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Interactions between introduced and native Anolis lizards in Florida and Grand Cayman Island

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To the Graduate Council:

I am submitting herewith a dissertation written by Glenn P. Gerber entitled "Interactions between introduced and native Anolis lizards in Florida and Grand Cayman Island." 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:

Gordon M. Burghardt, Gary E. McCracken, Tom Jennssen, Susan Riechert

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

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

To the Graduate Council:

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Gary F. McCracken

Susan E. Riechert

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

Interactions between Introduced and Native *Anolis* Lizards in Florida and Grand Cayman Island

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Glenn Philip Gerber

August 2000

FRONTISPIECE

Anolis carolinensis
The native anole of Florida

Anolis sagrei
The invading anole

Anolis conspersus
The native anole of Grand Cayman

DEDICATION

To my parents

Philip and Eugenia Gerber

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ABSTRACT

I investigated interactions between an invading species of lizard, *Anolis sagrei*, and native *A. carolinensis* in Florida and native *A. conspersus* in Grand Cayman. *Anolis sagrei* outnumbers both native species in some areas, particularly disturbed habitats, and is suspected of displacing them. *Anolis carolinensis* and *A. conspersus* are ecological analogs, and were the only anoles in Florida and Grand Cayman, respectively, until the introduction of *A. sagrei*. Because anoles are active, aggressive, territorial predators with size-structured populations and generalized feeding habits, I hypothesized that aggressive interference among adults and predation of juveniles by adults were important interspecific interactions. To investigate the importance of these mechanisms, I conducted behavioral experiments in both locations to determine the strength and symmetry of interspecific predation and aggressive interference. Based on the results of the behavioral experiments, I subsequently conducted experiments in the field and in enclosures to test hypotheses of interspecific interaction in relation to habitat structure and disturbance. Behavioral experiments demonstrated that (1) intraguild predation was asymmetrical in favor of *A. sagrei* in Florida and Grand Cayman, whereas (2) aggressive interference was minimal in Florida, but highly asymmetrical in Grand Cayman in favor of *A. conspersus*. A field experiment in Grand Cayman demonstrated that *A. sagrei* is restricted to open, disturbed habitats due to intense interspecific aggression and thus appears to have minimal impact on *A. conspersus*, despite its demonstrated potential to be an important intraguild predator. In contrast, enclosure experiments in Florida demonstrated that the survival of *A. carolinensis* juveniles is significantly reduced in habitats of low structural complexity due to intraguild predation from adult *A. sagrei* and competition from juvenile *A. sagrei*. My studies demonstrate that (1) both intraguild predation and interspecific aggression have important influences on anole community structure, (2) the effects of an introduced species on native congeners in one community cannot necessarily be predicted by knowing the effects of that same introduced species on native congeners in a different community, and (3) predicting the effects of one species on another, regardless of taxa, will be enhanced by understanding the nature, strength, and symmetry of the mechanisms of interaction.

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PART I

General Introduction:

A Mechanistic Approach to the Study of Interactions between Introduced and Native Anoles in Disturbed Landscapes

BACKGROUND AND RATIONALE

Habitat destruction and invasive species are postulated to be the first and second greatest threats to global biodiversity, respectively (e.g., Wilson, 1992; Vitousek et al., 1997; McKinney and Lockwood, 1999; Myers et al., 2000). Indeed, these processes are commonly associated. Anthropogenic disturbance of native habitats tends to create conditions favorable for invasive species, which are often introduced by humans and pre-adapted to exploit disturbed landscapes (e.g., Mooney and Drake, 1986; Simberloff et al., 1997; Cox, 1999). Consequently, interactions between native and exotic species are frequently imbedded within the framework of habitat disturbance (e.g., Hobbs, 1989; Hobbs and Huenneke, 1992). In many cases, exotic species dominate disturbed habitats, but are less successful in undisturbed habitats (e.g., Case and Bolger, 1991a; Case et al., 1994). The presence of ecologically similar native species is probably one of the most important reasons for this pattern (e.g., Case and Bolger, 1991a; Losos et al., 1993). Native species may be less adapted to disturbed habitats than invaders, but the reverse is generally true in undisturbed habitats. Thus, the success of invading species is frequently dependent upon the nature, strength, and symmetry of interactions with ecologically similar native species. Likewise, the persistence of native species may depend on their ability to coexist with ecologically similar invading species. Understanding interactions between exotic and native species may thus allow the impact of invading species on ecologically similar native species to be predicted. Further, species invasions, whether natural or human mediated, provide excellent opportunities to study interactions between species during the initial stages of contact and thus are likely to provide insight into the dynamics of species coexistence and exclusion (e.g., Petren et al., 1993; Petren and Case, 1996, 1998).

This dissertation focuses on interactions between an invading species of lizard and ecologically similar native species in Florida and Grand Cayman Island. All of the species belong to the genus *Anolis* (Sauria: Polychrotidae), which contains more than 400 described species and ranges throughout much of the new world tropics and subtropics. Anoles are small to medium sized lizards (approximately 30 to 200 mm in body length as adults) that are largely diurnal, insectivorous, and arboreal (Schwartz and Henderson, 1991). *Anolis* is the most specious genera of amniotes in the world and over 150 species have been described on the islands of the Caribbean alone (Crother, 1999). Within the Caribbean, independent but convergent adaptive radiations on each of the large islands in the Greater Antilles (Cuba, Hispaniola, Puerto Rico, and Jamaica) have produced remarkably similar anole assemblages (e.g., Williams, 1983; Losos, 1992; Losos et al., 1998), and there is considerable evidence that interspecific competition has been the primary force driving this process (reviewed in Losos, 1994). Thus, Caribbean anoles make excellent subjects for the study of interspecific interactions, as do island lizards in general (reviewed in Case and Bolger, 1991b).

With few exceptions, each of the large Greater Antillean islands has the same set of "ecomorphs," species that are adapted to use the same structural microhabitats (Williams, 1983; Losos et al., 1998). There are six basic ecomorphs, each named for that portion of the structural habitat most frequently used (i.e., grass-bush, trunk-ground, trunk, trunk-crown, twig, and crown giant). Each ecomorph has a characteristic size and morphology adapted to a particular niche. Additionally, on some of the large Greater Antillean islands, evolution has produced multiple species of the same ecomorph. However, on any given island, members of the same ecomorph are generally adapted to different climatic habitats (e.g., sunny and xeric versus shaded and mesic), and thus rarely, if ever, occur together. Indeed, comparative studies of anole assemblages suggest that members of the same ecomorph that do not differ in climatic habitat are too similar to coexist syntopically (e.g., Williams, 1983) and field studies support this conclusion (e.g., Jenssen et al., 1984).

Recent comparative analyses suggest that the ancestral morphotype of all Caribbean anoles was most similar to the present day trunk-crown or trunk-ground ecomorphs (Losos and de Queiroz, 1997; Beuttell and Losos, 1999), respectively named for their tendency to occupy the trunks and crowns of trees or the trunks of trees and the ground. This conclusion is consistent with ecological and distributional patterns as well, as trunk-crown and trunk-ground ecomorphs tend to be habitat generalists, and have been far more successful in colonizing other islands from their respective Greater Antillean source islands than have all other ecomorphs (Williams, 1969; Losos et al., 1993). Further, on small islands colonized by just one of these ecomorphs, the anoles have generally expanded their niches to include some of the resources normally used by the other ecomorph (e.g., Schoener, 1975; Lister, 1976a). On some of these islands, the anoles have also evolved a generalized morphology intermediate between that of the trunk-crown and trunk-ground ecomorphs (Lister, 1976b; Losos and de Queiroz, 1997; Beuttell and Losos, 1999). Thus, differences between trunk-crown and trunk-ground anoles appear to be maintained by interspecific interactions, such that in the absence of one ecomorph, the other is likely to undergo ecological and morphological release.

In this dissertation, I investigate the interaction between an invading trunk-ground anole, *A. sagrei*, and the native trunk-crown anoles of Florida (*A. carolinensis*) and Grand Cayman Island (*A. conspersus*). *Anolis carolinensis* and *A. conspersus* have been described as ecological analogs and prior to the introduction of *A. sagrei* were the only anoles in Florida and Grand Cayman, respectively (Williams, 1969). Both *A. carolinensis* and *A. conspersus* are believed to have evolved directly from Greater Antillean trunk-crown anoles that rafted to Florida and Grand Cayman, respectively, in the Pliocene. *Anolis carolinensis* is most closely related to *A. porcatus* of Cuba (Williams, 1969, 1976) and electrophoretic and albumin immunological data suggest a divergence time of 3 to 4 million years (Buth et al., 1980, and references therein). *Anolis conspersus* is most closely related to *A. grahami* of Jamaica (Grant, 1940; Underwood and Williams, 1959; Hedges and Burnell, 1990; Macedonia and Clark, in press) and mtDNA sequence data suggest a divergence time of about 2.8 million years (Jackman et al., unpublished manuscript). Both species are also known from Pleistocene fossils: *A. carolinensis* from Florida, Georgia, and Alabama (Holman, 1995), and *A. conspersus* from eastern Grand Cayman (Morgan, 1994). More importantly, no other fossil anoles have been found in North America (Holman, 1995) or Grand Cayman (Morgan, 1994), indicating that both species were indeed historically isolated from other anoles. Both *A. carolinensis* (e.g., Collette, 1961; Jenssen et al., 1998) and *A. conspersus* (e.g., Schoener, 1967; Avery, 1988) are habitat generalists with broad niches, and compared to their presumed progenitors on Cuba and Jamaica, respectively, both species appear to have undergone ecological release in the absence of other anoles (e.g., Collette, 1961; Schoener, 1975). In addition, recent morphological analyses suggest that *A. conspersus* has evolved a morphology intermediate between that of trunk-crown and trunk-ground ecomorphs (Beuttell and Losos, 1999), and data presented in Collette (1961) suggest that *A. carolinensis* may have done so also.

Anolis sagrei evolved on Cuba, where it occurs sympatrically with *A. porcatus*, the presumed progenitor of *A. carolinensis*, and subsequently colonized the Bahamas, Little Cayman and Cayman Brac, and several other small islands without human assistance (Williams, 1969). However, human assistance was required for *A. sagrei* to colonize Florida and Grand Cayman. *Anolis sagrei* was introduced to Florida about 60 years ago (Wilson and Porras, 1983, and references therein) and to Grand Cayman about 20 years ago (Minton and Minton, 1984). Since being introduced, *A. sagrei* has expanded its range in both Florida (Godley et al, 1981; Lee, 1985; Campbell, 1996) and Grand Cayman (Franz et al., 1987; Losos et al., 1993). Further, in some habitats, particularly those associated with human disturbance, *A. sagrei* now outnumbers native *A. carolinensis* (e.g., Christman, 1980; Wilson and Porras, 1983; Tokarz and Beck, 1987; Echternacht and Harris, 1993) and *A. conspersus* (Franz et al., 1987; Avery, 1988; Losos et al., 1993) in parts of Florida and Grand Cayman, respectively. Consequently, interspecific interactions and habitat disturbance are hypothesized to be important in both systems. The mechanisms of interaction and their connection with habitat disturbance are largely unknown, however.

A number of studies have now demonstrated changes in the resource use, growth rate, or population size of one *Anolis* species in response to the addition or removal of another (reviewed in Losos, 1994; see also Leal et al., 1998; Losos and Spiller, 1999; Campbell, 2000). However, the mechanisms of interaction between sympatric anoles have rarely been investigated (notable exceptions are studies by Oritz and Jenssen, 1982, Jenssen et al., 1984, and Stamps, 1983a, b). In general, studies of interspecific interaction in *Anolis* have taken a purely phenomenological approach (*sensu* Tilman, 1987) by looking for changes in one species in response to the removal or addition of another species without explicitly stating or providing evidence for the mechanisms of interaction. While such studies are extremely valuable for demonstrating population and community level effects of interspecific interactions (e.g., Connell, 1983; Schoener, 1983; Sih et al., 1985), many authors have argued that a mechanistic approach will provide greater understanding and predictability of interspecific interactions and community structure (e.g., Schoener, 1986; Tilman, 1987; Werner, 1992; Resetarits and Bernardo, 1998; Holway and Suarez, 1999). Studies of interspecific interaction can be defined as mechanistic (*sensu* Tilman, 1987) if they include the direct process by which interaction occurs as well as information on the physiology, morphology, and (or) behavior of individual species or functional groups relevant to that process.

Because most anoles (including the species studied here) are active, aggressive, territorial predators, interactions between species are likely to involve behavioral mechanisms. For example, although competition between similar species of *Anolis* may ultimately be for food, proximately, competition is likely to involve aggressive interference for space (e.g., Jenssen, 1973; Jenssen et al., 1984). In addition, because ontogenetic changes in size within species are generally much greater than size differences between species, the potential for intraguild predation in *Anolis* is great (reviewed in Gerber, 1999). Moreover, while overt aggressive and predatory interactions are difficult to overlook, the effects of interspecific aggression and intraguild predation may be much more subtle, particularly when interactions are highly asymmetric, as seems to be the rule rather than the exception. For example, individuals of one species may use different habitats than individuals of another species because of the threat of interference or predation. Consequently, both aggressive interference and intraguild predation are likely to be more important in structuring anole assemblages than is generally recognized.

EXPERIMENTAL APPROACH

I used a mechanistic approach to investigate the importance of aggressive interference and predation between *A. sagrei* and *A. carolinensis* in Florida, and between *A. sagrei* and *A. conspersus* in Grand Cayman. To do this, I first conducted behavioral experiments to determine the potential strength and symmetry of interspecific aggression and predation in Florida and Grand Cayman. Then, based on the results of the behavioral experiments as well as morphological, ecological, and physiological characteristics of the species, I conducted experiments in the field and in enclosures to test specific hypotheses of interspecific interaction in relation to habitat structure and disturbance.

Results of the behavioral experiments are presented in Parts II and III. In Part II, I show that the potential for intraguild predation of juveniles by adults is highly asymmetrical in Florida and Grand Cayman, and favors introduced *A. sagrei* in both locations. Thus, predation of native juvenile anoles by adult *A. sagrei* is a potentially important interaction in Florida and Grand Cayman. In Part III, I show that the potential for interspecific aggression among adult males is highly asymmetrical in Grand Cayman and favors native *A. conspersus*. Experimental tests for interspecific aggression were also conducted in Florida (Gerber and Kramer, unpublished data) but are not presented here as results confirmed earlier studies reporting little interspecific aggression between *A. sagrei* and *A. carolinensis* in Florida (Tokarz and Beck, 1987; Brown, 1988). Thus, interspecific aggression among adult males does not appear to be an important interaction in Florida, but is a potentially important interaction in Grand Cayman, favoring native *A. conspersus*.

Based on the results of the behavioral experiments, as well as species differences in habitat use, body size, and eco-morphology in Florida and Grand Cayman, I formed the following two hypotheses. In Grand Cayman, where *A. sagrei* is abundant only in highly disturbed habitats and *A. conspersus* is found in all habitats and most abundant in undisturbed woodlands, I hypothesized that introduced *A. sagrei* were being excluded from woodland habitats by the presence of the native *A. conspersus*, which are slightly larger and much more aggressive. If so, this should limit the potential impact of intraguild predation by *A. sagrei* adults on *A. conspersus* juveniles to disturbed habitats. In contrast, in Florida, where interspecific aggression and size differences are minimal and habitat overlap is extensive, I hypothesized that native *A. carolinensis* juveniles were significantly impacted by intraguild predation from adult *A. sagrei* and perhaps by competition with juvenile *A. sagrei*, which can be extremely abundant. Further, I hypothesized that interspecific interactions in Florida were mediated by the structural complexity of the habitat such that the impact of *A. sagrei* on *A. carolinensis* was most pronounced in areas of low habitat complexity.

To test these hypotheses, I conducted ecological experiments in Grand Cayman and Florida, which are presented in Parts IV and V, respectively. In Grand Cayman, I conducted a field experiment to determine whether *A. sagrei* would increase in abundance and shift its use of habitat toward that used by *A. conspersus* when *A. conspersus* was removed. As predicted, in the absence of *A. conspersus*, *A. sagrei* increased in abundance and shifted its use of habitat toward that previously used by *A. conspersus*. Thus, in Grand Cayman, interspecific aggression by native *A. conspersus* appears to restrict the distribution, abundance, and habitat use of introduced *A. sagrei*, thereby limiting the potential impact of this intraguild predator. In Florida, I conducted a series of experiments in small enclosures with low, medium, or high complexity habitats to determine the impact of adult and juvenile *A. sagrei* on the growth and survival of *A. carolinensis* juveniles. The survival of juvenile *A. carolinensis* was reduced by predation from adult *A. sagrei* and competition with juvenile *A. sagrei*, but only in habitats of medium and low structural complexity. Thus, in Florida, *A. sagrei* is most likely to impact *A. carolinensis* in areas of low structural complexity, such as disturbed habitats. I discuss the implications of these findings at length in Parts II through IV and summarize the results and conclusions of all the studies in Part VI. Illustrations of the *Anolis* species used in this study are provided in the frontispiece.

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PART II

Evidence for Asymmetrical Intraguild Predation between the Native and Introduced *Anolis* Lizards of Florida and Grand Cayman

ABSTRACT

Since its introduction, *Anolis sagrei* (Sauria: Polychrotidae) has been replacing native *A. carolinensis* in Florida and native *A. conspersus* in Grand Cayman Island as the common anole of urban environments and other open habitats. To assess the likelihood that predation of juvenile native anoles by *A. sagrei* adults is an important interaction in this process, the propensities for intraguild predation and cannibalism were assessed for *A. sagrei* and *A. carolinensis* in Florida and for *A. sagrei* and *A. conspersus* in Grand Cayman. Predation experiments were conducted in cages, using freshly captured lizards, in which adult males of each species were presented with conspecific and heterospecific juveniles. Adult *A. sagrei* were (1) significantly more likely to eat juveniles than were adult *A. carolinensis* or *A. conspersus*, and (2) significantly more likely to eat heterospecific than conspecific juveniles, whereas adult *A. carolinensis* and *A. conspersus* were not. Thus, the propensity for intraguild predation is asymmetrical in favor of introduced *A. sagrei* in Florida and Grand Cayman. Further study is needed, however, to determine the importance of intraguild predation under field conditions.

INTRODUCTION

Potentially competing species sometimes also interact as predator and prey, an interaction termed intraguild predation (Polis et al., 1989; Polis and Holt, 1992). Intraguild predation differs from simple predator-prey interactions in that intraguild predators not only benefit from the energetic and nutritional gains of predation, but also from the elimination of potential competitors. Intraguild predation can thus have important consequences for the structure of communities.

Among lizards, there are numerous reports of intraguild predation, but most of these are anecdotal. Consequently, little quantitative evidence exists regarding the frequency or significance of intraguild predation among lizards. Nevertheless, lizards often form assemblages of size-structured generalist predators, traits common in systems displaying intraguild predation (Werner and Gilliam, 1984; Ebenman and Persson, 1988; Polis et al., 1989). Furthermore, intraguild predation is reported to be an important interaction in guilds of other size-structured vertebrates with generalized feeding habits, such as fish (e.g., Werner, 1986; Persson, 1988), salamanders (e.g., Hairston, 1986; Gustafsen, 1993), and frogs (e.g., Hayes and Jennings, 1986; Werner et al., 1995). Intraguild predation may therefore be a more common and important interaction among lizards than is currently recognized.

Here, I report an investigation of the propensity for intraguild predation of two native lizards, *Anolis carolinensis* in Florida and *A. conspersus* in Grand Cayman Island, by an introduced congeneric competitor, *A. sagrei*. *Anolis sagrei* was introduced in mainland Florida around 1940 (Wilson and Porras, 1983) and in Grand Cayman around 1980 (Minton and Minton, 1984). Since its introduction, *A. sagrei* has successfully colonized much of Florida (Lee, 1985) and Grand Cayman (Losos et al., 1993), and is continually expanding its range in both areas. As it progresses, *A. sagrei* generally replaces *A. carolinensis* (Christman, 1980; Wilson and Porras, 1983; Tokarz and Beck, 1987; Echternacht and Harris, 1993) and *A. conspersus* (Minton and Minton, 1984; Losos et al., 1993) as the common anole in urban areas and other relatively open habitats. Interspecific interactions are thus suspected of causing the observed changes in species abundance. Because juveniles of the native anoles often appear to be disproportionately rare in areas where *A. sagrei* is abundant, I hypothesized that intraguild predation might be an important interaction in these systems.

Anolis sagrei, *A. carolinensis*, and *A. conspersus* are generalized arboreal anoles with broad niches and similar body-size distributions (Williams, 1969). Further, like many other anoles (Stamps, 1983a), each of these species has a social system based on territoriality and polygyny, and exhibits marked sexual size dimorphism (Schoener, 1967; Schoener and Schoener, 1980, 1982; Ruby, 1984; Jenssen and Nunez, 1998). Maximum recorded snout-vent lengths (SVL) for adult male and female *A. sagrei*, *A. carolinensis*, and *A. conspersus*, from the areas considered in this study, are 69 mm and 49 mm, 70 mm and 52 mm, and 77 mm and 52 mm, respectively (G. Gerber, unpublished data). Similarly, minimum recorded hatchling SVLs for these species are 17 mm, 20 mm, and 22 mm (this study). Thus, regardless of species, juvenile anoles in both guilds are small enough to be eaten by adult conspecifics or heterospecifics. If adult *A. sagrei* are, however, more prone to prey on juveniles (specifically those of other species) than are adult *A. carolinensis* and *A. conspersus*, intraguild predation could be asymmetrical in favor of *A. sagrei*. The intent of our study was (1) to determine if differences existed between species in Florida or Grand Cayman in the propensity of adults to prey on juveniles, and (2) to compare the propensities for intraguild predation and cannibalism.

To determine the propensity for intraguild predation and cannibalism in each species, I conducted captive predation experiments in Florida and Grand Cayman in which adult males served as predators and conspecific and heterospecific juveniles served as prey. My experiments demonstrate that adult *A. sagrei* are (1) more prone to prey on juveniles than are adult *A. carolinensis* or *A. conspersus*, and (2) more prone to prey on heterospecific than conspecific juveniles, whereas adult *A. carolinensis* and *A. conspersus* are not. Therefore, predation by introduced *A. sagrei* is a potentially important source of juvenile mortality for *A. carolinensis* in Florida and *A. conspersus* in Grand Cayman.

METHODS

I conducted predation experiments opportunistically in 1988, 1989, 1991, and 1993, between July and September, when hatchling anoles were most abundant. All predation experiments took place in small cages (described below) using freshly captured lizards. Predation experiments were conducted by placing juvenile anoles (≤ 30 mm SVL) in cages housing individual adult anoles for one day (24 h) and recording predation events. In addition, for juveniles that were not eaten, I checked for tail loss and other injuries that would indicate attempted predation. Cages were housed outside, near collection sites, in partial shade at ambient temperature and humidity. In Florida, I collected lizards near Lake Okeechobee in Palm Beach County and near Spring Lake in Highlands County, and conducted predation experiments at Archbold Biological Station.

In Grand Cayman, I collected lizards on the west side of the island near George Town, and conducted predation experiments at the Mosquito Research and Control Unit.

I choose to use only adult male anoles as predators, as males are significantly larger than females in all three species (see above). This served to maximize size differences between adults and juveniles (i.e., predators and prey) and to control for potential sexual differences in propensities for intraguild predation or cannibalism. To ensure that predators were not satiated when experiments began, adult anoles were fasted in their test cages for two days prior to conducting predation experiments (Windell and Saroken, 1976; Jenkins, 1980). Lizards were supplied with fresh water daily by spraying cages with a plant mister.

In Florida, I conducted two types of predation experiments using adult and juvenile *A. sagrei* and *A. carolinensis*: successive predation experiments and simultaneous predation experiments. In successive predation experiments, the propensities for cannibalism and intraguild predation were estimated separately by presenting individual adult anoles of each species with a single conspecific juvenile on one day and a single heterospecific juvenile anole on another day. Presentations were made on consecutive days and, based on random assignment, 50% of adults of each species were presented with a conspecific juvenile first and 50% were presented with a heterospecific juvenile first. In simultaneous predation experiments, the propensities for cannibalism and intraguild predation were estimated at the same time by presenting individual adult anoles of each species with one conspecific juvenile and one heterospecific juvenile anole on the same day. Successive predation experiments took place in one-gallon glass jars (16 cm diameter × 24 cm high), and simultaneous predation experiments took place in ten-gallon glass aquariums (60 cm × 25 cm × 30 cm high). Jars and aquariums were covered with screened lids (1.5 mm mesh) and provisioned with a sand substrate and a single, diagonally placed, wooden perch (2 cm diameter).

In Grand Cayman, I conducted simultaneous predation experiments similar to those conducted in Florida, but using adult and juvenile *A. sagrei* and *A. conspersus*. Successive predation experiments were not conducted in Grand Cayman due to difficulty locating juvenile anoles, and because the propensities for cannibalism and intraguild predation in the successive predation experiments conducted in Florida were statistically indistinguishable from those of the simultaneous predation experiments. I did, however, conduct predation experiments in Grand Cayman in which individual adult *A. sagrei* and *A. conspersus* were presented with a single *Sphaerodactylus argivus*, a tiny gecko (maximum SVL 30 mm) endemic to the Cayman Islands (Schwartz and Henderson 1991) and similar in size to hatchling *A. sagrei* and *A. conspersus*. These predation experiments (hereafter *Sphaerodactylus* predation experiments) were compared with the simultaneous predation experiments to investigate whether adult *A. sagrei* or *A. conspersus* differed in their propensity to prey on anoline versus non-anoline lizards of equivalent size. All predation experiments conducted in Grand Cayman took place in collapsible field cages (BioQuip® Products, Gardena, CA). Each cage consisted of a rigid cubic frame (30.5 cm sides), assembled from ¾ inch (2 cm) PVC tubing and three-way right-angled connectors, surrounded by a form-fitting bag of screened cloth (1.5 mm mesh) held shut by a strap secured around the tightly gathered open end.

Prior to conducting every set of predation experiments, I recorded the mass (± 0.01 g using an electronic balance) and snout-vent length (± 1 mm using a 200 mm rule) of all lizards. As an estimate of gape size, I also measured the head width (± 0.1 mm using vernier calipers) of adult anoles. To minimize variance in the ratio of prey size to predator size, I ranked all adult anoles and all geckos or juvenile anoles by mass and matched predators and prey accordingly. For simultaneous predation experiments, I also matched interspecific pairs of juvenile anoles presented to adult anoles by mass (± 0.02 g). The number, size, and species of lizards used as predators or prey in predation experiments conducted in Florida and Grand Cayman are summarized in Tables 2.1 and 2.2, respectively. After completing each set of experiments, I released adult anoles and surviving geckos or juvenile anoles at their site of capture.

RESULTS

Predation

Florida – Predation of juvenile anoles in Florida was asymmetric in favor of *A. sagrei* (Figure 2.1). Adult *A. sagrei* were more likely to eat juvenile anoles in simultaneous (*G*-test: $G = 13.924$, df = 1, $P < 0.001$) and successive ($G = 7.792$, df = 1, $P = 0.005$) predation experiments than were adult *A. carolinensis*. Furthermore, interspecific differences in predation were attributable to differences in the frequency of intraguild predation, not cannibalism. Adults of both species were unlikely to eat juvenile conspecifics, and adult *A. sagrei* were more likely to eat heterospecific than conspecific juveniles in simultaneous ($G = 10.299$, df = 1, $P < 0.001$) and successive ($G = 7.792$, df = 1, $P = 0.005$) predation experiments, whereas adult *A. carolinensis* were not (simultaneous experiments: $G = 1.127$, df = 1, $P > 0.2$; successive experiments: $G = 1.412$, df = 1, $P > 0.2$). It appears that predation was not affected by whether conspecific and heterospecific juveniles were presented to adults together or separately, as the propensities for cannibalism and intraguild predation were not significantly different between simultaneous and successive predation experiments for adult *A. sagrei* (maximum-likelihood ANOVA, experiment type × prey type × predation interaction: $\chi^2 = 0.20$, df = 1, $P > 0.6$) or adult *A. carolinensis* (experiment type × prey type × predation interaction: $\chi^2 = 0.47$, df = 1, $P > 0.4$).

Grand Cayman – Predation in Grand Cayman was also asymmetric in favor of *A. sagrei* (Figure 2.2). Adult *A. sagrei* were more likely to eat juvenile anoles in simultaneous predation experiments ($G = 7.362$, df = 1, $P = 0.007$) and geckos in *Sphaerodactylus* predation experiments ($G = 11.869$, df = 1, $P < 0.001$) than were adult *A. conspersus*. Furthermore, as in Florida, the interspecific difference in predation in simultaneous predation experiments was attributable to a difference in the frequency of intraguild predation, not cannibalism. Adults of both species were unlikely to eat juvenile conspecifics, and adult *A. sagrei* were more likely to eat heterospecific than conspecific juveniles ($G = 5.812$, df = 1, $P = 0.016$), whereas adult *A. conspersus* were not ($G = 1.158$, df = 1, $P > 0.2$). Results of the *Sphaerodactylus* predation experiments were similar to those of the simultaneous predation experiments, in that the overall frequency of predation did not differ between types of predation experiments for adult *A. sagrei* ($G = 0.238$, df = 1, $P > 0.6$) or adult *A. conspersus* ($G = 3.567$, df = 1, $P = 0.059$).

Florida and Grand Cayman compared – Because simultaneous predation experiments were conducted in both locations (Figure 2.1a and 2.2a), these experiments were used compare the predatory propensities of *A. carolinensis* and *A. conspersus*, and of *A. sagrei* populations from Florida and Grand Cayman. There were no significant differences in the frequency of cannibalism or intraguild predation between *A. carolinensis* and *A. conspersus* (maximum-likelihood ANOVA, species × prey type × predation interaction: $\chi^2 = 2.39$, df = 1, $P > 0.1$) or between *A. sagrei* from Florida and Grand Cayman (population × prey type × predation interaction: $\chi^2 = 0.05$, df = 1, $P > 0.8$). Thus, predatory propensities did not differ between the native species of Florida and Grand Cayman, or between the two introduced populations of *A. sagrei.*

Prey Injury and Tail Loss

Prey that were eaten sometimes shed their tails, as these were occasionally found in the cages of predatory adult anoles. In contrast, none of the 23 *Sphaerodactylus* or 218 juvenile anoles that were not eaten shed their tails or were visibly injured. These observations suggest that prey that were not eaten were not pursued by adults. Thus, there was no indication that the observed patterns of predation resulted from an inability of some adults to capture or subdue certain prey.

Morphological Considerations

Prey size – There was also no indication that the patterns of predation observed in Florida or Grand Cayman resulted from adult anoles being morphologically constrained by the size of prey used. First, there were no significant differences between the size (mass or SVL) of prey that were and were not eaten, for adults of any species in Florida or Grand Cayman (Table 2.3; *t*-tests: $P > 0.1$ in each case). Furthermore, these comparisons remained insignificant when the effect of adult size (mass or SVL) was statistically controlled for using analysis of covariation (ANCOVA: $P > 0.1$ in each case). Thus, within species, it does not appear that some adult anoles were constrained from predation because prey were too large to be eaten. Second, when prey size is expressed as a percentage of predator size [(prey mass or SVL/predator mass or SVL)100], it is apparent that prey presented to adult *A. sagrei* were (1) approximately the same relative size as prey presented to adult *A. carolinensis* in Florida (Table 2.3: smaller in relative mass, but larger in relative SVL) and (2) always relatively larger than prey presented to adult *A. conspersus* in Grand Cayman (Table 2.3). Thus, the high rate of predation exhibited by adult *A. sagrei*, relative to adult *A. carolinensis* and *A. conspersus*, was not associated with an advantage in relative prey size. Third, for those experiments using juvenile anoles as prey, juvenile *A. carolinensis* and *A. conspersus* were, on average, relatively larger than juvenile *A. sagrei* (Figure 2.1 and 2.2a). This was most pronounced in the successive predation experiments conducted in Florida (Figure 2.1b) in which conspecific and heterospecific juveniles presented to adult anoles were not matched by mass as they were in simultaneous predation experiments. Consequently, if prey size limited predation, adult *A. sagrei* should have eaten juvenile heterospecifics less frequently than juvenile conspecifics, not vise versa. Of course, by the same measure, I cannot rule out the possibility that some *A. sagrei* may have preferentially eaten juvenile heterospecifics due to their larger size.

Predator size and condition – Finally, the mass, SVL, head width, and body condition of adult anoles were examined to determine if there were intraspecific morphological differences between predatory and non-predatory individuals. Body condition was defined as $(\text{mass}^{0.3}/\text{SVL})100$, following Andrews (1991). Regardless of species, the average size and body condition of predatory males was consistently less than that of non-predatory males, though not all differences were significant (Table 2.4). For adult *A. carolinensis* and *A. conspersus*, predatory and non-predatory adults did not differ significantly in SVL or head width, but predatory adults were significantly smaller in mass and, consequently, had lower body condition values than non-predatory adults (Table 2.4). Thus, relative to other conspecifics tested, the few adult *A. carolinensis* and *A. conspersus* that ate lizards in our experiments were in poor physical condition and were probably the most in need of food. For adult *A. sagrei*, a similar association is suggested for Grand Cayman, but not for Florida (Table 2.4). Thus, the relationship between body condition and predation of lizards by adult *A. sagrei* is uncertain.

DISCUSSION

Asymmetry in Intraguild Predation

Adult *A. sagrei* were significantly more likely to prey on juvenile *A. carolinensis* and *A. conspersus* than adults of these species were to prey on juvenile *A. sagrei*. Thus, these experiments establish the potential for asymmetric intraguild predation. They do not, however, indicate how frequent predation of juvenile *A. carolinensis* and *A. conspersus* by adult *A. sagrei* is in nature. The experimental containers artificially constrained the juveniles and did not provide refuges. So, it is impossible to extrapolate from these experiments to the field. However, there is evidence that adult *A. sagrei* prey on juvenile *A. carolinensis* in Florida. In an analysis of stomach contents of 15 adult male *A. sagrei* and 15 adult male *A. carolinensis*, collected from an area of sympatry when hatchlings of both species were present, one hatchling *A. carolinensis* was found in the *A. sagrei* samples, whereas no hatchlings were found in the *A. carolinensis* samples (Campbell and Gerber, 1996). Also, at another site of sympatry in Florida, an adult male *A. sagrei* was observed to attack and eat a juvenile *A. carolinensis* released nearby (Campbell and Gerber, 1996). Similar evidence of intraguild predation is not available for Grand Cayman, but there have been no studies of anole diets conducted there since the arrival of *A. sagrei*.

The magnitude of predation by *A. sagrei* on the native anoles in Florida and Grand Cayman will depend on how frequently adult *A. sagrei* encounter, attack, and successfully capture juvenile *A. carolinensis* and *A. conspersus* in the field. This, in turn, will depend upon factors such as the degree of spatial overlap between adult *A. sagrei* and juvenile congeners, the relative abundances of the species, and the availability of refuges from predation.

Intra- and interspecific differences in microhabitat use suggest that spatial overlap between adult *A. sagrei* and juvenile *A. carolinensis* and *A. conspersus* may be relatively high. Within each species, juveniles typically perch lower than adults (Schoener, 1967, 1968, 1975; Losos et al., 1993), whereas between species, *A. sagrei* typically perch lower than *A. carolinensis* or *A. conspersus* (Schoener, 1968, 1975; Lister, 1976; Losos et al., 1993). A result of these differences is that juvenile *A. carolinensis* and *A. conspersus* tend to occupy the same vegetational strata used by adult *A. sagrei*, although they generally use thinner diameter perches. Thus, in those habitats where the species co-occur, adult *A. sagrei* probably regularly encounter juvenile *A. carolinensis* and *A. conspersus*.

As for the relative abundances of the species, *A. sagrei* reaches densities higher than those reported for any other anole, approaching $1/m^2$ in the Bahamas (Schoener and Schoener, 1980), and presently outnumbers *A. carolinensis* (Christman, 1980; Wilson and Porras, 1983; Tokarz and Beck, 1987; Echternacht and Harris, 1993) and *A. conspersus* (Minton and Minton, 1984; Losos et al., 1993) in parts of Florida and Grand Cayman, respectively. Consequently, even if individual adult *A. sagrei* only rarely prey on juvenile *A. carolinensis* and *A. conspersus*, overall predation rates may be high enough to have a significant effect on community dynamics. Intraguild predation might be particularly important to *A. sagrei* during the early stages of invasion when native juvenile anoles are most abundant relative to adult *A. sagrei*. This would not only facilitate the displacement of *A. carolinensis* and *A. conspersus*, but also the establishment of *A. sagrei*.

All else being equal, the frequency of intraguild predation should be inversely related to the availability of refuges from predation afforded by the habitat. This is consistent with observations that changes in species abundance in Florida (Christman, 1980; Wilson and Porras, 1983; Tokarz and Beck, 1987; Echternacht and Harris, 1993) and Grand Cayman (Minton and Minton, 1984; Losos et al., 1993) have been most pronounced in structurally simplified habitats, such as those characterized by human disturbance, even though *A. carolinensis* and *A. conspersus* thrive in such areas when allopatric. The replacement of native lizards by introduced competitors, particularly in disturbed habitats, has been reported for skinks (Case and Bolger, 1991; Rodda and Fritz, 1992) and geckos (Petren et al., 1993; Case et al., 1994) on islands in the Pacific as well. Moreover, there is also evidence for asymmetric intraguild predation in these systems (Bolger and Case, 1992; McCoid and Hensley, 1993; McCoid, 1995).

Finally, a review of intraguild predation in *Anolis* lizards (Gerber, 1999) suggests that predatory interactions between anoles are relatively common, often asymmetric, and likely affect the abundance and distribution of certain species. Perhaps the best documented case occurs on Grenada, a small island with two widely sympatric anoles differing considerably in body size. Stamps (1983b) has shown that juveniles of the smaller species, *A. aeneus*, are preyed upon by adults of the larger species, *A. richardi*, whereas juvenile *A. richardi*, likely due to their size, are not preyed upon by adult *A.*

aeneus. Furthermore, the threat of predation from adult *A. richardi* drives intense intraspecific competition among juvenile *A. aeneus* for territories in small forest clearings not inhabited by adult *A. richardi* (Stamps, 1983c). Thus, intraguild predation has important consequences for community dynamics on Grenada.

In brief, there is a growing body of data implicating intraguild predation as a widespread interaction in lizard assemblages. Further studies in the field are needed, however, to determine the actual importance of intraguild predation in most of these systems, particularly in relation to competitive interactions and other types of predation.

Possible Causes of Asymmetry in Intraguild Predation

Although my study demonstrates that adult *A. sagrei* are more prone to prey on *Sphaerodactylus* and juvenile anoles than are adult *A. carolinensis* and *A. conspersus*, the results do not provide an obvious explanation for this difference. Nor is there an obvious explanation as to why adult *A. sagrei* preyed more on *Sphaerodactylus* and juvenile heterospecific anoles than on juvenile conspecifics. Because the predation experiments took place in small cages without refuges, differences in the escape behavior of prey or the capture efficiency of adult anoles are unlikely explanations. The fact that *Sphaerodactylus* and juvenile anoles that were not eaten did not shed their tails, a tactic employed to avoid predation, and never sustained noticeable injury supports this conclusion as well. There was also no indication from the analysis of body sizes that the observed patterns of predation resulted from some prey being too large to be eaten by the adults to which they were presented. Consequently, the observed patterns of predation appear to reflect actual differences in the predatory tendencies of the species.

The most parsimonious explanation for why adult *A. sagrei* are more prone to prey on other species rather than on juvenile conspecifics is that they avoid cannibalism. This hypothesis is also supported by the observation that adult *A. sagrei* in Florida were no more likely to eat conspecific juveniles in the separate predation experiments than in the simultaneous predation experiments, even though alternative prey (i.e., similarly-sized heterospecific lizards) were not present in the former. Thus, the results of my experiments support the view that adult *A. sagrei* can and do discriminate juvenile conspecifics from similarly-sized heterospecific lizards. My results are inconclusive, however, as to whether adult *A. carolinensis* and *A. conspersus* can distinguish conspecific juveniles from similarly-sized heterospecific lizards because adults of these species were unlikely to prey on either.

Aside from *A. sagrei*, evidence that adults avoid cannibalism exists for at least one other species of anole: *A. cuvieri*, largest of the 11 species of anole native to Puerto Rico (Rand and Andrews, 1975). All five adult *A. cuvieri* (2♂, 3♀) in a breeding population maintained in a large outdoor enclosure ignored juvenile conspecifics presented on a tether, but readily accepted adult *A. limifrons* (a small Panamanian anole) the same size as the juvenile conspecifics similarly presented. Rand and Andrews also found small congeners, but no conspecifics, in the stomach contents of 3 of 14 museum specimens collected in Puerto Rico.

An explanation for why, and when, lizards with a territorial and polygynous social structure might benefit from not being cannibalistic is suggested by a study of curly-tailed lizards, *Leiocephalus schreibersi*, in Hispaniola (Jenssen et al., 1989) which found that large, territorial adults tended to be non-cannibalistic, whereas smaller, non-territorial adults generally were cannibalistic. Because territoriality and large size are good indicators of reproductive success in polygynous lizards (Stamps, 1983a), this suggests that cannibalism may be advantageous only for individuals with low reproductive success, as they run the least risk of eating their own offspring. Consistent with this prediction, the only juvenile anole found in a gut content analysis of *A. conspersus* (conducted on Grand Cayman prior to the arrival of *A. sagrei*) was eaten by a subadult male (Schoener, 1967). Because I intentionally used relatively large adult males as predators in this study, most of which were presumably territory holders and reproductively successful, this hypothesis might explain the relative lack of cannibalism observed as well as the tendency for smaller males to be more predatory than larger males.

Finally, there may be a historical explanation for why adult *A. sagrei* can distinguish juvenile conspecifics from similarly-sized heterospecific lizards, and, perhaps, why adult *A. carolinensis* and *A. conspersus* cannot. *Anolis sagrei* only recently colonized Florida and Grand Cayman from its native Cuba (Lieb et al,. 1983; Lee, 1992), where it occurs in sympatry with several other native anoles, whereas, until the arrival of *A. sagrei*, *A. carolinensis* and *A. conspersus* were the only anole species in Florida and Grand Cayman, respectively (Williams, 1969). Further, both *A. carolinensis* (Williams, 1969; Buth et al., 1980) and *A. conspersus* (Underwood and Williams, 1959; Hedges and Burnell, 1990) have been isolated long enough from their ancestral island populations in Cuba and Jamaica, respectively, for speciation to occur. Thus, isolation from other *Anolis* species may have led to a relaxation of selective pressures for conspecific recognition of juveniles in *A. carolinensis* and *A. conspersus* while maintaining a selected penalty to preying on any juvenile-sized lizards.

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APPENDIX: PART II

Table 2.1. Mass, snout-vent length (SVL), and head width of adult male *Anolis* used as predators, and mass and SVL of juvenile *Anolis* used as prey in predation experiments in Florida. Values are sample means, ± standard errors, and (ranges).

Predation Experiment Predators	Prey	*n*	Mass (g)	SVL (mm)	Head Width (mm)
Simultaneous					
A. carolinensis		27	3.8 ± 0.2 (2.4-5.3)	58.9 ± 0.8 (51-64)	9.0 ± 0.2 (7.6-10.5)
	A. carolinensis	27	0.29 ± 0.02 (0.15-0.51)	23.6 ± 0.5 (20-29)	—
	A. sagrei	27	0.28 ± 0.02 (0.14-0.49)	21.8 ± 0.4 (18-26)	—
A. sagrei		27	5.6 ± 0.2 (3.3-7.2)	59.3 ± 0.5 (54-63)	9.8 ± 0.2 (8.1-10.5)
	A. carolinensis	27	0.34 ± 0.02 (0.16-0.53)	25.1 ± 0.5 (21-30)	—
	A. sagrei	27	0.31 ± 0.02 (0.16-0.47)	22.9 ± 0.5 (19-27)	—
Sequential					
A. carolinensis		20	4.9 ± 0.2 (3.4-6.5)	63.0 ± 0.7 (59-70)	10.0 ± 0.1 (8.9-10.8)
	A. carolinensis	20	0.29 ± 0.02 (0.15-0.51)	23.9 ± 0.6 (20-29)	—
	A. sagrei	20	0.16 ± 0.01 (0.12-0.23)	18.6 ± 0.3 (17-21)	—
A. sagrei		20	6.3 ± 0.2 (4.0-7.9)	59.9 ± 0.7 (53-65)	10.0 ± 0.1 (8.7-10.6)
	A. carolinensis	20	0.32 ± 0.03 (0.17-0.53)	24.5 ± 0.7 (20-30)	—
	A. sagrei	20	0.23 ± 0.03 (0.12-0.50)	20.8 ± 0.7 (17-27)	—

Table 2.2. Mass, snout-vent length (SVL), and head width of adult male *Anolis* used as predators, and mass and SVL of *Sphaerodactylus argivus* and juvenile *Anolis* used as prey in predation experiments in Grand Cayman Island. Values are sample means, ± standard errors, and (ranges).

Predation Experiment Predators	Prey	*n*	Mass (g)	SVL (mm)	Head width (mm)
Simultaneous					
A. conspersus		20	7.7 ± 0.3 (6.1-11.4)	68.5 ± 0.6 (63-76)	11.4 ± 0.2 (10.1-13.0)
	A. conspersus	20	0.27 ± 0.01 (0.19-0.40)	23.6 ± 0.4 (22-28)	—
	A. sagrei	20	0.27 ± 0.02 (0.15-0.43)	22.8 ± 0.6 (19-27)	—
A. sagrei		20	4.7 ± 0.2 (2.8-6.6)	57.8 ± 0.7 (50-63)	9.3 ± 0.1 (8.2-10.3)
	A. conspersus	20	0.30 ± 0.02 (0.19-0.48)	24.9 ± 0.4 (22-28)	—
	A. sagrei	20	0.27 ± 0.02 (0.13-0.44)	22.8 ± 0.6 (19-27)	—
Sphaerodactylus					
A. conspersus		15	8.3 ± 0.4 (6.8-11.8)	68.3 ± 0.7 (64-73)	11.6 ± 0.2 (10.2-13.1)
	S. argivus	15	0.31 ± 0.03 (0.07-0.40)	23.1 ± 0.9 (14-26)	—
A. sagrei		15	3.8 ± 0.3 (1.9-5.3)	53.5 ± 1.3 (43-60)	8.7 ± 0.3 (7.1-9.8)
	S. argivus	15	0.26 ± 0.03 (0.07-0.38)	21.9 ± 1.2 (14-26)	—

Table 2.3. Absolute and relative mass and snout-vent length (SVL) of lizards used as prey in predation experiments classified by location, predator, and whether eaten. Data are combined for simultaneous and successive predation experiments in Florida, and for simultaneous and *Sphaerodactylus* predation experiments in Grand Cayman. Values are sample means, ± standard errors, and (ranges).

Location Predator	Eaten	*n*	Prey Mass (g)	Relative prey mass (% of Predator Mass)	Prey SVL (mm)	Relative prey SVL (% of Predator SVL)
Florida						
A. carolinensis	Yes	5	0.22 ± 0.03 (0.14-0.31)	6.3 ± 1.2 (3.3-10.3)	19.8 ± 1.0 (17-23)	33.4 ± 2.4 (28.3-41.8)
	No	89	0.26 ± 0.01 (0.12-0.51)	6.4 ± 0.3 (2.4-14.1)	22.3 ± 0.3 (17-30)	37.0 ± 0.6 (27.1-54.5)
A. sagrei	Yes	28	0.30 ± 0.02 (0.16-0.53)	5.3 ± 0.3 (2.6-8.9)	24.0 ± 0.5 (20-30)	40.6 ± 0.7 (33.9-48.4)
	No	66	0.31 ± 0.02 (0.12-0.53)	5.4 ± 0.3 (2.0-12.2)	23.4 ± 0.4 (17-30)	39.1 ± 0.7 (29.5-58.1)
Grand Cayman						
A. conspersus	Yes	4	0.23 ± 0.01 (0.22-0.24)	3.5 ± 0.1 (3.4-3.6)	22.5 ± 0.6 (21-24)	33.8 ± 0.8 (31.3-34.9)
	No	51	0.28 ± 0.01 (0.07-0.43)	3.6 ± 0.1 (1.0-5.7)	23.2 ± 0.4 (14-28)	33.8 ± 0.5 (20.9-40.0)
A. sagrei	Yes	20	0.26 ± 0.03 (0.07-0.48)	6.6 ± 0.5 (3.0-10.9)	23.0 ± 1.0 (14-29)	41.7 ± 1.2 (29.8-48.3)
	No	35	0.29 ± 0.01 (0.13-0.44)	6.1 ± 0.3 (2.8-8.7)	23.6 ± 0.4 (19-28)	40.8 ± 0.7 (32.2-47.2)

Table 2.4. Mass, snout-vent length (SVL), head width, and body condition of adult male *Anolis* used as predators in predation experiments classified by location, species, and whether predatory. Data are combined for simultaneous and successive predation experiments in Florida, and for simultaneous and *Sphaerodactylus* predation experiments in Grand Cayman. Values are sample means, ± standard errors, and (ranges).

Location Species	Predatory	n	Mass (g)	SVL (mm)	Head Width (mm)	Body condition $(\text{Mass}^{0.3}/\text{SVL})\times 100$
Florida						
A. carolinensis	Yes	5	3.6 ± 0.2 (3.0-4.2)*	59.6 ± 1.3 (55-63)	9.4 ± 0.3 (8.4-10.0)	2.46 ± 0.04 (2.34-2.57)*
	No	42	4.4 ± 0.2 (2.4-6.5)	60.7 ± 0.7 (51-70)	9.5 ± 0.1 (7.6-10.8)	2.55 ± 0.01 (2.29-2.71)
A. sagrei	Yes	25	5.8 ± 0.2 (3.8-7.9)	59.2 ± 0.5 (53-65)	9.8 ± 0.1 (8.7-10.6)	2.80 ± 0.02 (2.56-2.87)
	No	22	6.0 ± 0.2 (3.3-7.5)	59.9 ± 0.6 (54-63)	9.9 ± 0.1 (8.2-10.5)	2.84 ± 0.02 (2.63-2.97)
Grand Cayman						
A. conspersus	Yes	3	6.5 ± 0.2 (6.1-6.7)*	66.3 ± 1.8 (63-69)	10.8 ± 0.2 (10.5-11.0)	2.64 ± 0.05 (2.56-2.73)*
	No	32	8.1 ± 0.2 (6.1-11.8)	68.6 ± 0.5 (64-76)	11.6 ± 0.1 (10.1-13.1)	2.73 ± 0.01 (2.60-2.87)
A. sagrei	Yes	18	3.9 ± 0.3 (1.9-5.6)**	54.8 ± 1.2 (43-60)	8.8 ± 0.2 (7.1-9.9)*	2.72 ± 0.02 (2.56-2.88)*
	No	17	4.8 ± 0.2 (3.6-6.6)	57.5 ± 0.8 (52-63)	9.4 ± 0.1 (8.0-10.4)	2.78 ± 0.02 (2.65-2.96)

* $P < 0.05$, ** $P < 0.01$: predatory < non-predatory (t-test); Satterthwaite's approximation for the degrees of freedom was used when the F-test for equal variances had a $P < 0.05$; all differences in mass, but none in body condition, remain significant at the 0.05 level after applying the sequential Bonferroni technique (Rice, 1989) across groups for each variable to control the group-wide type-I error rate.

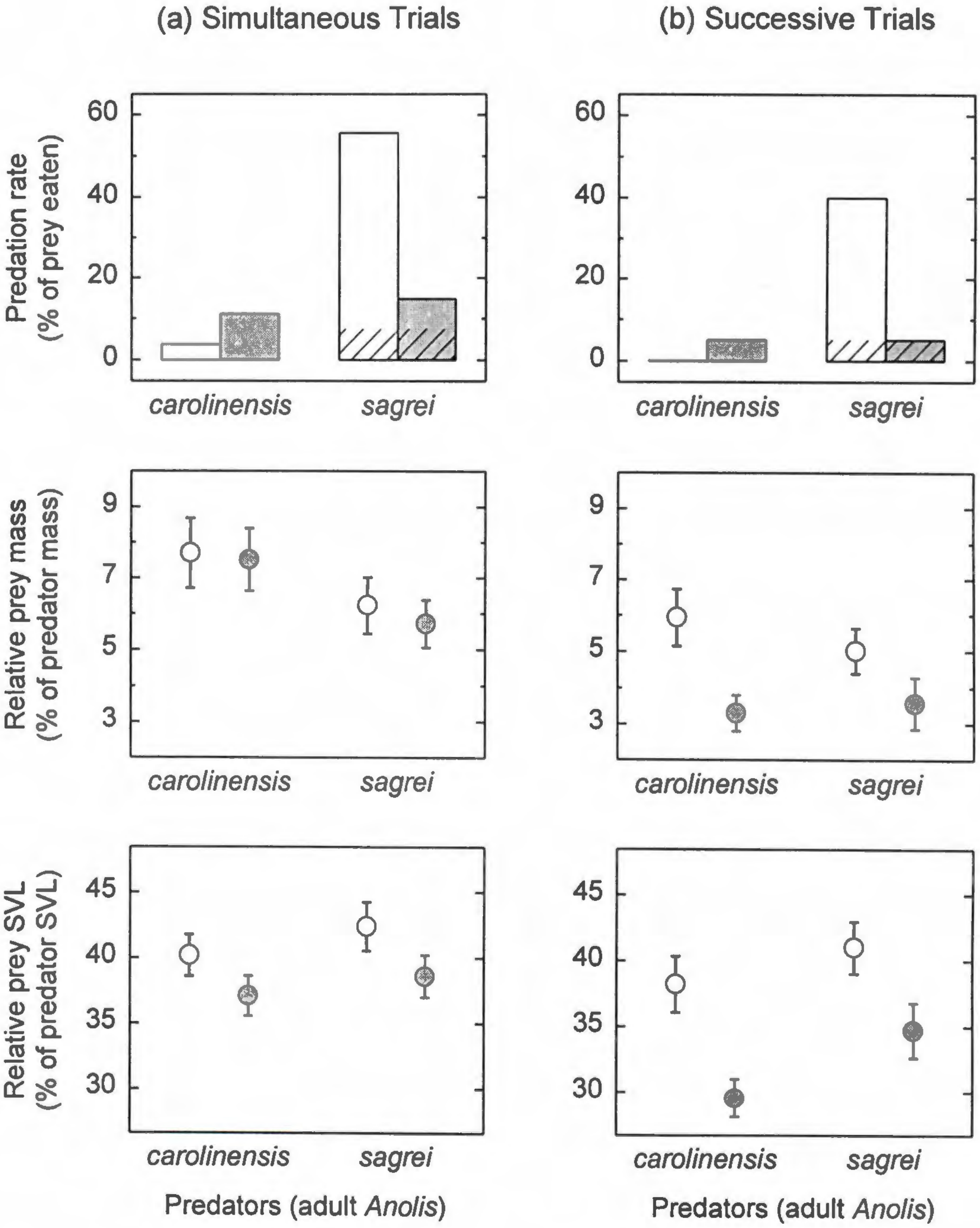

Figure 2.1. Predation, relative mass, and relative snout-vent length (SVL) of juvenile *Anolis carolinensis* (white) and *A. sagrei* (gray) used as prey in experiments with adult male *A. carolinensis* and *A. sagrei* predators in Florida. Two juvenile *Anolis*, one of each species, were presented to each predator simultaneously in (**a**) and successively in (**b**). Hatching indicates the percentage of predators that ate both prey. Error bars are 95% CIs of means. Refer to Table 1 for sample sizes and absolute mass and SVL of predators and prey.

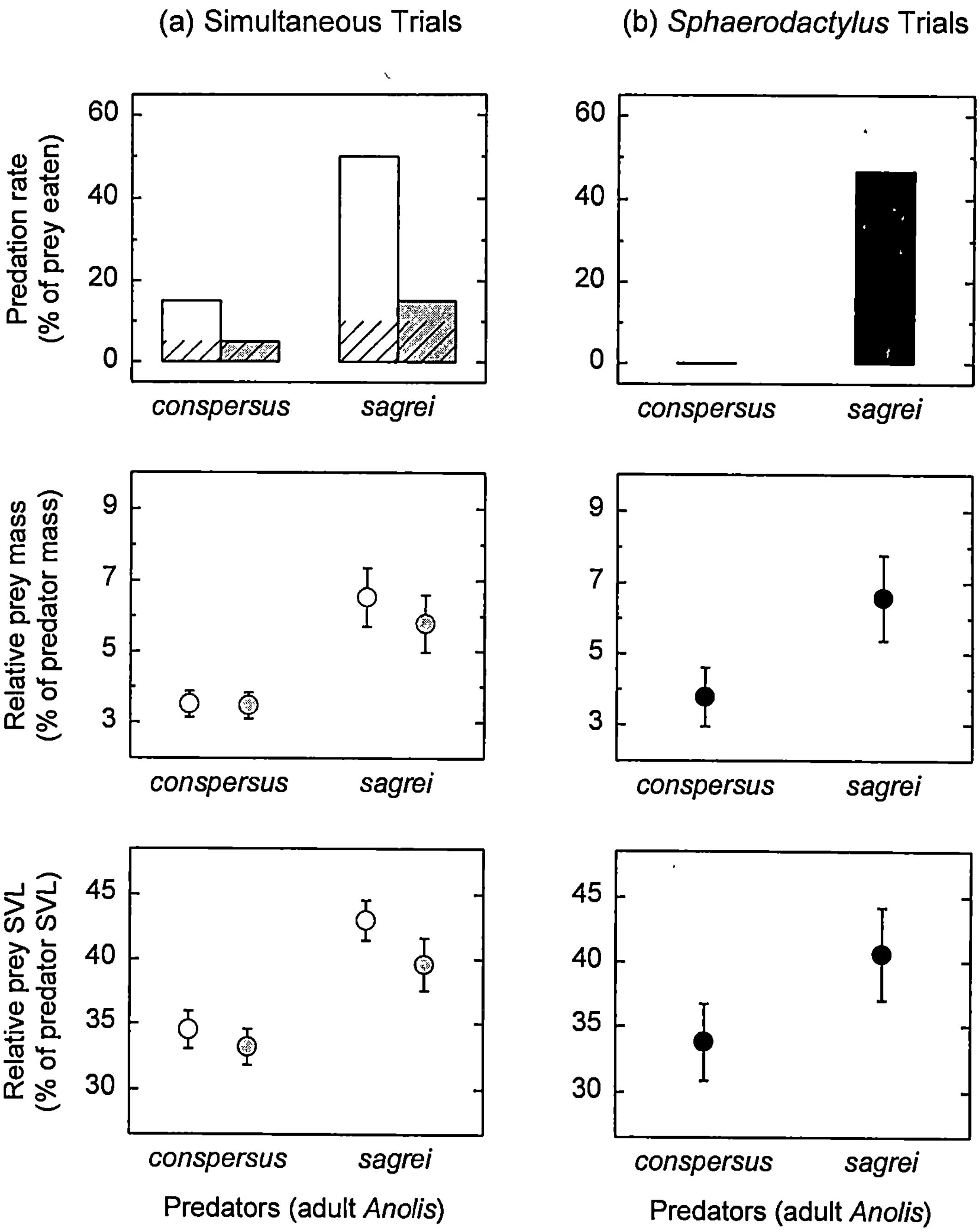

Figure 2.2. Predation, relative mass, and relative snout-vent length (SVL) of juvenile *Anolis conspersus* (white), juvenile *A. sagrei* (gray), and *Sphaerodactylus argivus* (black) used as prey in experiments with adult male *A. conspersus* and *A. sagrei* predators in Grand Cayman Island. Two juvenile *Anolis*, one of each species, were presented simultaneously to each predator in (**a**), whereas a single *S. argivus* was presented to each predator in (**b**). Hatching indicates the percentage of predators that ate both prey in simultaneous experiments. Error bars are 95% CIs of means. Refer to Table 2 for sample sizes and absolute mass and SVL of predators and prey.

PART III

Evidence for Asymmetrical Interference between the Endemic and Exotic *Anolis* Lizards of Grand Cayman

ABSTRACT

On the Caribbean island of Grand Cayman, the endemic anole, *Anolis conspersus* (Sauria: Polychrotidae), is ubiquitous but more abundant in wooded habitats than in open habitats, whereas the introduced anole, *A. sagrei*, is abundant in open habitats and rarely found in wooded habitats. Because *A. sagrei* occupies wooded habitats elsewhere, I hypothesized that *A. conspersus*, which are larger than *A. sagrei*, aggressively exclude *A. sagrei* from wooded habitats in Grand Cayman. To investigate this possibility, and to compare inter- and intraspecific aggression for each species, territorial intrusions were staged in the field by presenting free-ranging adult male residents of both species with tethered conspecific or heterospecific intruders. Residents of both species were highly aggressive toward conspecific intruders, but only resident *A. conspersus* approached and attacked heterospecific intruders. Thus, interspecific differences in size and aggression suggest that *A. conspersus* are both able and apt to aggressively exclude *A. sagrei* from preferred habitats. To investigate whether *A. conspersus* would respond aggressively to other anole species, resident *A. conspersus* were presented with intruders of a novel species, *A. maynardi*, endemic to Little Cayman Island and intermediate in size between *A. conspersus* and *A. sagrei*. Resident *A. conspersus* were equally likely to display to, approach, and attack *A. maynardi*, *A. sagrei*, and conspecific intruders. However, resident *A. conspersus* were less likely to exhibit postural modifiers (gular extension, sagittal expansion, or crest erection) with *A. maynardi* or *A. sagrei* than with conspecific

intruders. Further, although size differences between residents and intruders were often an important covariate, statistically adjusting for size differences between paired lizards could not explain the differences between conspecific and heterospecific encounter types for resident *A. conspersus* or *A. sagrei*. Thus, both intruder size and species were important determinants of resident behavior. These findings, particularly when combined with those of other studies, suggest (1) that both *A. conspersus* and *A. sagrei* distinguish conspecifics from heterospecific anoles, although possibly not among heterospecific anole species, and (2) that *A. conspersus* has a generalized territorial response to similarly-sized heterospecific anoles, whereas *A. sagrei* does not. Coexistence of *A. sagrei* with *A. conspersus* appears to hinge on interspecific differences that permit *A. sagrei* to exploit those habitats where *A. conspersus* are least abundant.

INTRODUCTION

Within guilds of territorial animals, interspecific differences in habitat use are often maintained through aggressive interaction (Morse 1974, 1980; Murray, 1981; Connor and Bowers, 1987). Because strength and fighting ability typically increase with increasing body size, larger species are usually socially dominant over smaller species. In contrast, because individual food requirements decrease with decreasing body size, smaller species are often more efficient exploitative competitors than larger species (Wilson, 1975; Persson, 1985). Consequently, in sympatry, subordinate species should experience a greater contraction of niche space than dominant species due to interference, but should have a competitive advantage in habitats where the dominant species is limited by the availability of resources other than space (Case and Gilpin, 1974). Such interactions frequently result in habitat partitioning, with socially dominant species occupying more productive habitats or patches than subordinate species (Jenssen et al., 1984; Robinson and Terborgh, 1995; Robertson, 1996).

When interference is highly asymmetrical, interspecific aggression does not have to be as intense as intraspecific aggression to cause exclusion or habitat partitioning (Case and Gilpin, 1974). Furthermore, exclusion or habitat partitioning may result from the avoidance of dominant species by subordinate species, rather than from overt aggressive interaction (Hixon, 1980; Morse, 1980; Erlinge and Sandell, 1988; Petren et al., 1993). In such situations, the importance of interspecific aggression may be overlooked and, consequently, other potential mechanisms of habitat partitioning may be overestimated.

When interspecific aggression occurs between closely related species it is generally hypothesized to result from misdirected conspecific aggression (i.e., mistaking other species for conspecific competitors) or from an adaptive response to present or past interspecific competition (Ortiz and Jenssen, 1982; Jenssen et al., 1984; Nishikawa, 1987; Hess and Losos, 1991). Thus, investigating the causal basis of interspecific aggression, in addition to its strength and symmetry, may provide valuable information regarding the origin and adaptive value of interference.

Here, I investigate the hypothesis that aggression between two territorial and polygynous species of *Anolis* (Sauria: Polychrotidae) found on Grand Cayman Island is asymmetric and consistent with expectations based on interspecific differences in body size and habitat occupancy. In addition, I investigate possible causes of interspecific aggression. The species are *A. conspersus*, endemic to Grand Cayman (Grant, 1940), and *A. sagrei*, inadvertently introduced to Grand Cayman about 20 years ago (Minton and Minton, 1984). As with many other territorial and polygynous lizards, including many other anoles (Stamps, 1983), adult male *A. conspersus* and *A. sagrei* are larger than adult female conspecifics and defend territories against adult male conspecifics (Schoener, 1967; Schoener and Schoener, 1980, 1982; Schwartz and Henderson, 1991; Losos et al., 1993). Compared with other anoles, *A. conspersus* and *A. sagrei* are considered medium-sized and ecologically unspecialized (Williams, 1969). *Anolis sagrei* are, however, somewhat smaller, less arboreal, and more heliothermic than *A. conspersus* (Losos et al., 1993). *Anolis sagrei* are considered "trunk-ground" anoles, as they typically utilize the trunks of trees and the ground, whereas *A. conspersus* are considered "trunk-crown" anoles, as they typically utilize the trunks and crowns of trees (Williams, 1969). *Anolis conspersus* are found almost everywhere on Grand Cayman, but are most abundant in wooded habitats (Schoener, 1967; Avery, 1988; Losos et al., 1993). In contrast, *A. sagrei*, which have colonized much of Grand Cayman since being introduced, are essentially absent from wooded habitats, but are locally abundant, often outnumbering *A. conspersus*, in urban areas and other disturbed habitats (Minton and Minton, 1984; Franz et al. 1987; Avery, 1988; Losos et al., 1993). Although species differences could account for the observed spatial segregation of *A. sagrei* and *A. conspersus* on Grand Cayman, two observations suggest that interference is involved. First, in other locations where *A. sagrei* occurs naturally, including the nearby islands of Little Cayman and Cayman Brac, it occupies wooded habitats similar to those on Grand Cayman (Lister, 1976; Losos et al., 1993; personal observation). Second, although overt interactions between *A. sagrei* and *A. conspersus* are rare, male *A. conspersus* have been observed chasing and supplanting male *A. sagrei*, but not vice versa (personal observation). Therefore, despite the considerable success of introduced *A. sagrei* on Grand Cayman, I hypothesized that *A. sagrei* was aggressively excluded from wooded habitats on Grand Cayman by native *A. conspersus*, which is larger and more widely distributed. In addition, because *A. conspersus* was the only anole on Grand Cayman prior to the introduction of *A. sagrei*, I ask whether interspecific aggression might be the result of misidentification, a learned response to interspecific competition, or a generalized preexisting (i.e., ancestrally acquired) adaptation to all potential anole competitors of similar size.

To investigate the symmetry of aggression between *A. conspersus* and *A. sagrei*, and whether, for either species, interspecific aggression might result from the misidentification of heterospecifics as conspecific, I presented free-ranging residents of both species with tethered conspecific or heterospecific intruders and recorded the occurrence, latency, and frequency of aggressive behaviors exhibited by residents. In addition, to determine if interspecific aggression in *A. conspersus* is specific to *A. sagrei* or generalized to all anoles of a similar size, I also measured the response of resident *A. conspersus* to intruder *A. maynardi*, a species endemic to nearby Little Cayman Island that is similar in size but not appearance to *A. sagrei* and with which *A. conspersus* had no prior experience. Results of these experiments suggest that (1) interspecific aggression is highly asymmetrical in favor of *A. conspersus*, (2) both *A. conspersus* and *A. sagrei* distinguish conspecifics from heterospecific anoles, although possibly not among heterospecific anole species, and (3) that *A. conspersus* has a generalized territorial response to similarly-sized heterospecific anoles, whereas *A. sagrei* does not. Thus, interspecific aggression in *A. conspersus* appears to be a conserved ancestral trait and coexistence of *A. sagrei* with *A. conspersus* appears to hinge on interspecific differences that permit *A. sagrei* to exploit those habitats where *A. conspersus* are least abundant.

METHODS

Study Sites

I conducted all fieldwork on Grand Cayman, a small (197 km^2), low-lying (maximum elevation 18 m), geographically remote island, located about 300 km from both Cuba and Jamaica at 19° N and 81° W (Brunt and Davies, 1994). Grand Cayman has a sub-humid tropical climate with distinct wet and dry seasons (Burton, 1994). Like many other low-lying limestone islands in the Caribbean, the native vegetation is predominantly dry evergreen woodland and thicket (Brunt, 1994). I used several different study areas located in semi-natural suburban habitats in the southwest part of the island, near George Town, where *A. conspersus* and *A. sagrei* are widely sympatric.

Subjects

Anolis conspersus is endemic to Grand Cayman and is most closely related to *A. grahami* of Jamaica (Grant, 1940; Underwood and Williams, 1959; Hedges and Burnell, 1990; Jackman et al., 1999). Males reach 77 mm snout-vent length (SVL) and 12.5 g (G. Gerber and A. Echternacht, unpublished data), have a heavily spotted or vermiculated pattern, and a brilliant sky-blue dewlap. Male body color varies from grayish-blue to yellowish-green in the light phase, and from reddish-brown to very dark brown in the dark phase.

Anolis sagrei evolved on Cuba and subsequently colonized parts of the Central American coast, the western Bahamas, and many small Caribbean islands, including two of the three Cayman Islands: Cayman Brac and Little Cayman (Williams, 1969). *Anolis sagrei* is, however, a recent addition to the fauna of Grand Cayman (Minton and Minton, 1984), likely introduced about 20 years ago with nursery stock imported from Florida (Franz et al., 1987; F. Burton, Personal Communication), where *A. sagrei* is also introduced (Godley et al., 1981; Lee, 1985). On Grand Cayman, males reach 69 mm SVL and 8.0 g (this study), and have a bright reddish-orange dewlap with a yellow border. Male body color and pattern varies from grayish-tan with faint brown mottling in the light phase to very dark brown with distinct, almost black mottling in the dark phase.

In addition, the sides of the body are patterned with small vertical yellow stripes and dots in the dark phase. Both *A. conspersus* and *A. sagrei* are β anoles (Etheridge, 1960).

Anolis maynardi is endemic to Little Cayman Island (Grant, 1940), located approximately 130 km west-northwest of Grand Cayman (Brunt and Davies, 1994), and is most closely related to *A. porcatus* of Cuba (Williams, 1969, 1976). Males reach at least 78 mm SVL and 7.8 g (this study), are nearly patternless, and have a pale yellow or peach-colored dewlap. Male body color varies from drab olive- to bright leaf-green in the light phase, and from tan to very dark brown in the dark phase. In addition, there are several pale, broken, horizontal stripes on the neck and shoulders, only distinct in the light phase, which sometimes turn turquoise. Compared with *A. conspersus* and *A. sagrei*, *A. maynardi* have a slender build and more elongate head. *Anolis maynardi* is an α anole (Etheridge, 1960) and member of the *carolinensis* superspecies (Williams, 1976).

Data Collection

I staged dyadic interactions between adult male anoles between late May and early August in 1989, 1990, and 1993. This period coincides with the summer wet season and with intense reproductive and territorial activity of all three species. I staged encounters by placing tethered intruders in the territories of free-ranging residents. Fifteen replicates of each of the following encounter types were staged: (1) resident *A. sagrei* and intruder *A. sagrei*, (2) resident *A. sagrei* and intruder *A. conspersus*, (3) resident *A. conspersus* and intruder *A. conspersus*, (4) resident *A. conspersus* and intruder

A. sagrei, and (5) resident *A. conspersus* and intruder *A. maynardi.* I staged encounters between 0830 and 1800 hours on warm (29 to 32 C), primarily sunny days.

Noose-poles were used to capture lizards used as intruders. Intruder *A. conspersus* and *A. sagrei* were captured on Grand Cayman the same day as staging encounters, and intruder *A. maynardi* were captured on Little Cayman and transported to Grand Cayman the day before staging encounters. Each intruder was placed in a plastic box (20 × 15 × 10 cm) with a screen lid until needed. Boxes were kept in the shade under ambient environmental conditions. Each anole was used in only one encounter.

To initiate an encounter, I positioned an intruder approximately 1 m from a perched resident. Because at least one species of *Anolis* has been shown to exhibit the dear enemy effect (i.e., to respond less aggressively to neighbors: Qualls and Jaeger, 1991), I presented residents with intruders from different field sites. Intruders were introduced by tethering them to the end of a wooden pole (about 2.5 m in length and 2 cm in diameter) with 0.5 m of green cotton thread (secured around the lizard's waist by a slip knot) and slowly extending the end of the pole toward a resident's perch from a distance of about 3 m. If the resident fled during this process, I aborted the encounter and repositioned the intruder near a different resident. Repositioning was required in approximately 10% of all encounters. Upon successfully positioning an intruder near a resident, I leaned the pole against the resident's perch (e.g., tree trunk), backed away to about 5 m, and observed the interaction through binoculars. I focused on the behavior of residents to determine their response to intruders. Because residents were not handled or tethered, I assumed their response would be similar to that during a naturally occurring territorial intrusion. However, the behavior of intruders could not be controlled, varied widely, and thus was a source of experimental error.

I was not concealed from the subjects during encounters, but anoles appeared to be unaffected by my presence, once the pole was in position. Furthermore, Sugerman (1990) demonstrated that *A. sagrei*, and thus likely other anoles, are insensitive to unobtrusive observers during staged agonistic encounters. My methods are similar to those used by other researchers investigating aggressive interactions between anoles (Evans, 1938; Gorman, 1968, 1976; Trivers, 1976; Stamps, 1983; Fitch and Henderson, 1987; Fitch et al., 1989; Hess and Losos, 1991; Losos, 1996).

For each encounter, I recorded the occurrence of the following agonistic behaviors (Table 3.1) exhibited by residents: display, gular extension, sagittal expansion, crest erection, approach, and attack. I chose these behaviors because they are common to all anoles, represent an increasing progression in aggressiveness (Greenberg, 1977; Jenssen, 1977), and can be reliably detected in the field. Using a stopwatch, I also recorded the latency (± 1 s) of these behaviors, from the moment the intruder was introduced, as well as the duration of each encounter. Finally, I recorded the total number of display bouts performed by residents. I defined a display bout as any continuous sequence of displays (dewlaps, headbobs, and pushups: see Table 3.1) temporally separated from other such sequences. I ended encounters when either subject attacked the other (to avoid injury to anoles) or any of the following occurred: (1) the resident moved away from and out of sight of the intruder, (2) no aggressive behaviors were recorded for a span of 10 min, or (3) 60 min elapsed without an attack.

At the end of each encounter, I captured the resident with a noose-pole and measured both subjects for SVL (± 1 mm) using a 150 mm rule, and mass (± 0.1 g) using a 10 or 30 g spring scale (± 0.3% accuracy: Pesola® Scales, Switzerland). To avoid using the same anoles in future encounters, I marked all subjects with a drop of paint before returning them to their respective capture sites. I returned *A. maynardi* to Little Cayman the day after staging encounters.

Data Analysis

To determine if there were significant differences between *A. sagrei* and *A. conspersus* residents in their reaction to conspecific intruders, I compared conspecific encounters of the two species. Then, separately for residents of each species, I compared encounters with conspecific intruders to those with heterospecific intruders to determine if there were significant differences between conspecific and heterospecific encounter types. Finally, for resident *A. conspersus*, I compared encounters with *A. maynardi* intruders to those with *A. sagrei* intruders to determine if there were significant differences between heterospecific encounter types. Consequently, I made five pairwise comparisons between the five encounter types (Table 3.2).

To determine if there were significant differences between encounter types in the occurrence of individual behaviors, I used a likelihood ratio chi-square test of independence (*G*-test) with Williams' correction to minimize the type-I error. Sokal and Rohlf (1995) recommend this test when the marginal totals of a contingency table are fixed for only one criterion (i.e., Model II tests for independence). To determine if there were significant differences between encounter types in the latency of each behavior, in display frequency, and in encounter duration, I used a sampled randomization test described by Adams and Anthony (1996). The test compares the observed treatment sum of squares for a given data set to a frequency distribution of possible treatment sum of squares generated by calculating the treatment sum of squares for each of 5000 random reassignments of the same data values into the treatment groups. The statistical power of this test is 0.999, thus it provides a significant advantage over more conventional tests (e.g., Wilcoxon rank-sum test), especially for small data sets (Adams and Anthony, 1996). For the analysis of latencies, I treated observations of residents that did not exhibit the behavior as missing.

To determine the approximate sequence in which residents exhibited behaviors, behaviors were ranked by their order of occurrence for each contest (following J. Macedonia, unpublished manuscript). When two or more behaviors occurred simultaneously, they were given an average rank value. Thus, for each behavior, a set of order of occurrence values (potentially one value per contest) was produced. Then, for each encounter type, behaviors were ranked against one another by their median order of occurrence values. All ties were settled using maximum and minimum rank order values.

To determine the significance of body size differences between paired lizards within encounter types, I used the Wilcoxon signed-rank test. To determine the significance of body size differences between paired lizards between encounter types, I first standardized the data by expressing the mass and SVL of intruders as the percent difference from the mass and SVL of the resident they were paired with. To do this, I used the following formula: relative intruder body size = ((intruder body size/resident body size) – 1)100. Differences between encounter types in relative intruder body size were then compared using the Wilcoxon rank-sum test.

Finally, because of variation in the body size difference between paired lizards, both within and between encounter types, I performed additional analyses to determine (1) if relative intruder body size had a significant effect on the behavior of residents, and (2) if adjustment for the effects of relative intruder body size could explain the observed differences in behavior between encounter types. I used logistic (maximum likelihood) models to investigate the effects of relative intruder body size on the occurrence of behaviors, and general linear (least squares) models to investigate the effects of relative intruder body size on the latency of behaviors, display frequency, and encounter duration. Because analysis of covariation (ANCOVA) assumes homogeneity of slopes across treatment groups, I first tested for interaction between relative intruder body size and encounter type. When a significant interaction was found, I ran a separate slopes analysis, by nesting relative intruder body size within encounter types, to determine the nature of the interaction. Only when the interaction was insignificant ($P > 0.05$) did I perform an ANCOVA.

I used SAS version 6.10 (SAS® Institute Inc., Cary, NC) for all statistical analyses, all tests were two-tailed, and probabilities ≤ 0.05 were considered significant. Because inferences were drawn by comparing the five encounter types or the five pairwise comparisons between encounter types (Table 3.2), the sequential Bonferroni procedure was used to maintain a group-wide type-I error rate of 0.05 (Rice, 1989).

RESULTS

Behavioral Comparisons between Encounter Types

Conspecific encounters compared for resident *A. sagrei* and *A. conspersus* - Most resident *A. sagrei* and *A. conspersus* paired with conspecific intruders exhibited all of the behaviors recorded (Figures 1 and 2), and there were no significant differences between species in latency (Figure 3.3). However, resident *A. sagrei* generally attacked conspecific intruders more quickly than did resident *A. conspersus*. Accordingly, encounters between *A. sagrei* were significantly shorter in duration than those between *A. conspersus* (Figure 3.4). Resident *A. sagrei* also displayed significantly more frequently to conspecific intruders than did resident *A. conspersus* (Figure 3.5). Behavioral sequences were similar for both conspecific encounter types (Table 3.3). Residents generally displayed first, then approached, postured, and finally attacked. There was, however, considerable sequential variability within encounter types, as evidenced by a comparison of the minimum and maximum rank order values for individual behaviors.

Heterospecific and conspecific encounters compared for resident *A. sagrei* - Resident *A. sagrei* exhibited significantly fewer behaviors in encounters with *A. conspersus* intruders than with conspecific intruders (Figure 3.1). In particular, resident *A. sagrei* were significantly less likely to erect a crest, approach, or attack in encounters with *A. conspersus* intruders than with conspecific intruders (Figure 3.2). Of the 14 *A. sagrei* residents that did not attack *A. conspersus* intruders, seven left the area, five remained but exhibited little aggression toward the intruder, and two were attacked by the intruder. The latter were the only staged encounters in which the intruder initiated an attack. When resident *A. sagrei* did exhibit aggressive behaviors with *A. conspersus* intruders, latencies tended to be longer than in encounters with conspecific intruders (Figure 3.3). Reflecting this, encounters with *A. conspersus* were significantly longer in duration than those with conspecific intruders (Figure 3.4). Furthermore, although resident *A. sagrei* were as likely to display to *A. conspersus* intruders as to conspecific intruders (Figure 3.2), they displayed significantly less frequently to *A. conspersus* intruders than to conspecific intruders (Figure 3.5). Behavioral sequences of resident *A. sagrei* with heterospecific intruders were similar to those with conspecific intruders (Table 3.3), suggesting that encounters with *A. conspersus* intruders were simply terminated at an early stage of assessment.

Heterospecific and conspecific encounters compared for resident *A. conspersus* - Resident *A. conspersus* exhibited significantly fewer behaviors in encounters with heterospecific intruders than in encounters with conspecific intruders (Figure 3.1). However, unlike resident *A. sagrei*, resident *A. conspersus* were as likely to approach and attack heterospecific intruders as they were conspecific intruders (Figure 3.2). Furthermore, resident *A. conspersus* tended to attack *A. sagrei* intruders more quickly than conspecific intruders (Figure 3.3). In contrast, resident *A. conspersus* were significantly less likely to exhibit gular extension, sagittal expansion, or crest erection in encounters with *A. sagrei* or *A. maynardi* intruders than with conspecific intruders (Figure 3.2) and, when they did, latencies were generally longer than in encounters with conspecific intruders (Figure 3.3). Resident *A. conspersus* were also less likely to display to *A. sagrei* intruders than to conspecific intruders (Figure 3.2). All of these patterns are evident in the rank ordering of behaviors exhibited by resident *A. conspersus* in encounters with heterospecific intruders as opposed to conspecific intruders (Table 3.3). No significant differences were observed in encounter duration or display frequency between the conspecific encounters and either heterospecific encounter type of resident *A. conspersus* (Figures 3.4 and 3.5).

Heterospecific encounter types compared for resident *A. conspersus* - Encounters between resident *A. conspersus* and *A. sagrei* or *A. maynardi* intruders were similar in the number of behaviors exhibited (Figure 3.1), encounter durations (Figure 3.4), display frequencies (Figure 3.5), and rank ordering of behaviors exhibited (Table 3.3). Resident *A. conspersus* were, however, significantly more likely to display to *A. maynardi* intruders than to *A. sagrei* intruders (Figure 3.2), and behavioral latencies of resident *A. conspersus* were generally longer in encounters with *A. maynardi* intruders than with *A. sagrei* intruders, although only the latency to attack was significantly different among encounter types (Figure 3.3).

Body Size Differences between Paired Lizards and Effects on Behavior

Because of randomly pairing adult males for each encounter type, there was considerable variation in the size difference between paired lizards in all encounter types (Table 3.4 and Figure 3.6). For conspecific encounter types, median differences in SVL and mass between paired lizards were not significantly different from zero (Table 3.4), and relative intruder SVL and mass did not differ significantly between species (Figure 3.6). In contrast, due to interspecific differences in the size of adult males, all heterospecific encounter types were marked by asymmetry in the size difference between paired lizards (Table 3.4 and Figure 3.6). *Anolis sagrei* residents were significantly smaller in SVL and mass than the *A. conspersus* intruders they were paired with, whereas *A. conspersus* residents were significantly larger in SVL and mass than the *A. sagrei* intruders they were paired with, and larger in mass (but not SVL) than the *A maynardi* intruders they were paired with (Table 3.4). Accordingly, for *A. sagrei* residents, relative intruder SVL and mass were significantly larger for heterospecific encounters than for conspecific encounters, whereas the opposite was true for *A. conspersus* residents, although *A. maynardi* intruders only differed in relative mass from conspecific intruders (Figure 3.6).

The effects of relative intruder size on the behavior of resident lizards are summarized in Tables 3.5, 3.6, and 3.7. Not surprisingly, within all encounter types, behaviors were often dependent upon relative intruder size, increasing or decreasing in frequency of occurrence or latency with relative intruder size (Tables 3.5, 3.6, and 3.7). However, the degree to which adjustment for size effects statistically removed or reduced the magnitude of behavioral differences between encounter types varied with the encounter types being compared. Although there were few significant differences in behavior between the conspecific encounters of *A. sagrei* and those of *A. conspersus*, none of these differences could be removed by adjusting for the effects of relative intruder size (Tables 3.5, 3.6, and 3.7). Thus, as expected, differences between the conspecific encounters of *A. sagrei* and *A. conspersus* appear to reflect behavioral differences between the species. In contrast, each of the significant differences in behavior between the encounters of resident *A. conspersus* with *A. maynardi* or *A. sagrei* intruders could be removed by adjusting for the effects of relative intruder size (Tables 3.5, 3.6, and 3.7). Thus, behavioral differences between these encounter types were adequately explained by differences in relative intruder size alone (i.e., the fact that *A. maynardi* are larger than *A. sagrei*), suggesting that resident *A. conspersus* may not differentiate *A. sagrei* intruders from *A. maynardi* intruders. Finally, for resident *A.*

sagrei and resident *A. conspersus*, some of the significant differences observed in behavior between heterospecific and conspecific encounter types could be removed or reduced in magnitude by adjusting for differences in relative intruder size, whereas others could not (Tables 3.5, 3.6, and 3.7). Furthermore, the effect of relative intruder size on resident behavior was frequently different for conspecific and heterospecific encounter types, as evidenced by significant interactions between relative intruder size and encounter type (Tables 3.5, 3.6, and 3.7). Thus, both the relative sizes and species of intruders were important determinants of the behavioral differences observed between conspecific and heterospecific encounter types, suggesting that resident *A. sagrei* and resident *A. conspersus* differentiate heterospecific intruders from conspecific intruders.

Finally, the nature of the relationship between behavioral measures and relative intruder size often varied when compared across encounter types, according to whether intruders were generally smaller than, equal to, or larger than residents in size. This was particularly evident for behavioral postures: gular extension, sagittal expansion, and crest erection (see Tables 3.5 and 3.6). In general, residents were more likely to exhibit postures with intruders that were similar in size than with those that were much larger or smaller. *Anolis conspersus* were generally larger than *A. sagrei* and *A. maynardi*, and resident *A. conspersus* were more likely to exhibit postures with relatively large heterospecific intruders than with relatively small heterospecific intruders, whereas the opposite was true for resident *A. sagrei* (Table 3.5). Furthermore, there was generally an inverse relationship between the likelihood of a behavior occurring and the latency until occurrence, as evidenced by a comparison of slopes in Tables 3.5 and 3.6 for the same behaviors and encounter types. In other words, behavioral latencies generally increased as the likelihood of occurrence decreased, indicating that residents were not only less likely to exhibit most behaviors in encounters with intruders that were much smaller or much larger, but also took longer to do so when they did.

DISCUSSION

Ecological Implications of Interspecific Aggression

Intraspecific aggression was intense and similar in *A. conspersus* and *A. sagrei*, but interspecific aggression was highly asymmetric. Resident *A. conspersus* were just as likely to attack heterospecific intruders as conspecific intruders, whereas resident *A. sagrei* were significantly less likely to do so. This is consistent with interspecific patterns of body size and habitat occupancy and supports the hypothesis that native *A. conspersus* aggressively exclude introduced *A. sagrei*, which are smaller, from wooded habitats on Grand Cayman. Nevertheless, the absence of *A. sagrei* from wooded habitats on Grand Cayman could also result from different habitat preferences or physiological requirements. On Grand Cayman, *A. sagrei* spend more time perched in the sun and maintain higher body temperatures than *A. conspersus* (Losos et al., 1993). Consequently, because wooded habitats are more shaded than open habitats, it's possible that *A. sagrei* are restricted to open habitats on Grand Cayman by thermoregulatory requirements (Losos et al., 1993). However, observations of *A. sagrei* from elsewhere in its range argue against this hypothesis. First, *A. sagrei* are abundant in wooded habitats on many of the islands where they occur naturally (Schoener, 1968; Lister, 1976; Schoener and Schoener, 1980), as well as in Florida where they are introduced (Lee, 1980; Salzberg, 1984; G. Gerber, unpublished data). Second, *A. sagrei* occupying wooded habitats on other islands (Lister, 1976) and in Florida (Lee, 1980; G. Gerber, unpublished data) spend less time perched in the sun and maintain lower body temperatures than conspecifics occupying nearby open habitats. This suggests that temperature regulation is quite plastic in *A. sagrei*, as it is in some ecologically similar anoles (e.g., *A. cristatellus*: Huey, 1974). Third, where *A. sagrei* occupy wooded habitats, they sometimes do so despite the presence of species ecologically similar to *A. conspersus* (Schoener, 1968; Schoener and Schoener, 1980). For example, in Florida, *A. sagrei* have invaded wooded habitats despite the presence of *A. carolinensis* (Wilson and Porras, 1983; G. Gerber, unpublished data), a native anole, closely related to *A. maynardi* of Little Cayman, which has been described as an ecological analog of *A. conspersus* (Williams, 1969). Unlike *A. conspersus*, however, *A. carolinensis* exhibit little aggression toward *A. sagrei* in staged encounters (Tokarz and Beck, 1987; Brown, 1988; G. Gerber and M. Kramer, unpublished manuscript). Fourth, because *A. sagrei* were most likely introduced to Grand Cayman only about 20 years ago (Franz et al., 1987; F. Burton, personal communication), it is unlikely that differences in habitat occupancy between Florida and Grand Cayman populations are genetically based (see also Lee, 1992). Finally, in an area of Florida where introduced *A. sagrei* are sympatric with introduced *A. cristatellus*, an interspecifically aggressive trunk-ground anole native to the Puerto Rican Bank (Ortiz and Jenssen, 1982; Jenssen et al., 1984; Hess and Losos, 1991), Salzberg (1984) documented an increase in the use of arboreal and shady perches by *A. sagrei* when *A. cristatellus* were removed. Thus, the results of my study combined with other available evidence suggests that the absence of *A. sagrei* from wooded habitats on Grand Cayman is most likely attributable to behavioral interference from *A. conspersus*, rather than to thermal constraints or narrow habitat preferences. Experimental manipulations of population densities will be required to test this hypothesis further, however. If habitat occupancy, and therefore abundance, of *A. sagrei* are limited through aggressive interference from *A. conspersus*, the removal of *A. conspersus* should result in *A. sagrei* invading wooded habitats and increasing in abundance (see Part IV).

Interspecific Aggression in *A. conspersus*

Results of my experiments demonstrate that male *A. conspersus* are highly aggressive toward male anoles of other similarly sized species. Why might this be? Interspecific aggression is generally hypothesized to result from either (1) misdirected conspecific aggression (i.e., mistaking other species for conspecific competitors) or (2) an adaptive response to interspecific competition (Ortiz and Jenssen, 1982; Jenssen et al., 1984; Nishikawa, 1987; Hess and Losos, 1991). In the case of *A. conspersus*, an island endemic long isolated from other anole species until the recent arrival of *A. sagrei*, the former hypothesis seems plausible at first glance. Upon closer examination, however, misidentification seems unlikely as *A. conspersus* and *A. sagrei* have unique head-bobbing patterns (Macedonia and Stamps, 1994) and differ markedly in physical appearance, including dewlap and body coloration. Moreover, although *A. conspersus* residents were just as likely to approach and attack *A. sagrei* intruders as conspecific intruders, they were less likely to exhibit most other behaviors with *A. sagrei* intruders and typically took longer to do so when they did. Furthermore, although some of these behavioral differences were attributable to interspecific differences in body size, encounters with *A. sagrei* intruders still differed significantly from encounters with conspecific intruders after adjusting for the effects of relative intruder size. Thus, at some point during encounters, *A. conspersus* residents identified *A. sagrei* intruders as non-conspecific. Consequently, the results of my experiments do not support a hypothesis of misidentification as an explanation for the aggression exhibited by *A. conspersus* toward *A. sagrei.*

An adaptive explanation for this behavior is not obvious either, as there seems to have been no opportunity for selection of interspecific aggression in *A. conspersus* until extremely recently (i.e., until the introduction of *A. sagrei*). It is possible, of course, that the interspecific aggression exhibited by *A. conspersus* is not heritable, but acquired through experience with *A. sagrei.* If so, however, resident *A. conspersus* should have discriminated between *A. sagrei*, a stimulus they had experience with, and *A. maynardi*, a stimulus they had no experience with. Yet after adjusting for the effects of relative intruder size, there was no indication that resident *A. conspersus* discriminated between intruder *A. sagrei* and *A. maynardi*, despite the pronounced morphological differences between these species. This suggests that interspecific aggression in *A. conspersus* is not a learned response to a specific stimulus (i.e., *A. sagrei*), but rather an innate, generalized response to all heterospecific stimuli within a certain size range.

Consequently, it seems probable that interspecific aggression in *A. conspersus* is a conserved ancestral trait. If so, there may be an adaptive, albeit historical, explanation for the origin of interspecific aggression in *A. conspersus*. The closest relative and presumed progenitor of *A. conspersus* is *A. grahami* of Jamaica (Underwood and Williams, 1959; Hedges and Burnell, 1990; Jackman et al., 1999). These two species, together with several other Jamaican anoles, comprise a clade known as the *grahami* species group (Underwood and Williams, 1959; Hedges and Burnell, 1990; Jackman et al., 1999). On Jamaica, *Anolis grahami* occurs sympatrically, in one location or another, with all of the other anoles in the *grahami* species group (Rand, 1967; Schoener, 1971; Williams, 1983). Thus, if *A. grahami* and other *grahami* species group members are interspecifically aggressive toward other anoles, this would suggest a possible ancestral and adaptive origin for interspecific aggression in *A. conspersus*. Consistent with this hypothesis, Rand (1967: page 9) stated, in an ecological study of the anoles around Kingston, Jamaica, that *A. grahami* and *A. lineatopus* (another member of the *grahami* species group) "defend their territories against other lizards of their own size regardless of species." Further, it has been demonstrated that male *A. grahami* distinguish between the displays of conspecifics and other anole species, but possibly not among those of other similarly-sized anole species (Macedonia and Stamps, 1994). Consequently, interspecific aggression in *A. grahami* is unlikely to result from heterospecific anoles being mistaken as conspecific, and may be a generalized response to any heterospecific anole of similar size, as hypothesized above for *A. conspersus*. Thus, it seems probable that interspecific aggression in *A. conspersus* represents a conserved trait that originated on Jamaica. This hypothesis warrants further study.

Interspecific Aggression in *A. sagrei*

Unlike resident *A. conspersus*, resident *A. sagrei* were less likely to exhibit all aggressive behaviors in encounters with heterospecific intruders as compared to conspecific intruders. As *A. sagrei* are generally smaller than *A. conspersus*, size differences may have been responsible for this. Adjusting for relative intruder size could not, however, account for most of the behavioral differences between the conspecific and heterospecific encounters of resident *A. sagrei*. Furthermore, in studies of interspecific aggression in Florida, *A. sagrei* exhibited little aggression toward *A. carolinensis* (Tokarz and Beck, 1987; Brown and Echternacht, 1991; G. Gerber and M. Kramer, unpublished data), a native species ecologically similar to *A. conspersus* (Williams, 1969) but very similar in size to *A. sagrei*. Consequently, even when presented with heterospecific intruders of the same size, *A. sagrei* are not very aggressive. Thus, unlike *A. conspersus*, *A. sagrei*, which belong to the Cuban radiation of anoles, do not appear to be indiscriminately aggressive toward other similarly-sized heterospecific anoles.

Intruder Size and the Costs and Benefits of Aggressive Behavior

Size difference alone could not explain all of the differences between conspecific and heterospecific encounter types for resident *A. conspersus* or *A. sagrei*, indicating that species identity was also an important determinant of their aggressive behaviors. Nevertheless, for all encounter types, the occurrence, latency, and frequency of aggressive behaviors exhibited by residents were often dependent on the relative size of the intruder and varied predictably with the degree of size asymmetry between contestants (Tables 3.5, 3.6, and 3.7). For example, when residents were presented with intruders (conspecific or heterospecific) that were significantly smaller or larger, they were less likely to exhibit postural threats (gular extension, sagittal expansion, crest erection) and took longer to do so when they did. That is, residents presented with much larger intruders generally did not escalate beyond low levels of aggression (headbobbing and dewlaping), whereas residents presented with much smaller intruders generally jumped to high levels of aggression (i.e., attack) without first exhibiting threat postures. This suggests that it was unnecessary (i.e., either excessively wasteful or risky) for resident anoles to employ postural threats in encounters with intruders that were significantly smaller or larger, as an accurate assessment of the intruders fighting ability, and thus the decision to retreat or attack, could be made without doing so. Hence, for resident *A. conspersus*, it may be only relatively large *A. sagrei* and *A. maynardi* (i.e., those most similar in size) were perceived as potentially threatening, and thus warranted the energetic cost of exhibiting postural threats prior to attacking. In contrast, for resident *A. sagrei*, it may be that relatively small *A. conspersus* (i.e., those most similar in size) were perceived as the least threatening, and thus warranted the potential risk of being attacked by exhibiting these behaviors. The general nature of the relationships observed between relative intruder size (but not necessarily species) and the likelihood, and latency, of residents to exhibit postural modifiers is depicted graphically in Figure 3.7. Despite its simplicity, the model provides a reasonable representation of the empirical data and indicates that when the variability in the behavior of resident anoles attributable to relative intruder size is examined across all encounter types it generally conforms to predictions of the sequential-assessment game (e.g., Enquist et al., 1990) and other similar game theory models of conflict (reviewed in Bradbury and Vehrencamp, 1998) in which opponents gradually increase their estimates of each other's relative fighting ability as the interaction proceeds and adjust their behavior to optimize their chances of winning while trying to avoid excessive risk.

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APPENDIX: PART III

Table 3.1. Description of agonistic behaviors recorded for adult male *Anolis* residents in staged encounters with con- or heterospecific adult male intruders.

Behavior	Description
Display	Raising and lowering the head (headbob), extending and retracting the dewlap (dewlap pulse), or raising and lowering the body by flexing and extending the limbs (pushup); typically performed in repetitive sequences comprising bouts
Gular Extension	Extension of the hyoid apparatus; increases the apparent size of the throat; independent from dewlap extension
Sagittal Expansion	Compression of the rib cage along the sagittal plane; increases the apparent size of the body
Crest Erection	Erection of a fold of skin along the dorsal mid-line of the neck and body; increases the apparent size of the neck and body
Approach	Movement toward the opponent, but without making physical contact
Attack	Rapid movement toward the opponent resulting in physical contact and biting

Table 3.2. Comparisons made between types of dyadic encounters staged between adult male *Anolis* residents and con- or heterospecific adult male intruders.

Comparison						
Encounter Type				Encounter Type		
Residents	Intruders	Abbreviation		Abbreviation	Residents	Intruders
sagrei	*sagrei*	S:S	↔	C:C	*conspersus*	*conspersus*
sagrei	*sagrei*	S:S	↔	S:C	*sagrei*	*conspersus*
conspersus	*conspersus*	C:C	↔	C:S	*conspersus*	*sagrei*
conspersus	*conspersus*	C:C	↔	C:M	*conspersus*	*maynardi*
conspersus	*sagrei*	C:S	↔	C:M	*conspersus*	*maynardi*

Table 3.3. Behaviors exhibited by adult male *Anolis* residents in staged encounters with con- or heterospecific adult male intruders, ranked by order of occurrence for each encounter type.

Encounter Type	(Rank) Behavior	*n*	Order of Occurrence		
			Median	Minimum	Maximum
S:C	(1) Display	13	1	1	3
	(2) Sagittal Expansion	6	1.5	1.5	3.5
	(3) Crest Erection	5	2	1	4
	(4) Gular Extension	7	2	1.5	4
	(5) Approach	3	4	3	5
	(6) Attack	1	6	6	6
S:S	(1) Display	13	1	1	5
	(2) Approach	12	2	1	5
	(3) Crest Erection	12	3	1	3
	(4) Sagittal Expansion	12	4.25	2	5
	(5) Gular Extension	12	4.5	2	5
	(6) Attack	15	6	1	6
C:C	(1) Display	12	2	1	5
	(2) Gular Extension	14	2.5	1	4
	(3) Approach	14	2.5	1	5
	(4) Crest Erection	12	3	2	5
	(5) Sagittal Expansion	12	4	2	5
	(6) Attack	13	6	4	6
C:S	(1) Approach	11	1	1	2
	(2) Display	7	1	1	3
	(3) Crest Erection	3	2	1	4.5
	(4) Attack	12	2.5	1	6
	(5) Gular Extension	6	2.75	1	3
	(6) Sagittal Expansion	3	4	2.5	4.5
C:M	(1) Display	14	1	1	3.5
	(2) Approach	13	2	1	3.5
	(3) Gular Extension	7	2	1.5	3.5
	(4) Attack	13	3	2	6
	(5) Crest Erection	5	3.75	1.5	5
	(6) Sagittal Expansion	5	4.5	3.5	5

Encounter types abbreviated as per Figure 3.2. *n* = number of encounters, out of 15, in which the behavior was exhibited. In the case of ties in the median order of occurrence, maximum or minimum values were used to determine rank.

Table 3.4. Snout-vent length (SVL) and mass of adult male *Anolis* residents and intruders used in different types of staged encounters, and differences in SVL and mass between paired lizards for each encounter type.

Encounter Type	*n*	SVL (mm) Residents	SVL (mm) Intruders	SVL (mm) Difference	Mass (g) Residents	Mass (g) Intruders	Mass (g) Difference
S:C	15	57 (51, 64)	63 (56, 69)	-6 (-15, 3) **	5.1 (3.0, 6.5)	5.6 (3.8, 9.5)	-0.6 (-4.6, 1.4) *
S:S	15	58 (55, 63)	59 (50, 69)	0 (-11, 7)	5.5 (4.6, 7.0)	4.6 (3.1, 8.0)	0.5 (-3.3, 3.0)
C:C	15	71 (60, 76)	68 (58, 75)	1 (-6, 16)	8.8 (5.1, 12.0)	8.8 (4.4, 11.0)	1.0 (-3.1, 7.1)
C:S	15	69 (62, 72)	58 (49, 63)	11 (5, 17) ***	8.3 (5.5, 10.0)	4.9 (2.6, 5.8)	3.2 (1.6, 4.6) ***
C:M	15	71 (67, 76)	67 (63, 78)	5 (-11, 9)	9.2 (7.4, 11.0)	5.8 (4.1, 7.8)	4.2 (0.4, 5.2) ***

Encounter types abbreviated as per Table 3.2. Numbers are sample medians with minimum and maximum values in parentheses. Differences between paired lizards: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ (Wilcoxon signed-rank tests). All differences in SVL and mass remain significant after applying the sequential Bonferroni test across encounter types.

Table 3.5. Summary of the effects of relative intruder size (RIS) and encounter type (ET) on the occurrence of agonistic behaviors exhibited by adult male *Anolis* residents in staged encounters with con- or heterospecifc adult male intruders.

				Effect on Behavioral Occurrence					
Behavior	ETs compared	RIS difference between ETs compared	n	ET main effect	RIS main effect	ET × RIS interaction	ET adjusted for RIS	r_L^2 of model fit	RIS measure used
Display	S:S & C:C	ns	30	ns	small > large *	ns	ns	0.47	length
	S:S & S:C	S:C > S:S	30	ns	small > large *	ns	ns	0.32	either
	C:C & C:S	C:C > C:S	30	C:C > C:S ?	ns	ns	C:C > C:S *	0.21	either
	C:C & C:M	C:C > C:M: mass only	30	ns	large > small ?	ns	ns	0.17	either
	C:S & C:M	C:M > C:S: length only	30	C:M > C:S *	large > small *	ns	ns	0.25	length
Gular Extension	S:S & C:C	ns	30	ns	small > large ?	ns	ns	0.21	length
	S:S & S:C	S:C > S:S	30	S:S > S:C ?	ns	ns	ns	0.10	either
	C:C & C:S	C:C > C:S	30	C:C > C:S **	large > small ?	large > small: C:S only *	--	0.21	length
	C:C & C:M	C:C > C:M: mass only	30	C:C > C:M *	large > small ?	large > small: C:M only *	--	0.25	mass
	C:S & C:M	C:M > C:S: length only	30	ns	large > small *	ns	ns	0.34	either
Sagittal Expansion	S:S & C:C	ns	30	ns	small > large ?	ns	ns	0.11	either
	S:S & S:C	S:C > S:S	30	S:S > S:C *	small > large ?	ns	ns	0.14	length
	C:C & C:S	C:C > C:S	30	C:C > C:S **	large > small ?	ns	C:C > C:S *	0.29	either
	C:C & C:M	C:C > C:M: mass only	30	C:C > C:M *	ns	large > small: C:M only *	--	0.28	either
	C:S & C:M	C:M > C:S: length only	30	ns	large > small *	ns	ns	0.29	either
Crest Erection	S:S & C:C	ns	30	ns	ns	ns	ns	0.04	either
	S:S & S:C	S:C > S:S	30	S:S > S:C *	ns	ns	S:S > S:C *	0.18	either
	C:C & C:S	C:C > C:S	30	C:C > C:S **	large > small ?	ns	C:C > C:S *	0.40	either
	C:C & C:M	C:C > C:M: mass only	30	C:C > C:M *	large > small *	large > small: C:M only ?	--	0.23	mass
	C:S & C:M	C:M > C:S: length only	30	ns	ns	large > small: C:M only *	--	0.37	mass

Table 3.5. (continued)

				Effect on Behavioral Occurrence					
Behavior	ETs compared	RIS difference between ETs compared	*n*	ET main effect	RIS main effect	ET × RIS interaction	ET adjusted for RIS	r_L^2 of model fit	RIS measure used
Approach	S:S & C:C	ns	30	ns	ns	ns	ns	0.13	either
	S:S & S:C	S:C > S:S	30	S:S > S:C **	small > large ?	ns	S:S > S:C *	0.28	length
	C:C & C:S	C:C > C:S	30	ns	ns	ns	ns	0.12	either
	C:C & C:M	C:C > C:M: mass only	30	ns	ns	ns	ns	0.03	either
	C:S & C:M	C:M > C:S: length only	30	ns	ns	ns	ns	0.05	either
Attack	S:S & C:C	ns	30	ns	ns	ns	ns	0.07	either
	S:S & S:C	S:C > S:S	30	S:S > S:C ***	small > large *	ns	S:S > S:C **	0.16	either
	C:C & C:S	C:C > C:S	30	ns	ns	ns	ns	0.08	either
	C:C & C:M	C:C > C:M: mass only	30	ns	ns	ns	ns	0.04	either
	C:S & C:M	C:M > C:S: length only	30	ns	ns	ns	ns	0.03	either

Encounter types are abbreviated as per Table 3.2. RIS differences between ETs compared as per Figure 1. Logistic analyses (Wald chi-square tests) were used to examine the effects of ET and RIS on behavioral occurrences (see methods for details). Results of all statistical tests are indicated as follows: ns = $P > 0.1$, ? = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. The direction of all statistically detected differences ($P < 0.05$) or tendencies ($P < 0.1$) are indicated by a greater than (>) symbol. In addition, differences or tendencies limited to only one measure of RIS or one ET are indicated after a colon. -- indicates that an ANCOVA was not appropriate (i.e., slopes ≠). r_L^2 is the proportional reduction in the model chi-square due to the independent variables (Menard, 1995): the reduced (main effects only) model was fit when ET × RIS was insignificant ($P > 0.05$), otherwise the full (main effects with interaction) model was fit. Results of chi-square tests are reported for the measure of RIS (mass or length) explaining the most variation in behavior; either indicates there was little difference between measures.

Table 3.6. Summary of the effects of relative intruder size (RIS) and encounter type (ET) on the latency of agonisitc behaviors exhibited by adult male *Anolis* residents in staged encounters with con- or heterospecific adult male intruders.

				Effect on Behavioral Latency					
Behavior	ETs compared	RIS difference between ETs compared	n	ET main effect	RIS main effect	ET × RIS interaction	ET adjusted for RIS	r^2 of model fit	RIS measure used
Display	S:S & C:C	ns	25	ns	ns	ns	ns	0.12	either
	S:S & S:C	S:C > S:S	26	S:C > S:S *	ns	ns	S:C > S:S *	0.25	either
	C:C & C:S	C:C > C:S	19	ns	ns	ns	ns	0.05	either
	C:C & C:M	C:C > C:M: mass only	26	ns	ns	ns	ns	0.03	either
	C:S & C:M	C:M > C:S: length only	21	ns	ns	ns	ns	0.09	either
Gular Extension	S:S & C:C	ns	26	ns	ns	ns	ns	0.01	either
	S:S & S:C	S:C > S:S	19	ns	large > small **	large > small: S:C only **	--	0.57	mass
	C:C & C:S	C:C > C:S	20	C:S > C:C ?	ns	ns	ns	0.17	either
	C:C & C:M	C:C > C:M: mass only	21	C:M > C:C *	ns	ns	C:M > C:C *	0.29	either
	C:S & C:M	C:M > C:S: length only	13	ns	ns	ns	ns	0.13	either
Sagittal Expansion	S:S & C:C	ns	24	ns	ns	ns	ns	0.05	either
	S:S & S:C	S:C > S:S	18	ns	large > small **	large > small: S:C only **	--	0.56	mass
	C:C & C:S	C:C > C:S	15	C:S > C:C **	small > large ?	ns	ns	0.54	length
	C:C & C:M	C:C > C:M: mass only	17	C:M > C:C ***	ns	ns	C:M > C:C **	0.63	either
	C:S & C:M	C:M > C:S: length only	8	ns	ns	ns	ns	0.22	either
Crest Erection	S:S & C:C	ns	24	ns	ns	ns	ns	0.01	either
	S:S & S:C	S:C > S:S	17	S:C > S:S ?	large > small **	large > small: S:C only **	--	0.71	mass
	C:C & C:S	C:C > C:S	15	ns	ns	large > small: C:S only *	--	0.48	mass
	C:C & CM	C:C > C:M: mass only	17	C:M > C:C **	ns	small > large: C:M only **	--	0.74	length
	C:S & C:M	C:M > C:S: length only	8	ns	ns	ns	ns	0.49	length

Table 3.6. (continued)

				Effect on Behavioral Latency					
Behavior	ETs compared	RIS difference between ETs compared	*n*	ET main effect	RIS main effect	ET × RIS interaction	ET adjusted for RIS	r^2 of model fit	RIS measure used
Approach	S:S & C:C	ns	26	ns	large > small *	ns	ns	0.21	mass
	S:S & S:C	S:C > S:S	15	S:C > S:S *	large > small **	large > small: S:C only ***	--	0.91	mass
	C:C & C:S	C:C > C:S	24	ns	large > small **	ns	ns	0.29	mass
	C:C & C:M	C:C > C:M: mass only	27	ns	ns	ns	C:M > C:C ?	0.14	mass
	C:S & C:M	C:M > C:S: length only	24	C:M > C:S ?	ns	ns	ns	0.14	length
Attack	S:S & C:C	ns	28	C:C > S:S ?	ns	ns	C:C > S:S ?	0.14	either
	S:S & S:C	S:C > S:S	16	ns	ns	ns	ns	0.08	either
	C:C & C:S	C:C > C:S	25	C:C > C:S *	large > small ?	ns	C:C > C:S ?	0.25	length
	C:C & C:M	C:C > C:M: mass only	26	ns	ns	ns	ns	0.04	either
	C:S & C:M	C:M > C:S: length only	25	C:M > C:S *	large > small *	ns	ns	0.26	length

Conventions as in Table 3.5, except that least squares analyses (*F*-tests) and the standard coefficient of determination (r^2) were used to examine the effects of ET and RIS on behavioral latencies. *n* = the number of encounters, out of 30, in which the behavior occurred.

Table 3.7. Summary of the effects of relative intruder size (RIS) and encounter type (ET) on the display frequency of adult male *Anolis* residents in staged encounters with con- or heterospecifc adult male intruders, and on the duration of encounters.

				Effect on Display Frequency or Encounter Duration					
Parameter	ETs compared	RIS difference between ETs compared	n	ET main effect	RIS main effect	ET × RIS Interaction	ET adjusted for RIS	r^2 of model fit	RIS measure used
Display Frequency	S:S & C:C	ns	30	S:S > C:C ***	ns	ns	S:S > C:C **	0.35	either
	S:S & S:C	S:C > S:S	30	S:S > S:C *	small > large *	ns	ns	0.23	either
	C:C & C:S	C:C > C:S	30	ns	ns	ns	ns	0.02	either
	C:C & C:M	C:C > C:M: mass only	30	ns	ns	ns	ns	0.03	either
	C:S & C:M	C:M > C:S: length only	30	ns	ns	ns	ns	0.02	either
Encounter Duration	S:S & C:C	ns	30	C:C > S:S *	ns	ns	C:C > S:S ?	0.16	either
	S:S & S:C	S:C > S:S	30	S:C > S:S *	large > small **	large > small: S:C only *	--	0.49	mass
	C:C & C:S	C:C > C:S	30	ns	ns	large > small: C:S only *	--	0.21	length
	C:C & C:M	C:C > C:M: mass only	30	ns	ns	ns	ns	0.01	either
	C:S & C:M	C:M > C:S: length only	30	ns	large > small ?	ns	ns	0.14	length

Conventions as in Table 3.5, except that least squares analyses (*F*-tests) and the standard coefficient of determination (r^2) were used to examine the effects of ET and RIS on display frequency and encounter duration.

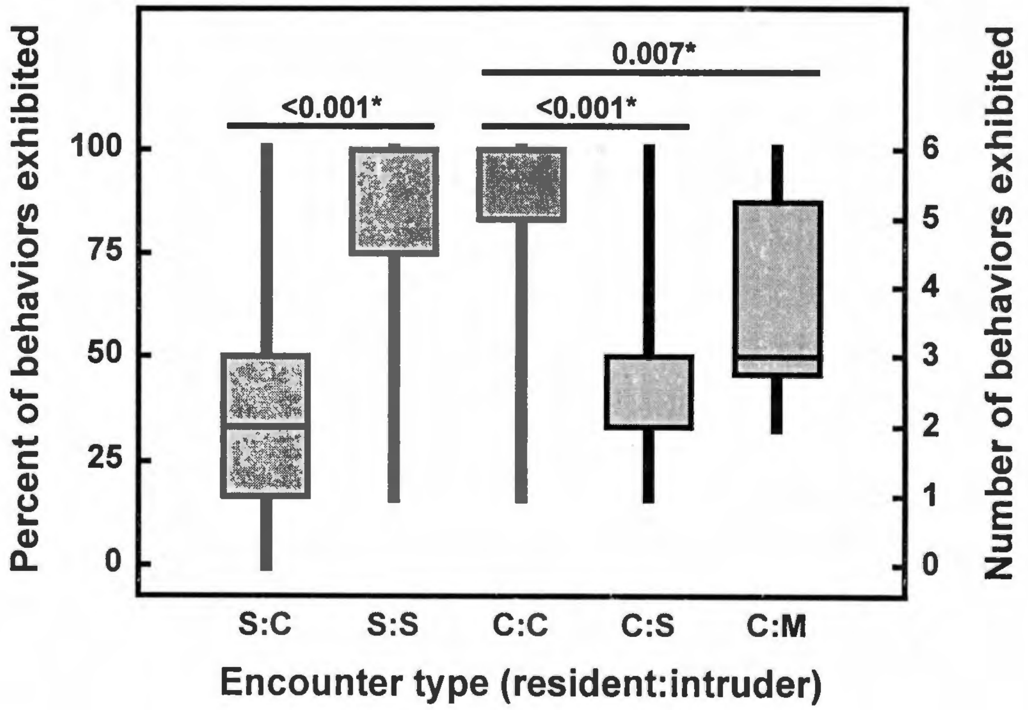

Figure 3.1. Percent, and number, of the six recorded agnostic behaviors (see Table 3.1) exhibited by adult male *Anolis* residents in staged encounters with con- or heterospecific adult male intruders (S = *sagrei*, C = *conspersus*, M = *maynardi*). Values are sample ranges (vertical lines), interquartile ranges (boxes), and medians (horizontal lines in boxes). All sample sizes are 15. Horizontal bars show *P*-values (sampled randomization tests) for differences between encounter types for the comparisons in Table 3.2. Asterisks denote differences that remain significant after applying the sequential Bonferroni test across all pairwise comparisons.

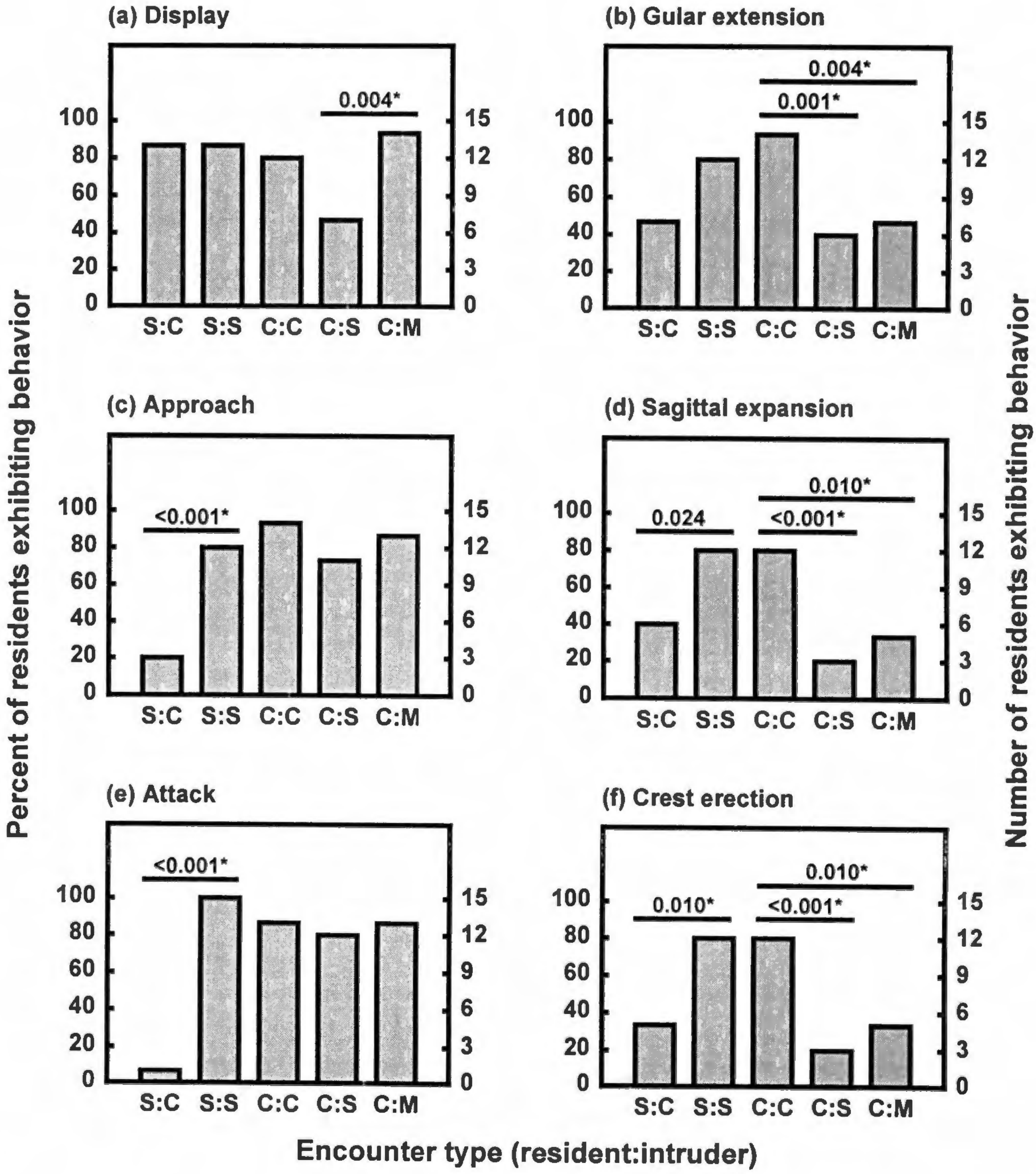

Figure 3.2. Percent, and number, of adult male *Anolis* residents that exhibited (**a**) display, (**b**) gular extension, (**c**) approach, (**d**) sagittal expansion, (**e**) attack, or (**f**) crest erection in staged encounters with con- or heterospecific adult male intruders (S = *sagrei*, C = *conspersus*, M = *maynardi*). Horizontal bars show *P*-values (*G*-tests with Williams' correction) for differences in occurrence between encounter types for the comparisons in Table 3.2. Asterisks denote differences that remain significant after applying the sequential Bonferroni test across all pairwise comparisons.

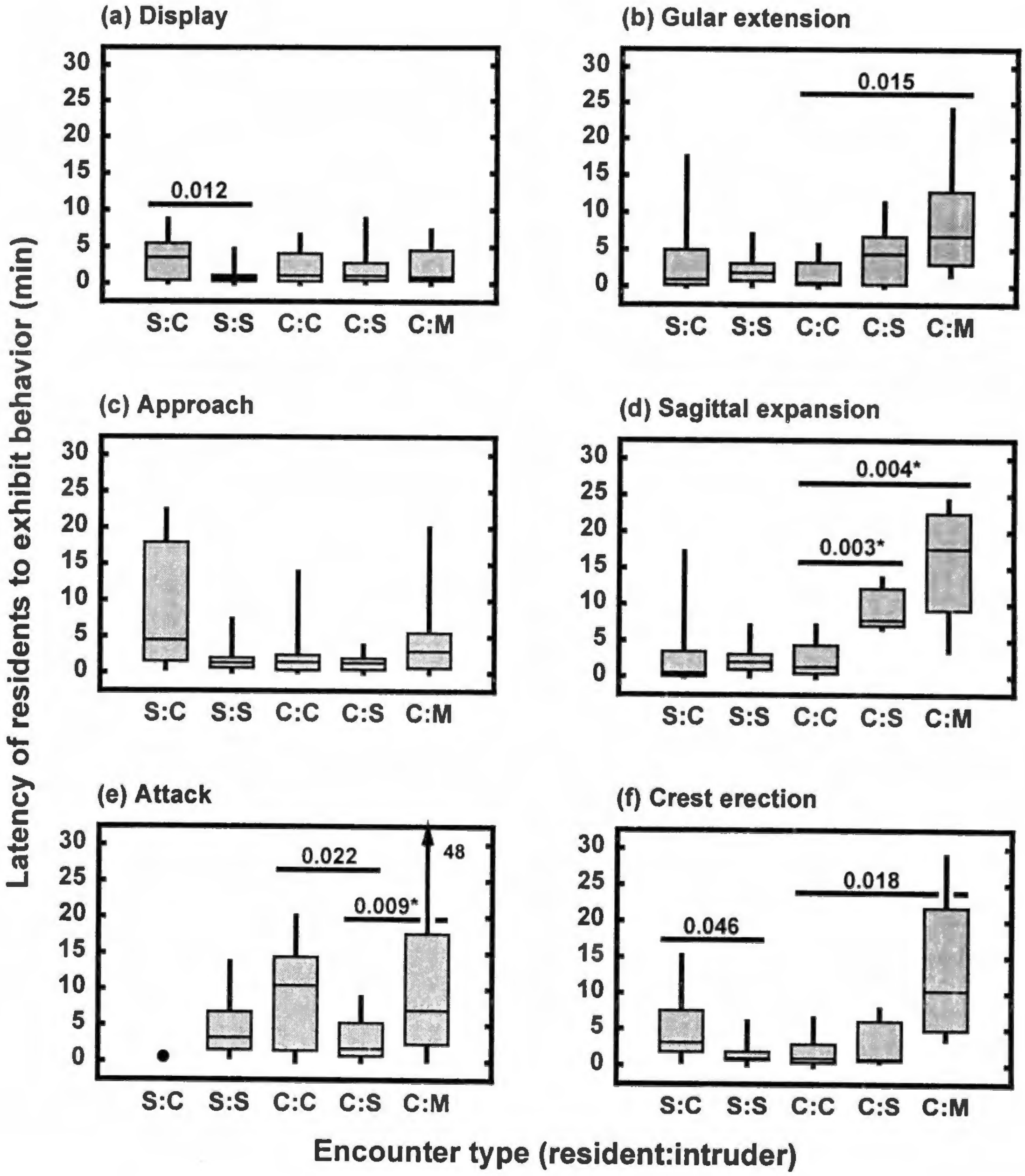

Figure 3.3. Latency to (**a**) display, (**b**) gular extension, (**c**) approach, (**d**) sagittal expansion, (**e**) attack, and (**f**) crest erection of adult male *Anolis* residents that exhibited these behaviors in staged encounters with con- or heterospecific adult male intruders (S = *sagrei*, C = *conspersus*, M = *maynardi*). Refer to Figure 3.2 for the number of residents that exhibited each behavior. Other conventions as in Figure 3.1. The maximum value is given for the range exceeding the y-axis (arrow).

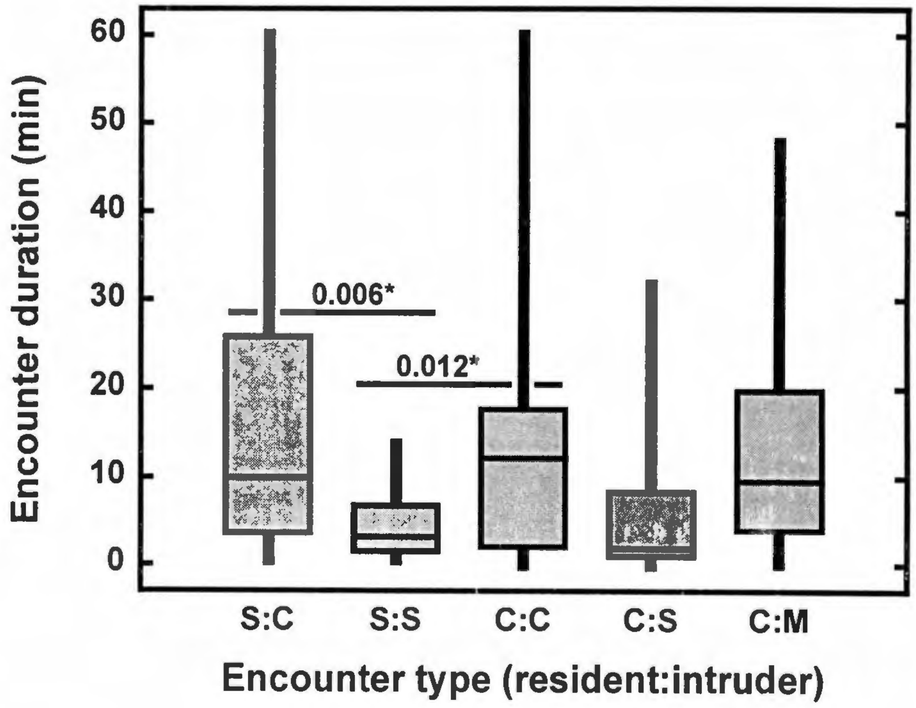

Figure 3.4. Duration of staged encounters between adult male *Anolis* residents and con- or heterospecific adult male intruders (S = *sagrei*, C = *conspersus*, M = *maynardi*). Conventions as in Figure 3.1.

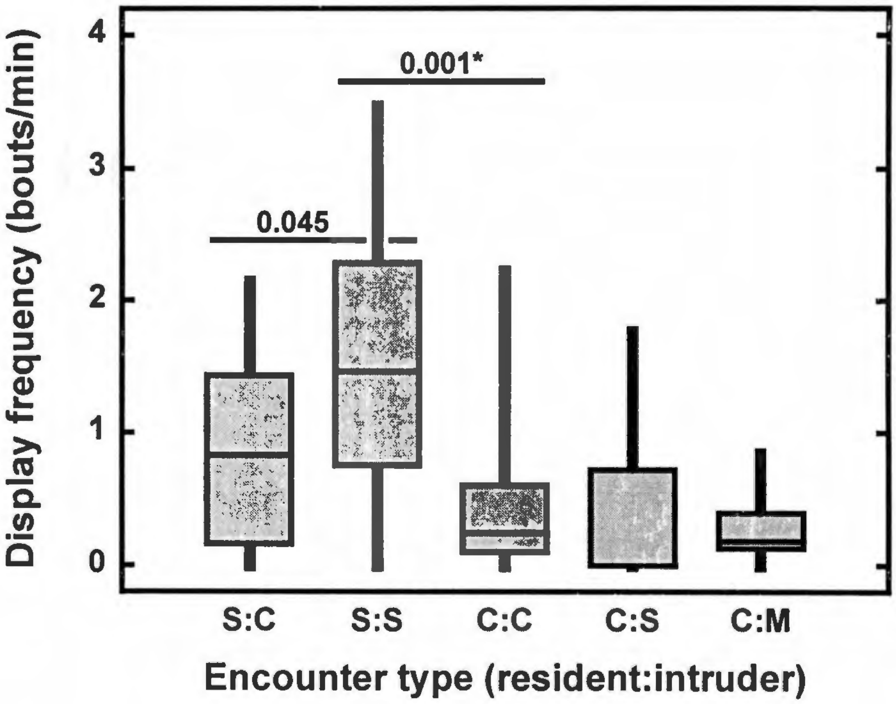

Figure 3.5. Display frequency of adult male *Anolis* residents in staged encounters with con- or heterospecific adult male intruders (S = *sagrei*, C = *conspersus*, M = *maynardi*). Conventions as in Figure 1.

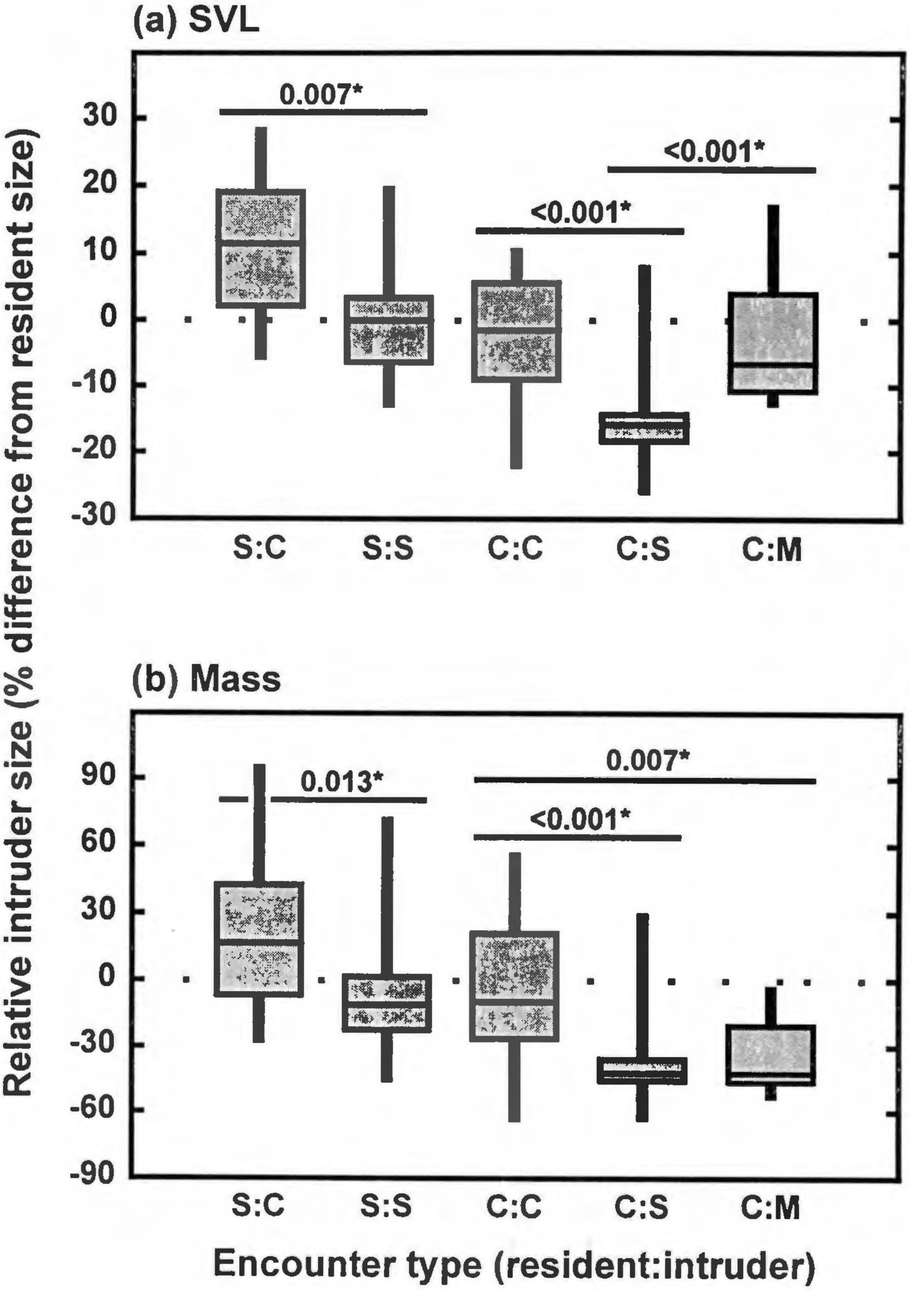

Figure 3.6. Relative (**a**) snout-vent length (SVL) and (**b**) mass of con- or heterospecific adult male intruders used in staged encounters with adult male *Anolis* residents (S = *sagrei*, C = *conspersus*, M = *maynardi*). Relative intruder size = ((intruder size/resident size) – 1)100. Conventions as in Figure 3.1, except that *P*-values are for Wilcoxon rank-sum tests.

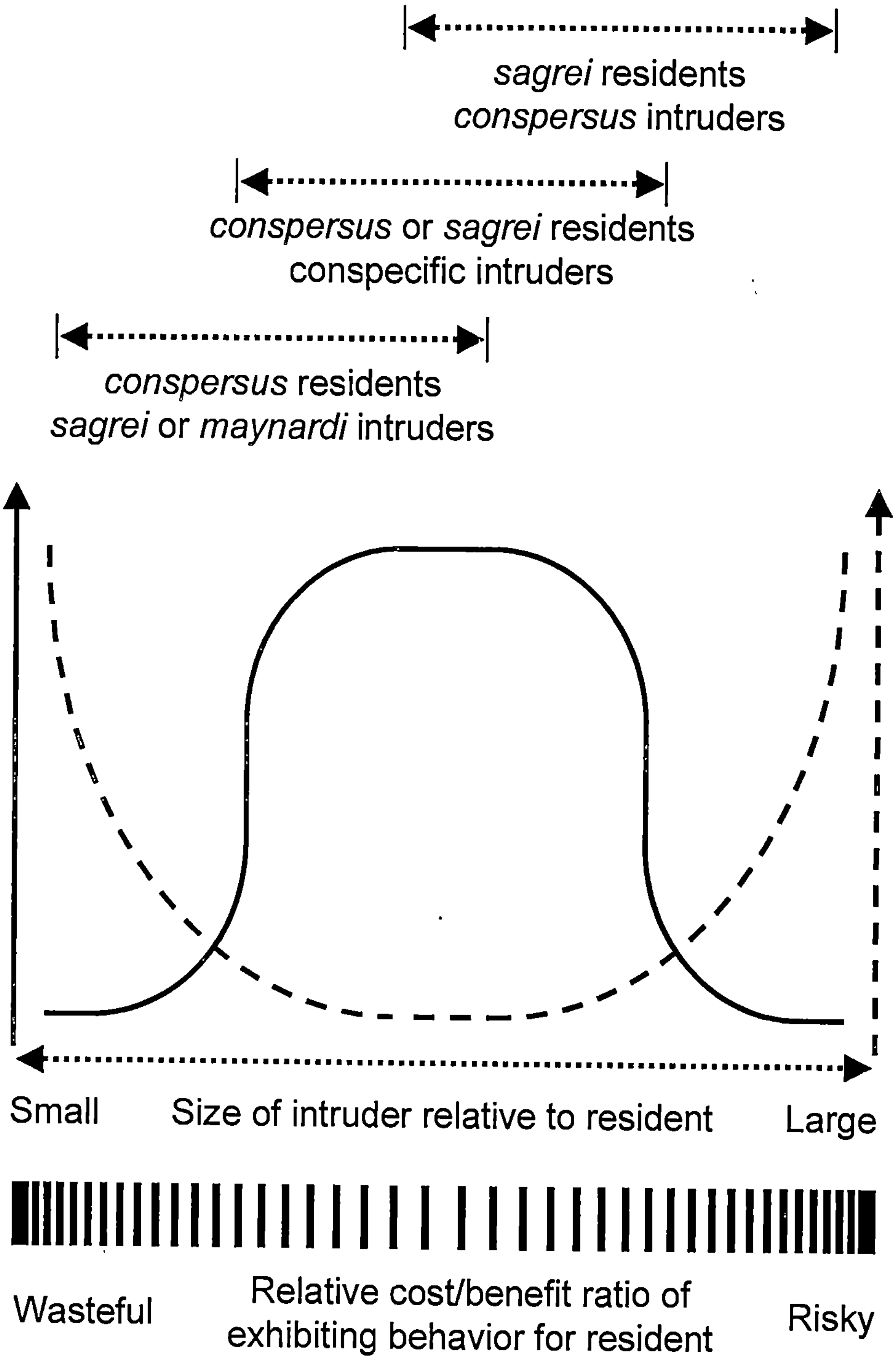

Figure 3.7. Qualitative graphical model depicting the general nature of the relationships observed between relative intruder size (but not necessarily species) and the likelihood, and latency, of adult male *Anolis* residents to exhibit agonistic behaviors (particularly postures: gular extension, sagittal expansion, crest erection).

PART IV

An Experimental Study of Density Compensation and Resource Partitioning between the Exotic and Endemic *Anolis* Lizards of Grand Cayman

ABSTRACT

Since its introduction, *Anolis sagrei* (Sauria: Polychrotidae) has invaded much of Grand Cayman and in some areas outnumbers the island's only native anole, *A. conspersus*. However, *A. sagrei* is conspicuously absent from habitats where *A. conspersus* is most abundant, such as undisturbed woodlands. Previous behavioral experiments found a pronounced asymmetry in interspecific aggression favoring *A. conspersus*, the larger of the two species, suggesting that the rarity of *A. sagrei* in woodlands may be due to competitive interference. This hypothesis was investigated using an asymmetrical BACI (before-after, control-impact) experimental design to compare the relative abundance and habitat use of *A. sagrei* and *A. conspersus* on three plots, located along a habitat gradient from relatively open to closed woodland, before and after removing *A. conspersus* from the middle plot. Following the removal of *A. conspersus*, *A. sagrei* increased in abundance on the experimental plot and shifted their use of structural and microclimatic habitats, and escape routes, toward those normally used by *A. conspersus*. In contrast, no niche shifts were observed on the control plots. Further, despite opposing patterns of relative abundance for the two species along the habitat gradient (i.e., among plots) prior to manipulation, and significant changes in species abundances following manipulation, the combined abundance of *A. sagrei* and *A. conspersus* did not vary significantly among plots or between study phases, suggesting complete density compensation between *A. sagrei* and *A. conspersus*. These findings support the hypothesis that the distribution, abundance, and resource use of *A. sagrei* in Grand Cayman is restricted by interference competition from *A. conspersus*. The success

of introduced *A. sagrei* in Grand Cayman appears due to (1) adaptations that allow it to exploit habitats that are relatively unprofitable for native *A. conspersus*, and (2) ongoing human disturbance that creates open habitats.

INTRODUCTION

Differences in the abundance and resource use of closely related sympatric species are often attributed to past or ongoing interspecific competition (Case and Bolger, 1991; Chesson, 1991; Losos, 1994). However, factors unrelated to interspecific interactions, such as physiological or morphological constraints, are usually important in determining the abundance and resource use of sympatric species as well (e.g., Toft, 1985). Further, competition is not the only interspecific interaction that can cause differences in abundance and resource use of closely related sympatric species. Intraguild predation (Polis et al., 1989; Holt and Polis, 1997), shared predators (Holt, 1977; Holt and Lawton, 1994), and shared parasites (Price et al., 1986; Schall, 1992) can mediate the effects of interspecific competition or produce complimentary patterns of abundance and resource use by themselves. Thus, it is important to consider alternative hypotheses for species differences. Even when interspecific competition is an important interaction, identifying its mechanism(s) will be important to understanding interspecific patterns of abundance and resource use (Schoener, 1986; Tilman, 1987; Werner, 1992; Resetarits and Bernardo, 1998, Holway and Suarez, 1999). For example, if competition is largely exploitative, its strength should be positively associated with resource overlap, whereas strong interference competition usually results in low resource overlap, at least where space is concerned (Case and Gilpin, 1974; Conner and Bowers, 1987; Abrams, 1998). Further, if interactions between sympatric species are asymmetric, as most cases of competition appear to be (Lawton and Hassell, 1981; Connell, 1983; Schoener, 1983), this asymmetry will have important ecological and evolutionary consequences for the species involved (Jenssen, 1973; Jenssen et al., 1984; Persson, 1985; Law et al., 1997). Thus, it is important to consider the history, mechanism(s), and symmetry of species interactions, as well as alternative hypotheses, when attempting to interpret patterns of abundance and resource use among sympatric species, and when designing experiments to test for interspecific interactions.

Here I present results of an experiment designed to test for interspecific competition between two species of *Anolis* lizard on Grand Cayman Island, one native and one introduced, for which important aspects of the history, mechanism, and symmetry of interaction are known. Historically, Grand Cayman was inhabited by a single species of anole, the endemic *A. conspersus* (Grant, 1940; Williams, 1969). Like many solitary species of *Anolis*, *A. conspersus* is moderate in size, has a broad ecological niche, and occupies a wide variety of habitats (Schoener, 1967; Williams, 1969; Avery, 1988). Around 1980, *A. sagrei*, another moderately-sized anole with a broad ecological niche (William, 1969) was introduced to western Grand Cayman (Minton and Minton, 1984). *Anolis sagrei* subsequently invaded much of the island and in some disturbed habitats it now outnumbers *A. conspersus* (Franz et al., 1987; Losos et al. 1993). *Anolis sagrei* has, however, had little success penetrating woodland habitats, where *A. conspersus* is most abundant.

Although *A. conspersus* and *A. sagrei* are both generalist anole species, they differ somewhat in body size, structural and microclimatic habitat use, active field body temperature, and escape behavior. Relative to *A. conspersus*, *A. sagrei* is smaller, perches lower and more often in the sun, maintains higher field body temperatures, and escapes downward more often than upward (Losos et al., 1993). Thus, these differences alone could account for why *A. sagrei* is found almost exclusively in non-woodland and disturbed habitats, which are relatively open and sunny with low vegetation, whereas *A. conspersus* is most abundant in woodlands, which are less open and more shaded with higher vegetation.

Alternatively, or in addition, the observed interspecific patterns of abundance and resource use might result from competition. If so, the abundance and resource use of each species should change in response to the addition or removal of the other. Losos et al. (1993) looked for an effect of *A. sagrei* on *A. conspersus* by comparing perch heights of *A. conspersus* before and after the introduction of *A. sagrei*. They found evidence that *A. conspersus* has shifted to higher perches in open (non-wooded) habitats, where *A. sagrei* is now common, but not in closed (wooded) habitats, where *A. sagrei* is essentially absent. Thus, there is evidence to suggest a competitive effect of *A. sagrei* on *A. conspersus*. However, their study did not address the mechanism of competition or an effect of *A. conspersus* on *A. sagrei*.

Studies of interspecific aggression suggest that behavioral interference is an important and highly asymmetric interaction between these species (Part III). In staged male-male encounters, resident *A. conspersus* were extremely aggressive toward intruding *A. sagrei*, whereas resident *A. sagrei* exhibited little or no aggression toward intruding *A. conspersus*. Thus, the rarity of *A. sagrei* in woodland habitats may be the result of aggressive interference from *A. conspersus*, the larger of the two species, rather than the result of pre-existing differences between the species.

In this paper, I present evidence supporting a hypothesis of competitive interference. When *A. conspersus* were removed from an area of sympatry, *A. sagrei* increased in abundance and shifted their use of structural and microclimatic habitats, and escape routes, toward those normally used by *A. conspersus*. Further, no niche shifts were observed for *A. sagrei* in adjacent control areas where *A. conspersus* were not removed. Thus, the rarity of *A. sagrei* in wooded habitats in Grand Cayman appears to result from the abundance of *A. conspersus* in these areas, not from distinct interspecific habitat preferences. Pre-existing differences between the species cannot be discounted, however, as the success of *A. sagrei* in Grand Cayman must be attributed to its ability to exploit those habitats least utilized by the larger, more aggressive *A. conspersus*. Human disturbance, which continually creates open habitats, also appears critical to the success and persistence of *A. sagrei* on Grand Cayman.

METHODS

Study Site

The study was conducted on the west coast of Grand Cayman near George Town in a zone of sympatry between *A. conspersus* and *A. sagrei*. The site was partially wooded and nearly level. Dominant trees on the site belonged to three introduced species: Australian pine (*Casuarina equisetifolia*), Indian almond (*Terminalia catappa*), and royal poinciana (*Delonix regia*). The most common shrub was cockspur (*Caesalpina bonduc*). On a fine scale, hereafter referred to as microhabitat, vegetation at the study site was patchy: bare ground and low herbaceous vegetation separated thickets of shrubs and young trees from stands of mature trees and their associated undergrowth. Table 4.1 describes the microhabitats recognized in this study. On a coarser scale, hereafter referred to as macrohabitat, a gradient existed across the study site with respect to how wooded (open versus closed canopy) the habitat was. Three plots were established along this macrohabitat gradient. Plot 1, on the coastal side of the study area, was 550 m^2 and relatively open; it contained 10 trees or 1.8 trees/100 m^2. Plot 3, on the inland side of the study area, was 360 m^2 and relatively closed; it contained 17 trees or 4.7 trees/100 m^2. Finally, plot 2, located between plots 1 and 3, was 500 m^2 and intermediate in habitat; it contained 16 trees or 3.2 trees/100 m^2. Figure 4.1 illustrates the distribution of plots along the macrohabitat gradient as well as distribution of microhabitats on each plot.

Experimental Design and Data Collection

The study entailed comparisons of relative abundance, sex ratio, and habitat use of *A. sagrei* on each of the three plots before and after removal of *A. conspersus* from plot 2. To document interspecific patterns in abundance, sex ratio, and habitat use, data were also collected for *A. conspersus* on each plot. The experimental design used in this study, an asymmetrical BACI (before-after, control-impact) design with replicated controls but a single experimental treatment, was developed for environmental impact studies where replication of experimental treatments (i.e., impacts) is not possible or desirable (Underwood, 1991, 1992, 1996). Consequently, the use this experimental design here is somewhat unorthodox. However, as for environmental impact studies, the decision to use this approach was born out of necessity. Because *A. sagrei* and *A. conspersus* tend to be spatially segregated in Grand Cayman, there are few areas of any size with reasonably abundant populations of both species. Indeed, despite considerable time and effort searching, the study area was the only area found in Grand Cayman that was suitable for conducting this field experiment. Further, based on the size, abundance, and vagility of the lizards, dividing the study area into more than three plots was deemed inappropriate. Thus, rather than not do the experiment, I adopted an asymmetrical design with one experimental plot and two control plots. To increase the statistical power and inference of the experiment, data were collected during multiple time periods on all plots, before and after the removal of *A. conspersus* from the experimental plot, and analyzed using a nested repeated measures design as described by Underwood (1992, 1996). Using this approach, a significant treatment effect is indicated when the change after treatment versus before treatment is significantly greater in the experimental area than the change (if any) in the control areas. This experimental design has relatively good statistical power and comes as close to providing a causal relationship of the manipulation as can be expected in an experiment without replication of the experimental treatment (Underwood, 1996).

Plot 2 was chosen to receive the experimental treatment (i.e., removal of *A. conspersus*) for three reasons. First, it allowed for interspersion of experimental and control plots, which is preferable to strict randomization when only a few plots are used (Hurlburt, 1984). Second, the trees on plot 2, unlike those on plots 1 and 3, formed a stand which was isolated from other trees by open areas of low herbaceous vegetation and few *A. conspersus*; this made it possible to remove *A. conspersus* from plot 2 without immediate recolonization through the crowns of adjacent trees. Third, because plot 2 was intermediate between plots 1 and 3 in habitat and relative abundance of both species, this positioned the experimental plot at the center of the continuum rather than at one of the ends, and thus maximized the power of statistical inferences based on comparisons of experimental and control areas.

Observations before removing *A. conspersus* from plot 2 were made between 28 June and 12 July 1991, hereafter the premanipulation phase. Observations after removing *A. conspersus* from plot 2 were made between 22 and 29 September 1991, hereafter the postmanipulation phase. During each phase, each plot was sampled on a daily (or bidaily) basis for a maximum of two hours (described below). Because each plot was sampled daily, it was not possible to sample all plots at the same time. Consequently, the order in which the plots were sampled was randomized each day to account for possible diel variation in activity and habitat use of the lizards. All sampling took place between 0800 and 1800 hours. Plots were sampled 10 times during the premanipulation phase and (due to time constraints) six times during the postmanipulation phase.

Anolis conspersus were removed from the experimental plot right after the premanipulation phase (13-19 July: 22 males, 20 females) and again right before the postmanipulation phase (19-21 September: 5 males, 13 females, 3 juveniles). In total, 63 *A. conspersus* (27 males, 33 females, 3 juveniles) were removed from the experimental plot. These lizards were marked and released in a wooded area about 100 m away that was separated from the study site by a paved road.

During each sampling period, data needed to quantify the relative abundance, sex ratio, and habitat use of lizards was gathered by slowly moving across a plot from one end to the other and recording data for each lizard encountered (without replacement), except those already fleeing when first sighted (< 10 %). Sampling periods were ended when the entire plot had been searched once or after two hours, whichever came first. Lizards were classified by species, sex, and age. For each species, three sex/age classes were distinguished: adult male lizards (hereafter males), which are larger and morphologically distinct from other sex/age classes, adult female-sized lizards (hereafter females), which included a small percentage of sub-adult males due to the difficulty of distinguishing some of these from adult females without capture, and juvenile lizards (estimated to be ≤ 30 mm in snout-vent length). Only data for males and females are presented because too few juvenile lizards were encountered to make useful comparisons between study phases.

For each lizard observed, microhabitat type (Table 4.1: wooded versus non-wooded) and arboreality (on standing vegetation versus on the ground, a rock, or a log) were recorded. For terrestrial lizards, microhabitat type was based on the immediate environment and available or observed escape routes. When lizards did flee, their escape direction (up versus down or lateral) was recorded. For arboreal lizards, perch diameter (mm), perch height (cm), and maximum height of the perch structure (cm; hereafter structure height) were recorded. Structure height was also recorded for terrestrial lizards that escaped arboreally. Perch measurements were taken with a rule except for inaccessible perch sites and structures (generally those > 3 m in height), which were estimated. When the sun was not obscured by clouds, the location of each lizard was characterized by its exposure to sunlight: shade versus full or dappled sun (hereafter perch microclimate). For each species, the number of lizards observed per hour of sampling in each sampling period was used to estimate relative abundance, and the frequencies of males and females observed in each sampling period were used to estimate sex ratio.

Data Analysis

For all analyses, daily sampling periods were considered sampling units. Thus, pre- and postmanipulation estimates of lizard resource use on plots were based on measures computed for sampling periods, not individual lizards. This was necessary because most lizards were undoubtedly represented in more than one sample, whereas sample periods represent random samples of plots (with replacement). For statistical analyses, sample period was nested within plot and study phase, and study phase was treated as a repeated measure.

Estimates of relative abundance, sex ratio, and resource use were analyzed two ways. First, data for the premanipulation phase were analyzed alone to provide an indication of differences between species and sexes, within and among plots, prior to manipulation. Second, data for the pre-and postmanipulation phases were analyzed together, but separately for each species, to test for changes across study phases attributable to the experimental treatment (i.e., the removal of *A. conspersus* from plot 2).

Differences between species, sexes, plots, and study phases were tested using least squares analysis of variance, for continuous variables, and logistic (maximum likelihood) analysis, for categorical variables. When significant interactions were found between classification variables (e.g., plot and study phase) in least squares analyses, contrasts within the interaction term of the model were used to determine which within plot differences were significant. Similarly, when significant interactions were found in logistic analyses, one-way analyses were used to determine which within plot differences were significant. Continuous variables describing resource use were analyzed using the median values for each sampling period: median values were used as the measure of central tendency for perch diameter, perch height, and structure height because these variables generally have a skewed distribution.

To provide multivariate comparisons and tests of (1) interspecific differences in habitat use during the premanipulation phase, and (2) habitat shift for each species between pre- and postmanipulation phases of the study, principal components analysis (PCA) was used. This approach was used in lieu of a multivariate analysis of variance, as four of the seven habitat variables measured were categorical. Further, even when the categorical variables were converted to continuous form by substituting the raw bivariate frequency data with the percentage of animals using the resource category most commonly used by *A. conspersus*, the distributions of these percentages were not normal. Some of the variables were likely correlated as well (e.g., structure height and microhabitat type), violating the assumption of independence for multivariate analysis of variance. However, variables need not be normally distributed (or even quantitative) to be used in PCA, and PCA can be used to transform correlated variables into a new set of independent variables that retain all of the information in the old set for subsequent statistical analysis (Green, 1979). Further, the principle components resulting from the PCA were approximately normal and homoscedastic, and thus were amenable to analysis of variance. All statistical tests were two-tailed and an alpha level of 0.05 was used to judge significance.

RESULTS

Relative Abundance

Premanipulation – For the premanipulation phase, relative abundance was analyzed by species and plot in a two-way factorial analysis of variance. The whole-model test ($F_{5,54} = 15.4$, $P < 0.001$) and the interaction of species and plot ($F_{2,57} = 37.6$, $P < 0.001$) were significant, indicating interspecific differences in relative abundance by plot (Figure 4.2, top). Contrasts of least square means indicated that *A. sagrei* was more abundant than *A. conspersus* on plot 1($t = -5.74$, df = 16, $P < 0.001$), the most open plot, whereas *A.*

conspersus was more abundant than *A. sagrei* on plot 3 ($t = 6.54$, df = 18, $P < 0.001$), the most wooded plot, and the species were equally abundant on Plot 2 ($t = 0.815$, df = 20, $P = 0.42$), intermediate between plots 1 and 3 in tree density. Thus, in relation to the macrohabitat gradient, species abundances during the premanipulation phase were opposite and complimentary. Indeed, the combined relative abundance of *A. sagrei* and *A. conspersus* did not vary significantly by plot (one-way ANOVA: $F_{2,57} = 7.814$, $P = 0.46$), suggesting density compensation (Figure 4.2, top).

Postmanipulation – To determine if the removal of *A. conspersus* from plot 2 resulted in (1) a significant reduction in the abundance of *A. conspersus* and (2) a significant increase in the abundance of *A. sagrei*, relative abundance was analyzed separately for each species by plot and study phase in a two-way factorial analysis of variance. For *A. conspersus*, the whole-model test ($F_{5,42} = 28.1$, $P < 0.001$) and the interaction of plot and study phase ($F_{5,42} = 13.1$, $P < 0.001$) were significant, indicating that relative abundance had changed more on some plots than others. Contrasts of least square means revealed that *A. conspersus* had not changed in abundance on plot 1 ($t = 0.034$, df = 10, $P = 0.97$), but had decreased in abundance on plots 2 ($t = -7.21$, df = 10, $P < 0.001$) and 3 ($t = -2.49$, df = 10, $P = 0.017$). Thus, removal efforts were successful in reducing the number of *A. conspersus* on plot 2, but *A. conspersus* numbers had also dropped on one of the control plots (Figure 4.2). Nevertheless, the magnitude of change on the experimental plot was significantly greater than that on the control plots (contrast of experimental plot versus both control plots: $F_{2,45} = 27.4$, $P < 0.001$).

For *A. sagrei*, a similar, but opposite, pattern was observed (Figure 4.2). The whole-model test ($F_{5, 42} = 11.0$, $P < 0.001$) and the interaction of plot and study phase ($F_{5, 42} = 3.92$, $P = 0.028$) were significant, and contrasts of least square means revealed that *A. sagrei* had not change in abundance on plot 1 ($t = 0.128$, df = 10, $P = 0.90$), but had increased in abundance on plots 2 ($t = 4.17$, df = 10, $P < 0.001$) and 3 ($t = 2.21$, df = 10, $P = 0.032$). As for *A. conspersus*, the magnitude of change on the experimental plot was significantly greater than that on the control plots (contrast of experimental plot versus both control plots: $F_{5, 42} = 27.4$, $P < 0.001$). Thus, removal of *A. conspersus* from plot 2 resulted in an increase in the relative abundance of *A. sagrei* on plot 2 that was greater than the observed changes in abundance on the control plots (Figure 4.2).

Finally, despite changes in the relative abundance of both species on plots 2 and 3 between study phases, the combined relative abundance of *A. conspersus* and *A. sagrei* did not vary significantly by plot or study phase (two-way analysis of variation with interaction: whole-model test, $F_{5, 42} = 0.307$, $P = 0.91$). Thus, the evidence for density compensation between these species is strong (Figure 4.2).

Sex Ratio

Premanipulation – To determine if there were species or plot differences in sex ratio prior to manipulation, the frequencies of males and females observed during premanipulation sampling periods were analyzed by species and plot in a two-way factorial logistic analysis. The whole-model test ($\chi^2 = 12.8$, df = 5, $P < 0.026$) and the main effect for species ($\chi^2 = 5.71$, df = 1, $P < 0.017$) were significant, but the there was no main effect of plot ($\chi^2 = 0.715$, df = 2, $P = 0.70$) and no interaction between species and plot ($\chi^2 = 3.10$, df = 2, $P = 0.21$). Thus, during the premanipulation phase, there was no difference between plots in sex ratios, but *A. sagrei* was characterized by a higher proportion of males than was *A. conspersus* (Figure 4.3, top).

Postmanipulation – To determine if there were significant changes in sex ratio between pre- and postmanipulation phases for either species, the frequencies of males and females observed during sampling periods were analyzed separately for each species by plot and study phase in a two-way factorial logistic analysis. For *A. conspersus*, the whole-model test ($\chi^2 = 27.6$, df = 5, $P < 0.001$) and the interaction of plot and study phase ($\chi^2 = 11.9$, df = 2, $P = 0.003$) were significant, indicating a difference between plots in the amount of change in sex ratio between pre- and postmanipulation phases (Figure 4.3). Analysis of sex ratio by study phase for individual plots revealed that the only significant shift in sex ratio for *A. conspersus* between study phases was on plot 2 (plot 1: $\chi^2 = 1.15$, df = 1, $P = 0.28$; plot 2: $\chi^2 = 21.0$, df = 1, $P < 0.001$; plot 3: $\chi^2 = 0.829$, df = 1, $P = 0.36$). Thus, in addition to lowering the overall abundance of *A. conspersus* on plot 2, efforts to remove *A. conspersus* from plot 2 were particularly effective in reducing the number of males, which, because of their large size and aggressiveness, are the individuals most likely to impact the abundance and habitat use of *A. sagrei*.

Changes in the abundance and sex ratio of *A. conspersus* on the experimental plot did not affect the sex ratio of *A. sagrei*, as the two-way logistic analysis of sex ratio by plot and study phase for *A. sagrei*, although significant (whole-model test: $\chi^2 = 19.6$, df =

5, $P = 0.0015$), showed that there was no interaction between plot and study phase ($\chi^2 = 0.019$, df = 2, $P = 0.99$). There was, however, a significant main effect of study phase ($\chi^2 = 12.6$, df = 1, $P < 0.001$) on the sex ratio of *A. sagrei*, indicating a decrease in the proportion of *A. sagrei* that were male throughout the study area between the pre- and postmanipulation phases (Figure 4.3).

Habitat Use

Premanipulation – To establish whether or not habitat use differed significantly by species, sex, or plot prior to manipulation, the premanipulation phase data for all seven habitat use variables were entered into a principal components analysis (PCA) and the resulting first and second principal components were each analyzed by species, sex, and plot in a three-way factorial analysis of variance. Plots of the first and second principle components for the premanipulation phase PCA of habitat use are presented in Figure 4.4. Analysis of the first principal component by species, sex, and plot was significant for the whole-model test ($F_{11,\,101} = 197.6$, $P < 0.001$), all main effects (species: $F_{1,\,111} = 590.8$, $P < 0.001$; sex: $F_{1,\,111} = 6.57$, $P < 0.012$; plot: $F_{2,\,110} = 13.3$, $P < 0.001$), and for the interaction between species and plot ($F_{2,\,110} = 12.9$, $P < 0.001$), but not for any of the interactions involving sex ($P \geq 0.37$ in each case). Analysis of the second principal component was significant as well (whole-model test: $F_{11,\,101} = 2.31$, $P = 0.015$), but only for plot ($F_{2,\,110} = 5.99$, $P = 0.004$) and the interaction of plot and species ($F_{2,\,110} = 4.92$, $P = 0.009$). Thus, as indicated in Figure 4.4, habitat use differed between the species, sexes, and among plots, and the amount of separation between species varied among plots. Significant differences among plots indicate the importance of considering resources availability when interpreting patterns of resource use. Separation of male and female conspecifics was similar, regardless of plot, however, suggesting that the sexes (although somewhat different from one another) respond similarly to differences in the availability of resources among habitats (Figure 4.4).

Postmanipulation – To look for significant changes in resource use between pre- and postmanipulation phases, a PCA was run for each species using data from both study phases and the resulting first and second principle components of each PCA were then each analyzed by sex, plot, and study phase in a three-way factorial analysis of variance (as described above). Data for the experimental plot was excluded from the analysis for *A. conspersus*, however, as too few data were available for this plot during the postmanipulation phase (due to removal efforts). For *A. conspersus*, analysis of the first principle component was significant for the whole-model test ($F_{7,53} = 16.2$, $P < 0.001$), but not for the main effect of study phase or for any of the interactions involving study phase ($P \geq 0.15$ in each case), and analysis of the second principle component was not significant (whole-model test: $F_{7,53} = 0.106$, $P = 0.99$). Thus, the resource use of *A. conspersus* did not change significantly between pre- and postmanipulation phases on either control plot. To confirm the validity of the analysis of variance of principle components, each of the seven habitat variables for *A. conspersus* was analyzed separately for each sex by plot and study phase in a two-way least square, or logistic, factorial analysis (Table 4.2). As expected, there was no interaction between plot and study phase for any variable for either sex. Thus, there was no evidence of habitat shift for male or female *A. conspersus*.

In contrast, *A. sagrei* did exhibit a shift in habitat use on the experimental plot, as can be seen from the principle components plots in Figure 4.5. Analysis of the first principle component was significant for the whole-model test ($F_{11, 78} = 46.4$, $P < 0.001$), and the three-way interaction of sex, plot, and study phase ($F_{2, 87} = 40.9$, $P = 0.0015$), indicating significant changes in resource use between pre- and postmanipulation phases on some plots. Contrasts of least square means by study phase were significant for both sexes on plot 2 (males: $t = 14.0$, df = 10, $P < 0.001$; females: $t = 3.66$, df = 10, $P < 0.001$) and insignificant for both sexes on plots 1 (males: $t = -0.204$, df = 10, $P = 0.84$; females: $t = 0.732$, df = 10, $P = 0.47$) and 3 (males: $t = 0.125$, df = 10, $P = 0.90$; females: $t = 0.303$, df = 10, $P = 0.76$). Analysis of the second principle component was also significant for the whole-model test ($F_{11, 78} = 12.7$, $P < 0.001$) and for the three-way interaction of sex, plot, and study phase ($F_{2, 87} = 4.55$, $P = 0.014$). Contrasts of least square means by study phase were significant for males, but not females, on plot 2 (males: $t = 9.55$, df = 10, $P < 0.001$; females: $t = 0.849$, df = 10, $P = 0.40$) and were insignificant for both sexes on plots 1 (males: $t = 0.834$, df = 10, $P = 0.41$; females: $t = 0.077$, df = 10, $P = 0.94$) and 3 (males: $t = 0.519$, df = 10, $P = 0.61$; females: $t = 0.040$, df = 10, $P = 0.97$). Thus, the postmanipulation resource use of *A. sagrei* was no different from the premanipulation resource use on either control plot, for males or females, but had shifted toward the resource use of *A. conspersus* on the experimental plot, and the shift was much more pronounced for males than females (Figure 4.5).

To better determine which of the seven habitat variables contributed to the observed shift in resource use by male and female *A. sagrei*, each habitat variable was analyzed separately for males and females by plot and study phase in a two-way least squares, or logistic, factorial analysis. As with the other analyses, when a significant interaction was found between plot and study phase, within plot differences between pre- and postmanipulation phases were tested with contrasts of least square means, or one-way logistic analyses. The results of these analyses are presented in Table 4.3. In all cases where a significant shift in resource use was found on the experimental plot, no shift was apparent on either control plot. Further, all significant differences presented in Table 4.3 remained significant when the sequential Bonferroni test (Rice, 1989) was applied across all habitat measures, for each sex, to maintain a table wide alpha of 0.05. As Table 4.3 illustrates, male *A. sagrei* on the experimental plot exhibited a shift in resource use for each of the recorded habitat measures except perch height, whereas the only significant univariate shift in resource use for female *A. sagrei* on the experimental plot was in arboreality. Further, as a comparison of Tables 4.3 and 4.4 demonstrates, all shifts in resource use by *A. sagrei* were directed toward the resource space typically occupied by *A. conspersus*.

Although no shift in median perch height was found for *A. sagrei* on the experimental plot (Table 4.3), there was a conspicuous change in the maximum perch height and display behavior of male *A. sagrei* on the experimental plot. After the removal of *A. conspersus*, male *A. sagrei* on the experimental plot were regularly observed displaying vigorously (dewlaping and headbobbing while doing four-legged pushups with the tail elevated) while perched on tree trunks at heights up to 3.4 m. In contrast, before removing *A. conspersus*, male *A. sagrei* were never observed above 1.7 m or displaying in this manner on trees. Consequently, when the maximum perch height of males was analyzed by plot and study phase in a two-way factorial analysis of variance, the whole-model test ($F_{5,42} = 7.03$, $P < 0.001$) and the interaction between plot and study phase ($F_{2,45} = 3.23$, $P = 0.049$) were significant, and the contrast between pre- and postmanipulation phases was significant for the experimental plot ($t = 4.25$, df = 10, $P < 0.001$) but not for either control plot (plot 1: $t = 0.580$, df = 10, $P = 0.57$; plot 3: $t = 0.999$, df = 10, $P = 0.32$). Thus, although median perch height didn't change, male *A. sagrei* did increase the range of perch heights used on the experimental plot after the removal of *A. conspersus*. A similar analysis for females was insignificant (interaction of plot and study phase: $F_{2,37} = 30.853$, $P = 0.43$), providing further evidence that habitat shift was more pronounced for male *A. sagrei*.

Finally, the shift or expansion in habitat use by *A. sagrei* on the experimental plot is particularly apparent when the number of individual trees occupied by *A. sagrei* before versus after manipulation is examined (Figure 4.6). *Anolis sagrei* were observed on significantly more trees on the experimental plot during the postmanipulation phase than during the premanipulation phase (*G*-test: $G = 10.008$, df = 1, $P = 0.002$), whereas there was no such difference between study phases for either control plot ($P >> 0.05$ for both comparisons). As expected, *A. conspersus* were observed on most of the trees on all three plots during the premanipulation phase (16 of 17 on plot 1, 14 of 14 on plot 2, and 9 of 11 on plot 3), and there were no significant changes between study phases for either control plot ($P \gg 0.05$ for both comparisons).

DISCUSSION

In a previous study on Grand Cayman, I demonstrated that male *A. conspersus* were highly aggressive toward male *A. sagrei*, but not vise versa (Part III). This finding, combined with the observation that male *A. conspersus* are generally larger than male *A. sagrei*, provided indirect support for the hypothesis that introduced *A. sagrei* were restricted to extremely open, sunny habitats on Grand Cayman as a result of interference from native *A. conspersus*, which occur in all habitats but are most abundant in undisturbed woodlands. Additional indirect support for this hypothesis was provided by observations that *A. sagrei* occupy woodlands similar to those on Grand Cayman elsewhere (Schoener, 1968; Lister, 1976; Lee, 1980; Schoener and Schoener, 1980), sometimes even in the presence of species ecologically similar to, but less aggressive than, *A. conspersus* (e.g., in Florida where *A. sagrei* is also introduced and occurs with native *A. carolinensis*: Tokarz and Beck, 1987; Gerber and Kramer, unpublished data).

This present study provides direct experimental evidence that the habitat occupancy, abundance, and resource use of *A. sagrei* on Grand Cayman is severely restricted by the presence of *A. conspersus*. Prior to manipulating the density of *A. conspersus* on the experimental plot, the abundance of the two species was inversely related along the macrohabitat gradient: *A. conspersus* were most abundant in wooded areas, whereas *A. sagrei* were most abundant in non-wooded areas (Figure 4.2). In addition, PCA showed that the two species were well separated in their habitat use on all plots prior to experimental manipulations (Figure 4.4). Compared to *A. conspersus*, during the premanipulation phase *A. sagrei* were less arboreal, occupied shorter vegetation, perched lower and on smaller diameter trunks and branches, spent more time in the sun, and escaped downward (rather than upward) most of the time (Tables 4.2 and 4.3).

In contrast, when the relative abundance of *A. conspersus* was reduced by two-thirds on the experimental plot (Figure 4.2), *A. sagrei* increased in abundance and shifted their use of structural and microclimatic resources to include much of what had been occupied by *A. conspersus* (Figures 4.2, 4.5, and 4.6; Table 4.3). The increase in abundance of *A. sagrei* on the experimental plot involved males and females equally, as the sex ratio of *A. sagrei* did not differ among plots during either study phase (Figure 4.3). However, the shift in habitat use of *A. sagrei* on the experimental plot was much more pronounced for males than females (Figure 4.5). Although both male and female *A. sagrei* on the experimental plot were significantly more arboreal (i.e., less likely to be on the ground) during the postmanipulation phase, only male *A. sagrei* significantly increased their use of wooded microhabitats, perched more frequently on taller vegetation and on trunks and branches of larger diameter, spent more time in the shade, escaped upward more often, and were regularly observed displaying from high vantage points on trees (Table 4.3). The greater shift in resource use for male than female *A. sagrei* is as expected though. First, most of the *A. conspersus* remaining on the experimental plot during the postmanipulation phase were females (Figure 4.3), which are smaller than male *A. sagrei* but slightly larger than female *A. sagrei*. Thus, the postmanipulation reduction in interspecific competition was likely more pronounced for male than female *A. sagrei*. Second, because interspecific asymmetries in size (and possibly aggressiveness) are more pronounced for males than females, and male *A. sagrei* overlapped more with *A. conspersus* in resource use to begin with (Figure 4.4; Table 4.2 and 4.3), male *A. sagrei* would be expected to shift more than females.

Finally, despite differences in the relative abundance of *A. conspersus* and *A. sagrei* among plots prior to manipulation, and changes within plots in the relative abundance of individual species between pre- and postmanipulation phases of the study, the combined abundance of the two species did not differ significantly among plots or between study phases (Figure 4.2). That is, changes in the abundance of *A. conspersus* (whether deliberate, as on plot 2, or not, as on plot 3) resulted in relatively rapid compensatory changes in the abundance of *A. sagrei*. Thus, in addition to demonstrating changes in abundance and resource use consistent with competition, the results of this study also provide strong evidence for complete density compensation between *A. conspersus* and *A. sagrei*. In summary, all of the findings of this experiment are consistent with the hypothesis that native *A. conspersus* restrict the distribution, abundance, and habitat use of introduced *A. sagrei* on Grand Cayman through aggressive interference.

Because interference between *A. sagrei* and *A. conspersus* is asymmetrical, the removal of *A. sagrei* would not be expected to produce a reciprocal response of equal strength in *A. conspersus*. Consistent with this prediction, the habitat occupancy and abundance of *A. conspersus* does not appear to have changed markedly since the introduction of *A. sagrei* (Losos et al., 1993) or to be noticeably different in areas of the island with and without *A. sagrei* (Losos et al., 1993, Gerber and Echternacht, unpublished data). There is evidence of a measurable competitive effect of *A. sagrei* on *A. conspersus* in those habitats where the species are sympatric, however, as *A. conspersus* have shifted their use of perch heights upward in open habitats, but not in wooded habitats, since the arrival of *A. sagrei* on Grand Cayman (Losos et al., 1993). The magnitude of this shift is, however, minor in comparison to that demonstrated here for *A. sagrei*.

Results of the recent studies on Grand Cayman are also consistent with those of Schoener (1975) where he compared the habitat use of the "species" in sympatry in Jamaica (i.e., introduced *A. sagrei* and native *A. grahami*, the ancestor of *A. conspersus* and its ecological analog) with the habitat use of the "species" in allopatry (native *A. conspersus* in Grand Cayman and native *A. sagrei* in Cayman Brac). After correcting for differences in habitat availability between sites, he found that both forms shifted their use of habitat in the presence of the other. In Jamaica, *A. grahami* occupied perches that were higher and larger in diameter than those occupied by *A. conspersus* on Grand Cayman, and introduced *sagrei* occupied perches that were lower and smaller in diameter than those used by native conspecifics on Cayman Brac. However, habitat shift was greater for *A. sagrei* than for *A. conspersus – A. grahami*, suggesting an asymmetry in the competitive relationship.

The correspondence between Schoener's (1975) results and those of this study and Losos et al. (1993), suggests a close similarity between the interaction of *A. sagrei* and *A. grahami* in Jamaica with that of *A. sagrei* and *A. conspersus* in Grand Cayman. Indeed, just as in Grand Cayman, the success of *A. sagrei* in Jamaica has been closely tied with human habitat modifications and the species is found only in open, sunny situations (e.g., Williams, 1969; Schoener, 1971). Thus, *A. grahami* may be restricting *A. sagrei* to open habitats in Jamaica (Schoener, 1971), just as *A. conspersus* does in Grand Cayman. Furthermore, because *A. grahami* "defend their territories against other lizards of their own size regardless of species" (Rand, 1967: page 9), interspecific aggression is likely to be an important and asymmetrical interaction between *A. grahami* and *A. sagrei* in Jamaica, just as it is in Grand Cayman between *A. conspersus* and *A. sagrei*. Indeed, interspecific aggression in *A. conspersus* is likely a conserved ancestral trait acquired from *A. grahami* (see Part III).

Detailed studies of interspecific resource partitioning have shown that such patterns are never attributable to a single mechanism, but rather always involve at least two mechanisms, often interacting in a complex fashion (Toft, 1985). The fact that *A. sagrei* has been able to expand its range on Grand Cayman, despite strong interference from *A. conspersus*, supports this conclusion. Coexistence of *A. sagrei* with *A. conspersus* appears to hinge on interspecific differences that permit *A. sagrei* to exploit open habitats more efficiently than *A. conspersus*. As shown by Losos et al. (1993) in a review of anole introductions, introduced anoles that differ significantly from their native counterparts are more successful than those that are similar to native species. Because *A.*

sagrei are typically more terrestrial and heliothermic than *A. conspersus*, they may have an advantage in open habits where arboreal perches and shade are less abundant (Losos et al., 1993). Further, because of their smaller size, *A. sagrei* should require less food per individual than *A. conspersus*. Indeed, smaller species are predicted to be more efficient exploitative competitors than larger species (Wilson, 1975; Persson, 1985) and thus should have a competitive advantage in habitats where the dominant species is limited by the availability of resources other than space (Case and Gilpin, 1974). In addition, while *A. sagrei* is clearly at a disadvantage with respect to aggressive interference, the situation appears to be opposite with regard to intraguild predation. In a study designed to examine the potential for intraguild predation between *A. sagrei* and *A. conspersus*, adult *A. sagrei* were significantly more likely to eat juvenile *A. conspersus* than juvenile conspecifics, whereas adult *A. conspersus* were unlikely to eat juveniles of either species (Gerber and Echternacht, in press). Thus, interspecific differences in physiology, morphology, and predatory behavior may explain how *A. sagrei* is able to numerically dominate *A. conspersus* in open habitats, despite its behaviorally subordinate status.

As noted previously by Losos et al. (1993), the availability of open habitats on Grand Cayman is a relatively new development arising from human settlement and the associated clearing of native woodlands. Thus, the recent colonization success of *A. sagrei* on Grand Cayman appears to be a human mediated phenomenon. Indeed, based on how effectively *A. conspersus* excludes *A. sagrei* from undisturbed areas, it is not clear that *A. sagrei* would persist on Grand Cayman if human habitat alterations were to cease. This view is also supported by the observation that *A. sagrei*, which originated on the Cuban Bank, colonized nearly every landmass surrounding Grand Cayman without human assistance, including Little Cayman and Cayman Brac, Swan Island, Half Moon Cay and coastal Belize, and Cozumel and coastal Yucatan (Williams, 1969). Consequently, it is likely that *A. sagrei* reached Grand Cayman in the past, without human assistance, but failed to colonize due to the presence of *A. conspersus* (Williams, 1969) and the relative scarcity of open habitats. In fact, the only landmass surrounding Grand Cayman that *A. sagrei* did not colonize of its own accord is Jamaica (Williams, 1969), where *A. grahami*, the interspecifically aggressive ancestor of *A. conspersus*, is native.

In conclusion, this study provides support for a mechanistic approach to species interactions that integrates observational and experimental techniques. Through an understanding of species differences in morphology (size) and behavior (interspecific aggression), it was possible to predict the nature of the interaction between *A. conspersus* and *A. sagrei* on Grand Cayman. Furthermore, without knowledge of the mechanism of competition, interspecific differences in distribution, abundance, and habitat use might have been overly attributed to pre-existing interspecific differences (Losos et al., 1993). Thus, although ecological differences between species may be required for coexistence of invading and native species, identification of such differences should not be interpreted as evidence that competition is negligible without experimental evidence. Further, even when competition is found to occur, it is important to consider other interactions, such as intraguild predation, that could potentially mediate its effects.

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APPENDIX: PART IV

Table 4.1. Description of the vegetation and microhabitat types recognized in this study. The two microhabitat types illustrate the dichotomy between perch structures that are relatively large, high, structurally complex, and well shaded and those that are relatively small, low, structurally simple, and poorly shaded. See Figure 4.1 for the distribution of vegetation and microhabitat types on the study plots.

Microhabitat	Vegetation	Definition
Wooded	Trees	Woody plants with stems > 5 cm in diameter at breast height (DBH); observed range 8 to 55 cm DBH
	Undergrowths	Plants (mostly woody) with stems < 5 cm in DBH and close enough to a tree to allow arboreal movement of lizards to and from the tree
Non-wooded	Thickets	Two or more woody plants with stems less < 5 cm in DBH, not part of an undergrowth, and close enough to allow arboreal movement of lizards between plants
	Open areas	Plants (mostly herbaceous) that were not trees or part of an undergrowth or thicket

Table 4.2. Spatial resource use of male (M) and female (F) *Anolis conspersus* on the study plots before and after removal of *A. conspersus* from plot 2. No significant shifts in resource use were observed between pre- and postmanipulation study phases for either sex, but plot differences were significant for some resource measures. Values are least square means and their standard errors. For convenience, categorical measures are presented as the percentage of animals using the most prominent resource category; however, statistical analyses were done on frequencies using logistic models (see text).

Resource Measure	Sex	Study Phase	Plot 1 Control	Plot 2 Experimental	Plot 3 Control
Arboreality (% on vegetation)	M	Pre	94.7 ± 4.1	93.0 ± 2.7	89.6 ± 3.0
		Pre	93.5 ± 3.7	—	94.0 ± 3.5
	F	Pre	92.0 ± 3.8	94.8 ± 2.5	87.5 ± 3.0
		Post	93.3 ± 3.5	—	94.1 ± 3.3
Microhabitat type (% in "wooded" areas)	M	Pre	58.7 ± 5.4	81.4 ± 3.9	88.3 ± 4.2
		Post	63.2 ± 5.9	—	90.0 ± 5.2
	F	Pre	60.0 ± 6.9	93.1 ± 4.5	95.0 ± 5.5
		Post	60.0 ± 6.3	—	91.2 ± 5.9
Microclimate type (% in shaded locations)	M	Pre	78.9 ± 5.8	74.4 ± 3.8	76.6 ± 4.1
		Post	80.4 ± 5.2	—	78.0 ± 5.0
	F	Pre	80.0 ± 9.7	70.7 ± 6.4	67.5 ± 7.7
		Post	80.0 ± 8.9	—	70.5 ± 8.3
Escape direction (% escaping upward)	M	Pre	39.1 ± 6.5	48.8 ± 4.7	57.1 ± 5.0
		Post	36.8 ± 7.1	—	62.0 ± 6.2
	F	Pre	36.0 ± 9.7	51.7 ± 6.4	50.0 ± 7.7
		Post	36.7 ± 8.9	—	52.9 ± 8.3
Median structure height (m)	M	Pre	5.88 ± 1.00	14.79 ± 0.73	14.40 ± 0.77
		Post	6.69 ± 1.10	—	15.00 ± 0.96
	F	Pre	5.66 ± 1.46	14.34 ± 0.96	13.33 ± 1.15
		Post	4.78 ± 1.33	—	13.99 ± 1.25
Median perch diameter (mm)	M	Pre	43.6 ± 17.6	90.2 ± 12.9	99.8 ± 16.9
		Post	50.7 ± 19.3	—	93.9 ± 13.6
	F	Pre	41.1 ± 22.0	90.5 ± 14.4	84.1 ± 17.4
		Post	37.0 ± 20.1	—	88.7 ± 18.8
Median perch height (cm)	M	Pre	103.6 ± 11.2	102.8 ± 8.2	93.3 ± 10.7
		Post	107.9 ± 12.3	—	91.4 ± 8.7
	F	Pre	107.2 ± 13.2	102.2 ± 8.7	69.3 ± 10.4
		Post	106.0 ± 12.1	—	67.9 ± 11.3

Table 4.3. Spatial resource use of male (M) and female (F) *Anolis sagrei* on the study plots before and after removal of *A. conspersus* from plot 2. Significant shifts in resource use between pre and postmanipulation phases are indicated by asterisks: ** = $P < 0.01$, *** = $P < 0.001$ (see text for details). Values are least square means and their standard errors. For convenience, categorical measures are presented as the percentage of animals using the most prominent resource category for *A. conspersus*; however, statistical analyses were done on frequencies using logistic models (see text).

Resource Measure	Sex	Study Phase	Plot 1 Control	Plot 2 Experimental	Plot 3 Control
Arboreality (% on vegetation)	M	Pre	74.2 ± 3.5	72.4 ± 3.5	60.0 ± 5.8
		Pre	72.1 ± 3.7	92.5 ± 3.3***	61.1 ± 5.7
	F	Pre	65.7 ± 7.8	53.3 ± 8.4	50.0 ± 11.5
		Post	66.7 ± 6.4	83.9 ± 5.8**	47.1 ± 7.9
Microhabitat type (% in "wooded" areas)	M	Pre	23.7 ± 4.9	24.5 ± 4.9	34.3 ± 8.2
		Post	14.0 ± 5.2	54.2 ± 4.7***	36.1 ± 8.1
	F	Pre	8.6 ± 4.9	10.0 ± 5.3	12.5 ± 7.2
		Post	9.8 ± 4.0	19.4 ± 3.7	11.8 ± 4.9
Microclimate type (% in shaded locations)	M	Pre	39.2 ± 6.3	43.9 ± 6.3	48.6 ± 10.5
		Post	37.2 ± 6.7	71.0 ± 6.0***	47.2 ± 10.3
	F	Pre	51.4 ± 8.6	53.3 ± 9.3	56.3 ± 12.8
		Post	51.0 ± 7.1	66.1 ± 6.5	52.9 ± 8.8
Escape direction (% escaping upward)	M	Pre	9.3 ± 2.4	6.1 ± 2.4	5.7 ± 4.0
		Post	11.6 ± 2.6	36.4 ± 2.3***	11.1 ± 3.9
	F	Pre	11.4 ± 4.6	6.7 ± 4.9	6.3 ± 6.8
		Post	11.8 ± 3.8	16.1 ± 3.4	8.8 ± 4.6
Median structure height (m)	M	Pre	1.85 ± 0.37	1.93 ± 0.37	1.87 ± 0.62
		Post	1.95 ± 0.39	4.50 ± 0.35***	1.76 ± 0.61
	F	Pre	1.46 ± 0.28	1.89 ± 0.30	0.95 ± 0.40
		Post	1.50 ± 0.22	1.95 ± 0.21	1.05 ± 0.28
Median perch diameter (mm)	M	Pre	14.1 ± 2.6	14.0 ± 2.6	26.5 ± 4.3
		Post	16.9 ± 2.8	41.8 ± 2.5***	23.3 ± 4.3
	F	Pre	12.6 ± 5.0	15.2 ± 5.4	17.2 ± 7.3
		Post	12.5 ± 4.1	22.4 ± 3.7	21.9 ± 5.0
Median perch height (cm)	M	Pre	67.0 ± 3.6	71.6 ± 3.5	39.9 ± 5.9
		Post	66.1 ± 3.8	67.9 ± 3.4	41.1 ± 5.9
	F	Pre	37.1 ± 5.9	46.6 ± 6.3	24.1 ± 5.9
		Post	41.1 ± 4.8	49.6 ± 4.4	21.0 ± 8.6

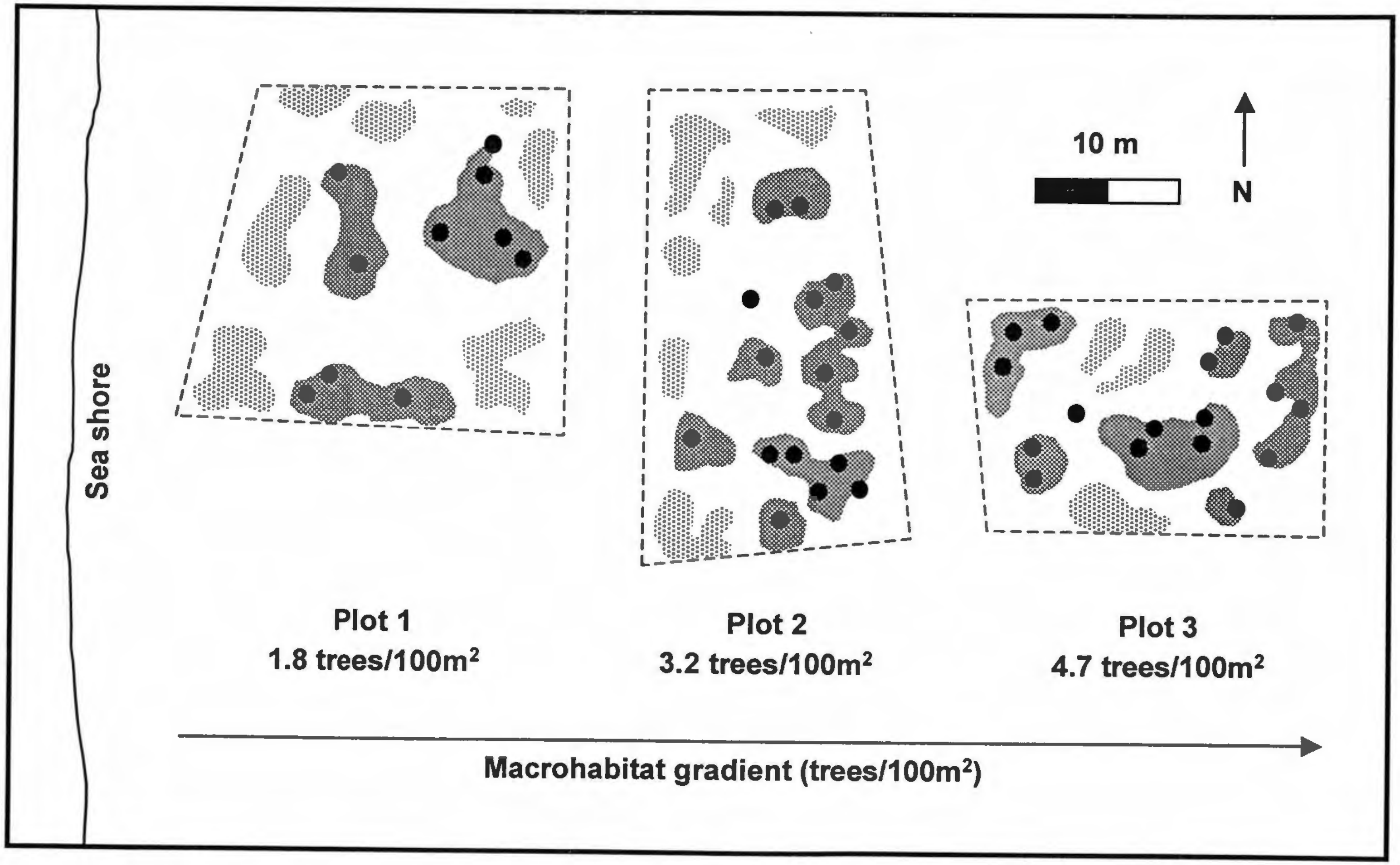

Figure 4.1. Diagram of the study site illustrating the position of plots as well as the distribution of vegetation on plots. Vegetation: trees (black dots), undergrowths (heavy stippling), thickets (light stippling), and open areas (white). See Table 1 for definitions of vegetation and microhabitat types. Plots were separated by open areas with a few thickets. The distance from plot 1 to the sea shore (about 30 m) is not drawn to scale. The study area was bounded by a paved road to the east and by fenced off residential properties to the north and south, none of which are shown.

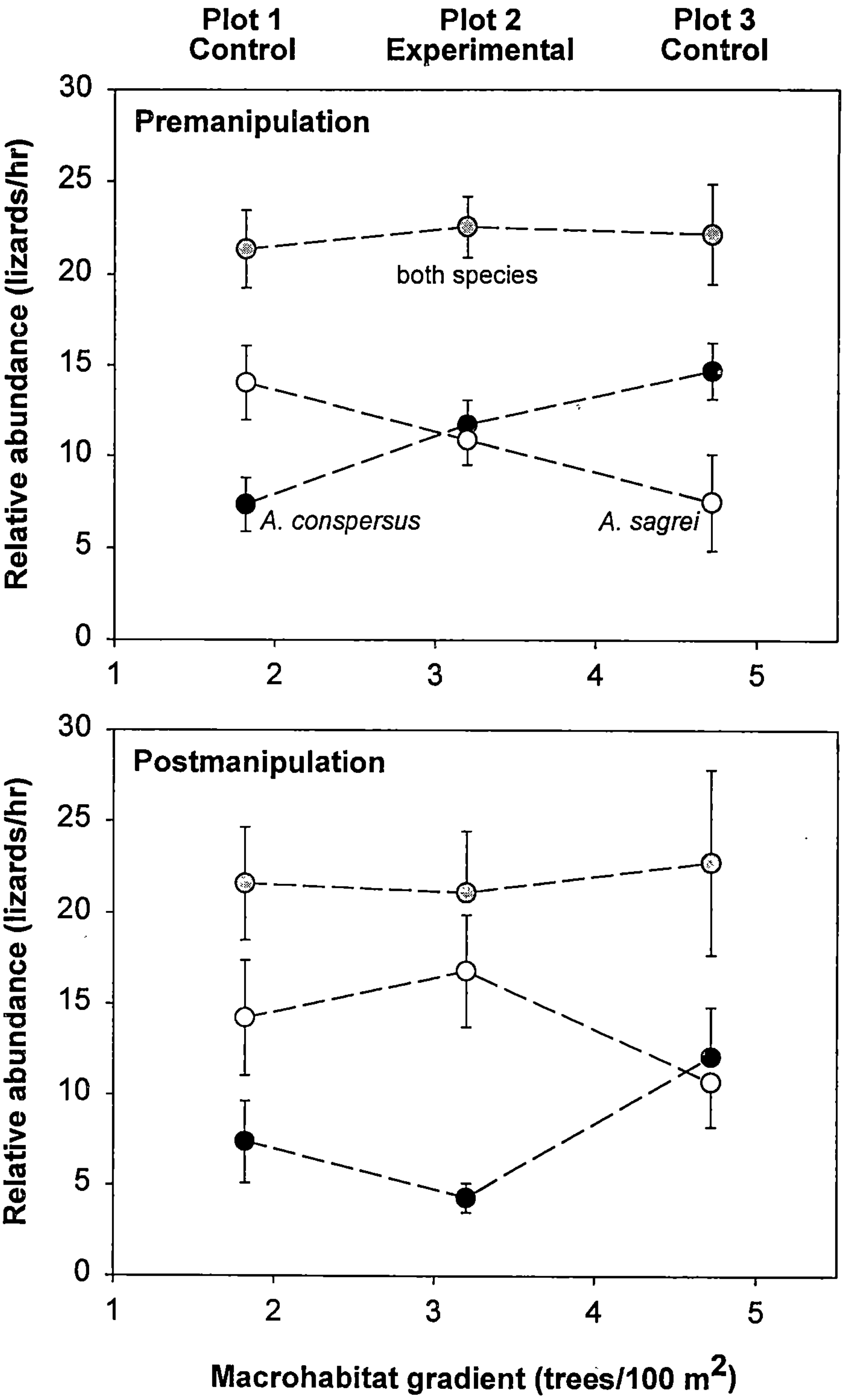

Figure 4.2. Relative abundance of *Anolis conspersus* and *A. sagrei* on experimental and control plots during pre- and postmanipulation phases of the study. Values are means and their 95% confidence intervals. Lines connecting means are for illustration only.

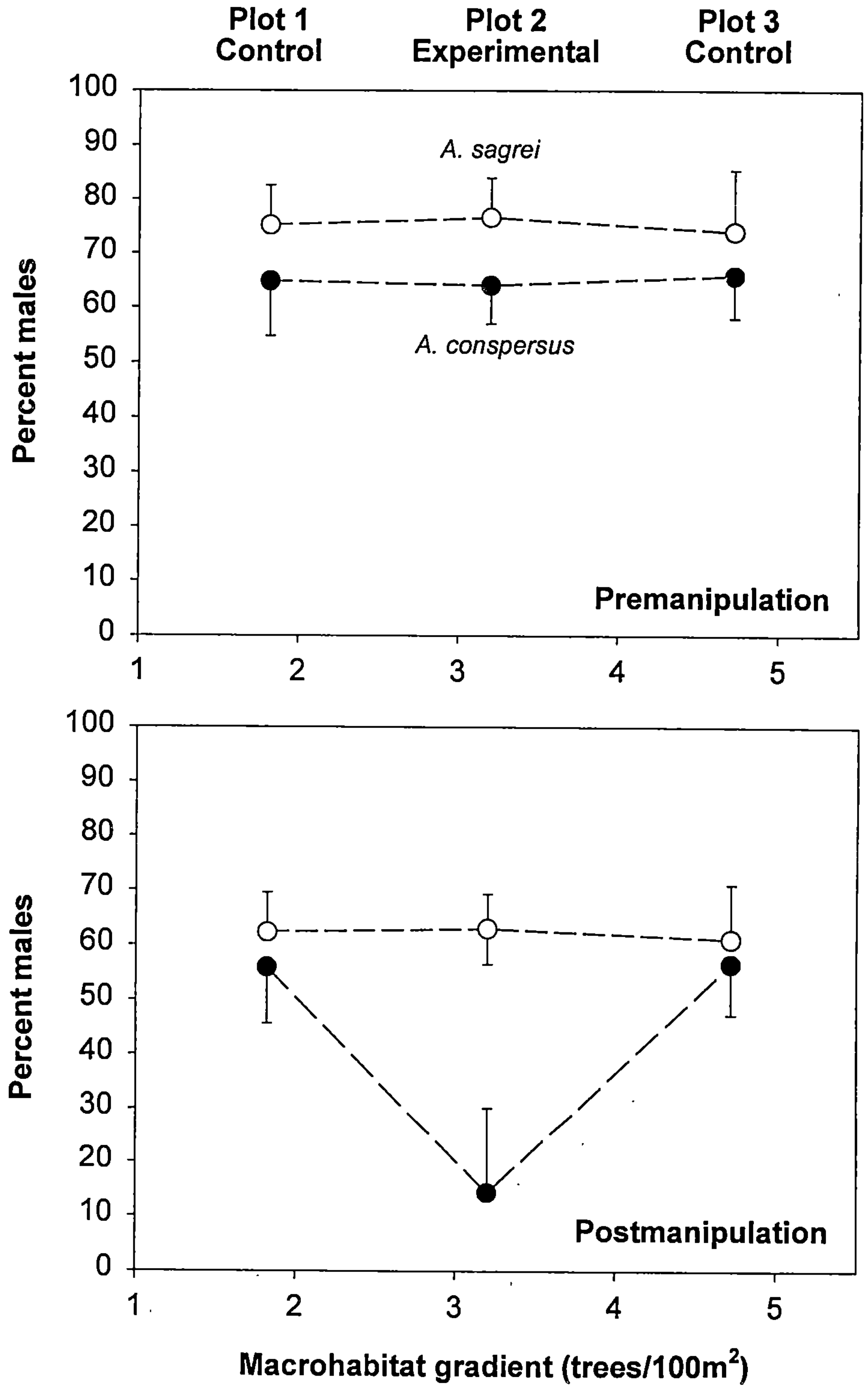

Figure 4.3. Percentage of *Anolis conspersus* and *A. sagrei* that were male on experimental and control plots during pre- and postmanipulation phases of the study. Values are means and their 95% confidence intervals. Lines connecting means are for illustration only.

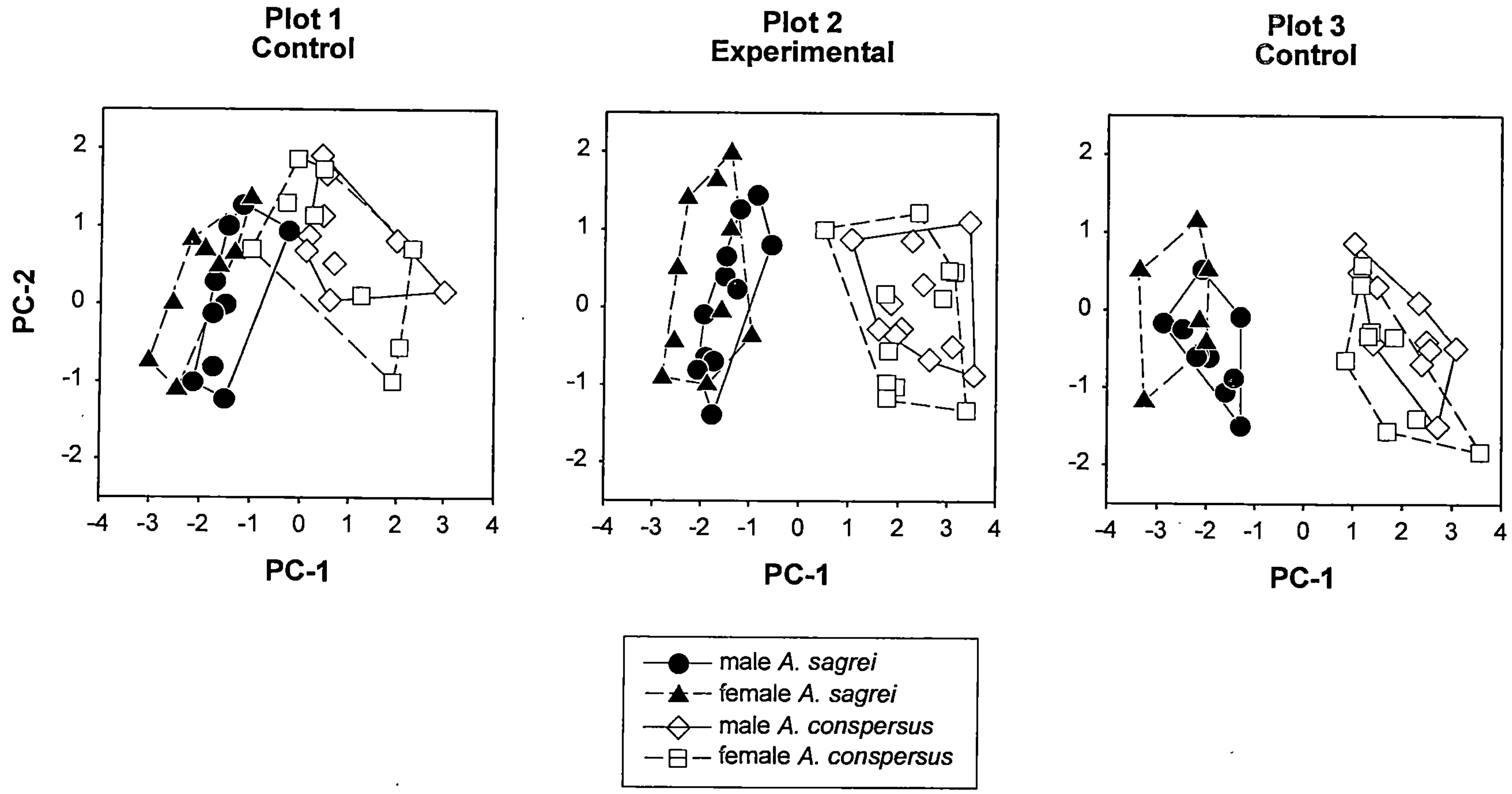

Figure 4.4. Plots of the first and second principle component scores for a PCA of the seven habitat use variables collected for male and female *Anolis conspersus* and *A. sagrei* on experimental and control plots during the premanipulation phase. PC-1 explained 60% of the variation and loaded highest for structural height, microhabitat type, and escape direction. PC-2 explained 13% of the variation and loaded highest highest for perch microclimate, arboreality, and perch diameter.

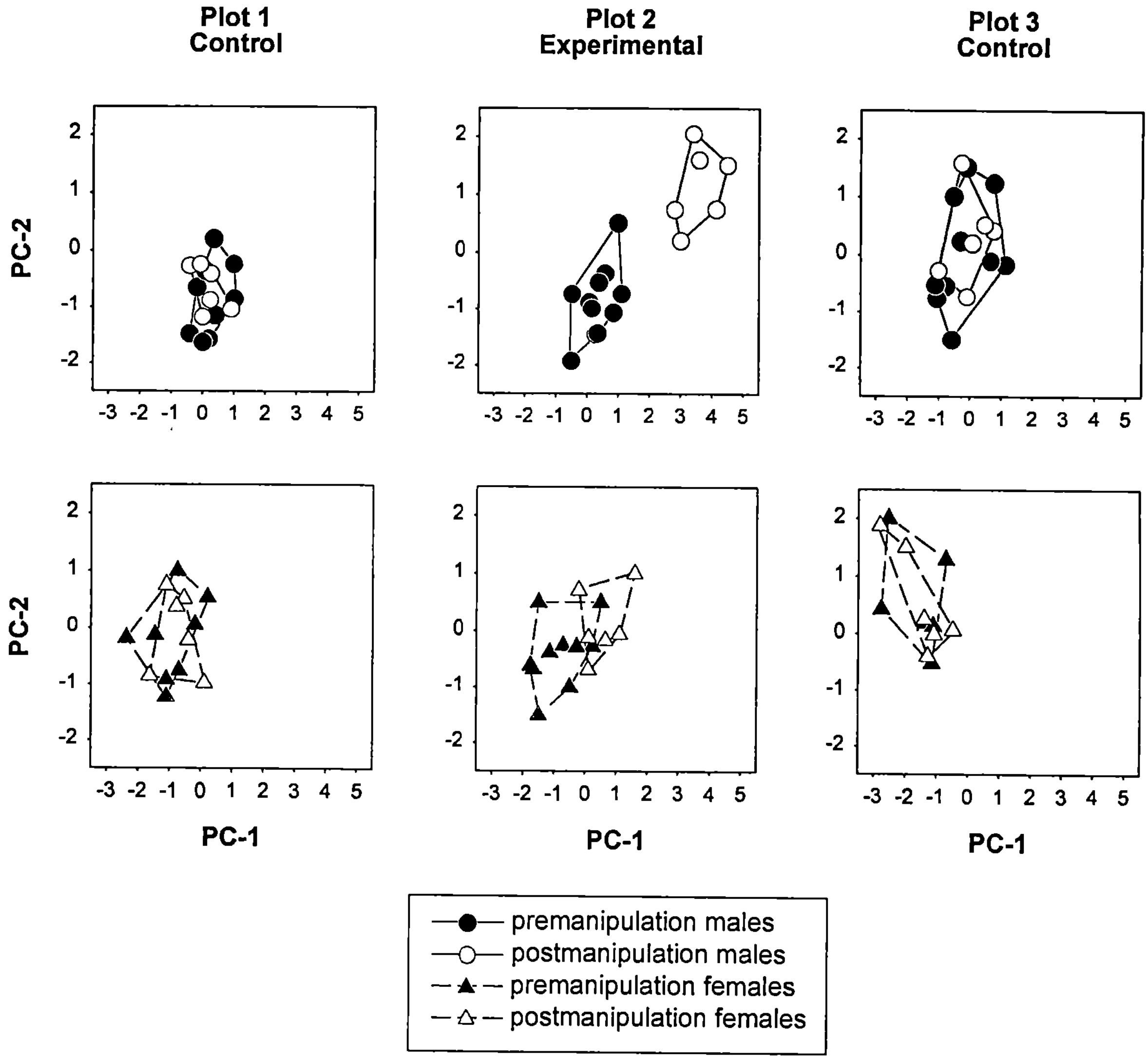

Figure 4.5. Plots of the first and second principle component scores for a PCA of the seven habitiat use variables collected for male and female *Anolis sagrei* on experimental and control plots during pre- and postmanipulation phases. PC-1 explained 38% of the variation and loaded highest for structure height, microhabitat type, and perch diameter. PC-2 explained 18% of the variation and loaded highest for microclimate type, escape direction, and perch height.

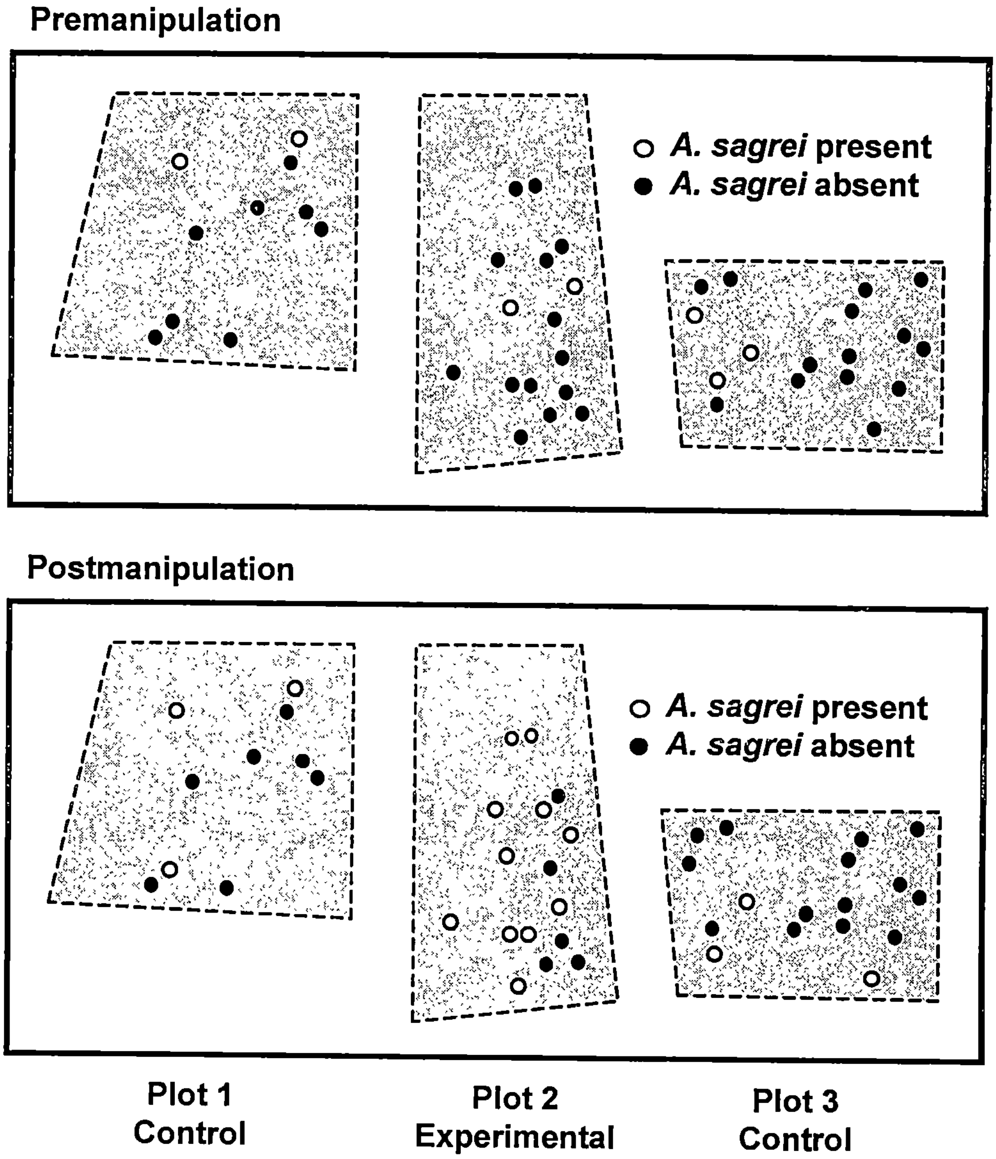

Figure 4.6. Presence and absence of *A. sagrei* on individual trees on the Study plots during pre- and postmanipulation phases of the study.

PART V

Effects of an Introduced Competitor and Predator on the Growth and Survival of Juvenile *Anolis carolinensis* in Habitats of Different Complexity

ABSTRACT

Since its introduction to Florida, the Cuban brown anole, *Anolis sagrei* (Sauria: Polycrotidae), has been replacing the native green anole, *A. carolinensis*, as the common anole of disturbed and open habitats. In a previous study, conducted in small cages lacking refuge, adult *A. sagrei* were significantly more likely to prey on juvenile *A. carolinensis* than on similarly sized conspecifics, whereas adult *A. carolinensis* were unlikely to prey on juveniles of either species. This suggested that intraguild predation might be an important and asymmetrical interaction between these species. To investigate the importance of intraguild predation under more natural conditions, as well as the strength of inter- versus intraspecific competition among juveniles, and the effect of habitat complexity on interspecific interactions, experiments were conducted in small outdoor enclosures in which groups of *A. carolinensis* juveniles were raised in habitats of low, medium, or high complexity in the presence or absence an adult male *A. sagrei*, and with or without *A. sagrei* juveniles. Juvenile *A. carolinensis* were not affected by the presence of adult or juvenile *A. sagrei* in the high complexity habitat, but experienced significant mortality in the presence of adult *A. sagrei* in the medium complexity habitat, and almost complete mortality in the presence of either adult or juvenile *A. sagrei* in the low complexity habitat. Further, even in the absence of juvenile and adult male *A. sagrei*, the growth of *A. carolinensis* juveniles decreased with decreasing habitat complexity and survival was reduced in the low complexity habitat. In contrast, *A. sagrei* juveniles exhibited reduced growth only in the low complexity habitat and survivorship was high in

all habitats. These results suggest that (1) predation, competition, and ecological differences are important components of the interaction between *A. carolinensis* and *A. sagrei* in Florida, and (2) that the numerical decline of *A. carolinensis* in disturbed and open habitats in Florida, following colonization by *A. sagrei*, may represent a return to a pre-evolved pattern of coexistence on Cuba, where *A. sagrei* is sympatric with *A. porcatus*, the progenitor and ecological analog of *A. carolinensis*.

INTRODUCTION

Interactions among closely related predatory species with size-structured populations and generalized feeding habits are likely to involve both competition and predation (Werner and Gilliam, 1984; Ebenman and Persson, 1988; Polis and Holt, 1992; Holt and Polis, 1997). The type, symmetry, and strength of interactions between such species will depend on many variables, including the relative sizes of the animals and the nature of the habitat in which interaction occurs. All else being equal, large animals are likely to physically interfere with or eat smaller animals and thus behaviorally dominate, whereas smaller animals are likely to be more efficient exploitative competitors than larger animals and thus dominate numerically (e.g., Case and Gilpin, 1974; Wilson, 1975; Persson, 1985). Similarly, the ability of large animals to interfere with or prey on smaller animals may be limited in high complexity habitats by morphological constraints, whereas the exploitative efficiency of small animals may be limited in low complexity habitats by increased risk of predation (e.g., Werner et al. 1983; Gotceitas and Colgan, 1989; Persson and Eklov, 1995). Further, because even closely related species are likely to differ in size, morphology, physiology, and behavior, their relative effectiveness as competitors and predators are likely to vary with differences in habitat complexity (e.g., Werner, 1992; Petren and Case, 1998; Briers and Warren, 1999).

Here I investigate the effects of habitat complexity on the strength and nature of interspecific interactions between two species of *Anolis* (Sauria: Polychrotidae) in Florida, one native and one introduced, that appear to be engaged in competitive and predatory interactions. The species are *A. carolinensis*, the only anole native to North America (Williams, 1969), and *Anolis sagrei*, a native of Cuba and the Bahamas that was introduced to Florida about 60 years ago (Wilson and Porras, 1983, and references therein). Both species are medium-sized anoles with broad ecological niches (e.g., Williams, 1969; Schoener, 1975; Lister, 1976), pronounced sexual size dimorphism (e.g., Schoener and Schoener, 1980; Jenssen et al., 1995), and exhibit a territorial and polygynous social structure (e.g., Evans, 1938; Schoener and Schoener, 1980; Ruby, 1984; Jenssen and Nunez, 1998). Like other anoles, *A. carolinensis* and *A. sagrei* are diurnal, primarily insectivorous, and largely arboreal. Both species are most abundant in edge situations (e.g., Collette, 1961; Williams, 1969), are heliotherms with similar preferred and field body temperatures (Corn, 1971; Gerber, unpublished data), and are considered excellent colonizers (e.g., Williams, 1969; Schoener, 1975; Lister, 1976). Relative to *A. carolinensis*, however, *A. sagrei* is stockier (generally shorter in length but greater in mass) with proportionately longer limbs, smaller toepads, and fewer subdigital lamellae (Collette, 1961; Glossip and Losos, 1997; Beuttell and Losos, 1999). Consequently, *A. sagrei* can run faster and jump further than *A. carolinensis* (Losos and Irschick, 1996), but is less adept at clinging and climbing (Irschick et al., 1996) and is thus typically more terrestrial (e.g., Collette, 1961; Schoener, 1968, 1975). In addition, *A. sagrei* has a lower rate of evaporative water loss than *A. carolinensis* (Claussen, 1967; Dunson and Bramham, 1981) and thus may be better adapted to xeric habitats. From an eco-morphological perspective, *A. carolinensis* is a trunk-crown ecomorph, occupying the trunks and crowns of trees, whereas *A. sagrei* is a trunk-ground ecomorph, tending to occupy the trunks of trees and the ground (e.g., Collette, 1961; Williams, 1969; Beuttell and Losos, 1999). Thus, while similar in many respects, the species differ enough that coexistence seems probable. Indeed, although *A. carolinensis* is endemic to the southeastern United States and has been isolated from other anoles for perhaps 3-4 million years (Buth et al., 1980), it belongs to a clade of Cuban origin whose members occur sympatrically with *A. sagrei* in Cuba, the Bahamas, and on several other small islands (Williams, 1969, 1976). Thus, *A. carolinensis* shares a coevolutionary history with *A. sagrei*.

Nevertheless, since being introduced to Florida, *A. sagrei* has colonized much of the state (Godley, 1981; Lee, 1985; Campbell, 1996) and has replaced *A. carolinensis* as the common anole in many areas as it has spread, particularly in disturbed and open habitats (e.g., Christman, 1980; Wilson and Porras, 1983; Tokarz and Beck, 1987; Echternacht and Harris, 1993). Consequently, the two species are generally assumed to compete (e.g., Case and Bolger, 1991a, 1991b), although documentation of this phenomenon is sparse (but see Campbell, 2000) and the mechanisms of interaction are largely unknown. Several researchers have investigated the potential for aggressive interactions between adult male *A. sagrei* and *A. carolinensis*, but these studies found interspecific aggression to be much less intense than intraspecific aggression in both species (Tokarz and Beck, 1987; Brown, 1988; Gerber and Kramer, unpublished data), suggesting other interactions are involved.

Because hatchling *A. carolinensis* often appear to be disproportionately rare where *A. carolinensis* is sympatric with *A. sagrei*, whereas hatchling *A. sagrei* are often abundant (Gerber, unpublished data), interspecific interactions between juveniles or between juveniles and adults may be important. For this reason, and because hatchling *A. carolinensis* and *A. sagrei* are small enough to be eaten by adults of either species, the potential for intraguild predation was investigated in an earlier study (Part II; Gerber and Echternacht, in press). Under captive conditions, where juveniles had no refuge from predation, adult male *A. sagrei* preyed heavily on juvenile *A. carolinensis* but rarely on juvenile conspecifics, whereas adult male *A. carolinensis* generally prey on neither juvenile conspecifics nor *A. sagrei*. Thus, an asymmetry in the potential for intraguild predation exists between the species that favors *A. sagrei*. Consequently, I hypothesized that hatchling *A. carolinensis* were the size-class most likely to be adversely effected by *A. sagrei*.

If hatchling *A. carolinensis* are regularly preyed upon by adult *A. sagrei* in the field, it is likely to be more common in habitats that afford little refuge from predation. Indeed, although hatchling *A. carolinensis* and adult *A. sagrei* occupy similar perch heights and may be found in close proximity to one another, hatchling *A. carolinensis* are generally found in microhabitats with considerable vegetational complexity (e.g., dense undergrowth), whereas adult *A. sagrei* are more often associated with structurally simple microhabitats (e.g., exposed tree trunks). The degree to which this pattern reflects the effects of predation, competition, or eco-morphological differences between species and size-classes is not known, however. Still, the fact that *A. carolinensis* populations in disturbed habitats, which tend to be structurally simple, undergo precipitous declines when *A. sagrei* invades, suggests that habitat complexity mediates interspecific interactions. Further, juvenile *A. sagrei* are frequently found alongside juvenile *A. carolinensis* in complex microhabitats, but like adult *A. sagrei* they tend to be more terrestrial and to be most abundant in structurally simple habitats. Thus, it seems probable that competition with juvenile *A. sagrei*, predation by adult *A. sagrei*, and eco-morphological differences between the species are all important factors in the decline of *A. carolinensis* in Florida.

To investigate the importance of intraguild predation under more natural conditions, the strength of inter- versus intraspecific competition among juveniles, and the effect of habitat complexity on interspecific interactions, I conducted a series of experiments in small outdoor enclosures in which groups of *A. carolinensis* juveniles were raised in habitats of different complexity in the presence or absence of an adult male *A. sagrei*, and with or without *A. sagrei* juveniles. I hypothesized that the effect of adult male and juvenile *A. sagrei* on *A. carolinensis* juveniles would increase as habitat complexity decreased, but that the survival and growth of *A. carolinensis* juveniles raised by themselves would not be significantly affected by habitat complexity. The results of these experiments show that the survival of juvenile *A. carolinensis* was reduced by adult *A. sagrei* in habitats of low and medium complexity, and by juvenile *A. sagrei* in the low complexity habitat. Thus, the magnitude of impact increases with decreasing habitat complexity. However, in the absence of juvenile and adult male *A. sagrei*, the growth of *A. carolinensis* juveniles decreased with decreasing habitat complexity and survival was also reduced in the low complexity habitat. In contrast, juvenile *A. sagrei* only experienced reduced growth in the low complexity habitat, and survival was high in all habitats. These results suggest that (1) predation, competition, and eco-morphological differences are all important components of the interaction between *A. carolinensis* and *A. sagrei* in Florida, and (2) that the numerical decline of *A. carolinensis* in open habitats following the colonization of Florida by *A. sagrei* may represent a return to the pre-evolved pattern of coexistence on Cuba, following the competitive release experienced by *A. carolinensis* when it colonized the North American mainland in the absence of interspecific competitors.

METHODS

The experiments were conducted in small outdoor enclosures (described below) near Knoxville, Tennessee, for a period of 35 days (5 weeks) from late July through early September in 1989, 1990, and 1991, respectively. This time period was chosen because it (a) coincides with the peak abundance of hatchling anoles in Florida and Louisiana, where lizards for the experiments were collected (discussed below), and (b) encompasses the life stage when *A. carolinensis* juveniles are most vulnerable to predation from adult *A. sagrei*. Differences in climate between Tennessee, Florida, and Louisiana are also minimal at this time of the year. Therefore, conducting the experiments in Tennessee, rather than in Florida (or Louisiana), was reasonable. Indeed, Knoxville is near the northern range limit of *A. carolinensis*, which appears to be set by winter, not summer, climatic conditions (Williams, 1969; Wilson and Echternacht, 1987).

Experiments were replicated in habitats of high, low, and medium complexity to determine if habitat complexity mediated the effects of competition and predation from *A. sagrei* juveniles and adults, respectively, on *A. carolinensis* juveniles. This was done by comparing the survival and growth of *A. carolinensis* juveniles in each habitat complexity type when (a) alone, (b) with *A. sagrei* juveniles, (c) with an adult male *A. sagrei*, and (d) with *A. sagrei* juveniles and an adult male *A. sagrei*. Survival and growth of juvenile and adult male *A. sagrei* were also measured to determine if these animals were affected by differences in habitat complexity or interactions with other anoles (i.e., presence of an adult male conspecific for *A. sagrei* juveniles, and presence of conspecific juveniles versus only *A. carolinensis* juveniles for adult male *A. sagrei*).

Enclosures and Habitat Complexity

Twenty-four enclosures, each measuring 1.2 m on a side and 0.9 m high, were established on top of a natural substrate. The enclosures comprised an interconnected array, 12 units long by 2 units wide, which shared adjoining walls. Enclosure walls consisted of rectangular wooden frames, built from 2 by 2 (5 cm by 5 cm) lumber, with galvanized aluminum window screening stretched across and stapled to one side. These frames were bolted together to form the walls of individual enclosures. Encircling and overhanging the inside, top perimeter of each enclosure was a 20 cm wide horizontal strip of clear polypropylene plastic, 3 mm thick. Plastic overhangs were attached to wooden frames, which were bolted to the top of each enclosure (see Pacala et al., 1983, for an illustration of this technique). To prevent the escape of lizards, all seams between enclosure sections were sealed with silicone caulk, the under-side of each overhang was sprayed with a silicone lubricant, and the base of each enclosure was buried in the substrate. In addition, each enclosure was fitted with a removable top constructed out of 2.5 cm hardware cloth attached to a wooden frame that rested on top of the plastic overhang. These tops served to exclude avian and mammalian predators while permitting the entrance of potential arthropod prey.

1989: High Complexity Habitat – In 1989, the habitat within the enclosures consisted of a dense mixture of wild herbaceous vegetation: grasses and broadleaved perennials and annuals. This was achieved by assembling the enclosures in an old field supporting a diverse, but relatively uniform, plant community. To facilitate enclosure assembly and to control for variation in vegetation height, all vegetation on the enclosure site was cut to a height of approximately 15 cm prior to enclosure assembly. The experiment did not commence, however, until the vegetation in the enclosures had grown to a height of about 60 cm.

1990: Low Complexity Habitat – In 1990, the habitat within the enclosures was radically simplified. Before assembling the enclosures, the ground was turned with a tiller to remove all vegetation from the site and landscaping fabric was placed over the soil to retard vegetation growth. Following assembly of the enclosures, two young shrubs (red tip, *Photinia fraseri*) were planted in opposite corners of each enclosure. Plants were obtained from a nursery and each was approximately 60 cm in height with one or two central stems supporting smaller branches with numerous leaves (approximately 10 cm by 4 cm). Following planting, the landscaping fabric in each enclosure was covered with three cubic feet (one bag) of pine bark mulch obtained from a commercial supplier.

1991: Medium Complexity Habitat – In 1991, the habitat within the enclosures was intermediate between the extremes of 1989 and 1990. This was accomplished through the natural growth of the shrubs planted in the enclosures in 1990. After pruning the shrubs to equalize differences in growth between plants in different enclosures, there was about a 5-fold increase over 1990 in the volume of space that shrubs occupied. As in 1990, the substrate was covered in pine bark mulch and thus was relatively open.

Lizards Subjects

All adult male and hatchling *A. sagrei* and approximately 25 % of the *A. carolinensis* hatchlings used each year were captured in Palm Beach County, Florida, just prior to commencing experiments, and transported to Knoxville, Tennessee. Due to the difficulty of collecting sufficient numbers of *A. carolinensis* hatchlings in Florida and a desire not to contribute to the depletion of existing populations, the other 75 % of *A. carolinensis* hatchlings were obtained from a commercial supplier (Snake Farm) in LaPlace, Louisiana (Parish of Kenner), where *A. sagrei* does not yet occur and *A. carolinensis* are more abundant. Prior to stocking enclosures, all lizards were weighed to the nearest 0.01 g using an electronic balance, measured for snout-vent length (SVL) to the nearest 0.5 mm using a metal rule, and permanently marked for future identification by clipping a unique combination of toes. At the conclusion of each year's experiment, all surviving lizards were collected and remeasured.

Experimental Treatments

In 1989 (i.e., the high complexity habitat), three enclosures each were stocked with two, four, six, eight, ten, and twelve *A. carolinensis* juveniles, respectively (18 enclosures in all). Two enclosures in each density treatment (12 total) also received an adult male *A. sagrei*. The other enclosure in each density treatment (6 total) did not receive an adult male *A. sagrei* and thus served as a control for the effect of adult male *A. sagrei* on the growth and survival of juvenile *A. carolinensis*. The six remaining enclosures each received four *A. carolinensis* juveniles and four *A. sagrei* juveniles. Four of these enclosures also received an adult male *A. sagrei*, whereas two did not.

In 1990 and 1991 (i.e., low and medium complexity habitats), the stocking design was simplified. Rather than varying the density of *A. carolinensis* juveniles, all enclosures received eight juveniles. Half of the enclosures (n = 12) received eight *A. carolinensis* juveniles each, and the other half received four *A. carolinensis* and four *A. sagrei* juveniles each. Within each of these two juvenile treatments, two-thirds of the enclosures (n = 8) received an adult male *A. sagrei*, whereas one-third (n = 4) did not.

In all years, assignment of treatments and individual lizards to enclosures was random. The SVL and mass of juvenile and adult male lizards used each year are summarized in Table 5.1. There were no significant differences between years in the initial SVL or mass of *A. carolinensis* juveniles, *A. sagrei* juveniles, or *A. sagrei* adult males, respectively (analysis of variance by year: $P > 0.2$ for all comparisons).

Food and Water Supplementation

In addition to arthropods that were already in the enclosures or colonized enclosures during the experiment, food was supplemented every three days with 3/8-inch

(1 cm) domestic crickets, *Acheta domesticus*, obtained from a commercial supplier. Supplementation with crickets was standardized by adding approximately 30 ml of crickets to each enclosure at each feeding (mean and standard deviation for 10 samples = 202 ± 14 crickets). In addition, enclosures with an adult male *A. sagrei* were supplemented with approximately ten 3/4-inch (2 cm) crickets at each feeding.

To minimize potential effects of environmental fluctuations in rainfall, cages were spayed with water from a hose, simulating an afternoon thunderstorm, when more than three days passed without measurable precipitation. This was rarely needed, however, as rainfall is generally frequent and abundant at this time of year (see Table 5.2 and below). Further, dew formed at the enclosure site every night throughout all years of the study. Thus, at a minimum, drinking water was available to the lizards every morning.

Confounding Between Years and Habitats

A central question of this study is the effect of habitat complexity on lizard interactions. However, because habitat complexity was held constant within years, habitat complexity is confounded by year. Consequently, differences in experimental results (i.e., survival and growth of lizards) between years could be attributable to variation between years other than habitat complexity level. Such effects were probably minimal, however, because (a) the experiments took place at the same time and location each year, (b) the lizards used each year were almost identical in size (Table 5.1) and were obtained from the same locations, and (c) the same method of food supplementation was used each year and drinking water, in the form of morning dew, was available daily in all years. Further, there were few climatic differences between years (Table 5.2). Only two environmental parameters, daily maximum temperature and daily percent of total possible sunshine, differed significantly between years. Daily maximum temperatures were significantly lower in 1989 (high complexity habitat) than in 1990 (low complexity habitat) and 1991 (medium complexity habitat), which did not differ from each other, whereas daily percent possible sunshine was significantly higher in 1990 (high complexity habitat) than in 1989 (high complexity habitat) and 1991 (medium complexity habitat), which did not differ from each other. The magnitude of these differences was not large, however, and thus may have been of little biological significance, particularly when compared with the magnitude of differences in habitat complexity.

Statistical Analyses

For the reasons just outlined, habitat complexity level (low, medium, high) was considered a treatment factor along with juvenile type (*A. carolinensis* juveniles alone versus with *A. sagrei* juveniles) and presence/absence of an adult male *A. sagrei*. The effects of these factors (or a subset of them) on the survival and growth of *A. carolinensis* juveniles, *A. sagrei* juveniles, and *A. sagrei* adult males were analyzed using standard analysis of variation (ANOVA) techniques. For those enclosures in the high complexity habitat (i.e., 1989) for which the initial density of *A. carolinensis* juveniles differed, regression analysis and analysis of covariation (ANCOVA) was also used to look for density dependent effects. The specific ANOVA, regression, and ANCOVA models used were different for each group of lizards (i.e., *A. carolinensis* juveniles, *A. sagrei* juveniles, *A. sagrei* adults) and thus are presented in the appropriate section of the results. For all analyses, individual enclosures were the unit of measure. Thus, analyses of growth and survival are based on enclosure means. Prior to analysis, growth measures were standardized (as the percent change in SVL or mass/day) to adjust for variation in the absolute size of lizards when experiments began. Similarly, survival was expressed as a percent to account for variation in the number of juveniles stocked in enclosures in 1989. All statistical tests presented are two-tailed and a P value of 0.05 was used to judge significance.

RESULTS

Survival and Growth of Juvenile *A. carolinensis*

Survival – The effects of habitat complexity level, presence/absence of *A. sagrei* juveniles, and presence/absence of an adult male *A. sagrei* on the survival of *A. carolinensis* juveniles (Figure 5.1, top) were analyzed in a three-way factorial ANOVA. The whole model test ($F_{11,60} = 23.5$, $P < 0.001$) and the three-way interaction ($F_{2,2} = 3.183$, $P < 0.048$) were significant, indicating that the survival of *A. carolinensis* juveniles was affected by all three factors and that the effect of each factor was dependent upon the level of the other factors. To sort these effects out, I used a series of contrasts between pairs of variables while holding the value of the third variable constant within the three-way interaction term of the ANOVA model.

Anolis carolinensis juveniles in enclosures without *A. sagrei* juveniles or adults exhibited high survivorship in medium and high complexity habitats (medium versus high: $t_7 = 0.038$, $P = 0.97$) but significantly lower survivorship in the low complexity habitat (low versus medium and high: $t_9 = 3.10$, $P = 0.003$), suggesting that conditions in the low complexity habitat were suboptimal for their survival. Compared to enclosures which had only *A. carolinensis* juveniles, survival of *A. carolinensis* juveniles in enclosures which also had an adult male *A. sagrei* was no different in the high complexity habitat ($t_{17} = -0.44$, $P = 0.66$) but decreased significantly in the medium complexity habitat ($t_{11} = 2.25$, $P = 0.028$) and dropped to almost zero in the low complexity habitat ($t_{11} = 3.59$, $P < 0.001$), indicating that the effect of an adult male *A. sagrei* on the survival of *A. carolinensis* juveniles was negative and inversely related to habitat complexity. When *A. carolinensis* juveniles were raised in enclosures with *A. sagrei* juveniles their survival was not significantly different than in enclosures with only conspecific juveniles for high ($t_7 = -1.32$, $P = 0.19$) and medium ($t_7 = -0.519$, $P = 0.61$) complexity habitats but dropped to almost zero in the low complexity habitat ($t_7 = 3.63$, $P < 0.001$), suggesting that *A. sagrei* juveniles are superior competitors in low complexity habitats. Finally, the presence of an adult male *A. sagrei* had no effect upon the survival of *A. carolinensis* juveniles when they were in enclosures together with *A. sagrei* juveniles (contrast of presence versus absence over all habitat complexity levels: $t_{29} = -0.15$, $P = 0.88$), whereas the presence of *A. sagrei* juveniles did have an effect upon the survival of *A. carolinensis* juveniles when they were in enclosures with an adult male *A. sagrei* (contrast of presence versus absence over all habitat complexity levels: $t_{29} = 6.99$, $P = 0.01$). However, the latter effect was only significant for the medium complexity habitat (high complexity: $t_{15} = -0.847$, $P = 0.40$; medium complexity: $t_{15} = -3.48$, $P < 0.001$; low complexity $t_{15} = -0.367$, $P = 0.72$), and the survival of *A. carolinensis* juveniles was increased, not decreased, by the presence of *A. sagrei* juveniles (Figure 5.1, top). Consequently, in these experiments, the effect of *A. sagrei* juveniles seemed to supersede, or even reverse (i.e., medium complexity habitat), the effect of an adult male *A. sagrei* on the survivorship of *A. carolinensis* juveniles.

Growth – As with survival data, the effects of habitat complexity level, presence/absence of *A. sagrei* juveniles, and presence/absence of an adult male *A. sagrei* on the growth of *A. carolinensis* juveniles (Figure 5.1, bottom) were analyzed in a three-way factorial ANOVA. Because survival of *A. carolinensis* juveniles differed significantly between treatments (Figure 5.1, top), and because the initial density of *A. carolinensis* juveniles was varied in the high complexity habitat enclosures, the number of juvenile anoles in enclosures at the end of the experiment was used to weight observations in the ANOVA model. The whole model test ($F_{11, 51} = 7.08$, $P < 0.001$) and the main effect for habitat complexity ($F_{2, 60} = 20.9$, $P < 0.001$) were significant, but all other effects were insignificant ($P > 0.35$ in each case). Growth of *A. carolinensis* juveniles was highest in the high complexity habitat, significantly lower in the medium complexity habitat (contrast of high versus medium: $t_{47} = 3.69$, $P < 0.001$), and lower still in the low complexity habitat (contrast of medium versus low: $t_{38} = 4.37$, $P < 0.001$). Thus, growth of *A. carolinensis* juveniles was not significantly affected by the presence of juvenile or adult male *A. sagrei* (although survival was), but was inversely related to habitat complexity.

Finally, because the initial density of *A. carolinensis* juveniles in the high complexity habitat was varied from 2 to 12 for enclosures that lacked *A. sagrei* juveniles, data from these 18 enclosures were used to test for an effect of intraspecific density on the growth of *A. carolinensis* juveniles. Regression of mean growth rate of *A. carolinensis* juveniles against the number of *A. carolinensis* juveniles stocked in enclosures was significant and negative (Figure 5.2), indicating a density dependent growth effect consistent with intraspecific competition. In contrast, growth rate of *A. carolinensis* juveniles was not affected by the presence of an adult male *A. sagrei* in some enclosures (Figure 5.2; effect of adult male *A. sagrei* in ANCOVA: $F_{1,16} = 0.342$, $P = 0.57$), suggesting that adult male *A. sagrei* were not significant competitors of *A. carolinensis* juveniles in this habitat.

Survival and Growth of Juvenile *A. sagrei*

Survival and growth of juvenile *A. sagrei* were each analyzed by habitat complexity level and presence/absence of an adult male *A. sagrei* in a two-way factorial ANOVA. The ANOVA of survival for *A. sagrei* juveniles was insignificant (whole model test: $F_{5,24} = 0.603$, $P = 0.70$), indicating that survival was not significantly affected by habitat complexity or the presence of an adult male conspecific (Figure 5.3, top). In contrast, the ANOVA of growth rate for *A. sagrei* juveniles was significant (whole model test: $F_{5,24} = 9.28$, $P < 0.001$) for both habitat complexity ($F_{2,27} = 17.5$, $P < 0.001$) and the presence of an adult male conspecific ($F_{1,28} = 5.35$, $P < 0.001$), and these terms did not interact ($F_{2,27} = 0.066$, $P = 0.94$). Growth of *A. sagrei* juveniles did not differ between medium and high complexity habitats ($t_{17} = 1.12$, $P = 0.27$), but was significantly different in the low complexity habitat (contrast of low versus medium and high: $t_{29} = 5.52$, $P < 0.001$). Thus, juvenile *A. sagrei* grew more slowly in the low complexity habitat and in the presence of an adult male conspecific in all habitats (Figure 5.3, bottom).

Survival and "Growth" of Adult Male *A. sagrei*

Adult male *A. sagrei* exhibited 100% survival but almost no change in SVL during the course of the experiment and tended to lose rather than gain mass in all habitats (Table 5.1). However, loss of mass by large males during the reproductive season is typical of *A. sagrei* and *A. carolinensis* in Florida (T. S. Campbell and S. Porter, personal communication) as well as *A. carolinensis* in Louisiana (Ruby, 1984), and could reflect natural senescence (e.g., Turner, 1977) of these short-lived species as well as energetic demands of territory defense (e.g., Ruby, 1984). Nevertheless, to determine if changes in mass differed by habitat complexity level, or whether males were in enclosures with *A. carolinensis* juveniles alone or together with *A. sagrei* juveniles (i.e., juvenile type), growth was analyzed in a two-way factorial ANOVA. Because survival of *A. carolinensis* juveniles differed significantly between treatments (Figure 5.1, top), and because the initial density of *A. carolinensis* juveniles was varied in the high complexity habitat enclosures, the number of juvenile anoles in enclosures at the end of the experiment was used to weight observations in the ANOVA model. The ANOVA was significant for the whole model test ($F_{5,40} = 2.45$, $P = 0.049$) and for the main effect of juvenile type ($F_{1,44} = 5.36$, $P = 0.026$), but not for habitat complexity ($F_{2,43} = 0.089$, $P = 0.92$) or the interaction of juvenile type and habitat complexity ($F_{2,43} = 0.572$, $P = 0.57$). Thus, changes in mass of adult male *A. sagrei* were not affected by habitat complexity but males lost significantly more mass in enclosures with only *A. carolinensis* juveniles than in enclosures that also had *A. sagrei* juveniles (Figure 5.4), suggesting that *A. carolinensis* juveniles had a significantly greater competitive effect on adult male *A. sagrei* than did conspecific juveniles.

Because the initial density of *A. carolinensis* juveniles in the high complexity habitat was varied from 2 to 12 for enclosures lacking *A. sagrei* juveniles, data from these enclosures were used to test for an effect of juvenile *A. carolinensis* density on the change in mass of adult male *A. sagrei*. Regression of adult male *A. sagrei* change in mass against the number of *A. carolinensis* juveniles stocked in enclosures was significant and negative (Figure 5.5, top), suggesting a density dependent competitive effect of *A. carolinensis* juveniles on the growth of adult male *A. sagrei*. Because adult male *A.*

sagrei in enclosures with some mortality of *A. carolinensis* juveniles appeared to lose less mass than males in enclosures with no mortality of *A. carolinensis* juveniles (Figure 5.5, top), ANCOVA was used to determine if this difference was significant. If significant, regressions of adult male *A. sagrei* change in mass against the number of juveniles in enclosures at the end of the experiment should have similar slopes for both groups (i.e., 100% survival versus < 100% survival), but different intercepts. Both regressions were significant (Figure 5.5, bottom) and homogeneity of slopes analysis revealed no interaction between survival level (100% versus < 100%) and the number of juveniles remaining at the end of the experiment ($F_{1,10} = 0.127$, $P = 0.73$), indicating that the regressions did not differ in slope. Consequently, adult male *A. sagrei* change in mass was analyzed by survival level using the number of juveniles in enclosures at the end of the experiment as a covariate. This ANCOVA was significant (whole model test: $F_{2,9} = 32.1$, $P < 0.001$) and revealed that males lost significantly less mass in enclosures where there was some mortality of *A. carolinensis* juveniles than in enclosures where there was no mortality of *A. carolinensis* juveniles (effect of survival level: $F_{1,10} = 15.4$, $P = 0.004$). This result indicates that adult male *A. sagrei* lost less mass in enclosures with some mortality of *A. carolinensis* juveniles than can be explained by density dependent interspecific competition alone (i.e., there was an unexplained benefit to these males). Consequently, it appears that mortality of *A. carolinensis* juveniles in these enclosures was due to predation by adult male *A. sagrei*.

DISCUSSION

In a previous study, I demonstrated that adult male *A. sagrei* are more likely to eat juvenile *A. carolinensis* than juvenile conspecifics, whereas adult male *A. carolinensis* are unlikely to eat juveniles of either species (Part II; Gerber and Echternacht, in press). This finding suggests that intraguild predation of *A. carolinensis* juveniles by *A. sagrei* adults might be an important interaction between these species, possibly contributing to the decline of *A. carolinensis* in areas of Florida invaded by *A. sagrei.* However, because these results were obtained in small cages that provided no refuge from predation for juveniles, extrapolating to the field is problematic.

The present study provides much greater realism by incorporating habitat complexity into the investigation of species interactions. The results demonstrate that adult male *A. sagrei* had a negative effect on the survival of juvenile *A. carolinensis* in vegetated enclosures, and that the magnitude of this effect was highly dependent upon the amount and complexity of the vegetation in the enclosures (Figure 5.1, top). Further, although predation of *A. carolinensis* juveniles was not observed in the enclosures, several observations support the conclusion that the effect of adult male *A. sagrei* on *A. carolinensis* juveniles was due to predation, not competition. First, whereas there was no detectable effect of adult *A. sagrei* on the survival of *A. carolinensis* juveniles in the high complexity habitat enclosures, which afforded the most protection to juveniles, the presence of an adult male *A. sagrei* reduced the survival of *A. carolinensis* juveniles by about one-third in the medium complexity habitat (but only in enclosures lacking *A. sagrei* juveniles: discussed below) and by about two-thirds in the low complexity habitat, which afforded the least protection to juveniles (Figure 5.1, top). Thus, the data are consistent with the expectation that the magnitude of intraguild predation is directly and inversely related to the availability of refuges from predation. Second, although adult male *A. sagrei* had a significant effect on the growth of *A. sagrei* juveniles (Figure 5.3, bottom), they had no effect on the survival of *A. sagrei* juveniles, regardless of habitat complexity level (Figure 5.1, top). Thus, adult male *A. sagrei* were clearly not preying on juvenile conspecifics, which is consistent with previous findings that adult male *A. sagrei* avoid cannibalism but prey on all heterospecific lizards of similar size (Part II; Gerber and Echternacht, in press). Third, even though a significant effect of adult male *A. sagrei* on juvenile *A. carolinensis* survival was not evident for the high complexity habitat, adult male *A. sagrei* lost less mass in high complexity habitat enclosures with some mortality of *A. carolinensis* juveniles than in enclosures with no mortality of *A. carolinensis* juveniles, and this difference could not be attributed to the effects of density dependent interspecific competition with juveniles (Figure 5.5). Thus, adult male *A. sagrei* received a growth benefit from the mortality of *A. carolinensis* juveniles in these enclosures that can only be explained by predation. Fourth, adult male *A. sagrei* were occasionally observed chasing *A. carolinensis* juveniles in what appeared to be predatory attempts, but were never observed chasing conspecific juveniles. Taken together, these observations provide a compelling case for predation, especially when combined with the results of previous behavioral experiments and field observations (Part II; Campbell and Gerber, 1996; Gerber and Echternacht, in press). In addition, because adult male *A. sagrei* experienced significantly greater mass loss in all habitat complexity types when with only *A. carolinensis* juveniles than when with juveniles of both species (Figure 5.4), *A. carolinensis* juveniles appear to have a significantly greater competitive effect on adult male *A. sagrei* than do conspecific juveniles. Thus, in addition to the obvious energetic and nutritional benefits, preying on juvenile *A. carolinensis* is also likely to benefit adult male *A. sagrei* by reducing interspecific competition for food. Consequently, given that these species share a coevolutionary history on Cuba, and that the *A. sagrei* introduced to Florida are from Cuba (e.g., Lieb et al., 1983; Lee, 1992) and occur sympatrically there with *A. porcatus* (e.g., Collette, 1961; Williams, 1969), the progenitor of *A. carolinensis* (Williams, 1976; Buth et al., 1980), predation of juvenile *A. carolinensis* by adult *A. sagrei* may represent an adaptive trait shaped by natural selection on Cuba.

Results of the experiments suggest that interspecific interactions among juvenile anoles are also important, and mediated by habitat complexity as well. Juvenile *A. sagrei* had no effect upon juvenile *A. carolinensis* in the high or medium complexity habitat treatments, but greatly reduced the survival of *A. carolinensis* juveniles in the low complexity habitat treatment (Figure 5.1). In fact, out of the four enclosures in the low complexity habitat treatment that had juvenile *A. carolinensis* and *A. sagrei* (but lacked an adult male *A. sagrei*), only a single *A. carolinensis* juvenile survived and this animal had one of the lowest growth rates recorded (Figure 5.1, bottom). These results suggest that *A. carolinensis* juveniles in the low complexity habitat treatment were affected much more by interspecific competition with *A. sagrei* juveniles than by intraspecific competition with other *A. carolinensis* juveniles. Further, *A. carolinensis* juveniles experienced reduced survival in the low complexity habitat treatment even when there were no *A. sagrei* adults or juveniles present, whereas *A. sagrei* juveniles, which were only in enclosures with juvenile *A. carolinensis*, exhibited no differences in survival across habitat complexity levels. Thus, *A. sagrei* juveniles appear to be better adapted to, and thus superior competitors in, low complexity environments than are *A. carolinensis* juveniles. Given that *A. sagrei* is a trunk-ground ecomorph and thus should be better adapted to terrestrial environments than *A. carolinensis*, a trunk-crown ecomorph, it is not surprising that juvenile *A. sagrei* were competitively superior in habitats lacking abundant and complex vegetation. Nevertheless, the magnitude of the effect *A. sagrei* juveniles had on juvenile *A. carolinensis* survival in the low complexity habitat treatment was not anticipated, especially given that food was supplemented and not believed to be limiting. Clearly, eco-morphological differences in competitive ability exist between these species and are mediated by habitat characteristics. Aside from the effects of interspecific competition, the reduced growth and survival of *A. carolinensis* juveniles in the low complexity habitat suggests that they may have a lower tolerance to desiccation than *A. sagrei* juveniles (see also Clausen, 1967; Dunson and Bramham, 1981). Although gross environmental humidity levels did not vary between habitat treatments (i.e., years; Table 5.1: water pan evaporation), microenvironmental humidity levels in enclosures were most likely affected by vegetational differences between habitat complexity treatments. In addition, because of their small body size and thus greater surface to volume ratio, hatchlings are likely more susceptible to desiccation than adults. Comparative studies of evaporative water loss and tolerance to physiological stress in these species are needed to investigate possible interactions between habitat structure, physiologic performance, and interspecific interactions.

Another unanticipated result of this study was the interaction between the presence of an adult male *A. sagrei* and the presence of juvenile *A. sagrei* on juvenile *A. carolinensis* survival (Figure 5.1, top). In the high complexity habitat, neither the presence of an adult male *A. sagrei* or *A. sagrei* juveniles, alone or together, had a measurable effect on *A. carolinensis* juveniles. In contrast, in the low complexity habitat, the presence of an adult male *A. sagrei* or *A. sagrei* juveniles, either alone or together, caused an equally large reduction in the survival of *A. carolinensis* juveniles. In the medium complexity habitat, however, the presence of an adult male *A. sagrei* significantly reduced the survival of *A. carolinensis* juveniles when all of the juveniles in the enclosure were *A. carolinensis*, but not at all when half of the juveniles were *A. sagrei*. Why? The most plausible explanation is that there is something different about intra- versus interspecific interactions among juveniles that caused juvenile *A. carolinensis* to differ in their vulnerability to adult male *A. sagrei* in the medium complexity habitat. Because the total abundance of juveniles in enclosures was held constant, there were eight juvenile *A. carolinensis* in enclosures lacking juvenile *A. sagrei* but only four juvenile *A. carolinensis* in enclosures with juvenile *A. sagrei.* Consequently, intraspecific competition for territories among *A. carolinensis* juveniles was likely more intense in enclosures with all *A. carolinensis* juveniles than in enclosures with juveniles of both species (and Figure 5.2 shows that *A. carolinensis* juveniles in enclosures were sensitive to intraspecific density dependent effects). If so, and if interspecific competition for territories was minimal (as it is appears to be among adults; e.g., Tokarz and Beck, 1987), then it is likely that more *A. carolinensis* juveniles were forced into situations where they were vulnerable to predation by adult male *A. sagrei* in enclosures where all juveniles were conspecific than in those enclosures where half of the juveniles were *A. sagrei.* Thus, it appears that competition for territories among juvenile *A. carolinensis* is much more consequential in those areas where *A. carolinensis* occurs sympatrically with *A. sagrei* than where *A. carolinensis* still occurs in allopatry. If so, the interaction between *A. carolinensis* and *A. sagrei* in Florida may be quite similar to the interaction between *A. aeneus* and *A. richardi* on the island of Granada in the Lesser Antilles (Stamps, 1983a, 1983b). In Grenada, Stamps (1983a) has shown that juvenile *A. aeneus*, the smaller of the two species, are preyed upon by adult *A. richardi*, whereas juvenile *A. richardi*, likely due to their size, are not preyed upon by adult *A. aeneus*. In turn, the threat of predation from adult *A. richardi* drives intense intraspecific competition among juvenile *A. aeneus* for territories in small forest clearings, which are not inhabited by adult *A. richardi* (Stamps 1983b). Thus, in both Florida and Grenada, an asymmetry in intraguild predation seems to have important consequences for community dynamics. Further, a review of intraguild predation in *Anolis* suggests that asymmetrical predatory interactions are common in anole assemblages (Gerber, 1999), just as they are in guilds of other animals (Polis et al, 1989).

Results of the enclosure experiments are also consistent with the findings of recent field experiments conducted on very small islands in Florida (Campbell, 2000) and the Bahamas (Losos and Spiller, 1999), which found that *A. carolinensis* (or a close relative in the case of the Bahamas) on islands without *A. sagrei* exhibited greater population densities and persistence than *A. carolinensis* on islands with *A. sagrei*. Both studies recognized the potential importance of intraguild predation as well as interspecific competition, but could not differentiate between these mechanisms because the studies were purely phenomenological in nature (i.e., based on changes in population size over time). Further, because *A. sagrei* and *A. carolinensis* tend to be short-lived (e.g., Gordon, 1956; Schoener and Schoener, 1982; T. S. Campbell, personal communication), separating effects that impact recruitment (e.g., intraguild predation) from those that impact mature adults (e.g., reduced fecundity resulting from interspecific competition) is difficult. My results do not address competition among adults, but suggest that recruitment of *A. carolinensis* juveniles is likely reduced in the presence of *A. sagrei* due to intraguild predation from adults and competition with juveniles, and that these effects will be most pronounced in habitats with little structural complexity. Thus, because small islands typically have less vegetational complexity than larger islands, my results suggest that these interactions were relatively important in the field experiments in

Florida (Campbell, 2000) and the Bahamas (Losos and Spiller, 1999). Finally, the results of these experiments are also consistent with observations in Florida that native *A. carolinensis* are most heavily impacted by introduced *A. sagrei* in urban environments and other disturbed habitats (e.g., Christman, 1980; Wilson and Porras, 1983; Tokarz and Beck, 1987; Echternacht and Harris, 1993), which generally have little vegetational complexity compared to undisturbed habitats and thus provide relatively little refuge for juveniles.

In summary, the results of this study suggest that asymmetrical intraguild predation of juveniles by adults, interspecific competition among juveniles, and eco-morphological differences between species are all important components of the interaction between *A. carolinensis* and *A. sagrei* in Florida. Further, although introduced *A. sagrei* appear to have caused the numerical decline of native *A. carolinensis* in many disturbed and structurally simple habitats, the results of this study suggest that *A. sagrei* are unlikely to have much effect on *A. carolinensis* populations in native habitats with moderately high levels of structural complexity. Indeed, although exacerbated by the magnitude of human habitat disturbance, the interaction between *A. sagrei* and *A. carolinensis* in Florida appears to represent a return to the pre-evolved pattern of coexistence on Cuba, following the competitive release experienced by *A. carolinensis* when it colonized the North American mainland in the absence of interspecific competitors.

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APPENDIX: PART V

Table 5.1. Snout-vent length (SVL) and mass of juvenile *Anolis carolinensis*, juvenile *A. sagrei*, and adult male *A. sagrei* at the start and finish of enclosure experiments in low, medium, and high complexity habitats. Values for SVL and mass are presented as means ± their standard deviations. *n* = number stocked at start or remaining at end of experiments.

		Low Complexity (1990)			Medium Complexity (1991)			High Complexity (1989)		
Lizards	Category	*n*	SVL (mm)	Mass (g)	*n*	SVL (mm)	Mass (g)	*n*	SVL (mm)	Mass (g)
Juvenile	Start	144	24.9 ± 1.65	0.35 ± 0.07	144	25.1 ± 1.29	0.35 ± 0.06	150	24.7 ± 2.35	0.32 ± 0.10
A. carolinensis	Finish	31	28.5 ± 2.64	0.54 ± 0.16	104	31.1 ± 2.96	0.71 ± 0.21	129	32.4 ± 3.30	0.70 ± 0.24
	Difference	31	+3.2 ± 1.70	+0.17 ± 0.12	104	+5.9 ± 2.34	+0.36 ± 0.17	129	+7.6 ± 2.58	+0.37 ± 0.18
Juvenile	Start	48	20.3 ± 3.15	0.26 ± 0.14	48	20.6 ± 2.48	0.27 ± 0.11	24	22.1 ± 1.79	0.29 ± 0.09
A. sagrei	Finish	40	25.7 ± 3.35	0.51 ± 0.21	42	28.7 ± 3.89	0.72 ± 0.31	24	30.5 ± 3.66	0.71 ± 0.30
	Difference	40	+5.4 ± 1.88	+0.25 ± 0.14	42	+7.9 ± 2.04	+0.44 ± 0.21	24	+8.4 ± 2.19	+0.42 ± 0.22
Adult male	Start	16	60.4 ± 2.06	6.31 ± 0.66	16	61.6 ± 1.86	6.54 ± 0.67	16	60.3 ± 1.88	6.38 ± 0.66
A. sagrei	Finish	16	60.8 ± 2.21	5.76 ± 0.70	16	61.9 ± 1.81	5.95 ± 0.69	16	60.4 ± 1.65	5.78 ± 0.70
	Difference	16	+0.2 ± 0.58	-0.60 ± 0.42	16	+0.1 ± 0.52	-0.59 ± 0.42	16	+0.3 ± 0.60	-0.55 ± 0.42

Table 5.2. Comparison of environmental parameters between years for the 54 day span, July 15 through September 6, encompassing the experimental period. Data are for Knoxville, Tennessee and were obtained from the U.S. National Oceanographic and atmospheric administration, Ashville, North Carolina (except for days with dew formation, which is based on personal observation). Values are presented as means ± standard deviations, or as frequencies. For frequency data, differences between years were analyzed using Chi-square tests. All other parameters were analyzed using Kruskal-Wallis tests. In the case of significant Kruskal-Wallis tests ($P \leq 0.05$), post hoc analyses were performed on all pairwise comparisons using Wilcoxon two-sample tests. The sequential Bonferroni test for simultaneous inference (Rice, 1989) was then used to determine statistically significant differences (underlined values differ from other values, which do not differ from one another).

	Year (Habitat Complexity)			
Environmental Parameter	1989 (High)	1990 (Low)	1991 (Medium)	*P*
Daily maximum temperature (C)	29.3 ± 2.2	30.6 ± 2.3	30.6 ± 2.6	0.01
Daily minimum temperature (C)	18.4 ± 2.6	18.1 ± 1.6	17.9 ± 2.0	0.08
Daily sunshine (% possible)	63 ± 23	73 ± 15	64 ± 18	0.01
Daily sky cover (10ths)	5.8 ± 2.5	4.6 ± 2.9	5.7 ± 2.9	0.06
Daily water pan evaporation (mm)	5.0 ± 1.6	5.1 ± 1.3	5.3 ± 2.2	0.74
Daily precipitation (mm)	3.2 ± 7.8	2.7 ± 8.6	4.0 ± 8.6	0.35
Days with measurable precipitation	16	12	17	0.47
Days between measurable precipitation	2.1 ± 3.2	3.2 ± 3.2	2.1 ± 2.6	0.44
Days with thunderstorms	13	10	14	0.63
Days with heavy fog	10	6	10	0.48
Days with dew	54	54	54	1.00

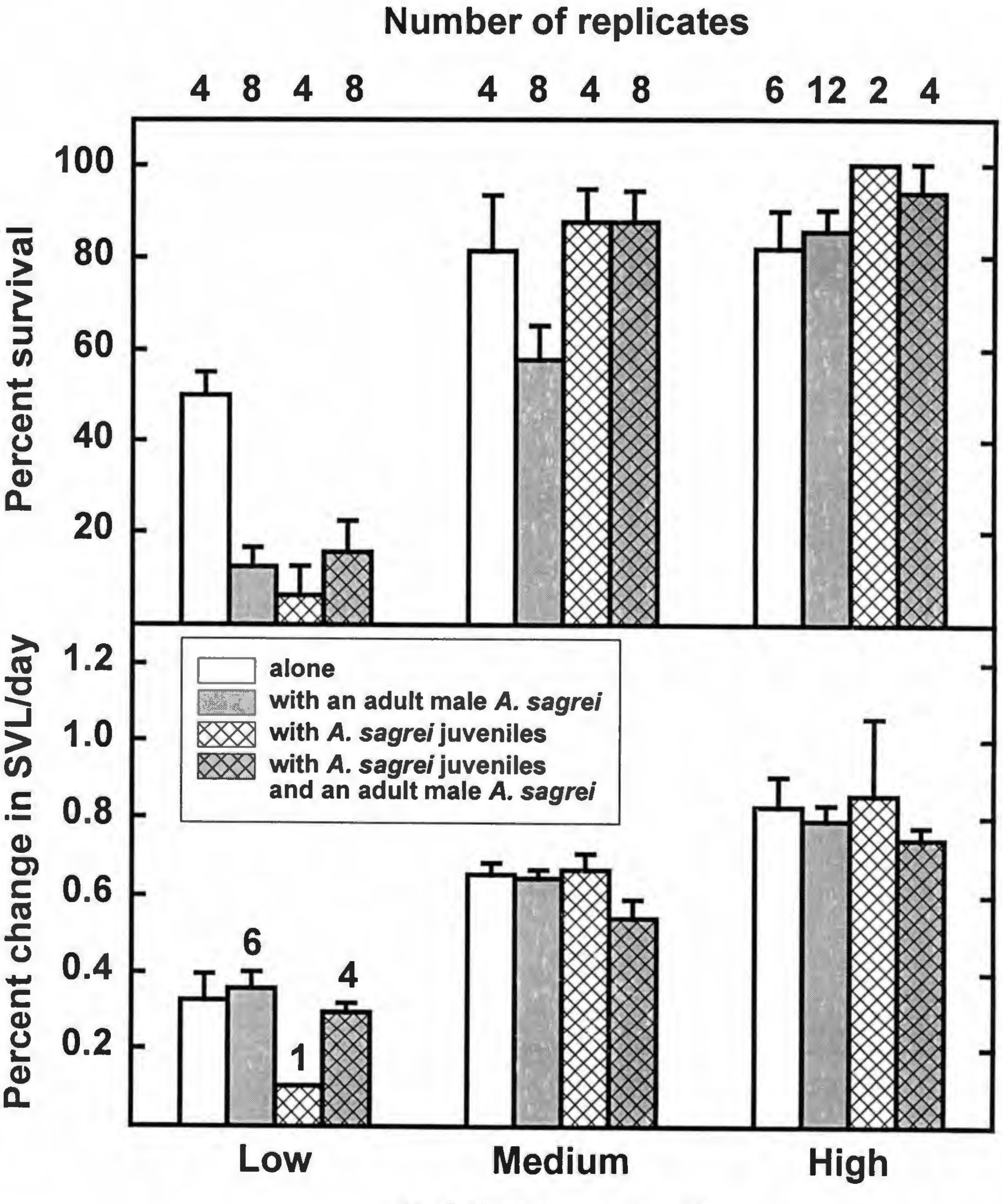

Figure 5.1. Mean survival and growth (± SE) of juvenile *Anolis carolinensis* in low, medium, and high complexity habitats in enclosures with and without *A. sagrei* juveniles and an adult male *A. sagrei*. Numbers above bars in bottom panel are the number of enclosures used to estimate the growth rate when different from the total number of replicates (i.e., the number of replicates that didn't experience 100% mortality).

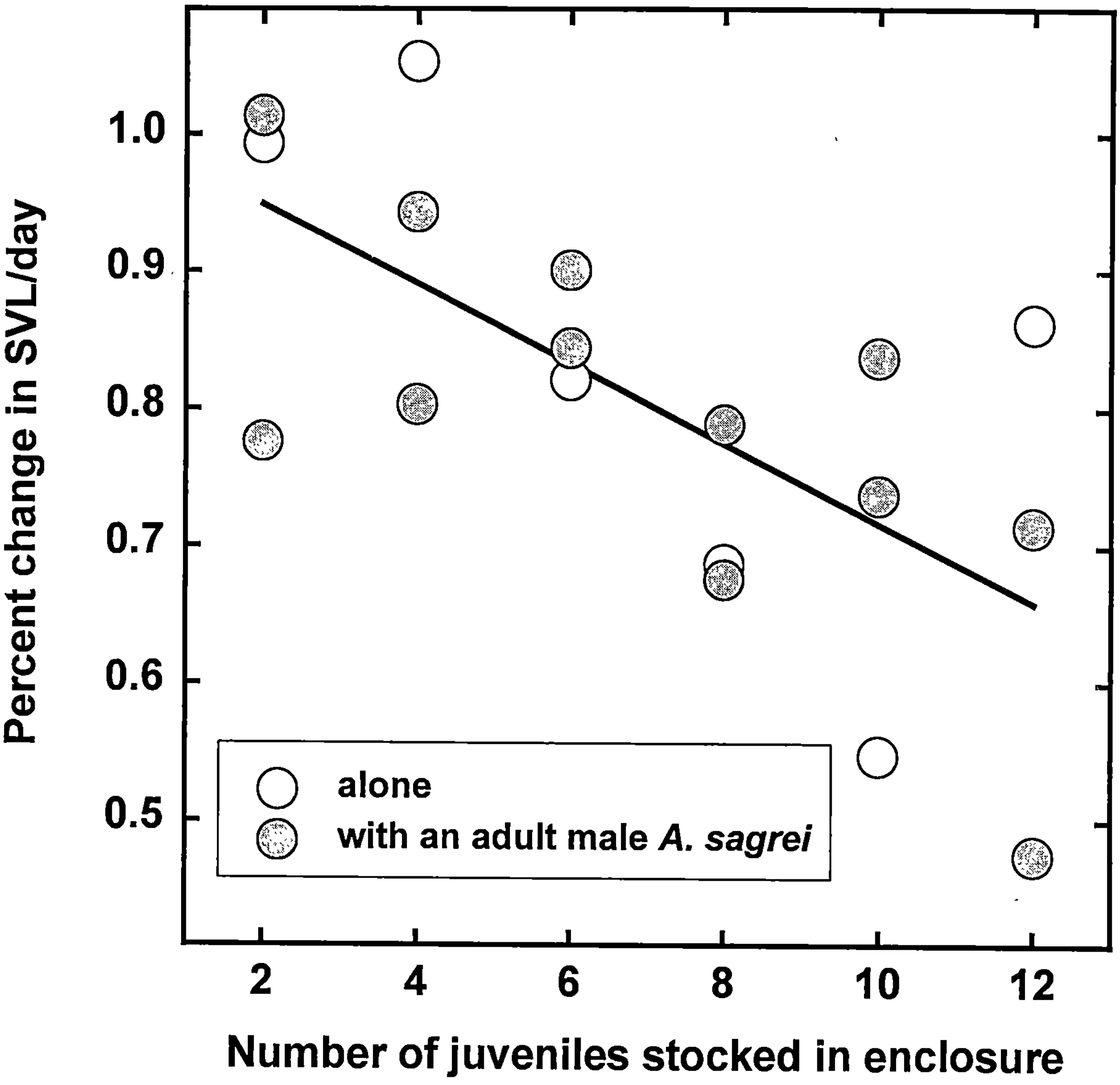

Figure 5.2. Mean change in snout-vent length (SVL) of juvenile *Anolis carolinensis* in the high complexity habitat in enclosures with different densities of juvenile conspecifics and with or without an adult male *A. sagrei*. Regression line is for all data points ($r^2 = 0.45$, $P = 0.002$).

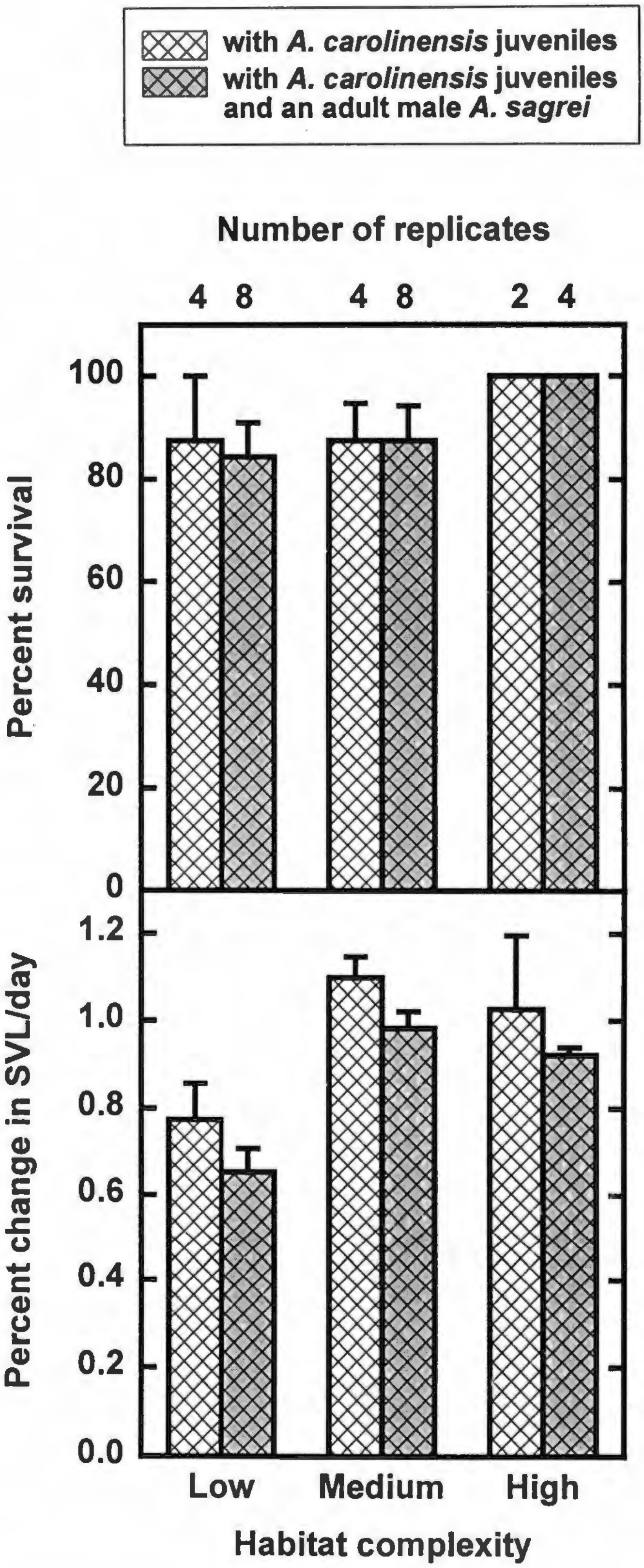

Figure 5.3. Mean survival and growth (± SE) of juvenile *Anolis sagrei* in low, medium, and high complexity habitats in enclosures with *A. carolinensis* juveniles and with or without an adult male *A. sagrei*.

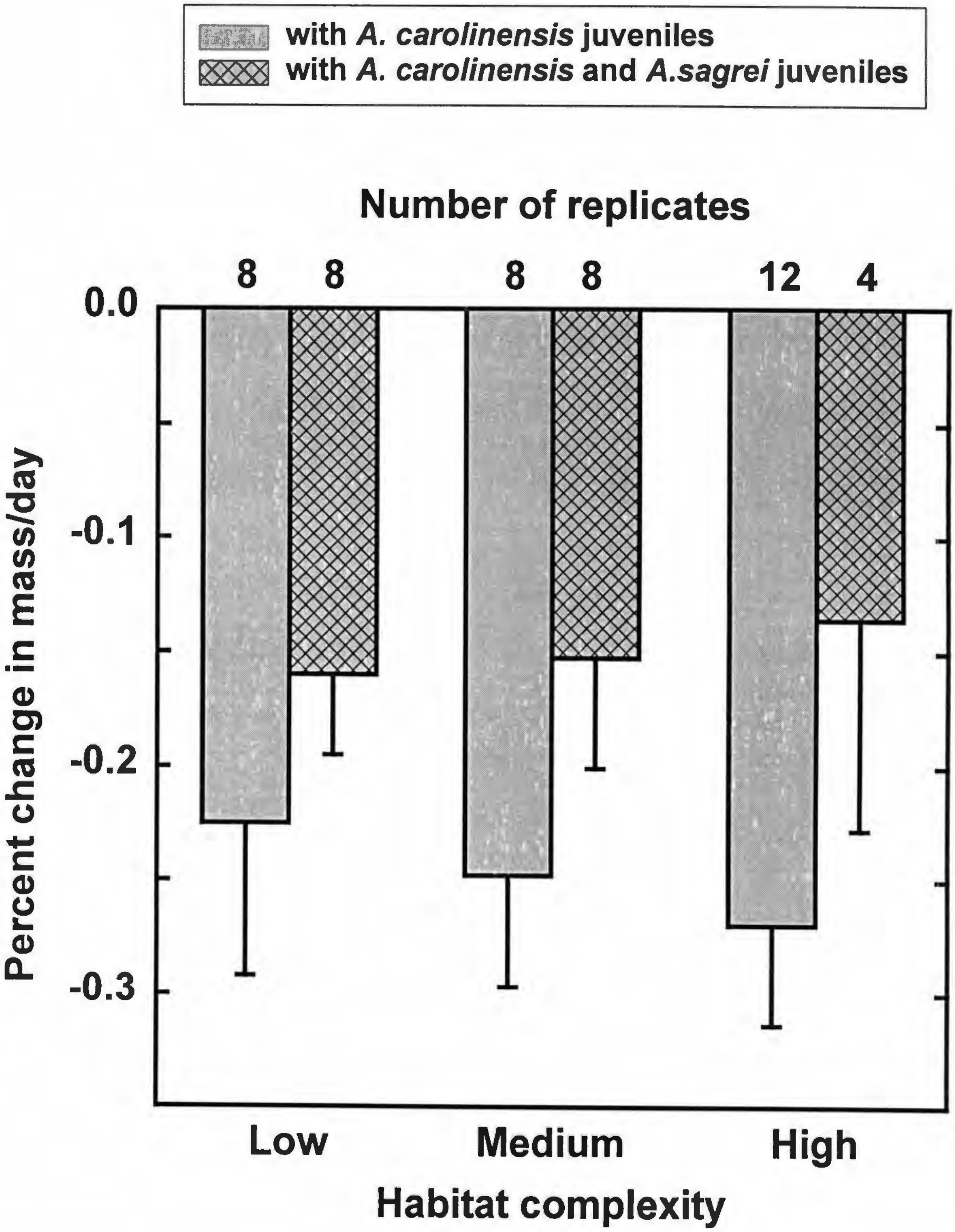

Figure 5.4. Mean change in mass (± SE) of adult male *Anolis sagrei* in enclosures with *A. carolinensis* juveniles or *A. carolinensis* and *A. sagrei* juveniles in habitats of low, medium, and high complexity.

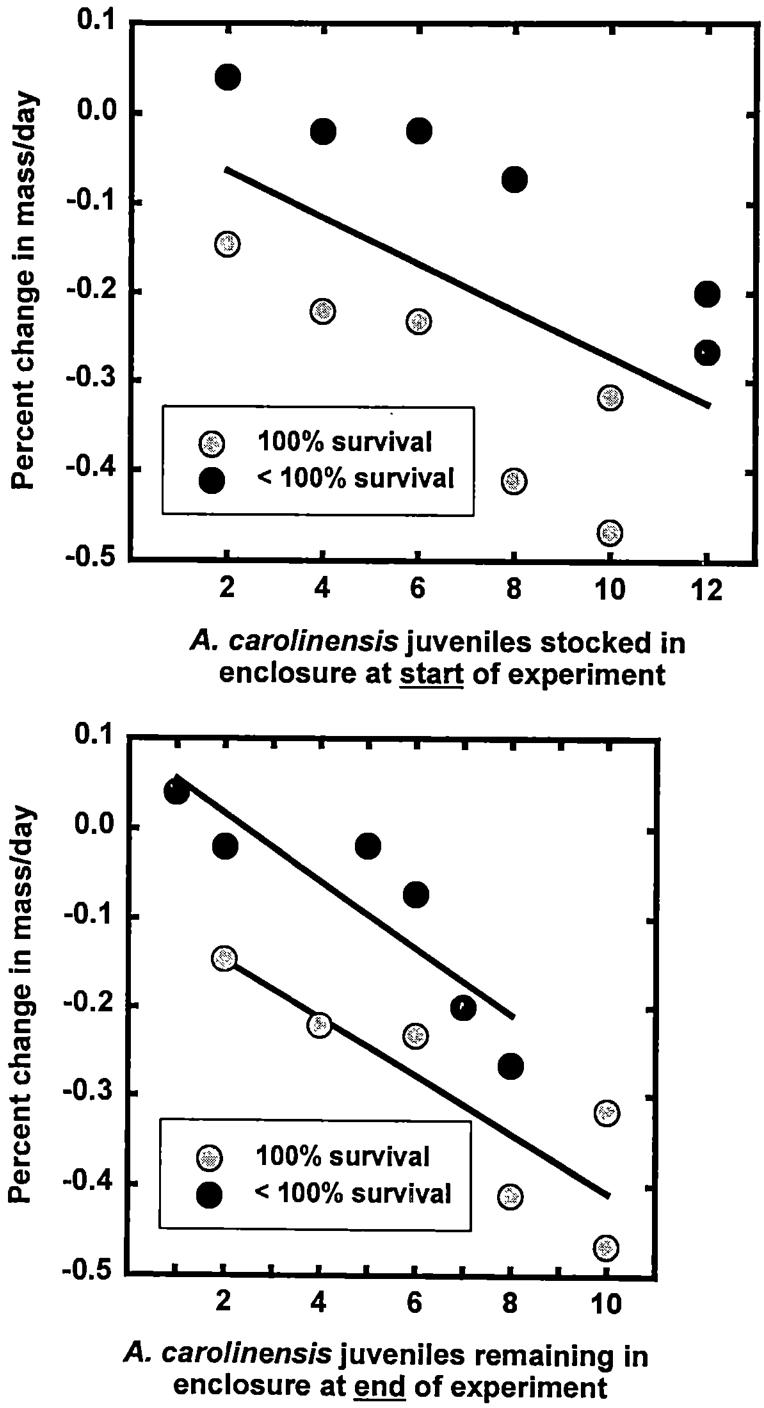

Figure 5.5. Change in mass of adult male *Anolis sagrei*, in enclosures with high complexity habitat, regressed against the number of *A. carolinensis* juveniles stocked in enclosures at the start of the experiment (top) and the number of juveniles remaining in enclosures at the end of the experiment (bottom). Each dot represents one enclosure. For comparative purposes, dots in both graphs are coded by survival status at the end of the experiment. Data are regressed collectively in the top graph ($r^2 = 0.35$, $P = 0.044$) and separately, by survival status, in the bottom graph (100% survival: $r^2 = 0.78$, $P = 0.019$; < 100% survival: $r^2 = 0.75$, $P = 0.025$).

PART VI

Summary and Conclusions

SUMMARY AND CONCLUSIONS

The past century has witnessed an unprecedented increase in the rate of extinction of species in the global biota (e.g., Myers et al., 2000, and references therein). Among those factors judged responsible for the loss of species, only habitat destruction has had a greater impact than introduced species (Wilson, 1992). Despite this, relatively few case studies have attempted to identify the mechanisms by which introduced species negatively impact elements of native biotas. It is not presently possible to predict, with any degree of certainty, which species are likely to invade, which of those that do invade will become established and, of those that become established, which will negatively impact their adopted biotic community (Williamson, 1996). Introductions of exotic species into the range of ecologically similar species provide excellent opportunities to study interactions between potential competitors during the initial stages of contact and thus are likely to provide insight into the dynamics of species coexistence and exclusion. Further, understanding the mechanisms of interaction between exotic and native species may allow the impact of invading species on ecologically similar native species to be predicted. Towards this end, I used a mechanistic approach to study interactions between an invading species of lizard, *Anolis sagrei*, and two ecologically similar native species, one in Florida (*A. carolinensis*) and one in Grand Cayman (*A. conspersus*). *Anolis carolinensis* and *A. conspersus* are both trunk-crown ecomorphs, have been described as ecological analogs, and were the only anoles in Florida and Grand Cayman, respectively, until the introduction of *A. sagrei*, a trunk-ground ecomorph (Williams, 1969). Thus, there are many similarities between these systems. Further, since being introduced, *A.*

sagrei has expanded its range in Florida (e.g., Campbell, 1996) and Grand Cayman (e.g., Losos et al., 1993) and presently outnumbers the native anoles in some habitats, particularly those associated with human disturbance (e.g., Echternacht and Harris, 1993; Losos et al., 1993). Consequently, it appears that *A. sagrei* has been displacing *A. carolinensis* in Florida and *A. conspersus* in Grand Cayman. However, the interspecific interactions involved and the role of habitat disturbance were largely unknown in both systems.

Because anoles are active, aggressive, territorial predators with size-structured populations and generalized feeding habits, I hypothesized that interactions between species were likely to involve aggressive interference among adults and predation of juveniles by adults. To investigate the importance of these mechanisms in Florida and Grand Cayman, I conducted behavioral experiments in both locations to determine the potential strength and symmetry of interspecific predation and aggressive interference. Then, based on the results of the behavioral experiments as well as morphological, ecological, and physiological characteristics of the species, I conducted experiments in the field and in enclosures to test specific hypotheses of interspecific interaction in relation to habitat structure and disturbance.

The propensity for adults to prey on juveniles was assessed by conducting predation experiments in small cages, using freshly captured lizards, in which adult males of each species were presented with conspecific and heterospecific juveniles. Similarly, the potential for aggressive interference was assessed by presenting free-ranging adult male residents of each species with tethered conspecific or heterospecific intruders and recording their response.

Results of the predation trials indicated that adult *A. sagrei* were (1) significantly more likely to eat juveniles than were adult *A. carolinensis* or *A. conspersus*, and (2) significantly more likely to eat heterospecific than conspecific juveniles, whereas adult *A. carolinensis* and *A. conspersus* were not (Part II). Thus, the propensity for intraguild predation was found to be asymmetrical in favor of introduced *A. sagrei* in Florida and Grand Cayman, suggesting that *A. sagrei* might be impacting the native anoles in both locations by preying upon juveniles.

In contrast, results of the aggressive interference experiments indicated that while residents of each species were highly aggressive toward conspecific intruders, only resident *A. conspersus* in Grand Cayman exhibited pronounced interspecific aggression (Part III). Thus, interspecific aggression appears to be a potentially important interaction only in Grand Cayman, where it is asymmetrical and favors native *A. conspersus*, rather than introduced *A. sagrei.*

Because *A. conspersus* is somewhat larger and more arboreal than *A. sagrei*, it was hypothesized that *A. sagrei* might be aggressively excluded from wooded habitats, where *A. conspersus* is most abundant, thereby limiting the impact of intraguild predation of juvenile *A. conspersus* by adult *A. sagrei* to highly disturbed habitats in Grand Cayman. This hypothesis was confirmed by conducting a field experiment in which the abundance and habitat use of *A. sagrei* was compared on experimental and control plots before and after the removal of *A. conspersus* from the experimental plot (Part IV).

Following the removal of *A. conspersus* from the experimental plot, *A. sagrei* increased in abundance and shifted their use of structural and microclimatic habitats, and escape routes, toward those normally used by *A. conspersus*. In contrast, no niche shifts were observed on control plots. Thus, the distribution and abundance of *A. sagrei* in Grand Cayman appears to be severely restricted by the presence of native *A. conspersus*, which are larger and more aggressive. The success of introduced *A. sagrei* in Grand Cayman appears due to (1) adaptations that allow it to exploit habitats that are relatively unprofitable for native *A. conspersus*, and (2) ongoing human disturbance that creates open habitats.

In contrast to Grand Cayman, *A. sagrei* has invaded a much wider variety of habitat types in Florida and generally occurs at higher densities, possibly because interspecific aggression with *A. carolinensis* is minimal compared to that with *A. conspersus*. This suggested that predation of juvenile *A. carolinensis* by adult *A. sagrei* might be a particularly important interaction in Florida. To investigate the importance of intraguild predation under semi-natural conditions, as well as the strength of inter- versus intraspecific competition among juveniles, and the effect of habitat complexity on interspecific interactions, experiments were conducted in small outdoor enclosures in which groups of *A. carolinensis* juveniles were raised in habitats of low, medium, or high complexity in the presence or absence an adult male *A. sagrei*, and with or without *A. sagrei* juveniles (Part V). Juvenile *A. carolinensis* were not affected by the presence of adult or juvenile *A. sagrei* in the high complexity habitat, but experienced significant mortality in the presence of adult *A. sagrei* in the medium complexity habitat, and almost complete mortality in the presence of either adult or juvenile *A. sagrei* in the low complexity habitat. Further, even in the absence of juvenile and adult male *A. sagrei*, the growth of *A. carolinensis* juveniles decreased with decreasing habitat complexity and survival was reduced in the low complexity habitat. In contrast, *A. sagrei* juveniles exhibited reduced growth only in the low complexity habitat and survivorship was high in all habitats. These results suggest that (1) predation, competition, and ecological differences are all important components of the interaction between *A. carolinensis* and *A. sagrei* in Florida, and (2) that the numerical decline of *A. carolinensis* in disturbed and open habitats in Florida, following colonization by *A. sagrei*, may represent a return to a pre-evolved pattern of coexistence on Cuba, where *A. sagrei* is sympatric with *A. porcatus*, the progenitor and ecological analog of *A. carolinensis.*

In conclusion, the research presented in this dissertation advocates a mechanistic approach to species interactions. By combining information on the type, strength, and symmetry of interspecific interactions with morphological, ecological, and physiological characteristics of the species, it was possible to predict the general nature and magnitude of interspecific interactions in relation to patterns of habitat disturbance and complexity. In Grand Cayman, where the native trunk-crown anole is larger and more aggressive than the invading trunk-ground anole, *A. sagrei* is restricted to very open or disturbed habitats due to intense interspecific aggression and thus appears to have minimal impact on *A. conspersus*, despite its demonstrated potential to be an important intraguild predator. In contrast, in Florida, where the native trunk-crown anole is more similar in size to the invader and interspecific aggression is minimal, *A. sagrei* has successfully invaded a variety of habitat types and appears to be significantly impacting *A. carolinensis* through intraguild predation and competition, both of which appear to be most severe in habitats of low structural complexity, where *A. sagrei* is likely most efficient as a predator and competitor. Thus, although *A. carolinensis* and *A. conspersus* have been described as ecological analogs and *A. sagrei* has become well established in both Florida and Grand Cayman, the impact of *A. sagrei* on these species appears to be very different due to differences in body size and the strength and symmetry of aggressive interference. These studies demonstrate that (1) both intraguild predation and interspecific aggression are important in structuring anole communities, (2) the effects of an introduced species on native congeners in one community cannot necessarily be predicted by knowing the effects of that same introduced species on native congeners in a different community, and (3) predicting the effects of one species on another, regardless of the taxa, will be enhanced by understanding the nature, strength, and symmetry of the mechanisms of interaction.

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VITA

Glenn Gerber was born in Salt Lake City, Utah, on 30 December 1960. He attended public schools in Brockport, New York, where he moved to in 1966 with his family after living briefly in San Luis Obispo, California, and Vermillion, South Dakota. He graduated from Brockport High School in 1979 and from Cornell University in Ithaca, New York, in 1983 with a Bachelor of Science degree in Biological Sciences. After spending a year in Colorado and Wyoming working in the Rocky Mountains and in Grand Teton National Park, he returned to New York State for graduate studies. In 1987, he received a Master of Science degree in Biological Sciences from the State University of New York College at Brockport, where he conducted behavioral and ecological studies of salmonid and centrarchid fish in Lake Ontario and its tributaries. Subsequently, he entered the doctoral program in Ethology at the University of Tennessee, Knoxville, to conduct the research presented in this dissertation. After completing his dissertation research on *Anolis* lizards in Florida and Grand Cayman, he spent several years studying the endemic iguanas of the Caribbean Islands. During this period, he conducted behavioral and ecological studies of iguana species in the Cayman Islands, the Turks and Caicos Islands, the British Virgin Islands, the Bahamas, and the northern Lesser Antilles. In August 2000, he finally completed his Doctor of Philosophy degree at the University of Tennessee in Ecology and Evolutionary Biology. In June 2000, he began a five-year postdoctoral fellowship at the Center for the Reproduction of Endangered Species of the Zoological Society of San Diego to continue his study of, and efforts to conserve, West Indian iguanas and the fragile island ecosystems in which they evolved.