMR sessions (plots not presented) indicated that lizards captured early in a given session were either the same size as those captured later (slopes not significantly different than zero) or were larger than those captured later in the session (slope significantly less than zero), indicating that at least one of the largest individuals was measured during each of the CMR sessions. This is consistent with the notion that the largest lizards of either sex will generally occupy the most commanding positions and most actively defend their territories, so might be more visible to the observer and more likely to be captured before smaller, less dominant lizards. Furthermore, Stamps and Andrews (1992) found that samples of 15 - 19 adult *Anolis limifrons* produced estimates of asymptotic size that were the same as the estimates obtained from very large samples, but that samples of less than 15 lizards underestimated the asymptotic size of the population by about 2 mm. Only five of the 20 island-sex-year combination samples contained fewer than 15 individuals: the sample of females on Island P2 in 1998 (10 lizards), and the donor lizard samples in 1994, the latter for which the SVL values for the entire population was known (Tables 2.3 and 2.4). Conversely, *A. sagrei* is very different from *A. limifrons* in ecology and behavior, and may be more (or less) visible to observers, so the sample size guidelines of Stamps and Andrews (1992) may not apply. Third, the coefficient of variation of the ZG adults was fairly small for both sexes on both islands (3.8 % in P1 females, 1.8 % in P2 females, 4.4% in P1 males, and 2.7% in P2 males), and the individual samples partitioned by island, sex, and year exhibited coefficients of variation under 5 percent, despite small sample sizes (Tables 3 and 4).

The absolute asymptotic sizes (SVL_{Max}) of females on Island P1 remained similar through 1997 (48-49 mm), then declined by 2 mm in 1998 (Table 2.3). However, the 1998 sample was taken in late June, nearly a month earlier than the latest samples in other years (Table 2.1), so the true SVL_{Max} may have been slightly underestimated. The largest females on Island P2 were present in 1996, but remained as large as 50 mm in following years (Table 2.3). Again, the 1998 sample was taken in late June, but also contains only 10 lizards, so the true SVL_{Max} may have been underestimated by as much as 2 mm (Stamps and Andrews 1992). More importantly, the largest females on Island P2 were equal in size to largest females on Island P1 during 1994 and 1995, but were larger during every year of the study after 1995 (Table 2.3). Overall, the mean SVL_{Max} of the females living on Island P2 between 1995 and 1998 (50.00 mm; s.e. = 0.67; n = 4) was almost 2 mm larger than the mean SVL_{Max} of the females living on Island P1 (48.25 mm SVL; s.e. = 0.67; n = 4), but the difference was not statistically significant (t = 1.849; df = 6; P = 0.1140; n = 8; four years pooled).

The SVL_{Max} of males on Island P1 reached their peak SVL of 65 mm in 1996, then declined rapidly to a low of 60 mm in 1998 (Table 2.4). Conversely, the largest males on Island P2 ranged between 65 and 67 in all years after 1994 (Table 2.4). Again, the 1998 samples were taken in late June, nearly a month earlier than the latest samples in other years, so may represent an underestimate for that year, but unlike females, male sample sizes were at least large enough for a valid comparison of SVL_{Max} between islands in 1998. Overall, the mean SVL_{Max} of the males living on Island P2 between 1995 and 1998 (66.00 mm; s.e. = 0.84; n = 4) was over 3 mm larger than the mean SVL_{Max} of the males living on Island P1 (62.75 mm SVL; s.e. = 0.84; n = 4), and the difference was significant (t = 2.751; df = 6; P = 0.0333; n = 8; four years pooled).

In summary, Mean SVL_{Max33} values were much smaller than SVL_{Max} values, as would be expected, but Mean SVL_{Max33} and Mean SVL_{ZG} tracked each other over time fairly well (Tables 2.3 and 2.4). Small sample sizes for SVL_{ZG} analyses precluded broad conclusions about yearly differences in asymptotic size based on these results alone. The largest third of the lizards in the samples should have given the best estimate of the *average* asymptotic size of brown anoles in the populations represented by those samples for at least two reasons: 1) brown anoles appeared to occur as fairly distinct seasonal cohorts that grew to full size by the beginning of their second summer, and all measurements were taken after that time, and 2) my sampling protocols kept me from capturing very many young lizards, even if they were present in great numbers. However, at least a few lizards that had not reached a zero-growth stage were likely included in these samples, so this method could have underestimated the real mean asymptotic size. Similarly, the largest individual in a given sample is likely an overestimate of the *average* asymptotic size reached by the population which it represents.

Body Size Distributions and Mean SVL

Size distributions constructed for each combination of island, sex, and year (Figures 2.8 - 2.11) reveal some distinct trends in body size over time, and strengthen the conclusions of asymptotic size analyses. Sample sizes were very small in 1994, especially for males, and merely show that moderate-sized adult donors were released on the islands in June of 1994. The 1995 histograms for both sexes on both islands have a fairly tight distribution about the mean. This indicates that the first generation progeny hatched within a fairly narrow range of time and grew at relatively equivalent rates. Moreover, it is clear that at this latitude, brown anoles are capable of growing to adult size by the beginning of their second summer, which is likely the beginning of their first reproductive season.

After 1995, the SVL histograms for females on Island P1 are fairly normal in shape, except for the 1997 plot, which is skewed to the left (Figure 2.8). Mean female SVL lies consistently around 44 mm on this island during each year of the study (Table 2.6). The histograms for females on Island P2 support previous conclusions that female lizards grew consistently larger on that island (Figure 2.9). In fact, mean SVL values lie above 46 mm from 1995 onward (Table 2.6).

The male histograms show a very different pattern (Figures 2.10 and 2.11), as do the mean values for male SVL over time (Table 2.7). Many small males lie outside the main concentration of data in the Island P1 plots (Figure 2.10): the 50 mm long lizard in the 1995 plot was captured on May 3, so *must* have hatched in 1994. After 1995, many more small males were represented in the samples, but all but one of these lizards were captured in mid-June, suggesting those lizards hatched the previous year. Together with the female plots, these plots support the notion that brown anoles reproduce seasonally at this latitude and grow together in fairly distinct yearly cohorts and that juveniles and small adults from the previous year merge into the year-old adult cohort some time after June. But more importantly, these plots indicate that, as years passed, male lizards on Island P1 were not able to achieve the June body size that their parents reached in the previous year, leading to the decrease in mean male body size observed on that island.

This did not occur on Island P2 (Figure 2.11). Males remained large, and although the histograms after 1995 are also skewed to the left, the proportion of small adults in each sample is lower, despite the fact that samples were taken on nearly the same day on each island (Tables 2.1 and 2.2). Furthermore, unlike Island P1, all the small males under 50 mm in 1995 and 1996 on Island P2 were captured in late July and August, and may have hatched earlier in the same summer in which they were measured.

The three-way ANOVA testing for differences in all the brown anole SVL values for each island-sex-year sample returned significant values for all three main effects and every interaction, but analyses of the residuals strongly indicate that this analysis was not appropriate for this data set, so the results were not presented. A highly irregular normal quantile plot and some very distant outliers indicated that the residuals were not distributed normally (18 residuals were over 10 standard deviations *below* the mean). I determined the location of the largest outlier residuals in each SVL histogram. All of the largest residuals corresponded to males between 40 and 50 mm SVL and females below 40 mm SVL. The failure of the ANOVA to properly model the data, combined with patterns revealed in visual analyses of the SVL histograms, suggest that 1) young adult lizards or even juveniles were included in data sets thought to consist of only year-old adult lizards, or 2) numerous year-old lizards that barely reached adult size were present in the samples, and 3) that the best data set for describing reproductive-sized adult lizards, $\text{SVL}_{\text{Max33}}$, might have already been analyzed.

Body Condition

The slope of the regression of Log_{10}Weight against Log_{10}SVL of these lizards (not shown) was 3.4345 ($R^2 = 0.9512$; $n = 912$), and the reciprocal of that value was 0.2912, so the CI value for each lizard was described by the formula: $\text{CI} = (\text{weight}^{0.2912}/\text{SVL}) * 100$. The three-way ANOVA testing for differences in mean CI values across island, sex, and year returned significant values for the main effects of island and year and both two-way interactions involving year (Table 2.8). Significant island*year and sex*year interactions dictated that I test for yearly differences in CI with four separate one-way ANOVAs: one for each sex on each island, using year as the factor. However, the non-significant values for sex and the island*sex interaction forced me to pool the data for males and females to test for differences between CI values on the two islands.

Mean CI values of Island P1 females declined progressively (Table 2.6) and significantly ($F_{4,318} = 35.6861$; $P < 0.0001$) over the five summers. After exhibiting significant declines in condition from one year to the next between 1995 and 1997 (Tukey-Kramer; $P < 0.05$), the P1 females suffered an even more dramatic decline between 1997 and 1998. The donor females were in the "best" condition on this island. Mean CI values of the P2 females remained stable and elevated through 1997, then plummeted in 1998 (Table 2.6). Although the overall trend is highly significant for P2 females ($F_{4,123} = 5.2101$; $P = 0.0007$), the pattern is different from that of the females on Island P1 in that none of the CI values were significantly different from each other between 1994 and 1997 (Tukey-Kramer; $P > 0.05$), whereas the 1998 CI values were significantly lower than the CI values for 1997 and all previous years (Tukey-Kramer; $P < 0.05$).

Mean CI values of Island P1 males exhibited almost the exact same general pattern as did P1 females (Table 2.7): a significant overall decline ($F_{4,313} = 32.6334$; $P < 0.0001$), significant incremental declines from one year to the next between 1995 and 1997 (Tukey-Kramer; $P < 0.05$), and a more dramatic decline between 1997 and 1998. Mean CI values of Island P2 males also declined steadily each year after reaching a maximum in 1995 (Table 2.7), and the overall pattern was highly significant ($F_{4,138} = 17.8069$; $P < 0.0001$), but only the individual difference between 1997 and 1998 values was significant (Tukey-Kramer; $P < 0.05$).

Brown anole CI values started out fairly similar on each island, but increasingly favored Island P2 as the study progressed (Table 2.9). Separate t-tests for each year (males and females pooled based on results from the 3-way ANOVA) show that mean CI values of the donor lizards placed on Island P1 were significantly larger than were mean CI values of the lizards placed on Island P2. This was probably due to sampling error resulting from randomly extracting four very small sets of lizards from an already small pool. Mean CI values of their progeny were almost exactly the same on the two islands in 1995, but were significantly different in 1996, favoring Island P2 by nearly 0.03 index units. This gap widened to over 0.06 index units in 1997. CI values remained significantly different in 1998 (by nearly 0.08 index units), despite small sample sizes and the fact that mean CI values for both islands were lower in 1998 than in earlier years.

Climatic Patterns During This Study

Daily weather was relatively consistent during the summer months of each year of the study. Sunrise occurred between 0630 and 0700 with calm winds and clear skies. As the land mass heated up, an on-shore breeze (sea-breeze) formed in late morning, bringing moist air onshore. The onshore movement of this moist air contributes to the intense thunderstorms that form over coastal areas in the middle to late afternoon for a few hours. Storms generally subsided by around 1800, after which the sun emerged from the clouds, then set with calm winds between 2000 and 2030.

I obtained data for the maximum, minimum, and mean monthly temperatures, and monthly precipitation totals from the NOAA weather station at Kennedy Space Center (KSC) for the period January 1994 through September 1998. During the reproductive period for these lizard species (May through August), monthly temperature extremes ranged from 13 to 39 degrees C, and mean monthly temperatures ranged from about 23 to 30 degrees C (Figure 2.12). Overall, June, July, and August were the warmest months during each year of the study, and the summer of 1998 was much warmer than any other year of the study (Figure 2.12). Mean monthly temperatures for June, July, and August of 1998 were over 3 degrees (C) warmer than for any other year. In fact, temperatures reached well into the 30s (C) every day during the summer of 1998.

Monthly precipitation totals plotted for each year of this study revealed two distinct rainy periods each year (Figure 2.13). The first, or minor wet period, occurred in February and March, followed by a distinct dry period. The main summer wet period begins with an abrupt increase of rain in June, followed by a steady fall-off between July and November. This pattern is very consistent with long-term weather data from this region of Florida (Fernald and Patton 1984).

Specific differences in rain patterns occurred each year of this study, some of which are relevant to anoles and their arthropod food supply. The early (minor) rain spike was particularly high in 1996 and 1998, and in 1997 the spike lasted into April and May. The lack of an early rain spike in 1995 was followed by a particularly wet summer that year, making up the deficit in cumulative monthly rainfall by about July (Figure 2.14), whereas in 1996, the early spike was followed by a relatively dry summer. More interestingly, summer rainfall was severely depressed during 1998, relative to all other years (Figure 2.13). Cumulative monthly rainfall totals for each year show that the rainfall deficit that started in May 1998 lasted through the end of that year (Figure 2.14). In fact, in the summer of 1998, the few rains I observed over Mosquito Lagoon were actually virga (rain that evaporates before reaching the ground). This was the driest year on record for this area (John Stiner, CANA, pers. comm.), and devastating fires raged throughout Volusia County, resulting in dense smoke and unsafe ozone levels for days on end.

DISCUSSION

Brown Anole Demographics

Analyses of growth data were limited by the manner in which the data were collected, and statistical analyses of growth data were not possible for at least two reasons. First, I was limited to performing this study on adults during four summer months (May - August), during which relatively little growth occurs. As far south as Miami, brown anole reproduction, growth, and survival appear to be seasonal phenomena (Lee et al. 1989), resulting in fairly distinct yearly cohorts. By April, the vast majority of lizards that hatched the previous summer were adults, and as a result, size distributions of summer lizards were relatively narrow until late July and August, when some hatchlings started recruiting into the adult population. For *Anolis sagrei* in the Bahamas, Schoener and Schoener (1978) were able to construct complete growth curves from data collected only between March 1 and May 17 (only 77 days), presumably because reproduction and growth is less seasonal and multiple size classes are present at all times of the year.

Secondly, to ensure that hatchlings and juveniles were not disrupted by my actions, a lower limit was imposed on the size of lizards that could be captured, limiting growth measurements to mature lizards that were often at or near asymptotic size. Hatchlings generally started appearing in late May, but were not captured and marked for reasons previously outlined. Since juvenile growth rates could not be calculated, any growth curve would be incomplete except for adult regions. This is the restriction of range problem in data analyses, where the true description of the data is not possible because of low variation in the variables in question. Without sufficient levels of variation in the plotted variables, complete growth curves (e.g. Von Bertalanffy, logistic-by-weight) could not be constructed from plots of SVL against time, nor from plots of growth against ending SVL (e.g. Dunham 1978, Schoener and Schoener 1978). But despite the limitations of this study, several important conclusions can be made regarding brown anole growth rates and life span, and rough comparisons can be made with other lizard species.

First, conservative lifetime growth rate estimates can be calculated from lizards living between 1994 and 1995. Donor females were released on June 10, 1994 (calendar day 161), which is the earliest date an egg could have been deposited on the island. Assuming an incubation period of about 25 days (A. C. Echternacht, pers. comm.), the earliest possible date of hatchling emergence would have been about July 5, 1994 (calendar day 186). Brown anoles hatch at about 15 - 18 mm SVL in Florida (Duellman and Schwartz 1958). Fully grown lizards (males over 60 mm, females over 46 mm SVL) were found during the brief visit on April 12, 1995 (calendar day 102 of 1995). By definition, these lizards must have grown to nearly full size in less than 281 days, or just over nine months. That corresponds to an average lifetime daily growth rate of 0.21 mm/day for males and 0.16 mm/day for females, assuming a 16 mm hatchling SVL. This is highly consistent with many other short-lived lizard species (Andrews 1982), such as *Uta stansburiana* (Tinkle 1967), *Sceloporus graciosus* (Tinkle et al. 1993), *Sceloporus merriami* (Dunham 1978), and *A. sagrei* in the Bahamas (Schoener and Schoener 1978). In fact, some have stated that lizards in general exhibit growth rates of 0.2 - 0.3 mm per day (Tinkle 1967). However, the female *A. sagrei* on the spoil islands in this study grew nearly 10 mm larger, and the male *A. sagrei* in Florida grew nearly 20 mm larger than their Bahamian counterparts (Schoener and Schoener 1978). This may be further evidence that Caribbean island anoles are limited by food relative to mainland anoles (Andrews 1979), even when the mainland sites being compared are themselves islands.

Second, the large numbers of large lizards of both sexes found on both islands in 1995, and the five lizards for which growth trajectories from small adult size were available indicate that brown anoles are capable of growing to reproductive size, and possibly, asymptotic size, by the beginning of their second summer, and may even reach reproductive maturity by their first fall. *Anolis* lizards are well known for their extraordinary individual growth rates (Andrews 1982, Schoener and Schoener 1978, Stamps et al. 1998). My data strongly suggest the possibility that brown anoles hatching early in the summer ("early lizards") can reach reproductive maturity (35 mm SVL in females and 40 mm SVL in males) before the end of that same summer. Using the lifetime growth rate estimates from above, assuming the initial hatchling size is 16 mm, and assuming that the earliest date of hatching is about May 1 (calendar day 120), early females growing at 0.16 mm/day could reach about 26 mm SVL by June 30 (day 181), 31 mm SVL by July 31 (day 213), and 36 mm SVL (adult size) by August 31 (day 244).

Early males growing 0.21 mm/day could reach 29 mm by June 30, nearly 36 mm SVL by July 31, and over 42 mm (adult size) by August 31. However, lifetime growth estimates are probably inappropriate for modeling hatchling or even juvenile *A. sagrei*, which clearly grow faster than adults (Schoener and Schoener 1978, Stamps et al. 1998). Thus, it is very likely that early lizards grow to adult size during their first summer. Again, this is consistent with many other short-lived lizard species, including anoles (Andrews 1982, Dunham 1978, Schoener and Schoener 1978, Tinkle 1967, Tinkle et al. 1993).

Despite the numbers obtained above, there is no way to determine from my data whether brown anoles 1) grow constantly through the winter, 2) grow rapidly to adulthood during their first summer and fall, or 3) remain fairly small through the first fall and winter, then grow rapidly to adulthood in the following spring. Winters can be fairly cold at this latitude, suggesting that these lizards do not usually grow at a constant rate from their first to second summers, and are probably not growing much from November through February.

If it is true that early lizards can grow to adulthood, establish territories, mate, and deposit a few eggs during their first summer, to do so they would have to successfully compete with larger lizards born the previous year that would be vigorously defending their territories through the end of August. However, early lizards would likely benefit by being the largest lizards at the beginning of the following summer, their first full breeding season. Lizards hatching after about June 30 (“late lizards”) are highly unlikely to reach maturity in their first summer, but will almost certainly be adults by the beginning of their second summer, and would presumably breed throughout that summer. However, they would on average be smaller than early lizards from the same cohort. Thus, it appears that brown anoles benefit greatly from being born earlier in the summer, but more detailed demographic studies are needed to determine the statistical validity of such statements.

Regarding life span, this study could not reveal the major sources of mortality, nor could it determine the exact timing of such events. However, the fact that none of the 916 lizards in this study were recaptured after their second summer indicates that brown anoles lived at most about 18 months on these islands. Thus, the brown anoles in this study exhibited a nearly complete population turnover each year.

Population Expansion Capabilities of Brown Anoles

The brown anole population expansions that followed both successful introductions seem extraordinary, but are easily explained by the reproductive biology of this species. In Miami, testis mass was largest in April, and declined steadily after July, and oviducal eggs were prevalent in females between April and September, and very few females ovulated between November and February (Lee et al. 1989). My study was conducted over 400 km north of Miami, so I assumed (conservatively) that the reproductive season for this species began on about April 1 and ended on about September 1. During this time, females should be able to deposit a single egg about every six days (Tokarz 1998, Vincent 1999). As stated above, although a few early lizards might reproduce during their first summer, it is very likely that brown anoles attain reproductive maturity by the beginning of their second summer regardless of their date of birth. Third, most brown anoles probably only live through a single reproductive season, so cohorts undergo an almost complete replacement, probably during the fall or winter of each year. These assumptions make calculations of population expansion much simpler than if reproduction occurred all year and populations consisted of numerous, overlapping cohorts of lizards at any given time.

Given the above assumptions, each donor female could have deposited 14 eggs between June 10 and September 1, 1994 (83 days), so the 12 donor females on Island P1 could have deposited 168 eggs and the 13 donor females on Island P2 could have deposited 182 eggs in 1994, assuming they all survived the entire summer. These "potential reproductive output" estimates (PRO) exceed the 1995 population estimations, but lie near the upper 95 % confidence interval of the Model Mth estimates for that year (Tables 2.1 and 2.2). In fact, I estimated the size of the one year-old adult population *only after they had experienced mortality* as eggs, hatchlings, juveniles, and over-wintering adults, so I must have underestimate the number of eggs that were deposited the previous summer. Thus, more eggs should have been deposited on an island during a given summer than are indicated by the population estimates of new adults in the following summer, and the difference should provide a fair estimate of the over-winter mortality rate.

This logic can be applied to the data for the following years by using half the value of the population estimate from each year as the number of females present during the reproductive season and by using the entire summer to calculate the reproductive period to obtain the PRO for that year. On Island P1, each of the 70 females in 1995 (Table 2.1) could have each deposited up to 25 eggs between April 1 and September 1 (154 days), so, up to 1,750 eggs could have been produced in 1995. This is well above the 1996 population estimate, and indicates that survival from egg to adult between 1995 and 1996 was around 30 percent. Similarly, in 1996, the approximately 238 female lizards should have been able to produce about 5,950 eggs, but the population estimate for 1997 is less than one-tenth of that value, indicating an over-winter survival rate of less than 10 percent. The approximately 288 females present in 1997 might have produced 7,200 eggs, but although the population was not visibly any larger or more dense than in 1997, this is based on anecdotal data (time between captures) rather than a CMR population estimate, so claims of higher mortality would be spurious at best.

The estimate of 109 lizards on Island P2 in 1995 (Table 2.2) translates to 54 females laying a total of about 1,350 eggs, but the 1996 population estimate is only about 15 percent of that PRO value, only about half of the 1995 - 1996 survival rate on Island P1. In 1996, the approximately 101 female lizards should have been able to produce about 2,525 eggs, but the population estimate for 1997 is less than 10 percent of that value. Considering the fact that population sizes were much smaller on Island P2 than on Island P1 throughout the study, and the fact that the former is over twice as large as the latter, the brown anole population on Island P2 did not expand as quickly as would be expected, based on the expansion on Island P1. On the other hand, the brown anoles on Island P2 were consistently larger and in better condition than those on Island P1.

Although the disparity in population growth rates on these islands cannot be directly explained by the data collected in this study, basic physical characteristics of the islands and anecdotal biological data point to three possible explanations. First, the Allee effect (Allee 1938) could explain the difference in speed of population expansion on the two islands. The Allee effect occurs when densities are so low that reproductive individuals not able to find each other easily. Island P2 is large relative to the 19 original donors, so lizards might have been less likely to find each other in the first few years than they were on the densely packed Island P1. However, PRO calculations for the Island P2 population indicate that it could easily have reached similar final densities as Island P1 within the four year study period. Moreover, the notion that female *A. sagrei* are able to store sperm (Tokarz 1998) would negate the importance of the Allee effect.

Second, the habitats on the two islands are strikingly different, as was my intention in picking them for the study. Island P2 is larger, contains dense and diverse vegetation, better developed leaf litter and soil, more diverse thermal microclimates and periodic fresh water, and is better buffered from the effects of harsh weather. Island P2 should support more arthropods and faster growing lizard populations, due to the "higher quality" of habitat found on this larger island, when in fact, more lizards occurred on the smaller island. The smaller size, smaller vegetation "volume," or some unknown physical aspect of the vegetation on Island P1 may have caused brown anoles to reach higher densities faster there than on Island P2. Possibly, brown anoles have an underlying preference for, and generally perform better in low, scrubby habitats like those found in the Caribbean (Williams 1969, Schoener 1975). However, the brown anole populations on Island P2 clearly preferred the forested zone during the first two years of the study when the island was not "full" with lizards and a choice of habitats was available, making this conclusion questionable. Something about Island P2 may have allowed its lizard population to remain below the island's carrying capacity for brown anoles, which was reflected in body parameters such as condition and asymptotic size.

The third and most likely explanation is that differences in the island habitats might have resulted in different predation pressures occurring on the two islands, with the lizards on P2 being exposed to more predatory birds, snakes, and mammals, all of which were seen regularly on that island. This would explain the smaller population estimates and higher mortality rates obtained on Island P2. Periodic culling of the lizard population by predators, including green anoles, which are known to consume brown anole hatchlings (Campbell, unpublished manuscript), might have kept the remaining brown anoles beneath the threshold at which intense intraspecific competition would occurs, which would in turn explain the consistently larger asymptotic body sizes and CI values of the lizards on this island. The opposite is probably true on Island P1, where predators were very rarely observed during CMR sessions.

Despite my inability to broadly generalize these results due to a lack of replication of the islands, certain results pertain to the study of the spread of this species within the main part of its range in Florida and from isolated populations that are springing up all over the southeastern United States (Campbell 1996). First and foremost, these results confirm the notion that this species can rapidly increase from a very small number of initial colonists in North America, which until now has been based on anecdotal evidence in numerous natural history records from Florida (e.g. Campbell 1996) and detailed studies in the Bahamas and western Caribbean (Losos et al. 1993, 1997, Losos and Spiller 1999, Spiller et al. 1998). Secondly, this study shows that although brown anoles are able to achieve high densities and spread very rapidly in isolated areas supporting either open, shrubby habitats or forested edge habitats, they may be less dense, grow larger, and remain in “better” condition (or at least, remain so for a longer time after invasion) in forested edge areas than in non-forested habitats. Thus, in contrast to the notion that it “does best in” or “prefers” low, open habitats (Schoener 1975, Williams 1969), when given a choice, this species may actually prefer the diverse spatial and climatic microhabitats of forested edge habitat over spatially limited and consistently hot shrub and high-marsh habitats, although it may not occur in such high densities in the former as it does in the latter. However, this finding may be restricted to North America, where only a single anole competitor is present (although this is changing rapidly in South Florida). Of course, this species may spread at different rates and achieve very different densities in these two different habitat types for some yet undetermined reason that can only be revealed with detailed experiments.

Ultimately, this study corroborates other studies placing *A. sagrei* among the densest of all terrestrial vertebrates. Oliver (1948) reported about 1,700 *A. sagrei* per hectare on Bimini, Lister (1976a) reported over 2,000 per hectare on Cuba, and Schoener and Schoener (1980) reported 9,700 per hectare on Bahamian islands. The population estimate for Island P2 (Table 2.2) corresponds to *A. sagrei* densities of between 1,100 and 3,100 adult lizards per hectare, although it is unclear whether or not this population has stopped expanding in number. The final estimate for Island P1 (Table 2.1) corresponds to an *A. sagrei* density of between 9,800 and 15,500 adult lizards per hectare. If this seems excessive, *A. sagrei* is vastly overshadowed in density by at least two gekkonid lizards: one *Sphaerodactyllus* species in the Caribbean (G. Rodda, pers. comm.), and one

Hemidactyllus species in the south Pacific (E. Campbell, pers. comm.), both of which reach densities of over 50,000 lizards per hectare. However, both of those species are smaller than *A. sagrei*. More importantly, assuming an average weight of 7 g for an average full-sized male (about 64 mm SVL), and 3 g for an average full-sized female (48 mm SVL), the spoil island densities correspond to between 49 kg and 78 kg of adult lizard biomass per hectare. Certainly, this puts at least some level of strain on natural systems invaded by this species. The strain was revealed in the body parameters of the lizards themselves as their populations expanded on these islands, especially on Island P1.

Intraspecific Density-Dependent Responses

Results of this study suggest a trade-off between populations supporting large numbers and densities of lizards that remain smaller in body size (Island P1) and populations that remain smaller in number and density, but consist of larger lizards (Island P2). Both male and female brown anoles exhibited significant declines in Mean SVL_{Max33} and apparent declines in absolute asymptotic size (SVL_{Max}) on the crowded island, but the decline was particularly dramatic in males. Moreover, lizards on the smaller island were in progressively poorer condition over time, whereas those on the larger island were in better condition over time, until 1998, which was apparently a "bad year" for all the lizards.

Because lizards that are already large in mid-summer often continue to grow in length (Figures 2.4 and 2.5), in this analysis it is very important to consider the latest calendar dates in which samples were taken (Tables 2.1 and 2.2). Although the 1994 donor samples contained the smallest values for SVL_{Max} in all the samples, this can only be attributed to the habitat in which they were collected (rocks on the shoreline of Lake Okeechobee). Most of their first year first-year progeny were taken fairly early in the summer, but a small number were measured in late July. The latest 1996 and 1997 samples were taken in August (late August in 1997), except for the Island P1 samples in 1996, which were taken in mid-July. All the 1998 lizards were measured on the same day in late June, much earlier than the latest samples taken in other years. Thus, asymptotic sizes could have been confounded by the date of the CMR sessions, and would explain the results on Island P2, but the results on Island P1 are opposite: despite being measured later in the season in successive years, lizards on Island P1 were still smaller over time. Although this could have been due to the presence of more younger individuals on that island, the results from asymptotic size analyses show that even maximum adult sizes were smaller over time.

Based on the yearly SVL data, there are two possible explanations for the decline in overall body size of the lizards on Island P1 over time: 1) new individuals were growing to late juvenile and even adult size by the end of their first summer and those individuals were recruiting into the population of the previous cohort of adults (from the previous year), thus, lizards from two separate cohorts were being measured, or 2) a substantial number of growing adult lizards of both sexes were beginning their second summer at progressively smaller sizes each year because their growth was somehow stunted, especially in the case of males on Island P1. It is not possible to *absolutely* differentiate between the above two explanations with my data, however, four different analyses strongly indicate that the second explanation was true.

First, although the lizards were not marked when they were juveniles, all the small lizards from Island P1 were collected in June, indicating that even the smallest of these lizards were adults in their second season of growth. Second, the SVL_{Max33} samples incorporated only the largest of the adult lizards in a given sample, which ensured that only the lizards that had been alive for one full year (a single cohort) were included in the analysis. That analysis was probably the best for determining true differences between the maximum sizes attained by adult lizards within a single cohort in any given year of this study, because the reduced sample probably contained only asymptotic individuals.

Third, the shifting positions and increasing leftward skew of the SVL histograms of P1 males in later years indicate that, as years passed, many of the males on this island were unable to reach a summertime SVL that would be normally expected in this species, or that was observed in their ancestors in 1995 (Figure 2.10). Although it is possible that a larger percentage of individuals grew to juvenile or small adult size in their first summer over time, this seems unlikely, based on the leftward shift of the entire histogram. Those small individuals were more likely severely stunted at the beginning of their second summer. The histograms describing summertime populations of P2 males also increased in their degree of leftward skew, however, the SVLs of most of these lizards remained large throughout the study (Figure 2.11), despite similar sampling effort and timing on each island.

The fourth, and probably the best indication that density dependent effects were responsible for the body size decline observed on Island P1, and lack thereof on Island P2, were the changes in body condition over time. Body conditions of both males and females generally declined as Island P1 filled with lizards, but similar declines were not observed on Island P2 during this study. In fact, the relative magnitude of differences in lizard CI values between the two islands became larger over time, favoring Island P2 after 1995 (Table 2.9).

In summarizing the results of the temporal analyses of body conditions for each sex and each island, four additional points can be made. First, both males and females exhibited significant declines in body condition over time on Island P1, but only males exhibited this pattern on Island P2 in final years. Second, on Island P2, female body condition remained elevated for a longer period than did male body condition. Third, in every case, the most significant declines in condition occurred between 1997 and 1998, an extremely hot and dry period. These first three points indicate that density dependent effects were realized very quickly on Island P1, that males might have filled Island P2 late in the study and were beginning to feel the effects of interspecific competition only during the last two years, which were hot and dry, and that females never came up against such a threshold during the study. Fourth, on Island P1, the donor lizards of both sexes were in the "best" condition, indicating that the habitat on Island P1 was of lesser quality than that of the shoreline rip-rap of their "native" Lake Okeechobee. This was not true for Island P2 females, which remained in better condition than the donors until 1998, nor was it true for males, which remained in better condition than the donors until 1996. Some type of ecological release may have been operating on the Island P2 donors and at least their first few cohorts of progeny.

Thus, negative intraspecific density-dependent effects may have occurred on growth, asymptotic body size, and body condition (CI) on Island P1, but not on Island P2, at least not during the four year study period. The islands were not substantially different in the size of their area of habitat suitable for anoles, yet the populations exhibited distinctly different invasion histories. This could have occurred because of differences in habitat "quality" and diversity and/or density of arthropod prey, as exhibited by the differences in growth rates in populations of *A. sagrei* in different Bahamian island habitats separated by only a few hundred meters (Schoener and Schoener 1978). However, this might also have been due to differences in the numbers and types of predators and competitors present on the two spoil islands.

Island P1 is sparsely vegetated, has thin soil, and only six isolated cabbage palms. It is exposed to waves and surrounded on all but one side by deep water, but is nearly connected to a larger spoil island to the north by a shallow mud flat. It was likely a part of this larger island in the past, but has been separated by erosion. Despite the connection, no other vertebrate species were ever observed on Island P1, and there was no evidence of regular use of the island by vertebrate predators, although wading birds certainly work the shoreline at least periodically. One emaciated green anole was found and marked in 1996, but was never seen again. Combined with my results on body parameters, the physical and vegetative characteristics of this island indicate that the lizards on this island were under intense competition as early as the summer of 1996, and that their populations were probably not culled by predators, as were the Island P2 lizards. Severe intraspecific competition between the lizards on this island was the most likely cause of the rapid declines in asymptotic body sizes and body condition.

Island P2 has deep leaf litter, well developed soil, a forested area about the size of Island P1, dense understory vegetation on the edge of the forest, fairly extensive high marsh habitat, and a small freshwater pond in the middle of the palm forest. It is completely surrounded by very shallow mud flats, algae beds, and seagrass beds, such that one must anchor over 30 meters away and carry equipment to the island. Wading birds were observed feeding along the shoreline during every sampling session on this island. A fish crow was observed capturing a living, wiggling food item from a cabbage palm trunk. A black racer (*Coluber constrictor*) was seen on the edge of the palm forest during five of the CMR sessions. This island is not connected to the mainland, but one could easily walk from the mainland to the island across the shallow lagoon, as do raccoons, which were regularly seen sleeping in the cabbage palms on this island (in fact, it was originally named Coon Island). A small population of green anoles was present throughout, and these lizards could have each consumed a few hatchling brown anoles each year of the study. Predation was likely an important limiting force on this island, or at least, was a more important force than on Island P1. Ultimately, predation pressures could select for larger body size on this island, since large lizards are presumably less vulnerable than are small lizards and might be differentially represented in future populations.

Anoles in general, and brown anoles in particular, are known to be excellent colonizers (Losos et al. 1993, Williams 1969). Extraordinarily plastic morphology may give them an edge in surviving colonization events, enable them to undergo rapid changes in asymptotic body size in the generations immediately following invasion, and subsequently aid them in rapidly evolving in response to predation or congeneric competition (Losos et al. 1997). Despite the simple design of this study and lack of replication of the two island types in this study, these results should help to set the stage for more rigorous studies of the expansion of *A. sagrei* throughout the Southeast, the evolutionary responses of this species to its new environment and the predators and competitors therein, and the effects of *A. sagrei* on its native green congener.

CHAPTER 3

Diversity and overlap in the diets of native green anoles (*Anolis carolinensis*) and exotic Cuban brown anoles (*A. sagrei*) in Florida

INTRODUCTION

The green anole (*Anolis carolinensis*, Polychrotidae) is a slender, trunk-crown anole, and the only *Anolis* lizard native to North America north of Mexico. In the Caribbean, it prefers the upper trunk and limbs of tall vegetation, about which it slowly searches for arthropod prey (Williams 1969, 1983, Schoener 1968, 1975). It has been present in North America since the Pleistocene (Williams 1969), during which time it experienced ecological release due to a lack of anole competitors, and can be found throughout the vertical range of forested habitat, from ground-to-crown. This arboreal insectivore is abundant in habitats with a high edge-to-interior ratios, and thus has remained abundant, until recently, in even the most highly disturbed urban environs.

The brown anole (*Anolis sagrei*) is native to Cuba and the Bahamas (Schwartz and Henderson 1991), but arrived in the Florida Keys in the late 1800s and was introduced to at least six separate ports in Florida in the 1940s (Lee 1985). Since that time, it has come to occupy most of peninsular Florida, and has spread north into Georgia and two other southeastern states with the assistance of humans (Campbell 1996, Campbell and Echternacht in prep.). This similar sized, but more robust trunk-ground anole is a sit-and-wait predator that generally prefers open habitats, and perches near the ground on large-diameter vegetation and fence-posts (Williams 1969, 1983, Schoener 1968, 1975).

The interaction between these two species and the apparent replacement of green anoles by brown anoles in urban areas of Florida has been mentioned repeatedly (e.g. Collette 1961, Wilson and Porras 1983, Case and Bolger 1991), and detailed natural history studies (e.g. Schoener 1968, 1975, Lister 1976a) and experimental manipulations (Losos and Spiller 1999, Spiller and Schoener 1998) have been conducted using the Bahamian populations of these two species, but there have been few studies of the interaction in North America. Interspecific behavioral interactions involving these two species are apparently less frequent and less intense than are intraspecific interactions (Tokarz and Beck 1987, Brown and Echternacht 1991). Although no definitive studies of exploitative competition have been performed in North America, their Bahamian analogs are known to consume similar arthropod prey (Schoener 1968). Results from a recent cage study suggest a negative effect of brown anole presence on egg production in female green anoles (Vincent 1999), and data from a recent study utilizing depletions and augmentations of dietary resources of sympatric populations of these species on small islands in Florida indicate that food limitation affects these species differently (Porter and Campbell, in prep.). Hatchling competition has been suggested (G. Gerber, pers. comm.), and hatchling predation by both species has been documented (Campbell and Gerber 1996). In fact, asymmetric intra-guild predation, in which resource competitors also consume each other (Polis et al. 1989), has been be invoked to describe this interaction (Gerber and Echternacht in press). However, the types of data needed to demonstrate the occurrence of resource competition and intra-guild predation in these species have never been gathered in natural systems. The fact that green anoles began disappearing from urban and disturbed areas of Florida only after the arrival of the brown anole, but persisted in natural habitats, suggests that green anoles are negatively affected through the combined negative effects of habitat alteration and interaction with brown anoles (Echternacht and Harris 1993).

To begin studying exploitative competition and intraguild predation between two species in natural situations, one must first demonstrate that prey resources are shared by the suspected competitors, that the shared resources are also limited during some stage of their life cycle, and that the competitors actually eat each other in the field. However, conclusive demonstration of the negative effects of exploitative competition (or intraguild predation) can only be made by manipulating prey resources or experimentally removing or adding one or more of the suspected competitors, and showing that these actions were the direct or indirect cause of the observed negative response (Underwood 1997).

Given the paucity of background information on this interaction, four questions come to mind: 1) what is the taxonomic identity and diversity of the prey items taken by each species? 2) to what extent do these two morphologically different species overlap in the prey taxa they consume, and is the extent of overlap influenced by differences in body size or feeding apparatus (or both)? 3) does the high level of sexual dimorphism in these species result in dietary differences within species, but across sex (intraspecific-intersexual) that are more dramatic than are differences across species, but within sex (interspecific-intrasexual)? 4) does sexual dimorphism in ecomorphology and microhabitat choice (e.g. perch height) of the lizards interact with the behavioral ecology and habitat choice of their prey to influence the number, volume, taxonomic identity and diversity of prey of the two species and sexes when they are sympatric? I set out to answer the first three questions with detailed stomach content analyses, and approached the fourth question qualitatively by integrating results from this study with numerous published accounts of the behavioral ecology of *Anolis* lizards and their terrestrial arthropod prey.

In this study, I document the taxonomic identities of all the prey items found in the stomachs of *Anolis carolinensis* and *A. sagrei* collected from sympatric populations occurring on three dredge-spoil islands in east-central Florida. I use multivariate methods to test the influence of island identity, lizard species, and lizard sex, on eight variables collectively: two numerical prey variables, two volumetric prey variables, and four lizard body variables. Next, I document lizard dietary diversities and dietary overlaps from a taxonomical perspective, and test hypotheses using one numerical and one volumetric prey variable, and quantitatively relate lizard morphological overlap to lizard dietary overlap. Finally, I integrate these results in a qualitative manner with known ecological and behavioral parameters of the lizards and the morphology, behavior, and ecology of the arthropods they consumed. To my knowledge, this is the first study documenting the dietary niche breadth and dietary overlap between these species in syntopy in the field in North America, and is the sole attempt at testing hypotheses about these two predators and their prey, using the full complement of species and sex as factors. As such, it addresses only two of the many evidential requirements for demonstrating interspecific exploitative competition and intraguild predation in this interaction.

METHODS

Study Area

I collected anoles from three dredge-spoil islands located in the Indian River Aquatic Preserve north of Ft. Pierce in St. Lucie County, Florida (Figure 3.1; all figures are in the Appendix). I chose these particular spoil islands because of their proximity to, and physical and vegetative resemblance with, nearby spoil islands that were being used for an experiment testing the effect of insect population depletion and enrichment on the outcome of the interaction between green anoles and brown anoles (Porter and Campbell in prep.). In short, it was necessary to determine whether or not the insects being depleted and enriched in that study were from the same taxa as were the insects being consumed by the lizards. More importantly, these spoil islands were similar to the highly disturbed, biologically invaded coastal habitats of central and south Florida, and supported reasonably dense populations of both species in relatively simple habitats where lizards were easy to capture in suitable numbers over short periods of time.

This chain of islands was created by the U.S. Army Corps of Engineers between 1958 and 1960 as a by-product of the construction of the intracoastal waterway. The islands I used were about 2 ha in area, dome-shaped, and dominated by the exotic Brazilian pepper (*Schinus terebinthifolius*) and Australian pine (*Casuarina* sp.), which form a canopy over 10 meters high. A few native cabbage palms (*Sabal palmetto*) remain in the interior, and red mangrove (*Rhizopora mangle*), black mangrove (*Avicennia germinans*), and buttonwood (*Conocarpus erectus*) line the shore. Sea grape (*Coccoloba* *uvifera*) and sea oxeye (*Borrichia frutescens*) occur in the understory, which is also dominated by small Brazilian pepper. Soil is well developed and covered by a thick layer of leaf litter contributed by mainly exotic vegetation. The eastern shorelines are generally dominated by mangroves, but the western shorelines were typically eroded and undercut by boat wakes from the intracoastal waterway, which lies about 100 meters to the west.

Island Choice and Sampling Period

I performed preliminary surveys in 1995 and 1996 to find islands in Indian River Lagoon near the study islands used by Porter and Campbell (in prep.) that contained large, syntopic populations of both species of lizards in complex habitat with vegetation at least 5 meters in height. At least five of the eleven large (2 ha) islands immediately north of Ft. Pierce met these conditions (Figure 3.1). I randomly chose three of these islands as replicates (SL6, SL8, and SL14), and collected lizards during the afternoons of May 30 and 31, 1996. Sufficient numbers of both species were collected on SL6 and SL8, but only two green anoles and only 14 brown anoles were captured on island SL14. I returned on June 11 and 12, 1997 to collect more lizards. Suitable numbers of both species were retrieved from island SL13, however, no green anoles were found on island SL6 a few days before the official survey date, and I was able to capture only a single green anole and only 32 brown anoles on island SL8 in 1997.

In summary, collections suitable for species comparisons were made from only three islands; two (SL6 and SL8) in 1996, and one (SL13) in 1997, giving total of 12 lizard sub-samples (two species and two sexes from three islands). Although the collections were separated by a full year, they were made within 14 days of each other on their respective calenders, so should be comparable from a seasonal standpoint. However, their value as true replicates was severely diminished by the confounding effect of year. Ultimately, because these islands were not chosen in a purely random fashion in the first place (e.g. they had to contain large numbers of both species and be close to the other study islands), "island" was simply considered a fixed effect in hypothesis testing, which guaranteed model simplicity, but revoked my ability to generalize to other systems.

Logistical considerations and time constraints forced the sampling periods to be brief, which limited my ability to generalize these results to other times of year. However, "point-samples" have a distinct biological advantage in a study of this type. First, the perch height distributions of these two species in sympatry are very different than perch distributions observed in allopatric populations (Campbell, in prep.), and removal of significant numbers of *Anolis* lizards should rapidly influence the spatial organization of remaining *Anolis* lizards (e.g. Leal et al. 1997). Thus, large-scale lizard removals over long periods of time would likely influence lizard spatial organization and prey choice, and ultimately confound results. Also, long-term removals (days or weeks) would be likely to influence the numbers and types of prey available to remaining lizards (e.g. Dial and Roughgarden 1995), especially if such resources were previously limited in supply, and would confound results in an ever increasing manner as lizards were collected.

This sampling regime brought with it a cost of not being able to generalize the results to different seasons, during which prey availability might be more (or less) limited. On the other hand, the value of this study lies in the high-resolution contrasts of stomach contents and body parameters of four behaviorally and ecologically distinct types of adult lizards, all of which may or may not be involved in intense competitive interactions. This is merely a study of the *potential* of the adults of these species to compete for food resources during the summer reproductive season.

Lizard Collection and Body Measurements

A team of three to six workers captured lizards during random-walk surveys conducted after 1000 AM to insure that the lizards had ample time to forage on the day they were captured. I established four rigid protocols for capturing lizards: 1) Although unintentional perception biases are inherent in any visual survey (e.g., conspicuous individuals), lizards were captured in the order they were found, to minimize intentional sampling biases such as the avoidance of lizards in dense vegetation. 2) Because green anoles (especially females) were less abundant and more difficult to find and capture, they were awarded the highest priority for capture, and were captured "at all cost," in order to equalize sample sizes as much as possible in the face of extremely dense brown anole populations. 3) After capturing a green anole, workers searched the immediate area and captured at least one brown anole of the same sex and approximately the same size. 4) To ensure that only adult lizards were utilized in the analyses, workers were instructed to visually estimate SVL and capture only reproductive-sized females and males (larger than 35 mm and 40 mm SVL, respectively; Lee et al. 1989). These protocols ensured that specimens of both species were spatially and temporally syntopic at the smallest scale possible, and as morphologically similar as possible.

Workers noosed, hand-grabbed, or used rubber-bands to stun lizards, which were immediately killed by inserting a metal probe into the rear of the braincase. I measured snout-vent length (SVL), tail length, and tail regeneration to 1.0 mm with a clear plastic ruler, and weight to 0.1 gram with a Precision Spring Scale (Avinet, Inc.), then tied a museum tag to the rear leg. To halt digestion as soon as possible, I injected 10% formalin into each lizard's body cavity within two minutes of capture. Lizards were fixed in 10% formalin for one week, then transferred to 70% ethanol for permanent storage. Following preservation, I measured head length (HL), head width (HW), and head depth (HD) to the nearest 0.1 mm with dial calipers (Helios, Inc.). Head length was measured as the point-to-point distance from the tip of the snout to the anterior edge of the ear aperture.

Stomach Content Analyses

First, I placed the stomachs into individual vials with matching museum tags, ensuring that lizard identities were unknown while their stomach contents were being identified and measured. I analyzed only stomach contents to avoid errors that might result from identification, measuring, and counting highly fragmented, decomposed prey items in the intestinal tract. I counted prey items as the minimum number of *whole* animals possible in each prey category, and measured the length and width of each prey item to 0.1 mm with dial calipers. I established a reference collection with at least one whole representative (or a disarticulated individual possessing all body parts) from each prey category. Disarticulated prey items were assembled for measurement, and the measurements of partial or badly damaged prey items were estimated from whole or reassembled animals from the reference collection. The volume of each prey item was calculated with the formula for a prolate spheroid (Dunham 1981, Vitt and Zani 1998):

$$\text{Prey volume} = {}^{4}/_{3}\pi(\tfrac{1}{2}\ \text{prey length}) \times (\tfrac{1}{2}\ \text{prey width})^2$$

Prey items were identified to the lowest taxonomic level possible (generally to family or genus) and segregated by size, life-history stage, and ecology, resulting in a matrix of 84 prey categories. The 84 groups vary widely in taxonomic level (species to class) and many disarticulated or damaged items had to be placed into miscellaneous or unknown categories. Thus, I established 28 "condensed" prey categories for data analyses, consisting of orders and higher taxa, with the exception of ants (Hymenoptera: Formicidae), which are routinely separated out for such analyses. I was able to place every prey item confidently within one of the 28 higher categories, hence, there was no need for an "unknown" category. Clearly, in comparisons of diet breadth and overlap, a trade-off exists between the logistics and errors inherent in using numerous, high-resolution, lower taxonomic categories, as opposed to the ease and accuracy of using a few higher taxa that give fairly low taxonomic resolution. I used categories that were generally equivalent to those used in previous studies (e.g. Pianka 1986, Vitt and Zani 1998) so the data would be valuable in a comparative sense, but refined the categories based on the ecomorphologies and behaviors of these differentially arboreal predators, so the categories might better resolve the reasons for any differences in the prey consumed by the two sexes of these species.

That non-prey items such as gut parasites, shed skin, or parts of plants might have a confounding effect on the numbers or sizes of prey items was carefully considered using basic statistics. I established five additional categories for stomach contents thought to be "non-prey" items (nematode, trematode, skin, plant, and empty). "Nematode" included any members of the phylum Nematoda, and "trematode" included any members of the class Trematoda in the phylum Platyhelminthes. These were considered gut parasites, although I have yet to identify these specimens to lower taxonomic levels. Nematodes and trematodes were generally very tiny (< 3 mm long and 0.1 mm in diameter), so were simply counted. "Skin" represented pieces of lizard skin, which anoles normally consume during the shedding process. "Plant" represents leaves, sticks, seeds, or other vegetative materials considered incidental to prey capture. Shed skin and plant material was ranked from 1 to 5 as the percent of space (by volume) occupied in the stomach *relative to all other stomach contents* (i.e., 1 = 0%-20%, 2 = 20%-40%, 3 = 40%-60%, 4 = 60%-80%, and 5 = 80%-100%).

Microhabitat Analyses

Microhabitat data were not gathered as the anoles were captured because time constraints and associated sample size considerations required a maximum number of lizards to be collected over the shortest possible time period, and relatively disruptive techniques were often used to capture, at "all cost," the first lizard seen, especially if it was a green anole. This often involved substantial disturbance of leaf litter and vegetation, so lizards were very likely disturbed prior to being seen by their ultimate captor. Thus, the position of lizards when first seen may have had little relation to their preferred perch and foraging positions a few hours prior to capture. Were perch data collected during this study, they would likely have been severely biased by the collectors and might have lead to spurious claims about the effect of microhabitat choice (e.g. vertical distribution) on dietary diversity and overlap.

In fact, the microhabitat preferences and perch height distributions of these two species are well known, as they have been studied intensively in the Caribbean for over 30 years (e.g. Schoener 1968, 1975), and extensive data sets exist for Florida as well (Campbell in prep., Gerber in prep.). Furthermore, between 1996 and 1998, perch height data was collected on hundreds of anoles on smaller spoil islands supporting the same vegetation and located adjacent to these islands in the Indian River Lagoon (Porter and Campbell, in prep.). These data were qualitatively compared with the numerical and taxonomic results from quantitative analyses.

Data Organization and Statistical Analyses

I summarized lizard and prey data by island, species, and sex, and performed statistical analyses of prey diversity, prey overlap, and lizard body parameters using multivariate and univariate analysis of variance (MANOVA and ANOVA, respectively) and principal components analyses (PCA) platforms in JMP (SAS Institute Inc. 1995). Although the fixed-effect ANOVA model is robust to unbalanced samples and departures of normality, particular attention was paid to assumptions of independence, equality of sample variances, and normality of the data and residuals from each model. All sample data sets were tested *a priori* for normality (Shapiro-Wilks test) and visual inspection of normal quantile plots, and for equality of the group variances (Levine's test, $\alpha = 0.05$).

Model adequacy was assessed by analyzing the model residuals for normality and lack of pattern when plotted against predicted values of the variables. When necessary, data were transformed using the Box-Cox method (Box and Cox 1964).

The comparison of greatest interest lies between green anoles and brown anoles. However, because adults of these species are highly sexually dimorphic in their body sizes, behaviors, and microhabitat utilization (e.g. Schoener 1975), analyses of differences between males and females, both within and across species, are also essential. Thus, four "species-sex" groups, or "SS groups" were recognized: green anole females (AcF), green anole males (AcM), brown anole females (AsF), and brown anole males (AsM). The three islands were used as replicates to test hypotheses about these four groups, so the data were also partitioned by island, resulting in 12 distinct "island-species-sex" (ISS) groups. Because of the manner in which islands were chosen (e.g. only islands containing large populations of both species and located near the islands in the Porter and Campbell study), island was considered a fixed effect in all analyses. This limits the ability of the results to be generalized to other habitats or even other spoil islands, but simplifies the models used in, and the results of, the hypothesis testing process.

In addition to simply documenting the taxonomic diversity and size distribution of prey items taken by these two species, this study tests four null hypotheses:

I. There are no differences in numerical or volumetric distributions of prey items taken by these lizards, when compared across ISS, SS, island, species, or sex,

II. There are no differences in body parameters of adult brown anoles and green anoles regardless of sex or island,

III. There are no differences in taxonomic breadths of the diets of these lizards, when compared across ISS, SS, island, species, or sex, and

IV. There are no differences in the dietary overlaps across the six possible comparisons of the four SS groups.

To prepare the data for testing Hypothesis I, two variables were calculated and summarized by ISS and SS group: 1) the number of prey items found in each stomach (n_{prey}) and 2) the number of prey taxa found in each stomach (n_{taxa}). Next, volumetric data for individual prey items were summarized by ISS and SS group for basic analyses of prey size distributions. However, individual lizards are the only appropriate sampling units for testing the hypothesis in this study (e.g. Aebischer et al. 1993), so I calculated two lizard-wise volumetric parameters: 1) the mean volume of the individual prey items in each lizard's stomach (Mean V_{ind}), and 2) the total volume of all the prey items found in each lizard's stomach (V_{tot}). It is clear that all four of these prey parameters are related, as they were calculated from the same individuals, so are non-independent, and must be analyzed with a multivariate model (e.g. MANOVA or PCA).

For a number of reasons, Hypotheses I and II were first tested simultaneously by including the four lizard body parameters (SVL, HL, HW, and HD) with the four prey variables in a multivariate MANOVA model. First and foremost, for statistical validity, the measured lizards clearly cannot be considered independent of the prey items they consumed. Secondly, and of greater biological relevance, lizard body size and shape of the feeding apparatus (the head) was included to tie morphological differences (if they occur) directly to any differences in the numbers or sizes of prey items consumed by different ISS or SS groups.

To control experiment-wise error rate, the effects of island, species, and sex were tested for a total of eight variables simultaneously, four describing the predator and four describing the prey. The eight variables were cast into a 3-way MANOVA ($\alpha = 0.05$) using island, species, and sex as factors. MANOVA serves to eliminate the inflation of Type I errors that results from using more than one univariate statistical test to address a single hypothesis, but is also valuable because it points directly to the main effects (or their interactions) that actually require *post hoc* univariate analyses. This is preferable to combining some or all of the variables to create new variables prior to the analyses (e.g. "head volume" calculated from HL, HW, and HD by the formula for a pyramid), because such parameters might miss differences in head shape.

To test Hypotheses I and II separately, the four body variables and four prey variables were analyzed *post hoc* with separate univariate ANOVAs ($\alpha = 0.05$), each a 3-way model using island, species, and sex as factors. However, only the statistically significant effects or interactions from the original MANOVA were considered *post hoc*, to avoid inflating experiment-wise error rate. Based on the results of the MANOVA and individual ANOVAs, I conducted additional *post hoc* analyses of differences in the four SS groups using principal components analysis (PCA) in order to better visualize any body and prey differences between the two species and sexes. PCA reduces the dimensionality of a multivariate data set by describing the structure of the data in as few variables as possible (Digby and Kempton 1987). Several abstract variables, the principal components, are constructed by using linear combinations of the original variables (standardized so the group means are zero and group variances are unity). Linear combinations maximize the variance of these components, each successive component being uncorrelated with the previous one. Eigenvalues describe the variance of each component, and sum to the number of variables in the analysis (in this case, 8). To visualize differences between the four SS groups, I plotted data clouds for each in two-dimensional principal components space using the first two principal components, which, by definition, should explain most of the variation in the model. The magnitude of differences between each group were assessed by calculating the distances between each combination of the four multivariate SS group means, or centroids.

Lastly, I used discriminant analysis (DA) on the body variables (SVL, HL, HW, and HD) to test the morphological distinctness of the four SS groups and to verify the analyses of body parameters that tested Hypothesis II. DA is similar to PCA, but it simply predicts the level of a one-way classification based on known response values, which are measured by Mahalanobis distance: the distance of each observation from each of the four multivariate group means, or centroids. DA was used to predict the identity of the four SS groups within which each lizard should fall, thus determined whether or not the four groups of lizards could be effectively distinguished using the four morphological characters that were measured. The degree of morphological distinction between the four groups was then discussed in terms of their observed dietary breadths and overlaps.

To prepare the data for testing Hypothesis III, dietary niche breadth (B) was calculated by constructing taxonomic distributions (as histograms) of the prey items represented in each of the 28 prey taxa. Numerical and volumetric data from prey items in each category were summarized for each ISS and SS group, then dietary niche breadth was calculated for two variables: 1) the proportion of the number of individuals (P_{ind}) in each of the 28 prey categories (hence, B_{ind}), and 2) the proportion of the total volume (P_{vol}) of prey items in each of the 28 prey categories (hence, B_{vol}). Both variables were calculated by the reciprocal of Simpson's index (Simpson 1949):

$$\text{Niche Breadth (B)} = 1 / \sum_{i=1}^{s} p_i^{\,2}$$

where p_i represents either the proportion of the number of individuals found in each taxon (P_{ind}, for B_{ind}), or the proportion of the total volume represented by each taxon (P_{vol}, for B_{vol}), and s is the number of taxa in the sample. This index, sometimes called Hill's N_2 (Hill 1973), has been used in a number of studies on dietary niche breadth in lizards (e.g. Pianka 1986, Vitt and Zani 1998). Whereas the original Simpson's index (D) determines the probability of randomly selecting two organisms from the *same* taxon, and Simpson's diversity index (1-D) represents the probability of randomly picking two organisms from different taxa from a sample, the 1/D modification represents the number of equally common prey taxa that must be present in the sample in order to generate the observed heterogeneity of the sample. This is a valuable comparative tool, because the value of 1/D ranges from a minimum of unity (a single prey taxon present from all the lizard stomachs in the sample) to a maximum of s (an equal utilization of all possible prey taxa by lizards in the sample). Also, in any form, Simpson's index tends to emphasize common species in a sample (Hill 1973), thus, probably considers the most valuable food items for lizards.

To test for differences in dietary diversity between the four SS groups (Hypothesis

III), Simpson's index values were pooled across the three island replicates. Because the two overlap variables were calculated from the same prey items, they were not independent variables, so the two were analyzed simultaneously with a 2-way MANOVA, using species and sex as factors, and the three islands as fixed replicates ($\alpha = 0.05$).

To test for differences in dietary overlap between the lizards of each ISS group on each island (Hypothesis IV), I first constructed resource-use matrices using P_{ind} and P_{vol} values from each of the 28 taxonomic groups, then calculated Pianka's index of dietary overlap (Pianka 1986, pp. 81) for each of the six possible group comparisons. The index, O, is a symmetric version of a niche overlap equation initially proposed by MacArthur and Levins (1967) and, although it is similar to a "competition coefficient," this index cannot confirm competition because it does not account for limitations in supplies of the resources in question. Moreover, while limited resources are required to implicate competition, only experimental manipulations can provide true evidence that competition actually occurs within or between species (Underwood 1986).

For each variable (P_{ind} and P_{vol}), I determined the species-wide dietary overlap (between all green anoles and all brown anoles) on each island by pooling data for males and females. Species-wide values were only used to obtain a general indication of overlap between the species, and were not analyzed statistically. Next, I calculated specific overlap values for every combination of the four individual SS groups, which resulted in six types of overlap values (henceforth, "SS overlaps") for each island as follows: two within-species, across-sex, or *intraspecific-intersexual* SS overlaps (AcF vs. AcM and AsF vs. AsM), four different within-species overlaps, two of which are *interspecific-*

intersexual SS overlaps (AcF vs. AsF and AcM vs. AsM) and two of which are *interspecific-intrasexual* SS overlaps (AcF.vs. AsM, and AcM vs. AsF).

To test Hypothesis IV, data were pooled across the three islands for each of the six SS overlap types and tested for differences among them using a 1-way ANOVA (α = 0.05), with SS overlap type as the factor (six levels). The magnitudes of overlaps between the four SS groups were then used to suggest the most likely sources of resource competition between the two species (and sexes), and to suggest the possible roles of microhabitat in the interaction, based on a knowledge of anole ecomorphs and their known perch distributions. Finally, the histograms showing prey taxonomic distributions for each ISS and SS group were qualitatively associated with the results from above hypothesis tests and published literature on the behavioral ecology of the prey items consumed, so the reasons for overlap or lack thereof could be viewed in a taxonomic light.

RESULTS

Stomach Contents Overview

A total of 197 adult anoles (65 *Anolis carolinensis* and 132 *A. sagrei*) were captured on the three islands (Table 3.1; all tables are in the Appendix). Different numbers of lizards were captured on the three islands, the fewest from SL6. Fairly equal proportions of each species were obtained from island SL6, but over twice as many brown anoles were collected on islands SL8 and SL13. A larger proportion of males were captured for each species and each island, except green anoles from SL6. Of the 197 stomachs opened, one was completely empty, eight contained only non-prey items, and 188 (95.4 percent) contained at least one prey item (Table 3.1). There were no obvious patterns describing empty stomachs or stomachs containing only non-prey items across island, species, or sex, other than a preponderance of nematodes in brown anoles on island SL8.

At least one nematode worm was present in 52 stomachs: 66 percent from island SL8, eight percent from island SL13, and none from island SL6 (Table 3.1). Only three green anole stomachs contained nematodes. Overall, very similar numbers of brown anole males and females contained at least one nematode (48 and 43 percent, respectively). Although nearly three times as many nematodes were found in the stomachs of males (mean = 9.48; s.d. = 14.79; n = 31) than were found in the stomachs of females (mean = 3.81; s.d. = 3.49; n = 21), the difference was not significant (t = 1.72; df = 50; P = 0.0915). A few tiny trematode worms were present in the stomachs of three brown anole females on island SL8, but these lizards also contained nematodes and prey items in their stomachs. These nematodes and trematodes were assumed to be gut parasites, and all the nematodes appear to be of the same species, but they have not been accurately identified to lower taxonomic levels.

The numbers of nematodes present in the stomachs were not associated with the body sizes (SVL) of the lizards containing them ($r^2 = 0.036$; $F_{1,50} = 1.8543$; $P = 0.1794$). More importantly, the number of nematodes in the stomachs had no significant influence on the number of prey items ($r^2 = 0.0011$; $F_{1,51} = 0.057$; $P = 0.813$) or the total volume of prey items ($r^2 = 0.0039$; $F_{1,51} = 0.197$; $P = 0.659$) in the stomachs. The vast majority of the stomachs contained less than 10 worms (mean 7.2; median 3.5; s.d. = 11.89; 95% C.I = 3.8-10.5; max. = 82), most of which were very tiny (< 3 mm long and 0.1 mm in diameter), thus occupied a small percentage of the stomach by volume. Although these worms likely feed on stomach contents, the results suggest that nematode presence was not a confounding factor in the stomach content analyses. This was an important result, as stomachs containing nematodes could not be excluded without severely compromising sample sizes, especially on island SL8 (Table 3.1).

Shed skin was found in 44 stomachs, ranging from a few scales to what appeared to be the entire body surface, but most stomachs were placed in the lowest of the five skin categories, thus contained less than 20 percent by volume relative to the other stomach contents (mean category = 2.0, median = 1.0; s.d. = 1.35; 95% C.I = 1.59 - 2.41). The vast majority of stomachs that contained shed skin (37 of 44 stomachs) also contained prey items. However, larger amounts of skin were associated with fewer prey items (r^2 = 0.093; $F_{1,43}$ = 4.304; P = 0.044) and smaller total volumes of prey (r^2 = 0.101; $F_{1,43}$ = 4.707; P = 0.036). In fact, all 5 stomachs from island SL6 and both stomachs from island SL13 that contained large amounts of shed skins lacked prey items (Table 3.1), but by definition, these seven lizards were not included in further analyses (they contained no prey items). For the remaining 37 lizards possessing skin and prey items in their stomachs, there was only a marginal effect of shed skin on prey numbers (r^2 = 0.105; $F_{1,35}$ = 4.097; P = 0.051) and volumes (r^2 = 0.117; $F_{1,35}$ = 4.620; P = 0.040). These results indicate that the shedding process influenced the diets of these lizards, but not to a degree that warranted excluding all 37 stomachs containing skin from further statistical analyses.

Plant material consisted of mostly small sticks, Australian pine leaves, or small seeds, and were considered a by-product of arthropod prey capture. Of the 24 stomachs in the study that contained plant materials, 22 stomachs had less than 20 percent of their contents represented by plant materials (category 1) and only two had between 60 and 80 percent plant material (category 3), relative to the amount of food in the stomach. Compared to the prey items, plant materials were infrequently consumed, and when consumed, comprised a relatively small volume of the stomach contents.

Sizes of Individual Prey Items

A total of 1,764 prey items were retrieved from the 188 lizard stomachs (Table 3.2), illustrating two important points regarding the sizes of individual prey items taken by these lizards. First, in all possible groupings (ISS, SS, species, island), standard deviations are larger than means, means are much larger than medians, and data ranges are much larger than 95% confidence intervals, indicating that lizards took prey items from a wide range of prey size classes, and that size distributions (not shown), which were severely skewed to the right, showing that the stomachs contained a few extremely large, influential outliers.

Second, the group means, medians, and 95% confidence intervals for individual prey volumes indicate that lizards consumed mainly small prey items, a finding consistent regardless of how the data are pooled; by sex, by species, by island, or any combination of these (Table 3.2). In fact, 90 percent of the 1,764 prey items were less than 26 mm^3 in volume, corresponding to a prey item less than 7 mm long and 3 mm in diameter. In every group, about 10 percent of the prey items were less than 0.20 mm^3 in volume, exemplified by an ant measuring only 1.5 mm in length and 0.5 mm in diameter. Group medians are especially illustrative. For example, the median volumes of prey items taken by females are about 4 mm^3 or less, corresponding to a fly measuring about 4.5 mm in length and 1.4 mm in diameter. Likewise, the median volume of prey items taken by males (highly variable, but generally around 9 mm^3) is equivalent to a beetle just over 4 mm long and 2 mm in diameter. Larger prey items, such as cicada crawlers and cockroaches ($\geq$ 300 mm^3) measured at least 16 mm long and 6 mm in diameter, but were represented in less than 0.5% of most samples. The largest prey item (942 mm^3) was an 18 mm long, 10 mm diameter cockroach taken by a large male brown anole on island SL8. Although lizards from all groups consumed extremely small prey items (minimum volumes are less than 0.5 mm^3 in all 12 groups), the largest individual prey items were taken by brown anole males.

Although volumetric data for individual prey items are useful in a descriptive sense, analyses of such data would completely miss the variation inherent in the predators, which were the main subjects of interest in this study. In fact, individual lizards are the only biologically and statistically appropriate sampling units for this type of a comparative study (e.g. Aebischer et al. 1993). In the following analyses, the lizards themselves were viewed as the sampling units (n = 188), and only the mean and total volumes of all the prey items in each lizard's stomach were used for testing hypotheses relating prey volumes to groups of lizards.

Multivariate Analyses of Prey and Body Variables

Although fixed-effect ANOVA and MANOVA models are relatively robust to violations of assumptions of data normality, unequal variance across groups, and even non-independence of data, transformations were necessary in this study. Data describing the numbers of prey (n_{prey}), numbers of taxa (n_{taxa}), mean volume of prey (Mean V_{ind}) and total volume of prey (V_{tot}) in each of the stomachs (n = 188) were not distributed normally within the 12 ISS groups, and group variances were significantly different among each variable, so data for all four variables were transformed using the Box-Cox method ($n_{prey}^{0.4}$ - 1 / 0.1221, $n_{taxa}^{0.6}$ - 1 / 0.3730, Mean $V_{ind}^{-0.2}$ -1 / -0.0074, and $V_{tot}^{-0.2}$ -1 / -0.0046, respectively). Transformed data were normalized and variances were equalized across all 12 ISS groups. Conversely, the raw data for the body parameters (SVL, HL, HW, and HD) met the assumptions required by MANOVA, so were left in their original form.

The 3-way MANOVA on the eight variables returned significant P-values for the three main effects and two of the 2-way interactions (Table 3.3). Dropping the non-significant island*species*sex interaction from the original model rendered the P-value for the island*sex interaction slightly less marginal (more significant), but did not change the outcome of any significance tests, despite the fact that two degrees of freedom were redistributed throughout the model. Residuals analyses for all eight of the variables in the full model indicated the MANOVA model was appropriate for testing Hypothesis I and II.

To test Hypothesis I and II, separate *post hoc*, univariate, 3-way ANOVAs were performed on each of the eight variables (Table 3.4). The results from each test are discussed below with reference to summary statistics for each associated variable: number of prey (Table 3.5), number of taxa (Table 3.6), mean volume of individual prey items (Table 3.7), total volume of prey items (Table 3.8), and the four body parameters (Table 3.9). Only the significant results from the original MANOVA were considered in these *post hoc* tests, to avoid inflating experiment-wise Type I error rates.

The average lizard stomach in this study contained about nine prey items in three to four taxa (Table 3.5). The range of the number prey items found in individual stomachs was large in every group. Between 39 and 61 percent of the 28 taxa were represented in each of the 12 ISS groups, and 57, 75, and 71 percent of the 28 taxa were retrieved from all the stomachs on islands SL6, SL8, and SL13, respectively (Table 3.5). Stomachs that contained more prey items also contained significantly more prey taxa ($r^2 = 0.20$; $F_{1,187} = 45.69$; $P < 0.0001$).

In the *post hoc* univariate ANOVAs for the numerical prey variables (Hypothesis I), island remained a significant effect on n_{prey}, but was not on n_{taxa} (Table 3.4). In fact, lizards from island SL8 contained the most prey items (Table 3.5) and taxa (Table 3.6) per stomach in almost every group comparison. Species was not a significant main effect for either variable, in stark contrast to the MANOVA results (Table 3.3). Stomachs of females contained significantly more prey items and prey taxa than did males in nearly every comparison, thus, sex remained a highly significant main effect for both variables in the univariate ANOVAs (Table 3.4). In fact, with only one exception (brown anoles on SL6), more prey items were present in fewer female stomachs (Table 3.5). For both variables, neither the marginally significant island-sex interaction, nor the highly significant species*sex interaction from the MANOVA (Table 3.3) were supported in the univariate

ANOVAs (Table 3.4). Thus, for both numerical variables, the identity of the island had no bearing on the direction or magnitude of the significant differences between the two sexes: females generally contained more prey items and taxa in their stomachs. Likewise, sexual differences in the numerical prey variables did not depend on species identity.

Separate ANOVAs for the two volumetric variables (Hypothesis I) returned the same result for each, in which species and sex were significant, but the significant island effect in the MANOVA (Table 3.3) disappeared in both univariate tests, as did both significant interactions (Table 3.4). Brown anole males and females consumed substantially larger prey items (Mean V_{ind}) than did their green counterparts on all but island SL13 (Table 3.7), on which female green anoles were slightly larger than female brown anoles.

Sexual differences in Mean V_{ind} were highly significant (Table 3.4) and substantial (Table 3.7). In fact, males consumed prey that were, on average, 2- to 11-times more voluminous than were prey consumed by females. Specifically, the mean individual prey volumes from male green anoles and brown anoles were 2- to 3-times larger and 3- to 11-times larger, respectively, than their female counterparts. Although this is not supported by a significant species*sex interaction, morphometric results (see later analyses) indicate a greater degree of dimorphism in the brown anoles collected in this study.

Regardless of these interspecific and intersexual differences, Mean V_{ind} data only describe the size of prey that lizards are capable of eating. Although this is important for relating prey size choices to lizard head sizes and shapes (see later analyses), the total volume of all the prey in each lizard's stomach (V_{tot}) combines all the food items taken in by these lizards during their most recent meals, thus serves to compare lizard stomach volumes. This variable is essential to estimate the relative ability of a given lizard group to deplete food, a particularly important consideration during times when food is limited in supply.

Species and sex were the only significant effects on V_{tot} (Table 3.4). Brown anoles consumed much larger total volumes of prey items than did green anoles on each island (Table 3.8), however, this finding was attributable mainly to males. Regarding sex, group means and maximum V_{tot} values show that males consistently consumed larger total volumes of prey than did females (Table 3.8). Moreover, the mean V_{tot} values for male brown anoles were between 2.5 and three times that of their female counterparts, whereas mean V_{tot} values for male green anoles were only about twice that of their female counterparts. This suggests different levels of dimorphism in body parameters (next analysis) are reflected in the prey sizes captured by the lizards, however, this was not supported by a significant interaction in the ANOVA model (Table 3.4).

Results from univariate 3-way ANOVAs for each body parameter (Table 3.4) clearly rejected Hypothesis II, and helped to define morphological differences in the lizards (Table 3.9). Island was a significant main effect for the variables SVL and HW, but not for HL or HD. In fact, the largest animals of all four SS groups were collected from island SL13 (Table 3.9), but for both species, mean SVLs from island SL13 were only about 2 mm larger for males and about 1 mm larger for females, relatively small differences by adult lizard standards for either species. This difference might have arisen because 1) the SL13 lizards were collected almost 14 calendar days later in the calendar year and were, on average, older than were the SL6 and SL8 lizards, 2) because they were collected during a more productive year for lizards or their prey, 3) because of some characteristic of the island SL13 promoted better growth than either SL6 or SL8, or 4) a combination of two or more of these explanations. The significant HW difference across island can be explained by the same factors explaining SVL, but the biological differences are minute (Table 3.9). This, combined with the lack of significant differences in HL and HD across islands indicates that SVL differences contributed the most to significant island differences in the original model.

Species was a highly significant main effect for all but SVL (Table 3.4), indicating that, although adults of these species were similar in body sizes, overall head size and shape were significantly different. Specifically, the heads of green anoles (especially males) are long and wedge-shaped (somewhat like a door-stop), and the heads of brown anoles are shorter, wider, and deeper. Sex was a highly significant main effect for all four variables (Table 3.4), as would be expected in these sexually dimorphic species. This may be a result of sexual differences in overall body sizes (SVL), but the head parameters of female lizards also appear to be very different than male head parameters in each species.

The significant island*sex interaction in the original MANOVA (Table 3.3) was not significant in any of the univariate ANOVAs (Table 3.4). In other words, sexual differences in individual parameters were not influenced by the identity of the island from which the lizards were collected. Conversely, the highly significant species*sex interaction in the original MANOVA model (Table 3.3) remained highly significant for three of the four morphological variables, and marginally significant for HL (Table 3.4). This is probably due to differences in the degree of sexual dimorphism exhibited by these two species. As expected, males were larger than females with respect to all body parameters, both within and across species, and on all islands (Table 3.9). However, the SVL of male brown anoles differed from that of females by about 14 mm, whereas green anole males and females differed by only about 10 mm. This pattern was also true for HW (2.5 mm and 2 mm differences, respectively) and HD (2 mm and 1.5 mm differences, respectively). However, the trend was opposite for HL, in which green anole males differed from females by about 4 mm, whereas brown anole males and females differed by only about 3.5 mm. Simply put, male green anoles had disproportionately long heads and male brown anoles had disproportionally short heads, relative to the other lizards in the study.

The above results indicate that, within SS groups (AcF, AcM, AsF, and AsM), lizard morphology was similar enough across the three islands that all the same-species, same-sex lizards could be pooled for additional *post hoc* analyses (PCA and DA). Although lizards from SL13 were slightly larger than those on the other two islands (Table 3.9), interactions with "island" were significant in only one out of 12 interactions containing island as a factor (Table 3.4). In short, lizards on island SL13 were larger, but proportioned the same as lizards on the other two islands. Furthermore, when pooled across the three islands, data for the four SS groups (Table 3.9) exhibited similar variances and approximated normal distributions.

Confusion remains about the use of data from multiple samples (i.e. islands) in a single PCA because of the potential for confounding within- and between-group variation (James and McCulloch 1990). To be safe, I first ran separate PCAs for each island and compared the results visually (Table 3.10). The amount of variation explained by PC-1 and PC-2 were similar for each island (over 97 % for each), and the eigenvectors of the first principal component for each of the four variables were strikingly similar on the three islands. Eigenvectors for PC-2 were also very similar, and the four SS groups clustered almost identically in separate scatter plots of PC-1 against PC-2 for each island (not shown). Thus, it was appropriate to pool the morphometric data from each SS group across the islands for the PCA.

Results from the PCA on the composite data sets (Table 3.11) confirmed the above statements about individual head parameters, and the formulas for each component better explained the contribution of each body parameter to the observed species and sexual differences. Over 88 percent of the variation was explained by PC-1 and over nine percent was explained by PC-2, thus the first two principal components describe over 97 percent of the variation in the analysis (Table 3.11). A plot of PC-1 against PC-2 (Figure 3.2) graphically illustrated the clear separation between the four SS groups. The variation explained by PC-1 reveals the extreme sexual dimorphism in the morphology of these two species. In fact, the formula for PC-1 (Table 3.11) indicates it was constructed almost entirely around head parameters HD and HW. Thus, the two variables describing the cross-sectional area of the head were the most important in separating the two sexes along this axis (Figure 3.2) and overall robustness of the head is probably the most important factor in describing intraspecific sexual differences. Although PC-2 reveals differences explained by lizard species, the influence of sex is also obvious: the data clouds for females were separate but adjacent, whereas the data clouds for males were separated by a distinct gap (Figure 3.2). The formula for PC-2 (Table 3.11) indicates that PC-2 was constructed mainly around the variation in HL.

Ultimately, differences between the four SS groups can be ordered from largest to smallest, using the group means, or centroids (Figure 3.2), as follows: 1) between males and females *across* species, 2) between males and females *within* species, 3) between males across species, and finally 4) between females across species. The sexes are most distinct because of the larger size and more robust heads of male lizards. A high level of male-male head distinction is achieved because male green anoles have long, narrow, wedge-shaped heads, whereas male brown anoles have short, robust heads. Heads of the adult females collected in this study are clearly the most similar in size and shape.

Using the four morphological variables, discriminant analysis (DA) was able to predict the correct SS groups in 195 of the 197 lizards in this study: one female green anole and one male brown anole were erroneously grouped with female brown anoles. The values of Mahalanobis' distances mirrored the results of the PCA, but was able to define the order of differences in the six possible SS group comparisons to an even greater degree as follows (again, in descending order of difference): 1) AcM vs. AsF, 2) AsM vs. AcF, 3) AsM vs. AsF, 4) AcM vs. AcF, 5) AcM vs. AsM, and 6) AcF vs. AsF (see PCA centroids in Figure 3.2). Despite the clarity of these results, lizard morphological relationships are only meaningful in this study when associated directly with patterns of prey taxonomic diversity and diet overlap.

In an attempt to associate lizard morphology with diet in one multivariate analysis and test Hypothesis I and II simultaneously, the data for all four prey variables (n_{ind}, n_{taxa}, Mean V_{ind}, and V_{tot}) and all four morphometric parameters (SVL, HL, HW, and HD) for all 188 adult lizards containing at least one prey item in their stomachs were cast into a single PCA. The first two principal components accounted for over 75 percent of the variation in the model, and the first four accounted for over 94 percent of the variance in the model (Table 3.12). A plot of PC-1 against PC-2 (Figure 3.3) indicates an almost complete absence of intersexual overlap, or a high degree of sexual dimorphism, for both species (PC-1), and substantial overlap between the two species within each sex (PC-2). The PCA formula for the first component (Table 3.12) indicates that two body variables (HD and HW) were again the most important parameters defining sexual differences. The PCA formula for the second component indicates that two prey variables (n_{ind} and n_{taxa}) were the most important in describing the extreme interspecific-intrasexual overlap between the numerical and volumetric diet variables and morphology of the two species. A plot of PC-1 against PC-3 (not shown) results in very similar groupings.

In summary, both Hypothesis I and II were rejected by the above results. Body parameters explained sexual differences, but were not as effective in explaining species differences, whereas prey parameters did not effectively separate either species or sex (Figure 3.3), indicating high overlaps in the number of prey items and taxa taken by the lizards. Volumetric parameters were not influential in any of the first four principal components (Table 3.12), probably because variation in these parameters was fairly high. Again, numerical and volumetric overlaps are taxon-free variables, so provide little indication of the taxonomic identities, taxonomic diversity, or taxonomic overlaps of prey items taken by these lizards. Detailed comparisons of the taxonomic diversity and overlap in the diets of these lizards can only be made by integrating these results with the distributions of arthropods taken by the lizards.

Dietary Niche Breadths

Measured by the proportion of the number of individuals in each taxon (B_{ind}), green anoles exhibited consistently higher Simpson's index values than did brown anoles, with the exception of males on island SL6 (Table 3.5). However, measured by the proportion of prey by total volume (B_{vol}), no consistent pattern across species or sex was evident (Table 3.8). Results from the 2-way MANOVA testing the influences of lizard species and sex on the two variables (B_{ind} and B_{vol}; islands pooled) were not significant for species (Pillai's Trace = 0.3027; $F_{1,8}$ = 3.4722; P = 0.0994), sex (Pillai's Trace = 0.0246; $F_{1,8}$ = 0.2016; P = 0.6653), or their interaction (Pillai's Trace = 0.0134; $F_{1,8}$ = 0.1084; P = 0.7504). Removal of the highly non-significant interaction from the model to re-distribute degrees of freedom slightly decreased the P-value for species (Pillai's Trace = 0.2998; $F_{1,9}$ = 3.8540; P = 0.0812), but barely altered the highly non-significant P-value for sex.

Although Hypothesis III cannot be rejected, it appears that raw numerical and raw volumetric dietary diversities of these species might be different, and further studies are warranted to resolve the marginal P-value obtained for the species effect. These results imply that brown anoles eat relatively large numbers of prey items from a few taxonomic categories, whereas green anoles eat relatively equal numbers of prey items from each prey taxa. However, the sexes may not differ with respect to these variables.

These variables were constructed from taxonomical distributions of prey items in the different groups, however, the 1/D index is only a single, dimension-free descriptor of the taxonomic evenness of each sample, with values ranging from one (a single prey taxon) to the total number of prey taxa in the sample (e.g. compare B_{ind} in Table 3.5 with the maximum number of prey taxa in each group in Table 3.6). However, it says nothing of the taxonomic identities of the prey items taken by the lizards. In fact, samples containing completely different numbers or types of prey items could exhibit similar values for this index. Only detailed analyses of differences in the proportions of individual prey taxa can provide true indications of dietary overlap.

Dietary Overlaps

Although the number of prey items, taxa, and Simpson's index of each sample are valuable in a comparative sense, only Pianka's dietary overlap index can actually quantify the degree of dietary overlap between samples. Values of Pianka's index calculated from the proportion of individuals (P_{ind}) in the 28 categories (Table 3.13) demonstrated that dietary overlap between the two species in general (sexes pooled) was around 0.91, that overlap was extensive regardless of the SS groups compared (ranging from a low of 0.75 to a high of 0.98), and that values were fairly consistent across the three islands.

Pianka's overlap values calculated by the proportion of total volumes of prey items (P_{vol}) in the 28 categories (Table 3.14) were much different than overlap values obtained from prey number data. It is clear that niche breadth and overlap values generated by volumetric data were influenced by different factors than were overlap values generated by prey numbers. Even the overlap values for the pooled species comparison (males and females combined) ranged between 0.60 and 0.87, indicating high overlap, but fairly substantial variation in the values as measured by prey volume. In fact, overlap values for the 18 individual comparisons ranged from a low of 0.12 to a high of 0.87, and were highly variable across the three islands.

Based on the above, it is not surprising that results from 1-way MANOVA using SS overlap as the factor (six levels), the values of Pianka's overlap for P_{ind} and P_{vol} as the two variables, and islands as replicates (n = 3), show no differences between any of the six contrasts (Pillai's Trace = 0.1151; $F_{5,12} = 0.3121$; P = 0.8963). Thus, with respect to the proportion of the total number of prey items and the proportion of the total volumes of prey items represented by prey in each of the 28 taxonomic groups, the four SS groups overlap in a similar manner regardless of which groups are being contrasted, and Hypothesis IV must be rejected. This analysis incorporated two variables that, although non-independent, were apparently very different with respect to their degree of variation across the 28 taxonomic groups. A deeper look into the sources of differences between the numerical proportions and volumetric proportions in each taxonomic group sheds light on the sources of variation in dietary diversity and overlap between these species, and leads to integration of morphology, diet, and ecology of the lizard predators and their arthropod prey.

Graphical Interpretation of Prey Data Distributions

Taxonomic influences on the values of Simpson's index and Pianka's overlap index were assessed graphically by constructing "prey histograms" showing the proportions of the numbers of prey items (P_{ind}) found in each of the 28 taxonomic categories. Prey histograms were constructed for each species (sexes pooled) and each SS group on each island, then plotted against each other by species overlap and by each of the six possible SS overlap types, resulting in seven sets of histograms (Figures 3.4A-G). The same exercise was performed on the data describing the proportions of the total volume of prey items (P_{vol}), and these seven sets of prey histograms (Figures 3.5A-G) were compared with those generated from the P_{ind} data sets. This technique facilitates a detailed, taxon-based assessment of the causes of high (or low) Simpson's index values and Pianka's overlap values, and an assessment of which variable might be the most important in future studies assessing exploitative resource competition between and across each sex of these species. These plots illustrate the high degree of dietary overlap in these species, but also revealed the subtle, but consistent differences in the diets of green anoles and brown anoles, as well as between males and females. When viewed together, the prey histograms, Simpson's index values, and Pianka's dietary overlap values allow powerful comparisons of the diets of the two species in general, and four SS groups in particular.

Prey histograms constructed from numerical proportions, P_{ind} (Figures 3.4A-G) clearly show the sources of large values in both Simpson's and Pianka's indices. Likewise, histograms for volumetric proportions, P_{vol} (Figures 3.5A-G) revealed the reasons for low Simpson's indices and high variability observed in Pianka's overlaps, and indicate that variability in P_{vol} was the main factor contributing to the highly non-significant results in the MANOVA testing for differences between the six SS overlap types. These distributions are especially illustrative when viewed in light of published biological information about the prey items themselves.

Numerically, ants (Form) were by far the largest components of the diets of both species. Overall, brown anoles consumed higher proportions of ants than did green anoles (Figure 3.4A) and males always consumed equal or larger proportions of ants than did females of the same species (Figures 3.4B and C). Comparisons across species but within sex (Figures 3.4D and E) illustrate that brown anoles consume more ants. Given the above, it is not surprising that brown anole males consumed higher proportions of ants than did green anole females (Figure 3.4F). However, even brown anole females consumed an equal or greater proportion of ants than did green anole males (Figure 3.4G).

Ants made up a much smaller proportion of the diets of these lizards by volume than by number, especially on island SL13 (Figure 3.5A). Also, female brown anoles consumed much larger proportions of ants than did male brown anoles (Figure 3.5C), female green anoles (Figure 3.5D), or male green anoles (Figure 3.5G). This was consistent with the respective numerical proportion data (Figure 3.4). Although brown anoles in general, and female brown anoles in particular, were clearly not ant specialists, a large proportion of their diet consisted of ants. Their vertical distribution (generally below 1.0 m above the ground) and foraging strategy (sit-and-wait) render ants, which are relatively small, very abundant, and constantly moving prey items, vulnerable to predation by brown anoles. This is true for green anoles as well, despite their more elevated perches, because ants often climb high in vegetation, but ant nests are generally ground-based, so they must "run the gauntlet" of waiting brown anoles before being exposed to green anoles. However, ants reach very high densities, and are unlikely to be limiting to either species.

Other prey taxa are not as well represented as ants, but illustrate differences in prey consumption by the two lizard species. Overall, green anoles consumed more flying and vegetation-perching insects such as wasps (Hym), adult flies (DipA), planthoppers (Hom), leaf bugs (Hem), dragonflies (Odo), and bark lice (Psoc), whereas brown anoles consumed more wingless, ground-dwelling, and larval taxa such as adult beetles (ColA), larval beetles (ColL), crickets and cockroaches (Orth), earwigs (Derm), centipedes (Chil), spiders (Aran), and as previously stated, ants (Figures 3.4A and 3.4D-G). There are also a few consistent differences between males and females with respect to the 27 non-ant prey taxa. For instance, females of both species consumed greater proportions of spiders than did their intraspecific male counterparts (Figures 3.4B and C).

The planthoppers (Hom) and leafhoppers (Hem) are sometimes combined as "bugs" in these types of studies (e.g. Pianka 1986) because they both obtain nutrients from the liquid contents of plants and are thought to be morphologically, behaviorally, and ecologically similar. I chose *a priori* not to combine these groups because they represent different insect orders, but it is noteworthy that green anoles consistently consumed greater proportions of both taxa than did brown anoles (Figure 3.4A). Furthermore, females were most responsible for the pattern (Figures 3.4B and D). But more interesting is the fact that larger proportions of planthoppers than leafhoppers were represented on islands SL6 and SL8 in 1996, whereas the opposite was true on island SL13 in 1997, indicating that planthopper deficits in the stomachs of lizards on island SL13 might have been offset by leafhoppers. The pattern of planthopper consumption seen on SL6 and SL8 was also observed in leafhopper consumption on SL13, where green anoles consumed larger proportions of leafhoppers than did brown anoles. Again, females were most responsible for the pattern, which may be evidence of a trade-off of similar prey species, reflecting different prey availability on different islands, or possibly in different years.

Noteworthy were four instances of anole hatchling predation documented in this study. Two male green anoles each contained one brown anole hatchling, and one female green anole contained two brown anole hatchlings. Although brown anoles are known to consume green anole hatchlings (Campbell and Gerber 1996, Gerber and Echternacht in press), this is the first demonstration that green anoles consume brown anole hatchlings under natural conditions, and the first indication that adult females might participate in hatchling predation. Although hatchling predation was infrequent, the hatchlings were large relative to most arthropod prey items consumed by these lizards. Similarly, many arthropod prey taxa that appeared to be unimportant in the diets of these lizards when viewed from a numerical perspective (Figure 3.4) were actually well represented from a volumetric perspective (Figure 3.5).

Volumetric diversity and overlap data were influenced by a few, large prey items. Most dramatic are the results for the Orthoptera (Ort), mostly represented by cockroaches (Blattidae) and various crickets. Of the 12 orthopterans found in lizard stomachs on island SL8, 11 were large cockroaches in brown anole males (Figures 3.5A, C, E, and F), and one small individual was found in a green anole female (Figure 3.5B, D, and F). The same pattern occurred on island SL13, where 6 out of the 7 cockroaches were taken by brown anoles (2 and 4 in females and males, respectively). However, on island SL6, only a single cockroach was found in the stomach of a male green anole (Figure 3.4), yet this individual prey item accounts for the apparent preference for orthopterans by green anoles on that island (Figure 3.5). Cockroaches from 3 mm to 20 mm occurred in large numbers on all the spoil islands, and nearly any habitat in Florida, and might be a significant food source for these lizards at all stages of their lives. Furthermore, although cockroaches and crickets are mainly ground-based arthropod that eat decaying vegetation (leaf litter), cabbage palms provide a source of large amounts of decaying vegetation, from ground to crown, in the crotches of dead frond-petioles, which are retained on the trunk for many years. These taxa and other detritivores are abundant on cabbage palm trunks, and may be significant source of food for vertically displaced green anoles where cabbage palms occur.

That the results for adult flies (DipA) in all the comparisons for SL6 and SL13 (but especially the latter) are opposite of results for numerical analyses is explained entirely by 10 very large mydas flies (Diptera: Mydidae). Only one mydas fly was taken by a green anole male on SL13, whereas six were taken by brown anole males, and one was taken by a brown anole female on that island (Figures 3.5A - G). On SL6, a female and a male brown anole contained one mydas fly each, but although the single fly had little affect on the results for male brown anoles, it dramatically affected the results for female brown anoles on that island (Figures 3.5C and D). Furthermore, all of these flies were either recently emerged with non-functional wings or were still in puparia, which places them writhing or crawling on or near the ground.

Also noticeable are values for the Homoptera (Hom), which appear contrary to the results generated by numerical data (Figure 3.4), especially on island SL6. This was due to large cicadas and their larvae (Homoptera: Cicadidae). Although both adults and larval “crawler” forms were represented, the latter was most numerous. Crawlers are large forms that emerge from a soil burrow and crawl slowly up shrubs and trees where they shed their last larval instar exoskeleton and hatch into adults. On island SL6, four of five cicadas were taken by brown anole males, and one was taken by a green anole male (Figures 3.5B, E, F, and G). This is the reverse of the pattern seen in the numerical data for that island (Figure 3.4). A similar pattern occurred on island SL13, where six of nine cicadas were taken by brown anole males, and the other three were taken by green anole males. Despite this, green anoles still exhibited larger volumetric proportions of homopterans in their diets on SL13, consistent with numerical data (Figure 3.4).

As previously stated, a number of large cockroaches were consumed by male brown anoles on SL8, but neither mydas flies nor cicadas were consumed by any lizards on SL8. Cockroaches are abundant on all these spoil islands, but large cicadas and mydas flies might have replaced cockroaches in the diets of male brown anoles on islands SL6 and SL13. This is plausible because all the individuals in both groups were emerging adults which would have been thrashing about while shedding the exoskeleton of their final instar. Thus, they might have been more vulnerable to brown anoles than would have been cockroaches.

Large dragonflies (Odonata) were taken on each island (Figure 3.5A), but mostly by male green anoles (Figures 3.5B, E, and G). Although dragonflies represented very small proportions of prey volumes on SL6 and SL13, a single dragonfly contributed nearly

30 percent of the prey volume taken by male green anoles on island SL8. Probably the most interesting results were the hatchling brown anoles found in both male and female green anole stomachs on SL13. For male green anoles, the proportional effect was not dramatic, but for female green anoles, over 40 percent of the prey volume in the sample was represented by only two brown anole hatchlings (Figures 3.5B, D and F).

In summary, these lizards consumed mostly very small prey items (Table 3.2), and as a result, values for Simpson's and Pianka's indices were often dramatically affected by a few large prey items distributed among a few prey taxa, especially when the SS groups being compared contained large prey items from different taxa. For example, comparisons of green anole females with either sex of brown anoles on island SL13 yield very low overlap values (Figures 3.5F and G), in part because of two brown anole hatchlings consumed by a single green anole female, and in part because of a few large prey items in a few arthropod groups (DipA, Hom, Hem, and Orth). This does not mean that overlap values calculated by volumetric data are meaningless. Rather, the interpretations of volumetric overlap data must be augmented by careful examination of the prey items that contribute to such results.

DISCUSSION

Parasite - Mediated Competition

Parasitic nematodes were present in many brown anole stomachs (except on island SL6), but were rare in the stomachs of green anoles (Table 3.1). These parasites did not appear to affect prey consumption. In fact, lizard stomachs from island SL8 contained large parasite loads (Table 3.1), but also contained the most prey items per stomach (Table 3.5). This does not mean that the nematodes had no effect on the anoles - they must have had a net negative effect, because they consume gut contents - but merely implies that the nematodes did not confound the results of the dietary analyses.

Parasite-mediated competition (Park 1948) has been documented in a number of species (Price et al. 1986). In short, because parasites negatively affect their host, they may also influence competitive relationships between their hosts and other species. Invading species often inoculate native species with novel parasites. Native species are usually harmed by novel parasites, but because the invaders generally have acquired some level of immunity, they are harmed less than the native species (Haldane 1949). The most dramatic examples of this phenomenon are the exterminations of many indigenous human populations by diseases brought by Europeans (Crosby 1986). In fact, colonizations of new sites by invaders are enhanced by this "natural biological warfare" (Price 1980).

Parasites such as malaria (*Plasmodium*) and intestinal nematodes are known to affect the outcome of anole competition (Schall 1992, Schall and Vogt 1993, Schall and Staats 1997) and anole micro-geographical distribution (Dobson et al. 1992). Because the helminth parasites in this study have yet to be identified, it is unclear whether brown anoles passed them to the green anoles, whether the green anoles or other Floridian lizards passed them to the brown anoles, or whether they are unique to each lizard species. If the worms were derived from North American lizards, brown anoles might have been infected at a higher rate because they are novel hosts without established defense mechanisms. Nematodes might negatively affect brown anoles, and in turn, help to ameliorate their negative effects on green anoles. But if the nematodes were introduced by brown anoles, green anoles are the novel host and might be affected by the parasites of brown anoles.

Clearly, this study does not provide evidence of parasite-mediated competition, but points to factors that must be accounted for in further studies of competition between these two species. Blood and gut parasite loads in these two species should be analyzed in both allopatric and sympatric portions of their ranges, especially at the leading edge of the geographical distribution of the brown anole (Campbell in prep.). Manipulative studies should be conducted to determine if they are passed between these lizard species, and if so, the rates of transmission and disease etiologies should be determined, so the potential for parasite-mediated competition can be assessed.

Lizard Size, Prey Size, and Resource Competition

Statistical analyses of the head parameters of the 197 adult lizards confirmed visual observations that: 1) the heads of adult males are larger than those of females, both within and across species, 2) adult green anoles have longer, narrower, and shallower heads than do adult brown anoles of the equivalent sex, and 3) adult females are more similar in head size and shape than are males. Similar results were obtained for these species on Bimini, where larger lizards consumed larger prey items, wider ranges of prey sizes, and fewer numbers of prey items than did small lizards (Schoener 1968, Schoener and Gorman 1968). Thus, one would predict the highest overlaps (by volume) to occur between females, based on the above facts and the similarities in their head parameters. Overlaps were high between females of these species on Bimini (Schoener 1968), but male green anoles could not be compared with any group because none were collected in that study. Although the volumetric overlaps between female lizards in my study were among the highest (Table 3.14), the data were highly variable and dramatically affected by a few very large prey items, and results were not significant.

Most of the lizards in this study ate very small prey items, none were wider than the lizard's head, and most were intact, indicating they were swallowed whole. Anoles generally swallow their prey whole but, unlike snakes, cannot disarticulate their jaws to accommodate large prey. To accommodate a large food item, an anole first chews it for a short period, then positions its long axis parallel to the lizard's body, then swallows it whole. Thus, head parameters directly influence the size of prey that lizards are able to eat and may influence the level of dietary niche overlap and the extent of resource competition (Schoener 1968, Schoener and Gorman 1968, Roughgarden 1995). Head length has been used in past studies to define head size and to correlate lizard size with the size of prey they can swallow (e.g. Lister 1976a, Schoener 1968). In this study, the heads of brown anoles were shorter, wider, and deeper than were similarly sized green anoles, and they consumed significantly larger prey items than did green anoles, which had longer heads

(Table 3.9). So, although head length positively correlates with prey size, it should not be used by itself in comparative studies, especially of these two species. Head length is mainly an indicator of gape size at the tip of the snout, and may be more important in fighting or prey capture, whereas head width and depth (or both combined as cross-sectional area) are better predictors of the ability of the lizard's head to accommodate a given prey item.

Lizards can swallow very long prey items (e.g. centipedes, millipedes, and beetle larvae in this study) and slowly pack them in the stomach as it expands and digestion proceeds. Thus, prey length *per se* may not affect the ability of a lizard to swallow a given prey item whole. For example, I watched a female brown anole consume a preying mantis longer than her own SVL. The extremely long prey items found in lizard stomachs in this study were not necessarily more voluminous than other prey items because they were also very narrow. However, the narrowness of such arthropods allows them to be consumed by even the smallest of lizards, introducing variability into volumetric data and potentially confounding dietary overlap values. Ultimately, the length of a prey item a lizard can swallow is more dependent on stomach size than head size, and is potentially confounding, so this parameter should be considered carefully if used as the sole measure of dietary overlap by prey size.

As a single measure, prey diameter is probably more meaningful than prey length in lizard dietary analyses because it relates more directly to the cross-sectional area of the mouth and throat opening of a lizard. Thus, the width or cross-sectional area of prey items might be the best predictors of dietary overlap by prey size, just as HW and HD (rather than HL) might be the best predictors of a lizard's ability to swallow prey. Measurements of the cross-sectional area of the mouth opening of each lizard (e.g. HW X HD) would provide the limits above which prey items could not be swallowed by a given group of lizards. Such calculations might especially help refine data sets that contain long and narrow, but relatively voluminous prey items.

In this study, with the exception of a few dragonflies, extremely voluminous prey items (e.g. mydas flies, cockroaches, and cicadas) were also large in girth; at or near the lizard's head width. Thus, analyses of mean prey volumes (Table 3.7) were probably appropriate for distinguishing the prey sizes these lizards could swallow. Measurements of total volumes of prey taxa in individual lizard stomachs describe the influence of lizard body or stomach size, rather than head size or shape, on dietary overlap by prey volume. Brown anoles are considerably more robust than are green anoles of the same size and sex (they weigh about twice as much as a green anole of the same SVL) and consumed larger total volumes of prey than did green anoles (Table 3.8). This implies that brown anoles are able to deplete arthropod resources more rapidly than are green anoles on a per-capita basis. Furthermore, brown anoles attain much higher population densities than do green anoles, are probably the most abundant lizard species in the Caribbean (Schoener and Schoener 1980), and I propose they are the most abundant terrestrial vertebrate species in urban Florida (Campbell and Echternacht in prep.). In fact, anoles are capable of depleting insect and spider populations (Dial and Roughgarden 1995, Pacala and Roughgarden 1984, Spiller and Schoener 1988, 1990, 1994, 1997, 1998). Thus, brown anoles are likely to affect the quantity of certain prey taxa available to green anoles, especially when the overall arthropod prey community is limited in supply.

By design, only adult lizards were collected in this study, so conclusions about diet diversity and overlaps must be restricted to the reproductive life stage. The results of this study suggest that sexual dimorphism in the adult morphologies and behaviors of these species result in differences in the types, numbers, and sizes of prey items taken by these lizards. In fact, sexual dimorphism in *Anolis* is thought to be the result of an evolutionary response to minimize the effects of intraspecific competition, in which sexual differences arose to decrease overlaps in the prey taxa consumed by the two sexes (Stamps 1983). Sexual dimorphism might also reduce the intensity of interspecific competition in this interaction, because there are four morphologically and behaviorally distinct players in the interaction, rather than just two, where lizards of the same sex and opposing species match more closely than do lizards of the same species but opposite sex. As a result, a given adult lizard should compete most strongly with same-sex congeners, and less so with opposite-sex congeners, cutting the negative effect of interspecific competition by a substantial amount. However, results of this study do not reveal consistent patterns in this regard. In addition, the body parameters of hatchling and juvenile stages are very similar across the four SS groups (Schoener 1968, 1975) and those stages may compete intensely for similar-sized arthropod prey (G. Gerber, pers. comm.). Clearly, more rigorous gut-content sampling is needed to determine whether or not the lowest adult dietary overlaps occur between the opposing sexes of opposing species, the highest adult dietary overlaps occur between same-sex congeners, and even higher overlaps occur between the juveniles and hatchlings of these two species regardless of their sex.

Arthropods and Energetics

Optimal foraging predicts that predators should maximize their energy gained (e) per unit time spent capturing and swallowing the prey (t): the e/t ratio (Schoener 1969a). For insectivorous lizards, small prey items are said to provide the best e/t ratio, and if available, should be the largest component of the diet (Schoener 1971, Pough and Andrews 1985). Results of this study are consistent with these predictions in that both species of anoles ate mostly very small prey items (Table 3.2). In particular, they consumed larger proportions of ants by number and volume (Figures 3.4 and 3.5). These results seem odd because small prey items by definition have high surface area-to-volume ratios relative to larger prey items, so indigestible exoskeleton makes up a larger proportion of an ant than, say, a cockroach. Therefore, a given mass of ants should contain less digestible material and should provide less energy per unit mass than a cockroach of the same mass. However, ants are available in great numbers, are much easier to catch, and require very little handling time. In fact, brown anoles in particular were regularly seen lapping up ants from long caravans as they marched by.

Despite the fact that large arthropods have lower e/t ratios (Pough and Andrews 1985) and are not as abundant as are small arthropods below 3 mm in length (Andrews 1979, Janzen and Schoener 1968), a large fraction of energy requirements of lizards are often met by large prey items because small items are unavailable (Pianka 1986, Roughgarden 1972). Although most of the prey items in this study were small, some very large prey items were represented (Table 3.2), and were negatively correlated with the number of prey items in the stomach. But the stomachs that contained large prey items probably contained fewer small prey items because they were extremely full rather than because fewer small prey items were available. Furthermore, the e/t ratio may not be the main driving force behind prey consumption in these lizards.

Energetic values of most arthropods are high enough, relative to the energetic costs of finding, catching, and swallowing them, that those costs can be ignored (Pough and Andrews 1985). It follows that the physical size of the prey rather than the energetic cost of consuming it sets the upper limit of what a lizard swallows. The risk of predation is likely substantial during the swallowing of a large prey item, and must be considered as well. In fact, on many occasions I have observed these species spend over 10 minutes consuming extremely large items on exposed perches, and they were extremely easy to capture during that period. Although the payoff of successfully swallowing a large item is surely grand, a lizard might pay for a mistake with its life. So, lizards must choose from a wide spectrum of prey ranging between 1) those that are smaller and less valuable in absolute terms but are more numerous, easily captured, and valuable in e/t ratio, and 2) those that are larger and more valuable as individual meals, but lower in e/t ratio, less abundant, and harder to capture and swallow.

Prey Availability and Resource Competition

Food availability clearly affects growth rate, reproduction, and survival, and may affect the outcome of exploitative competition. In this study, I did not attempt to determine the availability of arthropods in the field. Representative samples of arthropods can only be obtained by using multiple, time-intensive, and costly sampling strategies, such as pitfall traps, vacuum traps, sweep nets, and baited sticky-traps (Southwood 1978, McDonald et al. 1989). It can be argued that these techniques do not collect the prey types that are actually available to lizards, especially in arboreal situations (L. Vitt, pers. comm.). For example, such devices often capture arthropods that are really unavailable to lizards because they are too large or toxic for the lizards to eat or too cryptic for them to find. Moreover, lizards often capture prey items that cannot be captured using the above techniques. Despite the inherent circularity of such arguments, only analyses of the entire spectra of arthropods actually present in the guts of all the lizard species in the community in question can show which arthropods are really available to the lizards.

A number of studies have employed randomization algorithms to construct model "pseudo-communities" generated from Monte Carlo simulations of all the prey items taken by a number of predators, to which the diet of each individual predator is compared (Winemiller and Pianka 1990, Vitt and Carvalho 1995, Vitt and Zani 1996, 1998). This technique is extremely powerful when analyzing the diets of many different predators that eat very different prey. A detailed pseudo-community analysis would have been inappropriate in this study because the lizard "community" on these islands consisted of only two members (or four, if the two sexes are considered different "functional species") which consumed very similar prey taxa and were easily compared using simpler methods.

The results of this study simply define the prey diversity and overlap in the adults of these two species, and are enlightening despite the lack of arthropod abundance data or pseudo-community analyses. However, this study was merely a point-sample of the diets of these species. Seasonal and spatial aspects of prey availability must be considered in studies of resource competition between these, or any species.

Temporal Aspects of Resource Competition

Precipitation is a seasonal phenomenon in Florida, the highest volumes occurring between May and October (Fernald and Patton 1984). The effect of precipitation on vegetation growth and arthropod abundance have been documented in a number of systems (e.g. Hunter and Price 1998). Consequently, insectivorous lizards are affected indirectly by precipitation through its effects on vegetation and arthropod abundance (Dunham 1978, 1981, Anderson 1994, Guyer 1988, Stamps 1977, Stamps and Tanaka 1981). Because I conducted this study in early summer after the onset of the wettest part of the year, arthropods should have been abundant relative to other times of the year. It is possible that arthropod food resources were not limiting to these anoles when they were collected. Exploitative resource competition requires that a resource be limited in supply, thus should have been relatively relaxed if it occurs at all, and dietary overlap values should have been high relative to other times of the year.

During the summer, the energy requirements of adult green anoles and brown anoles are at a maximum due to their intense reproductive efforts. If prey items are unlimited, the reproductive efforts of these lizards should be unaffected. During times-of-plenty, lizard diets should overlap extensively, but prey choice should be influenced more by the lizard's choice of microhabitat or by the availability of its prey than by exploitative competition. But when prey are limited, these two species could either 1) exhibit a high degree of dietary divergence and specialization on exclusive prey types, or 2) undergo intense exploitative resource competition. More likely, if they compete at all for food, they minimally alter their foraging habits and reach some intermediate level of prey overlap in an attempt to ameliorate the effects of exploitative resource competition. Even minor changes in foraging habits might, however, affect lizard growth, reproduction, and/or survival, especially during hard times, or in habitats where food resources are highly variable due to disturbance by humans.

Spatial Aspects of Resource Competition

Both of these species are sit-and-wait foragers, but exhibit slightly different foraging behaviors. Brown anoles are more often seen perched for long periods in one or few spots in their relatively small territories near the ground, from which they pounce on moving prey. Green anoles are more variable in their method of hunting and capture. They utilize sit-and-wait methods, but also actively search for prey by slowly creeping along trunks and branches in their larger, more arboreal territories. One adult male was observed picking individual aphids (Homoptera) from leaves and flower heads as it slowly crept through a stand of sea oxeye, a low coastal herb. Green anoles were occasionally observed lapping nectar from saw palmetto (*Serenoa repens*) flower heads.

That green anoles in this study exhibited slightly higher dietary diversities than did brown anoles (but not significantly so) is contrary to results obtained on Bimini (Schoener 1968) and Exuma (Lister 1976a). Again, in the former study, male green anoles were not considered, and in both studies, additional anole species were present. My results show that, although green anoles did not consume different numbers of prey or taxa than their brown counterparts, they consumed prey more evenly from their chosen prey categories (Table 3.5). I propose this was a result of their use of more varied hunting techniques among larger and more arboreal territories than did brown anoles, which probably waited for more motile, ground-based prey to walk past. In the end, it is not surprising that these two similar sized, visually-oriented insectivores ate similar prey, given that they exhibit a high degree of similarity in their choice of habitat.

Despite high overlaps in habitat choice of these edge-preferring species, it is well-known that they perch at significantly different heights in vegetation (Lister 1976a, 1976b, Schoener 1968, 1975, Williams 1969, 1983). Although both utilize the ground, green anoles generally avoid the ground and low perches when in the presence of brown anoles (Lister 1976a). On adjacent islands in Indian River Lagoon green anoles perched higher (mean = 72.60 cm; s.e. = 2.86; range 0 - 420 cm) than did brown anoles (mean = 50.84; s.e. = 1.48; range 0 - 320 cm), which were most often found perched on dead branches near the ground (S. Porter, pers. comm.). Whether or not this difference is statistically significant or biologically meaningful in a habitat with a canopy over 10 m in height remains to be seen. However, the green anoles captured in this study were sparse on perches below 20 cm, and in a related study (Chapter 4), allopatric green anoles exhibited a perch height distribution not unlike brown anoles, whereas sympatric green anoles perched significantly higher, indicating that they were excluded from the lower perches by brown anoles. Specifically, male green anoles perched the highest, followed by green anole females, which often occupy perches over 1 m high but are also found near the ground. The vast majority of male brown anoles are found perched within 1 m of the ground, and most female brown anoles are found very near the ground or in leaf litter. But did brown anole stomachs contain more prey items because the lizards were closer to the ground, or simply because they were larger lizards?

The numbers, taxa, and biomass of arthropods also vary with vertical space in complex habitats (e.g. Brown et al. 1997). As a result, prey choices of anoles should be influenced by their spatial distributions relative to the distributions of the arthropods they consume, and likewise, the spatial distribution of anoles are probably influenced by the spatial distribution of the arthropods they consume (e.g. Patterson 1999). My results support these statements, as green anoles consumed more flying and herbivorous insects and brown anoles consumed more ground-dwelling detritivores. This is consistent with a study conducted over 30 years ago on these species in Bimini (Schoener 1968) except for ants, which in my study green anoles consumed in larger proportions. Also, lizards perching closer to leaf litter and soil (brown anoles) should have larger numbers and taxa of prey available to them, however, the green anoles in my study appeared to have the most diverse diets. Again, one must question whether brown anoles contain more prey because they are larger or because they perch closer to leaf litter and soil, the sources of the most arthropod prey.

Dietary overlap results (Table 3.13) are enlightening with respect to habitat overlap. Female green anoles overlapped least with male brown anoles (but not significantly so), the group with which they overlap most in vertical distribution, than with any other lizard group in this study. Again, this could be the result of their extreme difference in size. They also exhibited lower overlaps with brown anole females than with the other groups, although none of the differences were significant. High intraspecific-intersexual overlaps were contrary to that expected, especially within brown anoles, and may have been largely due to ant consumption.

With regards to volumetric data, Schoener (1968) found that on Bimini, intraspecific overlap values were larger than interspecific overlap values, and that lizard groups with higher microhabitat overlaps exhibited lower overlaps by prey size. However, no statistical support was given for either statement, minimal graphical support was given for the former (Schoener 1968, Figure 10, p. 719), and the origin of the latter does not appear to be supported by the data presented. My volumetric overlap data (Table 3.14) do not support either statement. First, perch height overlaps are the highest between male and female brown anoles or male brown anoles and female green anoles, and lowest between male green anoles and male or especially female brown anoles. In fact, intraspecific-intersexual overlaps for both species are among the lowest of all, and interspecific-intrasexual overlap values are the highest for both sexes when measured by volume (Table 3.14). This is probably explained by the fact that I analyzed only adult lizards, and intraspecific differences were more a result of lizard sexual size dimorphism than microhabitat choice. The fact that I analyzed only adults from two species and Schoener analyzed all age-classes of all four species of lizards present on Bimini (except adult male green anoles) limits the comparability of these two studies, and limits the applicability of his study to the seasonal cohorts present in Florida (Lee et al. 1989, Campbell and Echternacht, in prep). Furthermore, in volumetric analyses, it is impossible to separate the effects of lizard size from the effects of microhabitat distribution on lizard diet without experimentation.

The perch height shift observed in green anoles soon after the arrival of brown anoles is an important phenomenon regardless of our lack of understanding of the mechanism. Because arthropods are more abundant nearest the ground (e.g. Brown et al. 1997), fewer prey items and taxa might be available to green anoles than were available prior to the upward niche shift. Dietary plasticity probably helps to ameliorate the effects of the vertical shift, but the amount and quality (i.e. energy value) of prey items taken by green anoles in the presence of brown anoles is likely diminished by their being excluded from the ground level. Thus, interference competition (causing perch height shifts) and exploitative competition (causing diet shift) could be interacting to produce a substantial negative effect on green anoles. Clearly, the negative effects of "perch height-mediated dietary shifts" exhibited by green anoles would be most dramatic during times of limited resources (e.g. the dry season). However, because arthropods vary in abundance over vertical space, I propose that the negative effects of perch height-mediated dietary shifts might even be realized during times when resources are abundant and the effects of exploitative competition should otherwise be at a minimum. Of course, if this phenomenon even occurs, it can only be demonstrated with controlled experiments.

Hatchling Competition and Intraguild Predation

This study addresses only adult lizards, which are the most different in their morphologies and behaviors. Hatchlings and juveniles of both species increase in number and grow in size throughout the summer, and could be important elements in the competitive interactions between these species, if in fact competition occurs. Hatchlings and juveniles are very similar in size, regardless of sex, and likely overlap greatly in their prey resource use, because they can only consume the smallest of prey items. The more abundant brown anole (hatchlings and adults) might be able to decimate food resources enough to impact the reproductive output of adult green anoles and the growth rate and over-winter survival of young-of-the-year green anoles (Gerber pers. comm.). However, the smaller taxa of arthropods are also the most abundant, so are least likely to be limited in supply under natural conditions.

Hatchling lizards are both consumers of small prey items and potential prey items themselves. This study pre-dated the onset of extremely dense hatchling populations, thus could not address dietary overlap between adults and hatchlings, or between hatchlings of both species. In an earlier study on Bimini (Schoener 1968), the diets of adult male and female brown anoles overlapped marginally with hatchling and sub-adult green anoles and brown anoles. The juveniles of both species overlapped substantially, and green anole hatchlings overlapped substantially with adult female brown anoles, however, the overlap between adult male green anoles and hatchling brown anoles was not determined because adult male green anoles were not collected. Also, the results of that study might not be comparable with my study system because four anole species were present. Nonetheless, it is reasonable to assume that dense populations of growing hatchlings (especially brown anoles) are consuming a considerable amount of arthropod prey, possibly from taxa consumed by adult and hatchling green anoles.

At the latitude of my study site (Figure 3.1), hatchlings and juveniles are present in late May, but do not become abundant until about mid-June. In mid-summer, adults of both species eat mostly small prey items (Table 3.2) such as ants, plant hoppers, and spiders (Figure 3.4), all of which are probably also consumed by hatchlings (Schoener 1968). In late summer and fall when hatchlings become superabundant and arthropod populations presumably decline, small food items could become limiting to adult males and females of both species. If true, this might force adults to concentrate on larger prey items (including hatchlings) which are less abundant and more difficult to find, capture, and swallow. But without further studies incorporating hatchlings, conclusions regarding their impact on the arthropod fauna or the lizards that consume them remain conjecture.

On the other hand, hatchling lizards are a food source for anoles. The hatchlings of both species are consumed by the adults of both species (Campbell and Gerber 1996, Gerber and Echternacht, in press). Lizards are high quality prey items for at least two reasons. First, they are equivalent to medium to large arthropod prey items in volume and probably represent a substantial meal relative to other prey items, especially for female anoles (Figure 3.5). Second, they lack the tough, indigestible, and sometimes spiny exoskeleton possessed by many arthropods, so are easier to swallow and digest.

Hatchlings of both species increase in numbers during late June and might represent a significant protein source during late summer before they grow too large to be consumed. Of course, large males would be able to consume the growing hatchlings for much longer time periods than would females. Brown anole hatchlings become very abundant in low vegetation and leaf litter, and might represent a substantial dietary supplement for green anoles, especially for females, which perch lower in vegetation than do males. But green anoles become rare within a few years of becoming sympatric with brown anoles, and are unlikely to deplete dense brown anole hatchling populations after that time. They are likely harvesting a "doomed surplus" (Errington 1963) of brown anole hatchlings, the fraction which would undergo high mortality and not otherwise be recruited to adulthood (Guyer 1988).

Green anole hatchlings also perch low in vegetation, but do not become nearly as dense as their brown counterparts. However, they perch within the vertical range of both male and female brown anoles (Schoener 1968) and are highly vulnerable to brown anoles, which are more numerous and large enough to consume even large hatchlings. Because brown anoles become so dense, if even a small number of brown anole adults consume a single green anole hatchling during their lifetime, green anole populations would suffer considerably. So, although some proportion of green anole hatchlings are doomed to perish regardless of brown anoles, brown anoles are probably consuming more than just the "doomed surplus" of green anole hatchlings, thus causing the rapid declines seen within two years of the brown anole's arrival at a site.

General Applicability of This Study

The main concern in any sampling program is the ability to generalize the results to other localities or systems (Underwood 1997). Clearly, the three islands in this study were picked because they contained both lizard species in large enough densities that each could be collected in suitable numbers for statistical analyses. Thus, the results of this study are probably only applicable only to situations where the two species co-occur in fairly high densities and where food is unlimited, which would be expected in mainland habitats (Andrews 1976, 1979, but see Guyer 1988), especially after the onset of arthropod-inducing spring and summer rains (Dunham 1981).

It was unfortunate that lizards were collected from only three islands during only a single point in time. Species and sex are clearly fixed effects, but island also had to be considered a fixed effect because of the way in which the islands were selected and sampled. Fixed-effect models allow higher resolution of differences, but come at the cost of an inability to generalize beyond the study system. Statistically, these results cannot be extended to systems other than dredge-spoil islands in coastal Florida, but the results in this study were strong in most cases, make biological sense, and correlate with results from past studies (e.g. Schoener 1975, 1968). I propose that, at the very least, these results point to questions that should be addressed and design improvements that should be made during future studies. At best, the highly reductionist approaches I used in analyzing these data provide indications of the dietary niche breadth and degree of overlap of these two species in sympatry, especially in the extensive coastal regions of Florida that are dominated by the same, or similar exotic vegetation.

Based on a comprehensive faunal study of the islands (Florida Department of Environmental Protection 1989) and hundreds of hours of observation conducted over two summers, these islands supported few other potential competitors and predators of anoles (S. Porter, pers. comm.). Avian insectivores and potential anole predators (e.g. red-bellied woodpeckers, fish crows, herons and egrets) were occasionally observed. The mammal fauna was limited to introduced rats and mice, which probably eat anole eggs (A.

C. Echternacht, pers. comm.). Few snakes were observed on these islands and the only other small insectivorous lizard was the nocturnal Indo-Pacific gecko (*Hemidactylus garnoti*). This indicates that the spoil islands were species-depauperate in terms of vertebrates, relative to habitat islands isolated within an urban matrix, which would also have cats, mockingbirds, and other predators.

That large areas contain more species than do small areas has been known for some time (Gleason 1922), and was specifically demonstrated for invertebrates on small islands in Florida (Simberloff and Wilson 1969). Also, isolated oceanic islands generally support fewer species than do equivalent habitat areas on either continental islands or mainlands (MacArthur and Wilson 1967). As a result, it is often thought that island anoles are limited by food and mainland anoles are limited more by predation (Andrews 1976, 1979), although mainland anoles have also been shown to be limited by food (Guyer 1988). Dietary overlaps of the anoles in this study might have been high due to a limited number, biomass, or taxonomic scope of prey items available on the islands, forcing all the anoles to consume the same prey taxa, or due to an unlimited supply of the prey items and taxa that were taken by these lizards.

Although arthropod availability was not assessed, the speed with which discarded apple cores or unattended coolers are ravaged by ants, flies, and other species, and the presence of large numbers of both ground-dwelling and aerial web-building spiders suggest the second conclusion to be the most likely. The spoil islands used in this study were large (about 2 ha) relative to the extent of habitat required by anoles and their prey species. The islands lie in a lagoon system bordered by the mainland only 0.6 km to the west and a large barrier island only 0.4 km to the east (Figure 3.1). Each summer afternoon, prevailing on-shore breezes transport flying insects and ballooning spiders from the barrier island, and winds from storms to the west bring airborne arthropods from the mainland. Humans regularly transport terrestrial arthropods to the islands during camping trips, fishing excursions, and other water-based recreational activities, and leave huge amounts of arthropod-attracting garbage.

I propose that the arthropod faunas on these spoil islands are no less speciose than are isolated habitat islands on the mainland surrounded by a matrix of asphalt, and may actually contain more arthropods prey species than do many urban sites. In fact, if arthropod diversity is low on these islands, it is probably less likely due to size or isolation (e.g. MacArthur and Wilson 1967) than due to a predominance of exotic vegetation, which generally harbors less diverse arthropod populations (Schoonhoven et al. 1998). Arthropod faunas on these islands should closely resemble nearby coastal faunas on the mainland and barrier islands, which are also dominated by exotic plants. I propose the results of this study are applicable at the very least to coastal mainland systems dominated by exotic vegetation. In central and south Florida, such habitats are the norm.

Conclusions and Suggestions for Further Studies

Exploitative resource competition requires that resources be limited in supply. Large male anoles consumed larger prey items than did females, but they also consumed prey items from a large range of sizes, including small prey items within the size ranges consumed by females. Females of these species consumed very similar sized prey items.

Thus brown anoles, which maintained dense populations on these islands, likely consumed a large number of prey items that might otherwise have been available to green anoles. In a study of a mainland anole in Costa Rica (Guyer 1988), enhanced female survival was the main positive effect of food supplementation. It follows that food limitation might negatively affect females to the greatest degree. Although food limitation might not have been important during the period of my study, it might be during other times of the year when rainfall is lower.

Exploitative resource competition also requires that species overlap in resource use. In this study, high overlaps by numerical proportions point to two opposing conclusions. The first and most pessimistic is that the 28 categories utilized in the analyses were too general to differentiate the diets of these lizards. In fact, categories could be constructed so generally as to ensure high overlap or so specifically as to ensure very low overlap (Schoener 1968). Despite the high overlap values, this study revealed a number of consistent dietary patterns (e.g. green anoles consumed more vegetation-perching insects, and brown anoles consumed more ground-dwelling forms). Like many studies before, my ordinal level categories struck a balance between breadth and specificity in the prey items. Thus, I believe an alternative conclusion to be true - that overall, these species consume prey from the same taxa in similar numerical proportions, but that subtle dietary differences arise (Figure 3.4) that are largely consistent with their differences in morphology, behavior, and habitat use.

Overlap values generated from volumetric proportions were highly variable and revealed less consistent patterns both within and between lizard groups and islands. The low overlap values obtained in many of the volumetric comparisons indicated that the two species and sexes consumed prey in different volumetric proportions from the 28 different prey categories. In every case, the low overlaps could be attributed to a few large prey items consumed from different categories in each comparison (Figure 3.5). Thus, a few large prey items can create inconsistencies with overlap values established by numerical proportion data. However, volumetric data may be a better indication of true dietary overlap between these species because they describe lizard diets in terms of the energy derived from the different prey items. Green anoles might be able to ameliorate resource competition and persist in the face of brown anole invasions because they are able to shift their microhabitats and their diets and obtain energy from different prey types than are exploited by brown anoles. Unfortunately, a simple demonstration of overlap in dietary resources, or a lack thereof, can be evidence both for and against exploitative resource competition (Colwell and Futuyma 1971).

Because adult anoles consume prey from more than one trophic level (e.g. insects, spiders, and lizard hatchlings), they are both eating and competing with members of intermediate trophic levels (Pimm and Lawton 1978), a phenomenon termed intraguild predation (Polis et al. 1989). In the green anole-brown anole system, I propose that adult lizards compete with each other, their hatchlings, and with spiders for common arthropod prey, and also consume each other's hatchlings, their spider competitors, and each other's arthropod prey. Hatchling predation is probably the most significant cause of green anole population declines, given the speed with which green anole populations plummet. However, anoles are capable of depleting insect faunas (Dial and Roughgarden 1995) and eliminating all but the most common web-building spiders (Spiller and Schoener 1998), indicating that competitive forces are also at work. In the end, the relative strengths of the different forces that comprise intraguild predation in these lizard-spider-insect communities in Florida may depend on the relative abundances and identities of the players involved, the presence of other faunal elements such as anole predators and competitors, the habitat type at a given site, and the degree of spatial overlap of these lizards and their prey, all of which may change over time.

This study was merely a day in the life of these species. Clearly, the timing and duration of this study limits the ability of these results to be generalized over time. Only studies of temporal variations in dietary breadth and fluctuations in dietary overlap could refine the temporal aspects of exploitative competition between these species, if it occurs. Collections of lizards on a monthly basis or at least four times per year over a period of several years would better reveal the extent of variation in diet composition and overlap. This, combined with arthropod availability studies, might reveal periods when these two species compete for limited prey resources, if in fact they compete at all. Despite the probable futility of current arthropod sampling methods as a means of quantifying the prey available to lizards, arthropod availability (by number and biomass) should be determined concurrent with lizard gut content analyses, if only to determine overall temporal and spatial variation of arthropod populations.

Further studies should focus on dietary niche breadth and overlap during at least three additional time periods: 1) between August and October when hatchlings are present in great numbers, 2) between November and January when precipitation (and presumably arthropod prey) is at its minimum, and 3) in February and March when sub-adults from the previous summer's cohort are all about the same size and occupy similar microhabitats (Schoener 1968). Because of potentially limited prey supplies and the large numbers of lizards present, these two species probably exhibit greater dietary overlap and competition during these periods than during mid-summer.

Again, a simple demonstration of dietary overlap does not necessarily point to resource competition. An assessment of differences in the diets of these species in allopatry and sympatry would certainly be illustrative, but would still lack the direct causation required for unequivocal demonstration of exploitative competition. The nature and magnitude of exploitative competition between these two species and the specific effects on green anoles would best be demonstrated by analyzing the dietary profiles of green anoles before and after removals of brown anoles. The best design for this is probably a replicated split-plot design using lizard exclusion fences to separate control lizards (sympatric) from treatment lizards (allopatric green anoles) at the same site, so that arthropod populations are the same in the controls as in the treatments. Such a design would also reveal any niche-shift mediated dietary shifts and the potential for limited resources in elevated locations to contribute to exploitative competition.

For over 30 years, the decline of the green anole in south Florida has been blamed on the Cuban brown anole, but there have been no studies that definitively demonstrate exploitative or any other type of competition in this interaction. In keeping with the trend, this study does not demonstrate or refute competition between the two species or sexes on any level, nor does it reveal temporal aspects of their interaction. However, it was a step forward. My results indicate that 1) females of both species eat a wider range of smaller items from more diverse taxa, 2) males of both species eat smaller numbers of larger items from fewer taxa but also eat large amounts of small items, 3) brown anoles are larger in the most important head parameters, width and depth, and consume larger food items than do similar sized green anoles, 4) brown anoles also consume more food per-capita than do similar sized green anoles (by SVL) as a result of their more robust bodies, 5) these two species overlap greatly in their diets by numerical proportions of their prey, but less so by volumetric proportions, at least in mid-summer when prey may not be limited in supply with respect to these lizards, 6) despite high overlaps, green anoles consistently consume more arboreal forms whereas brown anoles consume more ground-dwelling forms, and these differences may be caused by behavioral-spatial phenomenon such as perch height-mediated dietary shifts, 7) green anoles consume the hatchlings of brown anoles, and 8) because both species consume lizard hatchlings, spiders, and their prey, this system might best be modeled by intraguild predation (Polis et al. 1989).

Only sampling of the diets of these lizards over a period of an entire year (or better yet, multiple years) can reveal temporal variations in dietary niche breadth and overlap, and only manipulative studies will unequivocally determine whether or not exploitative resource competition occurs between these species. My hope is that this study provides the background, methodology, and motivation for further research efforts addressing resource competition in these two species, and in other animal populations affected by invasive species.

CHAPTER 4

Effects of expanding populations of Cuban brown anoles (*Anolis sagrei*) on native populations of green anoles (*A. carolinensis*) on dredge-spoil islands in Florida

INTRODUCTION

Not long ago, the green anole, *Anolis carolinensis* (Polychrotidae), was abundant throughout the southeastern United States. As Lawson (1709) suggested nearly 300 years ago, these creatures coexist with humans quite nicely. His statement held true for over 250 years, until only a few decades ago, when this species began to decline in numbers, such that it is much more difficult to find in peninsular Florida today. Development continues to run rampant in even the most remote areas of Florida, and clearly threatens many native species, including the green anole, but the real threat to this lizard may not be coming directly from humans, but indirectly from a congeneric lizard species, the Cuban brown anole (*Anolis sagrei*). This species was introduced inadvertently by humans into several south Florida ports in the 1940s (Lee 1985), has been spreading northward ever since (Godley et al. 1981, Campbell 1996, Campbell and Echternacht, in prep.), and has become one of the most abundant, if not *the* most abundant, vertebrate species in peninsular Florida south of Orlando.

Few have studied the interaction between these two species in any respect (reviewed in detail in Chapter 1), and until very recently, no one had performed population-level manipulative experiments under controlled conditions in the field or otherwise. Aggressive interference competition is considered of minimal importance (Tokarz and Beck 1987, Brown and Echternacht 1991), and resource competition is often questioned, based on the thought that mainland anoles enjoy unlimited food supplies (Andrews 1976). Recent studies indicate that the two overlap substantially in their arthropod prey choices by number and taxa (Chapter 3), and that these species consume each others' hatchlings (Chapter 3, Campbell and Gerber 1996), such that the interaction might best be described as intraguild predation, or IGP (Polis et al. 1989, Holt and Polis 1997, Gerber and Echternacht, in press).

I studied this interaction in the field at the population-level using small islands along the east coast of Florida as experimental units. I introduced brown anoles onto islands occupied by green anoles, monitored the population increases of brown anoles and the population-level responses of green anoles for three subsequent years, and compared their responses with those of allopatric populations of green anoles on similar spoil islands. In the following study, I describe the temporal and spatial aspects of the invasion process, and the response of green anoles to increasing densities of brown anoles. I test hypotheses regarding density changes, niche shift, and competitive exclusion in green anoles as brown anole populations expanded on the islands. The islands also contained vegetation communities that enabled me to test hypotheses regarding the effect of habitat patchiness and vertical extent on the outcome of the interaction, so the results could be utilized to manage habitat for the continued viability of what should be an abundant species, before populations decline to the point that the trend becomes irreversible.

METHODS

Study Area

This study was performed on dredge-spoil islands in Mosquito Lagoon, an estuary within the boundaries of Canaveral National Seashore (CANA) and Merritt Island National Wildlife Refuge (MINWR) just north of Cape Canaveral in Brevard and Volusia Counties, Florida (Figure 4.1; all figures are in the Appendix). The spoil islands were created about 50 years ago by the U.S. Army Corps of Engineers (USACOE) as a by-product of the excavation of the Intracoastal Waterway (ICW), a large shipping channel along the east coast of Florida. In this study, I utilized seven spoil islands from a chain of more than 80 islands created along the ICW in Mosquito Lagoon (Figure 4.2). All are completely surrounded by water, and are very similar in age, shape, and distance to the mainland or barrier island, and range in size from about 25 m^2 to nearly 5 ha. Mosquito Lagoon is flanked by large natural areas on the mainland (MINWR) and barrier island (CANA), so similar native plant and animal communities have assembled on the islands.

The spoil islands of Mosquito Lagoon are dominated almost entirely by cabbage palm (*Sabal palmetto*), southern red cedar (*Juniperus silicicola*), buttonwood (*Conocarpus erectus*), black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), red mangrove (*Rhizophora mangle*), saw palmetto (*Serenoa* *repens*), prickly-pear cactus (*Opuntia* sp.), salt bush (*Baccharis halimifolia*), marsh elder (*Iva* spp.), oxeye daisy (*Borrichia frutescens*), saltwort (*Batis maritima*), and cordgrass (*Spartina alterniflora*), but a few other species are present in very small amounts (Table 4.1; all tables are in the Appendix). Brazilian pepper (*Schinus terebinthifolius*) and Australian pine (*Casuarina* sp.), both exotics, have colonized the mainland around Mosquito Lagoon. The former is becoming established on the spoil islands of Mosquito Lagoon despite the efforts of an eradication program, but the latter has only become established on spoil islands south of the Haulover Canal in Indian River (Figure 4.1). Overall, soil is very thin and poorly developed on the islands because of the coarse, well-drained, Miocene rock substratum (suction-dredge spoil), but a thick leaf litter layer is usually present in forested areas.

Experimental Design

A brief pilot study was conducted to assess the feasibility of this research (Chapter 2), but was done on two very small islands that contained very few green anoles, so I had no indication of the speed with which brown anole populations might expand on larger islands containing dense populations of green anoles. More importantly, there was no way to predict for statistical analyses the size of the post-invasion green anole populations that would remain on a particular island. Thus, it was difficult to choose islands small enough to ensure that brown anoles would reach high enough densities to have an effect on green anoles (if in fact they have a effect) within the study period, yet choose islands large enough to ensure that post-invasion green anole populations would remain large enough for statistical analyses. It was also clear that I could not have thoroughly sampled six, one-hectare islands containing huge anole populations without help from a small army.

I chose instead to use pairs of islands in three different size categories: small (~ 0.1 ha), medium (~ 0.2 ha), and large (~ 0.9 ha), in a simple un-replicated randomized block design, where brown anoles were added to three islands containing native green anoles (invasion treatments), and three islands containing native green anoles were monitored as single-species (allopatric) controls (Figure 4.3). So, the experiment was performed on six islands in three size-blocks: 1) a small treatment (ST) matched with a small control (SC), 2) a medium treatment (MT) matched with a medium control (MC), and 3) a large treatment (LT) matched with a large control (LC). After brief visits to all the islands in Mosquito Lagoon in March 1995, I simply picked two very similar islands from each size category and randomly assigned them to either an invasion treatment or allopatric control with the flip of a coin. This design incorporates the influence of island size and the extent of different habitats and habitat edges on the 'fill rates' of brown anole populations, the rates green anole declines, the post-invasion green anole population size, and the potential for long-term survival of green anoles.

A seventh island that contained large populations of both species in 1994 was monitored throughout the study as a two-species, sympatric control island, hereafter the "large two-species control" island (L2C). This island was used to assess densities and habitat utilization of sympatric populations of both species, compare density and habitat use of sympatric green anoles with allopatric green anoles on the large single-species control island (LC), and provide an indication of the outcome of this experiment, especially for the large treatment island (LT). Islands matching the small and medium islands in size and habitat, and containing both species of anoles, were not found in Mosquito Lagoon, so two-species controls for those islands were not available, nor were they established. Small and medium sized two-species islands were present to the south in the Indian River near Titusville (Figure 4.1), but were composed of entirely different vegetation (all Brazilian pepper and Australian pine), so were not utilized in this study.

Islands ST and SC lie on the east side of Mosquito Lagoon along the shallow "old channel" of the ICW, which was dredged circa 1920 and has not been maintenance dredged in many years (Figure 4.2). Only recreational boats can traverse this shallow waterway, so the islands along this channel are not subject to erosion from boat wakes, and the perimeter marshes are relatively extensive. Few of these islands are used as campsites, although they are occasionally boarded by recreational boaters and commercial fishermen. The two medium and three large islands lie in a chain of 53 islands along the west side of the lagoon that the USACOE piled along the west side of the ICW channel between Oak Hill and the Haulover Canal (Figure 4.2). They receive wakes from some very large vessels and barges, so their eastern shorelines are generally high energy, eroded, rocky, and lack stabilizing marshes or mangroves, whereas western shorelines are generally low energy depositional environments covered by low marsh vegetation and sometimes are extruded into long sandbar "tails." Good boat access is present on most of the large spoil islands in Mosquito Lagoon, so these islands are regular stop-overs for recreational boaters and commercial fishermen. Illegal camping occurs regularly but not frequently on all of these islands, and irresponsible campers often cut hedge vegetation for firewood and make pathways for additional boat landings.

The seven islands contained the same vegetation, but were different with respect to the presence and spatial distributions of four basic habitat types (Figure 4.3). For this study, "forest" is defined as any habitat dominated by large cabbage palms and cedars with a canopy layer over 4 m high. The small and medium islands consist of a central dome-shaped forest dominated by cedar and cabbage palm (Figure 4.4a). The dome is surrounded by salt marsh, usually with isolated mangrove shrubs embedded within (Figure 4.4a), hereafter termed "shrub-marsh" habitat. The large islands are high domes of dredge spoil, so a well-drained area occurs in the center of each island (Figure 4.4b). The central zone is a very open (20 - 30 percent vegetated), hot, and dry area with small patches of short (~ 2-3 m) cedars, cabbage palms, saw palmetto, and prickly pear cactus in a barren matrix of coarse, well-drained dredge spoil, and is hereafter termed "open-xeric" habitat. This hard surface is sorted like desert pavement and reaches extreme temperatures on a daily basis in summer, much like an asphalt parking lot. The open-xeric zone is surrounded by a partial ring of forested habitat (the "hedge"). The forested hedge is generally a 5 - 20 m wide strip of 5 - 8 m tall cedars, cabbage palms, buttonwood and other shrubs, and encircles much of the island except where interrupted by island erosion or human disturbance. Shrub-marsh habitat occurs along much of the shoreline, but is best developed waterward of the forested hedge. The hedge and shrub-marsh zones are essentially larger, longer versions of the small and medium islands, whereas the central xeric zone has no counterpart on the small or medium islands. Thus, the forest interior, forest edge, and shrub-marsh habitats are common to all seven islands, but open-xeric habitat is only found on the large islands.

Island Landscape Analyses

I utilized a combination of aerial photo-interpretation, ground-truthing, and map-and-compass techniques to accurately map the habitats of the seven islands and the lizards found therein. In 1995, I obtained black and white negative aerial photographs (9 x 9 inch format, 1:25,000 scale, 1992 flight) of the Mosquito Lagoon area from the Florida Department of Transportation (FDOT). Portions of the aerials showing the islands were scanned, enlarged 39.68 times (2.54 cm = 16 m), printed, and used to map island habitats. However, higher resolution images of more recent origin were required to accurately determine the locations of individual lizards relative to the physical features and vegetation that was present during the study period.

In 1996, I took color aerial photographs from a fixed-wing aircraft flying at about 500 feet above the ground with a 35mm camera outfitted with a 55 mm lens (Figures 4.5 through 4.11), after setting and measuring the distance between two aerial survey markers on the ground (2 m x 20 cm bars made from black plastic garbage bags). Individual branches can be discerned from these high-resolution photographs (except for island SC), so were used during lizard surveys to make vegetation maps for each island. However, because they were not taken from *directly* overhead, they were not appropriate for base maps or quantitative landscape analyses. Rather, they were used to construct accurate habitat maps from the FDOT aerials, on which I traced the edges of forest, shrub-marsh, and open-xeric habitats on each island image to make a simple habitat map for each island

(Figures 4.12 through 4.18).

I utilized the landscape analysis program FRAGSTATS (McGarigal and Marks 1995) to analyze the vegetation and habitats on the islands quantitatively. This platform is able to calculate many different landscape parameters and indices from a raster (grid) input file. To make the input file, I used a clear overlay sheet containing a grid for which each cell measured 2 m by 2 m on the habitat maps. The 4 m^2 grid cells were very small relative to the surface area of the islands (only 0.2 to 0.3 percent of the small and medium islands, and only 0.04 to 0.05 percent of the large islands), allowing a high level of resolution of the habitats within.

The grid overlay was used to "digitize" each island map with respect to habitat, where each grid cell was given a value corresponding to the preponderance of the habitat found within. The resulting raster input files for each island were run in FRAGSTATS using a pre-defined edge-width of two meters. Of the 100 parameters and indices that FRAGSTATS generates (McGarigal and Marks 1995), only 19 island-wide landscape parameters and indices, and 14 individual habitat (or "patch") parameters and indices were needed for a suitable comparison of the islands in this study (Appendix 4.2). Of primary importance were sizes of the islands and individual habitat patches, linear distances of habitat edges, calculations of the amount of "core" area (the area inside the edge) the shape of the habitat patches, and descriptions of the spatial distribution of habitats.

Lizard Introductions and Data Collection

Between March and May, 1995, I performed preliminary surveys and began collecting data on native green anoles on the treatment and control islands. Between May 10 and 27, I captured 160 brown anole "donor lizards" from urban areas around Mosquito Lagoon, including Bethune Beach, New Smyrna Beach, and Edgewater (Figure 4.2). Donors were immediately measured, weighed, and marked with exclusive numbers (see below), then released in groups at a single point on each treatment island within 48 hours of capture. Initially, 40 brown anoles (20M:20F) were released on the three treatment islands, but 40 more (20M: 20F) were released on island LT because of its larger size, and fears that the original introductions had failed.

I monitored all lizards with basic capture-mark-recapture (CMR) techniques and collected body, microhabitat, and location data for all captured and re-captured lizards. All the marking and measuring techniques that were performed on green anoles on the treatment islands were also performed on the control islands, thus the controls in this study are "procedural controls" (Underwood 1997). I established regular search routes in 1995 to allow complete coverage of all the vegetated areas of the islands, and made slow methodical searches around each island during daylight hours (between 07:00 and 20:00) until the island had been completely covered at least once. These individual "CMR sessions" lasted between a few hours on the small islands to many days on the large islands. To accurately estimate adult lizard population sizes each year, at least three full CMR sessions were conducted during every summer season on each island between May 1 and August 25 of 1995 through 1998. Population estimates were made for each species on each island in each year, without regards to sex, using Model Mth in the program CAPTURE (Otis, et al. 1978), as in Chapter 2. Estimates were multiplied by the vegetated area of each island to obtain the densities of each species on each island during each year of the study.

To make sampling as unbiased as possible, I captured lizards as they were seen, using a sort of random walk survey. Certain biases are inherent in this protocol (e.g. lizards that are performing territorial displays are more likely to be seen), but at very least it minimized the role of personal choice in deciding which lizards to capture. After spotting a lizard, I looked for a paint mark (see below), then mentally noted its location, body position, and the time of day to the nearest minute. The immediate area was quickly searched to determine if there were other lizards that would be disturbed by capturing the first. Those lizards were mentally noted, and capture strategy was planned that would accommodate as many lizards as possible. In sympatric situations, priority was always given to green anoles, so upon finding a brown anole, I always searched the immediate area for green anoles first so they would not be missed or scared up a tree. Of course, not all lizards could be captured, and the decision to abort a capture attempt was usually made based on the number of other perching lizards that would be disturbed by my actions.

I sampled only mature adult anoles in this study, for a number of reasons. First, at this latitude (Figure 4.1), green anoles are only 18-20 mm SVL upon hatching and brown anoles are only 15-18 mm SVL upon hatching, and are extremely difficult to toe-clip and measure without harming them (A. C. Echternacht, pers. comm.). Also, Gerber (pers. comm.) indicated that hatchling predation and interspecific competition between hatchlings could be important in the decline of green anoles, so I chose not to render hatchlings of either species more vulnerable to these phenomena by handling them in any way. Furthermore, I was only able to remain in Florida through late August, despite the fact that hatchlings continue to emerge through late September, thus could not have obtained samples representing the whole hatchling population. So, I limited this study entirely to reproductive-sized adults in summer months, which represent the final outcome of the reproductive effort of the previous year, minus mortality of hatchlings and juveniles. To sample only adults, I set an *a priori* lower size limit on lizards that could be captured, based on the known sizes of reproductive maturity for males and females of each species (Chapter 1). For both species, I used 35 mm and 40 mm as the lower size limits for females and males, respectively.

Adult lizards were captured by hand or noose, permanently marked with exclusive numbers by toe-clipping, and temporarily marked on both lateral surfaces with their number for rapid sight-identification with a black Sanford Sharpie® fine point permanent marker. I measured SVL, tail length, and tail regeneration to 1 mm with a clear plastic ruler, and measured weight to 0.1g with a Precision® spring scale, and noted any significant external injuries, parasites, and deformities. I checked females for the presence of shelled eggs by gently squeezing their abdomens with my thumb and forefinger ("palpation" method). Because these lizards are territorial, they were always released within 1 m of their point of capture. Any brown anoles found on control islands were either destroyed on-site or captured and transferred to the mainland.

I collected microhabitat data from the location where each adult lizard was first seen. Lizards that were moving upon first sight were captured, marked, and released, but perch-related parameters could not be recorded in those cases. I measured perch height (PH) to 1 cm using gradations drawn on a 1.25 m noose stick. Perch diameter (PDi) was measured to 0.2 cm if the perch was 0.2 - 10 cm, and to 1 cm if the perch was larger than 10 cm. Perch diameter was recorded as 'flat' for lizards perched on the ground surface or large, irregular surfaces (e.g. the center of large cabbage palm leaves). I also recorded total vegetation height (TH) directly above the perch by measuring the maximum height of the vegetation found within an imaginary cylinder one meter in diameter oriented vertically and centered around the perch (accurate to 0.2 m from 0 - 3 m, to 0.5 m from 3 - 5 m, and to 1 m above 5 m).

Because much of this study involves the effect of habitat type on the outcome of the interaction, I recorded descriptions of where each lizard was perched (e.g. east marsh, southeast forest edge, inside western hedge, etc.). I also took compass bearings and measurements from surveyed benchmarks or natural landmarks for all perched lizards, and plotted their locations on aerial photographs when benchmarks or landmarks were not visible. This information was used to assign lizards to one of the four habitat categories established above. Analyses of lizard parameters from different habitat types lead to questions about the effect of vegetation diversity, density, and architecture on the abundance of arthropod prey faunas, and in turn, anole body condition or demographics.

Body condition was calculated as a 'condition index' (CI) relating SVL to body weight using a formula modified from that presented by Andrews et. al (1983):

$$CI = (weight^{0.333} / SVL) * 100$$

where the mass exponent is calculated by taking the reciprocal of the slope of the regression of Log_{10}Weight on Log_{10}SVL (as in Chapter 2). I derived a mass exponent that was specific to the exclusive adult green anoles marked during the reproductive season in this study, rather than using the standard 0.333 value.

Arthropod Abundance

The effects of vegetation biomass, density, diversity, and architecture on the abundance and diversity of arthropods is well known, as is the effect of arthropod prey availability on lizard condition and demography (e.g. Dunham 1978, 1980). Because anoles generally differ in their preferred perch location over vertical space depending on the identity of syntopic competitors (Williams 1969, 1972), because these species are known to shift their perch position in response to those competitors (Schoener 1975), and because arthropods were likely be more abundant near the soil surface, I conducted a brief sticky-trap survey to assess differences in arthropod density and diversity over horizontal space (habitat type) and vertical space on the three large islands.

Because sticky traps are also effective devices for capturing small lizards, I chose not to deploy them on a regular basis in this study. In fact, during a brief sticky-trap pilot study in 1996, six anoles were captured on a single island in one day, in only 10 sticky-traps set on the ground surface. At best, death or injury of lizards in sticky-traps would result in slightly biased population estimates. At worst, sticky-traps might have negatively affected anole populations and undermined one of the assumptions of the population estimates: that on a short-term basis, these anole populations are closed. Ultimately, sticky-trap surveys may only be applicable in a general sense, as they may not capture many of the prey items that anoles consume, and may also capture many prey items that anoles do not consume (L. Vitt, pers. comm.). However, sticky-traps provide good relative measures of overall arthropod abundance.

To assess the difference in arthropods present in each of the habitat types, I performed a brief sticky-trap survey in 1998 on the four most closely spaced islands (MT, LT, LC, and L2C), in which Tanglefoot® was brushed onto paper plates which were attached to vegetation in a vertical position using a staple gun. Traps were deployed at 24 stations established on each large island: 12 in the forested hedge and 12 in the open-xeric area. Two traps were placed at each station: one at ground level and one at 2 meters above ground level in the same plant, thus, a total of 48 traps were deployed on each large island. Traps were placed on cabbage palms and cedars in equal numbers in each habitat. In summary, traps were placed at each of two trap heights (low and high) on equal numbers of each plant species (cabbage palm and cedar) and in equal numbers within forest and open-xeric habitats.

Statistical Analyses

Although thousands of lizards were captured during this study, islands were the experimental subjects. The contrasts of interest lie between green anole parameters on treatments (controls vs. invasion treatments), and over time within the treatments. I analyzed the effect of expanding brown anole populations on green anole populations by comparing temporal trends in the densities, body sizes as SVL_{Max33} (Chapter 2), body conditions as Mean CI (Chapter 2), and the two perch parameters (PH and Pdi) of green anoles on the invasion treatment islands to trends in the same parameters on the allopatric control islands. Yearly population-level parameters describing adult lizards on the six experimental islands (subjects) were cast into a repeated measures MANOVA (Von Ende 1993) with treatment (invaded or not) as the between-subject factor, and time (four years) as the within-subject factor, similar to Losos and Spiller (1999) and Leal et al. (1998). Analyses were performed using the programs JMP (SAS Institute, Inc. 1995).

With the exception of the population estimates, lizards captured more than once were included only once in statistical analyses. Data for the second (and subsequent) observations were excluded, so different lizards were utilized for analyses within and across year, ensuring that the data were statistically independent. All lizard body and perch data were partitioned by sex as well as species, as both of these species are highly sexually dimorphic in their body parameters and habitat utilization (Schoener 1975). In fact, as seen in Chapter 3, sexual differences within these species are often larger than are species differences. Moreover, because lizards were captured as they were seen, no attempt was made to capture the same numbers of males and females. Clearly, pooling across the sexes would result in severe biases if different relative numbers of the two sexes were represented in the samples being analyzed. In essence, this was a study of four very different types of lizards.

To analyze the sticky-trap data, I tested the effect of island (LT, LC, and L2C), plant species (cedar and cabbage palm), trap location (forested and open-xeric habitat), and trap height (ground level and 2 m above ground) on the number of individual arthropods and the number of arthropod taxa (orders) captured by 48 sticky-traps placed on each of the three large dredge-spoil islands in 1998, by casting these data into a four-way MANOVA.

RESULTS

Island Physical and Biotic Parameters

Results from FRAGSTATS analyses show the similarities between the matched treatment and control islands, and across all seven islands, with respect to total island size, total patch size and percent of the island occupied by each habitat type, and amount of edge of each habitat (Table 4.2). The shape indices, fractal indices, and diversity indices, evenness indices, and contagion were very similar as well, and are an indication that the landscape patterns were equitable between controls and treatments.

The small and medium islands and the habitats within them exhibit simple shapes with regular borders, whereas the large islands have larger edge-to-core ratios and more irregular shaped habitat patches. The small islands contain relatively small forest areas surrounded by relatively extensive shrub-marsh zones (Figures 4.5 and 4.6), whereas the medium islands support relatively larger forested areas surrounded by relatively narrower marsh zones (Figures 4.7 and 4.8). The forested areas of the large islands are not much larger than forested areas of medium islands (Figures 4.9, 4.10, and 4.11). In fact, the forest core area totals are very similar on medium and large islands (Appendix 4.2) because of the linear nature of the forested areas on the large islands. So, despite the larger size of the large islands, their forested core areas are similar in size to the forest core areas on the medium islands, and relatively more of the forested area is edge habitat.

On the large islands, about half of the forest edge lies toward the central, open-xeric habitat, a habitat very similar in landscape parameters on all three large islands (Table 4.2). This habitat is only 23 - 28 percent vegetated, entirely explaining the lower totals for island vegetated area for the large islands. In actuality, the "core" area of the open-xeric habitat (Appendix 4.2) is *only composed of edges*, as the vegetation within this zone consists of individual plants (or small clumps of a few plants) embedded in a matrix of bare dredge-spoil (Figures 4.9 - 4.11). A synthesis of the qualitative and quantitative aspects of each island are helpful for putting lizard and arthropod results into perspective.

The small treatment island **(ST)** is about 0.158 ha in area, including a 0.038 ha forested area and a 0.121 ha shrub-marsh zone (Figures 4.5 and 4.12). The dome-shaped forest is dominated by cedar and cabbage palm up to 6 m in height, with negligible understory vegetation, thus the only ground-canopy conduits are large tree trunks. The northwestern shoreline is eroded and some trees from the forested area are falling into the water. The forest dome has 100 m of edge dominated by dense salt bush, buttonwood and Brazilian pepper, and is bordered on three sides by the shrub-marsh area, which consists of numerous, short (2 - 3 m), isolated mangroves protruding from high marsh vegetation, mainly *Borrichia* and *Batis.* This island is contiguous with a low, regularly inundated *Batis* marsh and mud flat to the east in which fiddler crabs were abundant and anoles were never found. This area was deemed to be outside the limits of the island from an anole's perspective, and was not included in any surveys or maps, so the eastern edge (Figure

4.12) is largely a map feature, not a true shoreline. Soil is well developed throughout the forested area, but the shrub-marsh is regularly inundated, so has limited soil and numerous fiddler crab burrows. I never saw a boat land on this island; it is probably rarely used by humans as the approach is limited by oyster beds.

The small control island (SC) is about 0.100 ha in area, and consists of a 0.021 ha dome-shaped forested area dominated by cedar, cabbage palm, and Brazilian pepper up to 5 m in height, surrounded by a 0.078 ha shrub-marsh zone (Figures 4.6 and 4.13). The whole island, the forest, forested edge, and the shrub-marsh habitats are each about 60 percent of the size of the respective areas on island ST. The islands are very similar in vegetation density and configuration, except the perimeter of the central forest is dominated by mostly Brazilian pepper, followed by buttonbush and saltbush, and the forest canopy contains more gaps than does island ST. The forest is bordered on three sides by a shrub-marsh area dominated by short (< 2.5 m), isolated mangroves in a matrix of *Batis* marsh. The western shore is currently protected by a 4 m wide stand of larger mangroves, but is starting to show signs of erosion. Soil is of the same configuration as on island ST. Although it is possible to reach this island on foot via a narrow oyster bar, I never saw a boat land on this tiny island, and assume it is very rarely used by humans.

The medium treatment island (MT) is about 0.170 ha in area, and consists of an 0.095 ha dome-shaped forested area dominated by cedars and cabbage palms up to 8 m high, surrounded by three distinct, fairly narrow shrub-marsh zones totaling 0.076 ha (Figures 4.7 and 4.14). The central forest is open and walk-able, but large Brazilian pepper and buttonwood form a dense, 180 m perimeter around the forest on all but the very eastern tip. Shrub-marsh habitat consists of short, isolated mangroves within dense *Borrichia* marsh. Soil is very well developed and leaf litter is thick, except in the shrub-marsh areas. Shorelines exposed to easterly winds and boat wakes are eroded and rocky, whereas the protected western exposures are sandy. I saw only two fishing boats land on this island during the entire study.

A bird rookery consisting of about 50 crested cormorants became active on island MT in 1996, and was large in 1997 and 1998. Great egrets and great blue herons roosted with the cormorants, but were not observed nesting. An inordinate amount of feces, regurgitate (fish), and dead fledglings rained down from the central forest canopy onto my field assistants, and the ground was literally covered with feces, regurgitate, and dead birds from 1996 on. Flying insects were very obviously more abundant there than on any other island in the study, representing a natural food augmentation. Had the rookery been active in 1995, I would not have included this island in the study, as this represents a potential confounding factor for density, body size, and body condition.

The medium control island (MC) is 0.153 ha in total area, and consists of a 0.075 ha dome-shaped forested area dominated by cabbage palms and cedars up to 7 m high (Figures 4.8 and 4.15). Dense buttonwood and Brazilian pepper surround the forest edge on all but the north shore, where it is exposed on an eroding shoreline. The forest is bordered on the south by a 0.078 ha shrub-marsh zone consisting of short (<2 m), isolated mangroves protruding from a high *Borrichia* marsh. Overall, it is about 90 percent the size of island MT, the forested area is about 80 percent the size of the forest on island MT, and the shrub-marsh areas are nearly equal on the two islands, but the amount of edge on this island is considerably less than that on island MT. Soil and vegetation configuration are similar to that of island MT, but this island lacks a bird rookery (as do all the other islands). This island is used regularly by fishermen, recreational boaters, and overnight campers, due to its proximity to the boat launch at the Haulover Canal and good deep-water access on the southwestern tip of the island.

The large treatment island **(LT)** is 0.890 ha in total area (Figures 4.9 and 4.16). The forested hedge (0.205 ha total) is distributed as four unequal sized patches, and is tallest (up to 9 m) and widest (up to 15 m) to the south. At over 700 m long, the forest perimeter comprises about half of the total edge habitat on the island. The east shore is rocky, eroded, and supports minimal marsh vegetation, whereas the south, west, and northwest shorelines are low-energy and support dense marsh and mangrove vegetation totaling 0.202 ha in area. Overall, shrub-marsh habitat is best developed on the two sandbar 'tails' to the south and northwest, the latter of which contains a bomb crater created by pesticide ordinance dropped from a helicopter by Volusia County Mosquito Control Board. The central open-xeric zone is 0.483 ha in area, 25 percent vegetated, and contiguous with the eastern shoreline. Although illegal camping was a rare occurrence on this island, it was regularly used by recreational boaters and fishermen.

The large control island **(LC)** is 0.935 ha in area (Figures 4.10 and 4.17). Forested habitat (0.157 ha total) lies mainly along on the west and northwest edge as a long hedge, which is only about 70 percent of the area and perimeter of the forest on island LT. A narrow peninsula of low marsh vegetation connects to a small, sparsely vegetated area containing a few large cabbage palms and some Brazilian pepper, which will likely become a separate island in the near future. The east shore is a "sandy" beach, but the north and south shorelines are undercut by erosion. Shrub-marsh habitat (0.188 ha total) occurs mainly on the western tip of the island, similar to that of island LT. The central open-xeric area is 0.590 ha in area, about 23 percent vegetated, and is contiguous with the north, east, and south shorelines. This island is an official CANA backcountry campsite, and is occupied nearly every weekend during the summer months. It contains Indo-pacific geckos, and despite all attempts to keep it brown-anole-free throughout this study, they became unmanageable by August 1997, when numerous hatchlings were observed.

The large, two-species control island **(LC2)** is 0.931 ha in area, is configured similarly, and supports the same vegetation communities as islands LT and LC (Figures 4.11 and 4.18). Forested habitat (0.199 ha total) wraps around the west, northwest, and north edges, although a small patch occurs on the southeast edge as well. The eastern, southern shorelines are rocky and eroded and the south shore is undercut in many spots. Shrub-marsh habitat (0.126 ha total) lies mainly on the west tip of the island. The central open-xeric zone is 0.606 ha in area, 28 percent vegetated, and directly associated with the eastern and southern shorelines. This island also contains a large, lagoon-like red mangrove area to the north of the northernmost forested area that was not sampled during this study due to the presence of nearly continuous standing water, a 3 m-long American alligator (*Alligator mississippiensis*), and regular aerial assault from pesticide ordinance by the Volusia County Mosquito Control Board. Anoles were rarely seen during brief forays into this area, and similar habitat is not present on any other island. This region was ignored, so the northern "edge" of this island is merely a map feature.

Vertebrate faunas of the islands were fairly diverse (Table 4.3), likely due to their proximity to extensive natural habitats in the wildlife management area on the mainland to the west, and the national park to the east. Raccoons were regularly seen on every one of the islands during every year of the study. Insectivorous passerine bird species (e.g. parula warblers), fish crows, and a full complement of herons and egrets used the islands on a daily basis. Herpetofauna included black racers (*Coluber constrictor*), corn snakes (*Elaphe guttata*), yellow rat snakes (*E. obsoleta*), peninsula ribbon snakes (*Thamnophis sauritus*), salt marsh water snakes (*Nerodia clarkii*), and Florida box turtles (*Terrapene carolina bauri*) were seen on nearly every island at least one time during the study, although none were observed in high densities. The islands are well within the current geographic ranges of both anole species, most contain dense populations of native green anoles, and many contain brown anoles and Indo-pacific geckos (*Hemidactylus garnotii*) introduced by boat campers and commercial fishermen (Campbell 1996). Flying and ground-dwelling insects (especially ants) were abundant and diverse on the islands, as were arachnids (Table 4.3). Two intertidal crustaceans, the amphipod *Gammarus* and the isopod *Ligia*, were extremely abundant on all shorelines (thousands per square meter).

Changes in Population Size and Habitat Distribution

A total of 1,764 adult brown anoles and 719 adult green anoles were processed between May and August on the three invasion treatment islands (ST, MT, and LT) during the four years of this study. A total of 997 green anoles were processed on the three allopatric control islands (SC, MC, and LC), and 594 brown anoles and 346 green anoles were processed on island L2C during the same period. Thus, a total of 2,358 brown anoles and 1,343 green anoles were partitioned by year and used for population estimates in the program CAPTURE.

Brown anole populations expanded rapidly on the three treatment islands, but the numerical expansion was slowest on island ST, and greatest on the large island through 1998 (Figure 4.19). In terms of population density, the population on the large island (LT) exhibited a slight lag period relative to the other two islands, as would be expected for the largest invasion island, but brown anole population densities increased most rapidly on island MT (Figure 4.20), despite the fact that island ST was the smallest (Table 4.2). During the same period, green anole populations declined on each treatment island (Figure 4.21), whereas control island green anole population sizes remained fairly constant throughout the study period (Figure 4.22).

As evidenced by the non-synchronized yearly fluctuations in the plots, the covariance matrix of the yearly green anole density values did not exhibit compound symmetry (Mauchly criterion = 0.0025, P = 0.0061). The F-statistic for the within-subject effects resulting from a univariate repeated measures ANOVA for such a data set would be severely inflated, a fact not often considered in univariate repeated measures analyses in ecological data (Von Ende 1993). Thus, temporal trends in green anole density on the control islands could not be compared with trends on the treatment islands using a univariate repeated measures ANOVA.

Instead, I analyzed the green anole density values with less powerful, multivariate repeated measures (MANOVA) methods (Von Ende 1993) in which the four years were treated as four separate variables, with treatment (invasion vs. control) as the sole between-subject factor, and year as the within-subject effect, without the benefit of being able to partition experimental error into size-blocks. As main effects, year was not significant (Pillai's Trace = 0.9294, $F_{3,2} = 8.7708$, P = 0.1041), nor was treatment (Pillai's Trace = 0.1163, $F_{1,4} = 0.5263$, P = 0.5083). However, a significant treatment*year interaction was obtained (Pillai's Trace = 0.9903, $F_{3,2} = 67.7449$, P = 0.0146), indicating that changes in green anole densities observed on the treatment islands over the four years of the study (Figure 4.21) were significantly different from the changes in densities observed on the three control islands (Figure 4.22). Given these results, a detailed discussion of the spatial and temporal aspects of the expanding brown anole populations and declining green anole populations is warranted for each of the paired treatment and control islands.

Island ST: Overall, 521 brown anoles were marked and 471 recaptures were made on this island during 28 CMR sessions during the four summers of this study, thus, a total of 1,020 observations were made on these lizards (Table 4.4). Many lizards were recaptured two or more times in the early years when the population was relatively small. Of the 40 original brown anoles released in May 1995, a total of 23 of these lizards were recaptured later that year, and most of these lizards were recaptured more than three times. The first hatchling brown anole was seen on July 19, 1995, despite four prior surveys that month. Based on an incubation period of around 25 days at this latitude, brown anoles probably initiated egg laying shortly after their release on the island.

Numerous hatchlings were seen in subsequent sessions in 1995. Under ideal conditions, brown anole females lay, on average, one egg every 5 days (T. Vincent, pers. comm.). Assuming no female mortality, each of the 20 female propagules could have laid up to 24 eggs each between June 1 and October 1 (~120 days), for a total of about 480 eggs possible in 1995. I only marked a total of 90 brown anoles between May and August 1996, and the population estimate for that cohort was only 129 (Table 4.4), indicating that, either some females perished before laying eggs, fewer than 480 eggs were deposited by the 20 females, survival from egg to adult was only about 25 percent between 1995 and 1996, or some combination of these occurred.

Donors remained entirely within the forested area throughout 1995, and over 65 percent of their progeny were captured in the forested area in 1996, similar to the results from the forested island in the pilot study (Chapter 2). The population estimate for the brown anole cohort in 1997 was under 300, and in 1998, under 500 (Table 4.4). By 1997, they had spread to the farthest lone mangroves in the shrub-marsh zones (Figure 4.5), but were sparse there, and in 1998 at least three brown anoles could be observed in even the smallest of shrubs throughout the island. About half of the observations of brown anoles were made in the shrub-marsh area in 1997 and 1998.

Green anoles were abundant on this island in 1995, but their numbers declined over time (Figure 4.21). A total of 87 green anoles were marked in 1995 during three sessions before and five sessions after the inoculation of brown anoles was complete. The population estimate for the summer of 1995 was nearly 200 individuals, corresponding to a density of over 1,000 lizards per hectare for the entire island (Table 4.5). A nearly 30 percent decline occurred between 1995 and 1996, then only 49 green anoles were captured in 1997, and only 17 individuals were marked in 1998, despite eight full CMR sessions that included long periods standing in one spot marking brown anoles, and methodical searches of the canopy with binoculars. Frequent recaptures of these lizards indicated that most of the population had been marked. This estimate corresponds to an island-wide green anole density of about 300 lizards per hectare, only about 25 percent of the green anole density observed in 1995.

The number of observations of exclusive green anoles in the forested area declined from 61 percent in 1995 (25 percent of those in the interior, or core area of the forest) to 34 percent in 1996 (half in the core area), to 41 percent in 1997 (only six percent in the core area) and to just over 20 percent in 1998 (only six percent in the core area). During the same period, the number of observations of green anoles found in the shrub-marsh area steadily increased from 39 percent in 1995 to over 75 percent in 1998. I spent similar amounts of time in the forested area every year.

Island SC: A total of 130 green anoles were marked and 68 recaptures were made during 18 CMR sessions over the four summers of this study, totaling 198 green anole observations on this island (Table 4.6). The population hovered between about 70 and 90 individuals throughout the study (Figure 4.22), and remained much larger than that of the treatment island in both number and density through 1998 (Table 4.6), despite its smaller size (Table 4.2). Moreover, the proportions of green anoles observed in each of the habitats were similar during each year of the study: 10 -20 percent of the observations occurred in the forest core area, 50 - 60 percent occurred in the forest edge, and 20 - 30 percent were in shrub-marsh habitat (Table 4.6).

Island MT: Overall, 574 brown anoles were marked and 273 recaptures were made on this island during 23 CMR sessions over the four summers of this study, totaling 874 observations on these lizards (Table 4.7). Of the 40 original brown anoles released in May 1995, only 10 were recaptured later that year. The first hatchling brown anole was seen on July 24, 1995, however, no surveys were done between May and July, so hatchlings probably appeared sooner. As for island ST, up to 480 brown anole eggs could have been laid by the 20 females in 1995 under ideal conditions, but the estimate in 1996 was less than half of that value. I marked nearly 300 lizards in 1997, and recaptured about half of them, giving a reliable population estimate for that year of over 550 lizards. Although only 143 were marked in 1998, few recaptures indicated the population consisted of about 1,000 lizards, corresponding to a density of over one lizard for every two square meters of island surface area.

The green anole decline was most dramatic on this island (Figure 4.21). In 1995, nearly 100 green anoles were captured, and meager recaptures indicated the population almost certainly exceeded 200 (Table 4.8). In 1996, nearly the same number of lizards were marked and recaptured, and the estimate is about the same. However, in 1997, the green anole population had plummeted to the point where whole days would pass without seeing any. Only 17 were captured in 1997 (estimate less than 60), and only 11 were captured in all of 1998 (estimate less than 30), of which over half had been marked in 1997. These numbers correspond to a decline in the green anole population of over 90 percent!

As observed on island ST, in 1995 and 1996, many green anoles were captured from the cedars and cabbage palms in the forest core area, but in 1997 and 1998, they were only found only at, or within a few meters of the forest edge, or in the outer marshes. In fact, the number of observations of exclusive green anoles in the forested zone declined from over 60 percent in 1995, 1996, and 1997 to only 36 percent in 1998. Moreover, in the first two years, equal numbers of observations were made in forest core and forest edge habitat, whereas in 1997, only half of the observations from forested areas were in the core area, and in 1998, virtually every green anole seen in the forested zone was located on the edge. Observations of green anoles in the shrub-marsh zone jumped from about 40 percent in the first three years to over 60 percent in 1998.

Island MC: A total of 300 green anoles were marked and 87 recaptures were made during 16 CMR sessions conducted over the four summers of this study, totaling 387 observations of green anoles on this island (Table 4.9). This green anole population was estimated to include over 100 individuals during each year of the study, and remained much larger than that of the treatment island through 1998. Green anoles were observed in the three habitats types in similar proportions during each year of the study, generally about 25 percent of the observations occurring in forest core area, 50 percent in the forest edge, and 25 percent in the shrub-marsh habitat.

In 1998, a female green anole (40 mm SVL) was observed in Mosquito Lagoon floating toward the southwestern shoreline of the island on a southwest wind, indicating that it had dispersed across an approximately 100 m wide channel from the large island directly to the south that was known to support a large population of green anoles in

1996. This lizard was marked and released on the island, but was never recaptured. This was the only instance of over-water dispersal observed during this study. A total of three brown anoles were removed from this island in 1996, but no brown anoles were seen in 1997 or 1998.

Island LT: A total of 672 brown anoles were marked on this island during the 21 CMR sessions performed over the four summers of this study, and with 161 recaptures, over 800 observations were made on these lizards (Table 4.10). Despite releasing 80 brown anoles on the island in May 1995, no brown anoles were seen later that year. Although fears that the introduction had failed were unfounded, only 41 of their progeny were found in 1996, and the population estimate was only about 150 lizards. They had spread westward along the forested hedge, southward along the east shoreline, were present in many of the small shrubs in the north portion of the open-xeric zone, but except for a single adult male found in the southern hedge, they were entirely confined to the northern half of the island in 1996 (Figure 4.16, Figure 4.9). Although the 1996 surveys were relatively brief, two teams of three people each searched the island for two full days, and were specifically instructed to look carefully for brown anoles far from the release site. A large black racer was observed consuming a brown anole on the north end of the island in 1996; the only confirmed observation of predation on anoles in this study (but see Chapter 2).

By 1997, brown anoles had taken a firm hold throughout the island, but were present in very low densities far from the release site, such as the southern and western marsh tails (Figure 4.16). I marked over 200 brown anoles that year, and a population estimate of over 500 lizards was generated (Table 4.10). Brown anoles occupied most of the forested ring but remained sparse to the south, and a few were present in each shrub of the central zone. They had spread to all but the very southern tip of the island, and there was an obvious gradient in density from north to south at that time. In 1998, I marked over 300 brown anoles, and although the confidence limits are fairly wide, the small number of recaptures indicated the population was at least 1,000 lizards (Table 4.10). Brown anoles were fairly dense throughout the island in 1998, such that the difference in density between the north and south, if present, was not obvious. Consequently, in only three generations, brown anoles were able to spread throughout one-half hectare of very patchy vegetated habitat on this one-hectare island.

Green anoles declined as brown anoles filled the island, but not as rapidly as the decline observed on the other two treatment islands, especially island MT (Figure 4.21). In the summer of 1995, despite marking nearly 100 green anoles, the population was barely estimable due to insufficient recaptures, but probably contained at least 500 individuals (Table 4.11). This occurred in 1996 as well. In 1997, during more CMR sessions, fewer unmarked green anoles were captured, and more were recaptured, indicating the population, although still large, was probably only half that of the previous years. This occurred in 1998 as well, such that the population in the final year of the study was only about 60 percent smaller than the populations of 1995 or 1996.

The proportion of green anoles observed in forested habitats on this island increased from about 30 percent to over 50 percent between 1995 and 1998, but the proportions found in forest core and edge were similar each year. During the same period, the proportion of green anoles observed in the open-xeric habitat dropped from over 60 percent in 1995 to less than 20 percent in 1998. In 1998, green anole observations declined further in forested habitat and open-xeric habitat, but increased by over 1,000 percent in the shrub-marsh habitat. This is not to say that green anoles did not occur in shrub-marsh before 1998, only that the proportion captured in that habitat was lower in 1998 than in previous years. By 1998, the only habitat in which green anoles could be consistently found was dense forested edge habitat bordering on dense shrub-marsh habitat, which was the only habitat in which green anoles could be found in large numbers on the two-species control island (L2C).

The green anole decline appeared to mirror the brown anole expansion, especially in the open-xeric zone (Figure 4.16). In 1996, green anoles were not noticeably absent from any area of the island, but were more difficult to find within about 30 m of the release site, especially in forested areas with sparse understory vegetation, and in shrubs at the very northern end of the open-xeric zone (Figure 4.9). By 1997, few were found in the north hedge, in isolated plants in the north half of the open-xeric zone, or in open habitats along the east shore (Figure 4.16), but they were numerous in dense vegetation dominated by buttonbush and cabbage palm along the southern and western edges of the island. In 1998, green anoles were abundant only along the southwestern shoreline of the island, where the waterward forested edge borders on a narrow fringe of dense buttonwoods that had sent branches out over the water.

Island LC: A total of 567 green anoles were marked on this island and 227 recaptures were made during 24 CMR sessions over the four summers of this study, totaling nearly 800 observations of green anoles on this island (Table 4.12). Population estimates indicate that at least 250 individuals were present on this island during any year of the study. A decline of over 200 lizards was evident after 1997, the year with the largest population estimate, but although the differences between the 1998 estimate and the 1995 and 1996 estimates are smaller than the difference between the 1997 and 1998 estimates, nonetheless, they indicate a deficit of over 100 lizards in 1998 relative to other years. The only obvious difference between that year and any other was the weather (Chapter 2) and the presence of brown anoles.

Brown anoles were seen every year on this heavily used island, which is a National Park Service campsite. In fact, if randomness were not required by my experimental design, this highly vulnerable island would have been the best candidate for an invasion treatment, given the fact that it was certain to be colonized by brown anoles. Only seven brown anoles were observed on this island in 1996, and were either removed from the island or exterminated on-site. I was under the illusion I could effectively control brown anoles on this island, but I gave up after finding brown anole hatchlings in low densities throughout the island in August 1997. By 1998, adults were present in low densities throughout the island, and this island might not have represented a suitable control in 1998. Further declines probably occurred in the summers of 1999 and 2000, and the remaining green anoles were probably distributed much like those on island LT and the two-species control, island L2C. As such, the statistically significant difference obtained in the repeated measures MANOVA should be considered conservative for the density effects, and for the parameters tested in the following sections as well.

Island L2C: During brief surveys in August 1994, large numbers of both species were observed throughout this island. I anticipated that, at best, this island contained long-established, stable populations of both species at that time and, at least, if brown anoles had only recently arrived, they would occur at high enough densities by the beginning of this study in 1995 that it could be considered a suitable two-species control island. However, population estimates indicate that, although the latter statement was true, the former may not have been (Figure 4.23). Although the two species were very similar in their densities during 1995 and 1996, and the estimates were fairly reliable for both brown anoles (Table 4.13) and green anoles (Table 4.14), their densities diverged substantially in 1997, and again in 1998. Although the estimates were less reliable in 1997 and 1998, the 95 percent confidence intervals indicate the densities of the two species were significantly different during those years (Figure 4.23). Although this may have diminished the value of the island as a true two-species "control," it provided a huge amount of data regarding habitat utilization of these two species while in sympatry.

Spatial data indicate that the proportions of brown anoles observed in the three habitats were similar during each year of the study: about 60 percent in the forest and forested edge, and about 20 percent in the shrub-marsh and open-xeric habitats, similar to the pattern of brown anole distribution observed on island LT in 1998. Likewise, throughout the study, green anoles on island L2C were rare in the open-xeric zone, the same pattern observed at the end of the study on island LT. Furthermore, less than 20 percent of the green anoles found in the open-xeric zone on this island were located over 10 m from any forest edge or dense shrub-marsh habitat.

Changes in Microhabitat Parameters

To examine the potential effect of increasing densities of brown anoles on the island-wide perch choices of adult green anoles of each sex, perch height (PH) and perch diameter (Pdi) were analyzed across treatment and time. Males and females of both of these species have long been known to differ in perch height and diameter (e.g. Schoener 1968, 1975), and appeared to do so in this study, so the two sexes were analyzed separately with regards to microhabitat parameters, but were not compared statistically. Also, many of these arboreal lizards were observed perching in non-arboreal situations, for example, on the ground, on isolated rocks, or other debris protruding from the ground surface, such as fire-pit rocks, boards, tables, boats, and garbage. For these analyses, I did not distinguish between lizards perched in vegetation (a "true perch" *sensu* G. Gerber, pers. comm.) from those located on the ground or other non-vegetative surfaces. This was merely an examination of the effect of brown anoles on the overall perch position of green anoles in vertical space, as measured from the ground surface, and on the chosen perch surface, as measured by diameter.

PH data were not normally distributed within each sample or across all samples. The distribution of PH was generally skewed upward (not shown), but also contained a distinct spike in the lowest category, representing lizards "perched" on the ground, so could not be normalized with any technique. By separating out the ground-perching lizards for separate analyses, the data for the remaining vegetation-perching lizards would have been normalized (G. Gerber, pers. comm.), and mean PH values could have been used for further analyses. However, I chose to avoid segregating the lizards into two distinct groups, and included all perch data in one analysis to test for vertical shifts in perch choice, and simply utilized sample median PH values.

Perch diameter (Pdi) data were also problematic, for two reasons. First, lizards located on the ground occupied a "perch" of relatively meaningless diameter (e.g. the earth), as were lizards found under bark, in a hole, or on a large, flat, irregular surface such as the crotch of a cabbage palm leaf or plywood board. In these cases, perch diameters were recorded as "flat," thus could not be included with a numerical data set. Thus, unlike the PH data, I was forced to utilize Pdi data only for lizards found on perches that could be measured in terms of diameter. Second, of the lizards perched on surfaces exhibiting a measurable diameter, many were perched on the boles of cabbage palm trees, which were much larger in diameter than the largest trunks of the cedar trees or any other vegetation present on these islands at the time of this study. Thus, Pdi data were not normally distributed, but were somewhat bimodal, containing a large, normally distributed group representing the small-diameter perches of branched vegetation, and a smaller distribution representing lizards perched on large cabbage palm boles. I was unable to normalize these data, so I performed all Pdi analyses on sample medians.

I cast the median PH and median Pdi values for each sample into separate repeated measures MANOVAs (Von Ende 1993) using treatment as the fixed factor and year as the repeated factor, as in the density analyses above. Median PH values exhibited by male green anoles increased continuously on the treatment islands, but exhibited no regular temporal patterns on the control islands (Table 4.15). As main effects, treatment was significant (Pillai's Trace = 0.9695, $F_{1,4} = 126.9840$, P = 0.0004), as was year (Pillai's

Trace = 0.9952, $F_{3,2}$ = 138.0468, P = 0.0072), and the treatment*year interaction was also highly significant (Pillai's Trace = 0.9967, $F_{3,2}$ = 199.1305, P = 0.0050). These results indicate that significant upward shifts in the preferred perches of male green anoles on the treatment islands were mediated by increasing densities of brown anoles, and are strengthened by the data from island L2C, which also show an upward trend (Table 4.15).

Females appeared to exhibit an upward shift in their perch utilization (Table 4.15), with a significant result for treatment (Pillai's Trace = 0.8009, $F_{1,4}$ = 16.0877, P = 0.0160), however, year was not significant (Pillai's Trace = 0.8487, $F_{3,2}$ = 3.7382, P = 0.2182), nor was the treatment*year interaction (Pillai's Trace = 0.9050, $F_{3,2}$ = 6.3508, P = 0.1391). Although it does not appear that green anole females were affected by increasing densities of brown anoles with regards to perch height, the results from island ST were striking between 1995 and 1996, but PH decreased thereafter (Table 4.15), probably due to the horizontal shift out of the forested area. Green anole females perch lower than do male green anoles, and deposit eggs in soil, so might have an upward constraint on their perch preferences, however, an upward shift occurred on island L2C in 1998, after a period of elevated PH values (Table 4.15).

I also calculated the proportions of green anole males and females that were perched in vegetation (as opposed to being "perched" on the ground) during each year of the study and on each island, allowing a rough assessment of whether or not green anoles shift utilize plant perches more often in the presence of brown anoles. On island ST, MT, and LT, green anoles of both sexes occupied plant perches between 82 and 90 percent of the time in 1995, but plant perch utilization increased to 100 percent by 1998 in every case. The effect was largest for males on island ST, which were perched on vegetation in 100 percent of the observations from 1996 on. Both species exhibited this shift on island MT from 1997 on, but it only occurred on island LT in 1998. Conversely, the proportion of green anoles perching on plants on the control islands remained consistently between 76 and 90 percent, except in the case of males on island LC in 1997 and 1998, which were found perched in plants over 96 percent of the time.

Of the perches having a measurable diameter (Table 4.16), the diameter of perches chosen by males were not different over treatment (Pillai's Trace = 0.0398, $F_{1,4}$ = 0.1661, P = 0.7045), year (Pillai's Trace = 0.9444, $F_{3,2}$ = 11.3299, P = 0.0822), or the treatment*year interaction (Pillai's Trace = 0.7526, $F_{3,2}$ = 2.0821, P = 0.3471). Similar results were obtained for females by treatment (Pillai's Trace = 0.0238, $F_{1,4}$ = 0.0957, P = 0.7705), year (Pillai's Trace = 0.8596, $F_{3,2}$ = 4.0844, P = 0.2029), or the treatment*year interaction (Pillai's Trace = 0.7084, $F_{3,2}$ = 1.6195, P = 0.4038).

Although it appears that brown anoles have no effect on the diameter of perches chosen by green anoles of either sex, a significant upward perch shift should have placed green anole males in narrower branches, on average. However, both species regularly utilized cabbage palms, which have boles that change very little in diameter with increasing height, and may have sufficiently confounded these results. Separation of the data by plant species was warranted to account for cabbage palm, and was attempted, but resulted in very small sample sizes in many cases, especially on the treatment islands after 1996, so such analyses were not performed.

Prey Availability by Habitat and Height

Pooled group means illustrate that more individuals and orders of arthropods were captured in traps on island L2C, in cabbage palms, in forested habitats, and in traps near the ground (Table 4.17). Although the number of arthropod individuals and taxa were significantly different across habitat and height, neither island nor plant species were significant main effects, and none of the interactions were significant (Table 4.18).

The factors plant and island were removed from the model to reduce the analysis to a two-way MANOVA, using the same two variables, but only trap location and trap height as factors. Again, the number of individuals and orders of arthropods captured in the traps were significantly influenced by the location of the traps (Pillai's Trace = 0.0443; $F_{1,140} = 6.4849$; $P = 0.0120$) and the height of the traps (Pillai's Trace = 0.1511; $F_{1,140} = 24.9283$; $P < 0.0001$), however, these two factors did not interact (Pillai's Trace = 0.0028; $F_{1,140} = 0.3864$; $P = 0.5352$).

To refine these results further, the data for the number of individuals and number of orders were cast into separate univariate, two-way ANOVAs using trap height, trap location (habitat), and their interaction as factors. Significantly more individual arthropods were captured in traps located in forested habitats than in open-xeric habitats (DF = 1; SS = 629.1736; F = 8.3039; P = 0.0046), and significantly more arthropods were captured in traps placed near the ground than in traps placed two meters above the ground (DF = 1; SS = 2458.5069; F = 32.4475; P < 0.0001). However, the interaction between these two factors was not significant (DF = 1; SS = 37.0069; F = 0.4884; P = 0.4858). Significantly more arthropod orders were captured in traps located in the forested hedges than in the open-xeric habitat (DF = 1; SS = 16.3403; F = 11.1037; P = 0.0011), and significantly more orders were captured in traps placed near the ground than in traps placed two meters above the ground (DF = 1; SS = 65.3403; F = 47.2950; P < 0.0001). The interaction between these two factors was not significant (DF = 1; SS = 0.8403; F = 0.6082; P = 0.4368).

Changes in Body Size and Body Condition

Reproductive-sized adults of green and brown anoles overlapped substantially in size, as measured by SVL (Figures 4.24 and 4.25). Females overlapped substantially, reached about the same maximum size, and their mean size differed by only about 1 mm. Males overlapped in size as well, but their mean and maximum SVLs differed by about 5 mm. As a result, female brown anoles were on average about 70 percent as large as their male counterparts, whereas females green anoles were on average 80 percent as large as male counterparts, indicating that adult brown anoles were more dimorphic than were adult green anoles.

To test the effect of expanding brown anole populations on the ultimate body sizes (SVL) attained by adult green anoles of each sex, differences in the mean of the largest third of the green anole males and females in each yearly sample on each island (Mean SVL_{Max33} of Chapter 2) were examined across treatment and time. SVL_{Max33} data were normally distributed, so mean values were used as the test values. Although Mean SVL_{Max33} values appear to become larger over time in both males and females (Table 4.19), separate repeated measures MANOVAs (Von Ende 1993) using treatment, year, and their interaction as factors returned non-significant values for males by treatment (Pillai's Trace = 0.0412, $F_{1,4} = 0.0579$, P = 0.8217), year (Pillai's Trace = 0.9024, $F_{3,2} = 6.1650$, P = 0.1427) and their interaction (Pillai's Trace = 0.7842, $F_{3,2} = 2.4234$, P = 0.3055). Similar results were obtained for females by treatment (Pillai's Trace = 0.1208, $F_{3,2} = 0.5498$, P = 0.4996), year (Pillai's Trace = 0.8897, $F_{3,2} = 5.3769$, P = 0.1768), and the interaction (Pillai's Trace = 0.6848, $F_{3,2} = 1.4487$, P = 0.4333).

Brown anoles captured on island MT were very large during every year of this study, but were particularly large in 1996. In fact, the average size of all male brown anoles on that island in 1996 was 64 mm SVL and 8 g. The largest brown anole ever recorded (to my knowledge), a 73 mm, 11.8 g male, was captured on that island in 1996, along with a number of other males over 70 mm, numerous females over 52 mm in SVL, and the largest female brown anole ever recorded (to my knowledge): a 54 mm, 5 g individual! This trend continued in 1997 and 1998 as well. I anticipated that, if brown anoles had any effect on green anole body parameters, such as condition, it would occur on this island, as the green anole decline was most dramatic on this island.

Despite the extensive overlap in size by length, adult brown anoles were much more robust than were adult green anoles (Figure 4.26). Adult brown anole females weighed about one gram more than their green counterparts, but the pattern was especially evident in males above 50 mm, which weighed nearly twice as much as equivalent sized green anoles. The extensive overlap in their diets (Chapter 3) suggests that brown anoles, being the more robust species and presumably consuming more food, might have a negative effect on green anoles by depleting resources, which might be reflected in changes in body condition of green anoles, especially on island MT. So, differences in the relationship between green anole body mass and body length, a reflection of body condition (Chapter 2), were examined across treatment and time.

The slope of the regression of Log10 SVL against Log10 weight for 1,657 exclusively numbered green anoles in this study was 2.5542 ($R^2 = 0.86$), resulting in a mass exponent for the green anole condition index (CI) of 0.3915. To test the effect of increasing densities of brown anoles on the condition of adult green anoles of each sex, differences in mean green anole CI values for each year on each island (Mean CI) were examined across treatment and time with repeated measures MANOVA (Von Ende 1993).

Although Mean CI appears to differ over time in both males and females (Table 4.20), separate repeated measures MANOVAs for each sex, using treatment, year, and their interaction as factors returned non-significant values for males by treatment (Pillai's Trace = 0.0196, $F_{1,4} = 0.0802$, P = 0.7911), year (Pillai's Trace = 0.3723, $F_{3,2} = 3.955$, P = 0.7728) and their interaction (Pillai's Trace = 0.5038, $F_{3,2} = 0.6769$, P = 0.6424). Similar results were obtained for females by treatment (Pillai's Trace = 0.0014, $F_{1,4} = 0.0057$, P = 0.9434), year (Pillai's Trace = 0.8079, $F_{3,2} = 2.8040$, P = 0.2738) and their interaction (Pillai's Trace = 0.2500, $F_{3,2} = 0.2222$, P = 0.8750).

DISCUSSION

Relevance of this Study

The seven dredge-spoil islands I employed in this study were ideal "natural cages" for conducting an experiment on large numbers of lizards. They supported complex but relatively open vegetation generally less than 10 meters tall, allowing the entire range of vertical habitat to be searched thoroughly with small binoculars and some healthy tree climbing. Most importantly, they contained anole predators and arthropod prey faunas that were derived directly from the mainland and barrier island (Figure 4.1). I propose that these spoil islands were excellent models for isolated, disturbed habitat patches in coastal regions of peninsular Florida surrounded by asphalt and mowed lawns. Apparently, it is in these types of habitats that brown anoles are most dense and have the greatest effect on green anoles (Echternacht and Harris 1993).

Although the islands were considered at the outset of this study to be "closed" systems with regards to anole emigration and immigration, human influences were evident during the experiment, one over-water dispersal event was witnessed, and effort was required to keep two of the control islands free of brown anoles. In hindsight, that the integrity of the controls were maintained throughout the study on all but the large island in 1998 was fairly remarkable, given that at least five other islands in the Mosquito Lagoon chain were "naturally" colonized by this species (that is, without my assistance) during this short study (Campbell in prep.).

In real invasions and natural colonizations, new populations undergo a prolonged period when densities are too low for individuals to find each other effectively, termed the Allee effect (Allee 1938). Then, at some "critical threshold," the population expands rapidly. By using 40 lizards on island ST and island MT, and 80 lizards on island LT, the invader populations were probably just large enough to ensure sufficient short-term survival and reproduction in the first year so that large numbers of young lizards were present in the second summer, followed by immense numbers of lizards in third summer. Also, point releases insured that invader populations were dense enough to find each other in the first year, even on the large island. Despite these considerations, the as yet unconfirmed ability of females to store sperm (Tokarz 1998) would diminish the importance of any Allee effect.

Because the life spans of these species are less than two years (Lee et al. 1989), populations established using low numbers of invaders (e.g. a few placed on the islands each year at different points), would have taken more time to expand because many individuals would likely have perished before finding mates and reproducing. Although this would have better approximated a real invasion scenario, it probably would have taken an inordinate amount of time for the populations to expand. Furthermore, the populations might not have expanded at the same rate on each island, eliminating their value as replicates. On the other hand, the introduction level I used was also preferable to flooding the islands with brown anoles at or near the island's carrying capacity (e.g. thousands) over an abnormally short time period (e.g. a few days or weeks), which would have had no counterpart in reality.

Despite an inability to exploit more island replicates and increase the power of my statistical analyses, a number of notable results were obtained in this study, such as the overall timing of brown anole numerical and spatial spread, and the concomitant green anole density decline, habitat shift, and perch shift. Moreover, those results were based on means and medians of fairly large samples, even after the data was sorted by sex, island, and year. But these results came with great cost to the integrity of my experimental design, as intraspecific density-dependent effects and their interactions were clearly confounding across treatment. Moreover, this effect occurred only during the last years of the study and only in treatment populations. One solution to this problem would have entailed keeping densities of the treatment green anole populations stable via repeated introductions, while holding brown anole populations to a stable density (Goldberg and Scheiner 1993, Underwood 1997). This would not only have been futile under field conditions, but would have been an inadequate reflection of reality, and would have been better addressed in controlled study employing small cages: exactly the type of system I was attempting to avoid in studying this interaction.

Brown anoles invade and expand rapidly in number and density, and under most conditions, green anole populations respond with a reduction in their population density, probably to between 10 - 30 percent of their original size. The fact that they decline should be included in experimental studies of impacts on the fitness of surviving green anoles and their progeny, along with some type of experimental control for density-dependent effects. Despite the obvious declines observed in this study, the mechanisms remain elusive.

Niche Shift and Interference Competition

As brown anoles filled the treatment islands, green anoles exhibited significant declines in density and shifts in spatial distributions in the three main habitat types common to those islands, and a shift out of the open-xeric habitat on the large island. Although the cause cannot be absolutely attributed to brown anoles with these above analyses, similar trends did not occur on any of the matched control islands, indicating brown anoles were the agent of change. This suggests two possible explanations: first, that brown anoles induced a shift in green anoles remaining in the forested area to locations where they were much less likely to be seen by a ground-based observer, or that smaller proportions of green anole population utilized the forested area each year. The former explanation is unlikely, since, although an upward niche shift was expected, it was expected to be less than about 1 m, on average. Furthermore, the trees were relatively short (~ 6 m) and were regularly climbed in search of green anoles.

Green anole males on the three treatment islands exhibited an upward shift in the locations on which they perched, likely in response to the presence of brown anoles, the only experimental effect in this study. However, they did not choose perches of different diameters, and females showed no significant effects. A vertical shift, if it occurs, may have been important in conjunction with the temporal changes in the horizontal distribution, or habitat utilization, of green anoles on the treatment islands. Together, these spatial shifts might influence the outcome of resource competition in this two-species interaction, if it can be shown that the distribution of arthropods varies over horizontal or vertical space.

Biologists studying the effects of invaders on native species generally neglect cryptic behavioral interactions in favor of more obvious effects such as predation and population-level responses (Holway and Suarez 1999). Behavior is known to be an important factor in invader-native interactions in lizards (e.g. Petren et al. 1993). *Anolis* lizards, being active, highly conspicuous, and territorial, are amenable to the study of intraspecific and interspecific behavioral interactions, but only a few studies have addressed behavioral issues in the interaction between these two species. In keeping with this trend, my study demonstrated niche shifts but did not actually reveal any mechanisms because long-term behavioral observations were not conducted on focal individuals or a number of individuals in a given plant or habitat (e.g. Jenssen 1973).

Brown and Echternacht (1991) and Tokarz and Beck (1987) showed that intraspecific aggressive interactions (e.g. territorial behavior) occurred more frequently and with greater magnitude than did interspecific aggressive interactions between these species. My study was not specifically designed to reveal behavioral interactions, but field observations of interspecific interactions (or lack thereof) support this claim. I witnessed only two interspecific interactions, despite spending well over 1,000 hours searching carefully for perching anoles on the four islands where the two species were sympatric. In the first, I videotaped a female green anole being chased to over 4 m in a cabbage palm by a brown anole female. In the second (also videotaped), two males grappled and traded places on a low perch in a mangrove four times before the green anole gave up the perch and crept slowly up the trunk to a height of over 5 m. These were clear cases of aggressive interference causing an upward shift in green anoles, but very rare relative to the countless instances of interspecific territorial aggression observed during this study, mostly between male brown anoles. I propose that the latter observation best illustrates the perch shift mechanism. Green anoles are highly visual creatures (I regularly observed them pouncing on ground-based prey items from treetop perches over 5 m high), certainly know that brown anoles are present below them on a given plant, and may adjust their zone of activity based on some factor other than direct aggression. But given that interspecific interactions are so rare, what actually causes the shift?

Brown anoles are the more abundant (Chapter 2) and patrol smaller territories than green anoles, such that a given individual would, on average, have few interactions with a single territory-holding green anole, whereas a given green anole is likely to encounter a number of different brown anoles within the bounds of their larger territory. To exclude brown anoles from its territory, a green anole would have to continually interact with a number of brown anoles in addition to its intraspecific competitors. I posit that low-amplitude interactions, if frequent enough, and the "persistence" of brown anoles exhibited by the video-taped male discussed above, might be enough to create a measurable shift in the preferred perch height of green anoles. In other words, the interactions between these lizards might not have to be especially violent for green anoles to simply become tired of dealing with a large number of competitors that never seem to go away. But in the end, the cause may be even less complicated.

Green anoles exhibit "ground-to-crown" ecomorph in allopatric situations, but in fact, they are nicely pre-adapted for the trunk-crown life (Williams 1969). When faced with a trunk-ground competitor, green anoles occupy the microhabitat best suited to their eco-morphology (e.g. small branches in the shrub layer and crown of forested edge situations). Thus, the innate capacity to adopt their ancestral perch distribution was not lost during the thousands of years that green anoles have been isolated in North America. However, in deforested habitats, and even in native habitats such as the Florida scrub (Myers and Ewel 1990), there may be no "up" for green anoles to shift to, forcing them to move to a different habitat type. Although this appeared to occur in the open-xeric habitat of island LT from one year to the next, recapture data indicated that individual green anoles did not relocate to different areas of the islands: they were simply not replaced in that habitat by their progeny in the following year. This suggests that green anole females deposited fewer eggs in this habitat, that green anoles were excluded in hatchling or juvenile stages by resource competition or predation by brown anoles, or a combination of these, and potentially other factors.

If food limitation is caused by brown anoles, which perch lower than do green anoles, the latter may shift their perch upward to disperse themselves to better obtain food. If brown anoles deplete food resources as suggested above, and green anoles are able to assess this, they might move upward in response to the repeated and learned fact that they have had more successful hunting excursions higher in a given plant. Clearly, behavioral studies should be conducted in the field using a large number of marked individuals that have segregated themselves out 'naturally' in a habitat where most individuals will be visible, such as the larger shrubs in the open-xeric habitats of the large islands in Mosquito Lagoon. Some type of prey manipulation treatment would be in order, to remove the confounding effect of prey resource competition.

The arthropod survey was conducted over a very short period of time relative to the four-year life of this study, and during a fairly extreme climatic period (Chapter 2). However, the results point to factors that might influence the outcome of the interaction between these lizard species in harsh environs such as fragmented habitats, but especially urban areas with lone shrubs dispersed in a matrix of grass and asphalt, of which the open-xeric areas of these islands seem to be very suitable models. But the effects of habitat alteration on arthropod abundance are only meaningful in this interaction if it can be shown that the reduced arthropod abundance translates to a decline in growth, asymptotic size, body condition, or other variables describing individual fitness.

Exploitative Resource Competition

The body size and condition of the green anoles remaining on the treatment islands in later years did not appear to be affected by the increasing brown anole populations, contrary to the indication in Schoener (1969b) that they should be affected, but certain trends warrant further investigation. Although the sample sizes in these analyses (n = 3 islands in each treatment) may have been too small to accurately discern the true differences, if they occurred, between treatment and control populations over time, the sample means (or medians) used in these analyses were based on reasonable sample sizes, with the exception of the last two years on island ST and MT. The main issue in analyses of body parameters is that of the confounding effect of green anole density, which decreased on the treatments over time, presumably relaxing the level of intraspecific competition, and possibly influencing body parameters on those islands.

Alternatively, although island-wide and inter-island biotic and abiotic factors were relatively stable for such a large-scale field experiment (the islands span a length of over 10 km), large-scale factors such as climate may have had a greater influence on green anoles than did brown anoles, especially in 1998, which was a period of extreme climate in this area of Florida (Chapter 2). In fact, Mean CI values of green anole populations declined in value between 1997 and 1998 in many cases (Table 4.20), indicating a short-term trend that might have affected the outcome of significance tests on CI values.

Resource competition requires that resources utilized by both competitors also be limited in supply (Keddy 1989). The availability of food directly influences the growth of animals, and lizards have been particularly well studied in this regard (e.g. Dunham 1978, Pianka 1986, Roughgarden 1995, Petren and Case 1996). In turn, insectivorous vertebrates are known to influence their prey populations in both number and composition. Predation by birds is known to limit grassland arthropod densities (Bock et al. 1992, Fowler et al. 1991, Joern 1986), and predation by rodents has been shown to influence species composition and population sizes in ground beetle communities (Parmenter and MacMahon 1988).

In a number of studies, introduced brown anoles have been shown to devastate arthropod and spider populations on Bahamian islands (Schoener and Spiller 1996, 1999, Spiller and Schoener 1997, 1998). In fact, Caribbean island anoles generally occur at high densities and are probably limited by food, while mainland anoles occur at lower densities and are thought to be limited by predators (Andrews 1979), although a few exceptions have been demonstrated (Guyer 1988). However, it is highly plausible that brown anoles diminish the availability of arthropods even in mainland situations where prey were not previously limiting to green anoles. I have demonstrated a large overlap of prey choice in these two species in south Florida (Chapter 3), and presented data suggesting resources might be limited in the open-xeric habitats on the large islands in Mosquito Lagoon, which likely represent suitable models for disturbed habitats in Florida. But what features of disturbed habitats might cause arthropods to be limited in supply to anoles?

It is well known that diversity, density and distribution of arthropods is influenced by the spatial and structural diversity of their habitat, which is defined largely by vegetation (Greenstone 1984, Murdoch et al. 1972, Riechert and Gillespie 1986). The microspatial heterogeneity hypothesis (MacArthur and MacArthur 1961, Pianka 1966) predicts that more structurally diverse habitats will support more species, and the productivity hypothesis (Connell and Orias 1964, MacArthur 1969) states that, in more productive habitats, the resource base is able to support more species. The open-xeric zones of the large dredge-spoil islands of Mosquito Lagoon and analogous disturbed habitats in urbanized and agricultural areas on the mainland are much less structurally complex than are native, undisturbed habitats. By definition, competition, if it occurs between these two species, is likely to be more intense in habitats with low structural complexity, such as urban sites with groomed vegetation and mowed lawns.

The ecosystems of Florida have been fragmented into a patchwork of “habitat islands,” in the best cases consisting small native habitats under the influence of edge effects, and at worst consisting entirely of exotic vegetation on entirely landscaped earth, within which arthropod “pests” are managed intensively. This is where brown anoles appear to be having the most dramatic effect on green anoles. In order to properly model the interaction between these species, mainland food limitation issues should be re-evaluated in such habitats, in light of arthropod prey abundance and density, site conditions, and presence of exotic flora and fauna.

Roughgarden (1995) attempted to experimentally induce an increase in the level of competition between *A. bimaculatus* and *A. schwartzi* by placing cones around tree trunks, thereby forcing two species to perch closer to one another (all near the ground) than they would normally. However, a measurable increase in competition did not occur. Although the results of my study do not directly point to mechanisms, it is clear that there was an affect in the open-xeric habitats of these islands. In this habitat, green anoles and brown anoles were essentially forced to perch closer to one another, simply because all the plants were relatively short and highly isolated within a matrix of bare sand. Results from my brief arthropod survey indicate that competition for arthropod prey could have been more intense in this habitat, but other mechanisms, such as increased levels of hatchling competition or predation on hatchlings in less complex habitats (Gerber in prep.), cannot be ruled out.

CHAPTER 5

Summary and Conclusions

I have demonstrated that small numbers of brown anole propagules can give rise to large populations in only a few years (Chapter 2), and that increasing densities of brown anoles can rapidly and significantly affect green anole population size and density (Chapter 4). In light of these results, it is fairly obvious that these species compete on at least some level, and that the interaction is asymmetric (Figure 1.1; all figures are in the Appendix). Their activity periods overlap substantially (Campbell in prep.), and their micro-climatic niches are very similar (G. Gerber pers. comm., Campbell in prep.). When allopatric, their structural niches are very similar (low perches in fairly open, edge-rich habitat), but in sympatry, only green anoles are excluded from open habitats, and only green anoles shift their perch height (Chapter 4, Schoener 1975). This suggests some type of behavioral interference or avoidance, although interspecific interactions are fairly rare (Chapter 4, Brown and Echternacht 1991). The body sizes of the two species overlap substantially when comparing same-sex pairs, such that the Hutchinsonian ratio (using SVL) is about 1.04 between males and about 1.06 between females. Overlap is, however, much lower when comparing across sex (Hutchinson ratios are about 1.25 for green anoles and about 1.31 for brown anoles). This would seem to suggest that same-sex resource competition must be the most intense, and that these two species cannot co-occur without some type of structural niche shift (Schoener 1975), body size shift (Schoener 1969b), or dietary niche shift (Schoener and Schoener 1978). In fact, their diets are very similar (Chapter 3). Conversely, hatchlings and juveniles of these species are all about the same size, regardless of sex. Gerber (in prep.) has evidence that the presence of brown anole hatchlings affect green anole hatchling survival and growth, but the mechanism is yet unknown. The two species also share gut parasites (Chapter 3) and blood parasites (e.g. Schall and Vogt 1993) but, although the presence of parasite-mediated competition has been demonstrated in *Anolis* (Schall 1992), its role in this interaction has not been demonstrated. Finally, they consumed each other's hatchlings (Chapter 3, Campbell and Gerber 1996, Gerber and Echternacht in press), however, the importance of this phenomenon has not been studied under natural conditions using rigorous experimental designs. A number of habitat-related effects (Chapter 4) suggest that a synergism between habitat alteration and either resource competition, hatchling predation, or both factors (i.e. intraguild predation) could explain the rapid green anole declines in urban areas of Florida.

Brown anoles devastate arthropod prey faunas when introduced to small islands in the Bahamas (e.g. Spiller and Schoener 1998), and there is no reason to believe that they cannot do so in mainland Florida under certain situations. Given that habitat is often defined by the species of plants present, and that plants vary by species in their structural architecture, both of which influence the density of many arthropods (e.g. Schoonhaven et al. 1998), it follows that arthropod availability varies with habitat type. Generally, arthropods occur in lower densities in less taxonomically and structurally diverse plant communities, such as monocultures of row crops or ornamental vegetation. Thus, anole prey may be limited and resource competition may be more intense in certain habitat types, but especially in those with lower plant diversities, such as in agricultural landscapes or urban areas containing isolated shrubs in a matrix of grassed yards and asphalt. Green anoles were excluded from analogs of these habitats on dredge-spoil islands (Chapter 4), and appear to be excluded from urban areas in which they were formerly abundant.

Arthropods consumed by anoles also vary in vertical space, and with the exception of tropical rainforest, their densities are favored in locations nearest the ground (e.g. Brown et al. 1997). Thus, anole prey may be limited in supply only a few meters removed from the ground surface (Chapter 4). Dense populations of brown anoles cause green anoles to shift their perches upward in the Bahamas (Lister 1976b, Schoener 1975) and in Florida (Chapter 4) such that exclusion of green anoles from perches near the ground might affect their ability to obtain prey. So, dense populations of brown anoles may not only limit the supply of arthropods, which were once abundant and fully accessible to green anoles, but may also force green anoles to utilize a different guild of plant-based arthropods for food, which exhibit lower densities and diversities than do soil-based arthropod faunas.

But resource competition may not be of sufficient intensity to cause the rapid declines in green anoles observed on the spoil islands and in urban areas of Florida over the past 40 years. By definition, plant architecture defines the density of cover available for hatchlings, and in a recent study (Gerber, in prep.), hatchling green anoles were significantly less vulnerable to adult brown anole predators in cages containing dense, old-field successional vegetation than they were in cages containing mowed grass. I demonstrated a rapid exclusion of green anoles in the open-xeric habitat of the large treatment island, and the beginnings of this phenomenon on the large allopatric control island in 1998 after brown anoles finally took hold, both consistent with the distribution of green anoles on the two-species control island (Chapter 4).. Green anoles also appeared to be excluded from forested interior areas where the only ground-canopy conduits were large tree trunks occupied by the largest of the brown anoles. However, these exclusions were not physical relocations of lizards: there was simply no replacement of green anoles in the years immediately subsequent to the establishment of brown anoles. In fact, after the arrival of brown anoles on the treatment islands, green anoles could only be found in forest edge and shrub-marsh habitats that contained dense understory shrub and herb species. This strongly suggests that, in open habitats, expanding brown anole populations either consumed a large portion of food that, although limited, was previously available to green anoles in sufficient quantity, that brown anoles consumed large numbers of more vulnerable green anole hatchlings in habitats without dense understory vegetation, or these effects were combined.

None of these factors appear to be important in unfragmented forested habitats, or in the core of forest fragments, where both species, if present, occur in very low densities. So why are any of these factors are important, given that these two species can coexist under certain circumstances? The ecosystems of Florida continue to suffer from rampant development, in which developers most often clear-cut and grade their sites and re-plant with ornamental vegetation which is managed by pruning and chemically controlling the arthropod "pests" upon which anoles depend. Thus, despite artificial watering, which is clearly beneficial to arthropods and anoles, the replacement and thinning of vegetation results in limitations in the arthropods available to green anoles, and forces the offspring of surviving green anoles to "run the gauntlet" of brown anole predators under sparse cover.

Brown anoles reach densities that translate to a total adult biomass of up to 75 kg per hectare, and consume a lot of arthropods, but may also be a significant source of food for common predators of urban areas. More importantly, their hatchlings potentially represent a source of food for green anoles (Chapter 3). In the early stages of the invasion process, dense green anole populations might hold the rate of the brown anole expansion to a minimum by consuming their hatchlings (Chapter 4). After the inevitable brown anole expansion, the few surviving green anoles would derive great benefit from consuming part of the "doomed surplus" of brown anole hatchlings. However, it is highly unlikely that the green anole, which occurs in lower densities, could hold the brown anole expansion at bay for very long. After brown anoles become abundant, if only half of the adults present at a given site each consumed only a single green anole hatchling during their entire lifetime, they would probably be culling from more than the doomed surplus of green anoles, initiating diminished recruitment in the next cohort. However, management for the continued viability of this native species should be as simple as allowing a small amount of dense hatchling cover and arthropod habitat to remain on a site. Hopefully, this is not too much to ask of future generations.

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APPENDIX

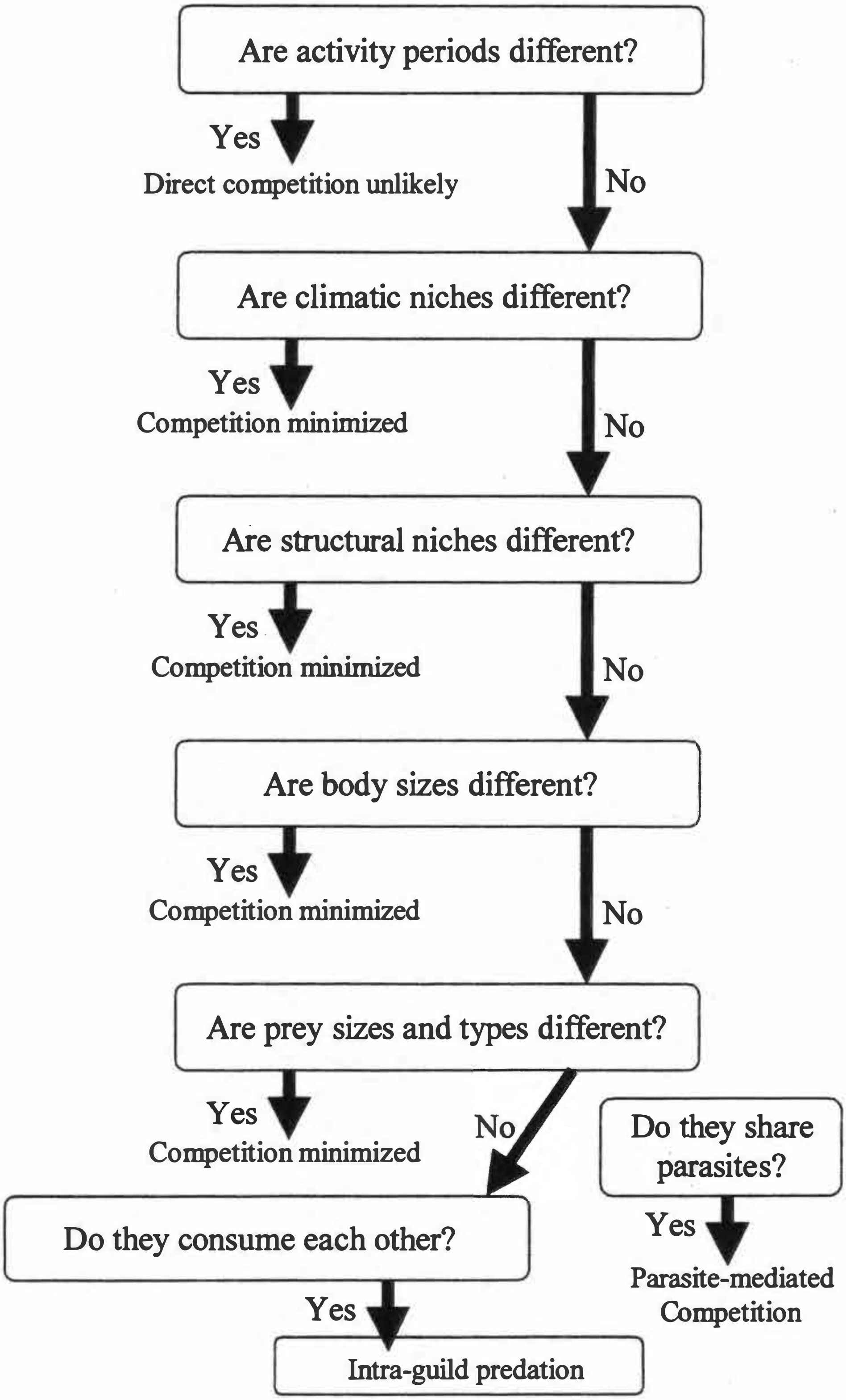


Figure 1.1. Competition flow-chart for *Anolis carolinensis* and *Anolis sagrei* constructed around the ideas in Schoener (1975) and Jenssen et al. (1984).

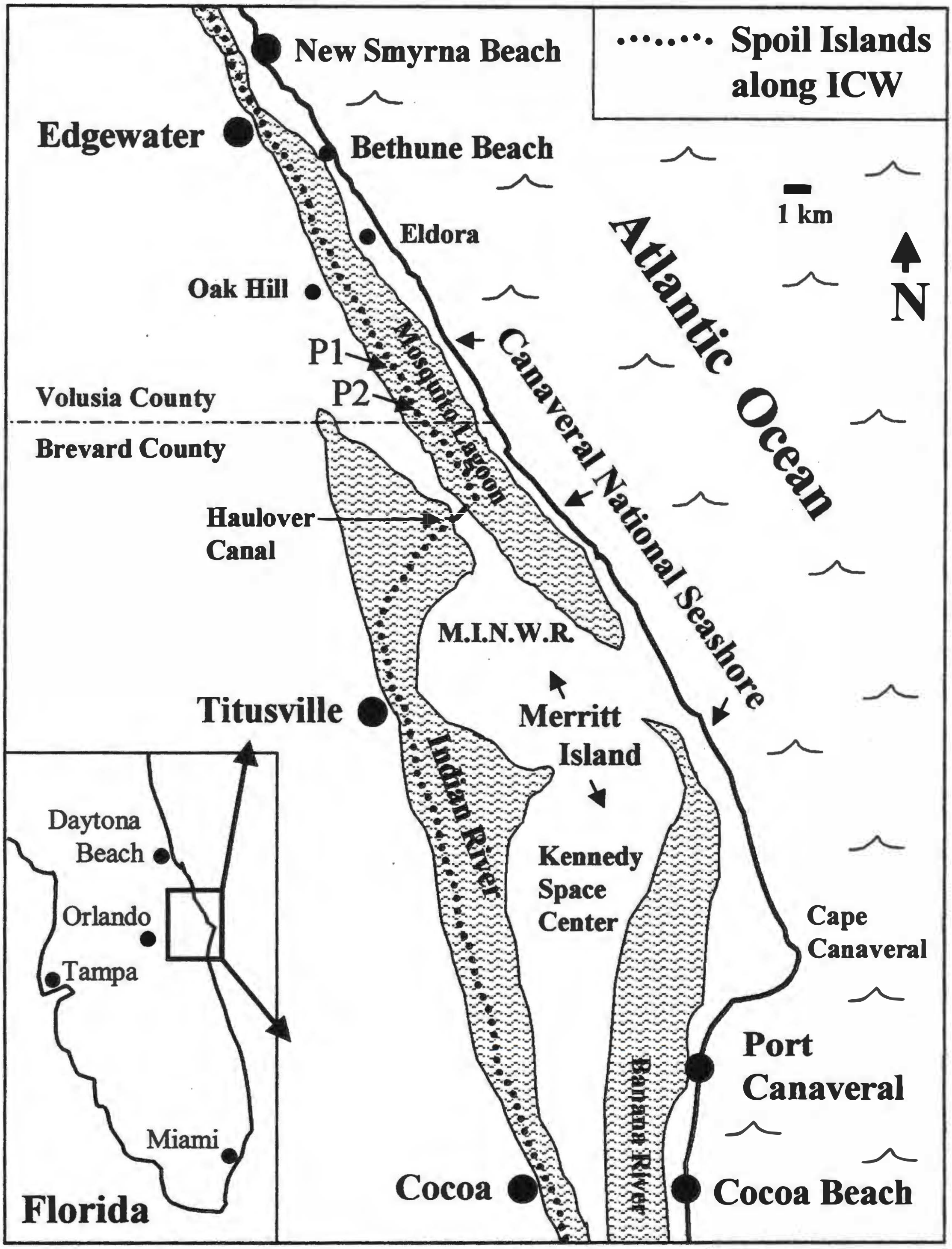


Figure 2.1. Location of the two pilot study islands (P1 and P2) used in this study. The two islands are located in a chain of dredge-spoil islands found along the Intracoastal Waterway (ICW) in Mosquito Lagoon, and are within the boundaries of Canaveral National Seashore and Merritt Island National Wildlife Refuge (MINWR). The latitude of Oak Hill is approximately 28^{0}52'30."

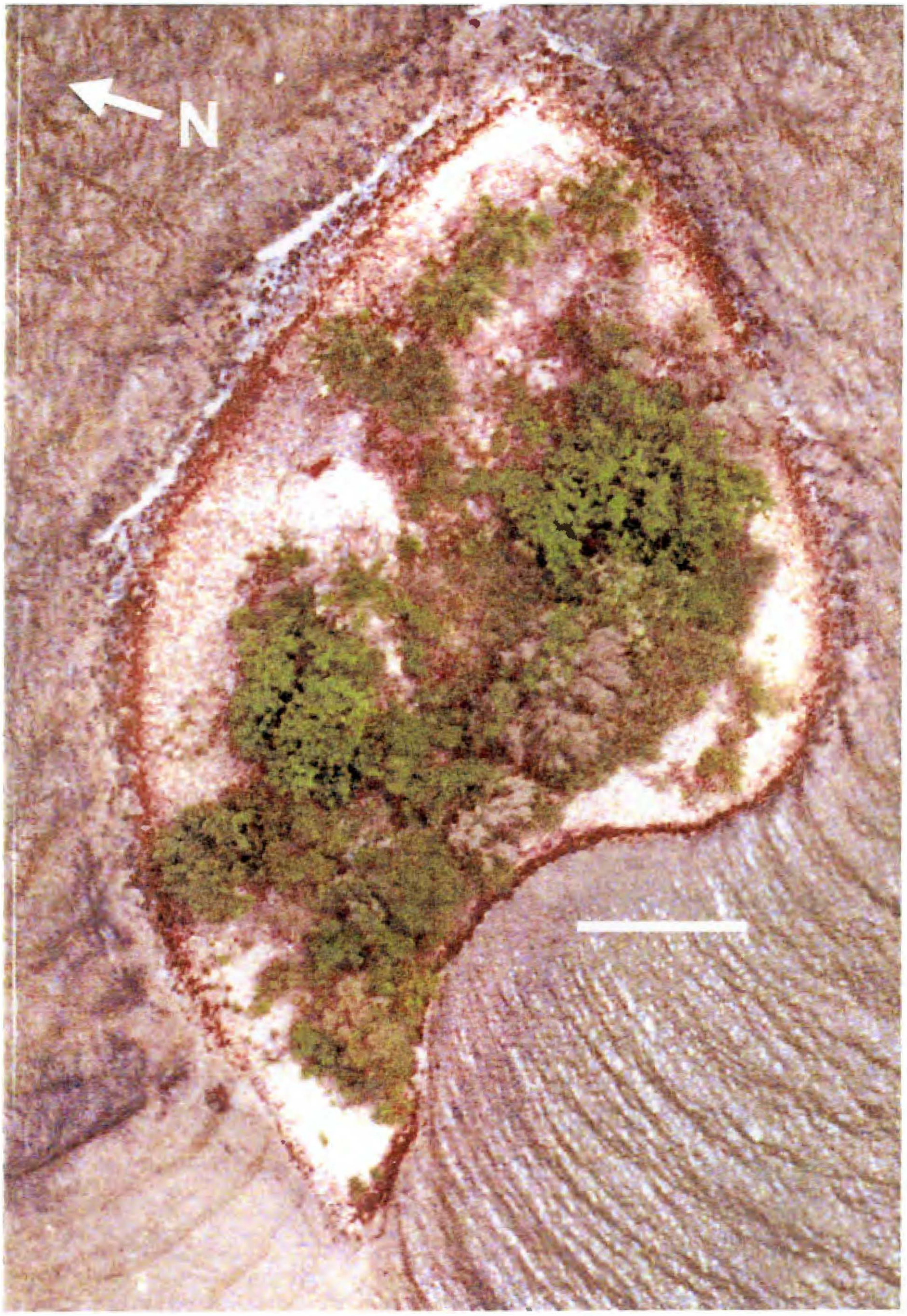


Figure 2.2. Color aerial photograph of Island P1 (scale 1: 236). White scale bar is approximately 5 m long.

Figure 2.3. Color aerial photograph of Island P2 (scale 1: 394). White scale bar is approximately 5 m long.

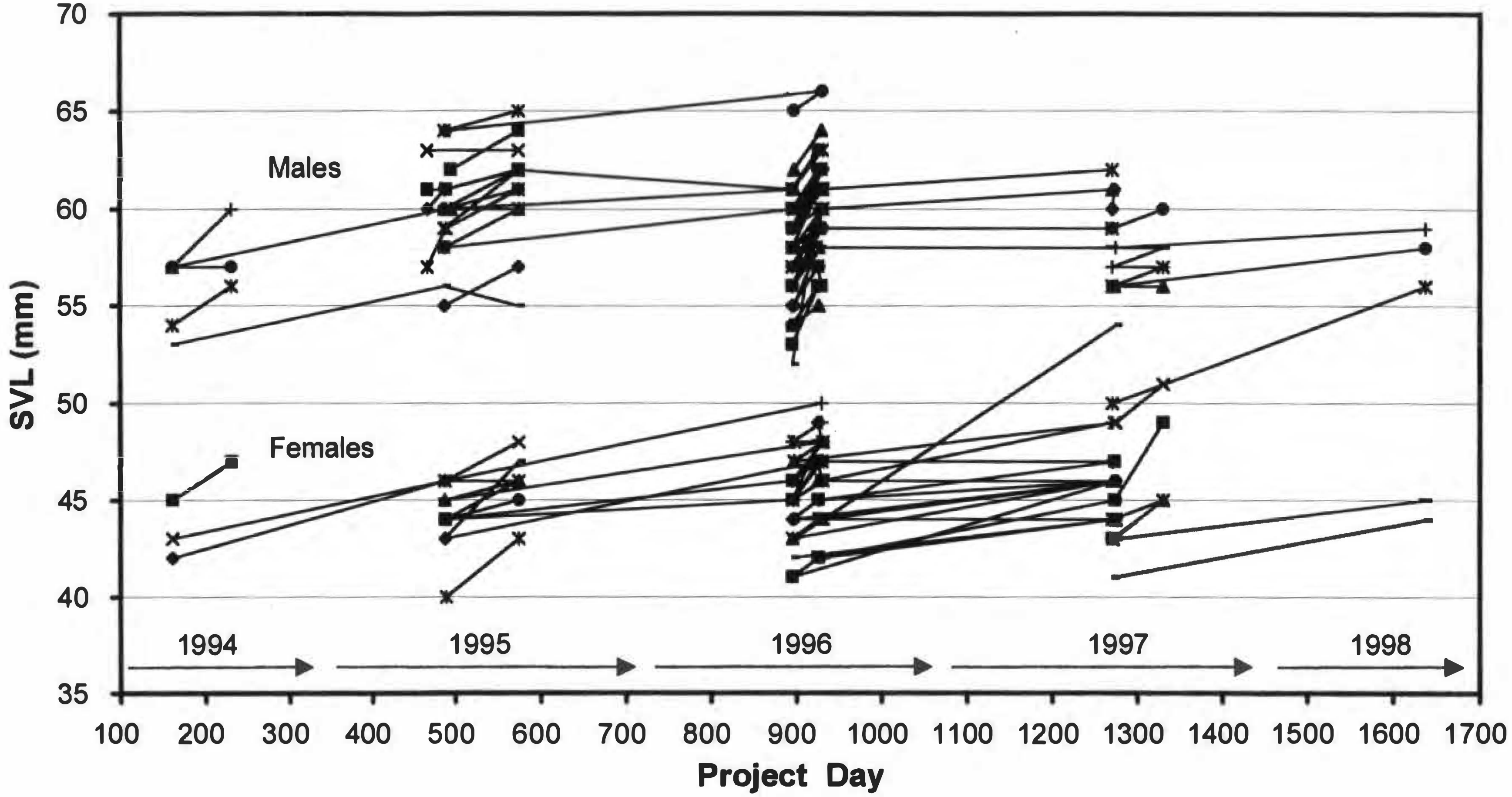


Figure 2.4. Individual growth trajectories for 136 brown anoles (51 females and 85 males) captured at least twice on Island P1 between 1994 and 1998. Project day is a running total of days beginning with January 1, 1994, such that January 1, 1995, 1996, 1997, and 1998 lie on days 365, 731, 1096, and 1461, respectively. Note that the male curves lie above the female curves, except for two males that were initially female-sized in 1996 and 1997.

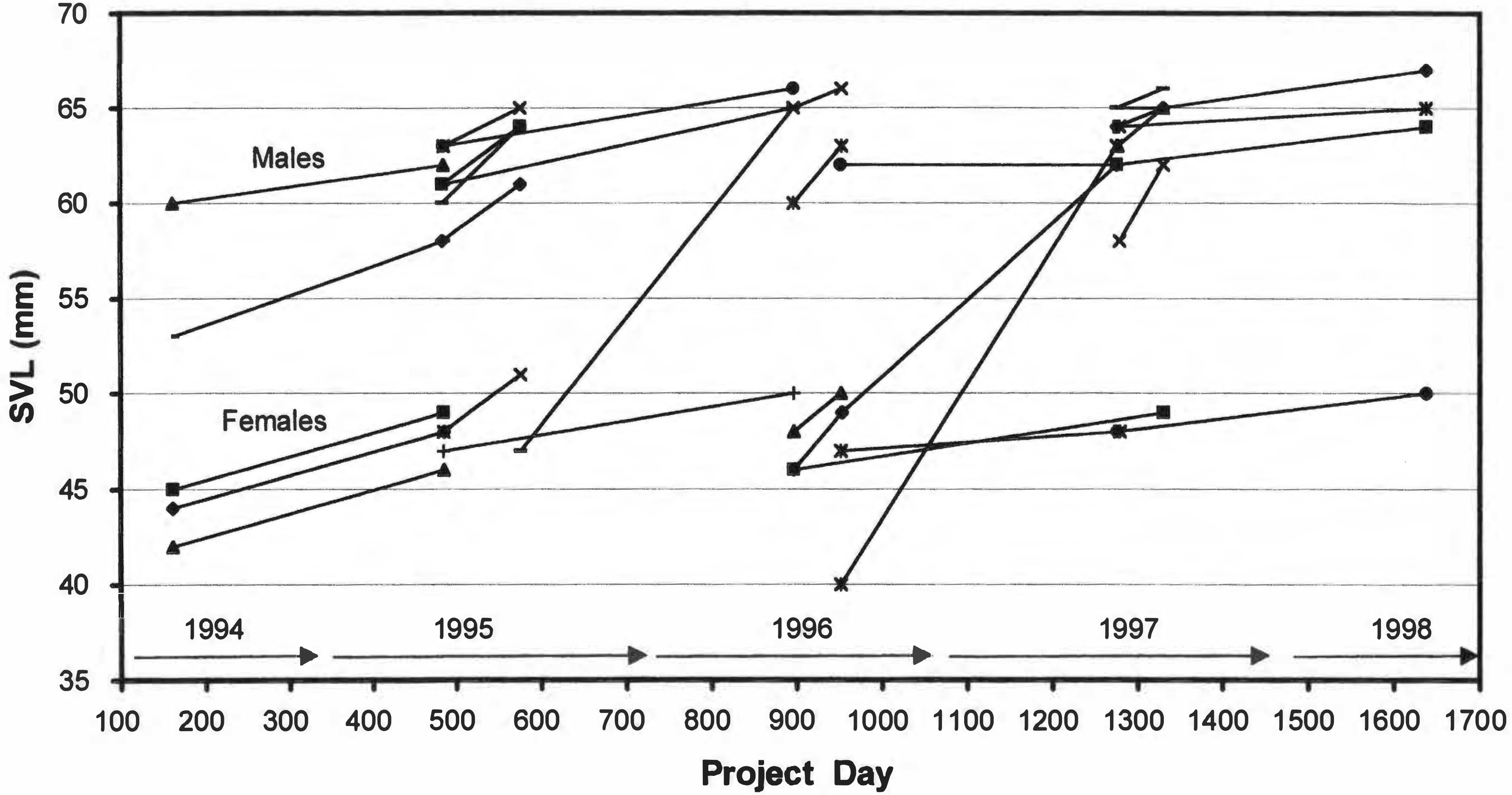


Figure 2.5. Individual growth trajectories for 32 brown anoles (11 females and 21 males) captured at least twice on Island P2 between 1994 and 1998. Project day is a running total of days beginning with January 1, 1994, such that January 1, 1995, 1996, 1997, and 1998 lie on days 365, 731, 1096, and 1461, respectively. Note that the male curves lie above the female curves, except for three males that were initially female-sized in 1995 and 1996.

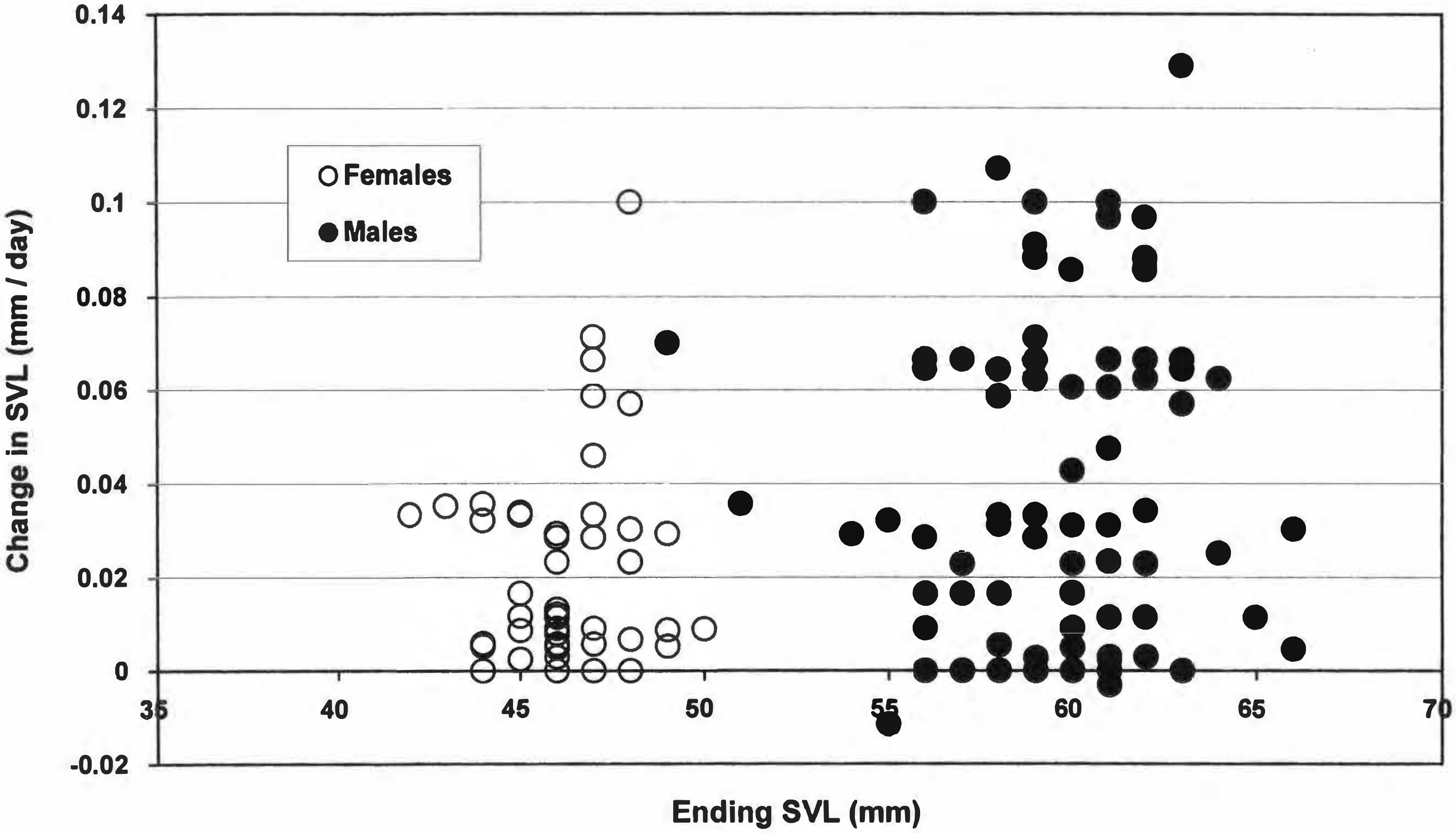


Figure 2.6. Brown anole growth rates (change in SVL in mm/day) on Island P1, plotted against the ending SVL of the measurement period. Plot includes 51 females and 85 males measured twice between 1994 and 1998.

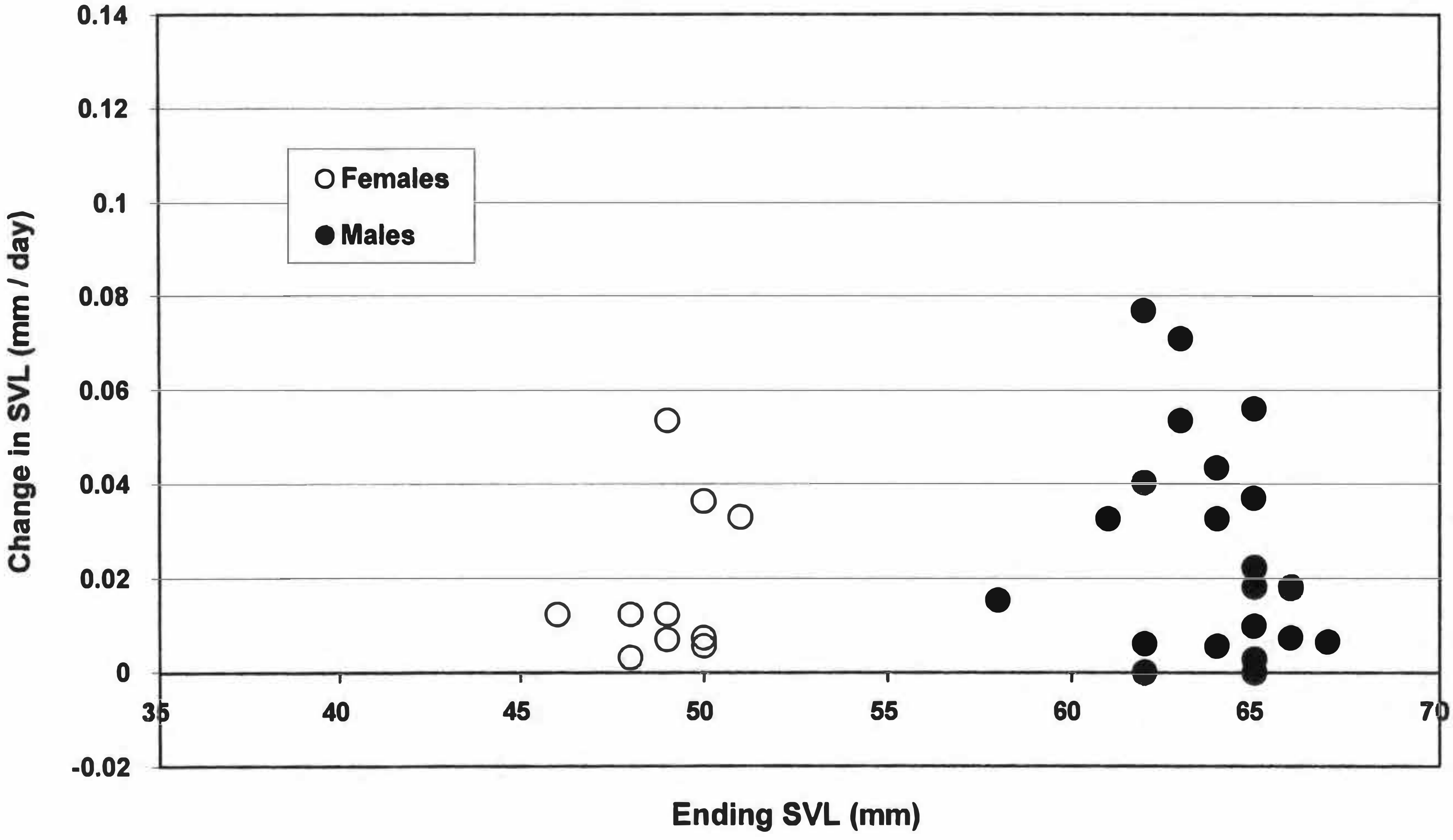


Figure 2.7. Brown anole growth rates (change in SVL in mm/day) on Island P2, plotted against the ending SVL of the measurement period. Plot includes 11 females and 21 males measured twice between 1994 and 1998.

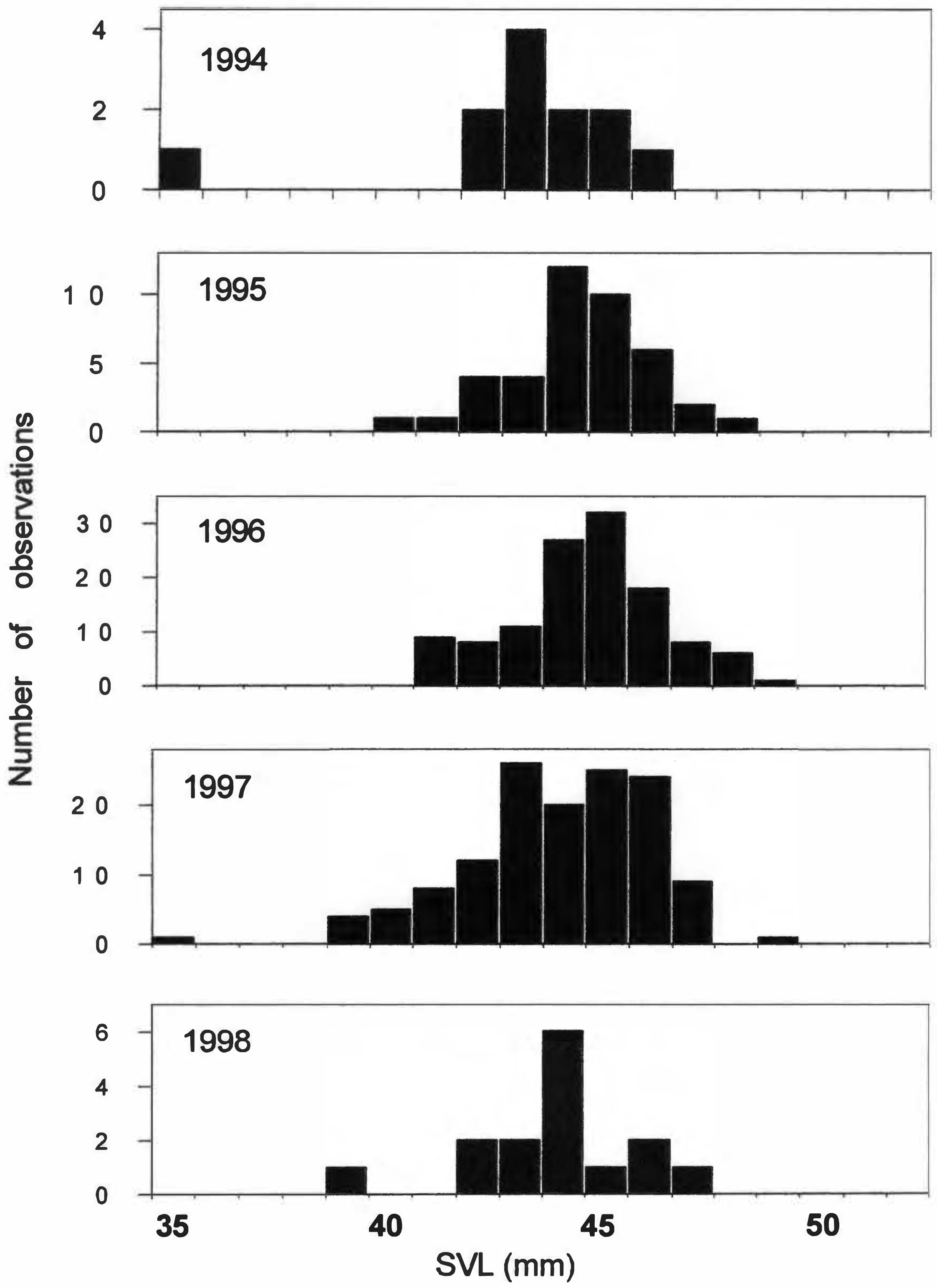


Figure 2.8. Snout-vent length (SVL) distributions of adult female brown anoles on Island P1 during each year of this study. Summary statistics for each year are provided in Table 2.6. Dates of surveys for each year are provided in Table 2.1.

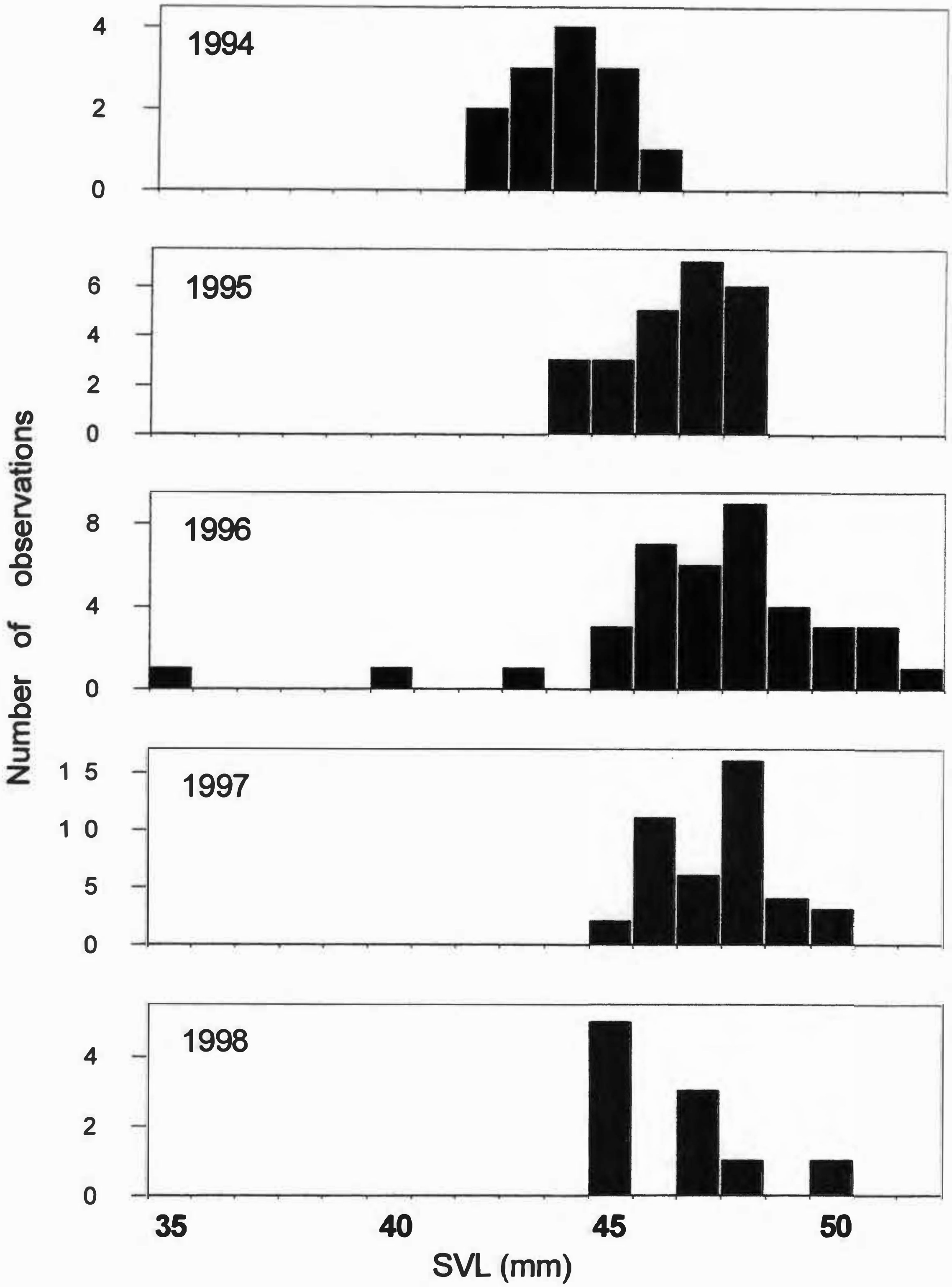


Figure 2.9. Snout-vent length (SVL) distributions of adult female brown anoles on Island P2 during each year of this study. Summary statistics for each year are provided in Table 2.6. Dates of surveys for each year are provided in Table 2.2.

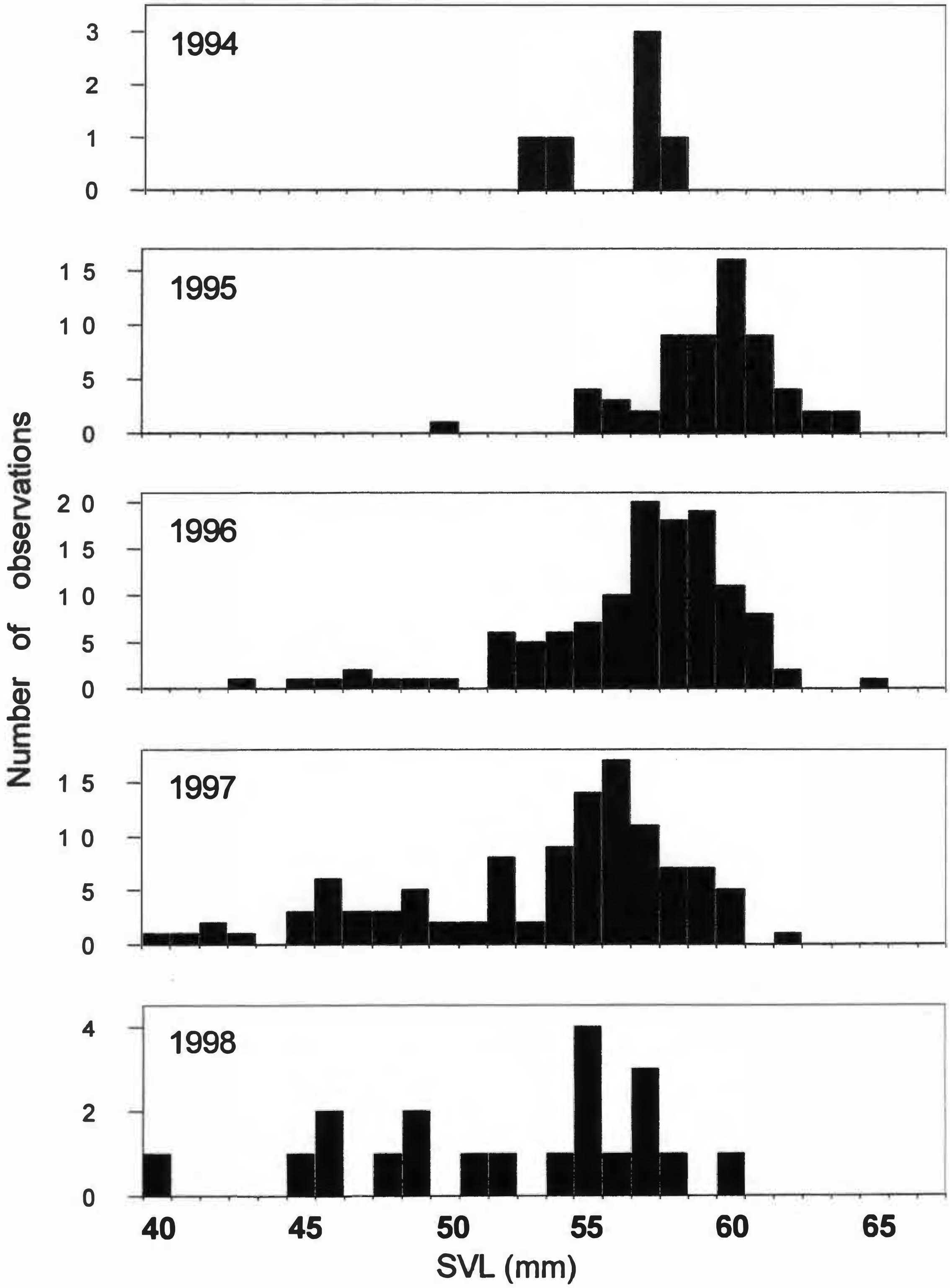


Figure 2.10. Snout-vent length (SVL) distributions of adult male brown anoles on Island P1 during each year of this study. Summary statistics for each year are provided in Table 2.7. Dates of surveys for each year are provided in Table 2.1.

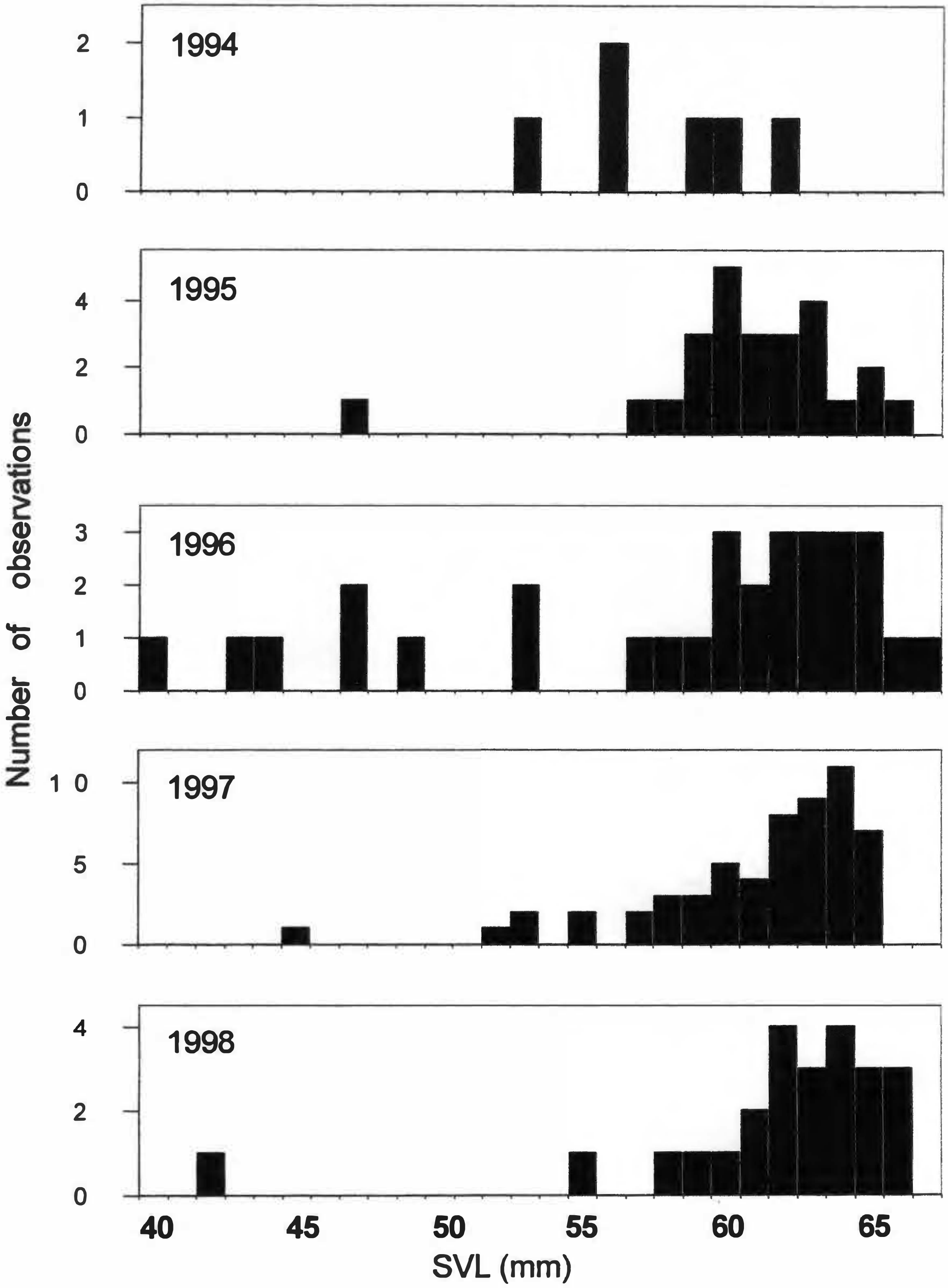


Figure 2.11. Snout-vent length (SVL) distributions of adult male brown anoles on Island P2 during each year of this study. Summary statistics for each year are provided in Table 2.7. Dates of surveys for each year are provided in Table 2.2.

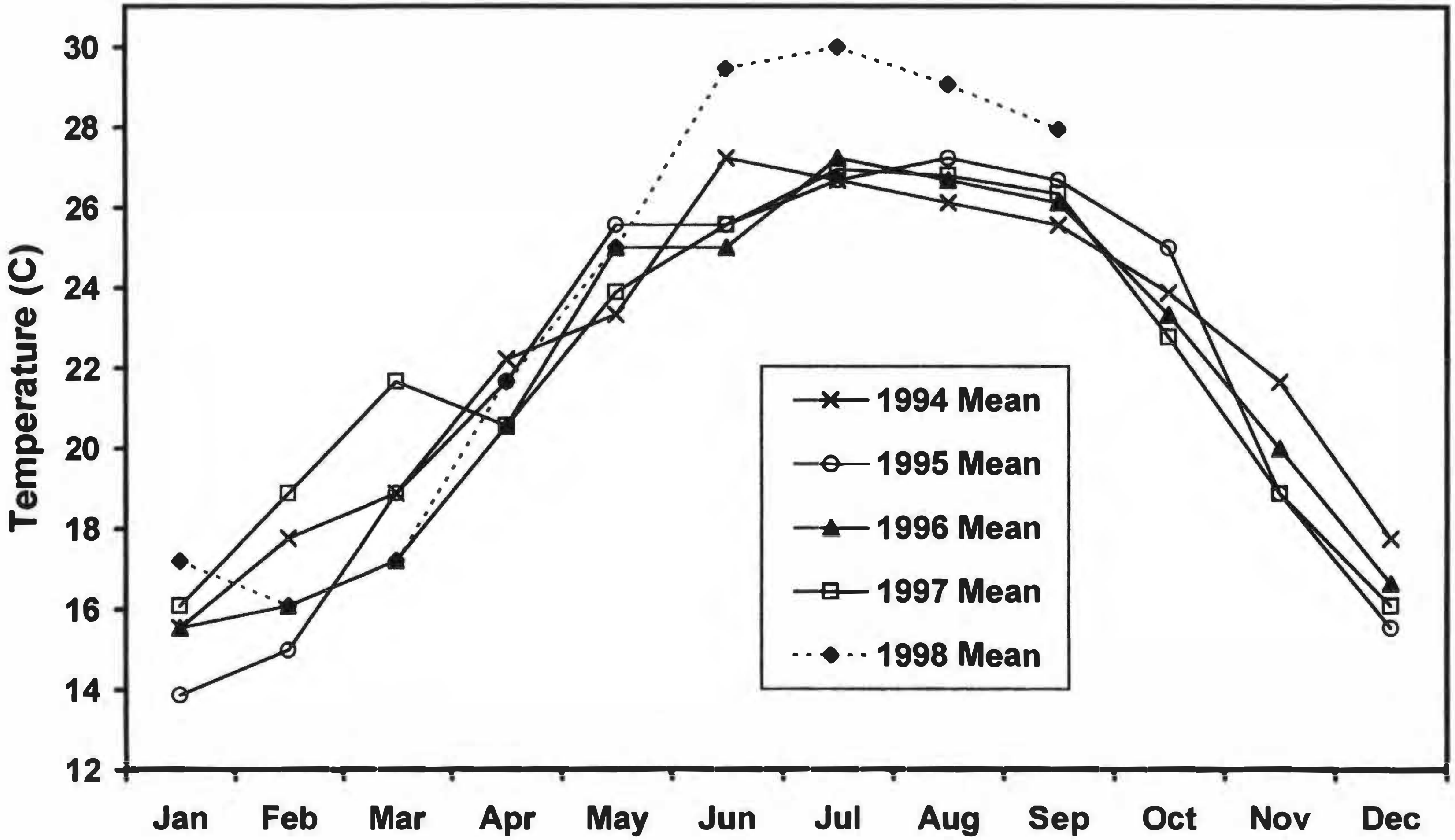


Figure 2.12. Mean monthly air temperatures during each year of this study. Data is from the NOAA weather station on Kennedy Space Center. Note the elevated temperatures exhibited during the summer of 1998.

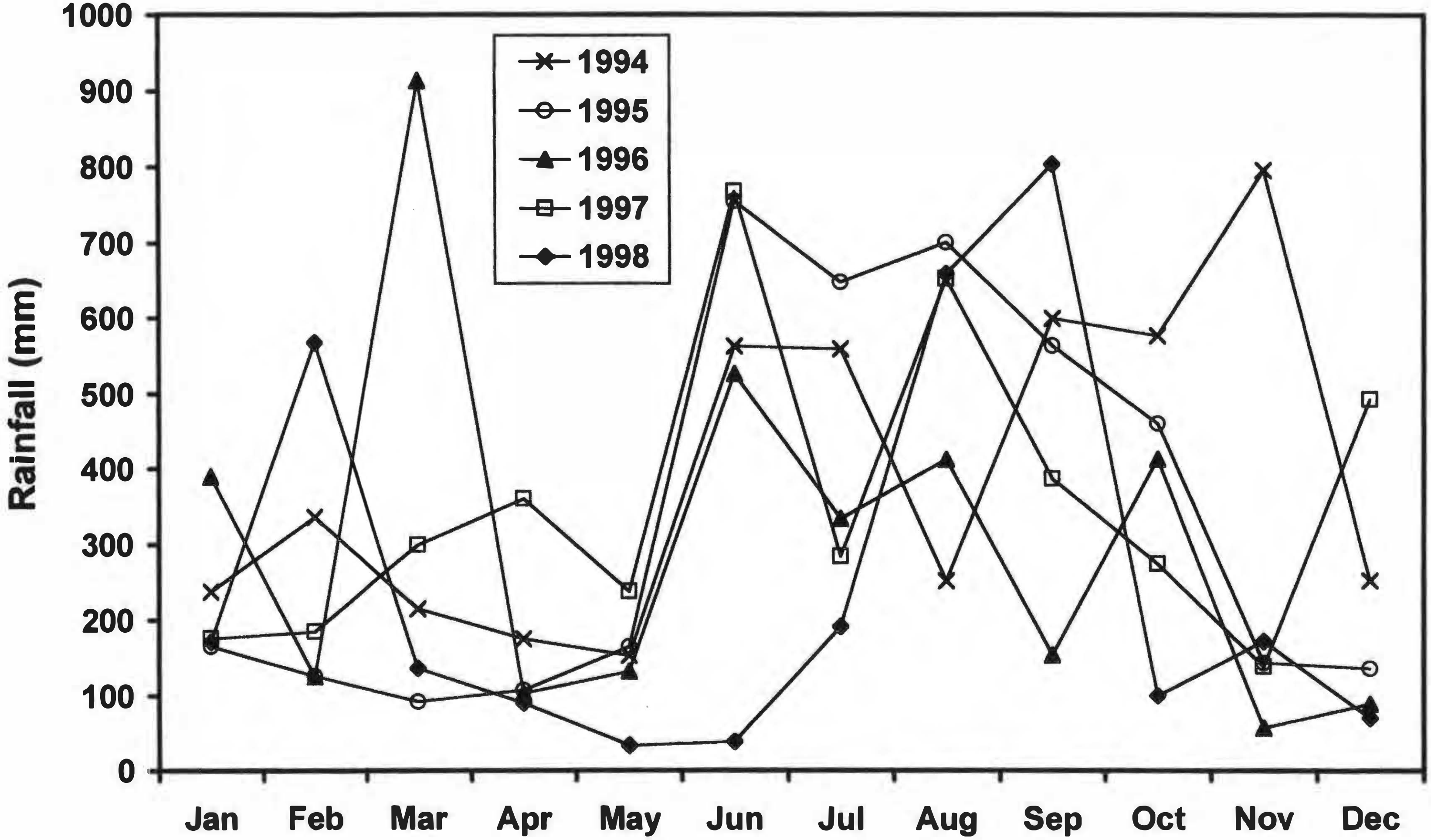


Figure 2.13. Monthly rainfall totals during each year of this study. Data was obtained from the NOAA weather station on Kennedy Space Center. Note the two-month lag in the onset of summer rains in 1998.

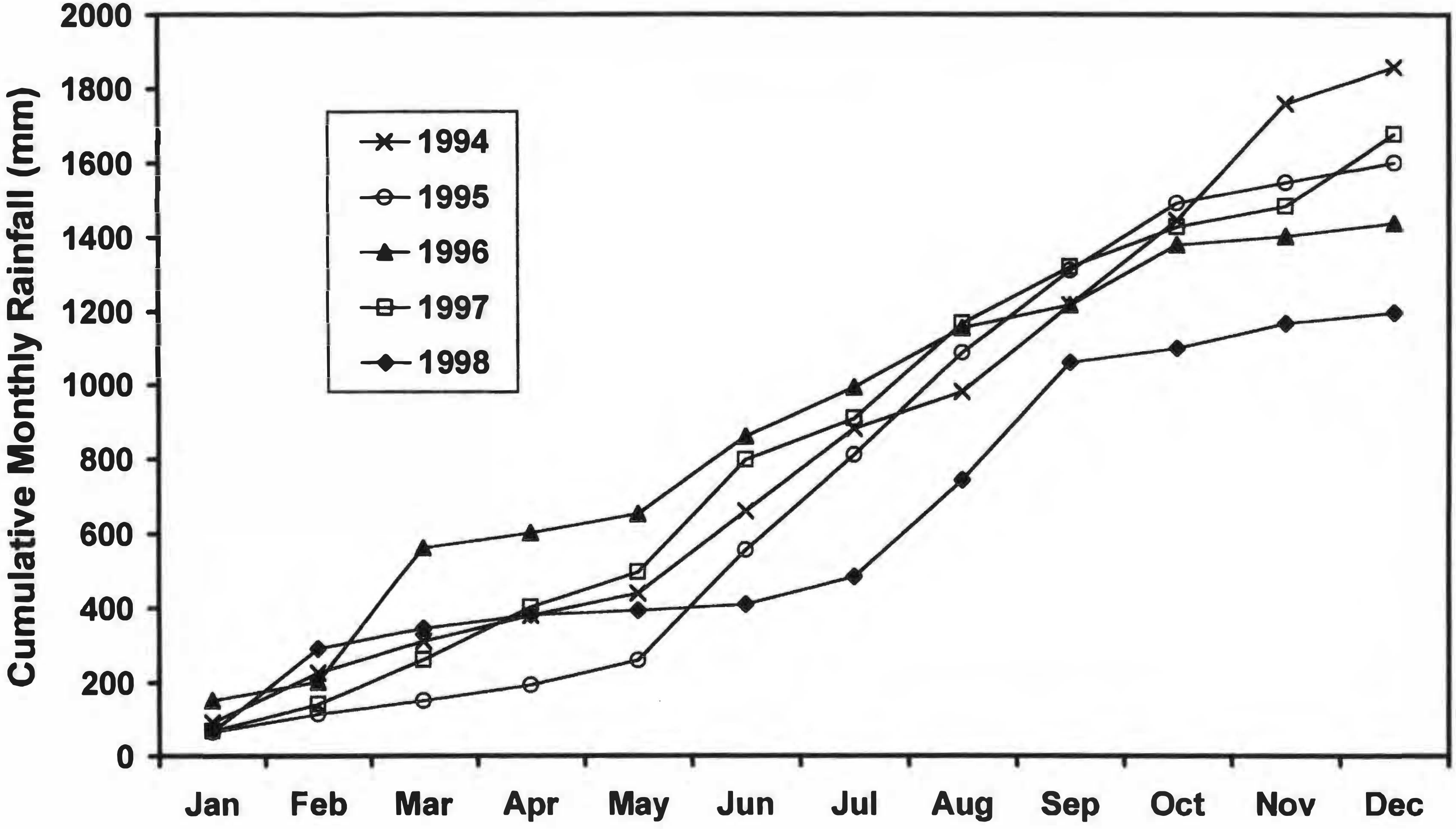


Figure 2.14. Cumulative monthly rainfall totals during each year of this study. Data was obtained from the NOAA weather station on Kennedy Space Center. Note the temporary lag in accumulation in early 1995, and the more dramatic lag in 1998.

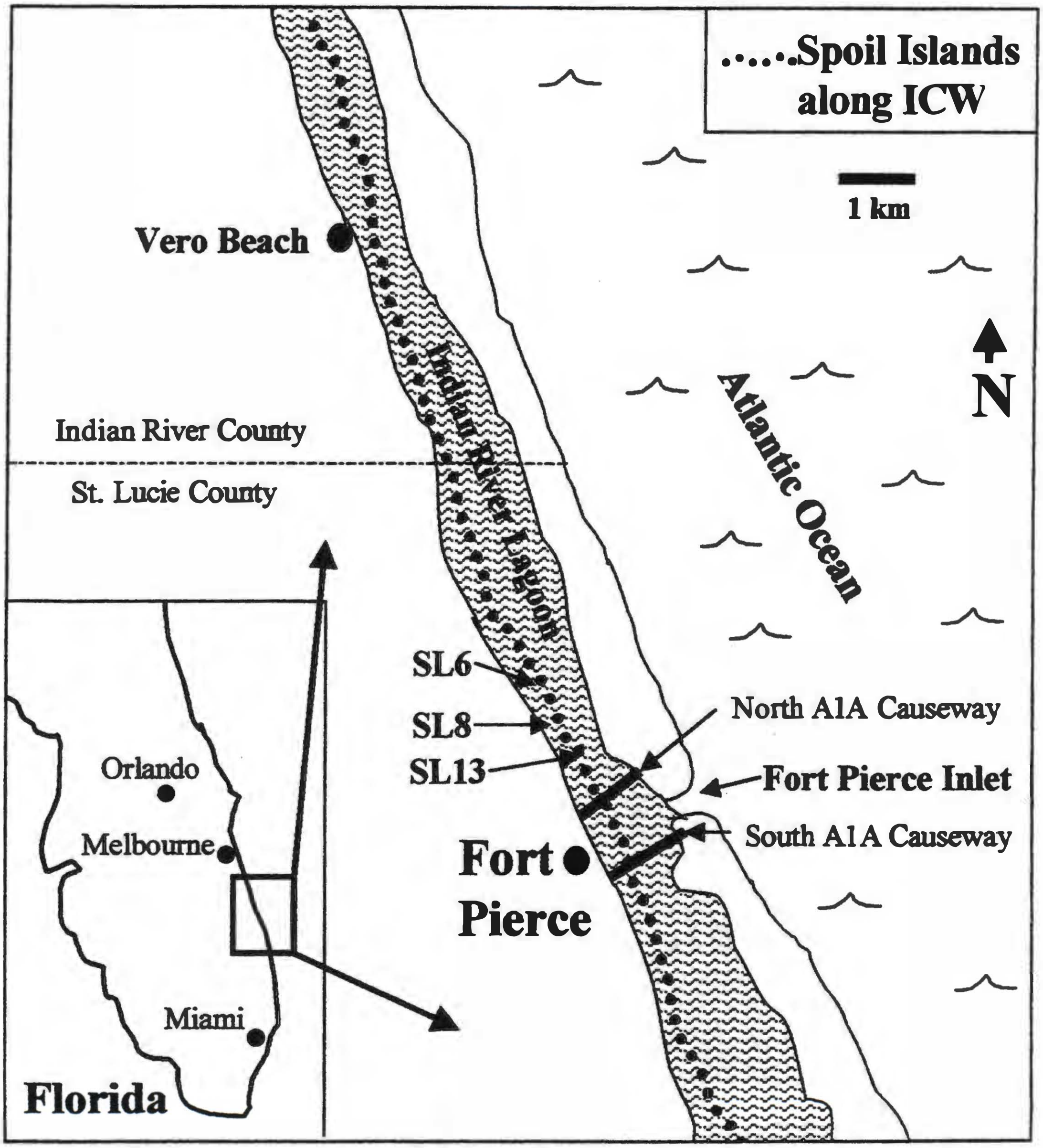
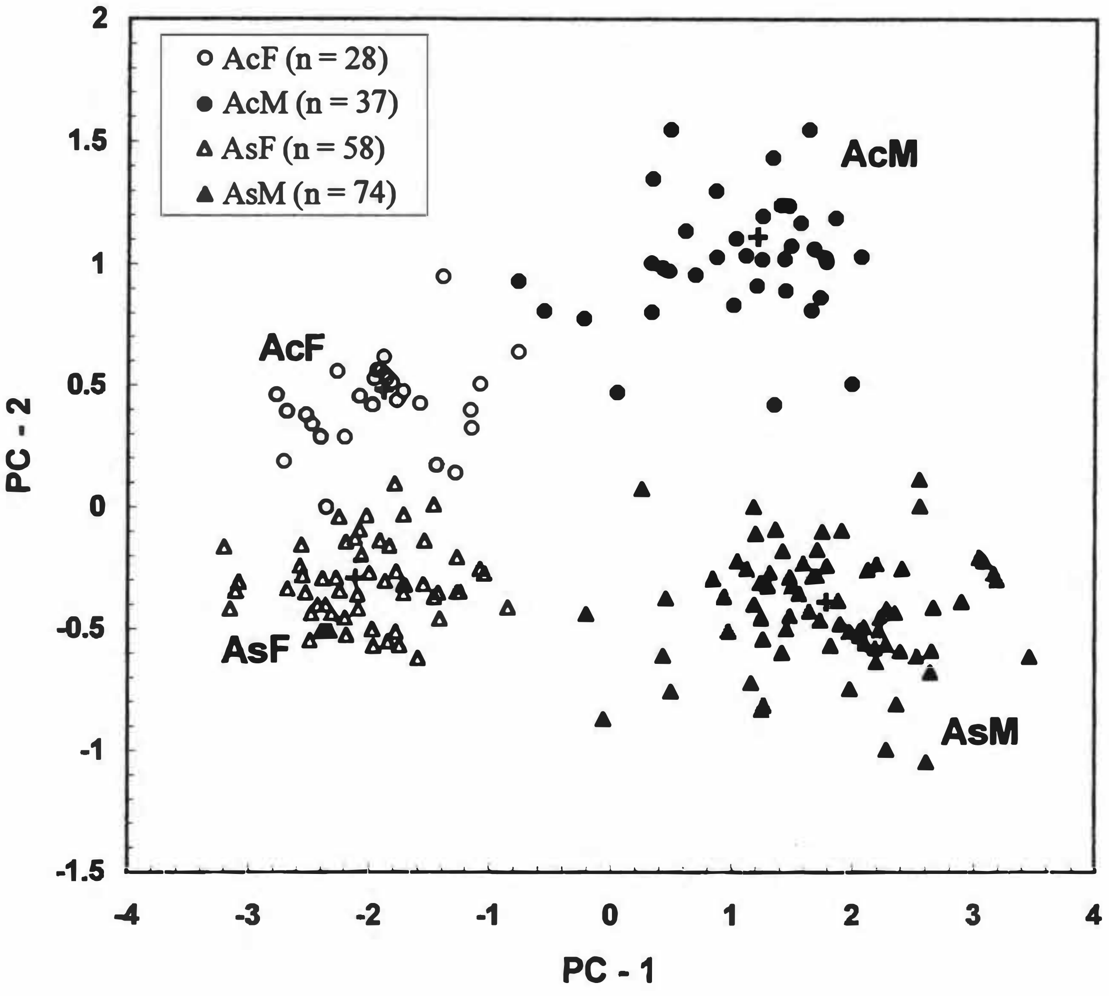
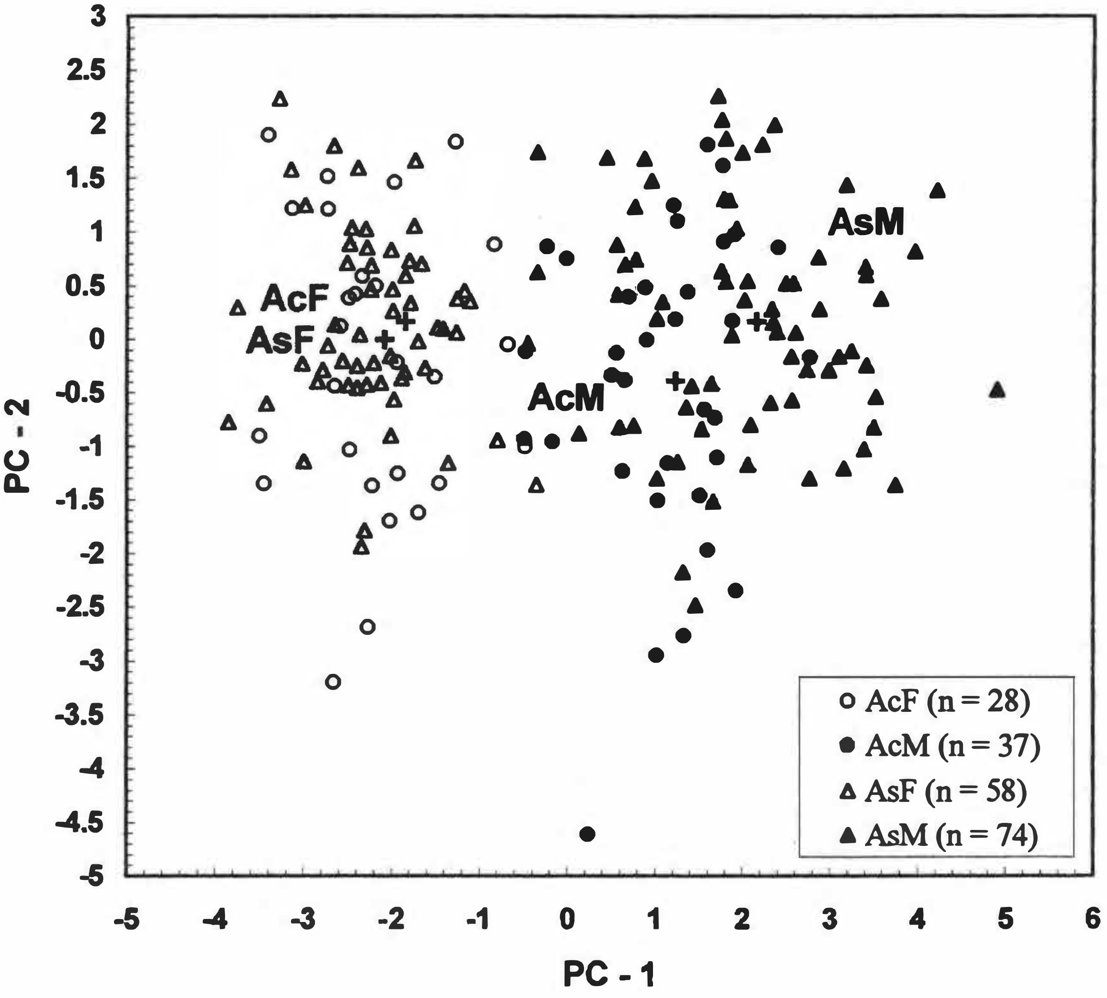


Figure 3.1. Location of the three dredge-spoil islands along the Florida Intracoastal Waterway (ICW) in Indian River Lagoon from which *Anolis carolinensis* and *A. sagrei* were collected for a comparative study of diet. Fort Pierce lies at approximately latitude 27°28'00".



Group centroid values (± 1 s.d.):
AcF: PC-1 = -1.89 (0.53); PC-2 = 0.43 (0.18)
AcM: PC-1 = 1.04 (0.71); PC-2 = 1.02 (0.25)
AsF: PC-1 = -2.02 (0.53); PC-2 = -0.32 (0.16)
AsM: PC-1 = 1.78 (0.76); PC-2 = -0.42 (0.24)

Figure 3.2. PCA results on four body parameters (SVL, HL, HW, and HD) for 65 adult *Anolis carolinensis* (Ac) and 132 adult *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = males, F = females. PC-1 and PC-2 together describe over 97% of the variation in the model. Note that PC-1 separates the two sexes of both species, and PC-2 separates the two species, such that females are more closely associated than are males. The four group means (centroids) are indicated by a "+".

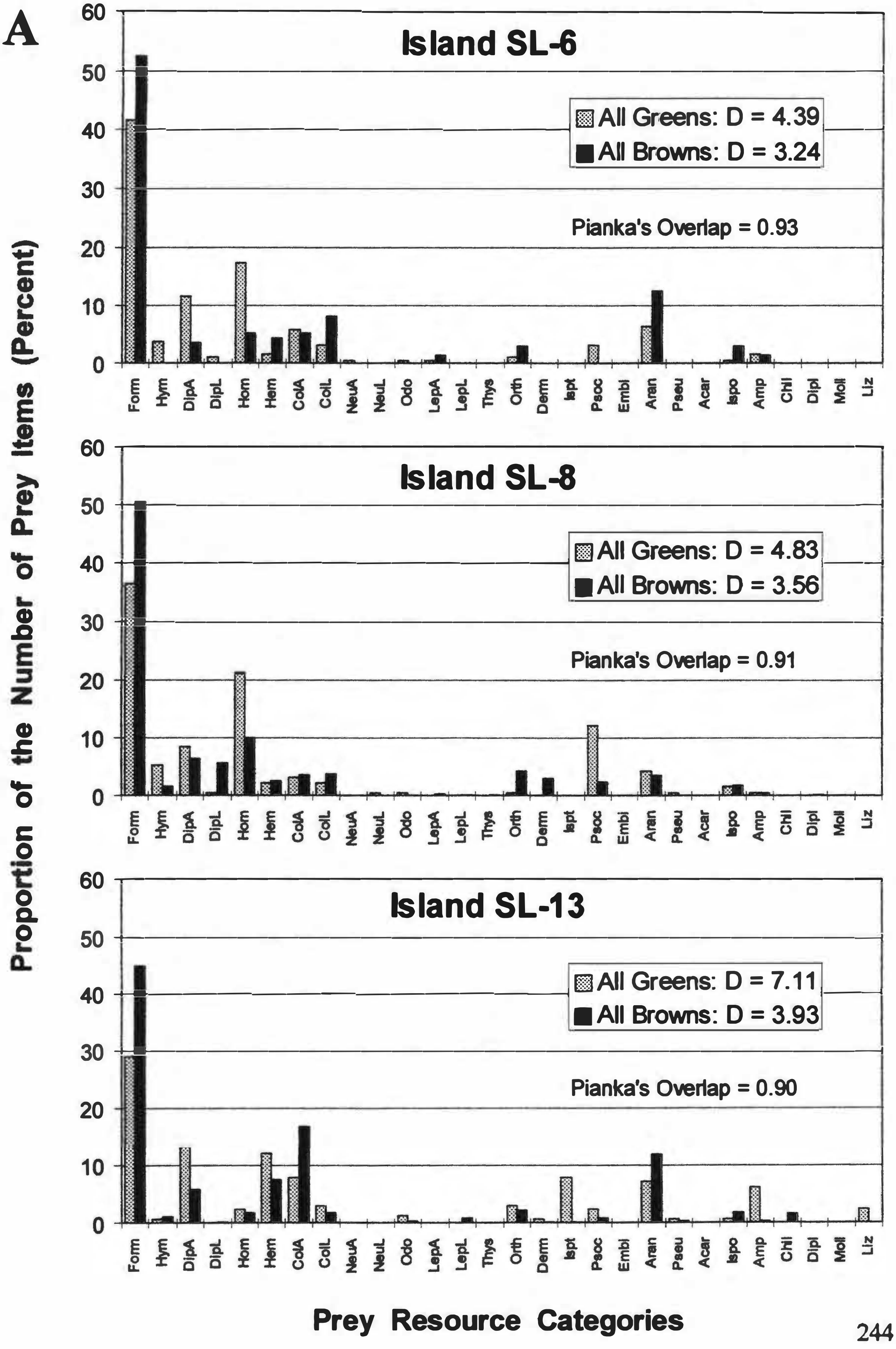


Group centroid values (+ 1 s.d.):
AcF: PC-1 = -2.19 (0.79); PC-2 = -0.24 (1.35)
AcM: PC-1 = 1.10 (0.80); PC-2 = -0.40 (1.41)
AsF: PC-1 = -2.18 (0.69); PC-2 = 0.13 (0.87)
AsM: PC-1 = 2.03 (1.13); PC-2 = 0.19 (1.05)

Figure 3.3. PCA results on four prey parameters (n_{prey}, n_{taxa}, Mean V_{ind}, and V_{tot}) and four body parameters (SVL, HL, HW, and HD) of the 61 adult *Anolis carolinensis* (Ac) and 127 *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon that contained prey items in their stomachs. M = males, F = females. PC-1 and PC-2 together describe over 75% of the variation in the model. Note that PC-1 separates the two sexes, but that PC-2 does not distinguish either species or sex. The four group means (centroids) are indicated by a "+".

Figures 3.4A-G. Proportions of the numbers of individual prey items (P_{ind}) found in each of the 28 prey categories in each species-sex (SS) group of *Anolis carolinensis* (Ac) and *A. sagrei* (As) collected from each of the three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Analogous plots for the three islands are shown in each figure, and the 28 prey categories (see below) are presented in the same order throughout. Values for Simpson's dietary niche breadth index (D) and Pianka's niche overlap values are included on the histograms for each island. Figure 4A shows the overall interspecific dietary overlap using pooled data for both sexes, or island-species (IS) group, such that all *Anolis carolinensis* are compared with all *A. sagrei*. Histograms in 4B and 4C show *intraspecific-intersexual* SS-overlap (AcF vs. AcM and AsF vs. AsM). Histograms in 4D and 4E show *interspecific-intrasexual* SS-overlap (AcF vs. AsF and AcM vs. AsM), and histograms in 4F and 4G show *interspecific-intersexual* SS-overlap (AcF vs. AsM and AcM vs. AsF).

In general, flying and potentially flying forms lie on the left side of each plot, and non-flying forms lie on the right, although larval, non-flying forms of certain taxa are presented adjacent to the adults of that taxa. Category names are abbreviated as follows, from left to right: Form = Formicidae (ants), Hym = non-ant Hymenoptera (wasps), DipA = adult Diptera (flies), DipL = larval or pupal Diptera, Hom = Homoptera (plant hoppers; cicadas), Hem = Hemiptera (leafhoppers), ColA = adult Coleoptera (beetles), ColL = larval Coleoptera, NeuA = adult Neuroptera (lacewings), NeuL = larval Neuroptera, Odo = Odonata (dragonflies and damselflies), LepA = adult Lepidoptera (moths and butterflies), LepL = larval Lepidoptera, Thys = Thysanoptera (thrips), Orth = Orthoptera (crickets and cockroaches), Derm = Dermaptera (earwigs), Ispt = Isoptera (termites), Psoc = Psocoptera (bark lice), Embi = Embioptera (webspinners), Aran = Aranaea (spiders), Pseu = Pseudoscorpionida (pseudoscorpions), Acar = Acarina (mites), Ispo = Isopoda (isopods), Amp = Amphipoda (beach-hoppers), Chil = Chilopoda (centipedes), Dipl = Diplopoda (millipedes), Moll = Phylum Mollusca: Class Gastropoda (snails), and Liz = Lizard (all lizard prey items were *Anolis sagrei*).


A
Island SL-6
▨ All Greens: D = 4.39
■ All Browns: D = 3.24
Pianka's Overlap = 0.93
Island SL-8
▨ All Greens: D = 4.83
■ All Browns: D = 3.56
Pianka's Overlap = 0.91
Island SL-13
▨ All Greens: D = 7.11
■ All Browns: D = 3.93
Pianka's Overlap = 0.90
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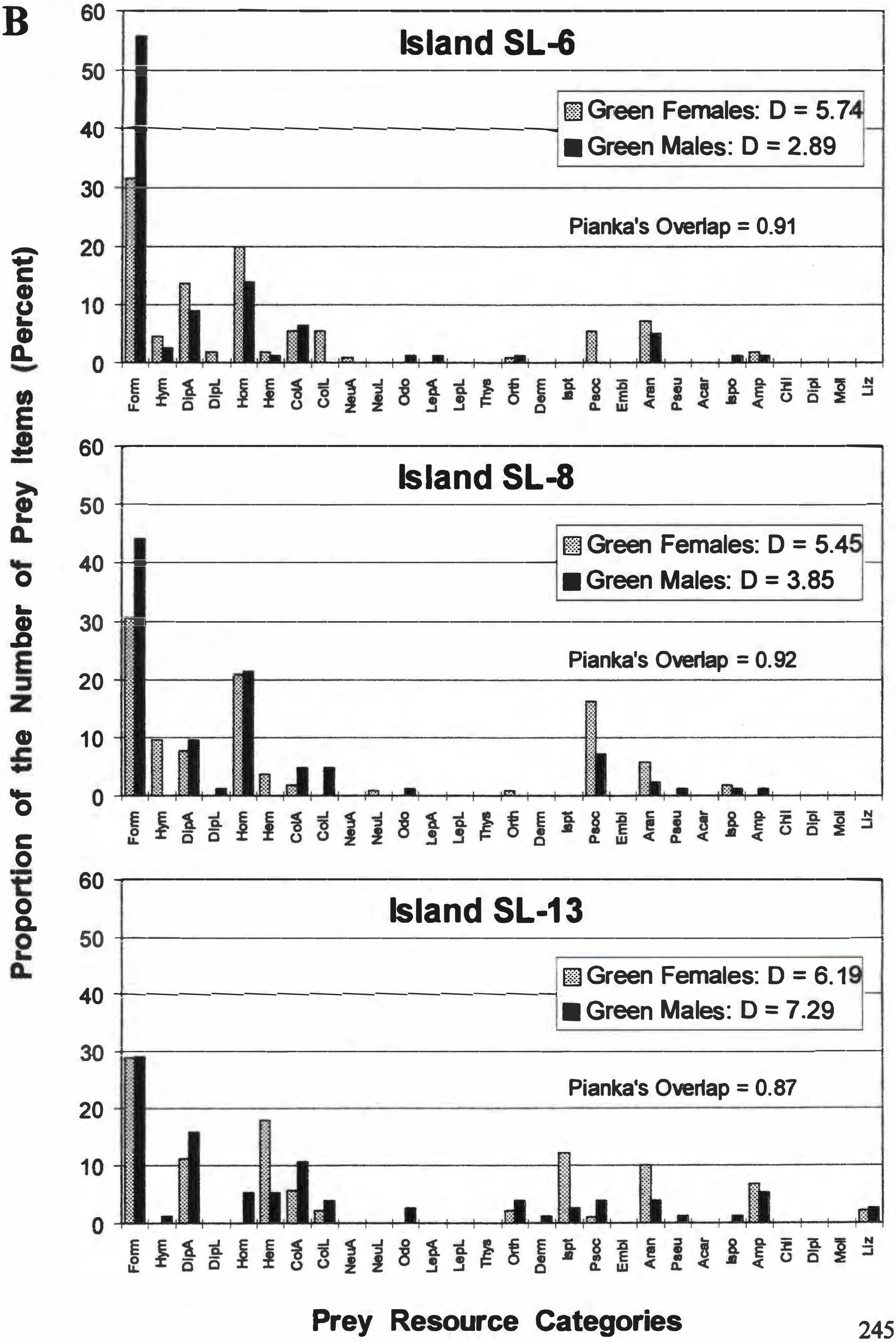
Liz
Proportion of the Number of Prey Items (Percent)
Prey Resource Categories

B


Island SL-6
Green Females: D = 5.74
Green Males: D = 2.89
Pianka's Overlap = 0.91
Island SL-8
Green Females: D = 5.45
Green Males: D = 3.85
Pianka's Overlap = 0.92
Island SL-13
Green Females: D = 6.19
Green Males: D = 7.29
Pianka's Overlap = 0.87
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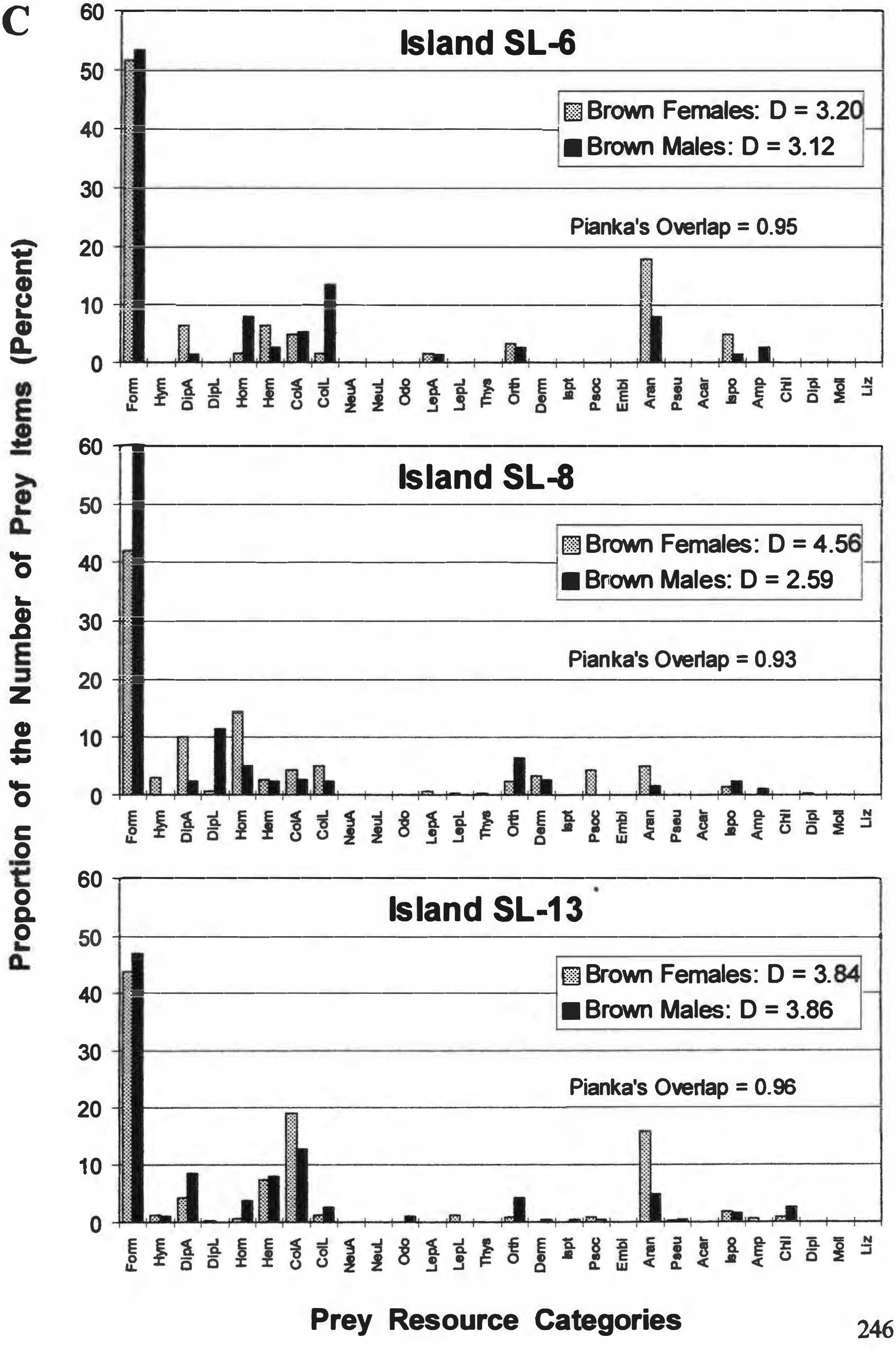
Proportion of the Number of Prey Items (Percent)
Prey Resource Categories

C


Proportion of the Number of Prey Items (Percent)
Island SL-6
Brown Females: D = 3.20
Brown Males: D = 3.12
Pianka's Overlap = 0.95
Island SL-8
Brown Females: D = 4.56
Brown Males: D = 2.59
Pianka's Overlap = 0.93
Island SL-13
Brown Females: D = 3.84
Brown Males: D = 3.86
Pianka's Overlap = 0.96
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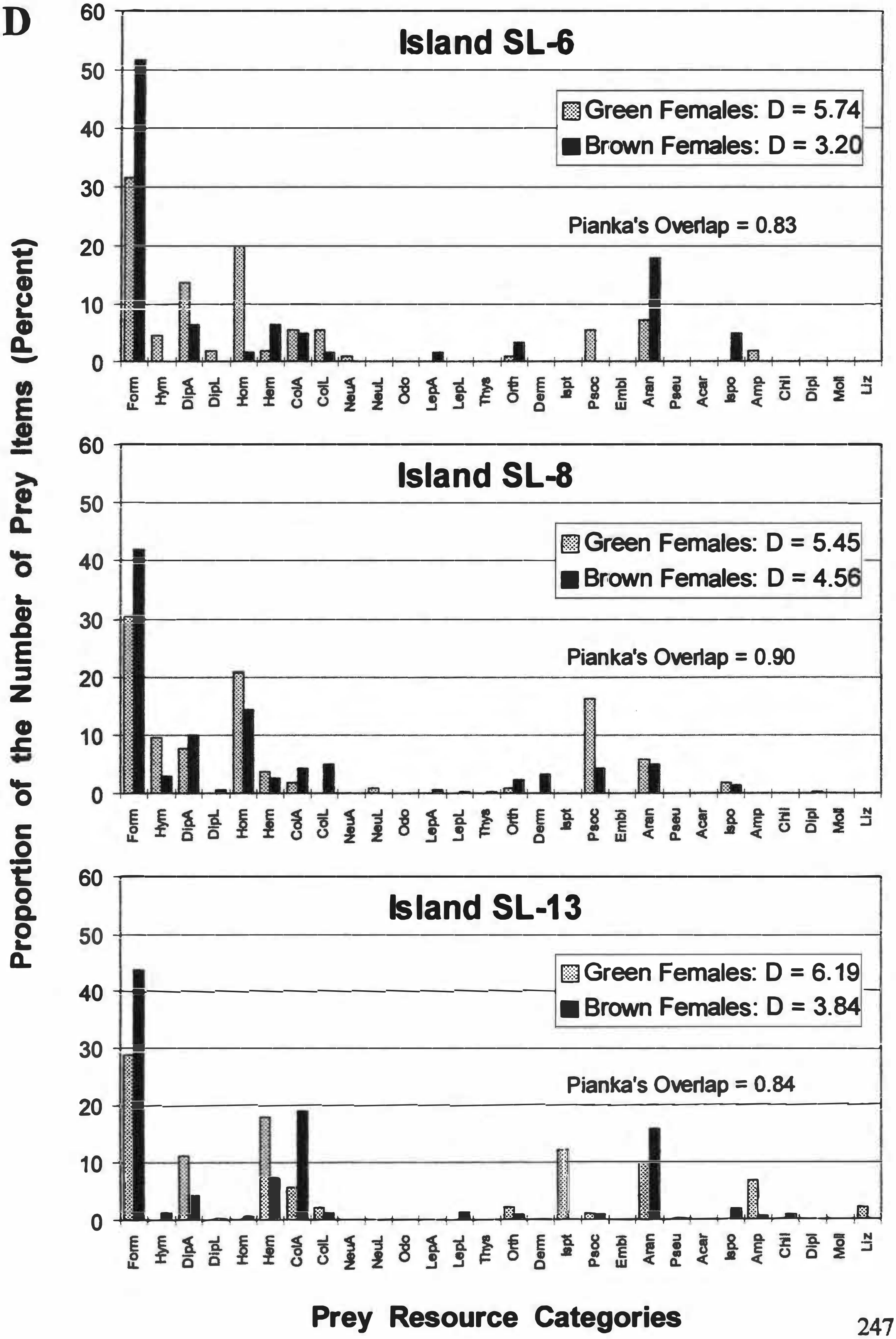
Prey Resource Categories

D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■ Brown Females: D = 3.20
Pianka's Overlap = 0.83
Island SL-8
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■ Brown Females: D = 4.56
Pianka's Overlap = 0.90
Island SL-13
▨ Green Females: D = 6.19
■ Brown Females: D = 3.84
Pianka's Overlap = 0.84
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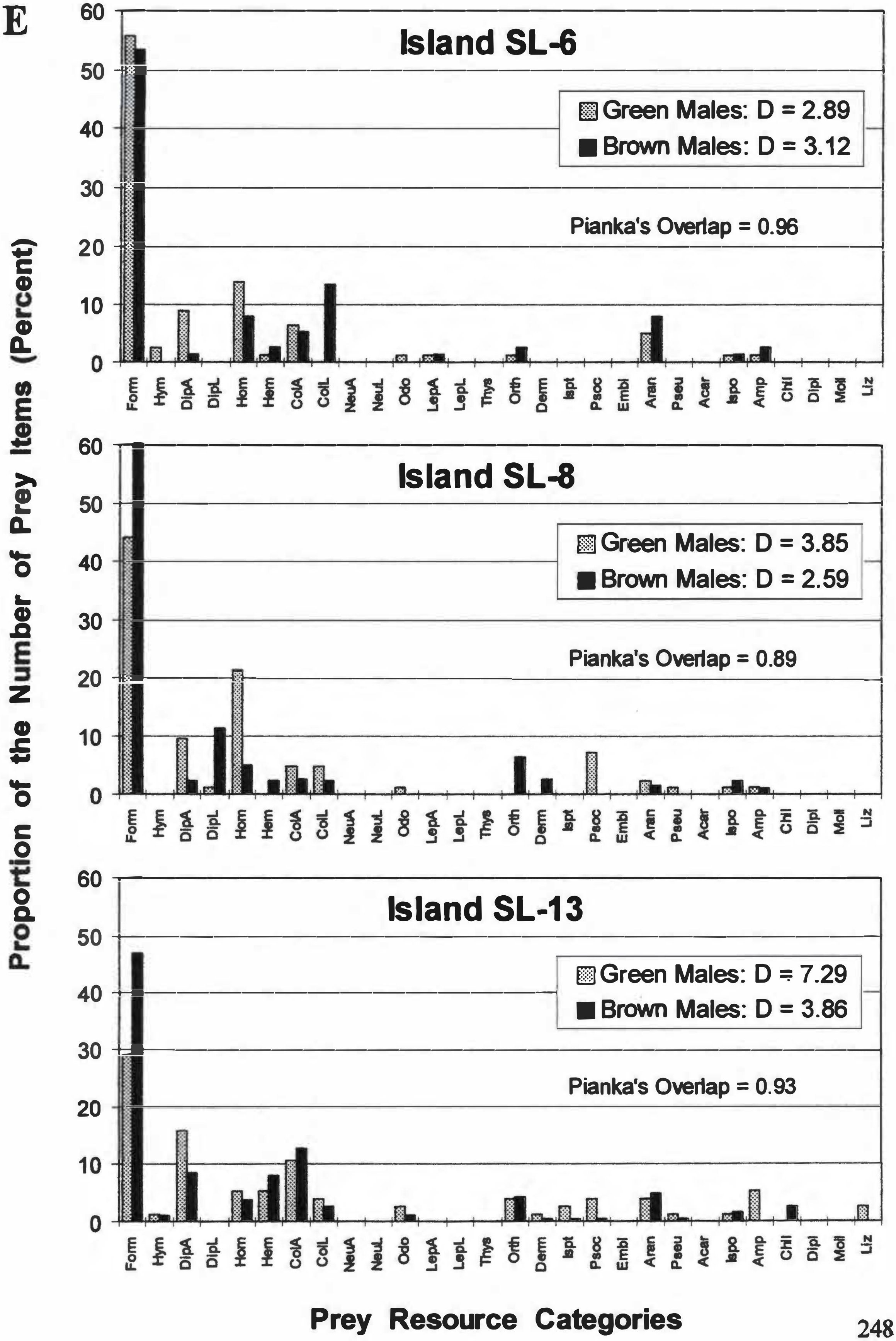
Proportion of the Number of Prey Items (Percent)
Prey Resource Categories

E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Brown Males: D = 3.12
Pianka's Overlap = 0.96
Island SL-8
Green Males: D = 3.85
Brown Males: D = 2.59
Pianka's Overlap = 0.89
Island SL-13
Green Males: D = 7.29
Brown Males: D = 3.86
Pianka's Overlap = 0.93
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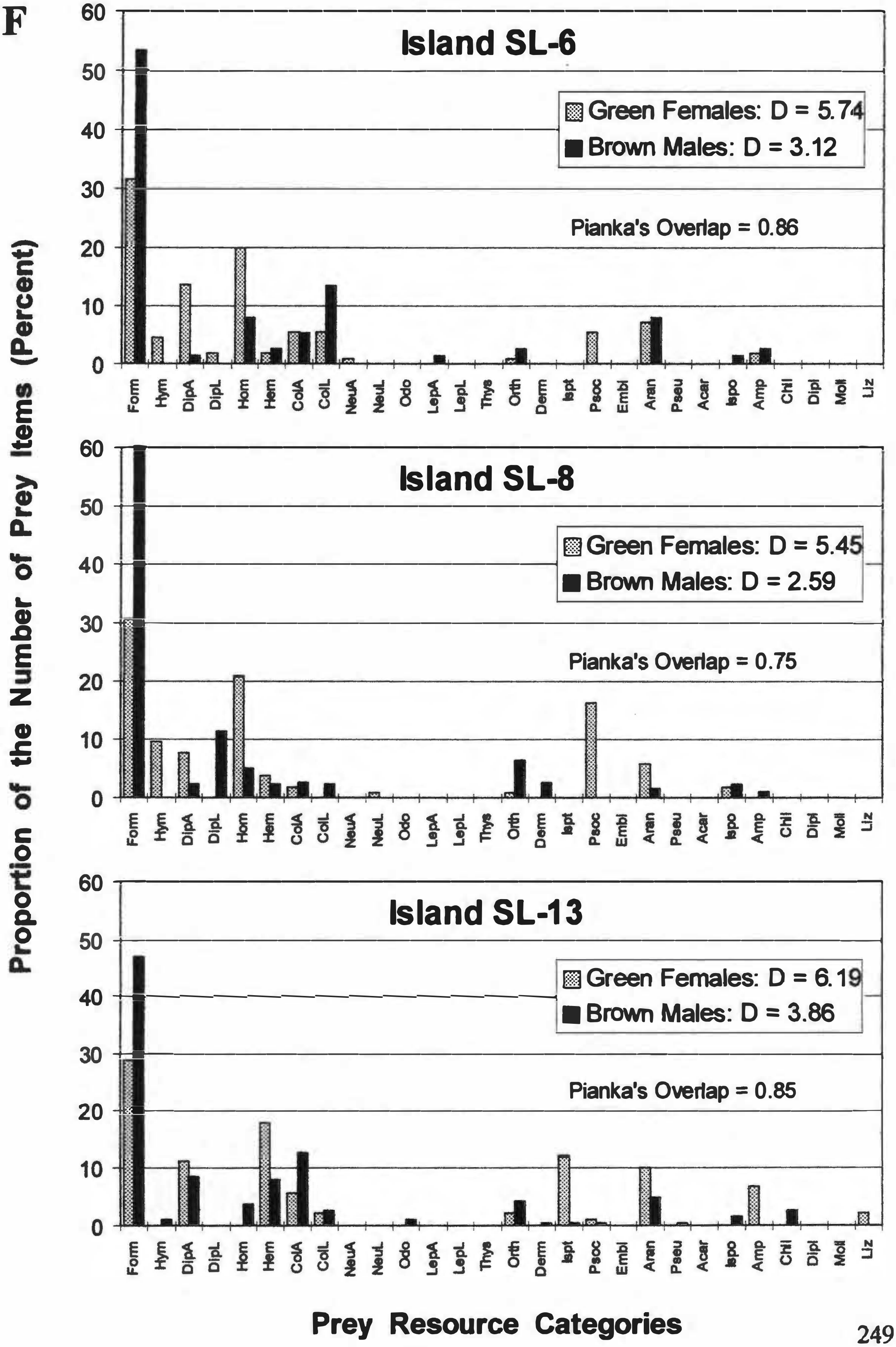
Liz
Proportion of the Number of Prey Items (Percent)
Prey Resource Categories

F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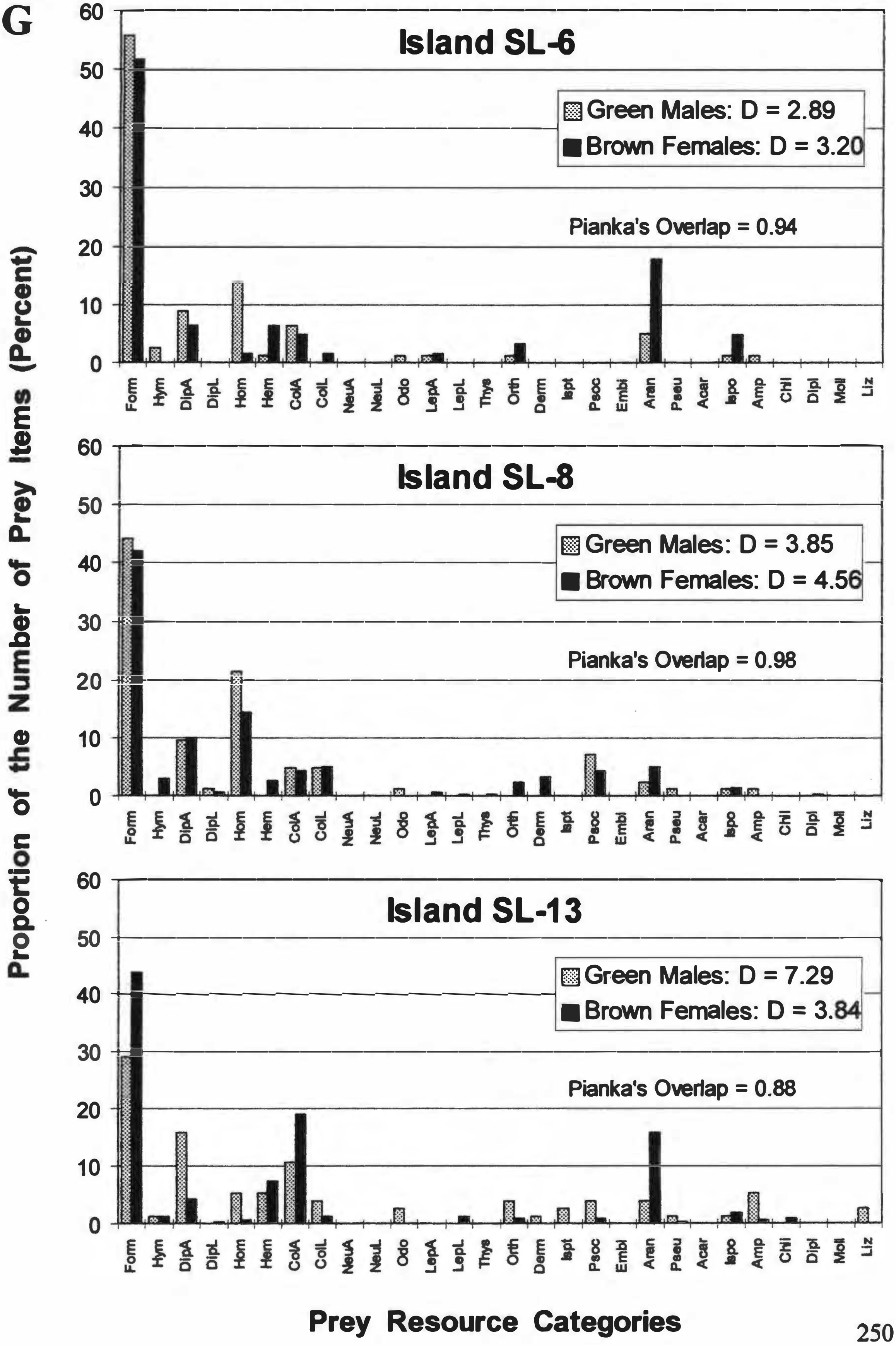
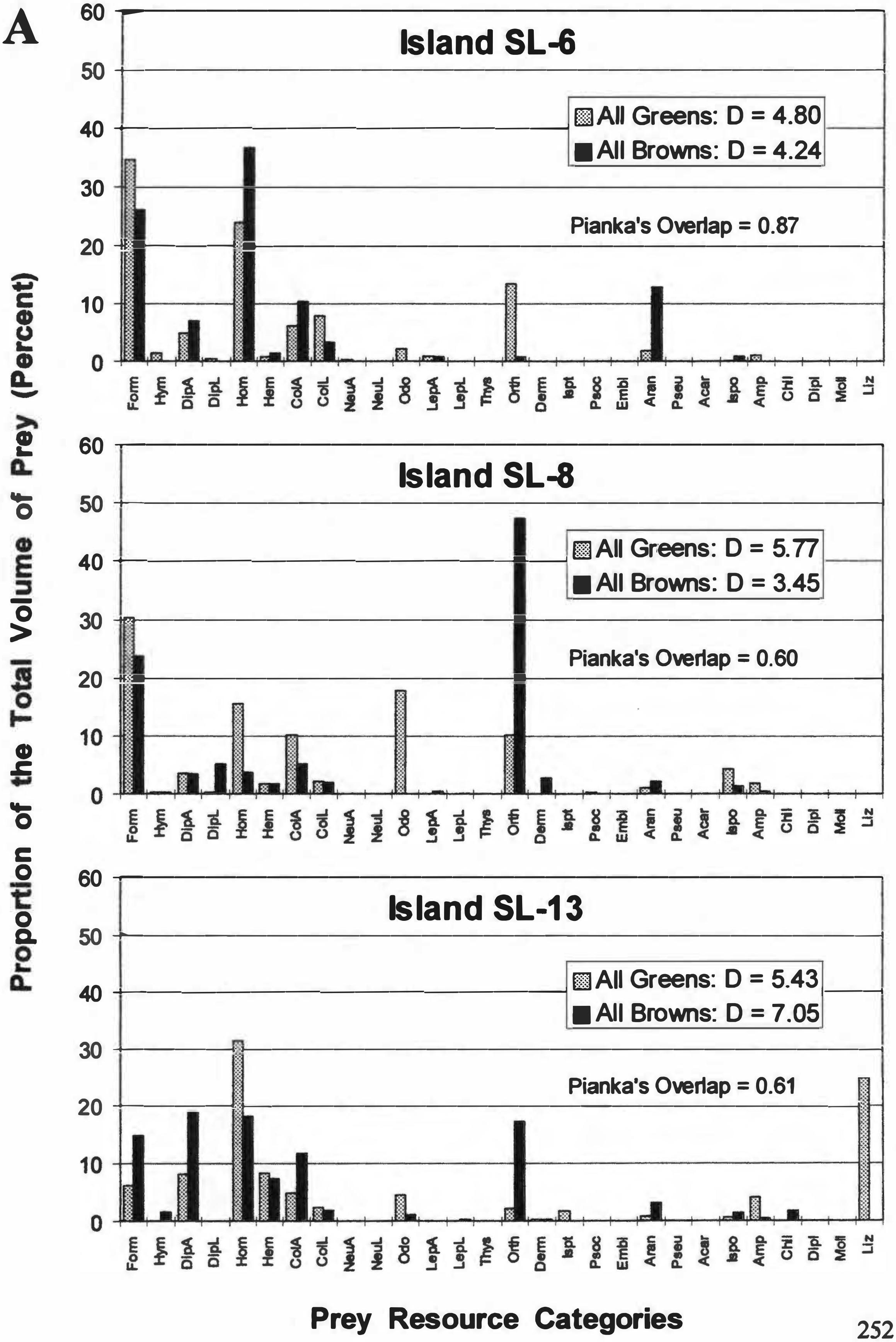
Brown Males: D = 3.12
Pianka's Overlap = 0.86
Island SL-8
Green Females: D = 5.45
Brown Males: D = 2.59
Pianka's Overlap = 0.75
Island SL-13
Green Females: D = 6.19
Brown Males: D = 3.86
Pianka's Overlap = 0.85
0
10
20
30
40
50
60
Proportion of the Number of Prey Items (Percent)
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Prey Resource Categories

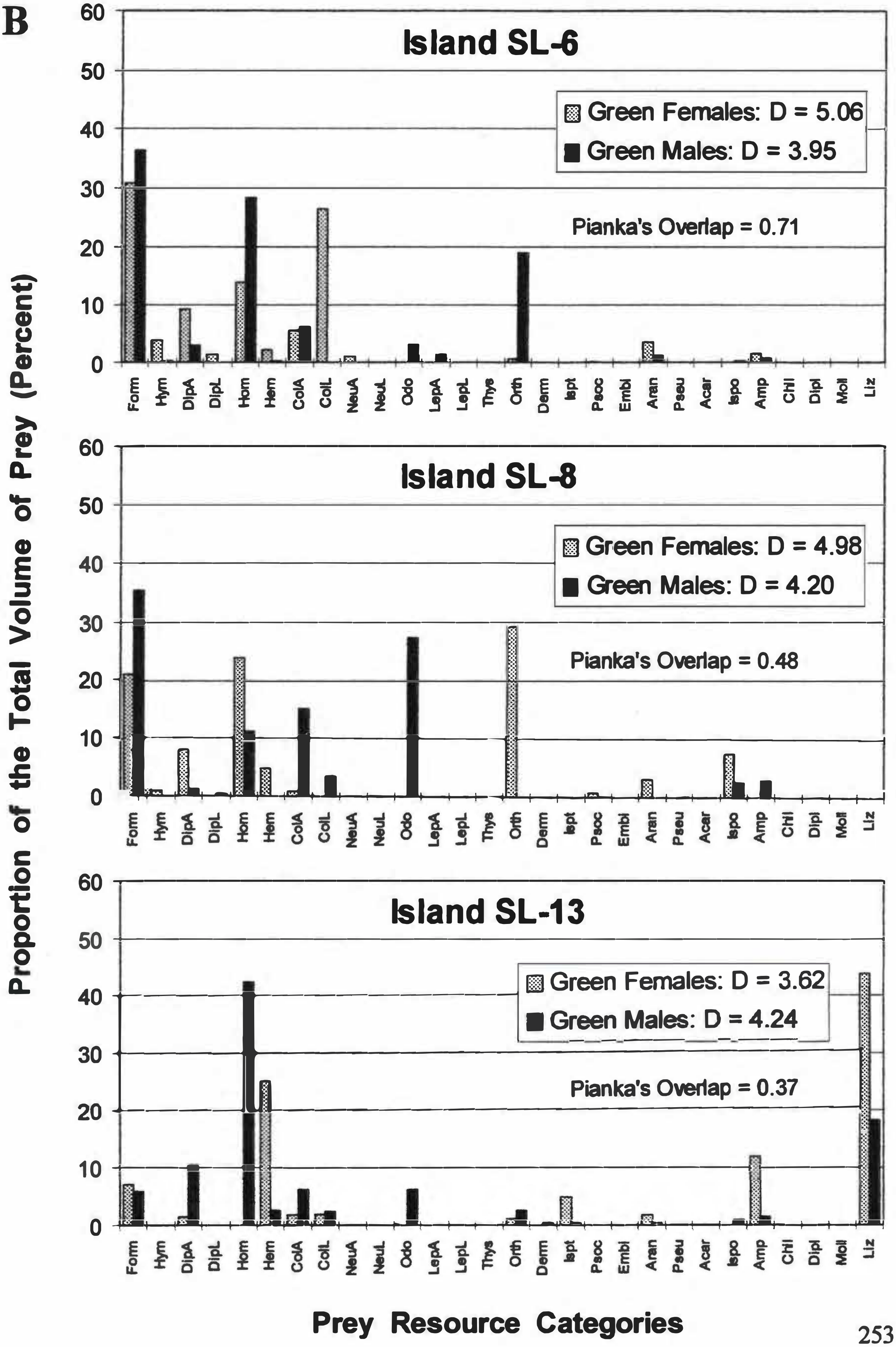
G

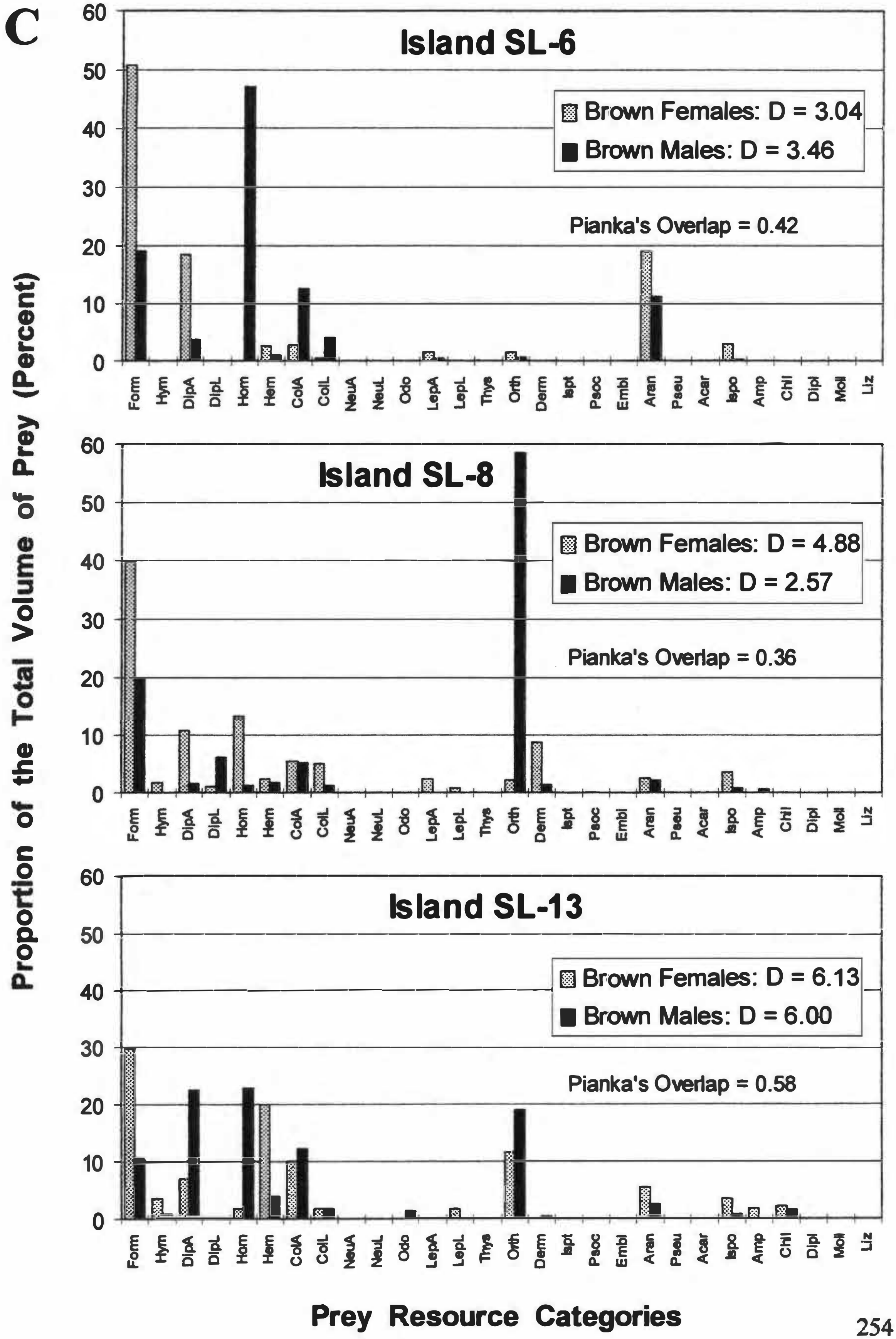

Island SL-6
Green Males: D = 2.89
Brown Females: D = 3.20
Pianka's Overlap = 0.94
Island SL-8
Green Males: D = 3.85
Brown Females: D = 4.56
Pianka's Overlap = 0.98
Island SL-13
Green Males: D = 7.29
Brown Females: D = 3.84
Pianka's Overlap = 0.88
0
10
20
30
40
50
60
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Proportion of the Number of Prey Items (Percent)
Prey Resource Categories

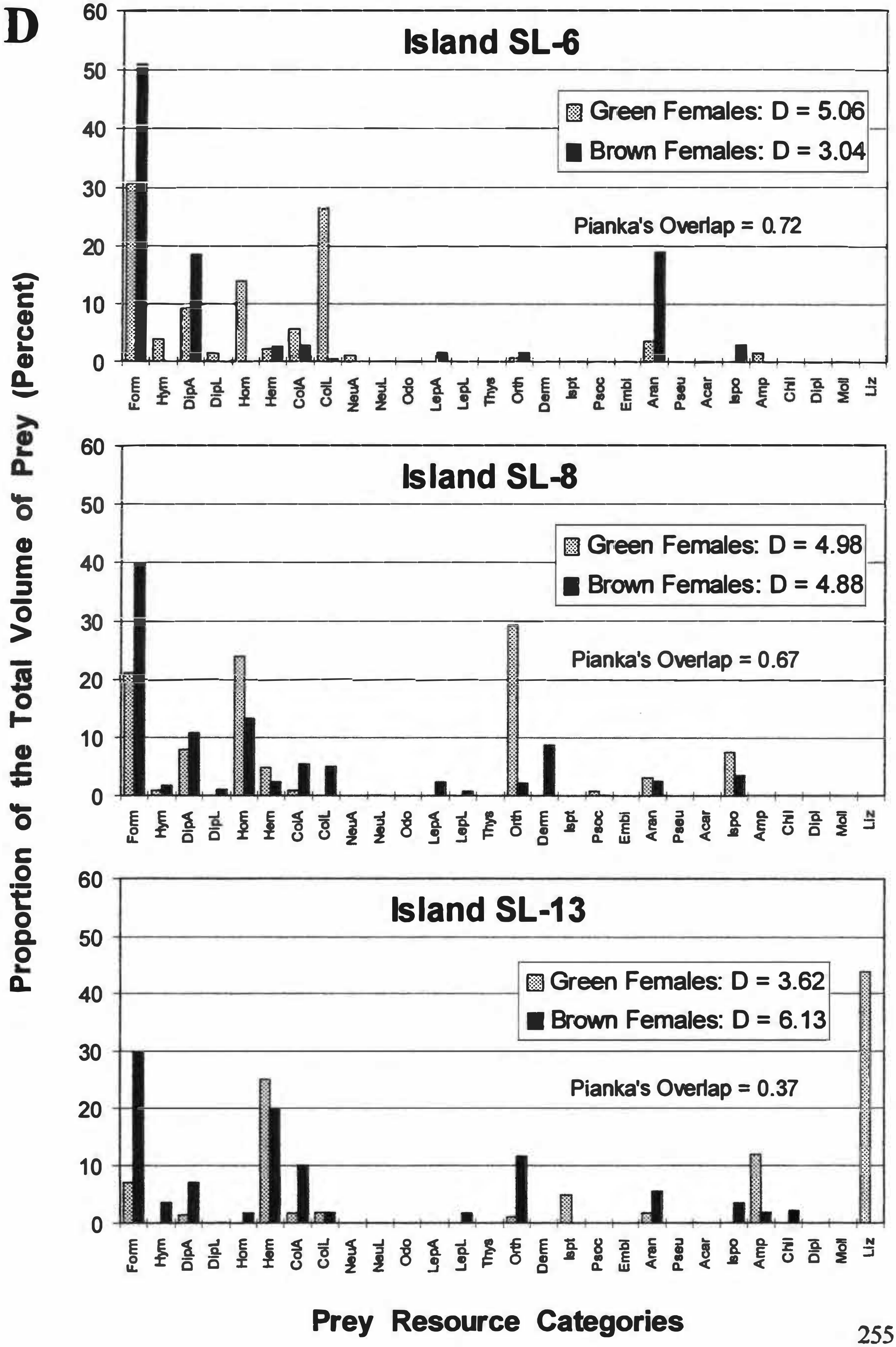
Figures 3.5A-G. Proportions of the total volumes of all prey items (P_{vol}) found in each of the 28 prey categories in each species-sex (SS) group of *Anolis carolinensis* (Ac) and *A. sagrei* (As) collected from each of the three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Analogous plots for the three islands are shown in each figure, and the 28 prey categories (see below) are presented in the same order throughout. Values for Simpson's dietary niche breadth index (D) and Pianka's niche overlap values are included on the histograms for each island. Figure 5A shows the overall interspecific dietary overlap using pooled data for both sexes, or island-species (IS) group, such that all *Anolis carolinensis* are compared with all *A. sagrei*. Histograms in 5B and 5C show *intraspecific-intersexual* SS-overlap (AcF vs. AcM and AsF vs. AsM). Histograms in 5D and 5E show *interspecific-intrasexual* SS-overlap (AcF vs. AsF and AcM vs. AsM), and histograms in 5F and 5G show *interspecific-intersexual* SS-overlap (AcF vs. AsM and AcM vs. AsF). M = male, F = female.

In general, flying and potentially flying forms lie on the left side of each plot, and non-flying forms lie on the right, although larval, non-flying forms of certain taxa are presented adjacent to the adults of that taxa. Category names are abbreviated as follows, from left to right: Form = Formicidae (ants), Hym = non-ant Hymenoptera (wasps), DipA = adult Diptera (flies), DipL = larval or pupal Diptera, Hom = Homoptera (plant hoppers; cicadas), Hem = Hemiptera (leafhoppers), ColA = adult Coleoptera (beetles), ColL = larval Coleoptera, NeuA = adult Neuroptera (lacewings), NeuL = larval Neuroptera, Odo = Odonata (dragonflies and damselflies), LepA = adult Lepidoptera (moths and butterflies), LepL = larval Lepidoptera, Thys = Thysanoptera (thrips), Orth = Orthoptera (crickets and cockroaches), Derm = Dermaptera (earwigs), Ispt = Isoptera (termites), Psoc = Psocoptera (bark lice), Embi = Embioptera (webspinners), Aran = Aranaea (spiders), Pseu = Pseudoscorpionida (pseudoscorpions), Acar = Acarina (mites), Ispo = Isopoda (isopods), Amp = Amphipoda (beach-hoppers), Chil = Chilopoda (centipedes), Dipl = Diplopoda (millipedes), Moll = Phylum Mollusca: Class Gastropoda (snails), and Liz = Lizard (all lizard prey items were *Anolis sagrei*).

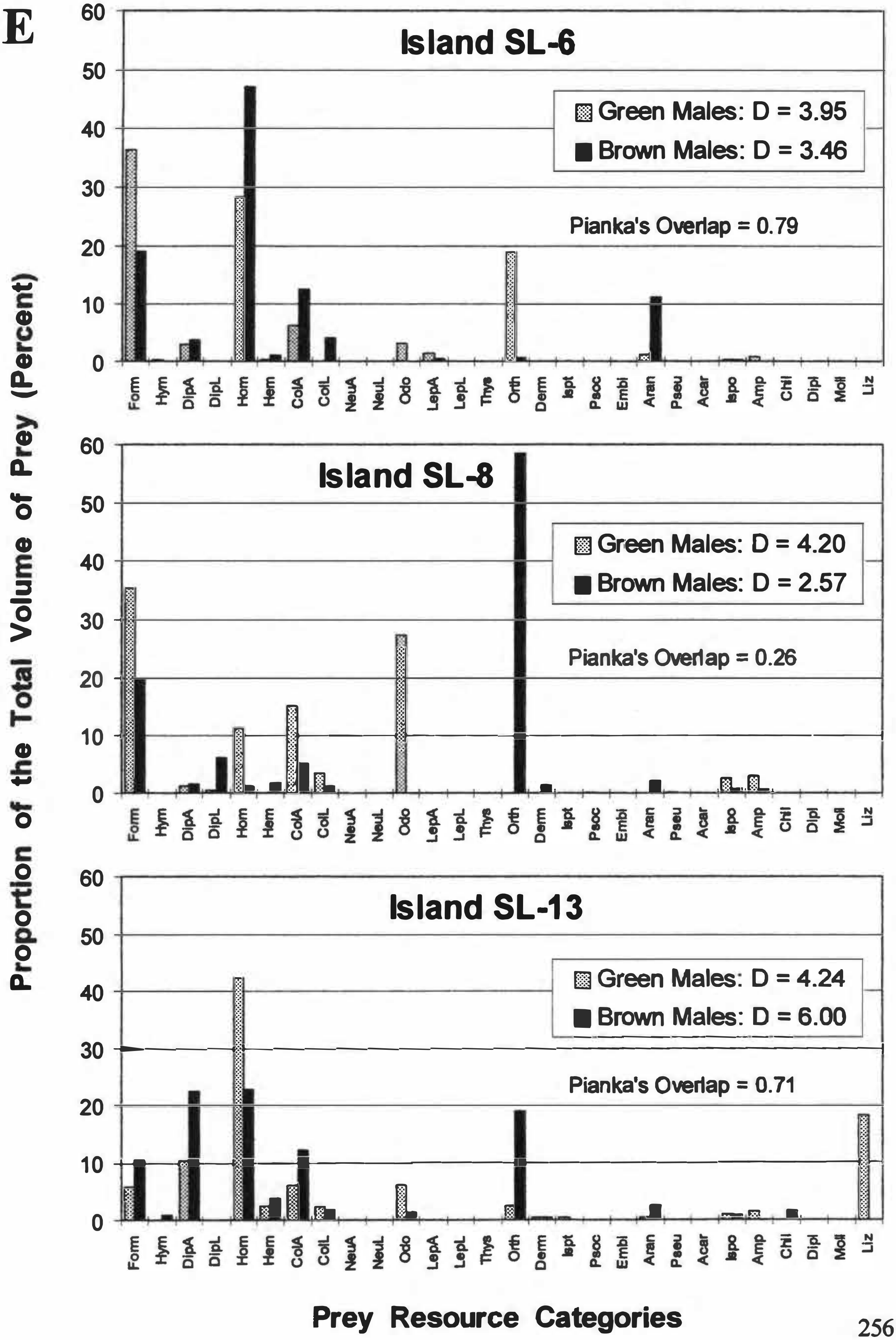

A
Proportion of the Total Volume of Prey (Percent)
Island SL-6
All Greens: D = 4.80
All Browns: D = 4.24
Pianka's Overlap = 0.87
Island SL-8
All Greens: D = 5.77
All Browns: D = 3.45
Pianka's Overlap = 0.60
Island SL-13
All Greens: D = 5.43
All Browns: D = 7.05
Pianka's Overlap = 0.61
0
10
20
30
40
50
60
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Prey Resource Categories


B
Proportion of the Total Volume of Prey (Percent)
Island SL-6
Green Females: D = 5.06
Green Males: D = 3.95
Pianka's Overlap = 0.71
Island SL-8
Green Females: D = 4.98
Green Males: D = 4.20
Pianka's Overlap = 0.48
Island SL-13
Green Females: D = 3.62
Green Males: D = 4.24
Pianka's Overlap = 0.37
0
10
20
30
40
50
60
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Prey Resource Categories

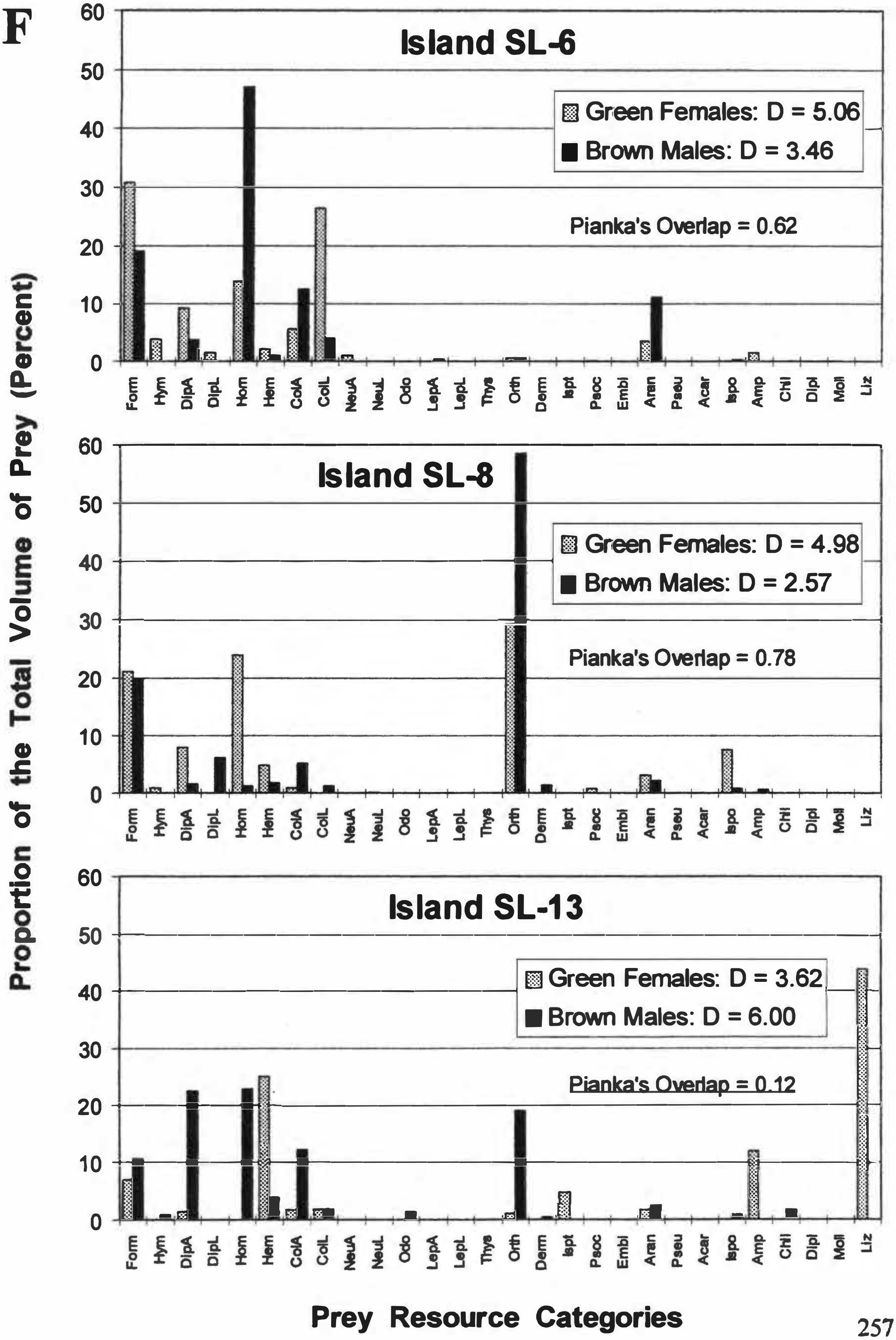

C
Island SL-6
▨ Brown Females: D = 3.04
■ Brown Males: D = 3.46
Pianka's Overlap = 0.42
Island SL-8
▨ Brown Females: D = 4.88
■ Brown Males: D = 2.57
Pianka's Overlap = 0.36
Island SL-13
▨ Brown Females: D = 6.13
■ Brown Males: D = 6.00
Pianka's Overlap = 0.58
0
10
20
30
40
50
60
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Proportion of the Total Volume of Prey (Percent)
Prey Resource Categories

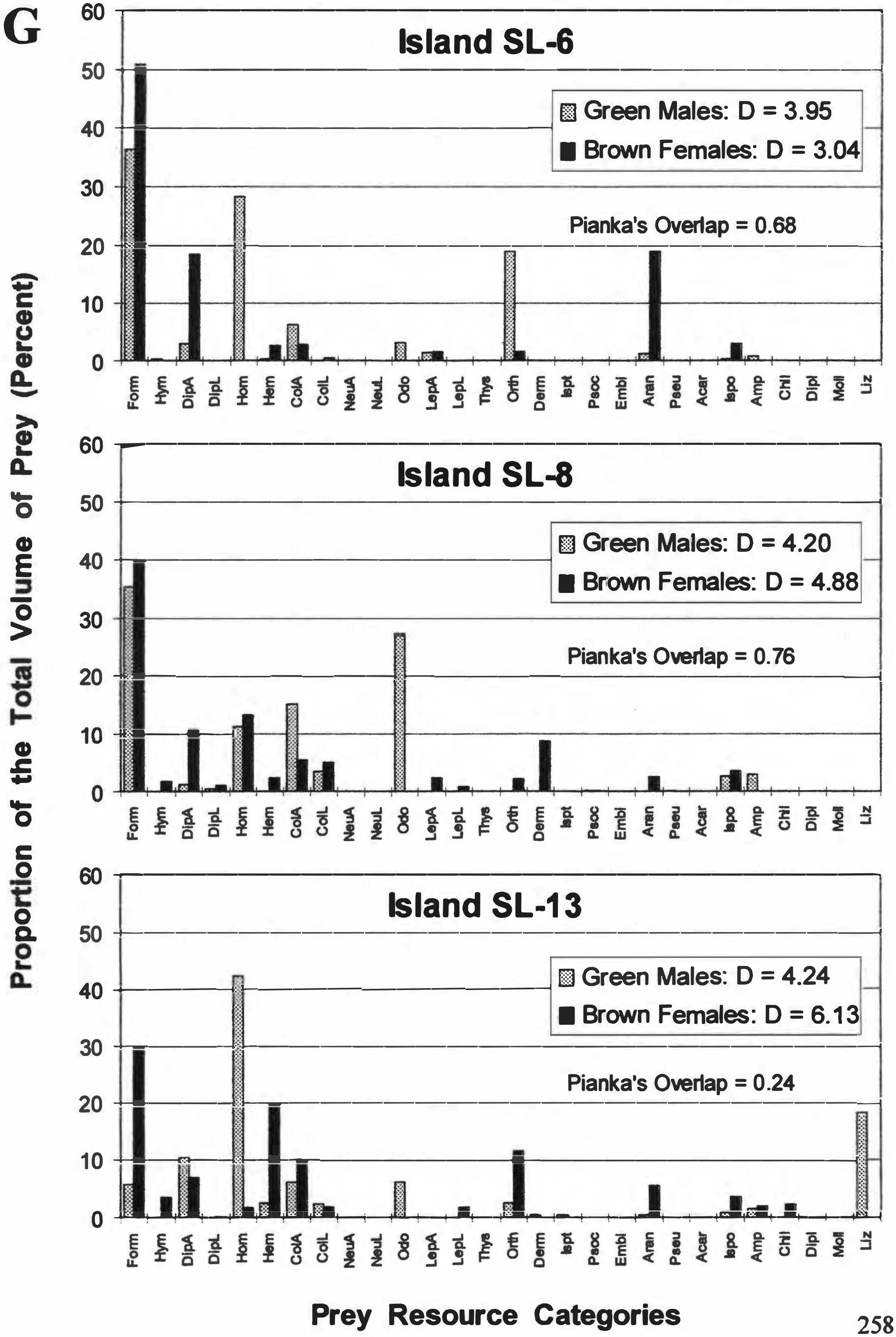

D
Proportion of the Total Volume of Prey (Percent)
Island SL-6
▨ Green Females: D = 5.06
■ Brown Females: D = 3.04
Pianka's Overlap = 0.72
Island SL-8
▨ Green Females: D = 4.98
■ Brown Females: D = 4.88
Pianka's Overlap = 0.67
Island SL-13
▨ Green Females: D = 3.62
■ Brown Females: D = 6.13
Pianka's Overlap = 0.37
0
10
20
30
40
50
60
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Prey Resource Categories

E


Island SL-6
▨ Green Males: D = 3.95
■ Brown Males: D = 3.46
Pianka's Overlap = 0.79
Island SL-8
▨ Green Males: D = 4.20
■ Brown Males: D = 2.57
Pianka's Overlap = 0.26
Island SL-13
▨ Green Males: D = 4.24
■ Brown Males: D = 6.00
Pianka's Overlap = 0.71
0
10
20
30
40
50
60
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Proportion of the Total Volume of Prey (Percent)
Prey Resource Categories

F


Island SL-6
Green Females: D = 5.06
Brown Males: D = 3.46
Pianka's Overlap = 0.62
Island SL-8
Green Females: D = 4.98
Brown Males: D = 2.57
Pianka's Overlap = 0.78
Island SL-13
Green Females: D = 3.62
Brown Males: D = 6.00
Pianka's Overlap = 0.12
Proportion of the Total Volume of Prey (Percent)
60
50
40
30
20
10
0
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Prey Resource Categories


G
Proportion of the Total Volume of Prey (Percent)
Island SL-6
▨ Green Males: D = 3.95
■ Brown Females: D = 3.04
Pianka's Overlap = 0.68
Island SL-8
▨ Green Males: D = 4.20
■ Brown Females: D = 4.88
Pianka's Overlap = 0.76
Island SL-13
▨ Green Males: D = 4.24
■ Brown Females: D = 6.13
Pianka's Overlap = 0.24
0
10
20
30
40
50
60
Form
Hym
DipA
DipL
Hom
Hem
ColA
ColL
NeuA
NeuL
Odo
LepA
LepL
Thys
Orth
Derm
Ispt
Psoc
Embi
Aran
Pseu
Acar
Ispo
Amp
Chil
Dipl
Moll
Liz
Prey Resource Categories

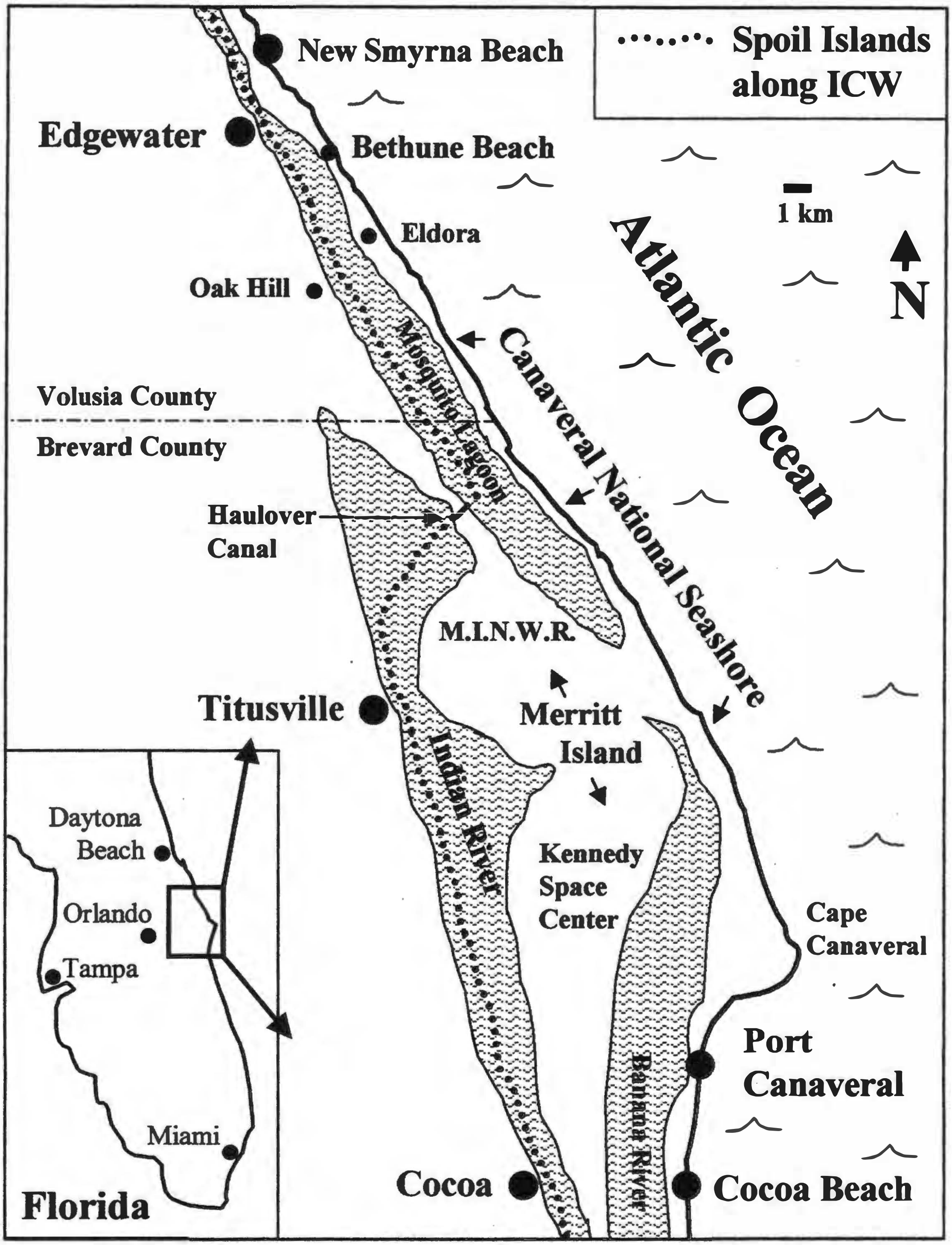


Figure 4.1. Location of the chain of dredge-spoil islands found along the Intracoastal Waterway (ICW) in Mosquito Lagoon, Brevard and Volusia Counties, Florida. These islands used in this study lie between Eldora (Latitude 28⁰54'00") and the Haulover Canal (Latitude 28⁰44'00") within the boundaries of Canaveral National Seashore and Merritt Island National Wildlife Refuge (MINWR).

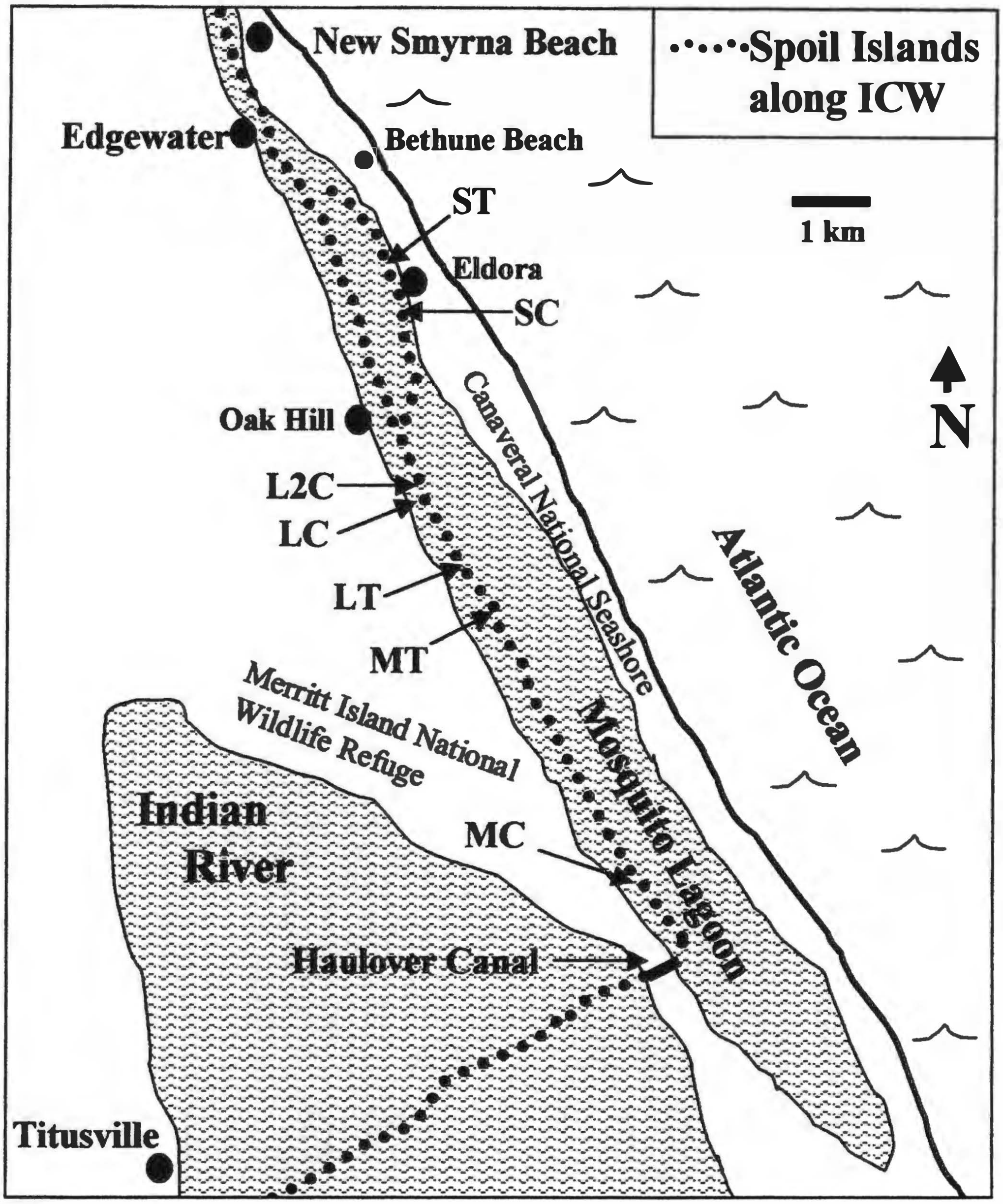


Figure 4.2. Location of the seven dredge-spoil islands in Mosquito Lagoon that were used as treatments and controls in this study, relative to Eldora, Oak Hill, the Intracoastal Waterway (ICW), and the Haulover Canal. ST = small treatment; SC = small control; MT = medium treatment; MC = medium control; LT = large treatment; LC = large control; L2C = large two-species control. Note that islands ST and SC are located along the “old channel” of the ICW on the east side of Mosquito Lagoon.

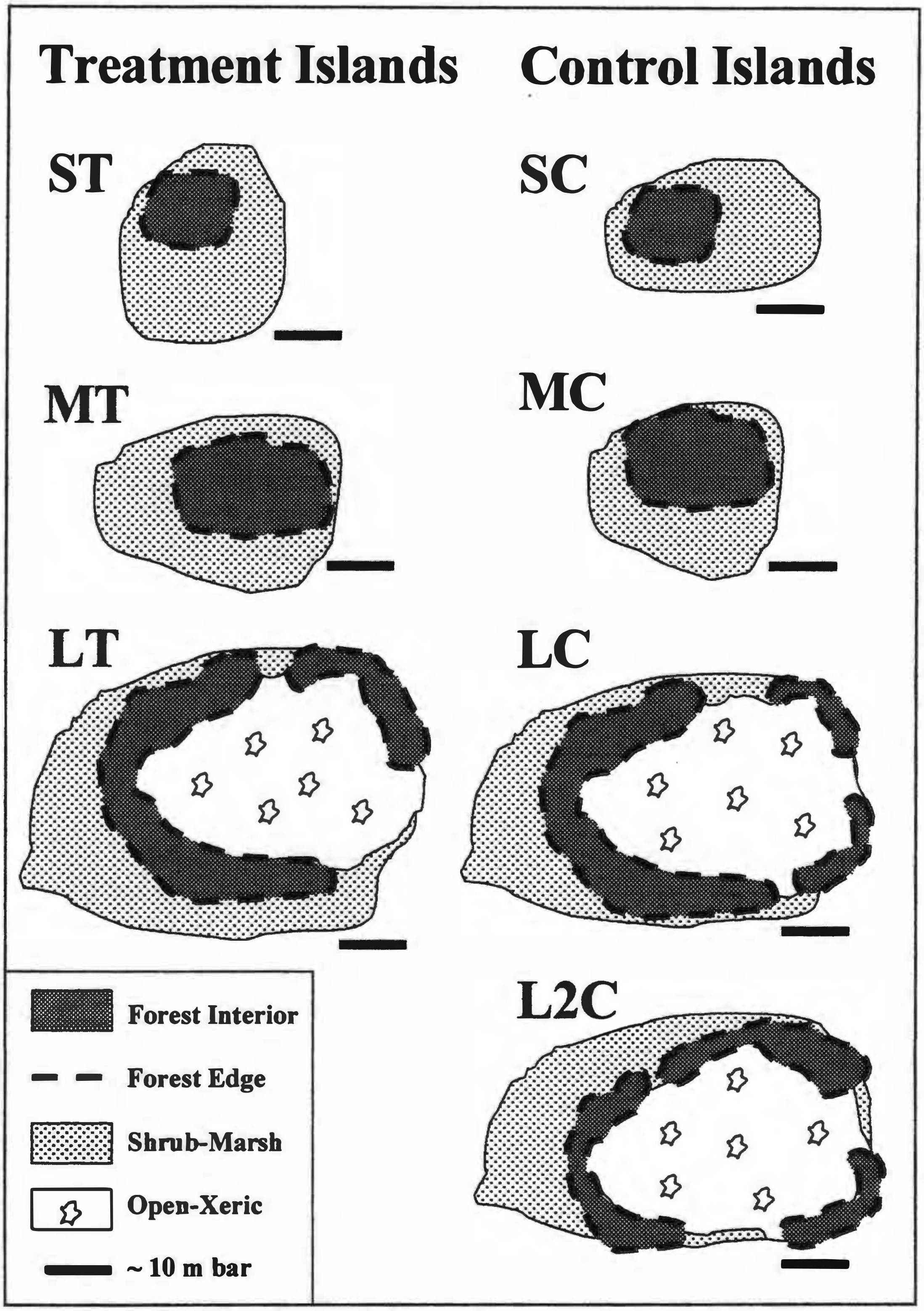
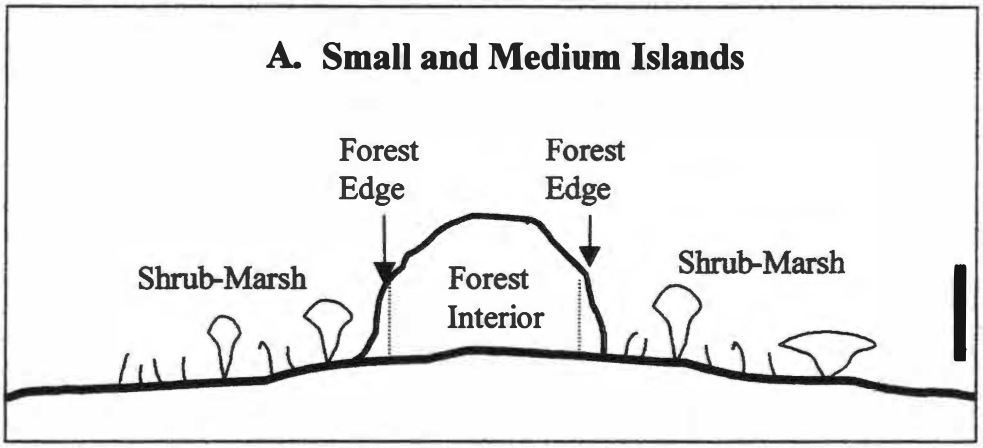


Figure 4.3. Graphical interpretation of the experimental design in this study, including rough illustrations of the seven dredge-spoil islands (three treatments and four controls) and the habitats occurring on each (abbreviations as in Figure 4.2).


A. Small and Medium Islands

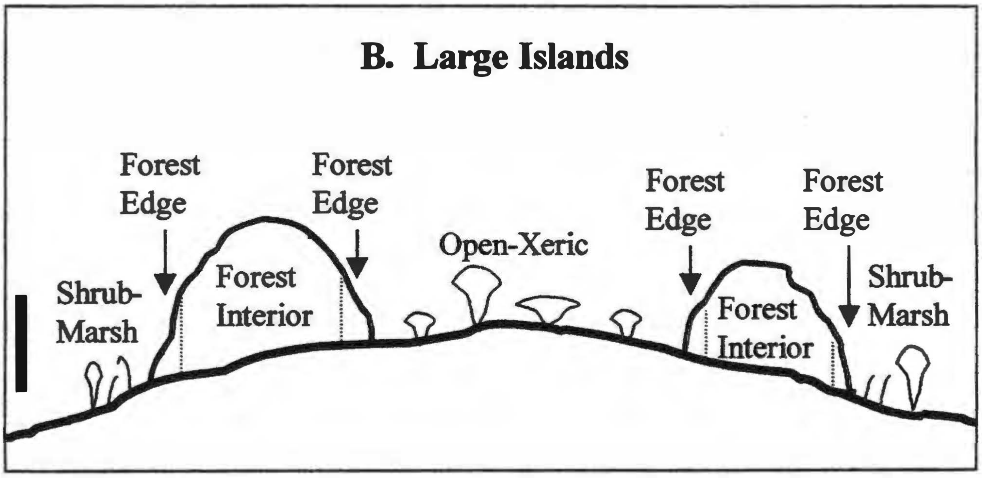

B. Large Islands

Figure 4.4. Cross sectional views through the center of a representative small and/or medium island (A) and a representative large island (B), showing the relative positions of the four habitat types present on each. The vertical scale bar is approximately five meters in height.

Figure 4.5. Overhead color aerial photograph of island ST.

Figure 4.6. Enlarged, enhanced, oblique aerial photograph of island SC.

Figure 4.7. Overhead color aerial photograph of island MT.

Figure 4.8. Oblique color aerial photograph of island MC.

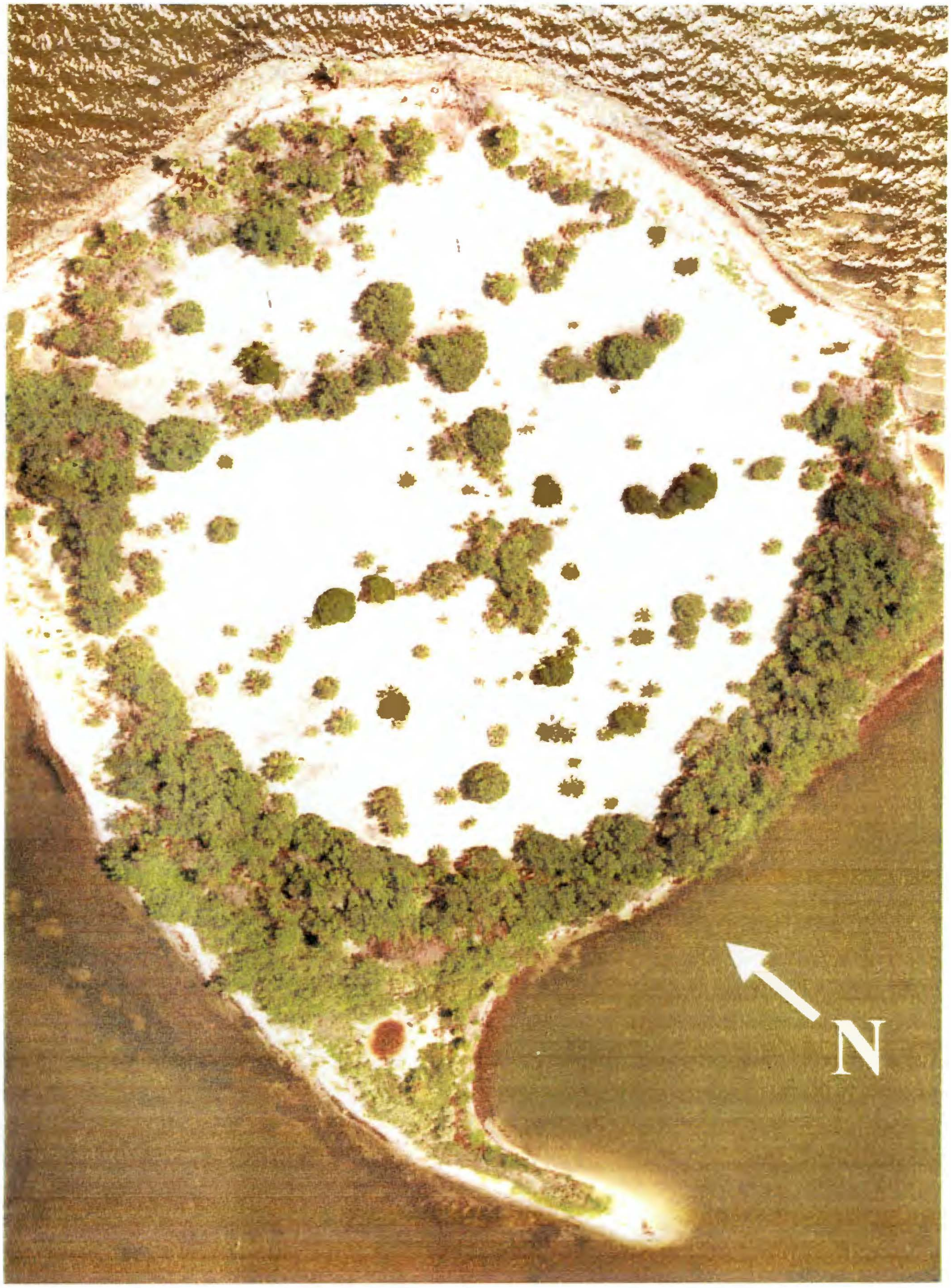


Figure 4.9. Overhead color aerial photograph of island LT.

Figure 4.10. Overhead color aerial photograph of island LC.

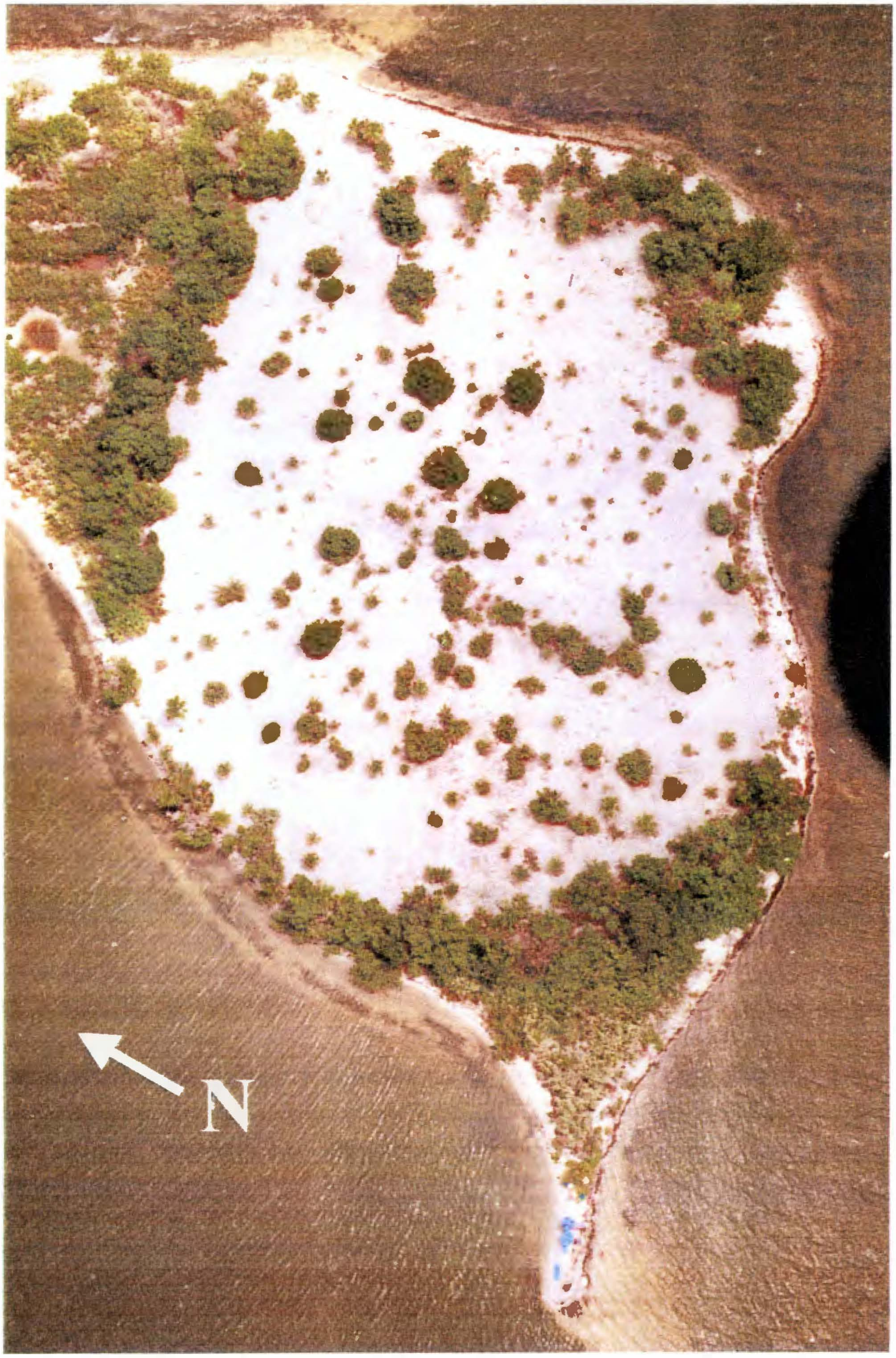


Figure 4.11. Overhead color aerial photograph of island L2C.

Figure 4.12. Schematic diagram of island ST used for FRAGSTATS analyses.

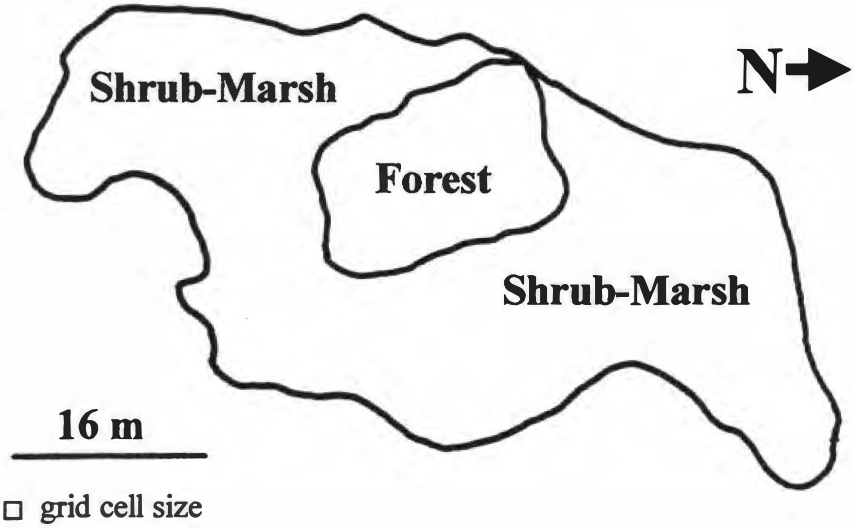


Figure 4.13. Schematic diagram of island SC used for FRAGSTATS analyses.

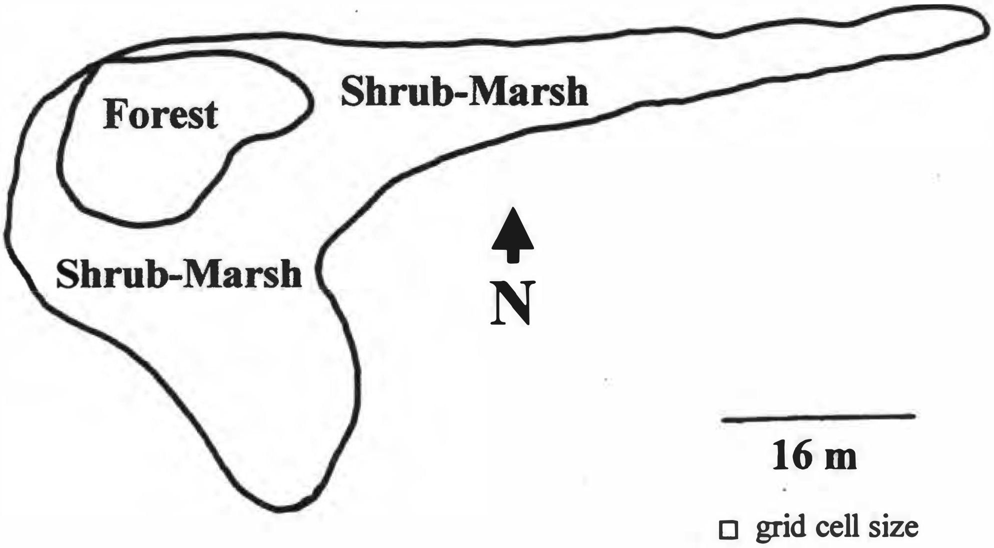


Figure 4.14. Schematic diagram of island MT used for FRAGSTATS analyses.

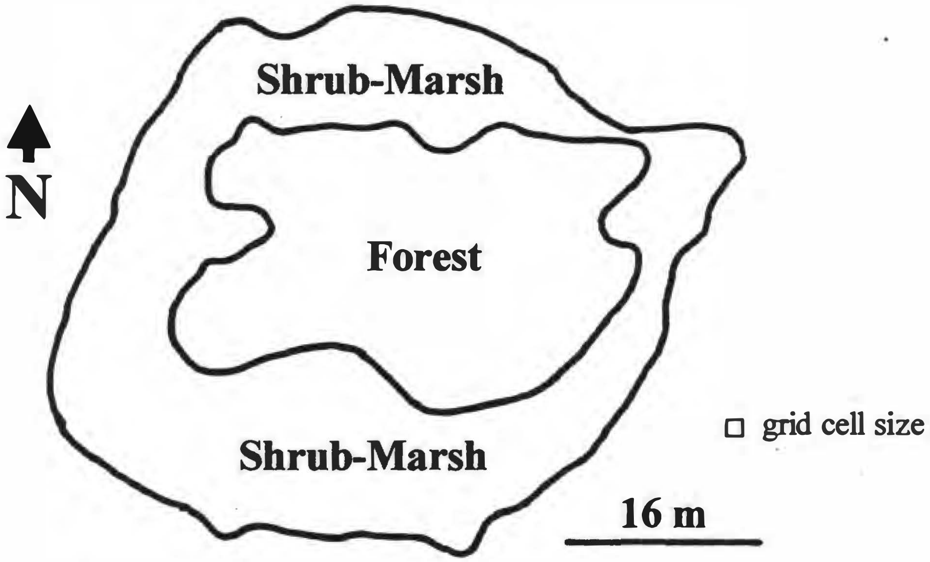
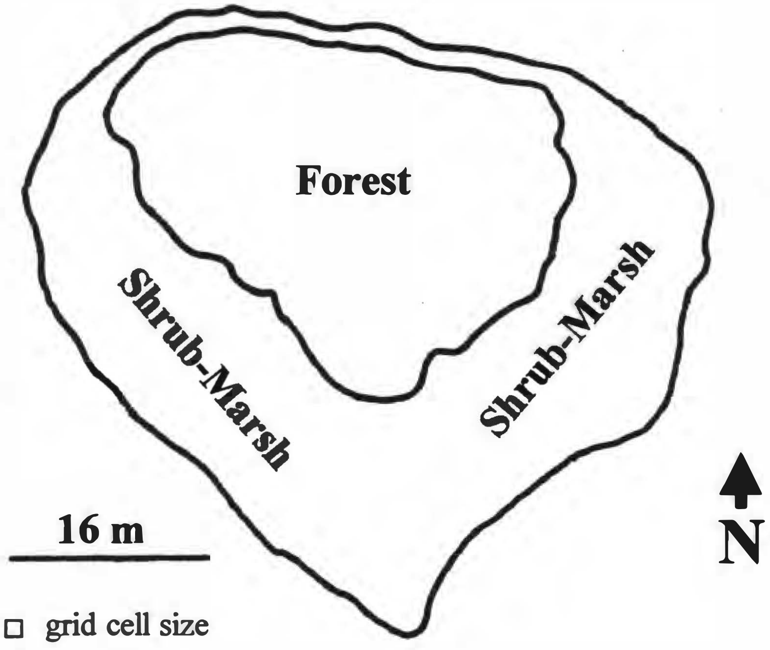


Figure 4.15. Schematic diagram of island MC used for FRAGSTATS analyses.



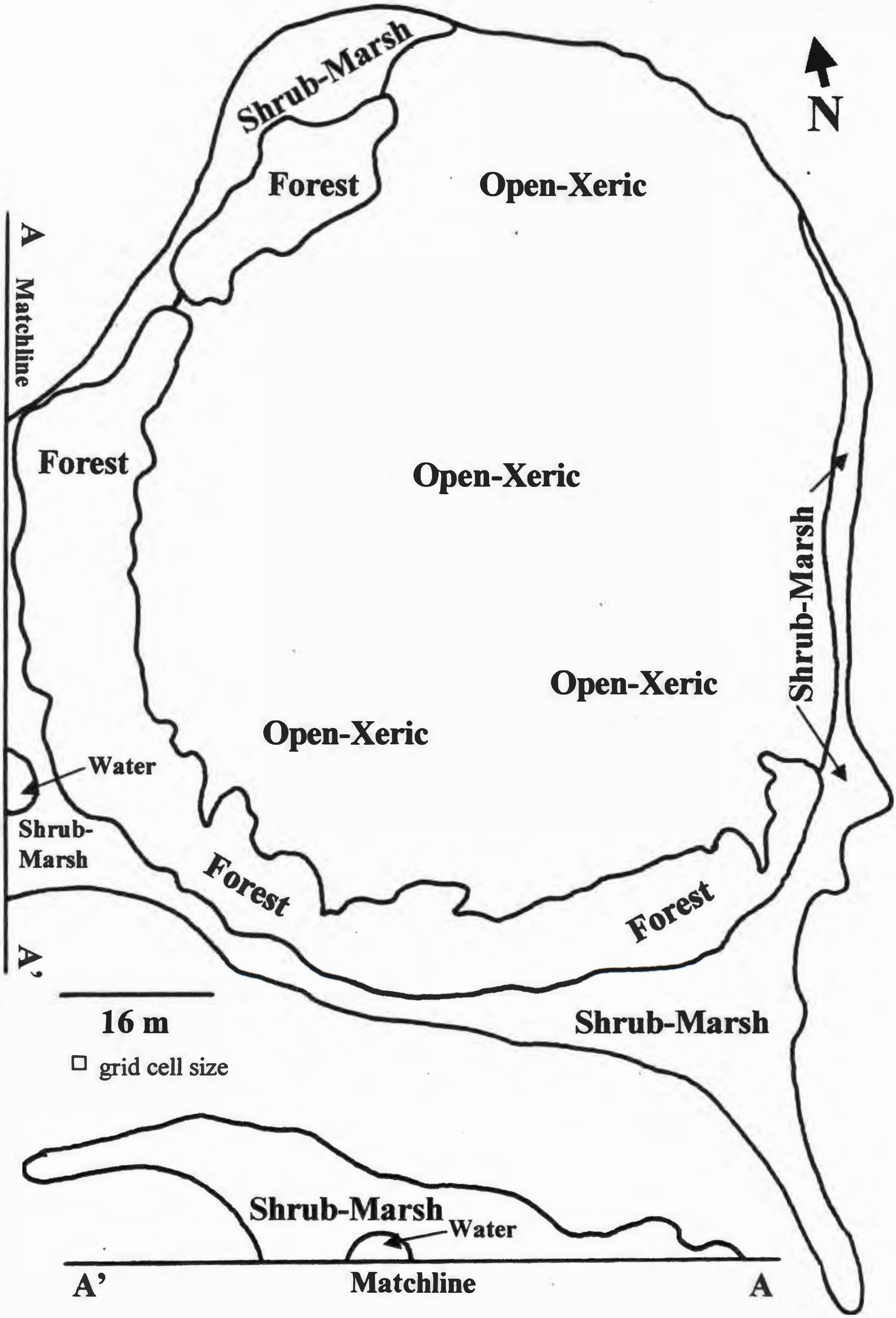


Figure 4.16. Schematic diagram of island LT used for FRAGSTATS analyses.

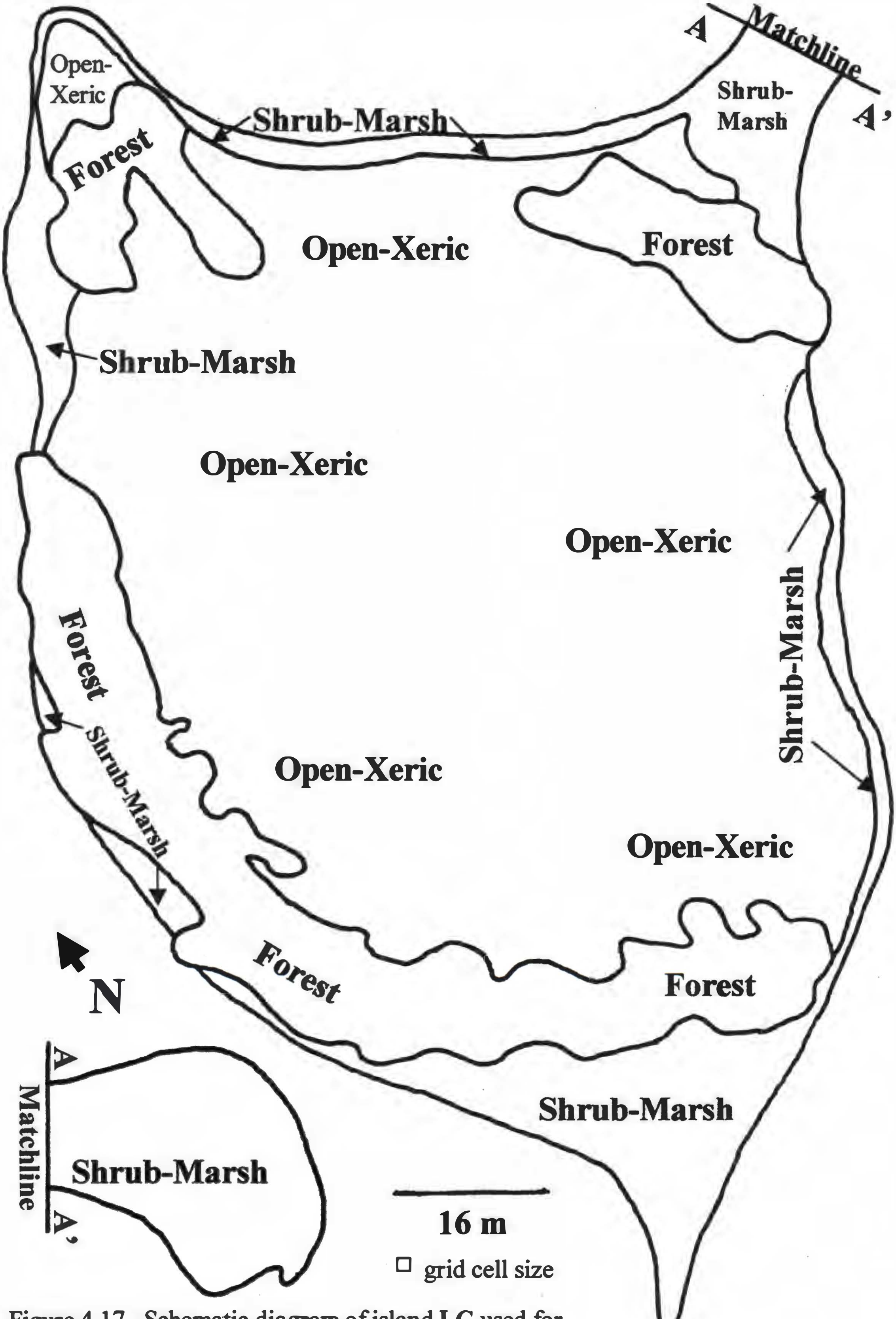


Figure 4.17. Schematic diagram of island LC used for FRAGSTATS analyses.

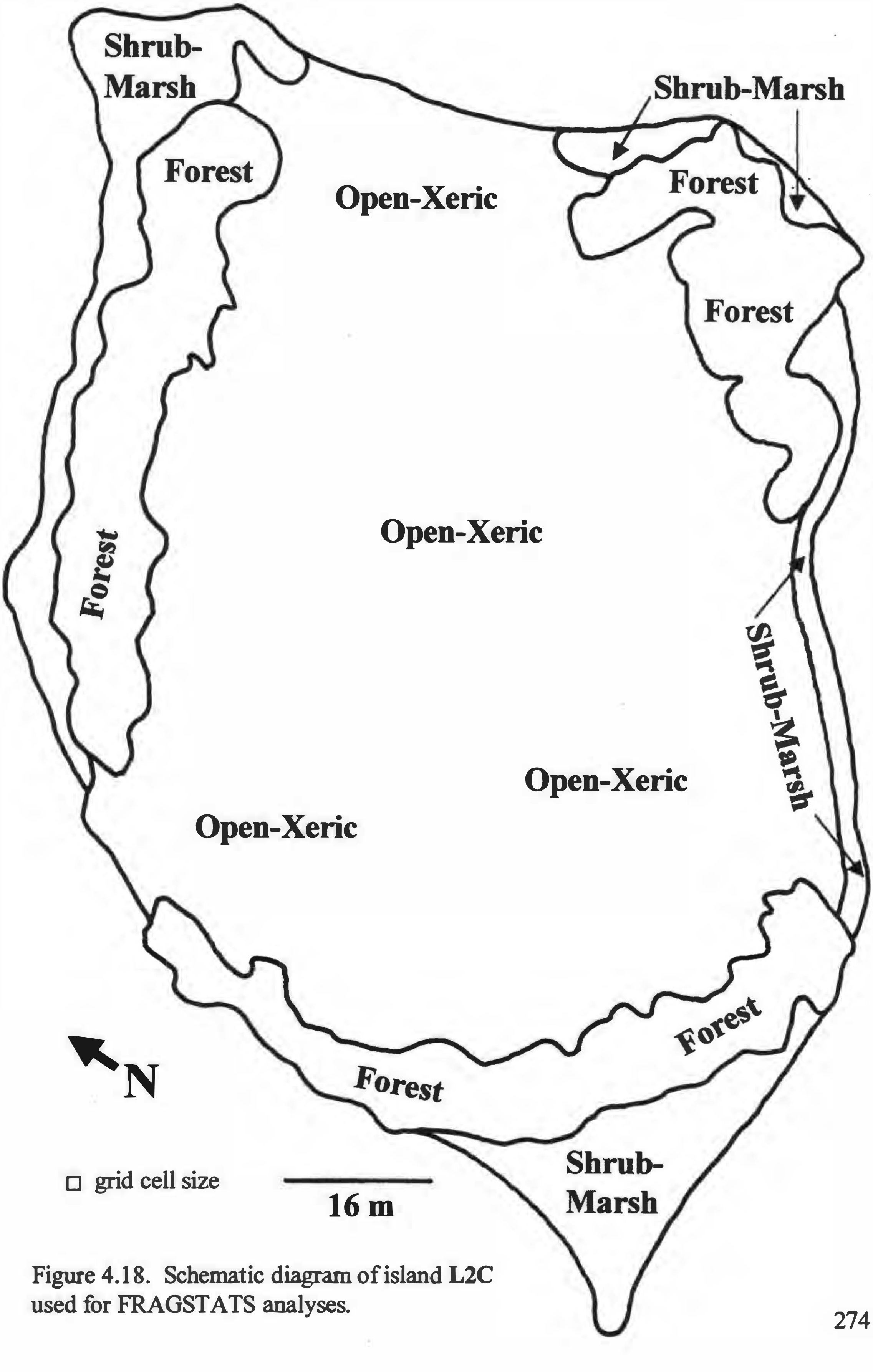


Figure 4.18. Schematic diagram of island L2C used for FRAGSTATS analyses.

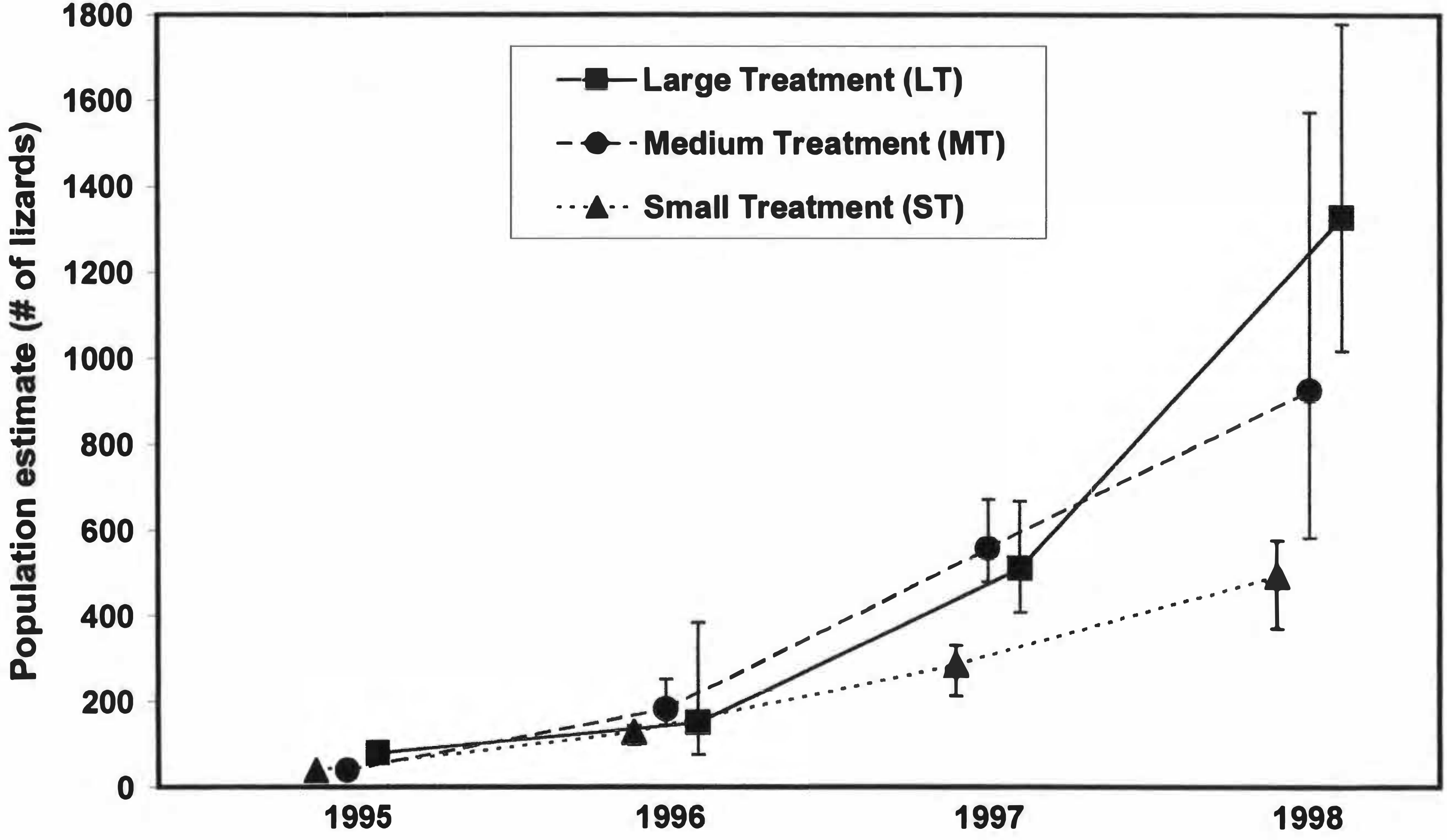


Figure 4.19. Population estimates for *Anolis sagrei* on the three treatment islands during each year of the study. Error bars represent 95 percent confidence intervals.

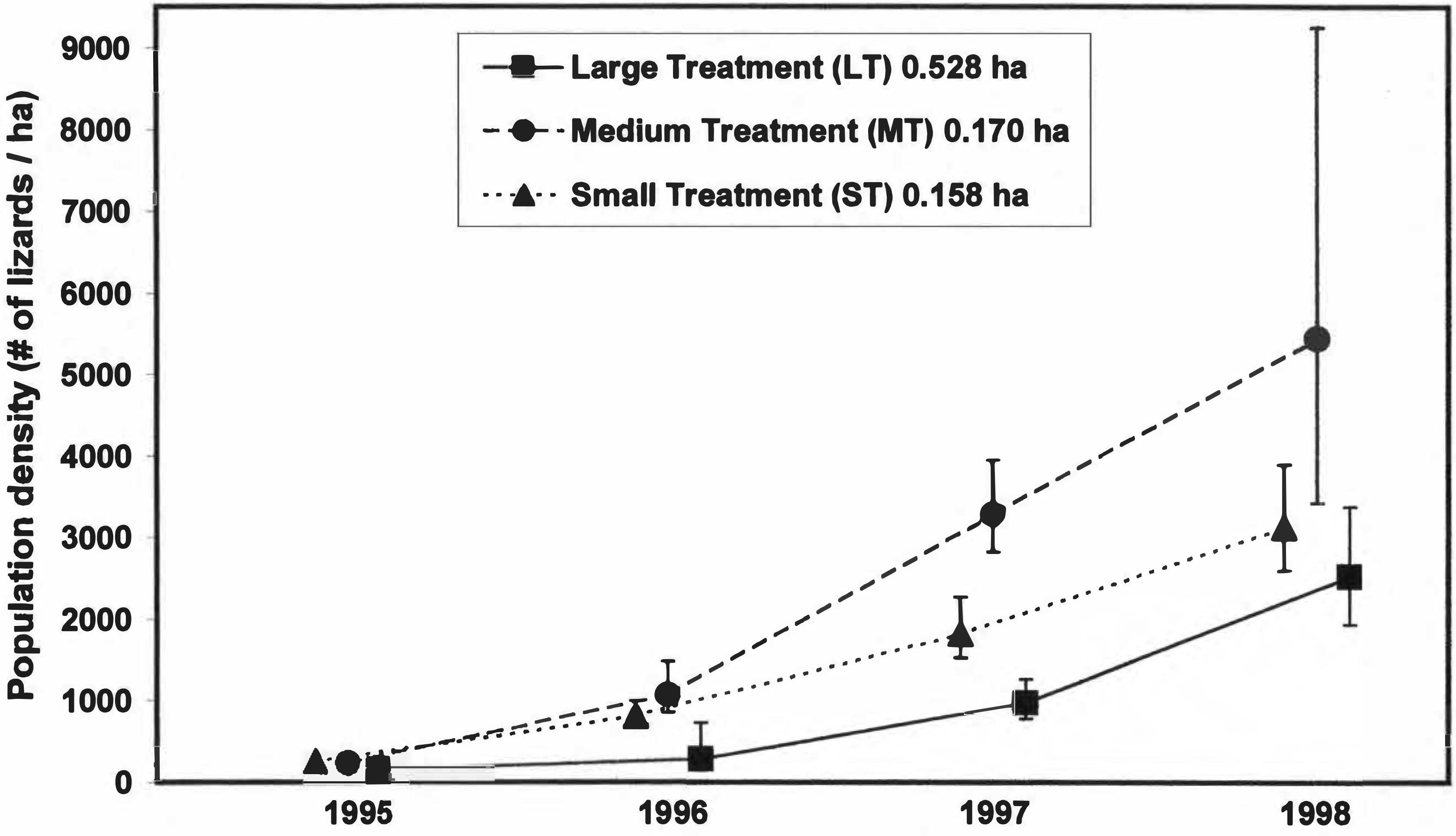


Figure 4.20. Population density estimates for *Anolis sagrei* on the three treatment islands during each year of the study. Density was calculated relative to the vegetated area of each island (see legend). Error bars represent 95 percent confidence intervals around the density estimates.

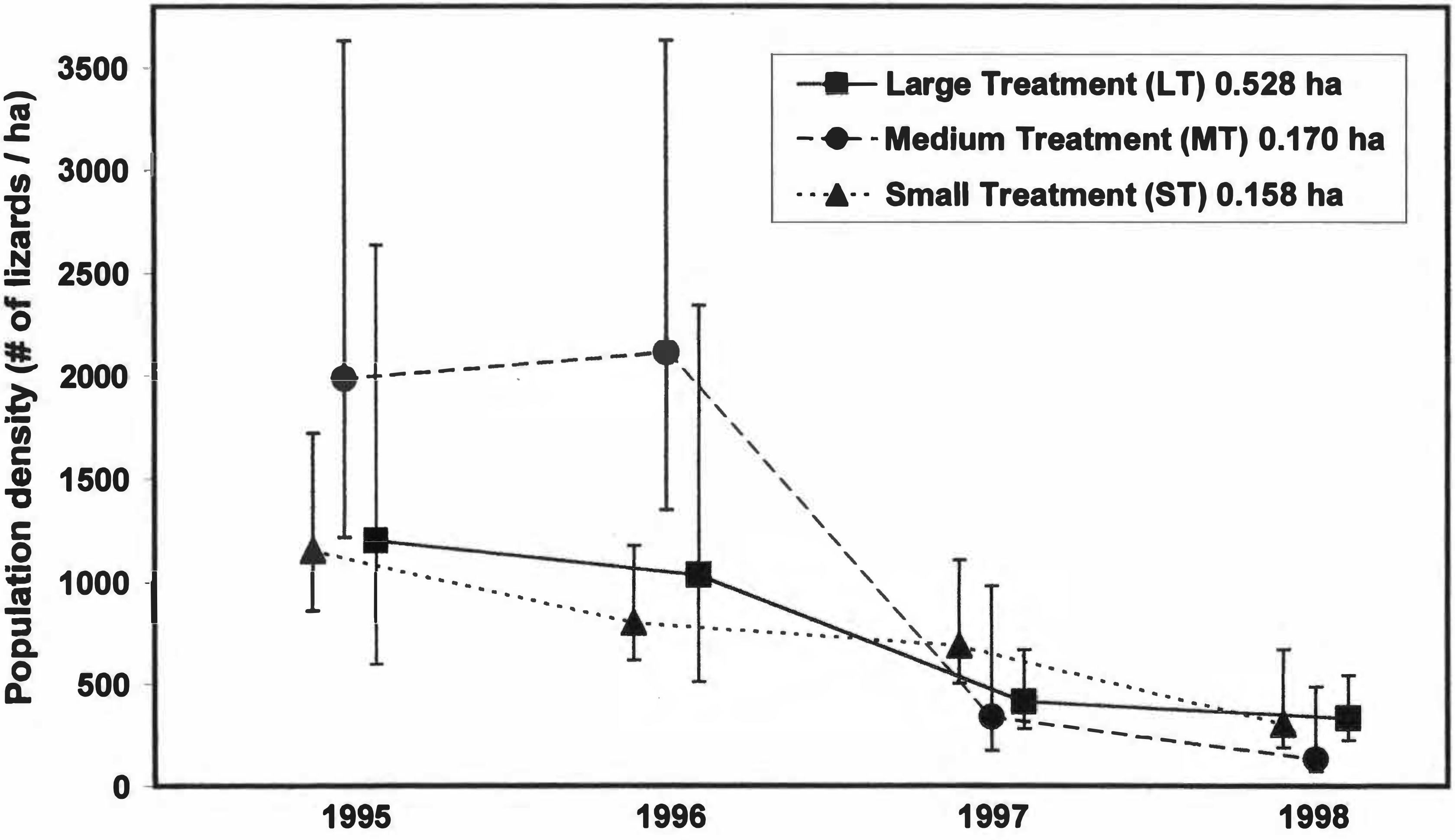


Figure 4.21. Population density estimates for *Anolis carolinensis* on the three treatment islands during each year of the study. Density was calculated relative to the vegetated area of each island (see legend). Error bars represent 95 percent confidence intervals around the density estimates.

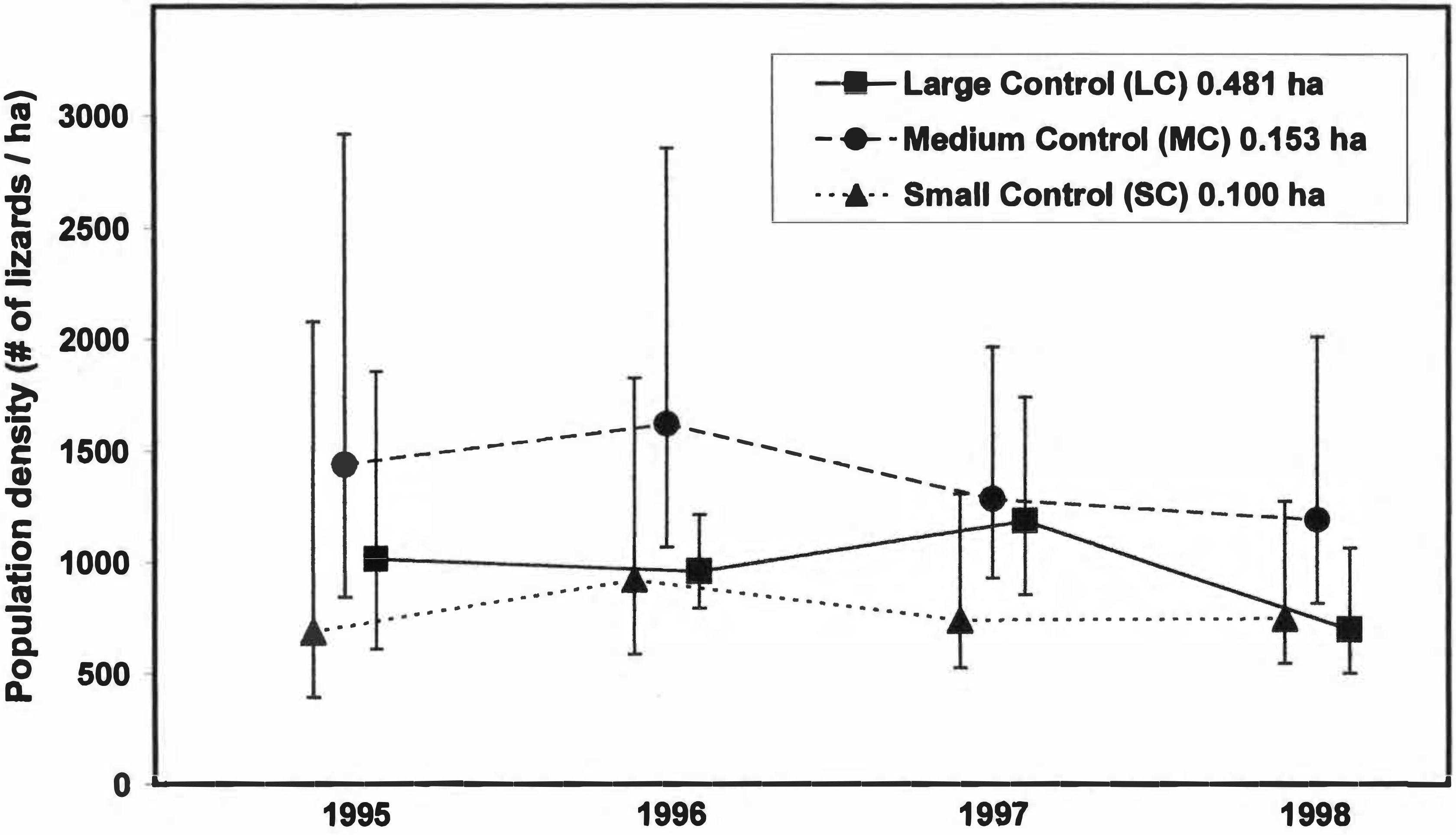


Figure 4.22. Population density estimates for *Anolis carolinensis* on the three control islands during each year of the study. Density was calculated relative to the vegetated area of each island (see legend). Error bars represent 95 percent confidence intervals around the density estimates.

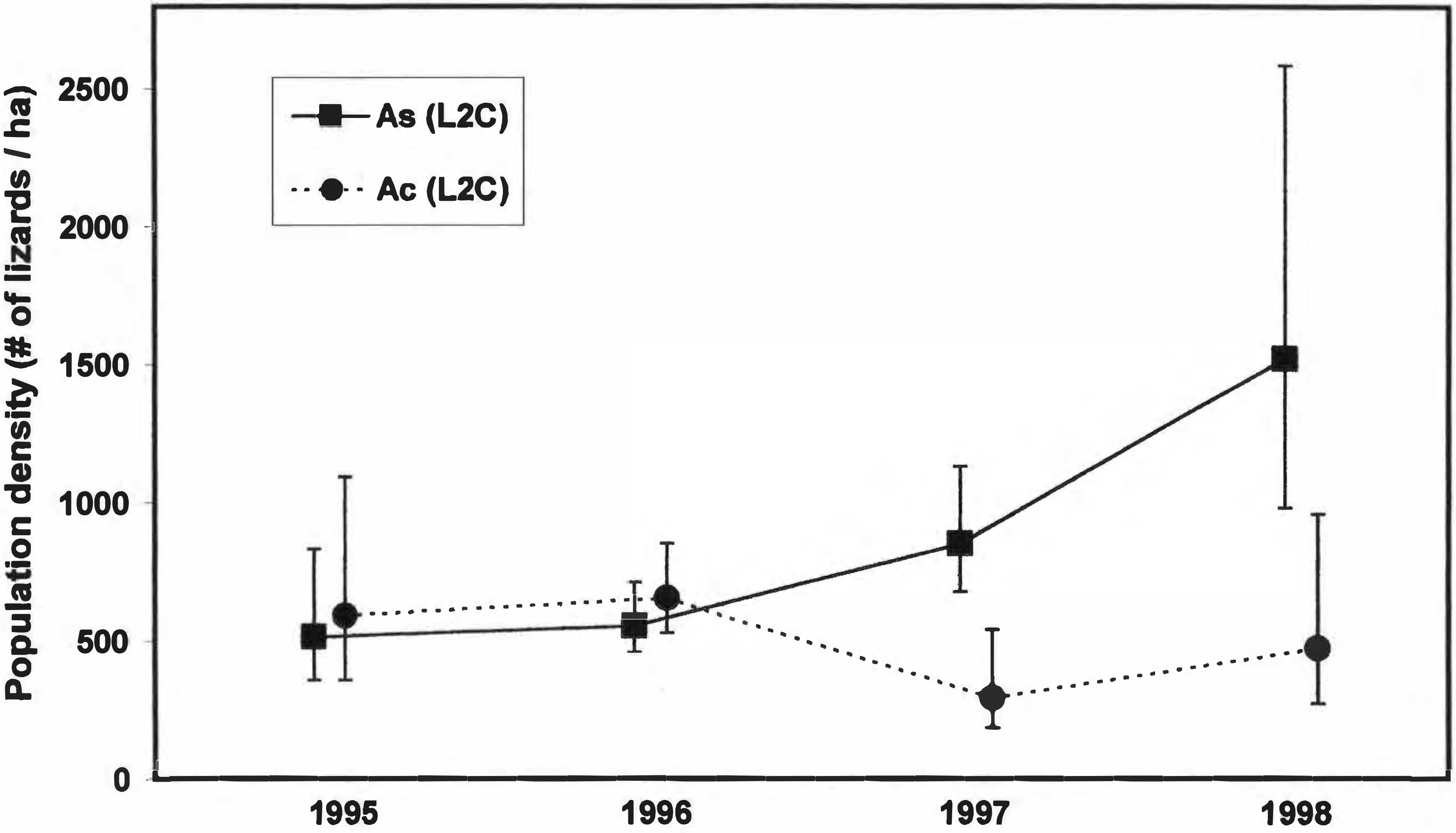


Figure 4.23. Population density estimates for *Anolis sagrei* (As) and *A. carolinensis* (Ac) on the large two-species "control" island (L2C) for each year of the study. Density was calculated relative to the vegetated area of the island (0.495 ha). Error bars represent 95 percent confidence intervals around the density estimates.

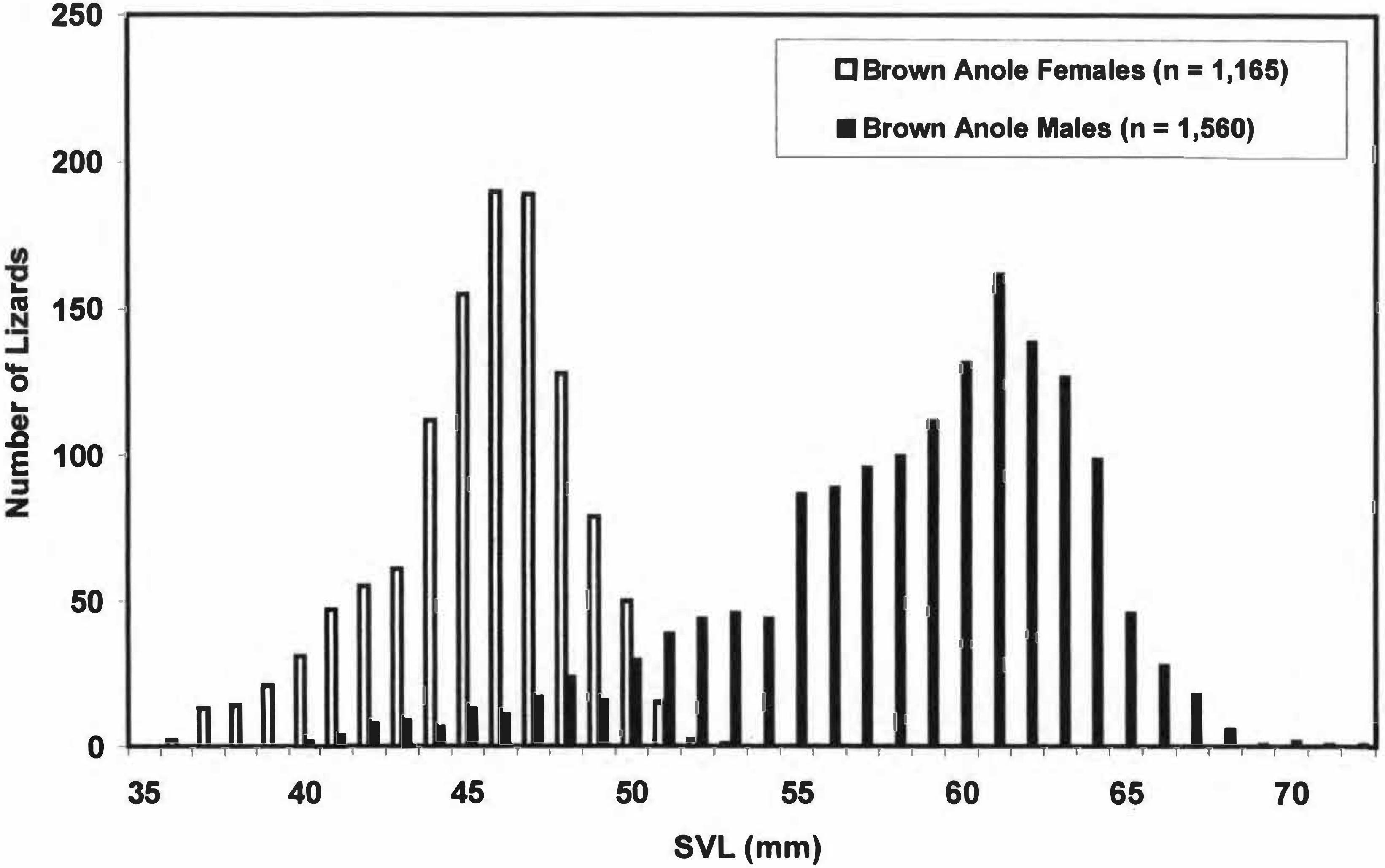


Figure 4.24. Distribution of snout-to-vent lengths (SVL) for 2,275 brown anoles (*Anolis sagrei*) measured between May and August on four dredge spoil islands (ST, MT, LT, and L2C) in Mosquito Lagoon.

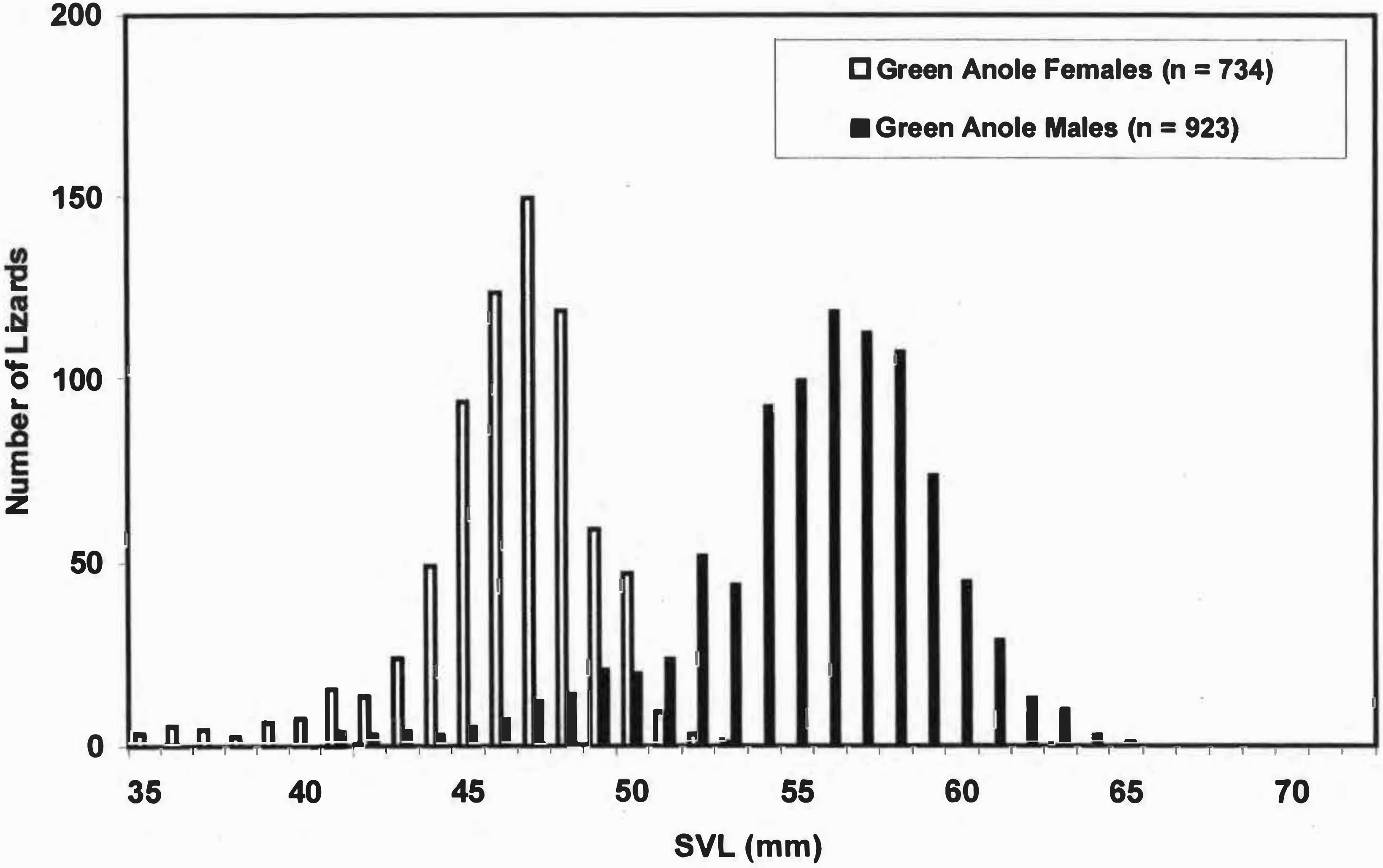


Figure 4.25. Distribution of snout-to-vent lengths (SVL) for 1,657 green anoles (*Anolis carolinensis*) measured between May and August on all seven dredge spoil islands used in this study in Mosquito Lagoon.

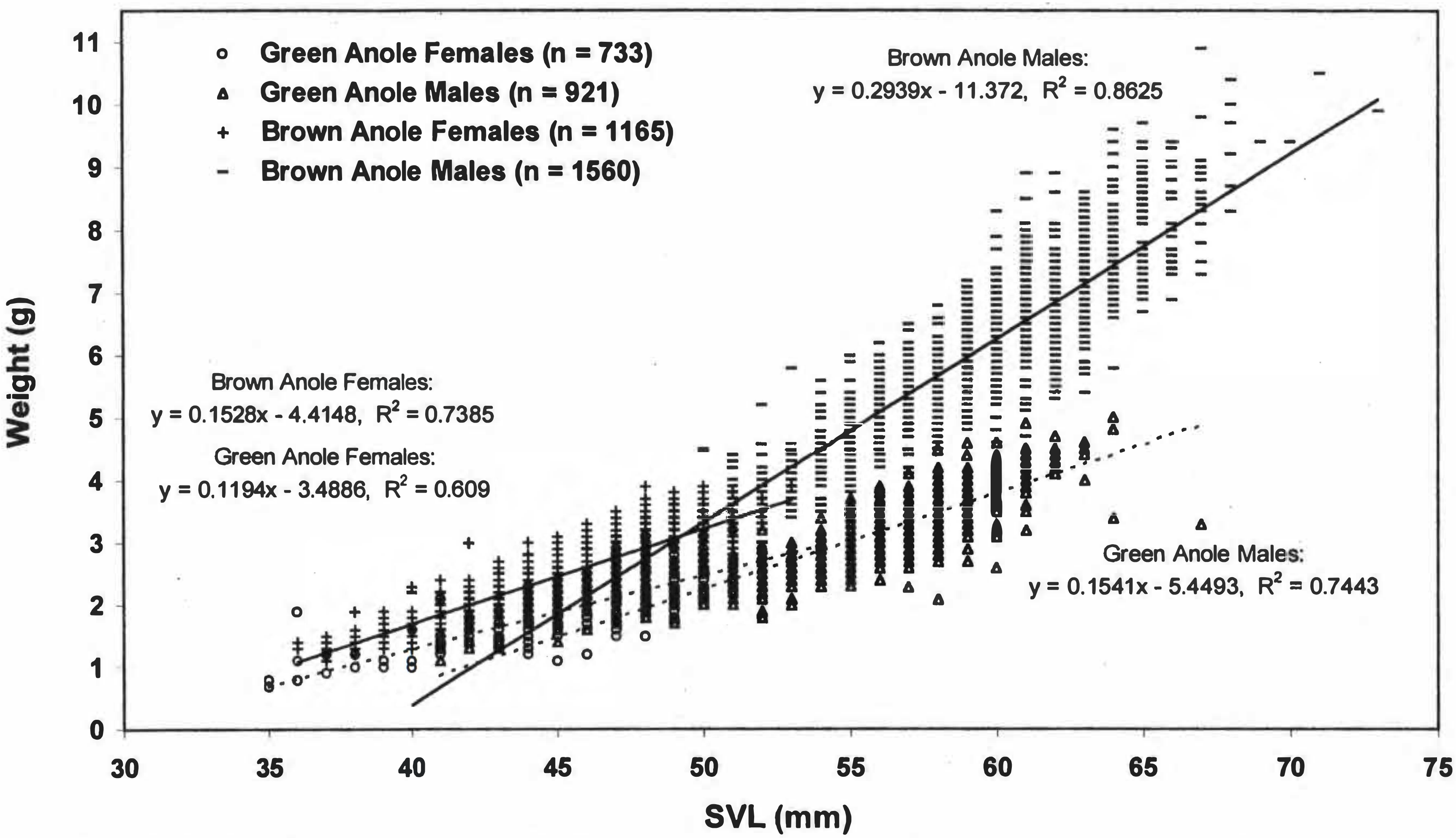


Figure 4.26. Regression of snout-to-vent length (SVL) against body weight for 4,379 *Anolis* lizards measured from six dredge-spoil islands in Mosquito Lagoon during four summer months (May-August) between 1995 and 1998. Data are plotted separately by sex for 1,654 green anoles (*Anolis carolinensis*) and 2,725 brown anoles (*Anolis sagrei*).

Table 2.1. Summarized capture data for 643 brown anoles marked and recaptured on Island P1 during 16 capture-mark-recapture (CMR) sessions. A CMR session is one complete capture survey, where the entire island is surveyed. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and multiplied by island area (0.048 ha) to obtain lizard densities and density ranges. The 1994 and 1998 populations were not estimated because the former were only donor lizards and the latter were sampled only once. Average p-hat is the average capture probability, or p-hat, of all the CMR sessions within a year. Field sampling dates include all the calendar dates (month/day) on which the island was visited.

	1994	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	18	103	241	246	35
Lizards from previous year	-	4	9	20	5
Total marked lizards	18	107	250	266	40
Number of recaptures	-	97	151	120	-
Total lizard captures	-	204	401	386	40
Population estimate (Mth)	-	140	477	576	-
Standard error of estimate	-	13.19	46.63	69.09	-
Average p-hat	-	0.29	0.14	0.17	-
Confidence interval	-	123 - 177	402 - 588	468 - 743	-
Lizard density (per m^2)	0.04	0.29	0.99	1.20	-
Density range (per m^2)	-	0.26 - 0.37	0.84 - 1.23	0.98 - 1.55	-
Field sampling dates	6/10; 8/19	4/12; 5/2-4; 5/10; 7/28	6/13,15,16; 7/13,15,18	6/24-28; 8/23	6/26
CMR sessions	-	5	6	4	1

Table 2.2. Summarized capture data for 273 brown anoles marked and recaptured on Island P2 during 14 capture-mark-recapture (CMR) sessions. A CMR session is one complete capture survey, where the entire island is surveyed. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and multiplied by island area (0.150 ha) to obtain lizard densities and density ranges. The 1994 and 1998 populations were not estimated because the former were only donor lizards and the latter were sampled only once. Average p-hat is the average capture probability, or p-hat, of all the CMR sessions within a year. Field sampling dates include all the calendar dates (month/day) on which the island was visited.

	1994	1995	1996	1997	1998
Newly marked lizards	19	51	69	100	34
Lizards from previous year	-	5	4	4	5
Total marked lizards	19	56	73	104	39
Number of recaptures	-	28	16	50	-
Total lizard captures	-	84	89	154	39
Population estimate (Mth)	-	109	202	246	-
Standard error of estimate	-	23.81	63.96	70.66	-
Average p-hat	-	0.13	0.11	0.21	-
Confidence interval	-	79 - 179	124 - 396	161 - 461	-
Lizard density (per m^2)	0.01	0.07	0.13	0.16	-
Density range (per m^2)	-	0.05 - 0.12	0.08 - 0.26	0.11 - 0.31	-
Field sampling dates	6/10; 8/19	4/29 - 5/1; 7/30	6/14; 8/8-9	6/29-30; 7/2; 8/23	6/26
CMR sessions	-	6	4	3	1

Table 2.3. Summary of asymptotic sizes of female brown anoles on each island during each year of the study calculated by three different methods. Mean SVL_{ZG} describes the mean SVL of only the zero-growth females in a sample (growth of donor lizards in 1994 was not measured). Mean SVL_{Max33} describes the largest third of the females in each sample. SVL_{Max} is simply the SVL of the largest female in each sample.

	1994	1995	1996	1997	1998
Island P1					
Mean SVL_{ZG}	-	46.00	46.86	45.93	44.5
s.e. Mean SVL_{ZG}	-	-	0.77	0.45	0.50
Sample size SVL_{ZG}	-	1	7	14	2
Mean SVL_{Max33}	45.00	45.93	46.40	46.02	45.60
Median SVL_{Max33}	45	46	46	46	46
s.e. Mean SVL_{Max33}	0.41	0.25	0.16	0.12	0.51
Sample size SVL_{Max33}	4	14	40	45	5
SVL_{Max}	46	48	49	49	47
Sample size SVL_{Max}	12	41	120	135	15
Island P2					
Mean SVL_{ZG}	-	-	50.00	48.50	50
s.e. Mean SVL_{ZG}	-	-	-	0.50	0.00
Sample size SVL_{ZG}	-	-	1	2	2
Mean SVL_{Max33}	45.25	47.75	49.77	48.71	48.33
Median SVL_{Max33}	45	48	50	48.50	48
s.e. Mean SVL_{Max33}	0.25	0.16	0.34	0.22	0.88
Sample size SVL_{Max33}	4	8	13	14	3
SVL_{Max}	46	48	52	50	50
Sample size SVL_{Max}	13	24	39	42	10

Table 2.4. Summary of asymptotic sizes of male brown anoles on each island during each year of the study calculated by three different methods. Mean SVL$_{ZG}$ describes the mean SVL of only the zero-growth males in a sample (growth of donor lizards in 1994 was not measured). Mean SVL$_{Max33}$ describes the largest third of the males in each sample. SVL$_{Max}$ is simply the SVL of the largest male in each sample.

	1994	1995	1996	1997	1998
Island P1					
Mean SVL$_{ZG}$	-	59.60	60.40	58.71	58.50
s.e. Mean SVL$_{ZG}$	-	(1.29)	(1.57)	(0.81)	(0.50)
Sample size SVL$_{ZG}$	-	5	5	7	2
Mean SVL$_{Max33}$	57.33	61.48	59.98	57.95	57.14
Median SVL$_{Max33}$	57	61	60	58	57
s.e. Mean SVL$_{Max33}$	0.33	0.27	0.19	0.24	0.59
Sample size SVL$_{Max33}$	3	21	40	37	7
SVL$_{Max}$	58	64	65	62	60
Sample size SVL$_{Max}$	6	62	121	111	20
Island P2					
Mean SVL$_{ZG}$	-	62.00	65.50	63.50	65.33
s.e. Mean SVL$_{ZG}$	-	-	0.50	1.50	0.88
Sample size SVL$_{ZG}$	-	1	2	2	3
Mean SVL$_{Max33}$	60.33	63.78	64.60	64.32	65.13
Median SVL$_{Max33}$	60	63	64.50	64	65
s.e. Mean SVL$_{Max33}$	0.88	0.43	0.40	0.13	0.30
Sample size SVL$_{Max33}$	3	9	10	19	8
SVL$_{Max}$	62	66	67	65	66
Sample size SVL$_{Max}$	6	27	30	58	24

Table 2.5. Results of a 3-way ANOVA testing the effect of island (2 levels), sex (2 levels), and year (5 levels) on the mean SVL of the largest third of the brown anoles (SVL_{Max33}) in each of the 20 island-year-sex groups (n = 307).

Source	**DF**	**Sum of Squares**	**F Ratio**	**Prob>F**
Island	1	453.5558	374.0326	< 0.0001
Sex	1	7536.1233	6214.7940	< 0.0001
Island*Sex	1	66.0592	54.4769	< 0.0001
Year	4	132.3612	27.2885	< 0.0001
Island*Year	4	75.3704	15.5389	< 0.0001
Sex*Year	4	33.0464	6.8131	< 0.0001
Island*Sex*Year	4	35.7626	7.3731	< 0.0001

Table 2.6. Summary statistics for female brown anole mean snout-vent length (SVL) and body condition indices (CI) on Island P1 (n = 323) and Island P2 (n = 128) during each year of the study. Yearly sample sizes apply to both parameters.

	1994	1995	1996	1997	1998
Island P1					
Mean SVL (mm)	42.92	44.32	44.56	43.87	43.80
Median SVL	43	44	45	44	44
s.e. Mean SVL	0.8021	0.2577	0.1639	0.1869	0.4995
Mean CI	2.9613	2.9326	2.8846	2.8356	2.7088
s.e. Mean CI	0.0206	0.0106	0.0061	0.0073	0.0228
n	12	41	120	135	15
Island P2					
Mean SVL (mm)	43.85	46.42	47.18	47.43	46.40
Median SVL	44	47	48	48	46
s.e. Mean SVL	0.3368	0.2753	0.4872	0.2020	0.5416
Mean CI	2.9054	2.9191	2.9062	2.9218	2.8115
s.e. Mean CI	0.0274	0.0126	0.0117	0.0100	0.0199
n	13	24	39	42	10

Table 2.7. Summary statistics for male brown anole mean snout-vent length (SVL) and body condition indices (CI) on Island P1 (n = 318) and Island P2 (n = 143) during each year of the study. Yearly sample sizes apply to both parameters.

	1994	1995	1996	1997	1998
Island P1					
Mean SVL (mm)	56.00	59.28	56.72	53.54	52.25
Median SVL	57	60	57	55	54.5
s.e. Mean SVL	0.8165	0.3111	0.3322	0.4615	1.1807
Mean CI	2.9535	2.9318	2.8705	2.8153	2.7266
s.e. Mean CI	0.0201	0.0083	0.0081	0.0877	0.0239
n	6	61	121	110	20
Island P2					
Mean SVL (mm)	57.67	60.80	58.23	61.10	61.75
Median SVL	57.5	61	61	62	63
s.e. Mean SVL	1.3333	0.7326	1.3860	0.5122	1.0184
Mean CI	2.8820	2.9460	2.9061	2.8664	2.7926
s.e. Mean CI	0.0416	0.0136	0.0159	0.0074	0.0103
n	6	25	30	58	24

Table 2.8. Results of a 3-way ANOVA testing the effect of island (2 levels), sex (2 levels), and year (5 levels) on the body condition index (CI) values of 912 exclusive brown anoles captured over the five summers of this study (includes donors).

Source	**DF**	**Sum of Squares**	**F Ratio**	**Prob>F**
Island	1	0.0555	9.2414	0.0024
Sex	1	0.0092	1.5294	0.2165
Island*Sex	1	0.0021	0.3463	0.5564
Year	4	1.4564	60.5903	< 0.0001
Island*Year	4	0.2329	9.6874	< 0.0001
Sex*Year	4	0.0686	2.8528	0.0229
Island*Sex*Year	4	0.0329	1.3670	0.2435

Table 2.9. Comparisons of mean body condition index (CI) values for 912 brown anoles (females and males pooled) on Island P1 and Island P2 during each year of this study. Standard errors are placed in parentheses below each CI value.

	1994	1995	1996	1997	1998
Island P1					
Mean CI	2.9587 (0.0150)	2.9322 (0.0065)	2.8775 (0.0051)	2.8265 (0.0055)	2.7189 (0.0166)
n	18	102	241	245	35
Island P2					
Mean CI	2.8980 (0.0224)	2.9328 (0.0092)	2.9062 (0.0095)	2.8897 (0.0066)	2.7981 (0.0093)
n	19	49	69	100	34
T ratio	2.229	0.058	2.655	6.571	4.125
d.f.	35	149	308	343	67
P	0.0324	0.9536	0.0083	< 0.0001	0.0001

Table 3.1. Stomach contents of 65 adult *Anolis carolinensis* (Ac) and 132 adult *A. sagrei* (As) collected on three dredge-spoil islands in Indian River Lagoon. Data are summarized by 12 island-species-sex (ISS) groups, by four species-sex (SS) groups, by six island-species (IS) groups, and by pooled data for the three islands. M = male, F = female. Values indicate the number of lizards collected (n_{lizard}), the number of stomachs that contained nematodes (n_{nema}), trematodes (n_{trema}), shed skin (n_{skin}), and plant materials (n_{plant}). Subtracting the number of stomachs containing only non-prey items (n_{np}) *and* the number of completely empty stomachs (n_{empty}) from the total number of lizards captured (n_{lizard}) gives the number of stomachs containing at least one prey item (n_{guts}).

Group	**Island**	**Species**	**Sex**	n_{lizard}	n_{nema}	n_{trema}	n_{skin}	n_{plant}	n_{np}	n_{empty}	n_{guts}
ISS	SL6	Ac	F	9							9
			M	14			2	1	2		12
		As	F	11			2		1		10
			M	14			6		2		12
	SL8	Ac	F	8				3			8
			M	8	2		1	1			8
		As	F	25	19	3	1	9		1	24
			M	29	25		10	2	1		28
	SL13	Ac	F	11	1		4		1		10
			M	15			3	1	1		14
		As	F	22	1		5	2			22
			M	31	4		10	5			31
SS	All	Ac	F	28	1		4	3	1		27
	All	Ac	M	37	2		6	3	3		34
	All	As	F	58	20	3	8	11	1	1	56
	All	As	M	74	29		26	7	3		71
IS	SL6	Ac	Both	23			2	1	2		21
		As	Both	25			9		3		22
	SL8	Ac	Both	16	2		1	4			16
		As	Both	54	44	3	11	11	1	1	52
	SL13	Ac	Both	26	1		7	1	2		24
		As	Both	53	5		15	7			53
Island	SL6	Both	Both	48			10	1	5		43
	SL8	Both	Both	70	46	3	12	15	1	1	68
	SL13	Both	Both	79	6		22	8	2		77
Total	All	Both	Both	197	52	3	44	24	8	1	188

Table 3.2. Individual prey volumes (mm^3) of 1,764 prey items removed from the stomachs of 65 adult *Anolis carolinensis* (Ac) and 132 adult *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Data were tabulated by 12 island-species-sex (ISS) groups, by four species-sex (SS) groups, by six island-species (IS) groups, and by pooled data for all prey on each of the islands.

Island	Species	Sex	n_{prey}	Mean	Med	S.D.	95% C.I.	Range
By ISS groups:								
SL6	Ac	F	111	7.30	4.71	12.64	4.92 - 9.67	0.13 - 102.07
		M	79	24.07	9.84	65.02	9.51 - 38.64	0.13 - 471.24
	As	F	62	15.68	8.18	22.57	9.95 - 21.41	0.20 - 135.83
		M	75	45.60	22.58	99.44	22.71 - 68.48	0.34 - 471.24
SL8	Ac	F	105	7.41	2.09	23.36	2.89 - 11.93	0.08 - 226.19
		M	84	17.31	6.03	45.70	7.39 - 45.70	0.15 - 395.97
	As	F	300	7.51	4.13	9.05	6.48 - 8.54	0.15 - 64.34
		M	264	32.00	7.12	94.44	20.55 - 43.44	0.15 - 942.48
SL13	Ac	F	90	9.05	3.32	27.97	3.19 - 14.91	0.08 - 235.62
		M	76	30.58	8.06	71.13	14.33 - 46.83	0.13 - 376.07
	As	F	329	6.57	2.15	14.49	5.00 - 8.14	0.03 - 210.18
		M	189	40.10	11.15	78.64	28.82 - 51.39	0.12 - 405.12
By SS groups:								
All	Ac	F	306	7.85	3.39	21.74	5.40 - 10.30	0.08 - 235.62
All	Ac	M	239	23.77	7.46	61.14	15.98 - 31.56	0.13 - 471.24
All	As	F	691	7.80	3.54	13.66	6.78 - 8.82	0.03 - 210.18
All	As	M	528	36.83	10.38	89.85	29.15 - 44.51	0.12 - 942.48
By IS groups:								
SL6	Ac	Both	190	14.27	5.42	43.67	8.02 - 20.52	0.13 - 471.24
	As	Both	137	32.06	12.57	76.37	19.16 - 44.96	0.20 - 471.24
SL8	Ac	Both	189	11.81	4.36	35.33	6.74 - 16.88	0.08 - 395.97
	As	Both	564	18.98	6.03	66.03	13.52 - 24.44	0.15 - 942.48
SL13	Ac	Both	166	18.91	3.63	53.27	10.74 - 27.07	0.08 - 376.07
	As	Both	518	18.80	2.66	51.41	14.37 - 23.24	0.03 - 405.12
By island:								
SL6	Both	Both	327	21.72	6.28	60.13	15.18 - 28.27	0.13 - 471.24
SL8	Both	Both	753	17.18	5.42	59.88	12.89 - 21.46	0.08 - 942.48
SL13	Both	Both	684	18.83	3.32	51.83	14.94 - 22.72	0.03 - 405.12
All	Both	Both	1764	18.66	5.42	56.93	16.00 - 21.32	0.03 - 942.48

Table 3.3. MANOVA results table for the fixed effects of island (three dredge-spoil islands in Indian River Lagoon), species (*Anolis carolinensis* and *A. sagrei*), sex, and their interactions on four Box-Cox transformed prey variables (n_{prey}, n_{taxa}, Mean V_{ind}, and V_{tot}) and four untransformed body parameters (SVL, HL, HW, and HD). P-values less than 0.05 are considered significant.

Source	**Pillai's Trace**	**F**	**DF $_{num}$**	**DF $_{den}$**	**P**
Island	0.2841	4.0456	14	342	< 0.0001
Species	0.8904	197.2104	7	170	< 0.0001
Sex	0.8154	107.2894	7	170	< 0.0001
Island*Species	0.1078	1.3915	14	342	0.1547
Island*Sex	0.1561	2.0680	14	342	0.0131
Species*Sex	0.6125	38.3819	7	170	< 0.0001
Island*Species*Sex	0.0872	1.1143	14	342	0.3436

Table 3.4. Results from eight univariate, 3-way ANOVAs for the fixed effects of island (three dredge-spoil islands in Indian River Lagoon), species (*Anolis carolinensis* and *A. sagrei*), sex, and their interactions on eight lizard-wise prey and body variables. These variables include four Box-Cox transformed prey variables: the number of prey items (n_{prey}), the number of prey taxa (n_{taxa}), the mean volumes of individual prey items in each stomach (V_{ind}), and the total volume of prey items in each stomach (V_{tot}), and four untransformed body parameters: snout-vent length (SVL), head length (HL), head width (HW), and head depth (HD). P-values less than 0.05 are considered significant.

Source	SS	F Ratio	DF	P
Box-Cox n_{prey}				
Island	348.6982	7.6421	2	0.0007
Species	12.1003	0.5304	1	0.4674
Sex	464.8380	20.3748	1	< 0.0001
Island*Species	195.2761	4.2797	2	0.0153
Island*Sex	94.7660	2.0769	2	0.1284
Species*Sex	1.3269	0.0582	1	0.8097
Island*Species*Sex	116.8932	2.5618	2	0.0800
Box-Cox n_{taxa}				
Island	10.1190	2.4824	2	0.0865
Species	3.8990	1.9130	1	0.1684
Sex	47.8987	23.5014	1	< 0.0001
Island*Species	6.7332	1.6518	2	0.1947
Island*Sex	7.7514	1.9016	2	0.1524
Species*Sex	0.2698	0.1324	1	0.7164
Island*Species*Sex	7.5522	1.8527	2	0.1599

Table 3.4, continued.

Source	SS	F Ratio	DF	P
Box-Cox V_{ind}				
Island	1218.718	2.5506	2	0.0809
Species	2501.535	10.4708	1	0.0014
Sex	14222.135	59.5303	1	<.0001
Island*Species	140.252	0.2935	2	0.7460
Island*Sex	464.542	0.9722	2	0.3803
Species*Sex	145.492	0.6090	1	0.4362
Island*Species*Sex	188.333	0.3942	2	0.6748
Box-Cox V_{tot}				
Island	11287.15	0.5510	2	0.5773
Species	78253.57	7.6406	1	0.0063
Sex	293694.71	28.6760	1	< 0.0001
Island*Species	3964.22	0.1935	2	0.8242
Island*Sex	3410.83	0.1665	2	0.8467
Species*Sex	19177.90	1.8725	1	0.1729
Island*Species*Sex	7271.20	0.3550	2	0.7017

Table 3.4, continued.

Source	SS	F Ratio	DF	P
SVL				
Island	120.9334	8.2940	2	0.0004
Species	0.2670	0.0366	1	0.8484
Sex	5540.4781	759.9654	1	< 0.0001
Island*Species	43.4015	2.9766	2	0.0534
Island*Sex	2.1497	0.1474	2	0.8630
Species*Sex	178.1029	24.4297	1	< 0.0001
Island*Species*Sex	10.2521	0.7031	2	0.4964
HL				
Island	1.1776	1.1828	2	0.3087
Species	77.0158	154.7033	1	< 0.0001
Sex	543.2220	1091.1820	1	< 0.0001
Island*Species	1.5074	1.5104	2	0.2227
Island*Sex	0.0919	0.0923	2	0.9118
Species*Sex	2.9495	5.9248	1	0.0159
Island*Species*Sex	0.4114	0.4132	2	0.6622

Table 3.4, continued.

Source	SS	F Ratio	DF	P
HW				
Island	1.9919	4.2677	2	0.0154
Species	14.1253	60.5270	1	< 0.0001
Sex	214.2015	917.8534	1	< 0.0001
Island*Species	0.9725	2.0836	2	0.1274
Island*Sex	1.1740	2.5154	2	0.0836
Species*Sex	4.1874	17.9432	1	< 0.0001
Island*Species*Sex	0.0359	0.0768	2	0.9261
HD				
Island	0.9329	2.9269	2	0.0560
Species	34.7952	218.3324	1	< 0.0001
Sex	120.2325	754.4322	1	< 0.0001
Island*Species	1.2482	3.9162	2	0.0216
Island*Sex	0.4705	1.4761	2	0.2312
Species*Sex	8.4948	53.3032	1	< 0.0001
Island*Species*Sex	0.2070	0.6495	2	0.5235

Table 3.5. Descriptive statistics for the number of prey items (n_{prey}) found in the stomach of each *Anolis carolinensis* (Ac) and *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Data are summarized four different ways: by 12 island-species-sex (ISS) groups, by four species-sex (SS) groups, by six island-species (IS) groups, and by the pooled data for each of the three islands. Simpson's dietary niche breadth index (B_{ind}) describes evenness in the proportion of prey items by numbers of individuals (P_{ind}) found in each of the 28 prey categories.

			Total	# Prey Items Per Stomach (n_{prey})			
Island	**Species**	**Sex**	**# Prey**	**Mean**	**S.E.**	**Range**	**B_{ind}**
SL6	Ac	F	111	12.33	2.89	4 - 30	5.74
		M	79	6.58	1.04	1 - 13	2.89
	As	F	62	6.20	1.08	1 - 11	3.20
		M	75	6.25	1.27	1 - 14	3.12
SL8	Ac	F	105	13.13	1.39	7 - 20	5.45
		M	84	10.50	1.04	6 - 14	3.85
	As	F	300	12.50	1.21	6 - 30	4.56
		M	264	9.43	1.10	1 - 22	2.59
SL13	Ac	F	90	9.00	1.86	3 - 19	6.19
		M	76	5.43	1.03	2 - 15	7.29
	As	F	329	14.95	1.82	5 - 37	3.84
		M	189	6.10	0.95	1 - 21	3.86
All	Ac	F	306	11.33	1.26	3 - 30	5.79
All	Ac	M	239	7.03	0.69	1 - 15	4.68
All	As	F	691	12.34	0.98	1 - 37	3.97
All	As	M	528	7.44	0.66	1 - 22	3.19
SL6	Ac	Both	190	9.05	1.48	1 - 30	4.39
	As	Both	137	6.23	0.83	1 - 14	3.24
SL8	Ac	Both	189	11.81	0.90	6 - 20	4.83
	As	Both	564	10.85	0.83	1 - 30	3.56
SL13	Ac	Both	166	6.92	1.02	2 - 19	7.11
	As	Both	518	9.77	1.11	1 - 37	3.93
SL6	Both	Both	327	7.60	0.85	1 - 30	3.98
SL8	Both	Both	753	11.07	0.67	1 - 30	4.00
SL13	Both	Both	684	8.88	0.84	1 - 37	4.56
All	Both	Both	1764	9.38	0.47	1 - 37	-

Table 3.6. Descriptive statistics for the number of prey taxa (n_{taxa}) found in the stomach of each *Anolis carolinensis* (Ac) and *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Data are summarized four different ways: by 12 island-species-sex (ISS) groups, by four species-sex (SS) groups, by six island-species (IS) groups, and by the pooled data for each of the three islands.

			Total	**# Prey Taxa Per Stomach (n_{taxa})**		
Island	**Species**	**Sex**	**# Taxa**	**Mean**	**S.E.**	**Range**
SL6	Ac	F	13	4.89	0.51	3 - 7
		M	13	2.92	0.36	1 - 5
	As	F	10	3.30	0.47	1 - 6
		M	11	2.58	0.34	1 - 5
SL8	Ac	F	11	4.63	0.50	3 - 7
		M	12	3.50	0.46	2 - 5
	As	F	17	5.17	0.36	3 - 9
		M	12	3.04	0.28	1 - 7
SL13	Ac	F	11	3.70	0.54	2 - 6
		M	17	3.50	0.42	1 - 6
	As	F	16	4.05	0.28	1 - 6
		M	16	3.16	0.25	1 - 6
All	Ac	F	13	4.37	0.31	2 - 7
All	Ac	M	17	3.29	0.24	1 - 6
All	As	F	17	4.39	0.23	1 - 9
All	As	M	16	3.01	0.16	1 - 7
SL6	Ac	Both	16	3.76	0.36	1 - 7
	As	Both	11	2.91	0.29	1 - 6
SL8	Ac	Both	16	4.06	0.36	2 - 7
	As	Both	18	4.02	0.27	1 - 9
SL13	Ac	Both	17	3.58	0.32	1 - 6
	As	Both	19	3.53	0.19	1 - 6
SL6	Both	Both	16	3.33	0.24	1 - 7
SL8	Both	Both	21	4.03	0.22	1 - 9
SL13	Both	Both	20	3.55	0.17	1 - 6
All 3	Both	Both	28	3.67	0.12	1 - 9

Table 3.7. Descriptive statistics for the mean volume (mm^3) of individual prey items (Mean V_{ind}) found in the stomach of each *Anolis carolinensis* (Ac) and *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Data are summarized four different ways: by 12 island-species-sex (ISS) groups, by four species-sex (SS) groups, by six island-species (IS) groups, and by the pooled data for each of the three islands.

				Mean Individual Prey Volume (Mean V_{ind})		
Island	**Species**	**Sex**	**n_{guts}**	**Mean**	**S.E.**	**Range**
SL6	Ac	F	9	9.39	2.53	4.07 - 28.00
		M	12	24.10	5.74	5.04 - 64.75
	As	F	10	28.02	13.02	2.88 - 135.83
		M	12	95.90	30.09	4.73 - 307.42
SL8	Ac	F	8	6.91	2.26	1.15 - 20.60
		M	8	18.07	4.97	3.61 - 49.47
	As	F	24	7.78	0.68	3.09 - 18.10
		M	28	65.99	23.52	4.75 - 603.20
SL13	Ac	F	10	9.34	2.66	1.81 - 25.33
		M	14	34.72	9.02	0.80 - 104.57
	As	F	22	7.87	1.24	1.30 - 26.81
		M	31	84.93	18.78	3.26 - 405.12
All	Ac	F	27	8.64	1.42	1.15 - 28.00
All	Ac	M	34	27.06	4.44	0.8 - 104.57
All	As	F	56	11.43	2.52	1.30 - 135.83
All	As	M	71	79.32	13.27	3.26 - 603.2
SL6	Ac	Both	21	17.80	3.75	4.07 - 64.75
	As	Both	22	65.04	18.61	2.88 - 307.42
SL8	Ac	Both	16	12.49	3.01	1.15 - 49.47
	As	Both	52	39.12	13.20	3.09 - 603.20
SL13	Ac	Both	24	24.15	5.90	0.80 - 104.57
	As	Both	53	52.95	12.12	1.30 - 405.12
SL6	Both	Both	43	41.97	10.25	2.88 - 307.42
SL8	Both	Both	68	32.86	10.19	1.15 - 603.20
SL13	Both	Both	77	43.97	8.65	0.80 - 405.12
All 3	Both	Both	188	39.49	5.61	0.80 - 603.20

Table 3.8. Descriptive statistics for the total volume (mm^3) of all prey items (V_{tot}) found in the stomach of each *Anolis carolinensis* (Ac) and *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Data are summarized four different ways: by 12 island-species-sex (ISS) groups, by four species-sex (SS) groups, by six island-species (IS) groups, and by the pooled data for each of the three islands. Simpson's dietary niche breadth index for volume (B_{vol}) describes the evenness in the proportion of total volumes of prey (P_{vol}) found in each of the 28 prey categories.

				Total Prey Volumes (V_{tot})			
Island	**Species**	**Sex**	**n_{guts}**	**Mean**	**S.E.**	**Range**	**B_{vol}**
SL6	Ac	F	9	89.98	14.80	23.96 - 151.81	5.06
		M	12	158.49	43.81	10.07 - 505.06	3.95
	As	F	10	97.23	19.96	11.53 - 186.60	3.04
		M	12	284.98	71.03	33.10 - 922.25	3.46
SL8	Ac	F	8	97.24	33.91	14.96 - 267.76	4.98
		M	8	181.76	50.72	43.34 - 494.74	4.20
	As	F	24	93.92	9.16	27.84 - 183.05	4.88
		M	28	301.73	45.47	14.24 - 964.35	2.57
SL13	Ac	F	10	81.43	26.64	5.44 - 285.21	3.62
		M	14	166.01	40.14	1.61 - 427.22	4.24
	As	F	22	97.29	12.17	26.09 - 216.01	6.13
		M	31	244.49	31.27	26.09 - 728.54	6.00
All	Ac	F	27	88.97	14.38	5.44 - 285.21	4.55
All	Ac	M	34	167.06	24.86	1.61 - 505.06	4.13
All	As	F	56	95.83	7.00	11.53 - 216.01	4.68
All	As	M	71	273.91	25.33	14.24 - 964.35	4.01
SL6	Ac	Both	21	129.13	26.43	10.07 - 505.06	4.80
	As	Both	22	199.64	43.99	11.53 - 922.25	4.24
SL8	Ac	Both	16	139.50	31.43	14.96 - 494.74	5.77
	As	Both	52	205.82	28.59	14.24 - 964.35	3.45
SL13	Ac	Both	24	130.77	26.88	1.61 - 427.22	5.43
	As	Both	53	183.39	21.36	26.09 - 728.54	7.05
SL6	Both	Both	43	165.20	26.21	10.07 - 922.25	4.82
SL8	Both	Both	68	190.21	23.23	14.24 - 964.35	4.18
SL13	Both	Both	77	166.99	17.05	1.61 - 728.54	8.02
All	Both	Both	188	174.98	12.42	1.61 - 964.35	-

Table 3.9. Summary data (mm) for anole snout-vent length (SVL), head length (HL), head width (HW), and head depth (HD) of 65 adult *Anolis carolinensis* (Ac) and 132 adult *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Data are summarized for the 12 island-species-sex (ISS) groups and four species-sex (SS) groups. Data were not tabulated by island-species (IS) group, by species, or by island, because both species were highly sexually dimorphic, such that the two sexes were not pooled for body analyses. Sample sizes are provided in Table 3.1.

			SVL		**HL**		**HW**		**HD**	
Island	**Species**	**Sex**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**
ISS groups:										
SL6	Ac	F	44.00	1.87	12.19	0.44	6.62	0.22	4.91	0.21
		M	53.07	3.08	16.07	0.89	8.53	0.51	6.23	0.52
	As	F	43.00	1.90	11.33	0.45	7.16	0.43	5.55	0.33
		M	57.14	2.96	14.71	0.73	9.64	0.46	7.97	0.49
SL8	Ac	F	44.75	3.06	12.44	0.68	6.91	0.50	5.13	0.26
		M	55.50	2.45	16.60	0.66	8.78	0.56	6.35	0.48
	As	F	42.24	2.40	11.26	0.57	7.01	0.44	5.53	0.32
		M	55.76	2.53	14.61	0.72	9.59	0.44	7.48	0.52
SL13	Ac	F	46.64	2.25	12.59	0.59	6.88	0.35	5.23	0.34
		M	55.87	2.29	16.45	0.77	9.10	0.49	6.51	0.37
	As	F	44.05	2.36	11.28	0.55	7.06	0.49	5.60	0.33
		M	58.13	3.57	14.80	0.90	9.94	0.61	7.83	0.80
SS groups:										
All	Ac	F	45.25	2.59	12.42	0.58	6.81	0.37	5.10	0.30
All		M	54.73	2.89	16.34	0.81	8.81	0.56	6.37	0.42
All	As	F	43.07	2.41	11.28	0.53	7.06	0.46	5.56	0.31
All		M	57.01	3.22	14.71	0.80	9.74	0.54	7.72	0.51

Table 3.10. Results of separate principal components analyses for the three dredge-spoil islands in Indian River Lagoon, using the four head variables (SVL, HL, HW, and HD) measured on 65 adult *Anolis carolinensis* and 132 adult *A. sagrei*. Note the similarities in eigenvectors across the three islands, especially for PC-1.

Island	Parameter	PC-1	PC-2	PC-3	PC-4
SL-6	Eigenvalues	3.4655	0.4435	0.0585	0.0326
	Percent of Variation	86.6378	11.0867	1.4614	0.8141
	Cum. Percent of Variation	86.6378	97.7245	99.1859	100.0000
	SVL Eigenvectors	0.5253	0.0712	-0.8392	-0.1215
	HL Eigenvectors	0.4553	0.7853	0.1308	0.2819
	HW Eigenvectors	0.5246	-0.2117	0.4136	-0.7134
	HD Eigenvectors	0.4916	-0.5775	0.1675	0.6299
SL-8	Eigenvalues	3.6099	0.3261	0.0392	0.0248
	Percent of Variation	90.2485	8.1527	0.9798	0.6190
	Cum. Percent of Variation	90.2485	98.4012	99.3810	100.0000
	SVL Eigenvectors	0.5159	0.2081	-0.7522	-0.3533
	HL Eigenvectors	0.4788	0.7091	0.3422	0.3883
	HW Eigenvectors	0.5136	-0.2885	0.5504	-0.5912
	HD Eigenvectors	0.4907	-0.6088	-0.1193	0.6118
SL-13	Eigenvalues	3.5726	0.3402	0.0516	0.0356
	Percent of Variation	89.3138	8.5051	1.2902	0.8908
	Cum. Percent of Variation	89.3138	97.8189	99.1092	100.0000
	SVL Eigenvectors	0.5186	0.1095	-0.7728	-0.3490
	HL Eigenvectors	0.4732	0.7500	0.2476	0.3902
	HW Eigenvectors	0.5170	-0.2119	0.5832	-0.5897
	HD Eigenvectors	0.4897	-0.6169	-0.0365	0.6150

Table 3.11. Results of the principal components analysis on the body variables SVL, HL, HW, and HD for 65 adult *Anolis carolinensis* and 132 adult *A. sagrei*, pooled over the three dredge-spoil islands in Indian River Lagoon from which they were collected.

Parameter	PC-1	PC-2	PC-3	PC-4
Eigenvalues	3.5467	0.3650	0.0528	0.0355
Percent of Variation	88.6669	9.1248	1.3202	0.8881
Cum. Percent of Variation	88.6669	97.7917	99.1119	100.0000
SVL Eigenvectors	0.5196	0.1271	-0.8073	-0.2494
HL Eigenvectors	0.4705	0.7503	0.3157	0.3407
HW Eigenvectors	0.5179	-0.2374	0.4980	-0.6538
HD Eigenvectors	0.4904	-0.6038	0.0266	0.6279

PCA formulas:

PC-1: 0.08*SVL + 0.23*HL + 0.38*HW + 0.43*HD + -12.96
PC-2: 0.02*SVL + 0.37*HL + -0.17*HW + -0.53*HD + -1.06
PC-3: -0.12*SVL + 0.15*HL + 0.37*HW + 0.02*HD + 0.62
PC-4: -0.04*SVL + 0.17*HL + -0.47*HW + 0.56*HD + -0.02

Table 3.12. Results of the principal components analysis on all four prey variables (n_{ind}, n_{taxa}, Mean V_{ind}, and V_{tot}) and all four body variables (SVL, HL, HW, and HD) for 65 adult *Anolis carolinensis* and 132 adult *A. sagrei*, pooled over the three dredge-spoil islands in Indian River Lagoon from which they were collected. Only the values of the first four principle components, which account for over 94 percent of the variation in the analysis, are presented.

Parameter	PC-1	PC-2	PC-3	PC-4
Eigenvalues	4.7221	1.3062	1.0068	0.5027
Percent of Variation	59.0258	16.3274	12.5847	6.2837
Cum. Percent of Variation	59.0258	75.3532	87.9379	94.2216
SVL Eigenvectors	0.43122	-0.02819	0.28455	-0.00153
HL Eigenvectors	0.38333	-0.08732	0.31996	0.07489
HW Eigenvectors	0.43050	0.01091	0.27067	0.00487
HD Eigenvectors	0.40825	0.06864	0.24741	-0.05209
n_{prey} Eigenvectors	-0.25556	0.51421	0.40262	-0.59232
n_{taxa} Eigenvectors	-0.24133	0.48534	0.35299	0.76137
MeanV_{ind} Eigenvectors	0.35377	0.27065	-0.52835	0.18547
V_{tot} Eigenvectors	0.25769	0.64306	-0.34108	-0.16347

PCA formulas:

PC-1: $0.06*SVL + 0.19*HL + 0.31*HW + 0.36*HD + -0.05*n_{prey} + -0.15*n^{taxa} + 0.02*MeanV_{ind} + 0.002*V_{tot} + -11.50$

PC-2: $-0.004*SVL + -0.04*HL + 0.01*HW + 0.06*HD + 0.09*n_{prey} + 0.31*n^{taxa} + 0.01*MeanV_{ind} + 0.01*V_{tot} + -4.41$

PC-3: $0.04*SVL + 0.16*HL + 0.20*HW + 0.22*HD + 0.07*n_{prey} + 0.22*n^{taxa} + -0.03*MeanV_{ind} + -0.003*V_{tot} + -6.12$

PC-4: $-0.001*SVL + 0.04*HL + 0.004*HW + -0.05*HD + -0.12*n_{prey} + 0.48*n^{taxa} + 0.01*MeanV_{ind} + 0.001*V_{tot} + -0.53$

Table 3.13. Comparison matrix of the six possible contrasts of Pianka's dietary overlap index values calculated from the proportion of the number of prey items contained in each of the 28 prey categories (P_{ind}) found in the stomach of each *Anolis carolinensis* (Ac) and *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Index values for species-sex (SS) overlap contrasts within each island are followed by the mean index value pooled over the three islands (in parentheses). Note the consistently high overlap values for every overlap contrast, as compared with the values in Table 3.14.

Group	Island	AcF	AcM	AsF	As (all)
AcM	SL6	0.91	-	-	-
	SL8	0.92	-	-	-
	SL13	0.87	-	-	-
	Mean	(0.90)	-	-	-
AsF	SL6	0.83	0.94	-	-
	SL8	0.90	0.98	-	-
	SL13	0.84	0.88	-	-
	Mean	(0.86)	(0.93)	-	-
AsM	SL6	0.86	0.96	0.95	-
	SL8	0.75	0.89	0.93	-
	SL13	0.85	0.93	0.96	-
	Mean	(0.82)	(0.93)	(0.95)	-
Ac (all)	SL6	-	-	-	0.93
	SL8	-	-	-	0.91
	SL13	-	-	-	0.90
	Mean	-	-	-	(0.91)

Table 3.14. Comparison matrix of the six possible contrasts of Pianka's dietary overlap index values calculated from the proportion of the total volume of all the prey items contained in each of the 28 prey categories (P_{vol}) found in the stomach of each *Anolis carolinensis* (Ac) and *A. sagrei* (As) collected from three dredge-spoil islands in Indian River Lagoon. M = male, F = female. Index values for each species-sex (SS) overlap contrast within each island are followed by the mean index value pooled over the three islands (in parentheses). Note that the values for these overlap contrasts are smaller and much more variable than those in Table 13.

Group	Island	AcF	AcM	AsF	As (all)
AcM	SL6	0.71	-	-	-
	SL8	0.48	-	-	-
	SL13	0.37	-	-	-
	Mean	(0.52)	-	-	-
AsF	SL6	0.72	0.68	-	-
	SL8	0.67	0.76	-	-
	SL13	0.37	0.24	-	-
	Mean	(0.58)	(0.56)	-	-
AsM	SL6	0.62	0.79	0.42	-
	SL8	0.78	0.26	0.36	-
	SL13	0.12	0.71	0.58	-
	Mean	(0.51)	(0.58)	(0.45)	-
Ac (all)	SL6	-	-	-	0.87
	SL8	-	-	-	0.60
	SL13	-	-	-	0.61
	Mean	-	-	-	(0.69)

Table 4.1. The names and growth forms of the live vegetation observed on the seven dredge-spoil islands in this study in Mosquito Lagoon between 1994 and 1998. Taxonomy follows Bell and Taylor (1982) and Taylor (1992).

Common name	**Scientific name**	**Growth form**
Cabbage palm	*Sabal palmetto*	canopy palm
Southern red cedar	*Juniperus silicicola*	canopy tree, shrub
Dahoon holly	*Ilex cassine*	canopy tree, shrub
Red mangrove	*Rhizophora mangle*	canopy tree, shrub
White mangrove	*Laguncularia racemosa*	canopy tree, shrub
Black mangrove	*Avicennia germinans*	canopy tree, shrub
Buttonwood	*Conocarpus erecta*	woody shrub
Saw palmetto	*Serenoa repens*	shrubby palm
Brazilian pepper	*Schinus terebinthifolius*	woody shrub
Salt bush	*Baccharis halimifolia*	woody shrub
False willow	*Baccharis angustifolia*	woody shrub
Wax myrtle	*Myrica cerifera*	woody shrub
Bamboo vine	*Smilax laurifolia*	climbing vine
Oxeye daisy	*Borrichia frutescens*	erect herb
Marsh fleabane	*Pluchea* spp.	erect herb
Marsh elders	*Iva* spp.	erect herb
Marsh mallow	*Kosteletzkya* spp.	erect herb
Sea blites	*Suaeda* spp.	erect herb
Glassworts	*Salicornia* spp.	erect herb
Beach carpet	*Philoxerus vermicularis*	mat-forming herb
Sea purslane	*Sesuvium* spp.	mat-forming herb
Sea blites	*Batis maritima*	mat-forming herb
Cord grass	*Spartina alterniflora*	marsh grass
Cord grass	*Spartina bakeri*	marsh grass
Black rush	*Juncus roemerianus*	marsh grass
Saltgrass	*Distichlis spicata*	marsh grass
Shore grass	*Monanthochloe littoralis*	marsh grass
Saltmarsh bulrushes	*Scirpus* spp.	marsh sedge
Umbrella sedge	*Cyperus* spp.	marsh sedge

Table 4.2. Selected island landscape parameters and indices for the seven dredge-spoil islands in Mosquito Lagoon used in this study, generated from the raster version of the program FRAGSTATS (McGarigal and Marks 1995). A list of 19 island-wide landscape parameters is followed by individual lists of 14 patch parameters for each habitat type. Edge and core parameters were calculated by FRAGSTATS using a fixed 2 m edge width. Definitions for each parameter and index follow the table.

Parameter or Index	**ST**	**SC**	**MT**	**MC**	**LT**	**LC**	**L2C**
Island-Wide Landscape Parameters and Indices							
Total island area (ha)	0.158	0.100	0.170	0.153	0.890	0.935	0.931
Total vegetated area (ha)	0.158	0.100	0.170	0.153	0.528	0.481	0.495
Total number of patches	2	2	4	2	10	14	10
Mean patch size (ha)	0.079	0.050	0.043	0.077	0.089	0.067	0.093
Patch size SD (ha)	0.042	0.028	0.041	0.001	0.143	0.149	0.173
Largest patch index (%)	76.3	78.63	55.63	50.9	54.3	62.6	65.1
Number of core areas	3	2	4	2	17	10	13
Total core area (ha)	0.100	0.064	0.101	0.106	0.618	0.696	0.694
Total core area index (%)	62.9	44.75	59.2	69.2	69.4	74.5	74.6
Mean core area index (%)	62.5	48.38	29.4	69.3	29.2	24.5	36.1
Total edge (m)	326	322	390	280	1578	1310	1166
Total edge area (ha)	0.065	0.064	0.078	0.056	0.316	0.262	0.233
Landscape shape index	2.048	2.556	2.180	1.788	4.181	3.387	3.021
Mean shape index	1.781	1.998	1.928	1.640	2.111	1.738	2.027
Mean fractal dimension	1.159	1.185	1.218	1.140	1.213	1.166	1.239
Shannon's diversity index	0.548	0.519	0.687	0.693	1.006	0.913	0.880
Simpson's diversity index	0.362	0.336	0.494	0.500	0.601	0.533	0.513
Shannon's evenness index	0.791	0.749	0.991	1.000	0.916	0.831	0.801
Simpson's evenness index	0.724	0.672	0.987	1.000	0.901	0.800	0.769
Landscape contagion (%)	44.7	45.3	25.5	33.9	39.0	44.5	46.8

Table 4.2, continued.

Parameter or Index	ST	SC	MT	MC	LT	LC	L2C
Forest Habitat Parameters and Indices							
Number of patches	1	1	1	1	4	2	3
Total forest area (ha)	0.038	0.021	0.095	0.075	0.205	0.157	0.199
Forest veg. area (ha)	0.038	0.021	0.095	0.075	0.205	0.157	0.199
Percent of landscape	23.7	21.4	55.6	49.1	23.0	16.8	21.4
Mean patch size (ha)	-	-	-	-	0.051	0.078	0.066
Patch size SD (ha)	-	-	-	-	0.055	0.047	0.009
Number of core areas	1	1	1	1	6	2	4
Total core area (ha)	0.023	0.012	0.070	0.057	0.112	0.091	0.111
Total core area index (%)	61.7	54.7	73.8	76.1	54.7	57.9	55.8
Mean core area index (%)	-	-	-	-	31.1	57.1	55.9
Core percent of landscape	14.6	11.7	41.1	37.3	12.6	9.7	11.9
Total edge (m)	100	68	180	136	708	492	656
Total edge area (ha)	0.020	0.014	0.036	0.027	0.142	0.098	0.131
Mean shape index	1.289	1.168	1.462	1.240	1.900	2.130	2.119
Mean fractal dimension	1.086	1.058	1.111	1.065	1.180	1.217	1.230
Shrub-Marsh Habitat Parameters and Indices							
Number of patches	1	1	3	1	5	10	6
Total shrub-marsh area (ha)	0.121	0.078	0.076	0.078	0.202	0.188	0.126
Shrub-marsh veg. area (ha)	0.121	0.078	0.076	0.078	0.202	0.188	0.126
Percent of island landscape	76.3	78.6	44.4	50.9	22.7	20.1	13.5
Mean patch size (ha)	-	-	-	-	0.040	0.019	0.021
Patch size SD (ha)	-	-	-	-	0.063	0.032	0.020
Number of core areas	1	1	3	1	10	6	8

Table 4.2, continued.

Parameter or Index	ST	SC	MT	MC	LT	LC	L2C
Total core area (ha)	0.076	0.033	0.031	0.049	0.074	0.086	0.041
Total core area index (%)	63.2	42.05	40.7	62.6	36.4	45.6	32.4
Mean core area index (%)	-	-	-	-	15.7	12.3	17.3
Core percent of landscape	48.2	33.1	18.1	31.8	8.3	9.2	4.4
Total edge (m)	316	316	384	228	1080	972	712
Total edge area (ha)	0.063	0.063	0.077	0.046	0.216	0.194	0.142
Mean shape index	2.273	2.829	2.309	2.041	2.401	1.721	2.075
Mean fractal dimension	1.231	1.312	1.432	1.214	1.262	1.165	1.268
Open-Xeric Habitat Parameters and Indices							
Number of patches	-	-	-	-	1	2	1
Total open-xeric area (ha)	-	-	-	-	0.483	0.590	0.606
Open-xeric veg. area (ha)	-	-	-	-	0.121	0.136	0.170
Percent of island landscape	-	-	-	-	54.3	63.1	65.1
Mean patch size (ha)	-	-	-	-	NA	0.295	NA
Patch size SD (ha)	-	-	-	-	NA	0.290	NA
Number of core areas	-	-	-	-	1	2	1
Total core area (ha)	-	-	-	-	0.432	0.520	0.542
Total core area index (%)	-	-	-	-	89.4	88.1	89.6
Mean core area index (%)	-	-	-	-	NA	52.7	NA
Core percent of landscape	-	-	-	-	48.5	55.6	58.3
Total edge (m)	-	-	-	-	420	516	456
Total edge area (ha)	-	-	-	-	0.084	0.103	0.091
Mean shape index	-	-	-	-	1.511	1.434	1.465
Mean fractal dimension	-	-	-	-	1.097	1.119	1.088

Table 4.2, continued.

Island-wide landscape parameters and indices (all patches of all habitat types):

***Total island area* (ha):** the total area of the island landward of mean high tide.
***Total vegetated (veg.) area* (ha):** the total area of the island above mean high tide occupied by live, rooted plant species exhibiting spacing closer than 1 m.
***Total number of patches*:** the total number of patches of all habitat types.
***Mean patch size* (ha):** the average size of all habitat patches of all habitat types.
***Patch size SD*:** the standard deviation of all habitat patches of all habitat types.
***Largest patch index* (%):** the percent of the island occupied by the largest habitat patch.
***Number of core areas*:** the number of core areas of all habitat types.
***Total core area* (ha):** the sum of the areas of all core areas of all habitat types.
***Total core area index* (%):** the percent of the island that is core area, of all habitats.
***Mean core area index* (%):** the average percent of a patch in the landscape that is core.
***Total edge* (m):** the sum of all the edge lengths of all habitat types and shorelines.
***Total edge area* (ha):** the total area of all edges, assuming a 2 m wide edge. This calculation (total edge x 2) was done by hand, not in FRAGSTATS.
***Landscape shape index*:** the shape index for all internal and external edges calculated together and adjusted by a square standard. Ranges between 1 (a single square) and a limitless value (many irregular edges within and surrounding the island).
***Mean shape index*:** the average shape index of all the individual habitat patches.
***Mean fractal dimension*:** the average fractal dimension for all individual patches.
***Shannon's diversity index*:** increases (from 0, no limit) as the number of habitat types increase or proportional distribution of areas becomes more equitable, or both.
***Simpson's diversity index*:** increases from 0 as in Shannon's index, but limit is 1.
***Shannon's evenness index*:** observed Shannon's diversity value measured against the maximum value that could be obtained if all habitat patches were found in equal proportions. Ranges from 0 (one patch) to 1 (perfectly even distribution of patches).
***Simpson's evenness index*:** observed Simpson's diversity value measured against the maximum value that could be obtained if all habitat patches were found in equal proportions. Ranges from 0 (one patch) to 1 (perfectly even distribution of patches).
***Landscape contagion* (%):** like evenness indices, but assesses patch interspersion relative to the maximum possible interspersion of the patch types in the landscape. Ranges from 0 when certain patch types are found only near certain other patch types (a very uneven distribution of adjacencies) to 100 when all patch types are found adjacent to all other patch types with equal frequency.

Table 4.2, continued.

Individual habitat parameters and indices (all patches within one habitat type):

Number of patches: the number of individual patches of a given habitat type.
Total habitat area (ha): the total area of all patches of a given habitat type.
Habitat vegetated (veg.) area (ha): the total area of the habitat occupied by live, rooted plant species exhibiting spacing closer than 1 m. Values for forest and shrub-marsh habitats equal their total habitat areas, but values for open-xeric habitat reflect the fact that, on islands LT, LC, and L2C, only 25, 23, and 28 percent of the open-xeric habitat was occupied by live plants, respectively. Values sum to *total vegetated area* (ha).
Percent of landscape: the percentage of a given habitat type on the island.
Mean patch size (ha): the average size of the patches of a given habitat type.
Patch size SD (ha): the standard deviation of the patch sizes of a given type.
Number of core areas: the number of separate core areas of a given habitat type, where core habitat is defined as the area inside the pre-defined 2 m wide edge.
***Total core area* (ha):** the sum of the areas of all the core areas of a given habitat type.
***Total core area index* (%):** the total percentage of a habitat type that is core area.
***Mean core area index* (%):** the average percentage of a habitat type that is core area.
***Core percent of landscape*:** the percent of the island landscape that is comprised of core area of the given habitat.
***Total edge* (m):** the total length of the edges between all patches of the given habitat type and all adjacent habitats, including interior edges and the island shoreline.
***Total edge area* (ha):** the total area of the edge of a given habitat, assuming a 2 m wide edge. This calculation (total edge x 2) was done by hand, not in FRAGSTATS.
***Mean shape index*:** the average shape index of all the patches of a given habitat type, where the shape index is a measure of divergence from a "square standard" (in raster) and ranges from 1 (a square patch) to a limitless number (a very irregular patch).
***Mean fractal dimension*:** indicates departure in the patch perimeter from euclidean geometry, and ranges from 1 (simple shapes) to 2 (highly convoluted shapes).

Table 4.3. Lists of the vertebrates and most common invertebrates observed on the dredge-spoil islands in Mosquito Lagoon between 1994 and 1998.

Common name	Taxonomy and/or scientific name
Amphibians:	
Green treefrog	*Hyla cinerea*
Squirrel treefrog	*Hyla squirella*
Cuban treefrog	*Osteopilus septentrionalis*
Reptiles:	
Gopher tortoise	*Gopherus polyphemus*
Diamondback terrapin	*Malaclemys terrapin tequesta*
Florida box turtle	*Terrapene carolina bauri*
Green anole	*Anolis carolinensis*
Brown anole	*Anolis sagrei*
Indo-Pacific gecko	*Hemidactylus garnotii*
Ground skink	*Scincella lateralis*
Southeastern five-lined skink	*Eumeces inexpectatus*
Six-lined racerunner	*Cnemidophorus sexlineatus*
Black racer	*Coluber constrictor*
Corn snake	*Elaphe guttata guttata*
Yellow rat snake	*Elaphe obsoleta quadrivittata*
Eastern garter snake	*Thamnophis sirtalis sirtalis*
Peninsula ribbon snake	*Thamnophis sauritus sackenii*
Atlantic salt marsh water snake	*Nerodia clarki taeniata*
Eastern diamondback rattlesnake	*Crotalus adamanteus*
Dusky pygmy rattlesnake	*Sistrurus miliarius barbouri*
Mammals:	
Racoon	*Procyon lotor*
Opossum	*Didelphis marsupialis*
Marsh rabbit	*Sylvilagus palustris*
House mouse	*Mus musculus*
Florida mouse	*Podomys floridanus*
Southeastern beach mouse	*Peromyscus polionotus niveiventris*
Hispid cotton rat	*Sigmodon hispidus*

Table 4.3, continued.

Common name	Taxonomy and/or scientific name
Birds:	
Double-crested cormorant	*Phalacrocorax auritus*
American anhinga	*Anhinga anhinga*
Wood duck	*Aix sponsa*
Brown pelican	*Pelicanus occidentalis*
Laughing gull	*Larus atricilla*
Miscellaneous terns	*Sterna* sp.
Black skimmer	*Rhynchops niger*
Great blue heron	*Ardea herodias*
Tri-color heron	*Egretta tricolor*
Great egret	*Casmerodius albus*
Snowy egret	*Egretta thula*
Reddish egret	*Dichromanassa rufescens*
White ibis	*Eudocimus albus*
Glossy ibis	*Plegadis falcinellus*
Black-necked stilt	*Himantopus mexicanus*
Plovers	*Charadrius* sp.
Sandpipers	*Calidris* sp.
Osprey	*Pandion haliaetus*
Red shouldered hawk	*Buteo lineatus*
Southeastern American kestrel	*Falco sparverius paulus*
Turkey vulture	*Cathartes aura*
Black vulture	*Coragyps atratus*
Belted kingfisher	*Megaceryle alcyon*
Red-bellied woodpecker	*Melanerpes carolinus*
Great crested flycatcher	*Myiarchus crinitus*
Fish crow	*Corvus ossifragus*
Blue jay	*Cyanocitta cristata*
Marsh wren	*Cistothorus palustris*
Northern mockingbird	*Mimus polyglottos*
Common yellowthroat	*Geothlypis trichas*
Northern parula warbler	*Parula americana*
Yellow-rumped warbler	*Dendroica coronata*
Red-winged blackbird	*Agelaius phoeniceus*
Boat-tailed grackle	*Quiscalus major*
Seaside sparrow	*Ammospiza maritima* spp.

Table 4.3, continued.

Common name	Taxonomy and/or scientific name
Arachnida:	
Golden silk spider	Araneidae: *Nephilia clavipes*
Spined micrathena	Araneidae: *Micrathena gracilis*
Black and yellow argiope	Araneidae: *Argiope aurantia*
Orchard spider	Tetragnathidae: *Leucauge* sp.
Jumping spider	Salticidae: *Phidippus audax*
Jumping spider	Salticidae: *Phidippus regius*
Funnel weaver	Agelenidae
Wolf spider	Lycosidae
Crab spider	Thomisidae
Insecta:	
Springtails	Collembola
Darner dragonflies	Odonata: Aeshnidae: *Anax* sp.
Skimmer dragonflies	Odonata: Libellulidae: *Libellula* sp.
Black-winged damselflies	Odonata: Calopterygidae: *Calopteryx maculata*
Cockroach	Orthoptera: Blattidae: *Blattus* sp.
Tree crickets	Orthoptera: Gryllidae: Oecanthinae
Ground crickets	Orthoptera: Gryllidae: Gryllinae
Mole crickets	Orthoptera: Gryllotalpidae
Grasshoppers	Orthoptera: Acrididae
Katydids	Orthoptera: Tettigoniidae
Termites	Isoptera
Earwigs	Dermaptera
Plant bugs	Hemiptera: Miridae
Stink bugs	Hemiptera: Pentatomidae
Leafhoppers	Homoptera: Cicadellidae
Planthoppers	Homoptera: Fulgoridae
Green plant hopper	Homoptera: Flatidae: *Anormenis septentrionalis*
Cicada	Homoptera: Cicadidae
Aphids	Homoptera: Aphididae
Scale insects	Homoptera: Coccidae

Table 4.3, continued.

Common name	Taxonomy and/or scientific name
Antlion	Neuroptera: Myrmeliontidae
Mantidfly	Neuroptera: Mantispidae
Lacewings	Neuroptera: Chrysopidae
Rove beetles	Coleoptera: Staphylinidae
Click beetles	Coleoptera: Elateroidae
Ground beetles	Coleoptera: Carabidae
Long-horned beetles	Coleoptera: Cerambycidae
Leaf beetles	Coleoptera: Chrysomelidae
Tortoise beetle	Coleoptera: Chrysomelidae: *Hemisphaerata cyanea*
Weevils (snout beetles)	Coleoptera: Curculionidae
Moths	Lepidoptera: Saturnidae
Skipper butterflies	Lepidoptera: Hesperiidae
Swallowtail butterflies	Lepidoptera: Papilionidae
Crane flies	Diptera: Tipulidae
Biting midges (no-see-ums)	Diptera: Ceratopogonidae: *Culicoides* sp.
Robber flies	Diptera: Asilidae
Horse flies and deer flies	Diptera: Tabanidae
Fruit flies	Diptera: Tephritidae
House flies	Diptera: Muscidae
Flesh flies	Diptera: Sarcophagidae
Salt marsh mosquito	Diptera: Culicidae: *Aedes* sp.
Spider wasps	Hymenoptera: Pompilidae
Cicada killer wasp	Hymenoptera: Sphecidae: *Sphecius speciosus*
Baldfaced hornet	Hymenoptera: Vespidae: *Vespula maculata*
Velvet ant	Hymenoptera: Mutillidae: *Dasymutilla occidentalis*
Ants	Hymenoptera: Formicidae
Red imported fire ant	Hymenoptera: Formicidae: *Solenopsis invicta*
Crustacea:	
Fiddler crabs	Decapoda: *Uca minor*
Scuds (side-swimmers)	Amphipoda: *Gammarus annulatus*
Beach roach (rock slater)	Isopoda: Ligiidae: *Ligia* sp.
Pillbugs (sowbugs)	Isopoda: Armadillidiidae: *Armadillidum vulgare*

Table 4.4. Summarized capture data for 521 adult *Anolis sagrei* marked and recaptured on island ST. A total of 28 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 33 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.158 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare. In 1995, the size of the donor population was known.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	40	90	163	228
Lizards from previous years	-	8	5	18
Total marked lizards	40	98	168	246
Number of recaptures	-	173	177	121
Total lizard captures	40	271	345	367
Population estimate (Mth)	-	129	287	494
Standard error of estimate	-	11.10	29.52	51.29
Average p-hat	-	0.20	0.10	0.07
Confidence interval	-	114 - 159	242 - 360	412 - 616
Lizard density (per ha)	253	816	1816	3127
Density range (per ha)	-	722 - 1006	1532 - 2278	2608 - 3899
Number of sampling days	-	11	14	8
Number of CMR sessions	-	8	12	8

Table 4.5. Summarized capture data for 205 adult *Anolis carolinensis* marked and recaptured on island ST. A total of 37 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 43 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.158 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	87	52	49	17
Lizards from previous years	-	20	7	6
Total marked lizards	87	72	56	23
Number of recaptures	46	44	46	14
Total lizard captures	133	116	102	37
Population estimate (Mth)	182	127	109	48
Standard error of estimate	33.23	21.21	22.87	16.95
Average p-hat	0.10	0.10	0.08	0.09
Confidence interval	136 - 272	98 - 186	80 - 175	30 - 106
Lizard density (per ha)	1152	804	690	304
Density range (per ha)	861 - 1722	620 - 1177	506 - 1108	190 - 671
Number of sampling days	10	11	14	8
Number of CMR sessions	8	9	12	8

Table 4.6. Summarized capture data for 130 adult *Anolis carolinensis* marked and recaptured on island SC. A total of 18 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 21 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.099 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	32	34	34	30
Lizards from previous years	-	4	6	13
Total marked lizards	32	38	40	43
Number of recaptures	9	7	21	31
Total lizard captures	41	45	61	74
Population estimate (Mth)	68	91	73	74
Standard error of estimate	34.44	28.75	17.93	16.61
Average p-hat	0.20	0.12	0.17	0.16
Confidence interval	39 - 206	58 - 181	52 - 129	54 - 126
Lizard density (per ha)	687	919	737	747
Density range (per ha)	394 - 2081	586 - 1828	525 - 1303	545 - 1273
Number of sampling days	3	4	7	7
Number of CMR sessions	3	4	5	6

Table 4.7. Summarized capture data for 574 adult *Anolis sagrei* marked and recaptured on island MT. A total of 17 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 19 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.170 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare. In 1995, the size of the brown anole donor population was known.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	40	97	294	143
Lizards from previous years	-	5	12	54
Total marked lizards	40	102	306	197
Number of recaptures	-	72	179	22
Total lizard captures	40	174	485	219
Population estimate (Mth)	-	183	559	926
Standard error of estimate	-	26.41	48.05	242.58
Average p-hat	-	0.19	0.11	0.06
Confidence interval	-	146 - 253	481 - 672	583 - 1573
Lizard density (per ha)	235	1076	3288	5447
Density range (per ha)	-	859 - 1488	2829 - 3953	3429 - 9253
Number of sampling days	-	5	9	5
Number of CMR sessions	-	5	8	4

Table 4.8. Summarized capture data for 209 adult *Anolis carolinensis* marked and recaptured on island MT. A total of 23 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 23 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.170 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	92	91	17	9
Lizards from previous years	-	8	3	2
Total marked lizards	92	99	20	11
Number of recaptures	17	28	5	2
Total lizard captures	109	127	25	13
Population estimate (Mth)	338	360	58	23
Standard error of estimate	99.23	94.39	29.84	13.93
Average p-hat	0.05	0.07	0.05	0.18
Confidence interval	207 - 618	230 - 618	30 - 167	13 - 83
Lizard density (per ha)	1988	2118	341	135
Density range (per ha)	1218 - 3635	1353 - 3635	176 - 982	76 - 488
Number of sampling days	7	5	8	3
Number of CMR sessions	7	5	8	3

Table 4.9. Summarized capture data for 300 adult *Anolis carolinensis* marked and recaptured on island MC. A total of 16 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 16 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.153 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	69	91	79	61
Lizards from previous years	-	3	6	15
Total marked lizards	69	94	85	76
Number of recaptures	15	21	18	33
Total lizard captures	84	115	103	109
Population estimate (Mth)	220	248	196	182
Standard error of estimate	74.84	65.82	38.85	44.19
Average p-hat	0.10	0.12	0.13	0.15
Confidence interval	129 - 447	163 - 437	142 - 301	125 - 308
Lizard density (per ha)	1438	1621	1281	1190
Density range (per ha)	843 - 2922	1065 - 2856	928 - 1967	817 - 2013
Number of sampling days	4	3	4	5
Number of CMR sessions	4	4	4	4

Table 4.10. Summarized capture data for 672 adult *Anolis sagrei* marked and recaptured on island LT. A total of 21 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 26 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.528 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare. In 1995, the size of the brown anole donor population was known.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	80	41	222	329
Lizards from previous years	-	2	6	24
Total marked lizards	80	43	228	353
Number of recaptures	-	8	96	57
Total lizard captures	80	51	324	410
Population estimate (Mth)	-	151	511	1328
Standard error of estimate	-	69.52	65.04	191.47
Average p-hat	-	0.08	0.08	0.04
Confidence interval	-	77 - 385	409 - 669	1019 - 1780
Lizard density (per ha)	152	286	968	2515
Density range (per ha)	-	146 - 729	775 - 1267	1930 - 3371
Number of sampling days	-	4	12	10
Number of CMR sessions	-	4	8	9

Table 4.11. Summarized capture data for 305 adult *Anolis carolinensis* marked and recaptured on island LT. A total of 11 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 30 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.528 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	88	88	73	56
Lizards from previous years	-	5	8	13
Total marked lizards	88	93	81	69
Number of recaptures	12	10	14	14
Total lizard captures	96	103	95	83
Population estimate (Mth)	634	546	219	176
Standard error of estimate	255.21	227.06	49.53	40.22
Average p-hat	0.05	0.06	0.09	0.9
Confidence interval	317 - 1393	272 - 1238	151 - 354	121 - 287
Lizard density (per ha)	1201	1034	415	333
Density range (per ha)	600 - 2638	515 - 2345	286 - 670	229 - 544
Number of sampling days	5	4	11	10
Number of CMR sessions	3	3	5	5

Table 4.12. Summarized capture data for 567 adult *Anolis carolinensis* marked and recaptured on island LC. A total of 24 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 41 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.481 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	117	204	151	95
Lizards from previous years	-	22	27	39
Total marked lizards	117	226	178	134
Number of recaptures	18	125	47	37
Total lizard captures	135	351	225	171
Population estimate (Mth)	488	461	569	335
Standard error of estimate	144.93	50.58	106.19	66.16
Average p-hat	0.06	0.08	0.08	0.10
Confidence interval	294 - 894	381 - 583	410 - 837	241 - 511
Lizard density (per ha)	1015	958	1183	696
Density range (per ha)	611 - 1859	792 - 1212	852 - 1740	501 - 1062
Number of sampling days	12	10	13	6
Number of CMR sessions	5	9	5	5

Table 4.13. Summarized capture data for 594 adult *Anolis sagrei* marked and recaptured on island L2C. A total of 22 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 41 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.495 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	100	157	182	155
Lizards from previous years	-	2	13	16
Total marked lizards	100	159	195	171
Number of recaptures	28	98	82	6
Total lizard captures	128	257	277	185
Population estimate (Mth)	256	275	422	753
Standard error of estimate	57.26	31.01	59.90	185.34
Average p-hat	0.10	0.12	0.11	0.07
Confidence interval	178 - 413	228 - 353	336 - 560	487 - 1281
Lizard density (per ha)	518	556	853	1521
Density range (per ha)	360 - 834	461 - 713	679 - 1131	984 - 2588
Number of sampling days	15	12	11	5
Number of CMR sessions	5	8	6	3

Table 4.14. Summarized capture data for 346 adult *Anolis carolinensis* marked and recaptured on island L2C. A total of 22 summertime (May - August) capture-mark-recapture (CMR) sessions were conducted over 41 days between 1995 and 1998. Population estimates and 95 percent confidence intervals were generated by program CAPTURE (Model Mth) and divided by vegetated area of the island (0.495 ha) to obtain lizard densities and density ranges based on the number of lizards per hectare.

Parameter	**1995**	**1996**	**1997**	**1998**
Newly marked lizards	77	161	48	60
Lizards from previous years	-	9	9	7
Total marked lizards	77	170	57	67
Number of recaptures	9	82	16	7
Total lizard captures	86	252	73	74
Population estimate (Mth)	294	324	145	236
Standard error of estimate	87.43	39.74	41.55	80.26
Average p-hat	0.06	0.10	0.10	0.11
Confidence interval	178 - 541	263 - 423	93 - 269	136 - 476
Lizard density (per ha)	594	655	293	477
Density range (per ha)	360 - 1093	531 - 855	188 - 543	275 - 962
Number of sampling days	15	12	11	5
Number of CMR sessions	5	8	6	3

Table 4.15. Median perch height (PH) values summarized by year for 1,657 *Anolis carolinensis* found in Mosquito Lagoon on six experimental dredge-spoil islands, and 594 found on an additional island containing both species (a two-species "control").

	1995	**1996**	**1997**	**1998**
Females				
Small Treatment (ST)	45	118	47	81
Medium Treatment (MT)	69	68.5	105	116
Large Treatment (LT)	53	80	115	91.5
Small Control (SC)	66	54	64.5	48.5
Medium Control (MC)	35	26	28.5	22
Large Control (LC)	28.5	37	25	41.5
Large 2-sp. Control (L2C)	75	78.5	70	137
Males				
Small Treatment (ST)	79.5	101	96.5	144
Medium Treatment (MT)	82	92	116	152
Large Treatment (LT)	75	113.5	122.5	160.5
Small Control (SC)	73	58.5	83	64
Medium Control (MC)	67	69	66.5	65
Large Control (LC)	61	59.5	77	62
Large 2-sp. Control (L2C)	83	81	102	114.5

Table 4.16. Median perch diameter (Pdi) values summarized by year for 1,657 *Anolis carolinensis* found in Mosquito Lagoon on six experimental dredge-spoil islands, and 594 found on an additional island containing both species (a two-species "control").

	1995	1996	1997	1998
Females				
Small Treatment (ST)	4.4	1.7	1.7	2.2
Medium Treatment (MT)	2.8	1.5	2	1.5
Large Treatment (LT)	4.2	2	3	1.6
Small Control (SC)	2	1.2	0.8	1.4
Medium Control (MC)	2.1	3.8	2	1.2
Large Control (LC)	4.5	3.3	2.4	1.9
Large 2-sp. Control (L2C)	2.3	2.2	2.1	1.2
Males				
Small Treatment (ST)	2.9	2.2	1.5	1.8
Medium Treatment (MT)	3.2	1.9	2.8	2.3
Large Treatment (LT)	4	2.2	3	2.8
Small Control (SC)	2	1.8	1	2
Medium Control (MC)	5	6.2	4	3.5
Large Control (LC)	3	2.5	2.8	2.2
Large 2-sp. Control (L2C)	3	2.8	2.2	1.8

Table 4.17. Pooled means and standard deviations for the number of individual arthropods and the number of arthropod orders captured in 144 sticky-traps placed on three of the large dredge-spoil islands in Mosquito Lagoon (LT, LC, and L2C). Traps were placed in plants of two different species (cabbage palm and cedar), within two different habitats (forested and open-xeric) and at two different heights (ground and two meters above ground). Traps were set in the morning and left for a 12-hours during a single day in June 1998.

Factor Type	Factor Level	# Traps	Mean # Individuals	S.D. # Individuals	Mean # Orders	S.D. # Orders
Island	LT	48	8.38	7.63	2.50	1.34
	LC	48	7.75	12.23	2.65	1.59
	L2C	48	11.52	8.73	2.79	1.22
Plant	Cabbage Palm	72	10.29	11.65	2.54	1.27
	Cedar	72	8.14	7.44	2.75	1.50
Location	Forested	72	11.31	11.68	2.97	1.44
	Open-Xeric	72	7.13	6.94	2.32	1.25
Height	Ground	72	13.35	11.89	3.32	1.41
	2 meters	72	5.08	4.17	1.97	0.98

Table 4.18. Results of a four-way MANOVA on arthropod data collected from three dredge-spoil islands in Mosquito Lagoon. This analysis tested the effects of island (LT, LC, and L2C), plant species (cedar and cabbage palm), trap height (ground and 2 m above ground), and trap location (forested and open-xeric habitat) on the number of individual arthropods and the number of arthropod taxa (orders) captured by 48 sticky-traps placed around each island during a single 12-hour period in 1998.

Source of Variation	**Pillai's Trace**	**F Ratio**	**DF Num.**	**DF Den.**	**P Value**
Island	0.0755	2.4485	2	60	0.0950
Location	0.1158	7.8580	1	60	0.0068
Plant	0.0336	2.0837	1	60	0.1541
Height	0.3739	35.8260	1	60	< 0.0001
Island*Location	0.0132	0.4013	2	60	0.6712
Island*Plant	0.0369	1.1491	2	60	0.3238
Location*Plant	0.0123	0.7501	1	60	0.3899
Island*Height	0.0405	1.2661	2	60	0.2894
Location*Height	0.0089	0.5393	1	60	0.4656
Plant*Height	0.0176	1.0736	1	60	0.3043
Island*Location*Plant	0.0254	0.7824	2	60	0.4619
Island*Location*Height	0.0276	0.8508	2	60	0.4322
Island*Plant*Height	0.0182	0.5575	2	60	0.5756
Location*Plant*Height	0.0211	1.2922	1	60	0.2602
Island*Location*Plant*Height	0.0383	1.962	2	60	0.3094

Table 4.19. Mean values of the largest third (Mean $\text{SVL}_{\text{Max33}}$) of the *Anolis carolinensis* in each of the island samples, summarized by sex and year. A total of 1,657 *A. carolinensis* were found on the six experimental dredge-spoil islands in Mosquito Lagoon, and 594 were found on the additional island containing both species (a two-species "control").

	1995	1996	1997	1998
Females				
Small Treatment (ST)	47.34	48.78	48.38	49.67
Medium Treatment (MT)	47.66	48.33	48.33	50
Large Treatment (LT)	48.17	48	49.36	50.83
Small Control (SC)	49.1	48.8	49.25	48.66
Medium Control (MC)	48.44	47.47	48.54	48.66
Large Control (LC)	47.5	48.19	48.13	49.66
Large 2-sp. Control (L2C)	48.75	47.97	48.6	49.07
Males				
Small Treatment (ST)	57.92	56.11	57.71	58.67
Medium Treatment (MT)	58.18	58.65	56	59.67
Large Treatment (LT)	59.23	58.47	58.5	61.75
Small Control (SC)	59.5	60.2	58.25	59.25
Medium Control (MC)	57.35	56.86	57.54	57.86
Large Control (LC)	60.36	58.35	58.4	59.32
Large 2-sp. Control (L2C)	55.00	56.17	57.42	58.19

Table 4.20. Mean values of the body condition indices (CI) of the *Anolis carolinensis* in each of the island samples, summarized by sex and year. A total of 1,657 *A. carolinensis* were found on the six experimental dredge-spoil islands in Mosquito Lagoon, and 594 were found on the additional island containing both species (a two-species "control").

	1995	1996	1997	1998
Females				
Small Treatment (ST)	2.9521	2.8900	2.9023	2.8336
Medium Treatment (MT)	2.8853	2.7925	2.8044	2.8091
Large Treatment (LT)	2.8646	2.8672	2.8449	2.8234
Small Control (SC)	2.9456	2.9380	2.9564	2.9129
Medium Control (MC)	2.8121	2.8600	2.8618	2.8090
Large Control (LC)	2.8998	2.8145	2.7671	2.7336
Large 2-sp. Control (L2C)	2.8287	2.8427	2.8271	2.7355
Males				
Small Treatment (ST)	2.7571	2.7270	2.7676	2.7766
Medium Treatment (MT)	2.7887	2.8121	2.7627	2.8001
Large Treatment (LT)	2.8313	2.8437	2.8329	2.7996
Small Control (SC)	2.8005	2.8252	2.8607	2.8167
Medium Control (MC)	2.8145	2.7689	2.8160	2.8092
Large Control (LC)	2.8448	2.7678	2.7524	2.7111
Large 2-sp. Control (L2C)	2.8014	2.7978	2.7486	2.7497

VITA

Todd S. Campbell was born in Chicago, Illinois on October 25, 1961. He spent his childhood in Mt. Prospect, Illinois, graduated from Prospect High School in May 1979, and entered William Rainey Harper College in Palatine, Illinois in August 1979. After two years, he transferred to Eastern Illinois University in Charleston, Illinois, where he obtained a Bachelor of Science in Zoology with a minor in chemistry in May 1984. He entered the Graduate Program in Zoology at Eastern Illinois University in August 1984, and was awarded a Master's in Zoology in August 1986. His thesis was an experimental study of predator-prey interactions between predaceous diving beetle larvae and two species of anuran tadpoles. After finishing the Master's, he obtained a regulatory position as Environmental Specialist with the Florida Department of Environmental Protection (FDEP) in Tallahassee, Florida in August 1986, then transferred to Orlando, Florida in 1988 and remained with FDEP until July, 1989. Between July 1989 and April 1993, he was based in Orlando as a Project Manager for Dames & Moore, Inc., a world-wide environmental consulting firm. He left that position in April 1993 in order to pursue a doctoral degree, but first spent the summer at the Nevada Test Site working on the Yucca Mountain Project and touring southwestern national parks. He married Kym Rouse Demora in July 1993 and returned to Orlando for the remainder of that year. In January 1994, he entered the University of Tennessee to pursue the Doctor of Philosophy degree in Ecology and Evolutionary Biology, and shortly thereafter, began the research project in this dissertation. The doctoral degree was awarded to him on May 12, 2000.