Anolis

Newsletter V

Ernest E. Williams

Edited by
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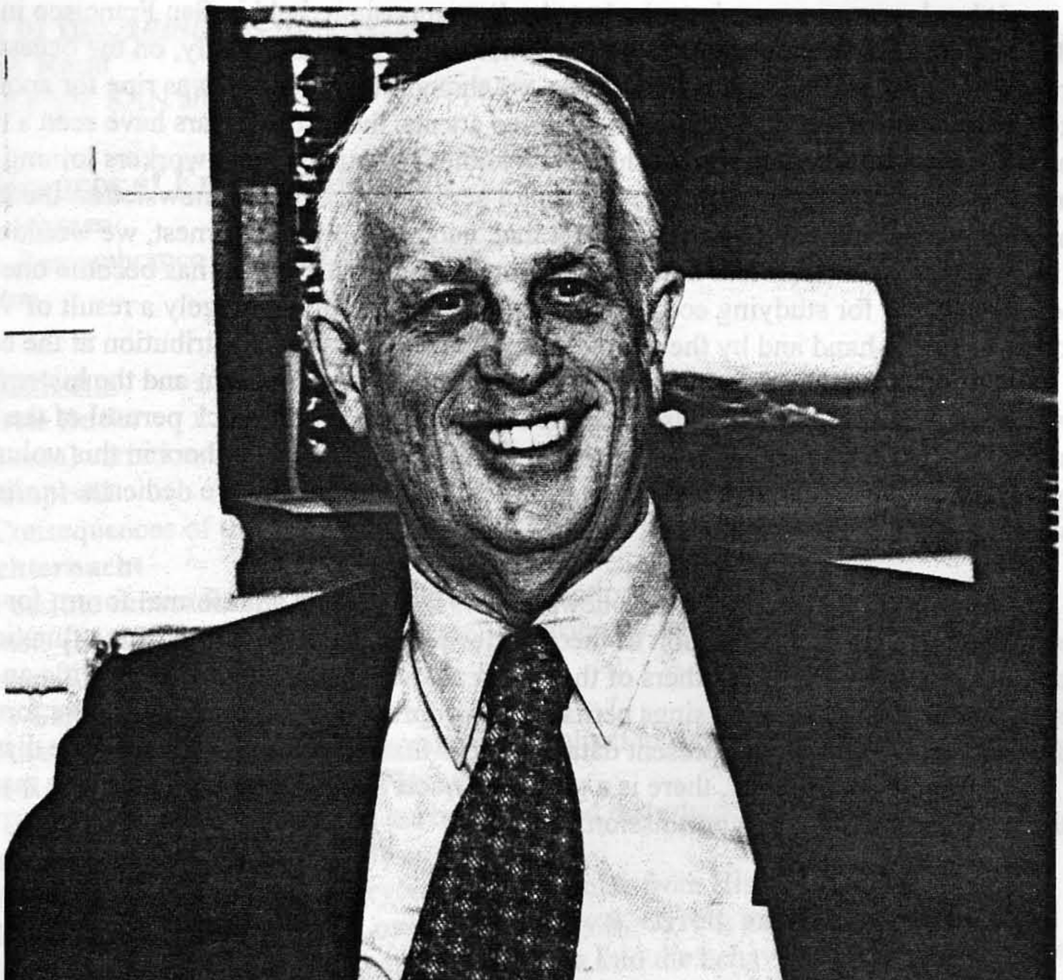

Ernest E. Williams

Preface

It has been ten years since the last *Anolis* symposium, held in San Francisco in 1989, and eight years since the publication of *Anolis Newsletter IV*. Consequently, on the occasion of the third *Anolis* symposium, held at Penn State, we thought that the time was ripe for another edition of the *Anolis* Newsletter series. As this volume attests, the last ten years have seen a remarkable expansion in the research being conducted on anoles, with many new workers joining the field. Nonetheless, the *Anolis* world has seen a major setback since the last newsletter: the loss of Ernest Williams. Surely, no one can doubt that, had it not been for Ernest, we would not be writing *Anolis* newsletters and holding *Anolis* symposia. That *Anolis* has become one of the model organisms for studying ecology, behavior, and evolution is largely a result of Williams' efforts, both first-hand and by the people he trained (Stan Rand's contribution at the beginning of the newsletter details the development of the Williams *Anolis* program and the history of the newsletters). Indeed, though he is gone, his legacy continues. A quick perusal of the Table of Contents indicates that (as far as is known to us) about half of the authors in this volume in some way are members of the Williams lineage. Ernest will be missed. We dedicate *Anolis Newsletter V* to his memory.

As with previous editions, the newsletter is meant to be an informal forum for the presentation of data and discussion of theory relevant to anoles. It serves three functions: to allow investigators to inform others of their current and future research; to provide an outlet for speculation and theoretical musings perhaps inappropriate for publication in more formal venues; and to give an opportunity to present data and ideas that otherwise might never be distributed. As with previous newsletters, there is a general request that nothing said herein be quoted without the authors' express permission.

Jonathan Losos and Manuel Leal
Washington University
St. Louis, MO
June 19, 1999

front cover: *Chamaeleolis porcus*, known in Cuba as the chipojo bobo. Drawing kindly provided by Kevin de Queiroz

back cover: One of the less-studied anole ecomorphs, bearing an uncanny resemblance, in the eyes of some, to Ernest Williams. From the cover of the *Third Anolis Newsletter*.

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Of FAN, SAN, and TAN - the WAN (Williams *Anolis* Newsletters)

The first three *Anolis* Newsletters were conceived and produced by Ernest Williams. I want to tell you a bit about him, the Newsletters and the golden age in which they were produced.

I have been out of *Anolis* research for many years except to help continue the annual *A. limifrons* census on Barro Colorado Island (BCI). I was an early grad student of Williams and maintained contact with Williams during the Newsletter years. Until just before he died last year, he spent 2 months each winter with us in Panama.

Williams as curator at the MCZ helped build one of the largest and most comprehensive herpetological collections and libraries in the world. In addition to *Anolis*, he worked with turtles, fossil snakes, and amphibians.

Williams was shy and particularly in groups had the disconcerting habit of not saying anything unless he had something to say. Still, he regularly gave parties with champagne and shrimp at the museum for up to 40-50 people.

At Harvard, he attracted a diversity of people. In the early days, they included Trivers, Gorman, Huey, Schoener, Gans, Crews, and myself. He wrote that he was best at reacting to other people's ideas--his reactions were perceptive and often useful. For him, the best students were those who brought new ideas for him to react to. He was interested in his students, employees, and other associates as people and treated them accordingly. However, because he did not go to meetings, most herpetological graduate students outside Harvard did not know him and he was to them a mysterious and forbidding figure.

Studies of Anolis have deep roots at Harvard that include Barbour, Noble and Lewellen Evans. Williams began his career in New York studying turtles, but became involved in anoles when he traveled to Jamaica in 1950 with Max and Bessie Hecht and Karl Koopman. They must have made a memorable team because guest house proprietors in rural Jamaica still remembered them when we visited more than a decade later.

Williams continued to visit the West Indies throughout his career. He wanted to see the anoles in the field. He was interested in them as animals and not just as a model system.

In the decades before the Newsletters, a number of lines of investigation of the evolution of *Anolis* were started. The major breakthrough in understanding the evolution in *Anolis* was in the late 50's when Etheridge discovered skeletal characters that defined groups of related species.

Bruce Collette described the ecological separation among the anoles in Havana on what came to be called structural niche. I elaborated this and added a microclimatic dimension. Schoener turned my natural history into science.

Ruibal presented his analysis of anole displays in the Milstead lizard ecology symposium in 1965.

Williams coined the term ecomorphs in 1972, formalizing the idea that anoles in similar niches evolved similar morphologies regardless of relationship.

Preston Webster and John Burns used allozymes to look at small scale geographic differences between populations and cryptic species.

My work on social organization in *Anolis lineatopus* in Jamaica followed up studies by Evans (1938) on *sagrei* in Cuba. Stamps was at work in Grenada.

Williams, with Garth Underwood, confronted the issues of geographical variation without barriers in their Anoles of Jamaica (1959).

Much, but not all, of this had been directly encouraged by Williams and supported by his NSF grants. The Newsletters were necessarily a product of their intellectual environment. Molecular systematics was just beginning, DNA sequencing was yet to come, Hennig had just been translated and cladistics was not yet popular. Continental drift was being taken seriously and resource partitioning was a hot topic. The causes of tropical diversity were being actively debated but were not satisfactorily resolved. The MCZ facilitated studies of anoles because of its large West Indian collections with many types and often large series.

In the late 60's and early 70's, fewer and fewer students did systematic theses and support for museums declined. Williams' NSF grants were among the largest at the MCZ and his students the most active, giving him clout in an institution where collections based research was becoming de-emphasized, but the study of evolution was still important. Mayr, Simpson, Ed Wilson, Steven J. Gould, Jim Watson, Don Griffin, and Phil Darlington were still on the staff. Williams gathered around him a bright, interactive group of students, post-docs and young faculty.

FAN, the First *Anolis* Newsletter, was sparked by the need for a progress report to NSF, but nothing of this scope was needed for NSF. In the covering letter to the NSF, Williams wrote: "In the interest of cross-communication and cross-fertilization I have instituted a "Lizard Ecology Discussion Group" at Harvard and we have had rather regular and quite profitable sessions, there has still been insufficient opportunity to fill in the general picture." He also wrote an in-house "Progress Report" which summarized the efforts of group members Webster, Schoener, Jenssen, Trivers, Rand, Kiester and Williams. This was the immediate predecessor of the Newsletters and its popularity may have lead to his writing FAN.

If Williams had enjoyed interacting with people he did not know well and had attended scientific meetings regularly during this period, it might have satisfied the need he felt for "cross-communication and cross-fertilization." The June 1972 Boston ASIH *Anolis* symposium was organized by George Gorman because he felt that the group "was coming apart."

Williams said: "... the Newsletter [is] neither a travelogue nor a gossip sheet nor a list of thesis topics, but a vehicle for exchange of information that in more expanded and documented form would be publishable somewhere in its own right." Clearly not intended as an alternative to publishing, though several things appeared there that should have been published but were not.

FAN, 29 pages, 13 contributors, was written by Williams in 1972. He organized the data being collected in terms of the number of species per island, an artificial sequence that Williams felt showed how the faunas of the more complex islands might have developed.

SAN, 73 pages, 18 contributors, produced in 1974, was the sequel to FAN promised to many people, but produced only when NSF forced Williams to write a report, though the Newsletter itself did not form part of the report. Individual reports were organized alphabetically by researcher, but abstracted by EEW. For the first time, SAN indicates the institutions of the researchers, reflecting the dispersal of the anole group.

TAN, 220 pages, 18 contributors, produced in 1977. Williams compiled it from the contributors' reports with little editing or rewriting.

Each successive Newsletter was longer and was less processed by Williams.

The contributors (Figure 1) were largely associates of Williams and almost all supported in one way or another by his research money. Of the 24 people who contributed to the Newsletters, 16 were either his current or past grad students or post docs. The group came from a variety of backgrounds.

It reflects Williams' egalitarian view of people that the contributors' academic status was not mentioned in the first two Newsletters.

The Newsletters made neither pretense at completeness nor any attempt to achieve it. Conspicuously missing were: Schwartz and Thomas who were collecting and describing anoles in the West Indies; Fitch and the Echelles who were doing ecology in Costa Rica; Sexton doing ecology in Panama; and Ruibal and Philibosian working on ecology and social behavior on St Croix.

What issues were addressed: aspects of the evolutionary biology of anoles particularly in the West Indies, phylogenetic relationships, biogeography, resource partitioning, factors structuring anole communities, social behavior, and alpha ecology and systematics within the West Indies and beyond to South America. Most of the papers scheduled for this Third *Anolis* Symposium would fit into those categories.

More than 200 copies of the Newsletters were xeroxed, stapled and mailed out to contributors, libraries and people requesting them. They qualify as publications under the International Code of Zoological Nomenclature, but Ernest was very careful to introduce no new names.

The MCZ has no record of who received them and Williams' secretary from those days doesn't remember that there ever was a list. The MCZ and Smithsonian Institution libraries cataloged them, but I could not find them in the on-line catalogs of the University of Texas, California at Berkeley, Michigan, or the AMNH. The Zoological Record did not index them. There are still copies that the MCZ would gladly send if requested.

Why did he stop? TAN promised more. I don't think that this was a conscious decision, but the result of how things were changing. NSF stopped umbrella grants in the late '70s so that Williams could no longer support the research of a group of independent anole studies, though he had funds for his own research. Williams retired in 1980 as curator in the MCZ, in 1985 as professor of biology.

Williams continued to study anoles and to go to the West Indies. But his old friends at the MCZ were dying or retiring. His old students had left Harvard and many changed research directions. Few new students replaced them. The Williams Newsletters had always been primarily an ingroup thing, reporting the activities of the group members to each other. As the group dissolved, the demand for Ernest's sort of Newsletters declined.

It was not until 1991 that Losos and Mayer produced the fourth *Anolis* Newsletter in conjunction with the 2nd *Anolis* symposium.

In conclusion, what do we learn? Did the Newsletters have an impact? Yes, particularly within the Harvard *Anolis* group.

Should they have been distributed more widely? Yes, because they contain information of more than ephemeral ingroup interest that was never published elsewhere.

Should they have been published? Possibly, but the loss of informality would be offset by the gain in distribution. Ernest felt not.

Should they have been associated with *Anolis* symposia or workshops? Definitely.

What else should have been done? Most importantly, Williams should have written the book on *Anolis* that he started at least four different times with different collaborators.

It seems appropriate to end by reiterating one of Ernest Williams contributions to the philosophy of field research: THE PRINCIPLE OF UNSYMPATHETIC MAGIC, which says "whenever one reaches a firm conclusion the next observation will contradict it."

I have presented my conclusions. I leave it to you to provide the contradictions.

Figure 1. Contributors to the Williams *Anolis* Newsletters

	1972 FAN	1974 SAN	1977 TAN	
R. Andrews	X	X	X	
S. Ayala	-	-	X	
D. Crews	-	X	X	
A. Dennison	-	-	X	
N. Greenberg	-	-	X	
G. Gorman	X	X	-	
W. Hall	X	X	-	
P. Hertz	-	X	X	
R. Holt	-	-	X	
R. Huey	X	X	-	
T. Jenssen	X	X	X	
R. Kiester	X	X	X	
B. Lister	-	X	-	
K. Miyata	-	X	X	
T. Moermond	X	X	X	
J. Peterson	-	X	-	
S. Rand	X	X	X	
J. Roughgarden	X	X	-	
R. Salvato	-	-	X	
T. Schoener	X	X	X	
D. Shochat	-	-	X	
J. Stamps	-	-	X	
R. Trivers	X	X	-	
P. Webster	X	X	X	
E. Williams	X	X	X	
Contributors	13	18	18	Total = 24
Pages	29	73	220	

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A Remembrance of Ernest E. Williams

I believe this passage is more about me than Ernest. Nonetheless, for me, Ernest was much more of a paternal presence than a lizard-chasing buddy about whom one tells stories. In his taciturn, New England demeanor, he seemed the keeper of truths. On a number of occasions, I recall dithering on for many minutes in a monologue of situational uncertainty about some data set. Then in a sentence, Ernest would provide a phrase that would part the clouds.

It was a heady time for me in 1969 when I took a 2-year postdoctoral fellowship at the Museum of Comparative Zoology. The alumni of those years, who had gathered under Ernest's guidance, have gone on to contribute much to evolutionary biology, and to distinguish the program Ernest developed on *Anolis* lizards. My own MCZ internship was mostly spent in Jamaica, following Stan Rand's lead in behavioral ecology. Working primarily with *Anolis opalinus*, I stayed in touch with Ernest through typed letters. But his exchanges, comments, and answers were always weeks away. Eventually my frustrations gave way to being on "Jamaican time." Still, not being close to his office and the noontime breaks at Chez Dreyfus left me wanting more.

I remember a particular week in August, 1970, when I really wanted his immediate input and sage appraisal. I had become curious that *opalinus* in Mandeville (where I was working) perched low, but had been described by Stan Rand and Tom Schoener as a "trunk-crown" species on their study sites near Kingston. So I checked into a Kingston guesthouse, and began focal observations on *opalinus* near Long Mountain. At first *opalinus* met my Mandeville expectations, but then I noticed a large *A. lineatopus* shifting over to the tree on which my observed *opalinus* was perched. In response to its new neighbor, *opalinus* went running up the tree. It happened twice more on other trees with different *opalinus* and *lineatopus*. I wanted to talk with Ernest, right now! Had I found direct field evidence for the elusive competitive interference? But then Ernest was in Cambridge, as far as I knew, and I would just have to wait til I got back to my typewriter and the Zen-like Jamaican mail system.

Several hours later, sitting at a dining table in the guesthouse, I had fallen into imaginary conversations with my mentor. On the verge of conjuring his image at my table as well, I noticed a figure coming through the doorway. It couldn't be. It was Ernest! I felt like an apostle at the resurrection. Serendipity had brought Ernest to Kingston, and in that moment I struggled with disbelief. After my animated recap of the day's observations, we laid plans for the next day. Then I "angst" through the night that I had seen an anomaly. Fortunately, the next day *opalinus* performed their displacement response for Ernest, and he pronounced it "confirming."

Steven Poe

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University of Texas at Austin

I suppose I was Ernest Williams' last student. I came to him after my junior year at Harvard, seeking an independent project to bolster my weak academic record and fool some unsuspecting herpetology department into accepting me for graduate study. Thanks mostly to Ernest, the ploy worked--an undergraduate thesis on anoles was produced and some graduate schools accepted me. But more importantly, my relationship began with the scientist and advisor who would most shape my academic future. Ernest believed in me when my record did not merit endorsement, advised me when he had little to gain from the relationship, and supported me financially because he thought the research should get done. Without him, I would not be working in anoles. Hell, I probably would not even be in science.

I have heard Ernest described as aloof and very Harvard, but in my opinion he had neither of these scornful qualities. Obviously, my views are limited to my time spent with him--when he was older--but in my judgement he was merely shy, quiet, and hard to get to know. We spent a lot of time together in my few years at the MCZ, but usually talked almost exclusively of anoles, anoles, anoles. Nearly every evening (and usually after finishing an entire pint of ice cream), Ernest would ask me, "What important discoveries have you made today?" More often than not, my "discovery" would be along the lines of a revelation that my medieval MCZ dissecting microscope really sucked. But sometimes the report would be of something novel that would pique Ernest's interest, and we would discuss the distribution of that character, and then other characters, and so on to anoles and evolution in general. For Ernest, many of the general principles could be gotten from anoles and I learned to share his view of the vast potential of this genus for answering evolutionary questions. The breadth and depth of his knowledge of anoles continually amazed me and a selfish scientific wish of mine would be to have just one more day to pick his brain on these lizards. Refreshingly different from those who would take pride in "problem-based" over "taxon-based" specialization, Ernest seemed to know something about everything that had been learned about his study animal. And he was incessantly intellectually curious in other areas as well. Working on my own to learn phylogenetic systematics, I photocopied papers from *Systematic Zoology, Cladistics*, and the like. No matter how obscure or cladomuddled the paper, Ernest wanted a copy of it for his own library. His thought was that if the paper was important enough for me to copy, he thought he should know about it himself. And incidentally, he was not as resistant to changes in systematics as some of his later papers might suggest. He retained a healthy skepticism, but, at least in his later years, he was not an anti-cladist. My undergraduate thesis under him was a parsimony analysis of some anoles, so one could say that I learned phylogenetic systematics under Ernest's tutelage!

Ernest and I went to the Dominican Republic for a month to collect anoles, and there, on my first real field work, I suppose I was Ernest's last field companion. He was very old by then, and it was difficult at times. Once, I returned from a half-hour of anole-catching to find Ernest prostrate on his back at the base of a muddy embankment, trying to right himself like a flipped turtle. Sadly, he was getting too old for the minor exertions of field work. But he endured, in good humor even, and my memories from that trip are treasured. One of my favorite recollections is the time when I returned from a difficult hill of terrain in the mountains, sweaty, bloodied from a fall, and without anoles, only to be greeted by Ernest's empty seat in the car.

Panicked by his unexpected absence, I followed the road up to the next house. At that house was "Ernesto," rocking in a chair on the porch, wearing a broad-brimmed straw hat and sipping a cool drink. Before I could thank the woman of the house for taking care of Ernest, she rebuked me in vitriolic Dominican Spanish for leaving my poor "grandfather" in the car alone. Even though Ernest had chosen to stay in the car, he did not protest her tirade, instead just looking at me accusedly--as if to say 'why, indeed, have you been so neglectful?'--while smirking to himself. As in this case, and in spite of his gringo Spanish, Ernest actually got along quite well with the locals. Once he even procured for us an invitation to the beach with a pair of fetching young ladies. Needless to say, we declined the proposition--there were anoles still to catch. But we did find time to enjoy the social life and cuisine of the area. For instance, in Puerto Plata we became regulars for brunch at Ernest's favorite local restaurant. One day, the syrup for the standard meal of pancakes was poured with a garnish of ants that apparently had entered the syrup bottle and died a sugary death. When I hastily pointed out to Ernest the drowned ants on his pancakes, he just shrugged and kept eating. "I'm old. I can't see them," he said.

So Ernest could adapt easily to challenging situations in the field, just as he would roll with the idiosyncracies of his diverse students. As we were both introverted, independent scientists, the two of us understood each other and worked well together. But this fertile work environment was not unusual. Ernest was able to foster the development of students of all kinds, at all levels of maturity and across almost all facets of evolutionary biology. His legacy as a great scientist is secure. In my opinion, his history as an inspiring mentor should be equally celebrated. And I will always remember him as my friend.

I was scoring an *Anolis wattsi* specimen for external anatomical characters when I heard that Ernest had died. I thought about what I would say if Ernest asked me at that moment "What important discoveries have you made today?" Then I got back to work on the anoles. I miss him.

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Sexual Variation and Adaptive Patterns

I am interested in the evolution of sexual dimorphism, particularly with regard to ecological factors which may influence sex differences. The amazing adaptive radiation and extensive evolutionary and ecological studies make *Anolis* a perfect group to investigate whether the evolution of sexual dimorphism is related to ecological factors, and also whether sex differences have a role in adaptive diversification. I have employed a comparative approach using field-collected morphological, ecological and behavioral data on 15 species of Puerto Rican and Jamaican anoles. This research was the subject of my doctoral dissertation and done in collaboration with Jonathan Losos and Thomas Schoener. My two main questions are: 1) are there any ecological influences in the evolution of sexual dimorphism, and if so, which evolutionary mechanisms are responsible, and 2) does sexual variation impact the pattern of adaptive diversification?

I believe that the ecological connection between intraspecific and interspecific processes is an important one, as it presents a much more complete picture of factors related to the evolution of sexual differences than either one alone. Recently, however, with the great number of studies on sexual selection, the balance of interest has weighed heavily on intraspecific processes.

The traditional explanations for the evolution of sexual differences are: independent adaptations of the sexes to their environment, selection pressure to reduce competition between the sexes, reproductive constraints which are unique to each sex, and sexual selection (male-combat or mate choice); ecology thus can have an important role in the evolution of sex differences. Even when the major mechanism is sexual selection, the ecological context of the species can greatly influence the degree to which sex differences can evolve.

Similarly, sexual differences can be informative for studies traditionally limited to interspecific comparisons. Just as species may have differences that reflect adaptation to their environment, sexes may also differ in ecologically relevant ways. Males and females may have different diets, rates of activity, social interactions, suites of predators, habitat use, thermoregulatory constraints and performance capabilities. Yet, sexual variation is usually not considered in the study of adaptive radiation and adaptive diversification in general (e.g., Liem 1974; Losos 1992; Schluter and McPhail 1993). Most studies have focused on one sex only or have pooled individuals regardless of sex. Greater Antillean *Anolis* lizards, which are famous for their adaptation to structural microhabitat and have repeatedly evolved six ecomorph types (trunk ground, trunk crown, trunk, grass-bush, twig, and crown giant), are an ideal group to investigate the possibility that sexes may act as independent ecospecies or otherwise contribute to adaptive diversity exhibited by the radiation.

Summary of Results

Patterns of sexual dimorphism and ecology

I began with size dimorphism and examined whether ecomorphs differ in sexual size dimorphism. Sexual dimorphism in size is strongly habitat-associated (Butler, Schoener, and Losos, in revision). That is to say, the trunk-crown and especially the trunk-ground species are highly sexually dimorphic, whereas the crown-giant, trunk, grass-bush, and especially the twig have very low sexual dimorphism. The pattern cannot be explained by allometry (increasing sexual dimorphism with increased overall body size), nor by phylogenetic inertia.

Shape dimorphsim is more complicated than size dimorphism. There are many hypotheses regarding the evolution of shape differences which link size, shape and ecology. Shape dimorphism may arise as an allometric response to changes in body size because different body parts tend to grow at different rates. Alternatively, if males and females utilize different microhabitats, then shape differences may reflect different adaptations that males and females have to their different environments. Finally, the relationship between males and females to their habitats may not differ, but the sexes may have different functional constraints. Lizards often provide good model systems for studies of locomotor adaptations, and the sexes may have different selective pressures. For example, males may be under stronger predation pressure and thus be in need of greater escape capabilities, or females may have to cope with the functional constraints imposed by egg-bearing such as altered load distribution or limited flexibility, all of which affect locomotion.

We found considerable dimorphism in shape in Puerto Rican and Jamaican anoles. Shape dimorphism is partially correlated with size dimorphism, but is not a direct consequence of size dimorphism (shape dimorphism cannot be explained as an allometric consequence of scaling differences between males and females).

What about differences in ecology? We examined whether shape variation has a direct relationship with ecology, whether this relationship differs between the sexes, and whether differences in habitat use between males and females can explain shape dimorphism. The relationship between shape and ecology is similar (but not perfectly so) between males and females. Males and females have nearly identical relationships between shape and perch height. However, the relationship between perch diameter and shape dimorphism differs between the sexes. They are not radically different, but different shape variables are more strongly related for perch diameter for males (relative forelimb and hindlimb) than for females (relative forelimb, mass, and lamella number). Finally, we tested whether dimorphism in shape can be explained by intersexual differences in ecology. We were indeed able to detect some significant relationships, even with only 12 species.

So, to summarize a rather complex pattern, although shape dimorphism cannot be accounted for by allometry, shape dimorphism (variation relative to body size) in limb length and lamella number is related to ecomorph type and possibly to body size. Thus, the shape dimorphism-by-ecomorph pattern suggests that the ecomorphs have very different lifestyles; in some ecomorphs, the sexes are very similar in shape whereas in others they are very different. There are also elements of shape dimorphism that are related directly with ecological variation, including dimorphism in relative SVL and mass. This pattern suggests that there are physical factors that are directly influencing the evolution of sexual dimorphism. Perch diameter is related to morphology in different ways for males and for females.

Sexual dimorphism and adaptive radiation

With all of this dimorphism in shape present, what consequences does sexual variation have for the adaptive radiation? Can ecomorphs even be classified accurately in the face of extensive sexual variation? We performed a discriminant function analysis on the shape data classifying individuals to species. When individuals were misclassified, we checked whether they were classified into the correct ecomorph category. When this analysis was performed on males only (or females only), we found that the classification worked well to the correct ecomorph type. However, when females were classified by the discriminant function described by the males, we found that there was a much higher misclassification rate, and that most of the errors occurred between trunk-ground and trunk-crown ecomorphs. Twig and grass-bush ecomorphs were well classified regardless of sexual variation.

If we consider sexes as separate morphospecies, does sexual variation increase morphological diversity in the radiation or increase "species packing?" With regard to morphological diversity, sexual variation does not increase clade-level morphological variation significantly (there is some additional variation on the extremes of morphological variation, but it is small relative to the variation already present when males are examined alone). However, sexual variation does significantly increase species packing (by reducing nearest-neighbor distance between groups) and this occurs with both morphology and ecology. Especially with trunk-ground and trunk-crown species, male and female clusters seem to be interdigitated. Trunk-ground females are morphologically more similar to trunk-crown males and trunk-crown females are ecologically more similar to trunk-ground males. In summary, sexual variation influences adaptive radiation in a very regular and evolutionarily repeated way. It greatly increases diversity in the form of ecological packing in two of the five ecological types examined. Thus, the niches of anoles are more complex and more tightly defined when both sexes are considered.

I also have a rather large data set of behavioral focal observations that need to be analyzed and synthesized and many, many diet samples ("barf") taken in the field. In the future, I would like to investigate sexual selection using genetic markers as well as locomotor differences between the sexes in the context of reproductive constraints.

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Consequences of the Cuban Brown Anole Invasion in Florida: It's Not Easy Being Green

Abstract: The Cuban brown anole (*Anolis sagrei*) is notorious for dispersing via anthropomorphic means and colonizing new habitats throughout the southeastern U.S. Because the native green anole (*A. carolinensis*) declines very quickly upon arrival of brown anoles, it has been difficult to determine the causes of such declines. As a result, many questions have remained unanswered for nearly 40 years. I studied the effect of brown anoles on green anoles by performing experiments on dredge-spoil islands in Florida. In 1995, I introduced brown anoles onto three islands occupied by greens and used three islands containing native greens as controls. Populations were monitored with capture-mark-recapture techniques. Body data, detailed microhabitat data and spatial data were collected. Green anole populations and habitat parameters were similar over time on the control islands. On treatment islands, brown anole populations increased dramatically and became dense in all habitat types within the study period. Green anole populations declined as brown anole populations expanded; survivors shifted their perch heights and utilized different habitats than did the original natives. Fall hatchling surveys, gut content analyses, and other lines of evidence suggest that intra-guild predation (competitors that eat each other) was the main cause of the rapid decline of green anoles. Sympatric green anole populations remained viable only in habitat patches containing dense understory vegetation, which may have ameliorated the effects of hatchling predation. Green anole populations might remain viable in urban or disturbed environs where the brown anole attains very high densities as long as sufficient understory vegetation is present to ensure successful yearly recruitment of hatchling green anoles to adulthood.

Caveat: At the time of this writing (April 1999), I have not finished analyzing the data from this study, so my results are presented in general terms without graphics or the "luxury" of statistical analyses. Any errors, omissions, inconsistencies with future publications, or otherwise ridiculous statements herein were borne of a desire to contribute *something* to this newsletter, stimulate candid appraisals, and generate further interest.

INTRODUCTION

An incredible number of excellent studies have been conducted on the natural history, ecology, and evolution of lizards of the genus *Anolis*, too many to review in this format. Studies of these interesting "model organisms" have contributed much to broader disciplines including community ecology and evolutionary biology, much to the chagrin of those working on lesser groups. In the interest of brevity, I only review the few studies of a specific problem: the potential impact of the exotic Cuban brown anole, *Anolis* (or, arguably, *Norops*) *sagrei*, on the native green anole (*A. carolinensis*) in Florida. General background information or data for certain species can be obtained from Schwartz and Henderson (1991), the 400 studies cited in Roughgarden (1995), and the recent studies by Leal et al. (1998), Losos and Spiller (1999), Spiller and Schoener (1998), and references therein.

The green anole, a slender trunk-crown anole, has been present in North America since the Pleio-Pleistocene (Williams 1969, 1983), during which time it experienced ecological release and came to occupy the entire vertical range of forested habitat (ground-to-crown). It is most abundant in habitats with a high edge-to-interior ratio and thus has remained successful in even the most highly disturbed urban environs. Until recently.

The brown anole, a more robust trunk-ground species (Williams 1969, 1983; Schoener 1968, 1975), arrived in the Florida Keys in the late 1800s and was inoculated to at least six separate ports in Florida in the 1940s (Lee 1985). It has spread throughout Florida and into Georgia and two other southeastern states since that time (Campbell 1996; Campbell in prep., an exhaustive review of all published and museum records documenting its spread).

The earliest written statements suggesting that the brown anole might negatively affect the native green anole were made by Collette (1961), followed by King and Krakauer (1966). This was reinforced by Lee (1985); Tokarz and Beck (1987) made the first attempts to study the interaction directly, followed by Brown and Echternacht (1991). These studies approached the problem from the standpoint of interference competition (territorial aggression) and found that intraspecific overshadowed interspecific interactions. Gerber (1991) studied hatchling competition and predation of hatchlings by adults in field cages and suggested that these two competitors also consumed each other's hatchlings (termed intraguild predation; IGP). In a brief note, Campbell and Gerber (1996) confirmed hatchling predation in the field. Vincent (this newsletter) studied the interaction in native hammock habitat and studied reproductive issues in field cages. Porter performed a field study on spoil islands that addressed the effects of food availability on the interaction. To my knowledge, these are the only studies of this problem in North America. However, detailed natural history studies and very interesting experiments have been conducted using the Bahamian populations of these two species (Schoener 1968, 1975; Losos and Spiller 1999).

The main objective of this study was to inoculate brown anoles into areas occupied by green anoles and follow the populations of both species over the next three years. The purposes of this study were many: (1) to determine whether or not brown anoles affect green anoles and, if so, (2) to reveal some of the mechanisms causing their decline, (3) to assess the spatial and temporal aspects of the invasion process and the subsequent green anole decline, and (4) to ascertain the conditions that allow green anole populations to remain viable.

STUDY AREA

This study was performed on dredge spoil islands in Mosquito Lagoon, an estuary within the boundaries of Canaveral National Seashore (CANA) and Merritt Island National Wildlife Refuge (MINWR) just north of Cape Canaveral in Brevard and Volusia Counties, Florida. The spoil islands were created about 50 years ago by the U.S. Army Corps of Engineers as a by-product of the excavation of the Intracoastal Waterway, a large shipping channel traversing the east coast of Florida. All are completely surrounded by water, and are very similar in age, shape, and distance to the mainland. Mosquito Lagoon is completely surrounded by two large protected areas, so very similar native plant and animal communities have assembled on the islands.

Islands are dominated by cabbage palm (*Sabal palmetto*), southern red cedar (*Juniperus silicicola*), buttonwood (*Conocarpus erectus*), black mangrove (*Avecinia germinans*), saw palmetto (*Serenoa repens*), salt bush (*Baccharis halimifolia*), sea-oxeye daisy (*Borrichia frutescens*), saltwort (*Batis maritima*) and Brazilian pepper (*Schinus terebinthifolius*).

Spoil islands are ideal "natural cages" for conducting experiments on anoles. They contain many anole prey species, but relatively few anole predators. Vertebrate faunas of the islands are somewhat depauperate, but not necessarily more so than urbanized areas of the mainland. Furthermore, they support complex but relatively open vegetation less than 10 meters tall, allowing the entire range of vertical habitat to be searched thoroughly with small binoculars. Finally, I believe spoil islands are excellent models for isolated, disturbed habitat patches in urbanized coastal regions of mainland Florida. It is in these types of habitats that brown anoles become most dense and have the most dramatic effects on green anoles.

METHODS

Island choice: Six dredge spoil islands had to be picked for the study: three were to be inoculated with brown anoles and three were to be left as allopatric controls. I had no indication of the speed with which brown anole populations would expand on islands that contained dense populations of their green-colored competitors. Nor could I predict the speed with which brown anoles would become dense enough to have measurable effects. Furthermore, I could not predict the size of the post-invasion green anole populations that would remain on a particular island. Thus, it was difficult to choose islands small enough to enable brown anoles to reach high densities within the period of my study, but large enough to allow post-invasion green anole populations to remain large enough for statistical analyses.

I chose instead to employ two small (0.03 - 0.07 ha), two medium (0.1 - 0.2 ha), and two large (0.8 - 1.0 ha) islands. Two islands were picked from pools of islands in each size category and each was randomly assigned to either an invasion treatment or allopatric control. This allowed me to utilize a few large islands with huge green anole populations; six large islands could not have been thoroughly sampled in this study without a small army. More importantly, it allowed me to determine the influence of island size (i.e., habitat patch size) on the "fill rates" of brown anole populations, the rates green anoles decline, the post-invasion green anole population size, and the potential for long-term survival of green anoles.

Island specifics: The small treatment island (Zero) consists of a ~ 0.03 ha dome-shaped forested area about 6 m high dominated by cedar, sabal palm, and buttonwood, bordered on three sides by a ~ 0.04 ha open shrub/marsh area dominated by small (2 m), isolated mangroves in a marsh matrix of *Batis* and *Borrichia*. The small control island (Fellers) consists of a ~ 0.02 ha dome-shaped forested area about 5 m high bordered on two sides by a ~ 0.02 ha open shrub/marsh area. The medium treatment island (Ant) consists of a ~ 0.09 ha dome-shaped forested area up to 8 m high bordered by four small shrub/marsh areas (~ 0.04 ha total). The medium control island (Tarp) consists of a ~ 0.07 ha dome-shaped forested area up to 7 m high bordered on one side by a ~ 0.04 ha open shrub/marsh area. Vegetation was similar on all.

The large islands are physically different from the small and medium islands. Because they are high domes of coarse sand, they have a centralized xeric area surrounded by a "ring" of forest and marsh vegetation along the shoreline. The central zone is a very open (30 - 40 %

vegetated), xeric area with lone or small clumps of short cedars and sabal palms (1 - 3 m high) and prickly pear cactus (*Opuntia*) in a barren matrix of coarse Miocene shell and coralline rocks (dredge spoil). The central xeric areas are important for determining the influence of habitat type (open vs. forested) on the outcome of the interaction; they are remarkably similar to sparsely vegetated urban areas (e.g., parking lots). The forested ring is generally a 5 - 20 m wide strip of 5 - 8 m tall cedars, sabal palms, buttonwood and other shrubs that wraps around most of the outer edge of the island, but is interrupted by erosion or human disturbance. Dense marsh zones and small patches of young mangroves lie waterward of the forested ring. The forested ring and marsh - mangrove zones are essentially larger, longer versions of the small and medium islands, whereas the central xeric zone has no counterpart on the small or medium islands.

The large treatment island (Yin) and large control island (Lizard) are very similar in size (0.8 - 1.0 ha), overall configuration, and vegetation composition, height, and density. A seventh island (Cedars Island), another large island like Lizard and Yin, contained large populations of both species in 1994 and was monitored in a second pilot study in early 1995 to determine if there were any measurable differences in habitat use and densities between allopatric and long-time sympatric green anoles. As a “two-species control” island, this island represented a vision of the treatment islands years in the future (and generated much needed funding), so I continued to monitor it throughout the study. Unfortunately, islands that contained both species of anoles and matched the small and medium islands in size and habitat were not found, so two-species controls for those islands were not available; nor were they established.

The manipulations: A total of 40 brown anoles (20M:20F) were captured from urban areas of the mainland around Mosquito Lagoon (e.g., New Smyrna Beach), marked and measured (see below) and released at a single point on treatment islands in May 1995 after background data was collected on native green anoles. Shortly thereafter, an additional 40 brown anoles were released on the large island to further ensure success of that invasion. Control islands were monitored in the same manner as treatments; any brown anoles found on these islands were either killed with a stout rubber band or captured and removed immediately.

Data collection: I monitored lizards with basic capture-mark-recapture (CMR) techniques and collected detailed microhabitat and positional data for all captured and re-sighted lizards. During “CMR sessions,” I made slow methodical searches around each island over a period of at least three days (depending on island size), or until most of the population had been marked (3 days on small, up to 10 days on large islands). Adult lizards were captured by hand or noose, permanently marked with exclusive numbers by toe-clipping, and temporarily marked on both lateral surfaces with their number for rapid sight-identification. I measured SVL, tail length, tail regeneration (to 1 mm), and weight (to 0.1g), and recorded female reproductive condition (gravid or not) and any external injuries, parasites, and deformities.

Microhabitat data consisted of perch height (to 1 cm), maximum vegetation height within a 0.5 m radius around the perch (to 0.2 m if below 3 m; to 0.5 m above 3 m), perch diameter (to 0.2 cm), perch plant species or perch type (16 categories), perch angle, general perch position (exposed or in deep cover), and anole position on the perch (e.g., head angle, insolation, and basking status). Positional data (accurate to 0.5 m^2) was taken for each anole captured or sighted by measuring and/or triangulating their position from previously surveyed benchmarks using a rangefinder and/or Suunto KB-14 compass accurate to 0.5 degrees.

Hatchlings, which are extremely delicate and difficult to handle without harming them, were not captured and marked in this study. Gerber (1991) indicated that hatchling predation might be the most important factor in the decline of green anoles, so I chose not to render hatchlings more vulnerable to predation by handling them. Instead, in the fall of each year, I monitored hatchling anoles of both species using distance sampling methods. Six transects were established on each island along which I walked slowly and recorded the perpendicular distance to each hatchling.

Data analyses: Population estimates will be made using the Jolly-Seber estimator. I will be casting this data on population sizes, anole densities and other parameters for each year into ANOVAs, similar to Losos and Spiller (1999) and Leal et al. (1998). Positional data will be analyzed with Geographic Information Systems (GIS), but because all data will be tied to lizard location, detailed spatio-temporal analyses will follow. Below I present a very general, non-statistical, and unfortunately non-graphical, summary of my results regarding population sizes, perch distributions, and hatchlings over space and time.

RESULTS

Treatment islands: Brown anole populations expanded dramatically on the three treatment islands and green anole populations declined, although both of these phenomena occurred at different rates on the three treatment islands. On the small treatment island (Zero), 23 of the 40 original brown anoles were seen again in 1995. The brown anole population exceeded 100 in 1996, 200 in 1997, and 400 in 1998. Nearly all were found within the central forested area in 1995 and 1996. At least two males were found on each tree trunk and at least as many females occupied low trunks and leaf litter by 1996. In subsequent years, frequent territorial squabbles rendered the forested area a busy battle zone and many brown anoles were observed in the canopy (5 - 6 m). They had expanded out into the perimeter marsh - mangrove region by 1997 and became dense (~ 5 per isolated mangrove) there by 1998.

Green anoles were dense on Island Zero in 1995 (more than 100 individuals) and were often found on the ground and perched low on tree trunks. Their numbers declined dramatically over time: only about 60 were present in 1996, 50 in 1997, and 20 in 1998. As early as 1996, green anoles were rarely seen on tree trunks in the central forested area and few were seen on narrow perches above eye-level. The forested area is very open underneath the canopy and the trunks of cedars and sabal palms are the main ground - canopy conduits. Only around the edges of the central forest do shrubs become dense. I found nearly all of the green anoles between 1996 and 1998 in this dense edge vegetation and even the low vegetation of the marsh - mangrove area, rather than in the forest canopy. I had expected them to survive only in the forest, based on their trunk-crown propensity when trunk-ground species are present.

The medium treatment island (Ant) generated interesting data. A bird rookery consisting of ~ 50 crested cormorants and a few great egrets became established on the island in 1996 and was large in 1997 and 1998. An inordinate amount of feces, regurgitate (fish), and dead fledglings rained down from the central forest canopy onto my field assistants. Flying insects were more abundant there than on any other island in the study and represented unintentional food augmentation. As a result, the 97 brown anoles captured during the summer of 1996 were extremely large. The average size of male brown anoles in June was 64 mm SVL and 8 g. The largest brown anole ever recorded (to my knowledge), a 73 mm, 11.8 g male, was captured on this island in 1996, along with a number of other males over 70 mm, and numerous females over 52 mm in SVL (largest 54 mm and 5 g!). The population exploded in 1997; I marked 297 lizards, but a meager recapture rate indicates the population was > 500. In 1998, I marked 254 lizards, but few recaptures indicate the population was much larger (~1000?).

The green anole decline was dramatic. In 1995, over 100 green anoles were captured and the population easily exceeded 200. In 1996, 89 lizards were marked, but recaptures indicate the population was ~150. By 1997, the green anole population plummeted to the point where whole days would pass without seeing any. Only 17 were captured that year (estimate ~ 40) and only 12 were captured in all of 1998 (nearly all recaptured; estimate ~ 20). In 1996, quite a few green anoles were captured by hand from high in the cedars and sabal palms of the central forest, but in 1997 and 1998, they were only found in or within a few meters of the edge of the central forest, or in the outer marshes.

Brown anoles required the entire study period to occupy the large treatment island (Yin). In 1996 their relatively small number of progeny (< 200 lizards from 80 propagules) were found mainly within 30 m of the release site in the forested ring on the north side of the island and in the north portion of the central open area. Very few individuals were found on the south end of the island more than 50 m from the release site. By 1997, the ~ 500 lizards on the island (220 marked) occupied most of the forested ring, but remained sparse to the south and a few were seen in each shrub of the central zone. They had spread to all but the very southern tip of the island; there was an obvious gradient in density from north to south at that time. By 1998, 496 brown anoles were marked with meager recaptures (rough estimate ~ 2000 lizards); they were fairly dense throughout the island and the difference in density between the north and south was not obvious (but may be revealed in subsequent GIS analyses).

Green anoles declined dramatically as brown anoles filled the island from north to south. In 1995, hundreds were marked. Unfortunately, the population may not be estimable due to insufficient recaptures, but likely contained at least 500 individuals. As early as 1996, green anoles were rare within about 30 m of the release site. By 1997, very few were found on the north side, in central open areas, or in open habitats along the east shore; most were found in outposts of very dense vegetation dominated by buttonbush (a very dense shrub), the same habitat in which greens can be found on the two-species control. By 1998, the only places green anoles could be reliably found were those areas containing dense understory vegetation.

Control islands: The population of green anoles on the small control island (Fellers) was roughly 40 - 60 individuals every year of the study and remained much larger than that of the treatment island through 1998, despite its smaller size. The population of green anoles on the medium control island (Tarp) was always over 100 individuals and remained much larger than that of the treatment island in 1996 through 1998, despite its slightly smaller size than the treatment. The green anole population on the large control island (Lizard) remained large throughout the study. I was able to capture a green anole every 4 - 6 minutes during every day of this study; the population probably consisted of at least 500 individuals each year.

Hatchling surveys: Hatchling transect data have not yet been converted to densities using distance sampling formulas and have not been analyzed statistically, but some general trends are worth noting. First, over twice as many green anole hatchlings were seen on the large control island (Lizard) than on the large, two-species control island (Cedars) during each of the fall hatchling surveys and during island-wide CMR sessions. This was probably due to the already smaller size of the adult green anole population on the two-species island, rather than due to hatchling predation *per se*. More importantly, hatchlings were only seen on that island in areas of dense marsh and shrub vegetation in and around the forested ring.

The number of hatchlings seen during transect surveys and CMR sessions declined on the treatment islands. In 1995, each treatment and control island yielded similar numbers of hatchling green anoles; the original brown anole invaders may have had little effect. In 1996, there was a difference between hatchlings on the small treatment (Zero) and control (Fellers), but this difference was not observed on the medium or large islands. The population of green anoles on the medium island was high in 1995 and 1996, but declined very rapidly between 1996 and 1997, indicating hatchling survival and adult recruitment was affected by the huge brown anoles present in fall 1996. On the large treatment island in 1997 and 1998, hatchling green anoles were rare on the north side of the island within 30 m of the release site and throughout the central open zone, whereas on the southern end they remained common through 1998.

DISCUSSION

Perch height mediated dietary shift: The perch height shift exhibited by green anoles as brown anole populations expanded and became dense on the treatment islands was expected of this species when sympatric with brown anoles (Schoener 1975). The ~ 30 cm shifts in mean perch heights observed on the treatment islands are biologically meaningless in habitats with 5 - 8 m canopies. However, the shift was manifested in the decline of green anole sightings on lower perches (0 - 0.5 m above the ground). This is noteworthy from a biological standpoint because of the vertical distribution of arthropods, which were more numerous and diverse near the ground than up in vegetation on the spoil islands (unpublished sticky-trap data from four islands).

The perch height shift observed in green anoles soon after the arrival of brown anoles is an important phenomenon regardless of our lack of understanding about the mechanism. Because arthropods are more abundant nearest the ground, fewer prey items and taxa might be available to green anoles than were available prior to the upward niche shift. These two species consumed similar sizes and taxa of prey items on three spoil islands in the Indian River Lagoon in St. Lucie County, where they have been sympatric for many years, but green anoles consumed more flying taxa and brown anoles consumed more ground-dwelling taxa and larvae (Campbell and Porter, unpubl. manuscript). Dietary plasticity probably helps to ameliorate the effects of the vertical shift, but the amount and quality (i.e., energetic value) of prey items taken by green anoles in the presence of brown anoles is likely diminished by their being excluded from the ground level. Thus, interference competition (causing perch height shifts) and exploitative competition (causing diet shift) could be interacting to produce a substantial negative effect on green anoles. Clearly, the negative effects of such “perch height-mediated dietary shifts” in green anoles would be most dramatic during times of limited resources (e.g., the dry season). However, because arthropods vary in abundance over vertical space, I propose that the negative effects of perch height mediated dietary shifts might even be realized during times when resources are abundant and the effects of exploitative competition should otherwise be at a minimum. Of course, if this phenomenon even occurs, it can only be demonstrated with controlled experiments.

Competitive exclusion: Brown anoles excluded green anoles from certain habitat types during this study. On the large treatment island (Yin), green anoles almost completely disappeared from the open central area and were rarely observed running on the ground in the open. By 1998, the green anole distribution on this island was very much like the long established two-species control island (Cedars) in that green anoles were rare in the central xeric area and only observed in the largest and tallest clumps of vegetation (> 3 m). On the large control island (Lizard Island), green anoles occurred in large numbers and high densities throughout the island during each year, remained abundant in the central zone in even the smallest, isolated plants, and were often observed running across the ground and perching on rocks. Although these results are strong and based on huge sample sizes, "competitive exclusion" in the strict sense of the word cannot be supported by my data. Based on data from hatchling surveys, simple predation may be the cause of exclusion in the low, open areas of the large islands.

Hatchling issues: In 1995, the treatment islands contained only 40 brown anoles (80 on Yin), a very low density for even the small island (Zero). Brown anoles probably had minimal impact on green anole hatchlings that year, although the green anole population was clearly smaller on the small treatment (Zero) as early as 1996. Brown anoles may have consumed a few hatchlings in fall 1995 before their demise, but it was not until 1996 that the cohort on the small treatment was large enough to affect the green anole hatchling population. The brown anoles on the medium treatment (Ant) grew extremely large in 1996 and probably were able to consume more and larger hatchlings and to do so for a longer period of time than on any other island. This is the most likely cause of the more dramatic and rapid decline of green anoles on Ant Island relative to its smaller counterpart, Island Zero. I made collections of anoles from all seven of these islands in August 1998 (370 lizards total) in order to document hatchling predation and food overlap, and thus IGP; hopefully they were not sacrificed in vain.

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

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

Ramifications: Hopefully, the above statements will hold up to statistical analyses. If they do, I further hope the results of this study will be applied to the management of green anole populations in urban and disturbed areas; the only habitats wherein I believe the brown anole affects the green anole. The green anole is not in danger of extinction, given that the two species evolved together in the Caribbean and should be able to coexist on some level. However, green anoles were clearly more abundant in urbanized areas of Florida until the arrival of brown anoles, and some local extirpations have probably occurred. Brown anoles clearly do not become as dense in native, "undisturbed" forested habitats, but will march into these areas as habitat alteration proceeds. In fact, green anoles often occur in higher densities in edge situations (e.g., well-vegetated suburbia) than in deep, undisturbed forest. Thus, only the introduction of the brown anole could have resulted in the declines and local eliminations of the green anole that even the most uninformed laypersons seem to have noticed. Based on the spatial data from these spoil islands, it appears that these two species can even coexist in non-forested urban areas as long as dense cover is provided for hatchlings to "run the gauntlet" of brown anoles. So, although its not easy being green in a progressively browning Florida, humans can make it easy for this important member of our native fauna and our sole native anole to remain locally abundant, so they may once again hang from every kid's earlobes.

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LITERATURE CITED

Brown, P. R. and A. C. Echternacht. 1991. Interspecific behavioral interaction of adult male *Anolis carolinensis* (Sauria: Iguanidae): A preliminary field study. Anolis Newsletter IV:21-30.

Campbell, T. S. 1996. Northern range expansion of the brown anole (*Anolis sagrei*) in Florida and Georgia. Herp. Review 27:155-157.

Campbell, T. S and G. Gerber. 1996. *Anolis sagrei*: Saurophagy. Herpetol. Rev. 27:106.

Collette, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. Bull. Mus. Comp. Zool. 125:137-162.

Gerber, G. P. 1991. *Anolis sagrei* and *Anolis carolinensis* in Florida: Evidence for interspecific predation. Anolis Newsletter IV:49-53.

Guyer, C. 1988. Food supplementation in a tropical mainland anole, *Norops humilis*: demographic effects. Ecology 69:350-361.

King, W. and T. Krakauer. 1966. The exotic herpetofauna of southeast Florida. Quart. J. Florida Acad. Sci. 29:144-154.

Leal, M., J. A. Rodríguez-Robles, and J. B. Losos. 1998. An experimental study of interspecific interactions between two Puerto Rican *Anolis* lizards. Oecologia 117:273-278.

Lee, J. C. 1985. *Anolis sagrei* in Florida: Phenetics of a colonizing species I. Meristic characters. Copeia 1985:182-194.

Losos, J. B. and D. Spiller. 1999. Differential colonization success and asymmetrical interactions between two lizard species. Ecology 80:252-258.

Roughgarden, J. 1995. *Anolis* Lizards of the Caribbean: Ecology, Evolution, and Plate Tectonics. Oxford University Press, Oxford.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. Ecology 48:704-726.

Schoener, T. W. 1975. Presence and absence of habitat shift in some widespread lizard species. Ecol. Monogr. 45:233-258.

Schwartz, A. and R. W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University of Florida Press, Gainesville.

Spiller, D. A. and T. W. Schoener. 1998. Lizards reduce spider species richness by excluding rare species. Ecology 79:503-516.

Tokarz, R. R. and J. W. Beck, Jr. 1987. Behaviour of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*: An experimental test for behavioural interference. Anim. Behav. 35:722-734.

Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quart. Rev. Biol. 44:345-389.

Williams, E. E. 1983. Ecomorphs, island size, and diverse end-points in island radiations of *Anolis*. Pp 326-370 In R. B. Huey, E. R. Pianka, and T. W. Schoener, eds., Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge.

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Possible Causes for the Rapid Decline in Population Density of Green Anoles, *Anolis carolinensis* (Sauria: Polychrotidae) Following Invasion by the Brown Anole, *Anolis sagrei*, in the Southeastern United States

Introduction. The brown anole, *Anolis sagrei* (Sauria: Polychrotidae) is native to Cuba, Jamaica, the Bahamas, Swan Island, Little Cayman Island and Cayman Brac (Schwartz and Henderson 1991) and invaded the mainland of North America about 60 years ago (Lee 1985). The first colonizations were in southern Florida and, subsequently, the species has expanded its range northward into at least southern Georgia (Godley et al. 1981, Campbell 1996). Established populations have been reported at multiple sites in Louisiana (Thomas et al. 1990, Platt and Fontenot 1994) and Texas (King et al. 1987, Krusling et al. 1995). The entire North American range of the brown anole is contained within that of its native congener, the green anole, *Anolis carolinensis*. The brown anole co-occurs with members of the *Anolis carolinensis* complex on at least five island banks in the West Indies (Williams 1969).

Green anoles utilize a wide variety of habitats, but their populations are densest in edge situations which feature small trees (dbh 5-15 cm) “imbedded” in an understory of low herbaceous vegetation and shrubs. We have been unable to locate any reports of population densities of green anoles prior to the arrival of brown anoles, but there are numerous anecdotal reports of rapid and dramatic declines in green anole populations following invasion by brown anoles. Observations indicate that these declines are most dramatic at disturbed sites, especially where the disturbance has included removal of the small trees, herbaceous vegetation and shrubs favored by the lizards. In general, however, it is only in the most disturbed sites that green anoles are completely excluded and in some habitats it is common to find adult males of both species defending largely overlapping territories. Anecdotally, the decline in population density of green anoles following invasion by brown anoles has been assumed to be the result of interspecific competition (e.g., Tokarz and Beck 1987). Here I present a preliminary model, based primarily on research conducted by our group, to account for the decline in population density of green anoles following invasion by brown anoles.

Behavioral Interference. In cage studies, Tokarz and Beck (1987) and Brown (1988) have demonstrated that levels of interspecific male-male aggression are reduced relative to intraspecific levels. Gerber (in prep.) has confirmed this with tether-release experiments in the field. Brown and Echternacht (1991), in observations of naturally-occurring interspecific encounters between non-tethered lizards in the field, noted that green anoles were more likely to chase and/or attack brown anoles than the reverse, and that brown anoles were more likely to retreat in the face of an interspecific encounter than were green anoles. Brown and Echternacht’s (1991) data were, however, weak because encounters were often already under way when they were first discovered, and because the history of the lizards relative to one another was unknown. Data available to date, however, does not support interspecific male-male aggression as playing a role in the decline in the population density of green anoles following invasion by brown anole.

Habitat Use. Green anoles have been characterized as occupying a trunk-crown ecological niche whereas brown anoles are said to occupy a trunk-ground niche (Williams 1969), but this applies to green anoles only where they occur in multi-anole (i.e., "complex," Williams 1969) communities. In the southeastern United States in areas not yet invaded by brown anoles, green anoles occupy a crown-trunk-ground niche that is, therefore, the sum of niches occupied by green and brown anoles where they occur together. Following invasion, the structural niche of green anoles shifts upward such that they occupy the trunk-crown niche observed in multi-anole communities elsewhere. If this is due to competition, the resource being contested has yet to be identified, although it may simply be space. In any case, this shift by green anoles may play a role in their decline following the appearance of brown anoles. Prior to invasion, green anoles should have access to more territories than following invasion (Fig. 1).

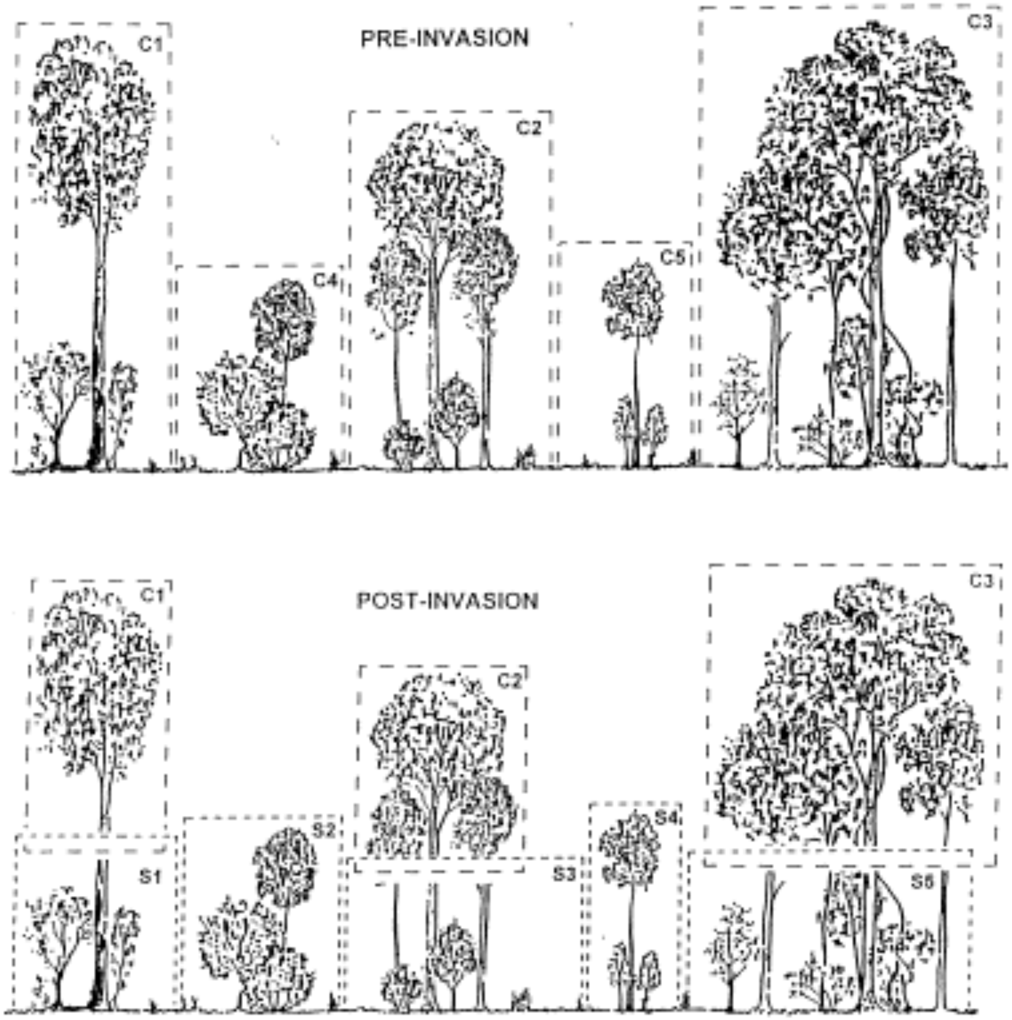
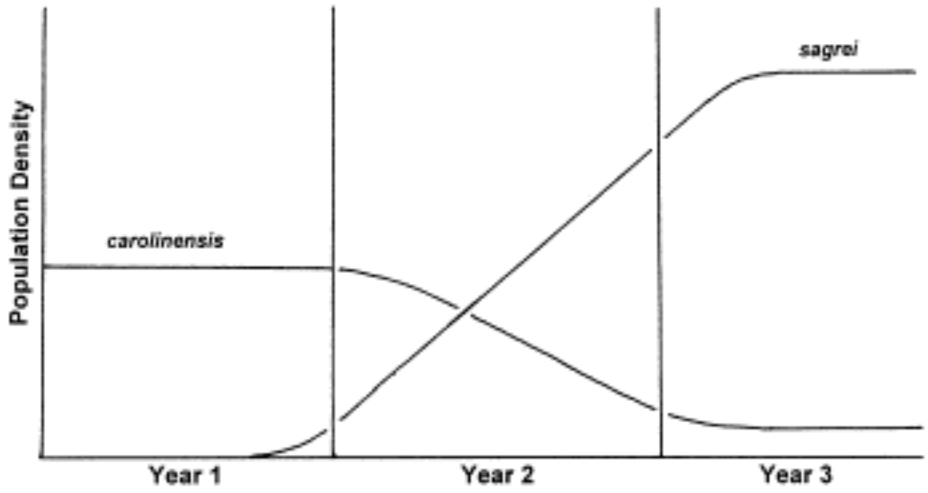


Figure 1. Hypothetical green anole (AC) territories at a site prior to (Upper) and following (Lower) invasion by brown anoles (AS). Note that the number of green anole territories is reduced from 5 to 3 following the invasion.

Intraguild Predation. Green anole hatchlings, like those of brown anoles, live close to the ground, often in low shrubs or herbaceous vegetation. Hatchlings of both species are, therefore, more likely to encounter adult brown anoles than adult green anoles. Using small cages and larger outdoor enclosures, Gerber (1991 and in prep.) has documented asymmetrical intraguild predation involving brown and green anoles. Adult male brown anoles exhibit a greater propensity for preying upon green anole hatchlings than on brown anole hatchlings, whereas adult male green anoles tend not to prey upon hatchlings of either species. Field observations and analyses of the stomach contents of the two species by Campbell and Gerber (1996) and Campbell (in prep.) have documented intraguild predation as well, although the extent to which it is asymmetrical in nature is as yet not clear. Campbell (in prep.) has documented very rapid increases in the population density of brown anoles following the introduction of known numbers of individuals onto spoils islands, on which brown anoles had not previously occurred, in the Florida intracoastal waterway and it is well-known that brown anole populations can be incredibly dense. Williams (1969:365) states that "More than any *carolinensis* it [*A. sagrei*] is a superabundant animal wherever it occurs. If any anole were to be singled out as a 'dominant' species, *A. sagrei* would be that species." Todd Vincent (in prep.) has documented green anole densities at two sites in Florida, one with brown anoles and one without. At *both* sites, densities of green anoles are substantially lower than is the density of brown anoles at the site where the two species co-occur. Given the disparity in densities at sites where the species co-occur, and the greater fecundity of brown anoles (see below) and their capacity for rapid population increase, individual brown anoles may need to prey upon no more than one or two green anole hatchlings in a season to bring about the near total collapse of the green anole population at a given site. Intraguild predation seems likely to play a major role in the decline in population density of green anoles following invasion by brown anoles.

Reproductive Interference. In enclosure studies, Todd Vincent (in prep.) has demonstrated that there is no difference in the quality (i.e., non-polar lipid content) of green and brown anole eggs in cages containing either a conspecific pair of anoles, two conspecific pairs, or a pair of each species. In both species, there is a density effect: fewer eggs per female are produced by females in the conspecific two-pair enclosures than when the enclosure houses a single pair of lizards, but the effect is greater in green anoles. In addition, in enclosures housing a pair of each species, the effect on brown anole females is not different from that observed in cages housing two pairs of brown anoles, whereas female green anoles exhibit a further decline in egg production. To what extent this phenomenon is a cage effect is not known. Vincent's field studies (in prep.) indicate that fewer green anole young-of-the-year survive to late Fall at the site where both species are present than at the site where brown anoles are absent, but it is not clear whether this is a result of reproductive interference or intraguild predation, or both.

The model. Our data suggest the following scenario (see Fig. 2). In Year 1, in an area yet to be invaded by brown anoles, green anoles occur at a relatively low population density. Sometime during that year, the site is invaded by brown anoles which increase in a nearly exponential fashion. As the population of adult brown anoles increases in late Year 1 and in Year 2, green anoles shift from the crown-trunk-ground niche to a trunk-crown niche, with a resultant reduction in number of available territories. At the same time, brown anoles are exerting increasing predator pressure on green anole hatchlings and, if the results of Vincent's enclosure studies are applicable in the field, female green anoles are producing fewer eggs than prior to the invasion. By Year 3, this model predicts that the green anole population will consist almost entirely of adults (which appear to be essentially annuals in Florida [Campbell, in prep.]) with recruitment reduced to essentially zero. In other words, in less than three years following invasion by brown anoles, the population density of green anoles will have exhibited the observed dramatic decline.



A. sagrei invades.

A. sagrei increases.
A. carolinensis undergoes niche shift and loss of space for territories, begins to suffer predatory loss loss of hatchlings, reduced fecundity, and population decline.

A. sagrei peaks.
A. carolinensis suffers virtually complete reproductive failure

Figure 2. A preliminary model for the decline in the density of a green anole population following invasion by brown anoles.

Caveats. Of course there are! The model I have presented applies only to disturbed areas, especially those impacted by habitat (as viewed by green anoles) destruction. In these areas, such as roadside parks and urban backyards, green anoles may be completely or nearly completely excluded following an invasion by brown anoles. If, however, enough habitat structure (again, as viewed by green anoles) remains, the two species may co-exist albeit at reduced densities of green anoles. The two species seem to be merely re-establishing the ecological relationships they exhibit on islands in the West Indies on which they co-occur. It seems likely that green anoles, or the ancestors of green anoles (*A. porcatus* of Cuba [Williams, 1969]) experienced ecological release and niche expansion upon colonizing the mainland of North America and are undergoing niche compression in the face of invasion by brown anoles. This model is probably not correct in all of its aspects and the careful reader has probably already identified some problems and, certainly, areas that warrant further investigation. The system offers an excellent opportunity to add to the meager list of case studies of the mechanisms by which invasive vertebrate species impact their native congeners.

Acknowledgments. I am deeply indebted to the graduate students and colleagues, collectively known as the Tennessee Green Anole Out-Group (to distinguish it from those whose studies of anoles are confined to the lab), who have contributed to this research. These include Pam Brown, Todd Campbell, Glenn Gerber, and Todd Vincent. If and when this model is formally published, all will co-author the paper. We have also had the assistance of a small army of undergraduate field assistants and their efforts have been greatly appreciated. In addition, Justin Congdon, Bob Gatten, Jim Jenkins, Luke Hasty, Tom Jenssen, Dan MacDonald, Ed Michaud, Jim Minesky, Dee Dee Truett, Gerry Vaughan, Julia Wade, and Mark Wilson have all contributed to our better understanding of the biology of green anoles. Our research would have been impossible without the cooperation of the Florida Game and Fresh Water Fish Commission, Division of Forestry of the Florida Department of Agriculture and Consumer Services, and Merritt Island National Wildlife Refuge, and the cooperation and logistical support of the personnel of the Division of Recreation and Parks of the Florida Department of Environmental Protection, Canaveral National Seashore, the Department of Biology of the University of Central Florida, and the Kennedy Space Center. Finally, We are indebted to the academic herpetologists of Florida for generally ignoring this area of investigation, leaving it open to carpet-baggers from Tennessee.

Literature Cited:

Brown, P. R. 1988. Intraspecific and interspecific behavioral interactions in adult male *Anolis* sagrei and gray-throated *Anolis carolinensis* (Sauria: Iguanidae). Unpubl. M.S. Thesis, Univ. Tennessee, Knoxville.

Brown, P. R. and A. C. Echternacht. 1991. Interspecific behavioral interaction of adult male *Anolis sagrei* and gray-throated *Anolis carolinensis* (Sauria: Iguanidae): A preliminary field study. Anolis Newsletter IV, pp. 21-30.

Campbell, T. S. 1996. Northern range expansion of the brown anole (*Anolis sagrei*) in Florida and Georgia. Herp. Rev., 27:155-157.

Campbell, T. S. and G. P. Gerber. 1996. *Anolis sagrei*: Saurophagy. Herp. Rev., 27:106.

Gerber, G. P. 1991. *Anolis sagrei* and *Anolis carolinensis* in Florida: evidence for interspecific predation. *Anolis* Newsletter IV, pp. 49-53.

Godley, J. S., F. E. Lohrer, J. N. Layne and J. Rossi. 1981. Distributional status of an introduced lizard in Florida: *Anolis sagrei*. Herp. Rev. 12:84-86.

King, K., D. Cavazos and F. W. Judd. 1987. *Anolis sagrei* (Sauria: Iguanidae) established in southern Texas. Texas J. Sci. 39:289-290.

Krusling, P. J., J. W. Ferner and J. Patterson. 1995. Geographic distribution: *Anolis sagrei*. Herp. Rev., 26:108.

Lee, J. C. 1985. *Anolis sagrei* in Florida: phenetics of a colonizing species I. Meristic characters. Copeia 1985:182-194.

Platt, S. G. and L. W. Fontenot. 1994. Geographic distribution: *Anolis sagrei*. Herp. Rev. 25:33.

Schwartz, A. and R. W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. Univ. Of Florida Press, Gainesville.

Thomas, R. A., P. J. Thomas, J. O. Coulson and T. Coulson. 1990. Geographic distribution: *Anolis sagrei sagrei*. Herp. Rev. 21:22.

Tokarz, R. R. and J. W. Beck, Jr. 1987. Behavior of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*: an experimental test for behavioral interference. Anim. Behav. 35:722-734.

Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quart. Rev. Biol. 44:345-389.

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A Review of Intraguild Predation and Cannibalism in *Anolis*

Introduction

Previously, I documented asymmetries in the propensity for intraguild predation between introduced *Anolis sagrei* and the native anoles of Florida and Grand Cayman Island, *A. carolinensis* and *A. conspersus*, respectively (Gerber, 1991; Gerber and Echternacht, in review). I found that adult male *A. sagrei* were likely to eat *A. carolinensis* and *A. conspersus* hatchlings, whereas adult male *A. carolinensis* and *A. conspersus* were not likely to eat *A. sagrei* hatchlings. Further, adults of all three species were unlikely to eat conspecific hatchlings. The propensity for intraguild predation in Florida and Grand Cayman is thus highly asymmetrical, favoring introduced populations of *A. sagrei*. Consequently, intraguild predation may be an important interaction in these systems.

Because of the low frequency of cannibalism exhibited by each of the anoles in my previous studies, and the relatively high frequency of intraguild predation exhibited by *A. sagrei,* I became curious about the occurrence of intraguild predation and cannibalism in other anoles. Do other anoles avoid cannibalism, as *A. sagrei* (and possibly *A. carolinensis* and *A. conspersus*) appear to do? Is intraguild predation asymmetrical in other anole assemblages, as it appears to be in Florida and Grand Cayman? In an attempt to answer these questions and put the results of my previous studies in context, I reviewed the literature for accounts of intraguild predation and cannibalism in *Anolis*. I included accounts of intraguild predation and cannibalism from field and captive settings resulting from direct observation, analysis of stomach contents, or manipulative experiments.

Intraguild Predation

The results of my review of intraguild predation in *Anolis* are summarized in Table 1. Although most accounts of intraguild predation between anoles were anecdotal, and therefore provided little information on the frequency of intraguild predation between specific species, taken together the accounts suggest that predatory interactions among anoles are relatively common. Approximately half of the accounts involve adult males and females of large species (> 90 mm max. SVL) preying upon adults, as far as is known, of medium-sized (60 to 90 mm max. SVL) and small (< 60 mm max. SVL) species. Adult males of medium-sized species preying upon adults and juveniles of small species and juveniles of other medium-sized species, make up most of the remaining accounts. Only one account was found in which a small species was the predator: it involved an adult male *A. opalinus* eating a juvenile of a medium-sized species (*A. valencienni*). Therefore, unlike intraguild predation in many taxonomic guilds (e.g., fish), in which adults of smaller species frequently prey upon juveniles of larger species (Werner and Gilliam, 1984; Werner, 1986; Polis et al., 1989), intraguild predation among anoles (and probably other lizards) is more often hierarchical. This is probably because, among anoles, juveniles of larger species are often too large to be handled by adults of smaller species. Therefore, although cross-predation of juveniles may occur among similarly-sized species, it appears that intraguild predation is usually asymmetric for sympatric anoles differing markedly in adult body size. This may have important ecological and evolutionary consequences.

For example, on Grenada, a small island with two widely sympatric anoles differing considerably in body size, Stamps (1983a) has shown that juveniles of the smaller *A. aeneus* are susceptible to predation by adult males and females of the larger *A. richardi*, whereas juvenile *A. richardi* (due to their size) are not at risk from adult *A. aeneus*. Furthermore, the threat of predation from adult *A. richardi* (and to a lesser degree adult male conspecifics) appears to drive intense intraspecific competition among juvenile *A. aeneus* for territories in small forest clearings not inhabited by adult *A. richardi* or adult conspecifics (Stamps, 1983b). If space in forest clearings is limiting, territorial competition among juvenile *A. aeneus*, in combination with intraguild predation from adult *A. richardi*, could place a bottleneck on adult recruitment.

On St. Martin, another small island with two species of anole differing in body size (but less markedly than those on Grenada), Roughgarden et al. (1983) reported adult males of the larger *A. gingivinus* capturing and eat juveniles and adults of the smaller *A. wattsi*. Roughgarden et al. suggested that adult *A. wattsi* are capable of eating juvenile *A. gingivinus* as well, but did not report any reciprocal predation. Furthermore, Roughgarden et al. speculate that the association of *A. wattsi* with rock piles may result from the avoidance of *A. gingivinus*, and other predators, rather than microclimatic considerations.

On Hispaniola, Fitch and Henderson (1987) found that all size classes of *A. bahorucoensis*, a small anole of the forest understory, are vulnerable to predation from adult male *A. coelestinus* and *A. cybotes*, medium-sized sympatric congeners inhabiting forest trees. When juvenile and adult *A. bahorucoensis* were tethered and presented to free-ranging adult male *A. coelestinus* and *A. cybotes*, they were attacked and eaten. Fitch and Henderson concluded that *A. bahorucoensis* is constantly in danger of attack from larger anoles and suggested that the rudimentary development of the dewlap and the small amplitude of movement involved in social displays in *A. bahorucoensis* were adaptations to reduce conspicuousness.

From these examples, it seems clear that intraguild predation by larger anoles is important in determining the resource use and population dynamics of smaller sympatric congeners. Thus, intraguild predation should be considered along with other factors, such as competition and physiological and morphological constraints, when interpreting patterns of resource use and abundance (see Toft, 1985, for a well balanced review of resource partitioning in reptiles and amphibians).

Finally, among the medium-sized anoles for which I found accounts of intraguild predation, the sex of the predator, when known, was always male. These same species were also invariably polygynous and sexually dimorphic with males being the larger and presumably more aggressive sex. Therefore, adult males of medium-sized polygynous species with marked sexual dimorphism appear to represent a greater potential threat to smaller anoles than do adult females. However, among the large species for which I found accounts of intraguild predation, both male and female predators were common (although sex was not given in many accounts). Thus, the threat of predation from large species for smaller anoles may be particularly acute.

Cannibalism Versus Intraguild Predation

The results of my review of cannibalism in *Anolis* are summarized in Table 2. In comparison to the review of intraguild predation, accounts of cannibalism were only about half as common. Also, whereas the accounts of intraguild predation that I found were approximately equally split between large and medium-sized species, all of the anoles for which I found accounts of cannibalism were medium-sized species. If absence of accounts of cannibalism for large anoles reflects the fact that smaller species have been studied more extensively, then the occurrence of intraguild predation by large species may be substantially greater than indicated here. My review suggests that large species are important intraguild predators that routinely avoid cannibalism. Strong evidence of this exists for *A. cuvieri*, largest of the 11 species of anole native to Puerto Rico (Rand and Andrews, 1975). Rand and Andrews found that each of five breeding adult *A. cuvieri* (three females and two males) maintained in a large outdoor enclosure in Panama ignored juvenile conspecifics presented on a tether, but readily accepted, when similarly presented, both adult *A. limifrons* (a small Panamanian anole), which are the same size as juvenile conspecifics, and large insects. They also found small congeners, but no conspecifics, in three of 14 museum specimens collected in Puerto Rico that contained food items in the stomach. Rand and Andrews suggested that larger species are more likely to regularly include smaller anoles in their diet and because of this are also more likely to have evolved mechanisms for avoiding cannibalism of juveniles. My reviews of intraguild predation and cannibalism in *Anolis* support this view.

For those anoles for which I found accounts of cannibalism (all medium-sized species), the sex of the predator, when know, was almost always male. In fact, only two instances of cannibalism by females were found (*A. cristatellus* and *A. whitemani*). One of these (*A. whitemani*), which involved the tail of a conspecific found in an analysis of stomach contents, is questionable because lizards are known to eat the shed tails of conspecifics and even their own shed tails (Grant, 1957; Clark, 1971; Vitt et al., 1977; Jenssen and Marcellini, 1986). In addition, results of the only manipulative experiment I found that systematically tested male and female adults of a medium-sized species for cannibalistic tendencies also found adult males to be more cannibalistic than adult females (Stamps, 1983a). Stamps presented tethered conspecific juveniles to 10 adult female and 10 adult male *A. aeneus* in the field. Juveniles were ignored by all 10 adult females, whereas three adult males attempted cannibalism and four others courted juveniles. Thus, adult males of medium-sized polygynous anoles, possibly because of their larger size and increased aggressiveness compared to females, appear to be more prone to cannibalism, just as they are to intraguild predation.

Unlike my review of intraguild predation among anoles in which adult-adult interactions were common, almost all of the accounts of cannibalism in anoles are of adults, or occasionally subadults, consuming juveniles. This is to be expected, however, given the costs associated with attacking larger prey (increased handling time and risk of injury) and morphologically imposed limits as to the size of prey which can actually be swallowed. Adult-juvenile interactions dominate accounts of cannibalism in other lizards as well (Polis and Myers, 1985; Mitchell, 1986). Nonetheless, I found an account of an adult male *A. valencienni* eating a subadult male conspecific and another in which an adult male *A. carolinensis* killed, but could not swallow, a subadult male conspecific. In the latter case, the subadult male (42 mm SVL) was not attacked and killed outright, but only after the adult male (50 mm SVL) made repeated attempts to copulate with it (Jenssen and Hovde, 1993). This is noteworthy given the extremely low frequency of cannibalism of juveniles by adult male *A. carolinensis* in my previous study (1 out of 47: Gerber, 1991). Combined with the observations by Stamps (1983a) for *A. aeneus*, in which some adult males attempted to court juveniles, whereas others attempted to eat them, these observations suggest that immature conspecifics represent an ambiguous stimulus for many adult male anoles. Thus, taken together, the accounts of cannibalism and intraguild predation for medium-sized anoles suggest that sexual differences in these behaviors stem from sexual differences in social roles and size associated with polygyny.

Finally, even among medium-sized anoles, cannibalistic tendencies appear to vary significantly. For example, Fitch and Henderson (1987), working in Hispaniola, found that all adult male *A. cybotes* presented with tethered juvenile conspecifics attacked and ate them. This is in stark contrast to the near lack of cannibalism exhibited by the adult male anoles in my previous studies (Gerber, 1991; Gerber and Echternacht, in review). Thus, interspecific differences in cannibalism (and intraguild predation) are not simply the result of size differences between species, but probably relate to different selection pressures which may, in general, be more similar for anoles of similar size.

In conclusion, my reviews of cannibalism and intraguild predation suggest that such interactions are important in the ecology and evolution of anoles. However, much obviously remains unknown, such as whether there is a strong phylogenetic component to eating other anoles or whether intraguild predation is an important factor (along with competition) in the evolution or maintenance of interspecific size differences within *Anolis* guilds. It is my hope that this review will provide an impetus for studies which will eventually provide a better understanding of the role that cannibalism and intraguild predation play in the dynamics and structuring of *Anolis*, and other lizard, guilds.

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One Last Thing

Predation is notoriously difficult to document. As such, it is not surprising that most accounts of intraguild predation and cannibalism in *Anolis* are anecdotal. Further, because they're anecdotal, these observations often go unpublished or get buried deep within papers on other topics. Accessing such data is thus an arduous task, at best. Therefore, I issue the following plea: if you are aware or in possession of additional accounts of intraguild predation or cannibalism in *Anolis,* published or not, PLEASE bring these to my attention. I am preparing an expanded review for publication and wish to be as thorough and up-to-date as possible.

Literature Cited

Brach, V. 1976. Habits and food of *Anolis equestris* in Florida. Copeia 1976:187-189.

Campbell, H. W. 1973. Ecological observations on *Anolis lionotus* and *Anolis poecilopus* (Reptilia, Sauria) in Panama. Amer. Mus. Nat. Hist., Novitates 2516:1-29.

Campbell, T. S., and G. P. Gerber. 1996. *Anolis sagrei* (brown anole). Saurophagy. Herpetol. Review 27:200.

Carr, D. K., R. Powell, and J. S. Parmerlee. 1989. *Anolis whitemani whitemani*. Food habits. Herpetol. Review 20:49-53.

Clark, D. R. 1971. The strategy of tail autonomy in the ground skink, *Lygosoma laterale*. J. Exp. Zool. 176:295-302.

Cochran, P. A. 1989. *Anolis sagrei* (brown anole). Behavior. Herpetol. Review 20:70.

Collette, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. Harvard Mus. Comp. Zool., Bull. 125:136-162.

Dalrymple, G. H. 1980. Comments on the density and diet of a giant anole *Anolis equestris*. J. Herpetol. 14:412-415.

Dial, R., and J. Roughgarden. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. Ecology 76:1821-1834.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Univ. Kansas Mus. Nat. Hist., Misc. Publ. No. 65.

Fitch, H. S. 1975. Sympatry and interrelationships in Costa Rican anoles. Univ. Kansas Mus. Nat. Hist., Occasional Papers No. 40.

Fitch, H. S., and R. W. Henderson. 1987. Ecological and ethological parameters in *Anolis bahorucoensis*, a species having rudimentary development of the dewlap. Amphibia-Reptilia 8:69-80.

Fitch, H. S., R. W. Henderson, and H. Guarisco. 1989. Aspects of the ecology of an introduced anole: *Anolis cristatellus* in the Dominican Republic. Amphibia-Reptilia 10:307-320.

Floyd, H. B., and T. A. Jenssen. 1983. Food habits of the Jamaican lizard *Anolis opalinus*: resource partitioning and seasonal effects examined. Copeia 1983:319-331.

Gerber, G. P. 1991. *Anolis sagrei* and *Anolis carolinensis* in Florida: evidence for interspecific predation. *Anolis* Newsletter IV:49-53.

Gerber, G. P., and A. C. Echternacht. In review. Predatory interactions between an introduced *Anolis* lizard and native congeners in Florida and Grand Cayman Island: evidence for asymmetrical intraguild predation. Oecologia.

Goldwasser, L., and J. Roughgarden. 1993. Construction and analysis of a large Caribbean food web. Ecology 74:1216-1233.

Gorman, G. C. 1968. The relationships of *Anolis* of the *roquet* species group (Sauria: Iguanidae) - III. Comparative study of display behavior. Harvard Mus. Comp. Zool., Breviora 284:1-34.

Grant, C. 1957. Autophagy in *Eumeces*. Herpetologica 13:156.

Hicks, R. A., and R. L. Trivers. 1983. The social behavior of *Anolis valencienni*, p. 570-595. *In*: Advances in herpetology and evolutionary biology: essays in honor of Earnest E. Williams. A. G. J. Rhodin and K. Miyata (eds.). Harvard Univ. Mus. Comp. Zool., Cambridge (MA).

Jenssen, T. A., and D. L. Marcellini. 1986. *Leiocephalus schreibersi* (curly-tailed lizard): Tail autonomy. Herpetol. Review 17:89.

Jenssen, T. A., and K. A. Hovde. 1993. *Anolis carolinensis* (green anole). Social pathology. Herpetol. Review 24:58-59.

Lando, R. V., and E. E. Williams. 1969. Notes on the herpetology of the U.S. Naval Base at Guantanamo Bay, Cuba. Stud. Fauna Curaçao and Carib. Is. 31:159-201.

Losos, J. B., R. M. Andrews, O. J. Sexton, and A. L. Schuler. 1991. Behavior, ecology, and locomotor performance of the giant anole, *Anolis frenatus*. Carib. J. Sci. 27:173-179.

Mitchell, J. C. 1986. Cannibalism in reptiles: a worldwide review. SSAR Herpetol. Circular No. 15.

Perez-Rivera, R. A. 1985. Nota sobre el habitat, los habitos alimentarios y los depredadores del lagarto *Anolis cuvieri* (Lacertilia: Iguanidae) de Puerto Rico. Carb. J. Sci. 21:101-103.

Polis, G. A., and C. A. Myers. 1985. A survey of intraspecific predation among reptiles and amphibians. J. Herpetol. 19:99-107.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev. Ecol. Syst. 20:297-330.

Powell, R., and J. S. Parmerlee, Jr. 1991. *Anolis chlorocyanus* (Hispaniolan green anole). Behavior. Herpetol. Review 22:130.

Rand, A. S., 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc. U.S. Nat. Mus. 122:1-79.

Rand, A. S., and R. Andrews. 1975. Adult color dimorphism and juvenile pattern in *Anolis cuvieri*. J. Herpetol. 9:257-260.

Reagan, D. P. 1992. Congeneric species distribution and abundance in a three-dimensional habitat: the rain forest anoles of Puerto Rico. Copeia 1992:392-403.

Roughgarden, J., J. Rummel, and S. Pacala. 1983. Experimental evidence of strong present-day competition between the *Anolis* populations of the Anguilla Bank - a preliminary report, p. 499-506. *In*: Advances in herpetology and evolutionary biology: essays in honor of Ernest E. Williams. A. G. J. Rhodin and K. Miyata (eds.). Harvard Univ. Mus. Comp. Zool., Cambridge (MA).

Schoener, T. W. 1967. The ecological significance of sexual size dimorphism in size in the lizard *Anolis conspersus*. Science 155:474-477.

Schoener, T. W., and G. C. Gorman. 1968. Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. Ecology 49:819-830.

Schwartz, A., and R. W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. Univ. Florida Press, Gainesville.

Simmonds, F. J. 1958. The effect of lizards on the biological control of scale insects in Bermuda. Bull. Ento. Research 49:601-612.

Stamps, J. A. 1983a. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behav. Ecol. Sociobiol. 12:19-33.

Stamps, J. A. 1983b. Territoriality and the defense of predator-refuges in juvenile lizards. Anim. Behav. 31:857-870.

Taylor, E. H. 1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull. 38:3-322.

Toft, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1-21.

Vitt, L. J., J. D. Congdon, and N. A. Dickson. 1977. Adaptive strategies and energetics of tail autonomy in lizards. Ecology 58:326-337.

Werner, E. E. 1986. Species interactions in freshwater fish communities, p. 344-358. *In*: Community Ecology. J. Diamond, and T. Case (eds.). Harper and Row Publishers, New York.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15:393-425.

Wolcott, G. N. 1923. The food of Puerto Rican lizards. J. Dept. Agriculture Puerto Rico. 7:5-37.

Table 1. Documented accounts of intraguild predation in *Anolis*.

Predator		Prey		Age Class & Sex[2]						
Species	Size[1]	Species	Size[1]	Predator	→	Prey	Frequency[3]		Location[4]	Source
biporcatus	L	*lemurinus*	M	**A**	→	**A**	1	GUT	Costa Rica	Taylor, 1956
capito	L	*polylepis*	S	A	→	A☝	1	GUT	Costa Rica	Fitch, 1975
carolinensis	M	*sagrei*	M	A☝	→	J	4/47	EXP	captivity	Gerber & Echternacht, in review
		sagrei	M	A☜	→	J	3	GUT	Florida	T. S. Campbell, personal comm.
chlorocyanus	M	*cristatellus*	M	A☝	→	A☜	1	OBS[5]	Hispaniola	Powell & Parmerlee, 1991
chrysolepis	M	*trachyderma*	S	A?	→	tail	1/25	GUT	Equador	Duellman, 1978
coelestinus	M	*bahorucoensis*	S	A☝	→	J	> 1	EXP	Hispaniola	Fitch & Henderson, 1987
		bahorucoensis	S	A☝	→	A	> 1	EXP	Hispaniola	Fitch & Henderson, 1987
conspersus	M	*sagrei*	M	A☝	→	J	1/20	EXP	captivity	Gerber & Echternacht, in review
cristatellus	M	*cybotes*	M	A	→	J	≥ 1	OBS	Hispaniola (I)	Schwartz & Henderson, 1991
		disticus	S	A☝	→	SA	1	EXP[6]	Hispaniola (I)	Fitch et al., 1989
cuvieri	L	*krugi*[7]	S	A?	→	A?	3/14	GUT	Puerto Rico	Rand & Andrews, 1975
		limifrons	S	A☝	→	A	2/2	EXP	captivity	Rand & Andrews, 1975
		limifrons	S	A☜	→	A	3/3	EXP	captivity	Rand & Andrews, 1975
		pulchellus	S	A☝	→	A☝	1	OBS	Puerto Rico	Perez-Rivera, 1985
		stratulus[8]	S	A?	→	A?	1	OBS	Puerto Rico	Dial & Roughgarden, 1995
cybotes	M	*bahorucoensis*	S	A☝	→	J	> 1	EXP	Hispaniola	Fitch & Henderson, 1987
		bahorucoensis	S	A☝	→	A	> 1	EXP	Hispaniola	Fitch & Henderson, 1987
		coelestinus	M	A☝	→	J	> 1	EXP	Hispaniola	Fitch & Henderson, 1987
		distichus	S	A☝	→	A	> 1	EXP	Hispaniola	T. A. Jenssen, personal comm.
equestris	L	*Anolis sp.*	S-M?	A?	→	A?	> 1	OBS	Cuba	Collete, 1961
		Anolis sp.	S-M?	A?	→	A?	> 1	OBS	Florida (I)	Brach, 1976
		carolinensis	M	A?	→	A?	> 1	OBS	captivity	Dalrymple, 1980
		sagrei	M	A?	→	A?	> 1	OBS	captivity	Dalrymple, 1980
evermanni	M	*stratulus*	S	A?	→	A?	≥ 1	OBS	Puerto Rico	Reagan, 1992

Table 1. (continued)

Predator		Prey		Age Class & Sex[2]						
Species	Size[1]	Species	Size[1]	Predator	→	Prey	Frequency[3]		Location[4]	Source
frenatus	L	*limifrons*	S	A☜	→	A☜	1	OBS	Panama	R. Ballinger (in Losos et al., 1991)
		lemurinus	M	A	→	A	1	OBS	captivity	R. Ballinger (in Losos et al., 1991)
garmani	L	*lineatopus*	M	A?	→	A☝	≥ 1	GUT	Jamaica	Schwartz & Henderson, 1991
gingivinus	M	*wattsi*	S	A☝	→	J	≥ 1	OBS	St. Martin	Roughgarden et al., 1983
		wattsi	S	A☝	→	A	≥ 1	OBS	St. Martin	Roughgarden et al., 1983
		wattsi	S	A?	→	A?	1	GUT	St. Martin	Goldwasser & Roughgarden, 1993
grahami	M	*lineatopus*	M	A	→	J	≥ 1	OBS	Jamaica	Rand, 1967
		valencienni	M	A☝	→	J	2	OBS	Jamaica	Hicks &Trivers, 1983
griseus	L	*trinitatis*	M	A☝	→	A☝	1	EXP[9]	St. Vincent	Gorman, 1968
gundlachi	M	*stratulus*	S	A?	→	A?	≥ 1	OBS	Puerto Rico	Reagan, 1992
lineatopus	M	*valencienni*	M	A☝	→	J	1	OBS	Jamaica	Hicks &Trivers, 1983
opalinus	S	*valencienni*	M	A☝	→	J	1/100	GUT	Jamaica	Floyd & Jenssen, 1983
richardi	L	*aeneus*	M	A☜	→	J	3	OBS	Grenada	Stamps, 1983a
		aeneus	M	A☜	→	J	≥ 1	GUT[10]	Grenada	Schoener & Gorman, 1968
		aeneus	M	A☝	→	J	1	OBS	Grenada	Stamps, 1983a
		aeneus	M	A☝	→	SA	1	OBS	Grenada	Stamps, 1983a
sagrei	M	*carolinensis*	M	A☝	→	J	1/15	GUT	Florida (I)	Campbell & Gerber, 1996
		carolinensis	M	A☝	→	J	1	OBS	Florida (I)	Campbell & Gerber, 1996
		carolinensis	M	A☝	→	J	23/47	EXP	captivity	Gerber & Echternacht, in rev.
		conspersus	M	A☝	→	J	10/20	EXP	captivity	Gerber & Echternacht, in rev.
smallwoodi	L	*Anolis sp.*	S-M?	A?	→	A?	> 1	OBS	captivity	Lando & Williams, 1969
smaragdinus	M	*sagrei*	M	A☝	→	J☜	1	OBS	Bahamas	J. B. Losos, personal comm.
valencienni	M	*lineatopus*	M	A?	→	J?	≥ 1	?	Jamaica	Schwartz & Henderson, 1991
vermiculatus	L	*Anolis sp.*	S-M?	A☜	→	A?	1	GUT	Cuba	Schwartz & Henderson, 1991

Footnotes

[1] L= large (max. SVL > 90 mm); M = medium (max. SVL 60 to 90 mm); S = small (max. SVL < 60 mm); ? = presumed max. size

[2] A = adult; SA = subadult; J = juvenile; ? = presumed age class

[3] OBS = observation; GUT = stomach contents; EXP = manipulative experiment

[4] (I) = predator is an introduced species

[5] Unsuccessful predatory attack; prey is an introduced species

[6] Tethered prey was attacked, chewed, and killed, but not swallowed

[7] One prey item identified as *A. krugi*; others only identified as non-conspecific

[8] Most likely *A. stratulus* (possibly *A. evermanni,* though)

[9] Decapitated head of prey was attacked and eaten during an experiment on species recognition

[10] Uncertain, but likely, prey species identification (possibly conspecific though)

Table 2. Documented accounts of cannibalism in *Anolis*.

		Age Class & Sex[2]						
Species	Size[1]	Predator	→	Prey	Frequeny[3]		Location[4]	Source
aeneus	M	A☝	→	J	1	OBS	Grenada	Stamps, 1983a
		A☝	→	J	3/10	EXP	Grenada	Stamps, 1983a
carolinensis	M	A☝	→	J	1/47	EXP	captivity	Gerber & Echternacht, in review
		A☝	→	SA☝	1	OBS[5]	North Carolina	Jenssen & Hovde, 1993
conspersus	M	A☝	→	J	3/20	EXP	captivity	Gerber & Echternacht, in review
		SA☝	→	J?	1/166	GUT	Grand Cayman	Schoener, 1967
cristatellus	M	A☝	→	J	1/31	GUT	Hispaniola (I)	Fitch et al., 1989
		A☜	→	J	1/35	GUT	Hispaniola (I)	Fitch et al., 1989
		A☝	→	J	1	EXP	Hispaniola (I)	Fitch et al., 1989
		A	→	J?	3/100	GUT[6]	Puerto Rico	Wolcott, 1923
cybotes	M	A☝	→	J	> 1	EXP	Hispaniola	Fitch & Henderson, 1987
evermanni	M	A?	→	J	≥ 1	GUT	Puerto Rico	Schwartz & Henderson, 1991

Table 2. (continued)

		Age Class & Sex[2]						
Species	Size[1]	Predator	→	Prey	Frequeny[3]		Location[4]	Source
grahami	M	A?	→	J?	2 + tail/176	GUT[6]	Bermuda (I)	Simmonds, 1958
lineatopus	M	A☝	→	J	1	OBS	Jamaica	Rand, 1967
		A	→	J	1	GUT	Jamaica	Rand, 1967
poecilopus	M	A☝	→	J	1	GUT	Panama	Campbell, 1973
roquet	M	A☝	→	J?	≥ 1	GUT	Martinique	Schoener &Gorman, 1968
		SA☝	→	J?	≥ 1	GUT	Martinique	Schoener &Gorman, 1968
sagrei	M	A☝	→	J	1	OBS	captivity	Cochran, 1989
		A☝	→	J	8/67	EXP	captivity	Gerber & Echternacht, in review
valencienni	M	A☝	→	SA☝	1	OBS	Jamaica	Hicks & Trivers, 1983
		SA☝	→	J	1	OBS	Jamaica	Hicks & Trivers, 1983
whitemani	M	A☜	→	tail	1/10	GUT[6]	Hispaniola	Carr et al., 1989

[1] L = large (max. SVL > 90 mm); M = medium (max. SVL 60 to 90 mm); S = small (max. SVL < 60 mm)
[2] A = adult; SA = subadult; J = juvenile; ? = presumed age class
[3] OBS = observation; GUT = stomach contents; EXP = manipulative experiment
[4] (I) = introduced species
[5] Prey was attacked and killed after the predator attempted to copulate with it, but attempts to swallow the smaller animal failed
[6] Uncertain prey species identification, but presumably conspecific

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The Effects of Agriculture and Hurricane Related Disturbance on Anole Communities

Throughout the West Indies, agriculture dominates the landscape and nearly all native forests have been replaced by agricultural habitats. Though it seems intuitive that this transition has had a negative impact on biodiversity, the impact of agriculture on West Indian lizards has never been studied in detail. In 1996, we began a study in the Los Haitises region of the Dominican Republic with the goal of determining the specific effects of agriculture on lizard communities. Detailed results from this study will be reported elsewhere (Glor et al., in prep.), but this note will briefly summarize the results we obtained for anoles in particular.

The Los Haitises region is located on the southern edge of Samana Bay in the northeastern Dominican Republic and has an interesting history of human disturbance. A part of the region was officially afforded protection with the establishment of Los Haitises National Park in 1976. However, extensive use of the park for small scale agriculture continued until 1993, at which time the Dominican government abruptly relocated all of the park's residents to the surrounding region. As a result, the park was left as a patchwork of different agricultural habitats ranging from clearcut pasture to the relatively undisturbed peaks of the region's haystack hills or *mogotes*. In the summer of 1996, we established 24 study plots in the park representing six different habitats. Additionally, we established nine plots outside the park in three different kinds of active agricultural habitats. Within each of these plots, we sampled diversity both with visual transects and mouse glue trap sampling grids. The glue traps proved to be a highly effective means of capturing anoles (Glor et al., in review). All sampling was conducted during three field trips in winter 96/97, summer 97, and winter 97/98 for a total of approximately 10 weeks of sampling.

Over the course of our sampling, 2,259 anoles representing five species were observed or trapped. These anoles dominated the lizard fauna and accounted for 89.7% of all lizards trapped and 98.7% of the lizards observed in transects. Though habitat was found to have a significant effect on anole abundance, there were no significant differences between anole abundance in the park versus abundance in the active agricultural plots. Anoles were by far the most abundant in active cacao plantations and were virtually absent from active pastures.

Anolis distichus, a trunk species, was dominant in all habitats with the exception of active oil palm plantations, where *A. cybotes* was dominant. *Anolis cybotes*, a trunk-ground species, was the second most common anole. *Anolis cybotes* had significantly higher relative abundance in the active agricultural plots relative to the park plots. The grass anole, *A. semilineatus*, was present in all habitats inside the park, but was completely absent from the active agricultural plots.

Not surprisingly, our results suggest that the abundance of anole species depends on the availability of appropriate structural microhabitat. For example, *A. semilineatus* was likely absent from active agricultural plots because undergrowth is actively weeded in these areas. Because of their distinct microhabitat specializations, anoles may serve as ideal indicator species not only for overall habitat quality, but also for the quality of particular microhabitats, such as undergrowth. Our results also suggest that anole communities outside the park are drastically different from those inside the park and that Los Haitises National Park is playing an important role in preserving the anole diversity of the region.

In the winter of 98/99, we returned to Los Haitises to survey anole populations in the same study plots following hurricane Georges. A previous study of anole populations indicated significant shifts in anole community structure following hurricane related disturbance in Puerto Rico (Reagan 1991). Reagan (1991) used data obtained during vertical and horizontal transects conducted before and after hurricane Hugo to conclude that crown dwelling species increased in relative abundance at ground level while trunk-ground species decreased in relative abundance. Though our results are not as thorough as those obtained by Reagan (1991), they do support his main conclusions. *Anolis chlorocyanus*, a trunk-crown species, increased in relative abundance in seven of eleven plots in which it was sampled, while *A. cybotes* decreased in relative abundance in seven out of the nine plots in which it was sampled.

Literature Cited

Glor, R.E., A.S. Flecker, M.F. Benard, and A. Power. In Prep. Lizard diversity and agricultural disturbance in a Caribbean forest landscape.

Glor, R.E., T.M. Townsend, M.F. Benard, and A.S. Flecker. In Review. The use of glue traps for sampling lizard diversity in the West Indies. Herpetological Review.

Reagan, D.P. 1991. The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rain forest. Biotropica 23:468-474.

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Phylogenetic Systematics of *cybotes* Group Anoles from Hispaniola

Many interesting aspects of anole evolution have yet to be addressed from a phylogenetic perspective. In particular, evolution within clades of particular ecomorphs has rarely been studied, despite the fact that these clades may be both species rich (up to 14 species) and ecologically diverse. A study of evolution within these clades may yield important lessons concerning habitat specialization, population structure, and speciation in anoles.

With eight recognized species, the *cybotes* group of trunk-ground anoles is the third largest clade of West Indian anoles comprised of a single ecomorph (Burnell and Hedges 1991, Jackman 1999). Restricted to Hispaniola, many members of the group are specialized for a particular habitat or microclimatic conditions (Schwartz and Henderson 1991). *Anolis cybotes* is the most widespread and can tolerate a range of ecological conditions, though it is generally considered mesophilic (Schwartz and Henderson 1991). *Anolis whitemani* replaces *A. cybotes* in xeric regions in the Cul de Sac plain as well as the northwest coast of Hispaniola (Williams 1963). Two members of the group are found primarily in upland pine forests, with *Anolis armouri* occurring in the Sierra de Baoruco and into Haiti and *A. shrevei* occurring in the Cordillera Central. *Anolis longitibialis* and *A. strahmi* are rock and cliff specialists found on the Barahona peninsula (Schwartz 1979). *Anolis marcanoi* is virtually ecologically indistinguishable from *A. cybotes* and is found on the southern slopes of the Cordillera Central (Williams 1975). *Anolis haetianus* is an ecologically poorly known species from the western edge of Tiburon Peninsula in Haiti.

Despite considerable taxonomic interest in the group (Williams 1963, Williams 1975, Schwartz 1979, Webster 1975, Schwartz and Henderson 1982, Schwartz 1989), evolutionary relationships within the group, and even the species status of many of its members, have always been unclear. One major challenge has been that few discrete or quantifiable morphological characters define most members of the *cybotes* group. However, most species do appear to be well defined on the basis of behavior, ecology or dewlap color. These distinctions, combined with the lack of suitable morphological characters, make this group ideal for a molecular phlyogenetic analysis. Working in collaboration with Dr. Allan Larson, our goal is to construct a phylogeny for the *cybotes* group based on mtDNA sequence coding for ND1, ND2, CO1 and eight tRNAs. To date, we have sequenced approximately 1,500 bp from seven of the eight species and up to six representative populations of some widespread species (i.e. *A. cybotes*, *A. whitemani*).

Though the results at this point are very preliminary, a number of well supported relationships have begun to emerge. First of all, *A. marcanoi* is sister to all other cybotoid anoles (decay index=12, bootstrap=100). Within the clade that includes all other members of the *cybotes* group, the next split occurs between *strahmi*/*longitibialis* and the other species. The sister species relationship between *A. strahmi* and *A. longitibialis* is strongly supported (decay index=12, bootstrap=100), but the other main clade, which contains *A. armouri*, *A. cybotes*, *A. whitemani*, and *A. haetianus*, is presently poorly supported (decay index=4, bootstrap=70).

Within the *armouri/cybotes/haetianus/whitemani* clade, *A. whitemani* appears to be paraphyletic. Representatives from three southern populations form a well supported clade (decay index=62, bootstrap=100), whereas representatives of three populations from northwestern Dominican Republic are falling within a well supported clade which also includes two populations of *A. cybotes* from the same region (decay index=21, bootstrap=100). A represenative of *A. whitemani* from a population in northwestern Haiti also appears to be distinct, though its relationships to other cybotoid anoles are not yet clear.

Anolis armouri appears to be the sister species to the northwestern *cybotes/whitemani* populations (decay index=5, bootstrap=90). Representatives from two insular populations *of A. cybotes* from Isla Soana and Isla Catalina are well supported as sister taxa (decay index=46, bootstrap=100), but the sister group to this clade is not yet well supported. Additionally, *A. haetianus* appears to be sister to a clade containing *armouri*, *cybotes*, and northern *whitemani*, but this relationship is not well supported (decay index=1, bootstrap=63).

Though several important branches in the group are not yet well supported, we feel that continued study of this group will improve the resolution of these relationships. In particular, we plan to add several more taxa to our analysis, including *A. shrevei* and a number of additional mainland populations of *A. cybotes and A. whitemani*.

The fact that a number of well-supported clades that make sense in term of biogeography have already been uncovered suggests that this group has considerable potential for a detailed study of within ecomorph evolution.

Literature Cited

Burnell, K.L. and S. B. Hedges. 1991. Relationships of West Indian *Anolis* (Sauria: Iguanidae): An approach using slow-evolving protein loci. Caribbean Journal of Science 26:7-30.

Jackman T.R., A. Larson, K. de Queiroz, and J.B. Losos. 1999. Phylogenetic relationships and the tempo of early diversification in *Anolis* lizards. *Systematic Biology*, In press.

Schwartz, A. and R. W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History.

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Anolis carolinensis Unplugged: Investigations into the Behavioral Ecology of the Green Anole

Overview

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For the last few years, my students and I have focused on the green anole, *Anolis carolinensis*, as a species with which to test hypotheses dealing with behavioral ecology (e.g., sexual selection theory). But the species comes with a history. From a literature search of the last three decades, I found almost a thousand papers with *A. carolinensis* listed in their titles. Perhaps because the species can be acquired through mail order (> 250,000 exported from Florida and Louisiana per year) and is tolerant of crowding and small cages, *A. carolinensis* has been commonly used as a laboratory subject, leading to its reputation as the “white rat” of reptiles. One might conclude from the sheer volume of studies that there is little left to investigate about this lizard. However, considering that exceedingly few investigations of *A. carolinensis* have been field-oriented, opportunities for investigations into the behavioral ecology of this species abound.

From Ruby’s (1984) initial field-validated assessment of the *A. carolinensis* mating system to our more recent field studies, the green anole is a polygynous, territorial species. But more importantly, it is emerging as an excellent species model for examining intrasexual selection. Classically, males of the species have been known for their proclivity to fight in aquaria and for their larger sexually dimorphic morphology (i.e., male-larger body size and dewlap area; e.g. Jenssen et al., 1995a; Jenssen et al., In press). Among competing hypotheses, the sexual dimorphisms appear to be best explained by sexual selection (e.g., Jenssen et al., 1995a; Ruby, 1984). These dimorphic traits have been commonly viewed as intersexually selected. In these female-choice arguments, large males have a fighting advantage for control of high quality territories attractive to females, or have large dewlaps as enhanced signaling structures attractive to females. However, the following data from free-ranging subjects suggest otherwise. We believe that these direct observations of trait use under natural conditions will yield the most reliable evidence of trait function, and the strongest inference for characterizing selection quality and intensity.

Our studies of intersexual activity profiles and spatial relationships with available habitat and neighbors have quantified a long list of large sexually dimorphic behavioral traits. The seasonal timing and magnitude of these intersexual asymmetries are evidence for the kind and intensity of selective pressures creating these intersexual divergences. For example, activity profiles recorded across seasons (Jenssen et al. 1995b; Jenssen et al., 1996; Nunez et al., 1997) show that the behavioral differences between adult sexes occur only during the breeding season. Thus, the observed behavioral dimorphisms reflect sexual selection for optimizing reproductive success and not natural selection (e.g., predator defense behavior, foraging behavior), which should operate all year around. Furthermore, the magnitude of sex-based activity divergence indicates relative intensity of differential selection on male and female reproductive responses. Consider that the average polygynous *A. carolinensis* male, approximately 10% larger and 30%

heavier than the average adult female (Jenssen et al., 1995a), has three resident females within his territory (Jenssen et al., 1995b; Jenssen and Nunez, 1998; Ruby, 1984). To maintain this level of exclusive mates, the male defends 800% larger territories (with no consexual overlap), displays at rates 3500% higher, and covers 700% more distance than does an average female (Jenssen et al., 1995b; Nunez et al., 1997). Furthermore, measurements of intersexual spatial relationships indicate that males are able to use a territorial response for their polygynous efforts because females are habitat (and dietary) generalists, meeting all their needs in stable, small (8 m^3), overlapping (20%) home ranges of available arboreal habitat (Jenssen and Nunez, 1998; Nunez et al., 1997). In their clumped home ranges, females are relatively tolerant toward consexual neighbors because inter-female aggression is infrequent in occurrence and brief in duration (once/8 h; 1.6 min, respectively; Nunez et al., 1997).

The *A. carolinensis* life history traits are also prime factors that reflect reproductive constraints, characterize the species' mating system, and imply the kind of selection. The single-egg clutch, unique to all *Anolis* species, is a peculiar vehicle for female reproduction. A female's "total clutch size" for a breeding season depends on the frequency with which she produces repeated clutches (i.e., mean clutch interval). There has been some contention for this estimate of female *A. carolinensis* reproductive potential. Early laboratory studies using mail-order subjects report a mean inter-clutch interval of 14 days. More recently, laying rates of captive females fresh from the field (Andrews, 1985; Lovern, Unpubl. data) and the intercopulatory durations of free-ranging females (Jenssen and Nunez, 1998) provide a mean cycling interval of once a week. Over the 4-month breeding season (approximately April - July), this twofold difference to the perceived female reproductive potential is significant, going from an estimated 8 eggs to at least 16 per season. Reproductive variance between females can be influenced by poor laying conditions (e.g., drought temporarily inhibits egg deposition) or female size (larger females tend to cycle faster; Andrews, 1985). But for the most part, inter-female variance in reproductive potential appears to be modest. However, for male reproductive success, each female ovulatory cycle becomes an event of competition with other males throughout the 4-month breeding period.

Two other life history traits have particular significance. The first is precocial neonates. With no post-hatching parental care from either the female or her mate, a female should have little interest in a male beyond insemination, reducing mate dependency for her reproductive success and eliminating any female need for mate guarding. In addition, it is obvious that females should not experience selection for maternal behavior nor its associated energetic drain away from egg production. The second trait is sperm storage. Females are able to lay multiple clutches of fertile eggs from a single copulation (Andrews, 1985). Given that (1) the population has a balanced sex ratio (Jenssen et al., 1995a; Ruby, 1984) and (2) territorial males attempt long term control over multiple, iteroparous females (Jenssen and Nunez, 1998; Ruby, 1984), we suggest that there are many floater males who should attempt to mate opportunistically with unguarded females. This means that sperm competition and extra-male paternity have a likely significance on territorial male fitness in the *A. carolinensis* mating system.

Longitudinal courtship and mating records constitute the last line of field data to distinguish between a male-controlled mating system (intrasexual selection) and a female-controlled mating system (intersexual selection). Continuous 8-day observations of individuals within *A. carolinensis* breeding groups (i.e., polygynous assemblages) found no obvious female-choice in the mating behavior (Jenssen and Nunez, 1998). Among various paradigms of polygyny, Jenssen and Nunez (1998) concluded that female *A. carolinensis* best fit a "neutral-mate-choice" model. In this model (Lightbody and Weatherhead, 1988), females exhibit little consexual competition, and settle into breeding territories with little differential response to one another or to variation in mate/territory quality. Female *A. carolinensis* largely conformed to this model by exhibiting: (1) no significant relationship between their potential reproductive rates (PRR) and any measured male or female variable; (2) no correlations between measured male and female variables (i.e., assortative mating); and (3) little inter-female competition for potential resources that might constrain reproduction (Jenssen and Nunez, 1998).

Historically, the "polygyny threshold" model (PTM) has been proposed for *A. carolinensis* (Crews, 1973). The PTM is a female-choice model developed for polygynous migratory birds (Orians, 1969). However, we have found no field support for it (Jenssen and Nunez, 1998). Critical to the PTM is an asynchronous temporal component, in which males (e.g., birds) enter breeding grounds a month or so before the arrival of females. During the pre-female period, males aggressively compete for high quality, limited habitat required for specialized nest sites and abundant food resources for parental care of altricial, homeothermic young. In this model, female-choice is driven by a cost/benefit relationship between mate/habitat sharing with other females and the relative compensation from resource quality. This scenario has little application to *A. carolinensis*. Not only are the life history traits a marginal fit, but past (Jenssen et al., 1996; Ruby, 1984) and current studies (Lovern and Jenssen, In prep.) have found no intersexual asynchrony to the winter/spring transitions from overwintering sites to nearby breeding sites. Behavioral, endocrinological, and gonadal measurements from the same individuals collected between late February to mid-April indicate a month-long transition to breeding state for the population, but not by sex.

Not only are territorial males devoting a majority of their time excluding rivals from resident females, but territorial males also appear to be controlling mating events within their territories. Jenssen and Nunez (1998) found four lines of evidence. First, at a distance, males significantly display more to non-receptive than to receptive resident females, suggesting an awareness of female reproductive state. Second, males bypassed 69% of copulatory opportunities with receptive resident females, a similar finding of Jenssen et al. (1995b). Third, when copulations did occur (< once/day), the preceding courtship sequence was always male-initiated. Fourth, copulations were long, averaging 23 min, and appeared to reflect a male-maintained duration**.** We speculate from these data that territorial males are managing copulatory events among resident females.

In conclusion, the sexually dimorphic traits of *A. carolinensis* appear driven by intrasexual selection. Without evidence of direct female choice, the distribution of reproductive females in space and time appears to facilitate prolonged female defense polygyny (a.k.a. male-contest endurance rivalry, Andersson, 1994). Male potential reproductive rate (PRR) was strongly correlated with number of resident females, size of resident male, and size of male territory (Jenssen and Nunez, 1998), but at an enormous energetic commitment to territorial activities, the extent to which was under appreciated before our observations. The intersexual energetics of this mating system should be particularly instructive.

Projects under investigation

I have been primarily interested in the communication system of *A. carolinensis* (e.g., DeCourcy and Jenssen, 1994), but I soon realized that to infer adaptive functions would require a better understanding of the species' natural history, social relationships, and mating system. Too often, data interpretation is dependent on one's theoretical overlay, and it is imperative to have a realistic perspective.

From DeCourcy and Jenssen (1994), Lovern et al. (1999), Jenssen et al. (In press), and Orrell and Jenssen (In manuscript), we know the following about the species' display number, structure, and function. Both sexes share three distinct headbob patterns, labeled A, B, and C, which may or may not be accompanied by dewlap extension. Although the relative frequencies of A, B and C displays can shift dramatically, both sexes use all three displays in each of the three basic social contexts: subject alone (except females, who generally do not advertise); consexual interactions; and heterosexual interactions. Therefore, it is a grave misrepresentation to label an *A. carolinensis* display (or any species' displays for that matter) by a social context (e.g., "assertion," "challenge," "courtship," or "submissive") because it obfuscates the fact that the species has a complex signaling system that uses more than one kind of headbobbing display in any one of their social contexts.

Furthermore, the A, B, and C headbob patterns demonstrate little temporal variance within and among individuals, and among populations, including those from individuals introduced 50 years ago in the Hawaiian Islands. This is a curious result considering the large geographic range of *A. carolinensis*, the wide variance of habitat types, and the potential function of displays as a female choice criterion during mate selection. Any one of these factors would predict phenotypic divergence between populations, especially in light of recent evidence for rapid shifts of body morphology in artificially colonized anoline populations (e.g., Losos et al., 1997).

Ontogeny and sex differences in behavior

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I have been interested in how juvenile male and female *Anolis carolinensis* develop into the dramatically sexually dimorphic adult endpoints described above. With the help of other graduate students and the members of my dissertation advisory committee, I have examined the ontogeny of behavior in free-ranging juveniles in the field and manipulated social interactions in the laboratory. Currently, I am investigating the potential role of androgens during development in producing sex differences in behavior. Overall, my hope with this research has been to see which, if any, of the traits that show prominent sexual dimorphisms in adults appear as dimorphic in juveniles, and to perhaps find proximate, endocrinological correlates to these differences. Such data would further reveal the extent to which sexual selection is influencing the life history of *A. carolinensis*, perhaps extending the effects of sexual selection to influencing the development of individuals before they are even reproductive.

Before doing any manipulative research, I simply went into the field to see what juveniles do. I examined variables related to space use, social interaction, and growth potential. Of these, I expected to find the biggest difference between males and females in behaviors that would affect growth, because of the great advantage of being a large adult male (able to overlap the territories of and mate with more females). Juveniles are not sexually dimorphic in body size at hatching, but growth rates demonstrate that juvenile males grow faster than females to attain the larger body size as adults (Michaud, 1990). My behavioral observations suggest that males grow faster because (1) they eat approximately 300% more often per hour than females (3 vs. 1 feeding event/h), and (2) they adopt an active foraging strategy, as opposed to sit-and-wait, significantly more often than females (84% vs. 63% of the feeding events for males and females, respectively). Because juveniles do not grow fast enough to become reproductive in the summer they hatch (Lovern, Unpubl. data), and because female growth rates are sufficient for surviving the winter dormancy period (based on sex ratios of animals coming into the following reproductive season; Jenssen and Lovern, Unpubl. data), the sexual dimorphism in feeding rate and foraging mode appear to be the result not of natural selection on immediate juvenile requirements, but rather sexual selection on future benefits.

I furthermore found that, contrary to adult dimorphisms in space use and social interaction, juvenile males and females differed very little in these parameters. In particular, I was interested in observing what types of social interactions juveniles expressed. The frequency and type of interactions observed, especially in comparison to adult interactions, could lead to inferences about what's "important" to juveniles (e.g., exclusive territories, advertisement of space use, consexual/heterosexual spacing). Apparently (and not surprisingly), inconspicuousness and general lack of activity are very important juvenile traits! Although I found that both juvenile males and females give headbobbing displays, display rates and other evidence of social interaction were identical between males and females (2 displays/h) and significantly lower in frequency than those seen in adults. Given that adults are only sexually dimorphic in the breeding season with respect to social behavior (Jenssen et al., 1995b; Jenssen et al., 1996), and that these dimorphisms are primarily a response to intrasexual selection on males, the relative inconspicuousness of juvenile males and females, which are not reproductive, is not surprising.

To further explore juvenile social behavior (because I was stubborn, interested in how past experience effects behavior, and to generate enough displays to analyze their structure!), I have collected gravid females and reared their offspring in the lab, and I have collected juveniles directly from the field. Individuals were housed in groups of four or in isolation and randomly paired periodically through development (between 0 and 120 d) to determine whether social condition, sex, or age had any effect on the type of social behavior observed. Like Cooper (1971) and Greenberg and Hake (1990), I found that juveniles were capable of headbobbing and expressing associated display modifiers (e.g., dewlap extension, sagittal expansion, gular extension) on the day of hatching. Furthermore, using the convention established by DeCourcy and Jenssen (1994) of labeling the three *A. carolinensis* display type structures A, B, and C, over 90% of displays given by juveniles were type C (statistically identical to adult type C displays), and the few A's and B's were predominantly given after 60 d of age. This result suggests that the motor ability to give headbobbing displays is fully present at hatching, but that the relative proportions of A, B, and C displays shows developmental changes. No animal, in over 100 h of videotape, ever displayed when alone, thus strongly rejecting a territory advertisement function of displays in juveniles (e.g., as in adult males). However, whether animals were housed in groups or in isolation, or were lab-reared or captured from the field, had no effect on the types of behaviors they expressed, and there were no differences in the intensities of male-male, male-female, and female-female interactions. These results suggest that overall, whatever is important to juveniles (i.e., why display?), it depends neither on the sex of other individuals nor on previous experience.

Although consexual and heterosexual interactions did not differ in intensity, males and females showed some developmental differences concerning social interaction. In the first week after hatching, males were much more likely than females to give a display in response to another lizard (60% vs. 13%, respectively), although male and female display rates on average did not differ. However, by 90 d, males and females were equally likely to display at other lizards (90% of the encounters included displays), but male display rate was significantly higher. Coupled with the allometrically increasing dewlap area in males, but not females, through development (Crews and Greenberg, 1981), these results suggest that sex steroids may have a role during development in producing sex differences in behavior and morphology. For the last part of my dissertation, I am examining potential endocrine correlates to sex differences in juvenile *A. carolinensis*.

To guide my endocrine research, I have used the organization-activation theory of sex differentiation. Sex steroids often act at two discrete developmental periods to produce sex differences in morphology and behavior. Hormonal "organization" of sexual dimorphism occurs when hormone exposure during early development is necessary for adult trait expression. Typically, organized traits are irreversible. Hormonal "activation" occurs when hormones must be present to produce and maintain a trait. Typically, activated traits are reversible, cycling with seasonal fluctuations in hormone concentrations. Whether sexual dimorphism in trait expression is regulated by organization, activation, or both, can be determined by hormone manipulation experiments during development. However, once again, I first wanted to document the natural state before performing manipulations. I examined testosterone (T) and dihydrotestosterone (DHT) plasma concentrations, two biologically active androgens known to be effective in activating adult *A. carolinensis* sexual dimorphisms (primarily testosterone; e.g., Adkins and Schlesinger, 1979). From blood samples collected in hatchlings on the day of hatch in the lab (17 males, 18 females), as well as from juveniles of all sizes in the field (35 males, 23 females), I found that males and females did not differ in T and DHT levels and that the majority of individuals showed no detectable levels of either androgen. Based on theoretical expectations and the above data, these results were a surprise. They suggest that androgens are not important in organizing sex differences in *A. carolinensis*, only in activating these differences in breeding adults. Perhaps juvenile sex differences in morphology (body size and dewlap) and behavior (display likelihood and/or rate) are mediated by other hormones or are hormone-independent. It's also possible that active levels of T and DHT fell below the sensitivity of my hormone assay (0.01 ng/ml) and are, in fact, sexually dimorphic, or that there is a maternal contribution to androgen differences (e.g., in yolk androgen concentration). To test some of these possibilities, I plan to finish my dissertation with yolk androgen analyses of freshly-laid eggs and with hormone manipulation experiments in juveniles. If there is no organizational role of androgens in *A. carolinensis*, then I expect to find no yolk androgens and that juvenile males and females will respond equally to elevated androgen levels.

Male mate-choice and energetics of reproduction

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Although mate choice is traditionally associated with female-controlled mating systems, males should also exhibit mating preferences whenever the reproductive benefits outweigh the costs of being choosy (Trivers, 1972; Parker, 1983). The type of mate choice strategy most frequently studied (for both sexes) is quality-based discrimination, in which individuals increase their reproductive success by choosing a mate that would produce greater numbers of offspring or superior offspring (reviewed in Andersson, 1994).

Another type of male-controlled mate choice strategy is the 'preference for novel females' (hereafter termed PNF). Based on the classic Coolidge effect in which males show greater sexual interest toward novel females than toward females with whom they previously copulated (Dewsbury, 1981), the PNF acts to increase male reproductive success by increasing the total number of different females inseminated. Despite the logical presumption that most males should practice mate choice (e.g., PNF), the phenomenon has not been widely tested among taxa and mating systems (e.g., mammals, review by Dewsbury [1981]; a salamander [Donovan and Verrell, 1991]; and two species of lizards: *Holbrookia propinqua* [Cooper, 1985] and *Anolis sagrei* [Tokarz, 1992]).

To test for the PNF in *Anolis carolinensis*, my investigation included both laboratory and field experiments. The laboratory protocol tested whether males can discriminate between resident and novel females, and whether males exhibit a preference for novel females by examining male courtship responses toward introduced resident (RF) and novel (NF) females. The field protocol validated the results obtained in the lab experiments with free-ranging lizards, and examined how PNF is expressed within a natural setting. Free-ranging novel females were released into a male's territory, and thus were encountered by resident males in the same way that males would encounter a novel female under natural conditions. Because males were simultaneously present with both resident and novel females, they could also choose which female(s) to interact with. For both laboratory and field experiments, male responses to novel and familiar females were videotaped, and variables were obtained from the videotaped records.

Results from the laboratory experiment (n = 16 trials) indicate that males can discriminate between resident and novel females; differential male courtship intensity strongly supports male preference for novel females. Intensified male courtship toward novel females as compared to resident females was supported by the following variables: 1) higher display rates (64 vs. 20 displays/h to NF and RF, respectively); 2) larger volley size (3.7 vs. 2.5 successive displays < 2 sec apart to NF and RF, respectively); 3) higher rate of display modifiers (2.9 vs. 0.1 modifiers/h to NF and RF, respectively); and, 4) higher proportion of movement toward novel females (58 vs. 30% of total distance moved in a trial [Wilcoxon signed rank tests, $P < 0.05$ for all comparisons]).

Results from the field experiment (n = 18 trials) validated the laboratory study. Males discriminated among resident and novel females, and a preference for courting novel females as compared to resident females was supported by the following variables: 1) greater proportion of time spent in interacting with novel females (53% vs. < 2% of time with NF and RF, respectively); 2) higher display rates (2.0 vs. 0.1 display/h to NF and RF, respectively); 3) performance of low amplitude displays (80% of low amp displays were to NF); 4) more frequent color changes (3.6 vs. 1.6 color changes/h toward NF and RF, respectively), and a very dark brown not typically seen during interactions with resident females; and, 5) males chased, grabbed, and/or crept slowly toward novel females, but did not make similar types of moves toward resident females (Wilcoxon signed rank tests, $P < 0.05$ for all comparisons).

We conclude that male *A. carolinensis* are able to discriminate among novel and resident females and that males do exhibit a PNF response in both laboratory and field environments. Our experiments suggest that free-ranging males encountering a novel female attempt to increase their reproductive success by directing intensified courtship behaviors toward a novel female.

The behavioral profile of breeding *A. carolinensis* is an obvious reflection of large intersexual differences in reproductive strategy and is likely to be associated with divergent patterns of energy allocation. For four months, males devote a great deal of time and energy to patrolling and defending a large arboreal territory (approximately 69 m^3; Jenssen and Nunez, 1998), using headbob displays at rates up to 209 displays/h while traveling at rates up to 73 m/h (Jenssen et al, 1995). In contrast, the reproductive strategy of breeding females appears to conserve energy for egg production; females exhibit little consexual aggression or territorial defense, and display and travel at rates less than 14 displays/h and 4 m/h, respectively (Nunez et al., 1997; Jenssen and Nunez, 1998). Based on respective activity profiles, we tested the prediction that male *A. carolinensis* energy expenditure in reproduction (i.e., in territorial behaviors, courtship) is equivalent to that of females producing eggs.

We examined the allocation of energy toward reproduction and territoriality in *A. carolinensis* lizards in Augusta, GA. During breeding and postbreeding seasons, we determined field metabolic rates (FMRs) of free-ranging lizards using the doubly-labeled water technique (Nagy, 1983), and maintenance metabolic rates (MMRs) of freshly captured lizards using metabolic chambers. We found no seasonal differences in FMRs for either sex, and both sexes had similar MMRs during both seasons (analysis of covariance; all $P > 0.15$). However, postbreeding MMRs were 30% higher than breeding MMRs for both sexes (Analysis of covariance; $P < 0.0001$). Partitioning daily energy into maintenance expenditure and activity expenditure indicated that 63% of daily energy was expended in breeding activity (776 J/day), compared to 40% in postbreeding activity (451 J/day). Over a 4-month breeding season, we estimated that a 5 g male and a 5 g female *A. carolinensis* expend about 74 and 67 kJ (respectively) in annual reproduction. We concluded that, despite differences in reproductive physiology and behavioral strategies, male and female *A. carolinensis* may expend the same energy in reproduction.

Sperm competition as a mechanism of sexual selection

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My dissertation research investigates the role of sexual selection in *Anolis carolinensis* by determining the occurrence of one mechanism of sexual selection, sperm competition. The life history and behavioral ecology of *A. carolinensis* seem to point to a system in which sperm competition is a viable mechanism for sexual selection.

Anolis carolinensis exhibits a polygynous mating strategy. Despite a 1:1 sex ratio observed from census data taken in the field, we have observed up to six resident females mated by a single territorial male, with an average of 3 females for every one male. While *A. carolinensis* males defend territories that contain female home ranges, the potential exists for multiple male paternity due to temporary invasion by “floater” males or female home ranges being overlapped by more than one male (Ruby 1984). This information implies that females could potentially mate with multiple males during a reproductive cycle, thus increasing the uncertainty of male paternity because of this threat by outside males.

Male *A. carolinensis* behavior exhibits the apparent effects of intense intrasexual selection. This intrasexual selection is very feasible because given the reproductive cycle exhibited by individual *A. carolinensis* females of approximately 16 weeks, a resident male with three females can have the paternity for approximately 48 ovulatory events for any breeding season at stake.

Sperm storage is present in *A. carolinensis*. Fox (1963) initially reported the presence of sperm storage tubules in *A. carolinensis*. Sperm enter the sperm storage tubules between two to six hours after insemination and if these sperm are being used to fertilize an egg, they enter the infindibulum six to 24 hours post mating (Conner & Crews 1980). The exact mechanisms of sperm transport and sperm release, however, are unknown in *A. carolinensis*.

Anolis carolinensis also has some unusual reproductive strategies present. Males reject 70% of copulation opportunities with receptive resident females and average only one copulation per day. This may indicate a limitation of available sperm. *Anolis carolinensis* also exhibits an abnormally long copulation duration of approximately 30 minutes. Manipulation of sperm in the female tract or mate guarding may be occurring at this time.

Although the behavioral profile of *A. carolinensis* suggests that sperm competition may be present, even after hundreds of hours of field observations, we have been unable to document the occurrence of extra-pair copulations. I am proposing to investigate the natural occurrence of extra-pair paternity in this species through the use of DNA fingerprinting.

I began field work for my dissertation research during the summer of 1998. *Anolis carolinensis* was observed in natural habitat located between the 16 km long Augusta Canal and Savannah River on the border of Georgia and South Carolina. Territory size was determined for ten male lizards. For each of these resident males, their resident females and any neighboring males were identified. Resident and neighboring males and resident females were captured and a blood sample was taken from each. Resident females were housed until they laid two eggs. Eggs were incubated until hatching and a tissue sample was collected from each of the hatchlings.

I am currently involved with performing DNA fingerprinting to determine the paternity of the hatchlings. Following analysis of these data, I will return to the field to continue observations on our study population. Based on the results of the analysis, I hope to be able to determine which habitat variables and territory characteristics should be measured in greater detail in order to determine conditions that favor extra-pair paternity in this lizard. If these data indicate that sperm competition occurs in this species, I will begin a study to investigate the role that female lizards play in controlling with which males they mate.

Literature Cited

Adkins, E., and L. Schlesinger. 1979. Androgens and the social behavior of male and female lizards (*Anolis carolinensis*). Horm. Behav. 13:139-152.

Andersson, M. B. 1994. Sexual Selection. Princeton Univ. Press, Princeton, NJ.

Andrews, R. M. 1985. Oviposition frequency of *Anolis carolinensis*. Copeia 1985:259-262.

Conner, J. and D. Crews. 1980. Sperm transfer and storage in the lizard, *Anolis carolinensis*. J. Morph. 163:331-348.

Cooper, W.E., Jr. 1971. Display behavior of hatchling *Anolis carolinensis*. Herpetologica 27:498-500.

Cooper, W. E., Jr. 1985. Female residency and courtship intensity in a territorial lizard, *Holbrookia propinqua*. Amphibia-Reptilia 6(1985):63-69.

Crews, D. 1973. Social factors associated with the male in the control of reproduction in the female lizard *Anolis carolinensis*: the role of courtship and aggression. PhD thesis, Rutgers Univ.

_______, and N. Greenberg. 1981. Function and causation of social signals in lizards. Amer. Zool. 21:273-294.

DeCourcy, K. R., and T. A. Jenssen. 1994. Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. Anim. Behav. 47:251-262.

Dewsbury, D. A. 1981. Effects of novelty on copulatory behavior: the Coolidge effect and related phenomena. Psychological Bulletin 89(3):464-482.

Fox, W. 1963. Special tubules for sperm storage in female lizards. Nature 198(4879):500-501.

Greenberg, N., and L. Hake. 1990. Hatching and neonatal behavior of the lizard, *Anolis carolinensis*. J. Herpetol. 24:402-405.

Jenssen, T. A., J. D. Congdon, R. U. Fischer, R. Estes, D. Kling, and S. Edmands. 1995a. Morphological characteristics of the lizard, *Anolis carolinensis*, from South Carolina. Herpetologica 51:401-411.

_______, N. Greenberg, and K. A. Hovde. 1995b. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. Herpetol. Monogr. 9:41-62.

_______, J. D Congdon, R. U. Fischer, R. Estes, D. Kling, S. Edmands, and H. Berna. 1996. Behavioural, thermal, and metabolic characteristics of a wintering lizard (*Anolis carolinensis*) from South Carolina. Func. Ecol. 10:201-209.

_______, and S. C. Nunez. 1998. Spatial and breeding relationships of the lizard, *Anolis carolinensis*: Evidence of intrasexual selection. Behaviour 135:981-1003.

_______, K. S. Orrell, and M. B. Lovern. In press. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. Copeia.

Lightbody, J. P., and P. J. Weatherhead. 1988. Female settling pattern and polygyny: tests of a neutral-mate-choice hypothesis. Amer. Nat. 132:20-33.

Losos, J. B., K. Warheit, T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387:70-73.

Lovern, M. B., T. A. Jenssen, K. S. Orrell, and T. Tuchak. 1999. Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis*: signal stability or lability? Herpetologica 55:222-234.

Michaud, E. J. 1990. Geographic variation of life history traits in the lizard, *Anolis carolinensis*. PhD thesis, Univ. of Tennessee.

Nagy, K. A. 1983. The doubly labeled water method: a guide to its use. UCLA Pub. No. 12-1417.

Nunez, S. C., T. A. Jenssen, and K. Ersland. 1997. Female activity profile of a polygynous lizard (*Anolis carolinensis*): Evidence of intersexual asymmetry. Behaviour 134:205-223.

Orians, G. 1969. On the evolution of mating systems in birds and mammals. Amer. Nat. 103:589-603.

Parker, G. A. 1983. Mate quality and mating decisions. In: P. Bateson, ed., Mate Choice. Cambridge Univ. Press, Cambridge, UK.

Ruby, D. 1984. Male breeding success and differential access to females in *Anolis carolinensis*. Herpetologica 40:272-280.

Tokarz, R. R. 1992. Male mating preference for unfamiliar females in the lizard, *Anolis sagrei*. Anim. Behav. 44:843-849.

Trivers, R. L. 1972. Parental investment and sexual selection. In: B. Campbell, Ed., Sexual Selection and the Descent of Man 1871-1971. Aldine Publishing Company, Chicago. Pages 136-179.

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Dwarfs, Giants, and Rock-Knockoffs: Evolution of Diversity in Antillean Anoles

I have long agreed with the orthodox neo-Darwinian view that new species evolve from populations peripherally isolated from their parental stocks in the Antilles by the simple, repetitive process of interglacial sea level rise. Thus, the new species are "daughter" species of their ancestral stocks, not "sister" species. Separate-but-equal dichotomous branching never occurs. The ancestral species remain essentially unchanged unless or until the new species invade the parental range, typically as a result of glacial maximum sea level drop. Then the opportunity for classic Darwinian character divergence emerges.

The ideal structure for speciation in isolation is a rock: a sheer-sided formation that, at interglacial high-stand sea level, is pounded by surf and provides scant or no opportunity for over-water waif dispersers to colonize and retard the speciation process by adding parental species genes. However, few anole populations stranded on such rocks persist and survive to evolve into new forms. On the Puerto Rico Bank, for example, at least four species of anoles were able to spread virtually throughout the area occupied by today's Virgin Islands at Wurm glacial maximum, 10-20 kya: *Anolis cristatellus*, *A. stratulus*, *A. pulchellus*, and *A. roosevelti*. It is highly probable that more species from Puerto Rico proper dispersed overland at glacial maximum into the Virgins area too, but, if so, none survived into historical times.

One of the four species, *A. roosevelti*, may now be extinct as a result of artificial, post-Columbian deforestation. Two, *A. stratulus* and *A. pulchellus*, have not survived on any of the several small islets that qualify as rocks. At least five islets qualify as rocks in my terms (and are locally called that): Carrot, Carval, Cockroach, Sail, and Watson. Of these, only Carrot and Cockroach seem to harbor anoles today, in both cases derivatives of *Anolis cristatellus wileyae*. One of these, *A. ernestwilliamsi* of Carrot Rock, is well differentiated and has occasionally colonized adjacent Peter Island to survive (however briefly) in sympatry with *A. c. wileyae*, its parental stock. Cockroach Rock anoles are less obviously differentiated from *A. c. wileyae*, but the few available specimens are unusually large, short-headed, and big-scaled. This population is certainly worth a closer look.

Dry rocks present a strong selection pressure for water retention, and this can be augmented by large size. Thus, dry rocks like Carrot and Cockroach may produce incipient giants. Wet rocks might present an opportunity for dwarfism, if small size were advantageous in the absence of selection for water retention. However, wet rocks -- that is, wet with fresh water-- are hard to find. There is a couple off the windward coast of Dominica that may repay investigation.

Long ago (*Copeia* 1964: 716-718), I suggested that *A. gingivinus* on Sombrero might undergo rapid speciation, but Ellen Censky tells me that population has apparently winked out. The nearby Anguilla Bank provides some outstanding prospects for rock-knockoffs. I never got to Pain de Sucre off St. Barts in the course of my field work of 30-40 years ago. Apparently, no one else has reached it since. Most amazing is the remotely isolated La Poule and Les Poussins cluster far northwest of St. Barts. These are “the Groupers” on tourist maps. I plan to make a try for these islets in the near future, before I get too stiff to climb.

But why me? Are there not others, far younger and more agile, who have thought of potential speciation in isolation too? Well, if one of you gets there before me here, are some predictions:

On the wet rocks off Dominica, I expect small anoles with big scales. In *A. oculatus*, scale size seems to correlate positively with moisture.

On the dry rocks near St. Barts, I expect relative giants (parental *A. gingivinus* is relatively small), but I cannot guess scale size. Indeed, the relationship of scale size to water seems reversed in some forms, like *A.ernestwilliamsi*. We need a good integumentary physiologist to look into this problem.

How does one know if there are no anoles surviving? Spiders. Small salticid or attid jumping spiders and little, plump orb weavers like *Argiope argentata* are densely abundant on islets lacking anoles (thanks, Tom Schoener, for pointing that out). If you find lots of spiders, there probably are no anoles.

The race is on. Good luck.

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Antipredator Responses in Puerto Rican *Anolis*

Two general statements can be found in a quick survey of the *Anolis* literature. First, predation pressure is a strong selective force. Second, the signal repertoire of *Anolis* is one of the most diverse of any lizard. Although the second statement has received considerable attention, currently there is a lack of knowledge of the mechanisms employed by *Anolis* to avoid or escape a predator attack. For the last six years, I have been working on the antipredator responses of *Anolis*. During my master's thesis I worked on the antipredator responses of *Anolis cristatellus* during caged predation episodes with a natural predator, the snake *Alsophis portoricensis*. One of the surprising results of this work was that *A. cristatellus* uses as antipredator responses the same elaborate visual displays that it uses during social interactions (Leal & Rodríguez-Robles 1995). The phenomenon of prey signaling to predators raises several questions. First, what is the purpose of the signals? Possibilities include that they are trying to misdirect the predator's attention or to deter the predator's attack. Second, if the prey is attempting to communicate, is it simply notifying the predator that it has been detected, or is it producing more specific information about its own abilities? If the latter, is this information likely to be accurate or deceptive? Particularly interesting is the observation that differences among species in the use of conspicuous displays against predators may be correlated with differences among species in physiological capacity. Finally, how did such signals evolve? An interesting observation is that the signals given by prey to predators are visually similar to signals used in intraspecific contexts. For my dissertation, I am addressing the previous questions using the antipredator responses exhibited by three species of Puerto Rican *Anolis* as a model system.

Predator-Prey Communication

After detecting an approaching predator, the prey can show a great variety of behavioral acts to avoid an attack. Prey may respond by avoiding detection by the predator or by using behavioral acts such as fleeing, cryptic movement or immobility. On the other hand, prey may respond by giving conspicuous signals that appear to increase the probability of detection by the predator (reviewed in Hasson 1991, Caro 1995). Two main hypotheses have been suggested to explain the evolution of conspicuous signals in predator-prey interactions. The "flash concealment" hypothesis suggests that the sudden exhibition of signaling behavior draws the attention of the predator strongly to one location and then allows the prey to escape to another location, usually in a cryptic movement pattern (Hailman 1977; Bildstein 1983). The "pursuit deterrent" hypothesis contends that because the chances of the predator successfully attacking its prey decrease when the prey is aware of the incoming predator, the prey have evolved signaling displays that communicate their alertness and ability to escape an attack to the predator, thus discouraging the attack (Zahavi 1987; Barker & Parker 1979).

A critical difference between the flash concealment hypothesis and the pursuit deterrent hypothesis is the behavior exhibited by the prey immediately after signaling. The flash concealment hypothesis predicts that the anoles should not repeatedly signal from the same location. Furthermore, the anoles should flee immediately after signaling to the predator in a cryptic movement making it difficult, if not impossible, for the predator to find the new location of the anole. The pursuit deterrent hypothesis predicts that anoles should signal repeatedly to the predator.

Anolis presents a unique opportunity for testing the effect of performance capabilities on the use of conspicuous signals as antipredator responses among closely related species that have similar morphology and ecological niche and that share the same predator. The ability of an animal to escape an attack by either outrunning the predator or repelling a predator after being captured is constrained by the animal's physiological capacity (reviewed in Bennett and Huey 1990). If the use of pursuit deterrent signals is constrained by the performance ability of the species (Caro 1994), closely related species with different performance capability should exhibit different responses to the predator. In anoles, performance capability varies greatly at the interspecific level among closely related species (Losos 1990; Losos & Irschick 1996), but there is a lack of knowledge about how this variation affects antipredator responses.

I am evaluating the effect of physiological capacity in the use of conspicuous displays by comparing the antipredator responses of *A. cristatellus, A. gundlachi* and *A. monensis*. The antipredator responses of each species will be correlated with the species' endurance capacity. If physiological capacity constrains the use of conspicuous displays, I predict that species with the higher performance ability should employ conspicuous displays, whereas the species with the lowest performance ability should rely mostly in flight or crypsis.

The Nature of the Signal

A major controversy regarding the evolution of signals, including those used as predator deterrent signals, is the nature of the message encoded in the signal. If signals are used as predator deterrents, a prediction of the hypothesis is that the prey can communicate to its predator not only that it has been detected, but also its condition or ability to escape (i.e. "honest signals" [Zahavi 1975]). Surprisingly, no empirical data have addressed this prediction. When prey is aware of the incoming predator, vulnerability to the predator may be related to the prey's physiological capacity (e.g., endurance capacity). Individuals with the highest endurance capacity may be able to flee for a greater distance from the predator, and/or, after being seized, may be more able to inflict damage (Arnold 1982; Bennett & Huey 1990; Garland & Losos 1994). As a result, if predators can assess the quality of prey, they may decide not to pursue high-quality prey. For example, when captured, *A. cristatellus* struggled vigorously while biting a snake predator for up to 28 minutes. Furthermore, subduing time (the amount of time that the snake spent subduing the lizard) of *A. cristatellus* increased linearly with the time the lizard spent biting the snake (Leal & Rodríguez-Robles 1995). The fact that long periods of activity in lizards are supported principally by aerobic capacity (Bennett 1978; Bennett & Huey 1990) suggests that anoles with higher endurance capacity should also be able to actively defend themselves from the snake for longer periods of time. Because predators become more vulnerable to predation themselves and can experience some damage from the prey while handling it (Formanowicz and Brodie 1988; Lima and Dill 1990), antipredator mechanisms that increase the prey-handling time may affect the decision of the predator about attacking or subduing certain prey. This observation suggests that endurance capacity in *A. cristatellus* may be a critical attribute during predator-prey interactions. Moreover, if the anoles are able to communicate their endurance to the snake, the snake should avoid individuals with high endurance capacity.

Studies on the physiological cost of anole displays have demonstrated that signaling is an energetically demanding behavior. For example, in *Anolis bonairensis*, male lizards that were actively giving signaling displays exhibited a significantly greater level of lactate content accumulation than males that were not signaling (Bennett et al. 1981), which suggests that the energetic cost of signaling may constrain the frequency and intensity of anole displays. Moreover, because anoles rely heavily on glycolysis to power short intervals of intense exercise (e.g., fleeing from a potential [Wine & Gatten 1992]), long periods of signaling may impair the lizard's ability to flee from a potential predator. Furthermore, *Alsophis portoricensis* sometimes attacks *A. cristatellus* even after the lizards have signalled (Leal & Rodríguez-Robles 1995), suggesting that cheaters would be heavily penalized if they signal to the snake and the snake subsequently attacks them. If the message encoded in the signal is "honest" and correlated with the ability of the anoles to escape from the predator, a positive correlation between endurance capacity and the intensity of signaling displays is predicted.

Background on the Predator-Prey System

The three species of anoles that I am using in this study are: *A. cristatellus, A. gundlachi*, and *A. monensis*, which belong to the same clade (Gorman et al. 1983; T. Jackman unpublished data). *Anolis cristatellus* is a medium-large (snout-vent length, SVL=56-76 mm), grey-brown, sexually dimorphic lizard that occurs in mesic to xeric areas (Rand 1964; Williams 1983; Schwartz & Henderson 1991). *Anolis gundlachi* is a medium-sized (SVL=45-69 mm), brown, mesophilic, sexually dimorphic anole that occurs only in highly shaded, closed canopy forest (Rand 1964; Williams 1983; Schwartz & Henderson 1991). *Anolis monensis* is medium-sized (SVL=57), grey, sexually dimorphic species that occurs in xeric areas and is endemic to Isla de Mona (Williams 1983; Schwartz & Henderson 1991). The three species have similar morphology (Williams 1983). All three species use tree trunks and the ground as their perching sites (Rand 1964; Williams 1983; Schwartz & Henderson 1991). All three species are sympatric with *Alsophis portoricensis* throughout their respective ranges and are commonly found in the diet of this snake, based on data from stomach contents from live snakes (Rodríguez-Robles & Leal 1993; M. Leal unpublished data).

In Puerto Rico, snakes (Henderson & Crother 1989; Schwartz & Henderson 1991) and birds (Pérez-Rivera 1985) are the principal natural predators of anoles. *Alsophis portoricensis* is the main snake predator of anoles in Puerto Rico and the only diurnal snake predator of anoles on Isla de Mona. *Alsophis portoricensis* is largely a ground-dwelling, actively foraging diurnal snake that uses mainly visual cues to locate prey (Rodríguez-Robles & Leal 1993; Leal & Thomas 1994). Although *A. portoricensis* is an opportunistic feeder that takes almost any small vertebrate encountered (Rodríguez-Robles & Leal, 1993), it preys primarily on reptiles, particularly anoles (Schwartz & Henderson 1991; Rodríguez-Robles & Leal, 1993).

Methodology

I have been carrying out a series of predation trials in which the anoles are approached by a model of the snake *Alsophis portoricensis*. Each episode involves presenting a single, previously undisturbed male lizard with an intact, stuffed skin of an *Alsophis portoricensis*. Recent work with *A. cristatellus* and *A. cuvieri* has demonstrated that a model of *Alsophis portoricensis* is as effective as a live snake in eliciting antipredator responses (Leal and Rodríguez-Robles 1997a, 1997b). These trials are carried out during daytime (900-1600 h), when *Anolis* and *Alsophis* are active. For each species, a total of 35 encounters will be performed.

Using a tape recorder, I recorded all the behaviors performed by the lizard 5 minutes before ("control period") and 5 minutes after ("experimental period") the field assistant began moving the snake toward the anole. See Leal (in press) for a detailed description of the methodology. The following data were recorded: display exhibited, number of iterations of each display, and behavior presented by the anoles following the signaling displays. I followed the behavioral descriptions of Jenssen (1977, 1978) and Greene (1988) to categorize the behavioral acts exhibited by the anoles. I considered displays of identical behavior patterns (e.g., dewlapping, pushups) separated by 30 s or more as belonging to different bouts (L. J. Fleishman, personal communication). The distance from the snake at which the lizard began to signal was recorded. After the predation trial, the lizards were caught to be measured and weighed and brought into the laboratory to perform endurance studies, described below**.**

Lizards collected during the predation trial were brought into the laboratory to measure their endurance capacity. Lizards were housed individually in plastic cages (28 cm long x 12 cm high x 17 cm wide) and provided with a perch site and water ad libitum. The room was on a 12 h photoperiod and at room temperature.

I measured endurance capacity using a circular race track 310 cm in circumference with fiberglass window screening substrate (1.6 mm mesh) that provided good traction. I began each trial by placing the lizard at a designated starting point. Lizards began immediately to run around the track. I chased the lizards around the race track by tapping their tails; if the lizard did not move after five consecutive taps, the trial was terminated (methods follow Brodie 1993). I used the time at which the lizard stopped moving as the measurement of endurance capacity. Using a stopwatch, I recorded the total amount of time until the lizard stopped running. Total distance traveled during each trial was also recorded. Each lizard was tested twice with a 24 h resting period between trials. The first test was performed after the lizards had been in the laboratory for a period of 24 h. Tests were performed at the preferred temperature for each species. After each test, the lizard's weight was recorded. The predictions of the honest signal hypothesis were tested using both the individual's greatest and its average endurance measurements.

Preliminary Results

Currently, all the data that I have collected is for *A. cristatellus* and *A. gundlachi*. Also, the data that are shown supporting the use of pursuit deterrent signals *by A. cristatellus* was recently published (Leal & Rodríguez-Robles, 1997a) and the data supporting honest communication in *A. cristatellus* were recently accepted for publication (Leal IN PRESS).

Antipredator Responses

The anoles performed six behavior patterns in response to the snake model: remaining still for at least 120 s while looking towards the snake model (immobility); movement toward the predator (predator inspection); movement at least 30 cm away (e.g., up the tree) from the snake model or movement to the opposite side of the trunk (flight); positioning of the body perpendicularly to the predator (lateral face-off); dewlapping; and pushups. Anoles flexed either two (two-legged pushups) or four (four-legged pushups) legs during the pushup displays.

The behavioral responses of *A. cristatellus* (*N*=35) and *A. gundlachi* (*N*=35) during the experimental period can be grouped in three main classes: non-signaling displays (immobility, flight), conspicuous signaling displays (pushups, dewlapping, lateral face-off), and predator inspection. Before the snake model reached the base of the lizard's perch, the most common behavior pattern presented by *A. cristatellus* and *A. gundlachi* was immobility. After the model reached the lizard's perch, 26 individuals of *A. cristatellus* gave conspicuous displays, whereas nine individuals did not display. In the case of *A. gundlachi*, only two individuals gave conspicuous displays, whereas 33 did not display. The ratio of 26:9 in *A. cristatellus* is significantly different from the 2:33 in *A. gundlachi* (two-tailed Fisher's exact test of independence, *P*<0.001 [Unpublished]). In 11 of the 35 trials, *A. cristatellus* approached the snake using a series of short, 'jerky' jumps (i.e., predator inspection) that were interrupted by dewlapping or pushup displays. However, predator inspection was never given by *A. gundlachi*.

The endurance capacity of *A. cristatellus* (mean ± *SE*, 46.7 ± 4.1 sec [range=19-85 sec, *N*=21]) was significantly greater than the endurance capacity of *A. gundlachi* (mean ± *SE*, 26.3 ± 1.7 sec; range=12-37 sec, *N*=21; t-test, *T*=4.64, *N*=41, *P*<0.001 [Unpublished data]). Two trends are apparent from this comparison. First, there is a difference between *A. cristatellus* and *A. gundlachi* in antipredator responses once the snake model has reached the lizard's perch. *Anolis cristatellus* responds by giving conspicuous displays, whereas *A. gundlachi* responds by remaining immobile or fleeing from the predator. Second, there is a significant difference between species in endurance capacity--the species with the highest endurance capacity is the one that gives conspicuous displays.

Predator-Prey Communication

Anolis cristatellus performed significantly more pushups during the experimental than during the control period (Wilcoxon's signed-ranks test, *T*=4.34, *N*=27, *P*<0.001), but there was no difference in the frequency of dewlapping between the two periods (*T*=0.42, *N*=8, *P*=0.32). Number of pushup bouts was significantly higher during the experimental than during the control period (*T*=4.52, *N*=26, *P*<0.001), but the number of dewlapping bouts was not (*T*=0.21, *N*=8, *P*=0.42). During the experimental period, pushup bouts were more frequent after the snake model reached the base of *A. cristatellus*' perch than during the time the snake was approaching it (*T*=3.14, *N*=17, *P*<0.001). Of the 26 lizards that performed pushups toward the snakes, only one lizard fled immediately (within 2 s) after performing the display, whereas 25 did not flee after the display and remained in the same location; thus, significantly more individuals remained in the same location after giving pushups (exact test using binomial distribution: *P*< 0.001). Furthermore, the anoles repeatedly signalled from the same location. The fact that *A. cristatellus* exhibited significantly more pushup displays after being exposed to the snake model than during the control period suggests that pushups are given as a response to the predator. Moreover, pushups were performed in accordance with the predictions of the pursuit deterrent hypothesis. This strongly supports the evolution of pursuit deterrent signals in *A. cristatellus*.

The Nature of the Signal

The correlation between performance ability and signal intensity during predation episodes has been examined for *Anolis cristatellus* (N = 21). Lizard body size was not correlated to either the number of pushups given in the presence of the snake (Spearman rank correlation: r_S= 0.07, N=21, P=0.7), nor to endurance capacity (r_S= -0.11, N=21, P=0.5). However, the number of pushups given in the presence of the snake and the endurance capacity of the individual were positively correlated (r_S=0.49, N=21, $P<$ 0.05). Number of pushups given in the presence of the snake was also positively correlated with the endurance capacity of the individual using the average score from both trials (Spearman rank correlation: r_S=0.47, N=20, $P<$ 0.05). By contrast, the number of pushups observed during the control period was not correlated to endurance capacity (r_S=0.10, N=21, P=0.6). Distance traveled in the laboratory trials was related to both endurance capacity (r_S=0.70, N=21, $P<$ 0.01) and number of pushups given in the presence of the snake (r_S =0.43, N=21, $P\leq$ 0.05). The lack of correlation between lizard size and signal intensity suggests that the size of the lizards is not a factor affecting the response that is given to the snake. Moreover, the lack of correlation between lizard size and endurance capacity suggests that the quality of the lizards does not depend on body size. The significant positive correlation between endurance capacity and signal intensity strongly supports the hypothesis of the use of honest communication by *A. cristatellus* during predator-prey interactions.

In summary, the results suggest that the antipredator responses of *A. gundlachi* and *A. cristatellus* are different. *Anolis cristatellus* responds to an approaching predator by giving conspicuous signals, whereas *A. gundlachi* relies on crypsis or fleeing. This difference seems to be related to the endurance capacity. However, data from *A. monensis* are needed to be able to evaluate this pattern. *Anolis cristatellus* is using conspicuous signals (i.e., pushups and predator inspection) in accordance with the pursuit deterrent signal hypothesis. The positive correlation between endurance capacity and the intensity of pushups suggests that *A. cristatellus* is not only communicating to the predator that it has been detected, but also its ability to escape an attack. Therefore, in *A. cristatellus,* pushups are honest signals. Despite extensive documentation and discussion of the signals that prey give to predators (reviewed in Caro 1995), this is the first study that demonstrates a direct correlation between the intensity of the signal given as a pursuit deterrent and a physiological attribute that may enhance the prey's likelihood of escaping an attack. Because pushups are widely used during anoline social interactions, including male-male competition and sexual selection (Crews 1975; Jenssen 1977; Ortiz & Jenssen 1982; Fleishman 1992), predation pressure and sexual selection may simultaneously favor the evolution of honest communication in *A. cristatellus* because both the predator and the potential mate or male rival may assess individual quality using the same signal. Additional data from *A. monensis* is critical to evaluate if this pattern is present in other species.

References Cited

Arnold, S. J. 1982. A quantitative approach to antipredator performance: salamander defense against snake attack. Copeia, 1982:247-253.

Baker, R. R. & Parker, G. A. 1979. The evolution of bird colouration. Philos. Trans. R. Soc. B., 287: 63-130.

Bennett, A. F. 1978. Activity metabolism of the lower vertebrates. Ann. Rev. Physiol., 40: 447-469.

Bennett, A. F. & Huey, R. B. 1990. Studying the evolution of physiological performance. Oxford Surveys Evol. Biol., 7: 251-284.

Bennett, A. F, Gleeson, T. T. & Gorman, G. C. 1981. Anaerobic metabolism in a lizard (*Anolis bonairensis*) under natural conditions. Physiol. Zool., 54: 237-241.

Bildstein, K. L. 1983. Why white-tailed deer flag their tails. Am. Nat., 121: 709-715.

Brodie, E. D., III. 1993. Consistency of individual differences in anti-predator behaviour and colour pattern in the garter snake, *Thamnophis ordinoides*. Anim. Behav., 45: 851-861.

Caro, T. M. 1994. Ungulate antipredator behaviour: preliminary and comparative data from African bovids. Behaviour, 128: 189-228.

Caro, T. M. 1995. Pursuit-deterrence revisited. Trends Ecol. Evol., 10: 500-503.

Crews, D. 1975. Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. Anim. Behav., 23: 349-356.

Fleishman, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. Am. Nat., 139: S36-S61.

Formanowicz, D. R., Jr., & Brodie, E. D. Jr. 1988. Predation risk and forager escape tactics. Anim. Behav., 36:1836-1838.

Garland, T., Jr. & Losos, J. B. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Ecological Morphology: Integrative Organismal Biology (Ed. by P. C. Wainwright & S. M. Reilly), pp. 240-302. Chicago: University of Chicago Press.

Gorman, G. C., Donald, G. B., Soulé, M. & Yang, S. Y. 1983. The relationships of the Puerto Rican *Anolis*: electrophoretic and karyotypic studies. In: Advances In Herpetology and Evolutionary Biology: Essays in Honor of Ernest Williams (Ed. by A. G. J. Rhodin & K. Miyata), pp. 626-642. Museum of Comparative Zoology: Cambridge, Massachusetts.

Greene, H. W. 1988. Antipredator mechanisms in reptiles. In: Biology of the Reptilia, Vol. 16, Ecology B, Defense and Life History (Ed. by C. Gans & R. B. Huey), pp. 1-152. New York: Alan R. Liss.

Hailman, J. P. 1977. Optical signals, animal comunication and light. Indiana University Press, Bloomington.

Hasson, O. 1991. Pursuit-deterrent signals: communication between prey and predator. Trends Ecol. Evol., 6: 325-329.

Henderson, R. W., & Crother, B. I. 1989. Biogeographic patterns of predation in West Indian colubrid snakes, p. 479-517. In: Biogeography of the West Indies: past, present, and future. C. A. Woods (ed.). Sandhill Crane Press, Gainesville, Florida.

Jenssen, T. A. 1977. Evolution of anoline display behavior. Am. Zool., 17: 203-215.

Jenssen, T. A. 1978. Display diversity in anoline lizards and problems of interpretation. In: Behavior and Neurology of Lizards (Ed. by N. Greenberg & P. D. MacLean), pp. 269-285. Maryland: National Institute of Mental Health.

Leal, M. & Rodríguez-Robles, J. A. 1995. Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). Copeia, 1995: 155-161.

Leal, M. & Rodríguez-Robles, J. A. 1997a. Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. Anim. Behav., 54: 1147-1154.

Leal, M. & Rodríguez-Robles, J. A. 1997b. Antipredator responses of the Puerto Rican giant anole, *Anolis cuvieri* (Squamata: Polychrotidae). Biotropica, 29: 372-375.

Leal, M. Honest signalling during prey-predator interactions in the lizard *Anolis cristatellus*. Anim. Behav. IN PRESS

Leal, M., and R. Thomas. 1994. Notes on the feeding behavior and the exhibit of caudal luring by juvenile *Alsophis portoricensis* (Serpentes: Colubridae). J. Herp., 28: 126-128.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool., 68: 619-640.

Losos, J. B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. Ecol. Monogr., 60: 369-388.

Losos, J. B. & Irschick, D. J. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. Anim. Behav., 51: 593-602.

Pérez-Rivera, R. A. 1985. Nota sobre el hábitat, los hábitos alimentarios y los depredadores del lagarto *Anolis cuvieri* (Lacerta: Iguanidae) de Puerto Rico. Carib. J. Sci., 22:101-103.

Rand, A. S. 1964. Ecological distribution in anoline lizards of Puerto Rico. Ecology, 45; 745-752.

Rodríguez-Robles, J. A. & Leal, M. 1993. Natural History Notes: *Alsophis portoricensis* (Puerto Rican Racer). Diet. Herpetol. Rev., 24: 150-151.

Schwartz, A., & R. W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. Univ. Florida Press, Gainesville, Florida.

Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In: Lizard ecology: studies of a model organism. (Ed. by R. B. Huey, Pianka E. R. & Schoener T. W.), pp. 326-370. Harvard University Press, Cambridge, Massachusetts.

Wine, R. N, & Gatten, R. E. Jr. 1992. Glycolytic support for locomotion in *Anolis carolinensis* and *Rana pipiens*: Simultaneous effects of temperature and duration of exercise. Physiol. Zool., 65: 724-741.

Zahavi, A. 1975. Mate selection - a selection for a handicap. J. Theor. Biol., 53: 205-214.

Zahavi, A. 1987. The theory of signal selection and some of its implications. In: Proceedings of the International Symposium of Biological Evolution (Ed. by V. P. Delfino), pp. 305-327. Bari: Adriatica Editrica.

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Our research on the Caribbean anole radiation continues apace. Integral to understanding patterns of evolutionary diversification is a robust hypothesis of phylogenetic relationships. Todd Jackman, soon to take up an Assistant Professorship at Villanova University, has been working feverishly in the laboratory of Dr. Allan Larson on this project. One paper, reporting the results of an analysis of approximately 1400 base pairs of mitochondrial DNA for 53 species, should appear soon *in Systematic Biology*. Papers on the anoles of Jamaica (Jackman et al., submitted) and the Lesser Antilles (Creer et al., in revision) are also submitted and projects on the evolution of the *cristatellus* group and a large clade of Cuban anoles should be completed shortly. The latter project also includes data from a nuclear gene, a rhodopsin intron; this gene seems to give broadly congruent results to the DNA data, though with less resolution deep in the tree. Kevin de Queiroz has also been an active collaborator in these projects. A related project on the relationships of *A. cybotes* and relatives is discussed in Rich Glor's contribution to the newsletter. Our ultimate goal is to derive a phylogeny for the entire Caribbean radiation, or as much of it as we can get. Currently, with the help of Blair Hedges, we have data for 85% of the Caribbean species, with tissues of a few other species in hand.

Field studies on the community ecology of Caribbean anoles are also continuing. Two trips in the past five years have explored the fauna of Cuba, which is the crown jewel of the anole radiation in many respects. First, one can find more sympatric species of anoles in Cuba than anywhere else in the world. In 1997, we visited Soroa, in the footsteps of the 1983 trip by Ernest Williams, Stan Rand, Dale Marcellini and Lourdes Rodríguez Schettino of the Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba. There, we (accompanied by Rodríguez Schettino) conducted a detailed study of microhabitat partioning among the 11 sympatric species. This work was performed in conjunction with Paul Hertz and Leo Fleishman, who examined differences in thermal biology and dewlap color of the four sympatric species of trunk-ground anoles (*A. allogus*, *A. homolechis*, *A. mestrei*, and *A. sagrei*). In the spring of 1999, we travelled to eastern Cuba. On the road to La Gran Píedra, less than an hour's drive from Santiago, we found an area that probably has 11 species as well (we actually only found nine, but two species were found at both higher and lower elevations along this road, and so presumably occur there as well).

Not only does Cuba have the most species, both at a given site and throughout the island, but it also has the most amazing species. Few anoles anywhere can match the marvelous twig giants (*Chamaeleolis*), not to mention the aquatic anole, *A. vermiculatus*, which not only runs across the water basilisk-style, but also catches prey under water, or the rock-wall inhabiting *A. bartschi*, with its long legs and beautiful coloration. And that's just a sampler. Cuba is truly Anole Heaven.

The experimental introductions being conducted in collaboration with Dave Spiller (see his contribution in the Newsletter) suffered a setback when they were demolished by Hurricane Lili. However, Spiller and Thomas Schoener are now studying the effects of the curly-tailed lizard, *Leiocephalus carinatus*, on island food webs in the Bahamas. Their results have clearly shown that *Anolis sagrei* populations are hard hit by the presence of curly-tails. Moreover, the anoles shift their habitat use radically, moving up into the vegetation to get off the ground and away from the rapacious curlies. As a result, their locomotor behavior appears very different. Future studies will document in great detail how these habitat shifts affect not only their locomotion, but also their foraging and social behavior. Ultimately, of course, such shifts could lead to selective pressure favoring the evolution of shorter legs or other morphological features. This, too, will be investigated.

A previous study (Losos et al., 1997) reported that *A. sagrei* populations introduced to small islands in the Bahamas differed in hindlimb length. Moreover, differences in limb length corresponded to differences in habitat use: populations using broader surfaces had relatively longer limbs than those using narrower surfaces. As we suggested in our paper, two processes could be responsible for this pattern: genetic adaptation and adaptive phenotypic plasticity.

To test the adaptive plasticity hypothesis, we raised baby *A. sagrei* from Florida at the St. Louis Zoo in two environments. Half were raised in aquaria with broad surfaces (2x4's), whereas the other half were raised on narrow (3/4" diameter) wooden dowels. The results were clearcut: lizards raised on narrow surfaces developed shorter legs than lizards raised on broad surfaces (Losos et al., in revision). These results have several implications. First, the differences among the experimental populations in the Bahamas may be the result of phenotypic plasticity (the magnitude of difference in hindlimb length in the growth experiment is comparable to that detected among islands). The next step will be to conduct a common garden experiment in which anoles from populations differing greatly in hindlimb length are raised under similar circumstances to see if the differences persist.

Second, the differences induced in the growth experiments are substantially less than those characterizing different ecomorph types. That is, although the lizards in the growth experiment differ in hindlimb length, they are all clearly recognizable as long-legged trunk-ground anoles. Hence, even when growing lizards under these extremely different environmental circumstances, the lizards did not exhibit differences in any way rivalling those observed between, for example, trunk-ground and twig anoles.

Third, these findings suggest the possibility that plasticity may have played a role in the anole adaptive radiations. By allowing populations to adjust to novel environmental circumstances, plasticity may facilitate habitat shifts. Once a population is using a new habitat, subsequent genetic mutations may arise and be incorporated, thus greatly extending the initial differences. In this way, plasticity may be an important initial step in adaptive radiation.

The next step in this work, then, is to determine whether this plasticity is a widespread trait in anoles. On the one hand, it may represent a basic result of how growing bone responds to different stresses and strains promoted by using different microhabitats. In this case, one would expect all anoles to exhibit similar plasticity. On the other hand, among anole species, *A. sagrei* probably uses the broadest range of different habitats. Thus, it is possible that *A. sagrei* has evolved this plasticity as an adaptation to its breadth of habitat use. By conducting similar growth experiments on other species, we hope to distinguish between these two possibilities.

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Color Signal Evolution in an Ancestor-Descendant Species Pair of Caribbean Anoles

Introduction

Signal evolution is driven to a large extent by details of signal perceivers' sensory systems. Male and female conspecifics, as well as predators, figure most prominently here because of their direct effects on a signaler's reproductive success (e.g. Endler, 1991, 1992). A signal's effectiveness depends not only on its design and on perceivers' sensory systems, however, but also on characteristics of the environment that enhance or attenuate its transmission. For visual signals, such environmental variables include attributes of the ambient light in which a signal is viewed, as well as features of the visual background against which a signal must be discriminated (e.g. Endler and Thery, 1996).

The stereotyped headbob motions and colorful dewlaps of anoles have long attracted the attention of researchers interested in the evolution of animal signals (e.g. Greenberg & Noble, 1944). Headbob patterns have been described and quantified in great detail for a number of species, with a considerable portion of this work having been carried out by Tom Jenssen and his students (e.g. Jenssen 1977, 1978; DeCourcy and Jenssen, 1994**).** For a few species, the evolutionary stages through which headbob patterns may have passed have been suggested, and predictions about the social correlates of display complexity have been made (e.g. Jenssen 1983).

In contrast to detailed descriptions and analyses of headbob patterns, dewlap color characterization has until recently been left largely to verbal descriptions, with instrument-based spectral analyses being comparatively rare. An exception to the rule has been Leo Fleishman's work on the visual ecology of anoles, which continues to provide insights into the evolution of *Anolis* motion and color displays (e.g. Fleishman 1986, 1988a,b, 1992, Fleishman et al. 1993,1995, 1997, Hertz et al., 1994). Last, aside from *Anolis carolinensis*, scant attention has been paid to the pigmentary bases underlying dewlap colors in anoles (e.g. Ortiz and Maldonado, 1966).

Against this backdrop, I would like to describe a portion of my current work on color signals in anoles. The research that I will report here is focused on an ancestor-descendant species pair in the Jamaican *Anolis* radiation (the *'grahami* series') whose dewlaps are dramatically different in coloration (Fig. 1). The ancestor, *Anolis grahami* on Jamaica, has a bright orange dewlap with a narrow yellow rim, whereas the dewlap of the descendant, *Anolis conspersus* on Grand Cayman, reflects light most strongly in the near ultraviolet (peak reflectance >40% at 340 nm). The fact that this dewlap appears blue to humans belies its true nature as an ultraviolet signal. A high level of confidence in the phylogenetic relationship of these two species provides a fortunate and fruitful context for a study of color signal evolution in anoles.

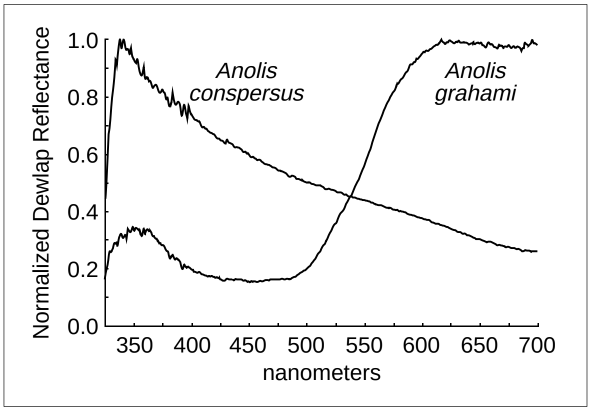

Fig. 1. Normalized mean dewlap reflectance spectra from *Anolis conspersus* and *Anolis grahami*.

Evidence For An *A. grahami/A. conspersus* Ancestor-Descendant Relationship

For over a century, *A. conspersus* and *A. grahami* have been viewed as sister species (Grant, 1940; Williams, 1969). Recently this proposal has received strong support from mtDNA sequences (Jackman et al., in review). Those data also indicate that *A. conspersus* and the southern/central (s/c), or 'Kingston,' population of *A. grahami* are much more closely related than either is to *A. grahami* in western Jamaica (Jackman et al., in review). The structure of headbob displays in these taxa likewise is consistent with this interpretation (Fig. 2; Macedonia and Clark, ms accepted pending revision). Furthermore, headbob display data indicate that *A. grahami* from eastern Jamaica (*A. g. aquarum*) lacks the synapomorphy of a plateau-shaped first unit that links *A. conspersus* specifically to the s/c *A. grahami* population (see also Jenssen, 1981).

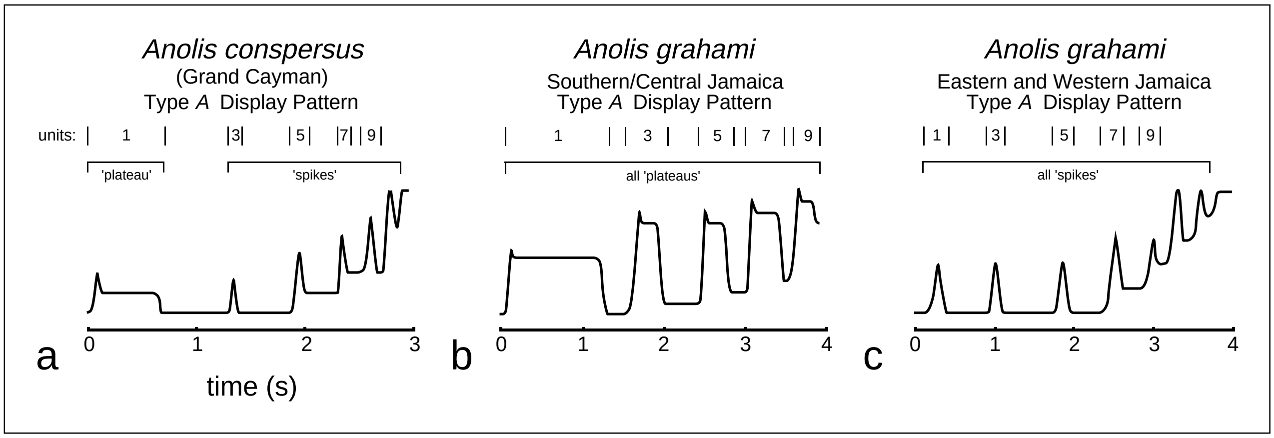

Fig. 2. Headbob displays from *Anolis conspersus* and the three *Anolis grahami* populations.

Although the statements above are consistent with a sister-taxon interpretation, they do not provide evidence for an ancestor-descendant relationship *per se*. Support for that particular argument emerges from the following four points:

1. Parsimony. The prospect that *A. grahami* rafted from Jamaica to Grand Cayman is simpler than the alternative that *A. conspersus* shared a common ancestor with *A. grahami* on Jamaica, rafted to Grand Cayman, and then became extinct on Jamaica. There is no support whatsoever for the idea that *A. conspersus* could have rafted from Grand Cayman to Jamaica and then given rise to any anole on that island.

2. Ocean Currents. Ocean currents flow from Jamaica toward the Caymans, not the reverse (e.g. Grant, 1940; Williams, 1969).

3. Sea Levels. No portion of Grand Cayman has been continuously above sea level for more than 3 MY (e.g. Haq et al., 1987), and perhaps closer to 2 MY (F. Burton, pers. comm.). For *A. conspersus* to be ancestral to any Jamaican anole, the radiation on Jamaica would have to have occurred less than 3 MYA (see below).

4. Molecular Clock. Molecular clock estimates for the first divergence in *Anolis* stock on Jamaica range from a minimum of 7 MYA (Hedges and Burnell, 1990) to a recently calibrated estimate of 13 MYA (Jackman et al. in review). The mtDNA research by Jackman et al. (in review) provides a molecular clock date of 2.8 MYA for the divergence of *A. conspersus* and the s/c *A. grahami* population. In contrast, *A. grahami* in western Jamaica is calculated to have diverged from the s/c *A. grahami* population about 7.5 MYA. All the evidence currently available therefore is consistent with the hypothesis that *A. grahami* from southern/central Jamaica is the direct ancestor of *A. conspersus* and that it colonized Grand Cayman by way of Jamaica approximately 2-3 MYA.

Skin Pigments and Dewlap Color Evolution in *Anolis conspersus*

Previous research on lizard coloration mechanisms has shown that skin color results from pigments (pteridines, carotenoids, and melanin) contained within dermal chromatophores and from structural colors produced by iridophores that lie beneath the chromatophores (e.g. Taylor and Hadley, 1970; Morrison et al., 1995, 1996). Together with several colleagues, I recently conducted a study of skin coloration in the *grahami* series anoles (Macedonia et al., in press). Among the goals of this work was to uncover the mechanisms responsible for the UV/blue dewlap of *A. conspersus*. We used thin layer chromatography to identify pteridines, spectrophotometry to measure carotenoid absorbance spectra, and histology to resolve patterns of melanin distribution in the dewlap.

Why is the dewlap of *A. conspersus* such a potent UV reflector? First, pteridine quantities in the *A. conspersus* dewlap are greatly diminished compared to those found in *A. grahami* and most other *grahami* series anoles (Macedonia et al., in press). In particular, pteridines responsible for the orange coloration of the *A. grahami* dewlap (drosopterins) have been reduced to trace amounts in *A. conspersus*. Because most pteridines absorb short wavelength light, their reduction in the *A. conspersus* dewlap results in more short wavelength light being reflected. Second, although the yellowish pteridine 'sepiapterin' is present in the dewlap skin of some *grahami* series species, including *A. grahami*, carotenoids are the primary source of yellow coloration in *Anolis* skin (e.g. Ortiz and Maldonado, 1966). Like pteridines, most carotenoids absorb short wavelengths (Fig. 3). The absence of carotenoids from the dewlap of *A. conspersus* (Fig. 3b) contributes greatly to that dewlap's reflectance profile.

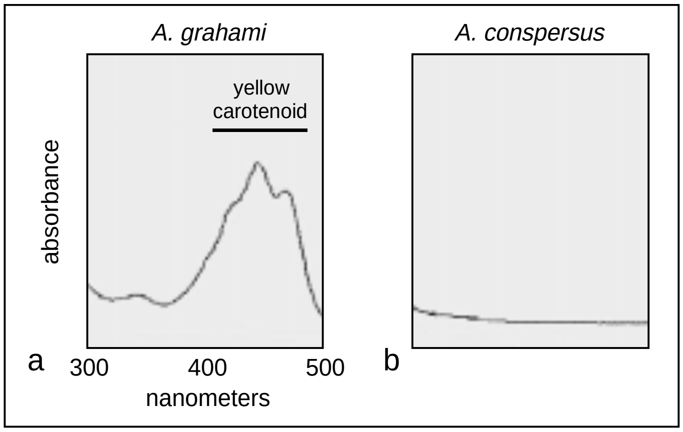

Fig. 3. UV-VIS spectrometry of dewlap extracts in 95% ETOH. (a) Characteristic 3-peaked shape of carotenoid absorption spectrum; (b) carotenoids absent from *A. conspersus* dewlap.

Third, histology revealed an additional layer of melanin in the *A. conspersus* dewlap unobserved in any other *grahami* series taxon. This melanin band lies directly above the fascia that separates the hypodermis from the muscle and cartilage that erect the dewlap (Fig. 4b). Virtually all wavelengths that pass through the iridophores and do not strike a melanophore should be absorbed by this melanin layer. The strong UV reflectance and blue color of the *A. conspersus* dewlap therefore is a product of (a) chromatophores with few pteridines or carotenoids, (b) short wavelength-reflecting iridophores, and (c) an additional melanin layer that greatly increases color saturation by absorbing long wavelengths (whose reflectance would make the dewlap appear pale blue - a condition occasionally witnessed in the brown morph, *A. c. lewisi*).

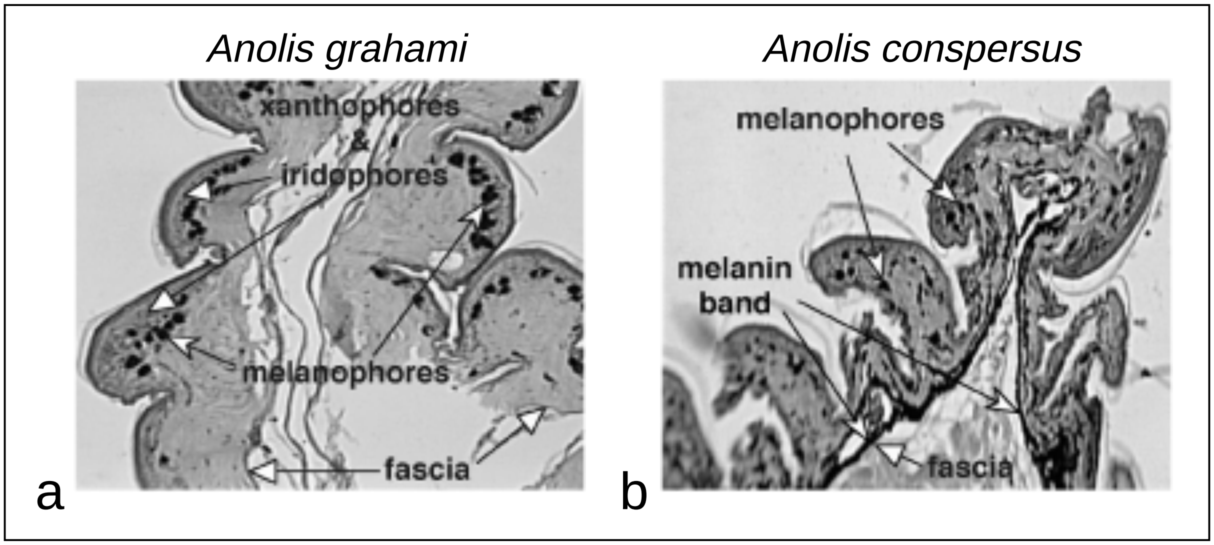

Fig. 4. Dewlap sections cut in the horizontal plane. The front of each dewlap is at the top of each illustration. Skin folds on the left and right side of each section allow the dewlap to extend in life. The open area interior to the fascia in 5a contained muscle tissue (seen in 5b) prior to sectioning.

Visual Photopigments and UV Signal Preadaptation

Might *A. conspersus* have evolved some visual system quirk that selected for its UV-bright/blue dewlap (i.e. 'sensory drive'; see Endler, 1992)? To assess this possibility, Ellis Loew at Cornell University used microspectrophotometry (MSP) to determine the classes of photopigments present in the retinas of these two species. Results showed that, despite their dramatically different dewlap colors, the differences in their visual pigment peaks are trivial and both species have a UV-sensitive visual pigment (*A. grahami* absorbance peaks: 565, 495, 460, 366 nm; *A. conspersus* absorbance peaks: 562, 500, 460, 365 nm; E. Loew, unpub. data).

Thus, a mechanism that facilitates perception of UV wavelengths did not evolve *de novo* in *A. conspersus* and is an ancestral trait. In fact, every *Anolis* species examined with MSP to date has been found to possess a UV-sensitive photopigment (Fleishman et al., 1993, and pers. comm.). Anoles in general therefore appear to be preadapted to make use of UV in signaling. If visual system changes did not play a role in *A. conspersus* dewlap color evolution, what did? In the last section of this report I will outline a hypothetical sequence of events that could have provided the impetus for the orange-to-UV/blue dewlap transition. Before getting to that, however, I would like to discuss another aspect of adaptive coloration in this anole.

Body Color Variation in *Anolis conspersus*

An interesting case of body color variation exists in *A. conspersus*, as three color morphs occur on Grand Cayman: a leaf green morph with a yellowish head (*A. c. conspersus*), a brown morph with brown or bluish legs (*A. conspersus lewisi*), and a taxonomically unrecognized turquoise blue morph. These distinctions apply to sexually-mature males; females and young tend to be uniform shades of tan or gray.

The green morph is restricted primarily to the George Town area in the southwest corner of Grand Cayman. This is the tourist center and the location of greatest rainfall (Fig. 5). The greater precipitation in this part of the island stems from convection currents that rise from a large (8,500 acres) central mangrove that abuts the eastern edge of the North Sound. The moisture condenses as it rises and cools to form clouds that drift directly over George Town and out to sea (Burton, 1994, and pers. comm.). The few plots of undisturbed habitat that can be found in this area often harbor large coconut palms and are relatively lush.

The brown morph, in contrast, is found to the east of the 900 mm isohyet that runs longitudinally roughly from Half Moon Bay to the north coast (Fig. 5). The highly porous, exposed limestone substrate in this region results in vegetation that ranges from open woodland to xeric habitat. Mangrove also is present in some areas.

The blue morph is the most widespread color variant. It occurs in all types of habitats west of the brown morph's distribution, with the exception of enclaves in the southwest containing only the green morph. The blue morph also is the most variable of the three forms in coloration. Curiously, island-wide collections made in the 1930's (e.g. Grant, 1940) make no mention of a blue morph. Moreover, Grant (1940) describes *A. conspersus* in West Bay (Fig. 5) to be yellow-green in color. In a number of surveys of West Bay made during the 1990's by Sandy Echternacht, Glenn Gerber, and myself, the blue morph is the only color variant we have seen there. This part of Grand Cayman has undergone extensive development over the past half-century and, apparently, the blue morph has displaced the green morph as old-growth forest has given way to residential and commercial development.

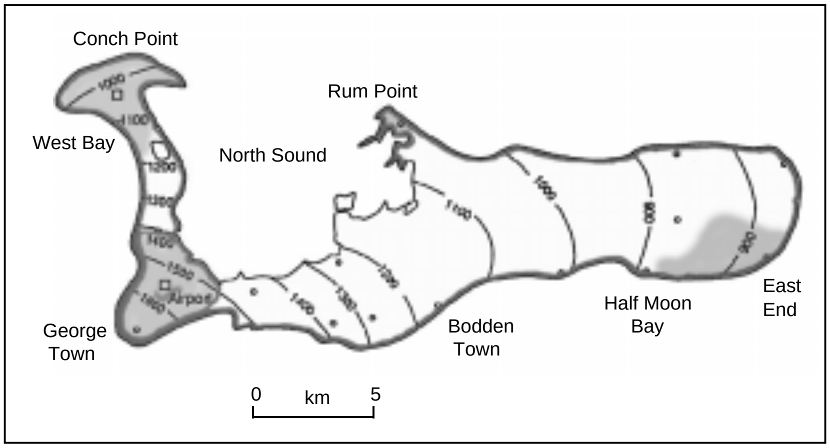

Fig 5. Areas on Grand Cayman surveyed for *Anolis* in June 1998. Coastline outlined in dark gray was sampled at irregular geographic intervals. Lighter gray patches depict areas sampled repeatedly. Isohyets (mm) show rainfall in 1987, a relatively typical year (after Ng and Beswick, 1994).

Quantifying Color Morph Distinctiveness

From 2-11 June 1998, Sandy Echternacht and I mapped the distribution of the three color morphs on Grand Cayman. Although our survey was not exhaustive, over 40 sites distributed along the coast and inland were examined (Fig. 5).

Several types of data were obtained routinely, such as road map location, global positioning system (GPS) coordinates, topographic description, dominant plant species, quantity and color morph of each *A. conspersus* sighted, and quantity/species of other lizards seen. To quantify coloration in adult male *A. conspersus*, I gathered spectral radiance data from six body locations: head, dewlap, back, belly, leg, and tail. Readings were obtained through a fiber optic cable connected to an Ocean Optics S2000 portable spectrometer leading into a laptop computer. A reflectance standard was used to calculate reflectance from the radiance data.

Spectral data were gathered for 44 adult males (9 brown, 12 green, and 24 blue) at a resolution of (approx.) 0.37 nm steps. Over the region of interest, which was 325 to 700 nm, this produced 1085 data points per reading. For most statistical comparisons, these spectra were converted into a more manageable form that retained the basic attributes of the original data set (see Endler, 1990:339-340). I divided each spectrum into 'color segments' containing 217 points each that correspond roughly to ultraviolet (325-400 nm), violet-blue (400-475 nm), green (475-550 nm), yellow-orange (550-625 nm), and red (625-700 nm). Each 217-point color segment then was summed, producing one value per segment. Finally, each of these 5 values was divided by the sum of the unsegmented spectrum (325-700 nm) to produce five 'color scores' that summarized the relative brightness of each color segment.

The color scores were not normally-distributed and were highly correlated among themselves, but these problems can overcome with a principal components analysis (PCA). PCA creates hierarchically-ordered factors that are normally-distributed, uncorrelated, and weighted linear combinations of the original variables (Kleinbaum and Kupper, 1978). The first few factors usually explain most of the variance in the data set, i.e. these are the 'principal' components. The factors then can be rotated so that they are more readily interpretable in terms of the original input variables.

From 30 color scores (five color segments X six body locations), a PCA created eight factors meeting Jolliffe's criterion (Eigenvalues >0.7; Jolliffe, 1986) that accounted for 90.4% of the variance in the original variables. The first two factors alone explained 57% of the variation (PC1 = 41.8%; PC2 = 15.2%; Fig. 6). Following axis rotation, PC1 was weighted on *head*, *back*, and *tail* color scores, and PC2 on *leg* color scores.

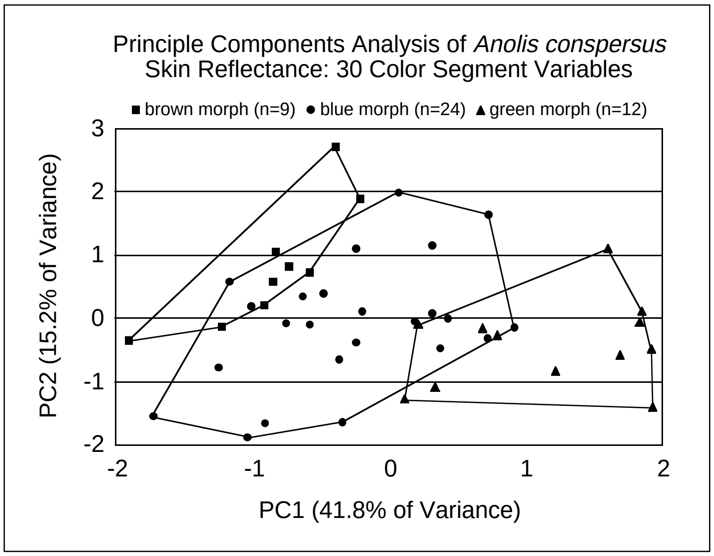

Fig 6. PCA of 30 skin reflectance variables ('color scores') for *A. conspersus*.

When creating factors, PCA does not consider which groups contribute which data points. This means that the PCA should only separate green, brown, and blue morphs in principal component space if that separation minimizes data set variance. It is evident from this analysis that the three color morphs are 'natural groups,' although not all groups are equally distinctive. The blue morph, which exhibits the most color variation, has four individuals within the green morph color space and two individuals within the brown morph color space (Fig. 6). I tested for population distinctiveness in coloration by entering the PCA factors into a One-Way ANOVA, with morph color as the grouping variable. Results showed four factors to differ significantly among the color morphs, and protected post-hoc tests (Duncan's Multiple Range Test) revealed which morphs differed in pairwise comparisons: PC1 ($F_{2,42}=10.02$, $P<0.001$; $P<0.05$ for green vs. blue and green vs. brown), PC4 (variance explained: 7.9%; weighted on 'belly' scores: $F_{2,42}=5.49$, $P<0.01$; $P<0.05$ for green vs. blue), and PC7 (variance explained: 3.2%; weighted on 'head' scores: $F_{2,42}=7.50$, $P<0.01$; $P<0.05$ for green vs. brown and blue vs. brown). The only factor that reliably distinguished the blue morph from the green was roughly equivalent to *belly* coloration, which in the green morph is yellowish and in the blue morph is bluish-white.

Having shown that the three color variants of *A. conspersus* are statistically distinguishable, I would like to turn to the topic of habitat lighting and its potential relationship to the color variation observed in *A. conspersus*.

Light Habitats and Color Signal Evolution

To a large extent, sensory systems define the parameters of effective signal design. For animals that rely on vision as their primary sensory modality, the quality of light in their natural habitats is crucially important for life-sustaining activities like finding food and mates, defending resources, and avoiding predators. All visual signals involve light in some manner, and because most anoles are arboreal, this typically means forest light.

John Endler (1992, 1993) has characterized six types of light conditions in forest environments. Four of these vary with forest geometry (i.e., 'forest shade,' 'woodland shade,' 'small gaps' and 'large gaps'), one varies with time of day ('early/late'), and one with weather ('cloudy'). Endler's research in this area centers on the implications of 'light habitats' for the evolution of animal color patterns. His studies on courtship in guppies (e.g. Endler, 1991) and birds (Endler and Thery, 1996) in the neotropics reveal how the costs and benefits of signal conspicuousness are balanced between the attraction of predators and mates.

Likewise, Leo Fleishman has spent well over a decade elucidating the interplay between visual physiology/behavior in anoles and the light habitats in which their visual displays are used. His efforts have broadened our understanding of how response properties of the *Anolis* visual system and characteristics of the habitats in which they live have influenced the design of their motion and color signals (Fleishman 1988a, b; 1992, 1993, 1995, 1997; this volume).

Inspired by these researchers' work, I have been investigating the potential relationship of ambient light to skin coloration in *A. conspersus*. I used a hemispherical cosine receptor to acquire spectral irradiance (habitat lighting) readings; data collection was restricted to relatively clear days. Four types of readings were obtained in locations where only one type of color morph was present. The measures included (1) *down-welling irradiance* (cosine receptor oriented directly upward); (2) *side-welling irradiance* (cosine receptor parallel to the ground, pointing away from me); (3) *line-of-sight radiance* (colimmating lens positioned parallel to ground at a tree trunk location where a lizard had just been with a reading taken in each direction an eye had been oriented); and (4) *tree reflectance* (reading taken of the tree bark on which a lizard had just been perched, followed immediately by a reading of a white standard at the same location).

Figure 7 illustrates three differences in irradiance spectra found in the shade of the color morph-specific sites: (1) wavelengths in the blue-blue/green region of the spectrum (475-515 nm) were proportionally stronger in the blue morph sites, (2) longer wavelengths (yellow, orange, brown: 570-610 nm) were proportionally stronger in the brown morph sites, and (3) although the middle wavelengths (green) are strongest in absolute terms in all sites, the irradiance spectrum is narrowest in the green morph sites. It is intriguing that irradiance spectra from the blue and brown morph sites exhibited greater intensity in the parts of the spectrum that should reflect best from their bodies.

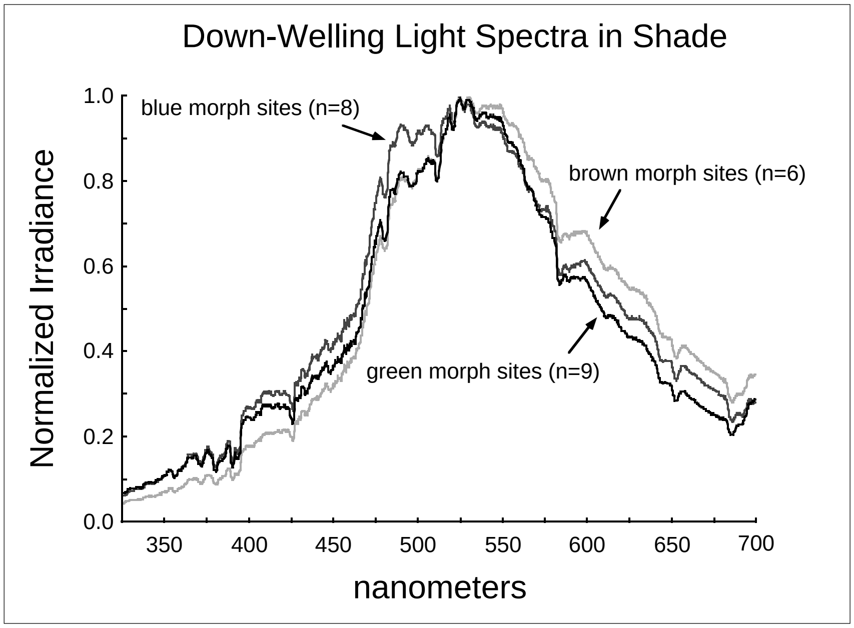

Fig. 7. Normalized irradiance spectra from sites containing only one of the three *Anolis conspersus* color morphs. Light gray = brown morph sites, dark gray = blue morph sites, black = green morph sites.

To determine if these differences would hold when the spectra were converted to color scores (and sample sizes decreased from n=1085 to n=5 per spectrum), twenty color scores (four variables X five color segments) were calculated and entered into a PCA. The PCA produced six factors with Eigenvalues >0.7 that together accounted for 93.6% of the variation in the data set. The first two factors explained 59.5% of the variance. After rotation, PC1 was weighted primarily on *down-welling irradiance* (41.4%) and PC2 on *side-welling irradiance* (18.2%).

To address the question of color morph habitat distinctiveness in another way, the PCA factors were entered into a One-Way ANOVA with morph color again as the grouping variable. Three factors differed significantly among the morph-specific habitats, and Duncan's Multiple Range Test revealed which pairs were responsible: PC1 ($F_{2,20}$=10.31, P<0.001; P<0.05 for blue vs. brown and green vs. brown), PC2 ($F_{2,20}$=9.09, P<0.01; P<0.05 for blue vs. brown and blue vs. green), and PC3 (variance explained: 11.6%; weighted on *tree trunk reflectance*: $F_{2,20}$=4.74,P<0.05 for green vs. brown).

I conclude at this point that results above are sufficiently consistent with the idea that the three *A. conspersus* color variants, as well as the ambient light characteristics of the habitats in which they reside, are different enough to be considered distinctive. Although I find this interesting, what I really wish to determine is whether or not habitat lighting and *A. conspersus* coloration are meaningfully related. I will address this issue in two ways here. First, I will describe a discriminant function 'cross-validation' analysis of an unusual kind that provides some insights. Then, I will push the speculation envelope by proposing a sequence of events that could have led to the dewlap color and some of the body color traits observed in *A. conspersus* today.

A Test for a Morph Color/Habitat Lighting Relationship

I used a procedure in stepwise discriminant function analysis (DFA) known as 'cross-validation' to investigate the strength of a relationship between light habitats and coloration in *A. conspersus*. As typically applied, a cross-validation is simply the case where half of a data set is used to create discriminant functions that then are used to classify the other half of the data set. Its purpose is to determine how well the discriminant functions perform in distinguishing groups containing individuals other than those which the functions were specifically tailored to discriminate. I reasoned that if the lizard color/habitat lighting association were strong, then the functions generated to discriminate among light habitats should also be able to classify the lizard reflectance PC scores above the level of chance. To test this idea, I entered the ten PCA factors with Eigenvalues >0.1 that were created from the habitat lighting data into a stepwise DFA. The DFA selected four significant factors to create its classification functions. These four factors, and the two subsequent functions that they generated, are identical to those described on the previous page which classified the habitat lighting PCA scores. This time, however, those functions were used to classify the lizard reflectance PCA scores.

Nine permutations are possible in classifying the three color morphs (blue classified as blue, blue classified as brown, blue classified as green, brown classified as blue, etc.). I used a chi-square test to determine if the observed classifications were significantly greater than those expected at random. Results showed that brown morph subjects were correctly classified in 7 of 9 cases (chi-square = 8.67, $P<0.02$) and green morph subjects were correctly classified in 7 of 12 cases (chi-square = 6.5, $P<0.05$). Blue morph subjects, the most variable in coloration, were not classified at a level differing from random (chi-square = 1.65, NS). In sum, these results suggest that the relationship between morph coloration and habitat lighting is so predictable that information about the *spectral habitats alone* can determine, for the two taxonomically recognized color morphs, which morph belongs with which light habitat. Now *that* is impressive!

A Scenario for Color Signal Evolution in *Anolis conspersus*

In this final section, I will present a scenario regarding how *A. conspersus* came to possess a short wavelength-reflective dewlap despite the fact that its direct ancestor and all other members of its clade sport long wavelength-reflective dewlaps. Some aspects of this scenario are factual; others, purely speculative. Fortunately, the *Anolis* Newsletter is an appropriate forum to convey ideas that require additional research.

Molecular clock dating of mtDNA sequences suggests that *A. conspersus* arose from *A. grahami* about 2.8 MY ago (Jackman et al., in review). The current stance on the geological history of Grand Cayman is that at least part of the island has been continuously above water for approximately 2 MY (F. Burton, pers. comm.). Accepting some error in one or both estimates, *Anolis grahami* must have colonized Grand Cayman soon after the final emergence of that island from the Caribbean Sea 2-3 MYA.

Grand Cayman is a low-lying island, reaching 17 meters in elevation at its highest point in the east. Most of the island, however, is less than 4 meters above sea level (Ng and Beswick, 1994). Western Grand Cayman, being roughly 13 m lower than the highest areas in the east, might have taken an additional several hundred thousand years to break the ocean surface. Although the elevation of the island above the sea floor has been stable for at least the past 0.5 MY (Vezina et al., 1999), sea levels have fluctuated. Wave-cut notches indicate that the most significant highstand occurred 125k years ago when the Caribbean Sea was 6 meters higher than now (Jones and Hunter,1990). The only significant portion of the island remaining above water was roughly a 40 km^2 area in the east (my estimate from map in Jones and Hunter,1990).

Today, the eastern end of Grand Cayman consists primarily of mixed woodland and scrubland. The eastern end is drier than the west (Fig. 5) because (a) it takes the westerly winds directly, (b) much of the ground is porous limestone with poor soil to none at all, and (c) it doesn't have the benefit of the central mangroves which provide convection-based rainfall to the west. If eastern Grand Cayman emerged above sea level between 2 and 3 MYA, it must have been at that time a small mound of porous limestone containing little else but low-stature, salt-tolerant, scrubby vegetation.

How did the *A. grahami* colonists deal with such an inhospitable place? *Anolis grahami* is somewhat preadapted to survive such rigors, as it is heliophilic (Wingate, 1965; Rand, 1967;

Schoener, 1970, 1971; Losos, 1996) and is a hardy anole in general (pers. obs.). Under colonizing conditions, however, thermoregulation and water balance might have been forces with substantial influence on how and where this species spent its time.

It has been shown that anoles reduce evaporative water loss (EWL) by decreasing skin permeability through the deposition of lipids at the epidermis. A reduction in EWL reaching a 50% maximum occurs in about a week's time (e.g. Kobayashi et al., 1983; Kattan and Lillywhite, 1989). Importantly, EWL increases with increasing temperature and with decreasing humidity. Even with this adaptation, however, conditions on emergent Grand Cayman must have been extremely challenging. Perhaps the most direct means to reduce EWL in this environment would have been to maintain lower body temperatures by remaining *in the shade* whenever possible. Contemporary *A. conspersus* prefers the shade and cannot tolerate temperatures as high as those enjoyed by *A. grahami* (e.g. Schoener, 1967; Losos et al., 1993; pers. obs.).

Early in this report I stated that the orange coloration in the *A. grahami* dewlap is the result of two kinds of pigments: yellow carotenoids and reddish-orange pteridines. These pigments selectively absorb short wavelengths, but are transparent to long wavelengths, which reflect back into the environment. The orange dewlap serves *A. grahami* well as a long wavelength reflector and is best suited for signaling in sunlight. The same dewlap would make a rather miserable reflector in an open, desert/woodland shade environment, however, which consists mostly of UV/blue skylight. If the colonists spent much time in the shade to reduce EWL, they would have done so at the price of a major reduction in dewlap signal effectiveness. If so, selection should have favored mutations that interfered with deposition of short wavelength-absorbing pigments in the dewlap. It is conceivable that such mutations could spread rapidly through an initially small population.

Reducing short wavelength-absorbing pigments *per se* would be insufficient to convert a long wavelength reflector into a short wavelength reflector. This could, however, produce an *all*-wavelength reflector. A white (or grayish-white) dewlap would have functioned much better than an orange one in short wavelength-biased shade, as at least it would be reflecting the short wavelengths rather than absorbing them. But a good short wavelength reflector requires absorption of at least some of the middle and long wavelengths. This solution eventually manifest itself in the form of a melanin layer deposited directly above the silvery fascia in the dewlap - a trait that is unique to *A. conspersus* in the *grahami* series anoles.

As Grand Cayman continued to rise above the sea floor, more of the western portion of the island was exposed, vegetated, and inhabited by *A. conspersus*. The alternation of glacial and warming periods would have elicited a number of expansions and contractions of Grand Cayman's land surface (e.g. Vezina et al., 1999), but sea levels began to recede for the last time about 125k years ago (Jones and Hunter, 1990). *Only since this time period* could the extensive central mangroves have formed permanently on the island and altered the botanical makeup of western Grand Cayman.

As mentioned earlier, moisture rising from the central mangroves causes clouds to form and move westward, with the prevailing winds taking many of them over the George Town area (Burton, 1994). This rainfall pattern selected for more water tolerant vegetation, like palm forest. Until the central mangrove was established and became a climatic influence on western Grand Cayman, i.e. less than 100k years ago, there is no reason to consider that a green morph existed. (This can be tested. If the brown morph from eastern Grand Cayman has been on the island for 2MYor longer, but the green morph has been around for less than 100k years, considerable differences in genetic variation between the two morphs should be detectable with molecular methods).

As *A. conspersus* began to occupy these wetter, greener areas, they found themselves in an ironic situation: a UV-bright/blue dewlap is a poor signaling device in a habitat rich in middle wavelengths but comparatively weak in short wavelengths. Even the orange dewlap of *A. grahami* would have served them better, although a yellow dewlap would perhaps be best. Yet, the green morph still exhibits a UV-bright/blue dewlap like the other color morphs. Why should this be? I speculate that the genetic change responsible for the loss of carotenoids in the dewlap was a kind of Rubicon for *A. conspersus* from which there was no turning back. This may explain the yellowish head of the green morph, which can be very yellow in some of the more dimly lit forest shade sites where it is found (Fig. 8). A yellow head cannot function with the efficacy of a yellow dewlap, of course, because it can never be hidden. But it *can* serve as a color/motion signal when headbobbing, and so may constitute a sort of "panda's thumb" solution to re-establishing a superior color signal in this morph of the Grand Cayman anole.

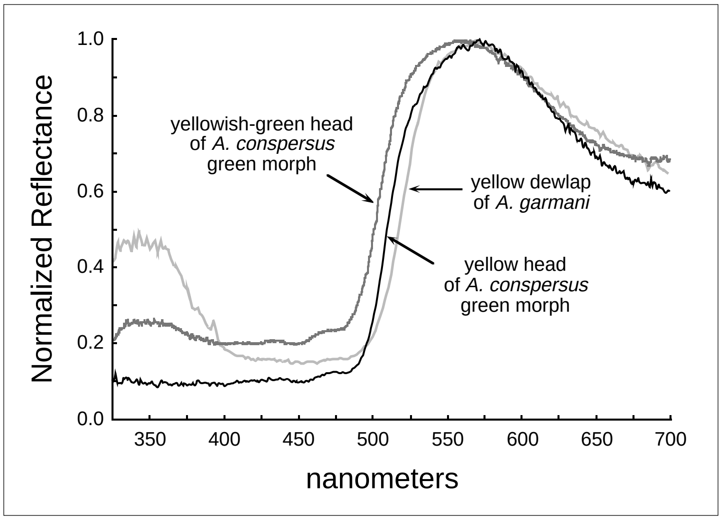

Fig 8. *A. conspersus* green morph: reflectance of individual with average yellowish-green head (dark gray) and individual with yellow head (black) compared with yellow dewlap of *A. garmani* (light gray).

Last, some thoughts on the blue morph: what is it, where did it come from, and when? Given that neither Lewis nor Grant (1940) mentioned it in their writings, I think it possible that the blue morph has existed for less than 50 years. Perhaps much less. Although it is intermediate in many characteristics of coloration between the green and brown morphs, my impression is that it is a reduced-melanin version of the brown morph, *A. c. lewisi*. Both have considerable UV/blue reflectance from their legs and tails, and the blue morph always has some brown on its back. Whether the brown or the green morph gave rise to the blue morph should be able to be determined with molecular techniques.

The presence of the blue morph in western Grand Cayman and its apparent displacement of the green morph hints that the relationship between morph color and habitat lighting is a real phenomenon. It also suggests that the blue morph has an advantage in open habitats where skylight contributes more to the shade than does a green canopy of leaves. John Endler (1997) recently pointed out in a conservation context how important light environments are both for color signals and for crypsis. Animals, like anoles, that have evolved color advertisement signals in particular light environments are likely to be vulnerable in general to habitat light alterations. Importantly, Endler suggests that among the most vulnerable will be those having evolved in 'forest shade' environments, whereas among the least vulnerable should be those from more open habitats (e.g. woodland/desert shade). The parallel with the green and the blue morphs of *A. conspersus* is uncanny. Of what precious little undisturbed green morph habitat still exists in southwest Grand Cayman, hopefully, at least a portion will remain for some time to come.

Literature Cited

Burton, F. J. 1994. Climate and tides of the Cayman Islands. In: The Cayman Islands: Natural History and Biogeography (Ed. By M. A. Brunt and J. E. Davies), pp. 51-60. Kluwer Acad. Publishers, The Netherlands.

Cooper, W. E. and Greenberg, N. 1992. Reptilian coloration and behavior, pp 298-422 in: Biology of the Reptilia, Vol. 18, Physiology E, Hormones, Brain and Behavior (C. Gans and D. Crews, eds.). University of Chicago Press: Chicago.

Decourcy, K. R. and Jenssen, T.A. 1994. Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. Anim. Behav. 47:251-262.

Endler, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns. Biol. J. Linn. Soc. 41:315-352.

Endler, J. A. 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. Vis. Res. 31:587-608.

Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. Am. Nat. 139:S125-153.

Endler, J. A. 1993. The color of light in forests and its implications. Ecol. Monogr. 63:1-27.

Endler, J. A. and Thery, M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. Am. Nat. 148:421-453.

Endler, J. A. 1997. Light, behavior, and conservation of forest-dwelling organisms. In: Behavioral Approaches to Conservation in the Wild. (Ed. by J.R. Clemmons and R. Buchholz), pp. 329-355. Cambridge Univ. Press: U.K.

Fleishman, L. J. 1986. Motion detection in the presence and absence of background motion in an *Anolis* lizard. J. Comp. Phys. A. 159:711-720.

Fleishman, L. J. 1988a. Sensory influences on physical design of a visual display. Anim. Behav. 36:1420-1424.

Fleishman, L. J. 1988b. Sensory and environmental influences on display form in *Anolis auratus*, a grass anole from Panama. Behav. Ecol. Sociobiol. 22:309-316.

Fleishman, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. Am. Nat. 139:S36-61.

Fleishman, L. J., Loew, E. R. and Leal, M. 1993. Ultraviolet vision in lizards. Nature 365:397.

Fleishman, L. J., Marshall, C. J. and Hertz, P. E. 1995. Comparative study of temporal response properties of the visual system of three species of anoline lizards. Copeia 1995:422-431.

Fleishman, L. J., Bowman, M., Saunders, D., Miller, W. E., Rury, M. J. and Loew, E. R. 1997. The visual ecology of Puerto Rican anoline lizards: habitat light and spectral sensitivity. J. Comp. Physiol. A 181:446-460.

Grant, C. 1940. The herpetology of the Cayman Islands. Bull. Inst. Jamaica, Sci. Series, 2, 1-65.

Greenberg, B. and Noble, G.K. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Voigt). Physiol. Zool. 17:392-439.

Haq, B.U.,Hardenbol, J. and Vail, P.R. 1987. Chronology of fluctuating sea levels since the Triassic. Science 235:1156-1167.

Hedges, S.B. and Burnell, K.L. 1990. The Jamaican radiation of *Anolis* (Sauria: Iguanidae): An analysis of relationships and biogeography using sequential electrophoresis. Carib. J. Sci. 26:31-44.

Hertz, P. E., Fleishman, L. J. and Armsby, C. 1994. The influence of light intensity and temperature on microhabitat selection in two *Anolis* lizards. Func. Ecol. 8:720-729.

Jackman, T., Irschick, D.J., de Queiroz, K, Losos, J.B. and Larson, A. in review. A molecular phylogenetic perspective on the evolution of *Anolis* lizards of the *Anolis grahami* series.

Jenssen, T.A. 1977. Evolution of anoline lizard display behavior. Am. Zool. 17:203-215.

Jenssen, T.A. 1978. Display diversity in anoline lizards and problems of interpretation. In N. Greenberg and P.D. Maclean (eds.), Behavior and Neurology of Lizards: An Interdisciplinary Conference, pp. 268-285. N.I.M.H., Rockville.

Jenssen, T.A. 1981. Unusual display behavior by *Anolis grahami* from western Jamaica. Copeia 1981:728-733.

Jenssen, T.A. 1983. Display behavior of two Haitian lizards, *Anolis cybotes* and *Anolis distichus*. In A. G. J. Rhodin and K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams, pp. 552-569. Mus. Comp. Zool., Cambridge Massachusetts.

Jolliffe, I. 1986. Principle Components Analysis. Springer-Verlag, New York.

Jones, B. and Hunter, I.G. 1990. Pleistocene paleogeography and sea levels of the Cayman Islands, British West Indies. Coral Reefs 9:81-91.

Kattan, G.H. and Lillywhite, H.B. 1989. Humidity acclimation and skin permeability in the lizard, *Anolis carolinensis*. Physiological Zoology 62:593-606.

Kleinbaum, D.G. and Kupper, L.L. 1978. Applied Regression Analysis and Other Multivariate Methods. Duxbury Press, Boston.

Kobayashi, D., Mautz, W.J. and Nagy, K.A. 1983. Evaporative water loss: humidity acclimation in *Anolis carolinensis* Lizards. Copeia 1983:701-704.

Losos, J.B. 1996. Dynamics of range expansion by three introduced species of *Anolis* lizards on Bermuda. J. Herpetol. 30:204-210.

Losos, J.B., Marks, J.C. and Schoener, T.W. 1993. Habitat use and ecological interactions of an introduced and native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. Oecologia 95:525-532.

Macedonia, J.M. and Stamps, J.A. 1994. Species recognition in *Anolis grahami* (Sauria: Iguanidae): evidence from responses to video playbacks of conspecific and heterospecific displays. Ethology 98:246-264.

Macedonia, J. M. and Clark, D. L. (accepted pending revision). Display behavior of male *Anolis conspersus*: structural analyses and phylogenetic implications. J. Herpetol.

Macedonia, J.M., James, S., Wittle, L.W. and Clark, D.L. in press. Skin Pigments and Coloration in the Jamaican Radiation of *Anolis* Lizards. J. Herpetol.

Morrison, R. L., Rand, M.D. and Frost-Mason, S.K. 1995. Cellular basis of color differences in three morphs of the lizard Sceloporus undulatus erythrocheilus. Copeia 1995:397-408.

Morrison, R. L., Sherbrooke, W.C. and Frost-Mason, S.K. 1996. Temperature-sensitive, physiologically active iridophores in the lizard *Urosaurus ornatus*: an ultrastructural analysis of color change. Copeia 1996:804-812.

Ng, K.-C. S. and Beswick, R.G.B. 1994. Ground water of the Cayman Islands. In: The Cayman Islands: Natural History and Biogeography (Ed. By M. A. Brunt and J. E. Davies), pp. 61-74. Kluwer Acad. Publishers, The Netherlands.

Ortiz, E. and Maldonado, A. A. 1966. Pteridine accumulation in lizards of the genus *Anolis*. Carib. J. Sci. 6:9-13.

Rand, A. S. 1967. The ecological distribution of the anoline lizards around Kingston, Jamaica. Breviora 272:1-18.

Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size of the lizard *Anolis conspersus*. Science 155:474-478.

Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patch habitats. Ecology 51:408-418.

Schoener, T. W. 1971. Structural habitats of West Indian *Anolis* lizards. 1. Lowland Jamaica. Breviora 368:1-24.

Taylor, J. D., and Hadley, M. E. 1970. Chromatophores and color change in the lizard, *Anolis carolinensis*. Z. Zellforsch. 104:282-294.

Underwood, G. and Williams, E.E. 1959. The anoline lizards of Jamaica. Bull. Inst. Jamaica, Sci. Series 9:1-48.

Vezina, J., Jones, B and Ford, D. 1999. Sea-level highstands over the last 500,000 years: Evidence from the ironshore formation on Grand Cayman, British West Indies. J. Sedimentary Res. 69:317-327.

Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Q. Rev. Biol. 44:345-389.

Wingate, D.B. 1965. Terrestrial fauna of Bermuda. Herpetologica 21:202-218.

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The Dynamics of Population Differentiation in Lesser Antillean Anoles

This is a brief summary of the work of our group, which began over 10 years ago. This has formed the subject of most of our Ph.D. dissertations, some of which are only just being written. Our work mainly focuses on the single-species islands, i.e., the larger central islands (Guadeloupe, Dominica, Martinique and St. Lucia). All are relatively young (5-10 my), at least in part, and are as a result extremely mountainous with considerable habitat diversity. The endemic species on each of these islands are morphologically variable, to varying extents.

Much of our work has taken place on Dominica. This is an extremely mountainous island which receives an extremely high rainfall from the easterly Trade winds, with over 7m/yr estimated to fall on the higher peaks. The distribution of rain over the whole island is very unequal, and results in variable habitats: rainforest over much of the centre of the island, with more xerophytic vegetation on the coasts (especially on the leeward Caribbean coast which experiences both the lowest rainfall and the most pronounced dry season). The vegetation of the windward coast, on the other hand, is strongly influenced by the salt-laden onshore winds, which give it a characteristic combed appearance. *Anolis oculatus* is common in all these habitats and shows corresponding morphological variation, from orange-brown with many small white spots containing enlarged white scales, and a prominent neck and tail crest, to yellow in hue with prominent white marbling and black patches, and even green with bluish-green markings.

We have investigated population differentiation in this species using a number of different approaches, including a quantitative description of morphological variation and studies of the correlation of morphological patterns with environmental variation using matrix correlation tests. We also gathered further lines of indirect evidence favouring natural selection from studies of parallel patterns in other species (mainly *A. marmoratus* from Basse Terre, Guadeloupe). In order to assess how much phenotypic plasticity contributes to these patterns, we carried out a “common-garden” experiment in which animals from different populations were hatched and raised in a common environment and their morphological characters recorded after six months. If morphological variation is induced, then lizards should show the similar morphological traits to each other, rather than to their parental populations, but, in fact, they retain the characteristics of their parental populations. We can assume, therefore, that the pattern we see is not simply a direct effect of the environment, but is largely due to genetically controlled variation. We also directly measured selection intensity by carrying out a series of manipulative experiments (only the first series have been published so far) in which populations were translocated between habitats. These experiments were a logistical nightmare, but we have been able to show that selection intensity (measured as the magnitude of the multivariate morphological difference between survivors and non-survivors within each translocated population) is related to the magnitude of the ecological change experienced and is also affected by season.

We are now investigating the underlying genetic variation in both the mitochondrial and nuclear genomes (microsatellites) to assess the historical component of morphological variation. Like most of the work we have done on *Anolis,* this has turned out to be extremely labour intensive because of the extreme variability they show. All the species we have looked at so far show marked genetic structuring at mitochondrial loci, which is consistent with what we know of the turbulent volcanic history of these islands. However, in all cases we have examined so far, this historical legacy has been largely overwritten by natural selection. A few exceptional instances of congruence between morphological patterns and mitochondrial lineages have been identified. In at least one case (*A. roquet* on Martinique), speciation appears to be complete, producing the first example of 2 sister species co-existing on the same Lesser Antillean island. In *A. oculatus*, patterns are suggestive of some form of reproductive isolation in only part of the island. These patterns could be more widespread in the single-species islands than is currently realized. Further work on these “hybrid zones” is planned, which will integrate genetic and behavioural data.

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Preliminary Report on DNA-DNA Hybridization Studies of Anoles

Anoles are an ecologically, behaviorally and morphologically diverse group of lizards with over 250 species distributed from the U.S. to Brazil and throughout the West Indies. These characteristics have made them a favorite and favorable system for studies of adaptive radiation, many of them carried out by the late Ernest Williams, his students, and collaborators. Study of adaptive radiation and related phenomena requires an understanding of the phylogenetic relationships of the taxa involved, and, since the pioneering studies of Richard Etheridge, many workers have endeavored to provide this phylogenetic framework. Many recent studies have utilized the techniques of molecular systematics; here we provide a preliminary overview of our study of anole phylogeny using DNA-DNA hybridization. The present report summarizes a presentation made at the *Anolis* Symposium held at Penn State on 27 June 1999.

Twelve species of anoles, representing mainland (*humilis, limifrons*) and island (*grahami, sagrei*) beta anoles, island alpha anoles of both the *punctatus* (arrow interclavicle: *cristatellus, distichus*, *leachii, longitibialis, richardii*) and *carolinensis* (T-shaped interclavicle: *porcatus*) subsections (sensu Williams), *Chamaelinorops*, and *Chamaeleolis* were used. Although no mainland alphas were available, *richardii* (and its close relatives) is generally thought to be closer to mainland alphas than to the other island alphas. The agamid *Hydrosaurus* was used as an outgroup.

Divergence in DNA sequence was measured using single-copy whole-genome DNA-DNA hybridization. In this method, an excess of single stranded DNA of one species (the driver) is hybridized with radioactive-iodine labeled DNA of another (the tracer). The thermal stability of the resultant heteroduplex DNA is compared to that of homoduplex DNA prepared in a similar manner, except that driver and tracer are from the same species. The difference in stability was indexed by the difference in median melting temperature of the hybridized DNA of heterologous versus homologous hybrids.

A complete 11x11 matrix of reciprocal comparisons, with each cell replicated 3-9 times, was carried out for all species except *limifrons* and *richardii*. *Limifrons* was included as an unlabeled driver (4-6 replications) for all eleven tracers, while *richardii* was included as an unlabeled driver (1-3 replications) for eight of the drivers. Missing cells in the 13X13 matrix were filled by reflection from known reciprocals after symmetrization, or, in three cases involving *richardii*, where no reciprocal was available, by an additive estimation procedure.

Phylogenetic trees were estimated by the least squares method for additive trees using Felsenstein's FITCH program. The stability of the results was assessed by the frequency with which clades appeared in trees derived from 1000 bootstrap pseudoreplicate matrices, and by the average consensus of all 7813 single and multiple deletion weighted jackknife trees.

The average consensus weighted jackknife and bootstrap consensus tree was found to be

(*Hydrosaurus*(*longitibialis*(*porcatus*(*richardii*(*sagrei*(*grahami*(*humilis*, *limifrons*))))
((*Chamaeleolis*, *Chamaelinorops*)(*leachii*(*cristatellus*,*distichus*))))))

Four aspects of this tree are worth noting. Two of these are groupings found to be especially well-supported in the analysis. First, a grouping of all the beta anoles had a bootstrap frequency of .795; within the betas, *grahami* joined *humilis* and *limifrons* in all bootstrap trees, while the latter were joined to one another with a frequency of .996. Thus, a holophyletic beta group is supported, embracing both island and mainland species. While both island series of betas are represented, the greater diversity of mainland betas is represented by only two species, and thus this conclusion must be tempered by this sparse sampling.

Second, a group of northeast Caribbean alphas (*leachii*, *cristatellus*, *distichus*) is found in all bootstrap trees, with the latter two joining with each other at a frequency of .700. Much previous evidence has also supported a grouping of these geographically annectant forms. *Longitibialis*, a cybotoid anole at times inferentially associated with this grouping, does not appear to be closely related.

Third, there is little or no evidence for a holophyletic alpha group; indeed, the only evidence for it is that it is not formally excluded by the most conservative trees arrived at by collapsing branches with bootstrap frequencies less than 0.50. It is likely that the betas have their closest relatives within a paraphyletic alpha group.

The previous three items accord with the *a priori* expectations of GCM, sufficiently so to make us doubt that they could really be true. We are thus happy that the fourth item, which is related to the apparent paraphyly of the alphas, is not what was expected. This is that there is no strong evidence that either of the morphologically peculiar genera, *Chamaeleolis* or *Chamaelinorops,* are basal to the other anoles. There is modest evidence that their relationships lie within the alphas. The mixture of primitive and autapomorphic features in these two genera has led to the suggestion that they are old forms, but our data are in accord with the results of Hass, Hedges and Maxson, who were moved to formally synonimize these genera with *Anolis*.

In order to provide a tree suitable for assigning divergence times to the events of anoline cladogenesis, the above topology was forced onto a tree from Felsenstein's KITSCH program using Jukes-Cantor corrected distances from median melting temperatures of the total DNA (T50-H), thereby providing a tree with ultrametric pathlengths among the species. To calibrate this phylogeny, we used the emergence from a period of transgression by Jamaica in the early to mid-Miocene (ca. 18 myrbp). Assuming that the dichotomy of the Jamaican *grahami* and its sister group is accounted for by this event gives a sequence divergence rate of about 0.48%/myr, remarkably close to rates calculated for a wide range of other vertebrates using similar methods of estimation. Note that this estimate also supports the notion that, while older than the divergence of the *grahami* series on Jamaica, *Chamaelinorops* and *Chamaeleolis* are relatively recent derivatives, and are not relics of an older anoline fauna.

We will comment here on two biogeographic issues of some interest. The first is the independence (or lack thereof) of the radiations of the anole faunas of the Greater Antilles. Our sampling is insufficiently dense to address this issue in any detail, but we do note that the previously known heterogeneity of the faunas of Cuba and Hispaniola is supported, as well as relationship between Hispaniola and Puerto Rico.

The second is the geographic origin of the betas. Williams suggested a scenario of a Central American origin of betas, followed by colonization of Jamaica, from thence to Cuba, and finally a back-colonization (perhaps human assisted) from Cuba to Jamaica by *sagrei*. Gorman, in discussing some of the evidence indicating that some alphas were closer to betas than to other alphas, suggested that the betas had a West Indian origin, and that they had subsequently colonized the mainland (Etherdige had considered a similar possibility earlier, but rejected it). Our results, indicating holophyletic betas and possibly paraphyletic alphas, can be interpreted in Gorman's framework: betas originate in Cuba, then disperse to Jamaica, and from Jamiaca to the mainland, where they spread out and diverge.

We prefer a different scenario. Although only supported by a bootstrap frequency of .412, *richardii*, a mainland-like alpha, appears as sister to the betas in our tree, and thus betas have a mainland origin. The first divergence within betas, of *sagrei*, marks the colonization or separation of Cuba from the mainland. Jamaica, which was largely or totally submerged from the Eocene to the Miocene, did not receive its anoles (or, at least, its surviving anoles) from Central American progenitors until it had emerged, and thus is a later split from the mainland betas. One reason we prefer this scenario is that the high species-level endemism of anoles on the individual Greater Antilles and mainland, combined with the widespread occurrence of little-differentiated anoles on small, recent islands, implies that anoles disperse relatively easily, but become established in rich faunas only with difficulty.

Our data alone cannot distinguish between these scenarios, and many questions remain unanswered, most notably, who are the betas' nearest relatives among the alphas? Etheridge considered (but rejected) the West Indian T-shaped interclavicle alphas as the betas' progenitors, and neither our nor others' data indicate a relationship with these alphas, but rather with arrow interclavicle alphas. There are, however, mainland alphas with T-shaped interclavicles, and perhaps closer relatives of the betas should be sought among them.

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Research and Thoughts on the Knight Anole (*Anolis equestris*) From Extreme Southern Florida

Southern Florida is currently home to eight West Indian species of *Anolis*. Like anoles in general, nearly all the Florida anoles are small and medium-bodied in length. Unlike these and most other anoles, *A. equestris*, also established in southern Florida, is a very large-bodied species. Typical of the few other large, or "giant," anoles, *A. equestris* is most often found on large branches well above the ground. Exceptional in its body size, *A. equestris* also differs from many other West Indian anoles in that both sexes share a similar body color and pattern and both sexes have and use a fully functional dewlap. Both sexes also appear to use the same features of the habitat. Because of its unusual combination of characters, findings of growth and activity could be interpreted within the framework of large versus small anoles. With that in mind, and because of its ubiquity within walking distance of my home, the fact that its ecology has gone practically unstudied anywhere, and because I'm enamored with the impressive appearance of this species, I began toe-clipping individuals in September 1996.

I have marked nearly 100 animals; most are adults, and the sex ratio of my sample is1:1. From my mark-recapture study, that will probably terminate September 1999, I am relatively certain of a few things. From approximately 30 mm SVL at hatching, growth is equally rapid for both sexes until they reach their mean adult SVLs (160 mm for males, 140 for females), after which time growth asymptotes. Because of El Niño and La Niña, southern Florida has experience mixed up wet (May - October) and dry (November - April) seasons. Moreover, dry season growth data have been difficult to come by because of reduced activity during the dry season. However, wet season and early dry season data indicate that both sexes grow at about 10 mm/month, thereby reaching maturity in 8-9 months. This being the case, males and females reach their mean body size at about 14 and 12 months, respectively. Scattergrams corroborate the rapid growth. However, more data are needed to measure growth rates for the rest of the dry season. What also remains unclear to me is the age of larger individuals. I want to continue this project for at least one more year because even with up to two years of individual recapture data, little if any growth is apparent after they reach their mean body size. I am left with the question: how old are the largest males (180 mm) and females (150 mm)? Could it be that the largest individuals are four or five years old? More data will tell.

From my mark-recapture data, I found that *A. equestris* is most conspicuous during May - (mid) November. This period coincides with average monthly low temperatures of 22.1° C and high temperatures of at least near 28° C. During these months, adults of both sexes are commonly seen in a head down and out position at various heights on tree trunks. Although individuals in this position will capture and eat insects tossed to them, the main function of this display appears to be territorial. From my three day per week visits, I have found that the period May - October does coincide with most territorial display and conspicuous activity. Because activity wanes at temperatures less than 27° C, during November - April activity declines in number of days each month and number of hours each day in which individuals have available to be actively moving around. General activity also does not include the head down and out posture, although hunting individuals may face straight down as they approach terrestrial prey or those on the trunk of the tree. Otherwise, if lucky, bright green individuals are spotted on limbs, broadside to the sun. I am hoping that with more data to come, I can identify patterns of winter/dry season activity and relate those to degree of breeding activity. For example, presumably, *A. porcatus* is not territorial during the dry season in Cuba, whereas *A. sagrei* courts and mates throughout the year, even if sparingly, in Miami. Having many summer copulation records and only one winter (late January) one suggests the gonadal cycle of *A. equestris*, like that of *A. sagrei*, is dictated by day length, which is also true of the Cuban treefrog. That being the case, perhaps winter breeding by *A. equestris* in extreme southern Florida, like that of the other Cuban colonizers, occurs but uncommonly.

Lastly, watching this species has led me to wonder about the function of *A. equestris* in the activity and composition of the *Anolis* community. Rather nonchalantly, I have often referred to *A. equestris* as the *T. rex* of the trees. This is true in more ways than one. They eat frogs, birds, and anoles. Ernest Williams accurately defined the structural niche partitioning among the West Indian anoles, and subsequent studies have demonstrated the role of competition in the enforcement of *Anolis* habitat partitioning. I suggest here that ample evidence exists that lizard predation by *A. equestris* has its role as a mechanism that enforces the structural niche partitioning, and, perhaps, regulating the temporal use of the habitat by at least a displaced Cuban anoline community. I wonder if, with respect to *A. equestris*, predation is the overwhelming mechanism that enforces where and when heterospecifics are active. Testing what its looming presence in the upper reaches of the tree does to the temporal and spatial patterns of activity would be a fun project that combines field and enclosure replicates. With the exception of the grass and small twig anoles, the other ecomorphs are present, sometimes in duplicate, in southern Florida. Somewhat unique to Florida, another way to approach this scenario is to ask if the presence of a predatory anole enforces the natural structural niche placement of both historically familiar anoles like *A. sagrei* and *A. porcatus*, as well as other species like *A. distichus* and *A. cristatellus*, that contend with ecological analogs of *A. equestris*, but not with *A. equestris* itself.

Beyond the question of activity, by knowing which species are most susceptible to predation, this study could answer the question: how does the presence of a predator (*A. equestris*) shape the very structure of the anole community? Do the activities *of A. equestris* give one competitor an advantage over another, or does *A. equestris* act as an anole lawn mower preventing any one species reaching abundances above which they could negatively impact a potential competitor?

For example, at my study site, *A. sagrei* is very uncommon, and even males have not been observed at heights greater than 2 m. *Anolis carolinensis* is also present and found from ground level to at least 3 m. *Anolis equestris*, generally active above 2 m from the ground, has been observed hunting and displaying at less than 0.2 m above the ground. Is *A. sagrei* easier to capture than *A. carolinensis*? If so, is the resulting dearth of *A. sagrei* responsible for the relative abundance and ecological release of *A. carolinensis*? In this regard, it would be fascinating to know if *A. carolinensis* has any mechanisms to avoid contact with *A. equestris*. An interesting way to interpret those findings would be in relation to any behavioral mechanisms used by its ecological analog, *A. porcatus,* that is present in southern Florida.

I hope that this progress report, as it were, on my mark-recapture project *on A. equestris* and my thoughts on predation as a mechanism that shapes both activity and structure of the anoline community provide a little insight and a spark for projects on where in the world of *Anolis* do the giant anoles belong?

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Phylogenetic Analysis of *Norops* (Beta *Anolis*) Species: Preliminary Data

Introduction

Much attention has been afforded to the phylogenetic relationships among *Anolis* species, yet resolution has been long in coming. Work in recent years has led to some elucidation of relationships (e.g., Jackman *et al.* 1999), but one group of anoles has been largely understudied to date: the beta anoles or *Norops* (*sensu* Savage and Talbot 1978, Guyer and Savage 1986, Savage and Guyer 1989). This article presents some relationships among *Norops* as discovered via molecular data collected to date[1].

The current status of *Anolis* (*sensu lato*) systematics stems from the work of Etheridge (1959) and Williams (1974, 1976). The genus *Anolis* was subdivided into an alpha section (inhabiting the Caribbean islands, South America and Central America north to Costa Rica; ~180 species) and a beta section (inhabiting Mexico, Central and South America, Jamaica, and Cuba; ~140 species) on the basis of a single osteological character: the beta section was characterized as possessing anterolaterally directed transverse processes on their caudal vertebrae, whereas the alpha section lacked these processes. Some challenges to the monophyletic status of the beta anoles have been raised (Burnell and Hedges 1990; Gorman *et al.* 1984; Shochat and Dessauer 1981; Wyles and Gorman 1980) but these studies suffer weaknesses rendering their results speculative[2]. More rigorous phylogenetic studies making comprehensive use of data from the

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[1] This article presents preliminary results of my dissertation work which are in progress. At the time of this writing, sequences for approximately 10 additional taxa have been collected and it is anticipated that several more will be collected prior to the commencement of these meetings. Therefore, the results presented at the meetings will likely be different from those presented here. In addition, this work is anticipated to be completed by fall 1999 and thus much data not presented here nor at the meetings will be accumulated and analyzed and could render different relationships than those presented at the meetings.

[2] A few studies have challenged the alpha-beta dichotomy of *Anolis* systematics, but there are serious problems with these studies. Three studies used albumin immunological data (Gorman *et al.* 1984; Shochat and Dessauer 1981; Wyles and Gorman 1980), but made one-way comparisons from the one reference species to the study species only. Non-reciprocity of immunological data necessitates reciprocal crosses to ensure confidence in data used in phylogenetic analyses (e.g., A->B=10, B->A=15; see Guyer 1992 and Page and Lydeard 1994). More problematical, all immunological comparisons were made to only one (Gorman *et al.* 1984) or a few (Shochat and Dessauer 1981; Wyles and Gorman 1980) reference species. The combination of one-way

literature (Guyer and Savage 1986, 1992) or using new molecular data (Jackman *et al.* 1999) have established the monophyletic status of the beta section of *Anolis*, hereafter referred to as *Norops*[3].

Relationships below the section level are not resolved and are of less certain phylogenetic status. The alpha and beta sections were subdivided into series (largely by Etheridge) and subseries and species groups (largely by Williams) on the basis of morphological (osteology, external morphological attributes), karyological and ecological features. These groups were erected on the basis of overall similarity; cladistic analysis of their data (Nicholson, unpublished) resulted in little resolution among the series. Guyer and Savage's (1986, 1992) analysis of data synthesized from the literature resulted in some resolution among the series, but they assumed each series to be monophyletic (their results have been criticized [Cannatella and de Queiroz 1989; Williams 1989] and not accepted by the systematic community at large). Of the seven proposed series of *Norops*, only one, the *grahami* series, forms a monophyletic group; the remaining six series are unresolved. These series may be monophyletic, but there are no data to support these designations currently.

The focus of this research is to resolve the phylogenetic relationships among the series of *Norops*. The following two broad questions are addressed: (1) Does each of the seven proposed *Norops* series comprise a natural, monophyletic group; and (2) if each series is monophyletic, what are the evolutionary relationships among the series? If the series are not monophyletic, what alternative groups are supported by the data and what are the evolutionary relationships among those groups?

Methods

Taxon sampling consists of approximately 67 species spanning all seven *Norops* series plus two outgroup species representing the two closest lineages to *Norops* (*carolinensis* and

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comparisons and few reference species renders their phylogenetic results suspect because very close or identical values (in i.d. units) for distantly related species can be obtained; these distantly related taxa will then be incorrectly linked in a phylogenetic analysis. Burnell and Hedges (1990) produced protein electrophoretic data for alpha and beta taxa, but presented only one of 2000 trees obtained from their analyses and bootstrap values for all but two nodes were well below 50%. Page and Lydeard (1994) note that obtaining such high numbers of most parsimonious trees is a direct result of the large number of character states relative to taxa. They state "In the absence of character state trees for the alleles each locus is treated as unordered multistate character, and so as the number of character states increases the informativeness of the characters decreases" (p. 32). Thus the interpretation of Burnell and Hedges results is suspect.

[3] Savage and Talbot (1978) called for this monophyletic group to be recognized as the genus *Norops* because it was well recognized as being monophyletic and distinct. Because additional studies have confirmed the monophyletic status of this group, I refer to it by its proposed generic name. Some workers have challenged this recognition apparently on the basis that *Anolis (sensu lato)* could not be completely resolved with current data and thus no monophyletic groups should be named and recognized. I disagree with this stance and until procedures for agreeing on names in situations such as these are proposed and or new taxonomic procedures are instituted, I propose that the beta anoles be recognized as *Norops*.

cristatellus groups [Guyer and Savage 1986, 1992; Jackman *et al.* 1999]; see Table below). Taxa were selected to represent the geographic and morphologic variation exhibited by each series. Specimens and tissues from all taxa have been obtained by personal collection or via museum loans.

Series (# species)		Native Range	# taxa in this project
auratus	(68)	Mexico, C. Am., S. Am.	25
fuscoauratus	(26)	Mexico, C. Am., S. Am.	10
grahami	(7)	Jamaica and Grand Cayman	7
meridionalis	(1)	S. Am.	1
onca	(2)	S. Am.	1(?; permits pending)
petersi	(12)	Mexico, C. Am., S. Am.	8
sagrei	(12)	Cuba	12
cristatellus	(OG)		1
carolinensis	(OG)		1

Molecular characters in the form of DNA sequences for the nuclear ITS – 1 (internal transcribed spacer unit) region are being collected and reported on here (additional data being collected include nuclear ITS – 1 and morphological data, but are not discussed here). Preliminary ITS-1 data for *Norops* species reveal suitable levels of variation (3 – 23% sequence divergence) supporting their use for this study.

DNA sequences were aligned by eye and or using Sequencher 3.0 (1995, Gene Codes Corporation). Gap insertions were coded as missing data. Phylogenetic analyses were conducted using PAUP* (ver. 4.0b2; Swofford 1999). Trees were searched under the strict parsimony approach and evaluated via consistency indices (C.I.), retention indices (R.I) and decay indices. Decay indices were calculated using the program Autodecay (Eriksson, 1998). The heuristic search option was employed with 1000 replicates of random taxa addition.

Results

Of 1098 aligned base pairs, 731 characters were constant, 367 were variable, and 139 were parsimony informative (=38%, or 12.6% of 1098 characters). The structure of ITS-1 is similar to 28S rRNA, but in miniature, with several variable regions interspersed with conservative regions. Phylogenetic analysis of 1098 aligned base pairs of ITS-1 resulted in 3 most parsimonious trees with a CI of 0.811 and an RI =0.525. The cladogram presented (Figure 1) represents a strict consensus of the three trees; numbers at the nodes indicate decay indices. Species names are indicated and the proposed series and subgroups (either subseries or species groups) each taxon has been assigned to are indicated to the right of each species label. Although the tree does lack some resolution at some of the nodes, none of the proposed groups forms a strictly monophyletic group. Some of the decay indices are low suggesting low support for those nodes; those relationships may change with the addition of more data and taxa.

Discussion

This section should begin with a note of caution, as these data are preliminary, the work is in progress and many more characters and taxa will be added (prior to and post-symposium meeting); thus, these results should be treated with caution. However, if these results are supported with additional data and characters, they would prove interesting indeed. As observed from the cladogram, none of the proposed *Norops* series form monophyletic groups. There are two primary clades generated from this analysis: an "island" clade comprising the Cuban (*sagrei* series) and Jamaican (*grahami* series) taxa and a "mainland" clade formed of the remaining taxa. However, two Mexican taxa emerge within the island clade: *N. sericeus* and *N. nebulosus*, both *auratus* series taxa, but assigned to different subgroups (the *auratus* and *laeviventris* groups, respectively). In addition, none of the mainland series represented here (*auratus, fuscoauratus, petersi*) form monophyletic groups, although not all nodes are resolved. It is perhaps not surprising that the series themselves do not form monophyletic groups, but the subgroups (subseries, species groups) might have been expected to cluster together, yet they also do not form clusters. For example, *N. capito* and *N. biporcatus* are assigned to the *petersi* subgroup of the *petersi* series, but do not fall out together in this phylogenetic analysis.

It would be premature to speculate on the biogeographic implications of these data, but if additional data support inclusion of the Mexican species within the island clade, then this has interesting implications. There has been much discussion over the years regarding the origin of Caribbean taxa and whether vicariance or over-water dispersal is the best explanation (e.g., see Crother and Guyer 1997 for a review) and some workers postulate that some species have traveled from the Caribbean back to the mainland (Crother, per. com.). The placement of *N. sericeus* suggests an over-water dispersal from Cuba to Mexico. The placement of *N. nebulosus* is harder to explain; this can really only be elucidated with the addition of Jamaican taxa.

By the time of the symposium, additional taxa will have been added and I hope that I might elucidate further the phylogenetic relationships among the series of *Norops*.

Acknowledgments

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Literature Cited

Burnell, K.L. and S.B. Hedges. 1990. Relationships of West Indian *Anolis* (Sauria: Iguanidae): an approach using slow-evolving protein loci. Caribbean Journal of Science 26:7-30.

Canatella, D.C. and K. de Queiroz. 1989. Phylogenetic systematics of the anoles: is a new taxonomy warranted? Systematic Zoology 38:57-69.

Crother, B.I. and C. Guyer. 1997. Caribbean historical biogeography: was the dispersal-vicariance debate eliminated by an extraterrestrial bolide? Herpetologica 52:440-465.

Eriksson, T. 1998. AutoDecay ver. 4.0. Department of Botany, Stockholm University. Stockholm.

Etheridge, R.E. 1959. The relationships of the anoles (Reptilia: Sauria: Iguanidae): an interpretation based on skeletal morphology. Ph.D. Thesis, University of Michigan, Ann Arbor.

Gorman, G.C., C.S. Lieb, and R.H. Harwood. 1984. The relationships of *Anolis gadovi*: albumin immunological evidence. Caribbean Journal of Science 20:145-152.

Guyer, C. and J.M. Savage. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). Systematic Zoology 35:509-531.

Guyer, C. and J.M. Savage. 1992. Anole systematics revisited. Systematic Biology 41:89-110.

Jackman, T.R., J.B. Losos, A. Larson, and K. De Queiroz. In press. Phylogenetic relationships of anoles.

Page, R.D. and C. Lydeard. 1994. Towards a cladistic biogeography of the Caribbean. Cladistics 10:21-41.

Savage, J.M. and J.J. Talbot. 1978. The giant anoline lizards of Costa Rica and western Panama. Copeia 1978:480-492.

Savage, J.M. and C. Guyer. 1989. Infrageneric classification and species composition of the anole genera *Anolis, Ctenonotus, Dactyloa, Norops,* and *Semiurus* (Sauria: Iguanidae). Amphibia-Reptilia 10:105-116.

Shochat, D. and H.C. Dessauer. 1981. Comparative study of albumins of *Anolis* lizards of the Caribbean islands. Comparative Biochemistry and Physiology 68A:67-73.

Swofford, D. 1999. Phylogenetic Analysis Using Parsimony ver. 4.0b2 (licensed to Brian Crother and Mary White and used with their permission). Sinauer Associates, Sunderland, MA.

Williams, E.E. 1974. A case history in retrograde evolution: the *onca* lineage in anoline lizards. I. *Anolis annectens* new species, intermediate between the genera *Anolis* and *Tropidodactylus*. Breviora 440:1-21.

Williams, E.E. 1976. West Indian anoles: a taxonomic and evolutionary summary. I. Introduction and a species list. Breviora 440:1-21.

Williams, E.E. 1989. A critique of Guyer and Savage (1986): cladistic relationships among anoles (Sauria: Iguanidae): are the data available to reclassify the anoles? Biogeography of the West Indies, pp.433-478. C.A. Wood, Ed., Sandhill Crane Press, Gainesville, FL.

Wyles, J.S. and G.C. Gorman. 1980. The classification of *Anolis*: conflict between genetic and osteological interpretations as exemplified by *Anolis cybotes*. Journal of Herpetology 14:149-153.

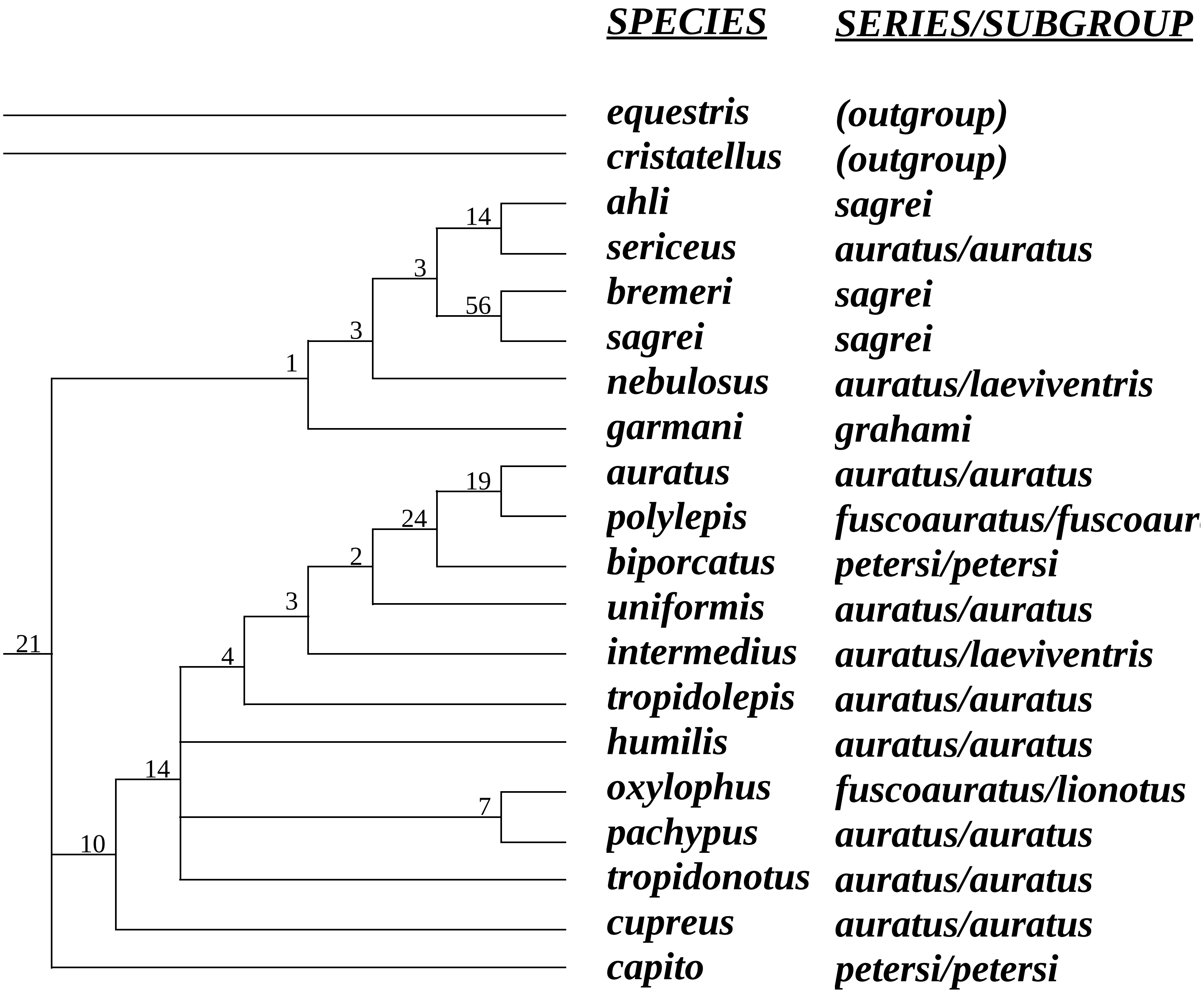

Figure 1. Strict consensus of three most parsimonious trees generated using 1098 bp of the nuclear ITS-1 region for 18 ingroup and 2 outgroup taxa. Numbers at nodes indicate decay indices. Species names and the series and subgroup (subseries or species group) to which they have been assigned by previous workers are indicated.

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Observations of a Population of Cuban Knight Anoles, *Anolis equestris*

"Considering the disproportionate amount of attention anoles have received in the past 30 years, it is surprising that an autecological approach to studying anoline ecology has been ignored. One spectacular segment of the anoline fauna has been neglected completely: the giant species…"

Robert W. Henderson and Robert Powell, 1999, In:
Caribbean Amphibians
and Reptiles, Academic Press

Introduction

This symposium is testament to the importance of anoles to science, yet as the quote above suggests, relatively few species within this adaptive radiation of nearly 400 species have been studied, and a paucity of data exist for canopy or giant anoles. Giant canopy dwelling *Anolis* inhabit mainland and Caribbean forests but little is known of their ecology and natural history (Collette 1961; Ruibal 1964). Only two ecological publications exist to our knowledge, both on the diet (with other observations) of *A. equestris* in South Florida (Brach 1976; Dalrymple 1980). It is because of this lack of information, combined with our own particular fascination, that we have studied a population of *A. equestris* in South Florida.

Neill (1957) first reported the occurrence of *A. equestris* in South Florida and King and Krakauer (1966) noted details regarding the introduction of individuals to the Coral Gables area. The species appears to be doing quite well where it occurs; it can be found in the Miami area (Miami-Dade County) in suburban settings and ranges north to Broward County, Florida. Urban myth holds that one *A. equestris* resides in every large tree in Coral Gables and during near or below freezing, cold dead individuals have been observed littering the street (J.M. Savage, pers. comm). In this study, we sought basic natural history and ecological information regarding *A. equestris*. This article presents our preliminary data on numbers, sex ratios, home range size, movement patterns and behavioral observations over the course of 9 months (the project is still in progress) for a population of *A. equestris* in South Florida, USA.

Methods

We conducted this study in the Gifford Arboretum and Microbiome complex behind the Cox Science building on the Coral Gables campus of the University of Miami during the months of August 1998 to May 1999. Our study site is approximately 14,659.2 km^2 and includes two major types of habitat. The first is predominantly open habitat dedicated to the display of tropical tree and shrub species including subtropical Florida species. The second is a less open habitat that was developed as a microbiome to represent native South Florida subtropical hammock habitat. These areas are adjacent to each other, but separated by a parking lot driveway approximately 5m wide and 20m long.

Sampling periods varied from once a week (during colder periods) to seven days a week and spanned all times of the day. During each sampling period, we attempted to capture each new individual *A. equestris* we observed. Lizards were captured either by hand or using dental floss tied as a noose attached to an approximately 6m collapsible fishing pole (e.g. 17' Sunny Day Pole, model SD-17, South Bend Inc, NorthBrook, Il 60065). Once captured, all individuals were weighed to the nearest gram, measured for snout-vent length (SVL) and tail length to the nearest millimeter, examined for injuries or unique marks, sexed, and marked. Each lizard was marked by sewing colored glass beads with surgical suture to the base of the tail using unique combinations of 1-3 beads per lizard. After marking, lizards were either released immediately or outfitted with a radio transmitter and released at the point of capture.

The radio-transmitters used were G3 two-stage transmitters with LiBR 2030 batteries or SM1 single-stage transmitters with Renata 357 (AVM Instrument Company LTD, Livermore, CA). Each transmitter plus battery set-up was coated 2-3 times with Plasti-Dip (PDI brand, PDI Inc., P.O. Box 130, Circle Pines, MN 55014), painted green to blend with the lizard using tempura paint (American Glue Corporation, Taylor, MI 48180), and sealed with quick drying epoxy (Devcon 2-ton Crystal Clear Epoxy, Devcon Consumer Products, Des Plaines, IL, 60018). Four-pound monofilament line was tied around the transmitter set-up and sealed on with the last coat of epoxy. Harnesses were constructed of quarter-inch elastic (Stretch-Rite brand, Rhode Island Textile Company, Pawtucket, RI 02862) in a dog-harness style with two loops, one in front and one behind the forelimbs. The radio-transmitters were tied via the monofilament line to the harnesses after the harness was attached to the lizards. Total mass of the transmitter and harness combination was a maximum of 6g for two-stage transmitters and a maximum of 4.5g for the single stage transmitter. Numbers of active transmitters varied over time (between 8 to 12) as batteries sometimes failed and were retrieved for battery. Lizards were tracked using a hand-held Yagi 3-element antenna and a CE-12 receiver (Custom Electronics, Urbana, IL).

During each sampling period, lizards were tracked and the study area was surveyed for additional individuals (marked lizards without radios or unmarked individuals). For each sampling period, we attempted to sight the transmittered individual, but in some cases they were high in trees or so cryptic that sighting was not possible.

The study area was mapped using a Trimble GPS unit detailing nearly all vegetation and other pertinent features (e.g., trails, trail markers, parking lots). A grid was overlaid so that coordinate points could be recorded for each sighting locality. Using these coordinates, home ranges were calculated using the CalHome program (John G. Kie, James A. Baldwin, and Charles J. Evans, 1994, U.S. Forest Service, Pacific Southwest Region and the California Dept. of Fish and Game).

Results and Discussion

Sixty-nine lizards (35 male, 27 female, 5 juveniles, 2 unsexed) were marked in the study area over the course of nine months. The observed sex ratio was 1.3:1 (males:females). There was a distinct lack of juveniles observed similar to that found in Dalrymple's (1980) study. Four juveniles were located low to the ground (<1m) perched on shrub limbs or on the ground. However, we did observe one juvenile on a horizontal branch 2.5 meters above the ground.

Anolis equestris are cryptic and difficult to spot unless they are perched low on the trunks of trees. We could regularly spot our transmittered individuals, but occasionally these individuals could not be spotted, which was probably due to the height of their location. We did resight and recapture marked (not transmittered) individuals, but these numbers are low due to difficulty in sighting them; it is perhaps no surprise that few ecological studies have been performed on this species. Only one of our transmittered individuals left the study area, although it moved to a courtyard on the opposite side of a building bordering out study area. We later observed a very large male in this prior resident's area, so perhaps the disperser lost a battle to this larger male. It is possible that the road and adjacent buildings bordering the study area prevents dispersal from happening regularly, but this seems unlikely given that the species can be found throughout the Miami area. Alternatively, it is possible that all of our marked adults have established territories and only juveniles disperse. Because lizards without radio-transmitters were so difficult to sight, our recapture/resight data are low and we have not attempted to estimate population size or densities from them.

A subset of our data were used to estimate home ranges for 11 individuals (5 males, 6 females) for which we had greater than 12 data points (range = 12 – 47 points spanning two of the nine months). Using the 90% area calculated using minimum convex polygon method, home range size spanned 69.25 – 944.4 m^2 and averaged 289.2m^2. Male home ranges spanned 108.9 – 297.1 m^2 and averaged 232.1 m^2, whereas female home range size spanned 69.25 – 944.4 m^2 and averaged 336.8 m^2. However, the lowest (69.25 m^2) and highest (944.4 m^2) female home range size estimates were substantially different from the next lowest (137.8 m^2) and next highest (346 m^2) estimates and, if removed from the calculation, an average home range estimate of 251.8 m^2 obtains. It appears that male and female home ranges do not differ substantially and there appears to be no correlation between body size and home range size. However, these data are preliminary, sample sizes are small, and conclusions from these data should be treated cautiously at this time. If further data support these findings, then this would present an interesting departure from most other lizards. The usual trend for anoles and other territorial lizards is for male territory to be larger than female and for males to overlap between two and several female territories (e.g., Dunham 1980; Guyer 1988). It is not known with certainty that *A. equestris* is territorial, but males are suspected to be territorial given studies of other *Anolis* and observations of the ferocious fights males may engage in (Nicholson, personal observation; Dalrymple 1980).

Although diet was not explicitly studied via stomach or fecal contents, we did record food items observed eaten, attempted to be eaten, or removed from study animal's mouths. On two occasions, we observed adults lunging after *A. distichus*, which is abundant in our study. In one case, an adult male *A. equestris* captured and consumed an *A. distichus.* One adult female was observed to capture and consume a blue-gray gnatcatcher and another adult female was observed with a gecko (*Hemidactylus mabouia*) in its mouth. One juvenile had the remains of a spider in its mouth. The two published studies of *A. equestris* diet (Brach 1976; Dalrymple 1980) differ in their conclusions. Brach (1976) reported that 80% of their diet was fruit, whereas Dalrymple (1980) reported ~93% of their diet was animal matter (primarily insect/arthropods; he did observe individuals eating *Ficus* fruit as well). Other items reportedly consumed by *A. equestris* include tree frogs and young birds (Ruibal 1964) and other small anoles (Collette 1961). It appears that *A. equestris* probably eats whatever it can get into its mouth, but it would be interesting to examine feeding preferences and sexual and seasonal differences in foraging habits.

On several occasions, we observed *A. equestris* copulating. We have seen them mate early in the year when temperatures begin to rise (late March) and we have seen them copulating as late early October, suggesting a lengthy breeding season. Most tropical species of *Anolis* are known to breed nearly year round with seasonal differences in intensity between wet and dry seasons (e.g., Andrews *et al.* 1983). In contrast, South Florida populations of *A. sagrei* are known to breed from March to August and are thought to not breed at all or rarely in the intervening months (Lee *et al.,* 1989). *Anolis equestris* might conform to this latter breeding trend, but this should be examined with greater detail.

A. equestris is an interesting species that appears to differ in some ecological respects from other anoline species. This report presents a subset of our data and will be expanded in future publications. However, we encourage others to more completely study *A. equestris* to elucidate differences between it and other anoles, and to add to our knowledge of the natural and life history of canopy dwelling anoles.

Literature Cited

Andrews, R., A.S. Rand and S. Guerrero. 1983. Seasonal breeding and long-term population fluctuations in the lizard *Anolis limifrons.* In E. Leigh, A.S. Rand, and D. Windsor, (eds) The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes. Pgs. 441-454. Museum of Comparative Zoology.

Brach, V. 1974. Habits and food of *Anolis equestris* in Florida. Copeia 1976:187-189.

Collette, B.B. 1961. Correlation between ecology and morphology in anoline lizards from Havana, Cuba, and southern Forida. Bulletin of the Museum of Comparative Zoology 125:135-162.

Dalrymple, G. 1980. Comments on the density and diet of a giant anole *Anolis equestris*. Journal of Herpetology 14:412-415.

Dunham, A.E. 1980. An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. Ecological Monographs 50:309-330.

Guyer, C. 1988. Food supplementation in a tropical mainland anole, *Norops humilis:* demographic effects. Ecology 69:350-361.

King, W. and T. Krakauer. 1966. The exotic herpetofauna of southeast Florida. Quarterly Journal of the Florida Academy of Science 29:144-154.

Lee, J.C., D. Clayton, S. Eisenstein, and I. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. Copeia 1989: 930-937.

Neill, W.T. 1957. Historical biogeography of present-day Florida. Bulletin of the Florida State Museum 2(7):176-220.

Ruibal, R. 1964. An annotated checklist and key to the anoline lizards of Cuba. Bulletin of the Museum of Comparative Zoology 130:473-520.

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Although I am interested in all aspects of anole biology, my work thus far has been in phylogeny reconstruction. My main project is to collect morphological data to help elucidate the phylogeny of anoles, and a long term goal is to collect morphological phylogenetic data for all anole species. So far, I have scored over 2000 specimens of approximately 175 species for over 100 characters of osteology and squamation. Additional projects include a molecular and combined phylogeny of the Puerto Rican and Hispaniolan giant anoles (*cuvieri* series) and continuing maintenance of the *Anolis* Handlist, but these projects are not far along. I am also very interested in becoming involved in work on species-level problems, especially in undersampled areas such as northern South America.

Aspects of my preliminary results for large scale anole phylogeny are highlighted below. The "series" designations used are listed in Table 1 and mostly refer to the smallest units recognized by Savage and Guyer. I use the series designation to facilitate communication of results, and so that points of agreement and disagreement with earlier studies are evident (these particular names are used because Savage and Guyer's treatment is the most comprehensive). Although I agree with Williams that the recognition of informal groups is useful as a convenience, I do not think these should be used as proxies for clades. I can think of very few--almost no--anoline groups that are unequivocally monophyletic (the former *Chamaeleolis* is one of the few that comes to mind). Rigorous phylogenetic work in many laboratories should change this state of affairs, but until that work is completed, all informally recognized groups should be treated with suspicion.

In order to best estimate the large-scale phylogeny of *Anolis*, I have included at least two members from almost all informally recognized groups (Table 1). This approach is designed to maximize the amount of taxonomic, geographic, and morphological diversity sampled from the genus. Any worker interested in the phylogeny of a particular *Anolis* species is welcome to contact me, and if specimens are available I will do my best to include that species in phylogenetic analysis.

Skull characters come mainly from Poe (1998). Postcranial characters are mostly from Etheridge (1959). External characters are gleaned from the many papers covering lower level groups and alpha taxonomy (e.g., Williams, Fitch, Schwartz), as well as personal observation.

Current phylogeny results (subject to change, of course), based on collected morphological characters combined with allozyme, chromosome, morphological, and DNA sequence data from the literature:

--Etheridge's *latifrons* series (Guyer and Savage's *Dactyloa*) appears to be a paraphyletic basal group.

--*Phenacosaurus* is nested within a basal clade of *Anolis* that includes members of Williams' *tigrinus* and *punctatus* groups.

--The Hispaniolan green anoles (*chorocyanus* series) and *hendersoni* series each diverge early, before the remaining main Caribbean radiation.

--Guyer and Savage's *Ctenonotus* (*cybotes* series + *distichus* series + *acutus* series + *bimaculatus* series + *cristatellus* series) is monophyletic.

--The *cuvieri* series of Puerto Rican and Hispaniolan crown giants forms a clade with the anoles formerly recognized as *Chamaeleolis*.

--The Cuban (*alutaceus*) and Hispaniolan (*semilineatus*) grass anoles form a clade.

--Etheridge's beta section (*Norops* of Guyer and Savage) appears to be monophyletic and nested within his alpha section.

--The Caribbean betas (*sagrei* and *grahami* series) do not form a monophyletic group. The Jamaican series is more closely related to mainland betas than to other island betas.

--The mainland betas are monophyletic.

--The giant mainland beta anoles (*petersi* series) form a clade with *A. meridionalis*.

--The *gadovi* and *schiedi* groups form a clade.

--Several of the small series identified by Etheridge, Williams, Lieb, Burnell and Hedges, Gorman, and others are monophyletic, at least relative to the species I have analyzed (Table 1). Examples include the *roquet*, *latifrons* sensu stricto (giant mainland alpha anoles), *chlorocyanus*, *hendersoni*, *carolinensis*, *insolitus*, *semilineatus*, *equestris*, *cristatellus*, *distichus*, *nebuloides*, *crassulus*, *schiedi*, and *cupreus* series.

--A few series were not monophyletic in my preliminary analysis, but are likely to become so when more data are added. These include the *grahami*, *bimaculatus*, *sagrei*, *humilis*, and *lucius* series.

--Some series (again, as I have recognized them) appear unlikely to be monophyletic based on current evidence: *punctatus*, *monticola*, *fuscoauratus*, *acutus*, *auratus*, and *alutaceus.*

I consider the many ongoing anole molecular phylogenetic projects to be complementary to this anole morphology project, and I look forward to combining and comparing these data and results.

Table 1. Species for which I have collected morphological phylogenetic data. External data has been collected for all species listed. Skull and postcranial data have been collected for almost all species.

1a. Alphabetical by series composition		1b. Alphabetical by species name	
Anolis species	Series	*Anolis* species	Series
acutus	*acutus*	*acutus*	*acutus*
evermanni	*acutus*	*aeneus*	*roquet*
stratulus	*acutus*	*aequatorialis*	*aequatorialis*
aequatorialis	*aequatorialis*	*agassizi*	none
ventrimaculatus	*aequatorialis*	*ahli*	*sagrei*
alutaceus	*alutaceus*	*aliniger*	*chlorocyanus*
clivicola	*alutaceus*	*allisoni*	*carolinensis*
cyanopleurus	*alutaceus*	*allogus*	*sagrei*
spectrum	*alutaceus*	*altae*	none
vanidicus	*alutaceus*	*altavelensis*	*distichus*
angusticeps	*angusticeps*	*alutaceus*	*alutaceus*
argillaceus	*angusticeps*	*angusticeps*	*angusticeps*
loysiana	*angusticeps*	*antonii*	*fuscoauratus*
aquaticus	*auratus*	*apollinaris*	*petersi*
lineatus	*auratus*	*aquaticus*	*auratus*
townsendi	*auratus*	*argenteolus*	*lucius*
auratus	*auratus*	*argillaceus*	*angusticeps*

bitectus	*auratus*	*armouri*	*cybotes*
chrysolepis	*auratus*	*auratus*	*auratus*
granuliceps	*auratus*	*bahorucoensis*	*hendersoni*
tropidogaster	*auratus*	*baleatus*	*cuvieri*
bimaculatus	*bimaculatus*	*barahonae*	*cuvieri*
gingivinus	*bimaculatus*	*barbouri*	*Chamaelinorops*
leachii	*bimaculatus*	*barkeri*	none
lividus	*bimaculatus*	*bartschi*	*lucius*
marmoratus	*bimaculatus*	*bimaculatus*	*bimaculatus*
nubilis	*bimaculatus*	*biporcatus*	*petersi*
oculatus	*bimaculatus*	*bitectus*	*auratus*
wattsi	*bimaculatus*	*bonairensis*	*roquet*
allisoni	*carolinensis*	*brevirostris*	*distichus*
brunneus	*carolinensis*	*brunneus*	*carolinensis*
carolinensis	*carolinensis*	*capito*	none
isolepis	*carolinensis*	*carolinensis*	*carolinensis*
longiceps	*carolinensis*	*chamaeleonides*	*chamaeleolis*
maynardi	*carolinensis*	*chloris*	*punctatus*
paternus	*carolinensis*	*chlorocyanus*	*chlorocyanus*
porcatus	*carolinensis*	*christophei*	*monticola*
smaragdinus	*carolinensis*	*chrysolepis*	*auratus*
barbouri	*chamaelinorops*	*clivicola*	*alutaceus*
chameleonides	*chameleolis*	*cobanensis*	*schiedi*
aliniger	*chlorocyanus*	*coelestinus*	*chlorocyanus*
chlorocyanus	*chlorocyanus*	*compressicauda*	*humilis*
coelestinus	*chlorocyanus*	*conspersus*	*grahami*
crassulus	*crassulus*	*crassulus*	*crassulus*
sminthus	*crassulus*	*cristatellus*	*cristatellus*
cristatellus	*cristatellus*	*cupreus*	*cupreus*
desechensis	*cristatellus*	*cuprinus*	*subocularis*
gundlachi	*cristatellus*	*cuvieri*	*cuvieri*
krugi	*cristatellus*	*cyanopleurus*	*alutaceus*
poncensis	*cristatellus*	*cybotes*	*cybotes*
pulchellus	*cristatellus*	*darlingtoni*	unknown
cupreus	*cupreus*	*desechensis*	*cristatellus*
dollfusianus	*cupreus*	*distichus*	*distichus*
baleatus	*cuvieri*	*dollfusianus*	*cupreus*
barahonae	*cuvieri*	*dunni*	*gadovii*
cuvieri	*cuvieri*	*equestris*	*equestris*
ricordii	*cuvieri*	*etheridgei*	*monticola*
roosevelti	*cuvieri*	*evermanni*	*acutus*
armouri	*cybotes*	*fasciata*	*punctatus*
cybotes	*cybotes*	*fowleri*	*monticola*
longitibialis	*cybotes*	*fraseri*	*latifrons*

marcanoi	*cybotes*	*frenatus*	*latifrons*
shrevei	*cybotes*	*fuscoauratus*	*fuscoauratus*
strahmi	*cybotes*	*gadovii*	*gadovii*
whitemani	*cybotes*	*garmani*	*grahami*
altavelensis	*distichus*	*gingivinus*	*bimaculatus*
brevirostris	*distichus*	*grahami*	*grahami*
distichus	*distichus*	*granuliceps*	*auratus*
equestris	*equestris*	*griseus*	*roquet*
luteogularis	*equestris*	*gundlachi*	*cristatellus*
noblei	*equestris*	*hendersoni*	*hendersoni*
smallwoodi	*equestris*	*heterodermus*	*phenacosaurus*
antonii	*fuscoauratus*	*homolechis*	*sagrei*
fuscoauratus	*fuscoauratus*	*humilis*	*humilis*
kemptoni	*fuscoauratus*	*insignis*	*latifrons*
limifrons	*fuscoauratus*	*insolitus*	*insolitus*
maculiventris	*fuscoauratus*	*intermedius*	*laeviventris*
mariarum	*fuscoauratus*	*isolepis*	*carolinensis*
ortonii	*fuscoauratus*	*jacare*	*punctatus*
polylepis	*fuscoauratus*	*jubar*	*sagrei*
tolimensis	*fuscoauratus*	*kemptoni*	*fuscoauratus*
dunni	*gadovii*	*krugi*	*cristatellus*
gadovii	*gadovii*	*laeviventris*	*laeviventris*
liogaster	*gadovii*	*latifrons*	*latifrons*
taylori	*gadovii*	*leachii*	*bimaculatus*
conspersus	*grahami*	*lemurinus*	*lemurinus*
garmani	*grahami*	*limifrons*	*fuscoauratus*
grahami	*grahami*	*lineatopus*	*grahami*
lineatopus	*grahami*	*lineatus*	*auratus*
opalinus	*grahami*	*liogaster*	*gadovii*
reconditus	*grahami*	*lividus*	*bimaculatus*
valencienni	*grahami*	*longiceps*	*carolinensis*
bahorucoensis	*hendersoni*	*longitibialis*	*cybotes*
hendersoni	*hendersoni*	*loveridgei*	*petersi*
compressicauda	*humilis*	*loysiana*	*angusticeps*
humilis	*humilis*	*luciae*	*roquet*
notopholis	*humilis*	*lucius*	*lucius*
tropidonotus	*humilis*	*luteogularis*	*equestris*
insolitus	*insolitus*	*luteosignifer*	*sagrei*
placidus	*insolitus*	*marcanoi*	*cybotes*
sheplani	*insolitus*	*mariarum*	*fuscoauratus*
proboscis	*laevis*	*marmoratus*	*bimaculatus*
intermedius	*laeviventris*	*maynardi*	*carolinensis*
laeviventris	*laeviventris*	*megapholidotus*	*nebuloides*
fraseri	*latifrons*	*meridionalis*	none

frenatus	*latifrons*	*mestrei*	*sagrei*
insignis	*latifrons*	*micropholidotus*	*nebulosus*
latifrons	*latifrons*	*microtus*	*latifrons*
microtus	*latifrons*	*monticola*	*monticola*
squamulatus	*latifrons*	*nebuloides*	*nebuloides*
lemurinus	*lemurinus*	*nebulosus*	*nebulosus*
tropidolepis	*lemurinus*	*noblei*	*equestris*
oxylophus	*lionotus*	*notopholis*	*humilis*
poecilopus	*lionotus*	*nubilis*	*bimaculatus*
argenteolus	*lucius*	*occultus*	unknown
bartschi	*lucius*	*oculatus*	*bimaculatus*
lucius	*lucius*	*olssoni*	*semilineatus*
vermiculatus	*lucius*	*onca*	*onca*
christophei	*monticola*	*opalinus*	*grahami*
etheridgei	*monticola*	*ophiolepis*	*sagrei*
fowleri	*monticola*	*ortonii*	*fuscoauratus*
monticola	*monticola*	*oxylophus*	*lionotus*
megapholidotus	*nebuloides*	*parvicirculatus*	*schiedi*
nebuloides	*nebuloides*	*paternus*	*carolinensis*
micropholidotus	*nebulosus*	*pentaprion*	*pentaprion*
nebulosus	*nebulosus*	*perracae*	*punctatus*
agassizi	none	*petersii*	*petersi*
altae	none	*placidus*	*insolitus*
barkeri	none	*poecilopus*	*lionotus*
capito	none	*polylepis*	*fuscoauratus*
meridionalis	none	*poncencis*	*cristatellus*
darlingtoni	none	*porcatus*	*carolinensis*
occultus	none	*maculiventris*	*fuscoauratus*
onca	*onca*	*proboscis*	*laevis*
pentaprion	*pentaprion*	*pulchellus*	*cristatellus*
vociferans	*pentaprion*	*punctatus*	*punctatus*
apollinaris	*petersi*	*quadriocellifer*	*sagrei*
biporcatus	*petersi*	*reconditus*	*grahami*
loveridgei	*petersi*	*richardi*	*roquet*
petersii	*petersi*	*ricordii*	*cuvieri*
heterodermus	*phenacosaurus*	*roosevelti*	*cuvieri*
chloris	*punctatus*	*roquet*	*roquet*
fasciata	*punctatus*	*rubribarbus*	*sagrei*
jacare	*punctatus*	*ruizii*	*tigrinus*
perracae	*punctatus*	*sagrei*	*sagrei*
punctatus	*punctatus*	*semilineatus*	*semilineatus*
transversalis	*punctatus*	*sericeus*	*sericeus*
aeneus	*roquet*	*sheplani*	*insolitus*
bonairensis	*roquet*	*shrevei*	*cybotes*

griseus	*roquet*	*smallwoodi*	*equestris*
luciae	*roquet*	*smaragdinus*	*carolinensis*
richardi	*roquet*	*sminthus*	*crassulus*
roquet	*roquet*	*solitarius*	*tigrinus*
trinitatus	*roquet*	*spectrum*	*alutaceus*
ahli	*sagrei*	*squamulatus*	*latifrons*
allogus	*sagrei*	*strahmi*	*cybotes*
homolechis	*sagrei*	*stratulus*	*acutus*
jubar	*sagrei*	*subocularis*	*subocularis*
luteosignifer	*sagrei*	*taylori*	*gadovii*
mestrei	*sagrei*	*tolimensis*	*fuscoauratus*
ophiolepis	*sagrei*	*townsendi*	*auratus*
quadriocellifer	*sagrei*	*transversalis*	*punctatus*
rubribarbus	*sagrei*	*trinitatus*	*roquet*
sagrei	*sagrei*	*tropidogaster*	*auratus*
cobanensis	*schiedi*	*tropidolepis*	*lemurinus*
parvicirculatus	*schiedi*	*tropidonotus*	*humilis*
olssoni	*semilineatus*	*valencienni*	*grahami*
semilineatus	*semilineatus*	*vanidicus*	*alutaceus*
sericeus	*sericeus*	*ventrimaculatus*	*aequatorialis*
cuprinus	*subocularis*	*vermiculatus*	*lucius*
subocularis	*subocularis*	*vociferans*	*pentaprion*
ruizii	*tigrinus*	*wattsi*	*bimaculatus*
solitarius	*tigrinus*	*whitemani*	*cybotes*

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Natural History of Some *Anolis* Lizards: A Summary of Work in the Last Decade

I have been taking undergraduate students into the Neotropics, primarily the Dominican Republic, since 1986 — primarily to study anoles. Spurred on in large part by the dearth of information on natural history (Schwartz and Henderson 1991), my students, a few loyal colleagues, and I have been looking at various aspects of natural history in *Anolis* lizards. Below I summarize by category the results of many studies often of very short duration. Nevertheless, an accumulation of such information over time can provide a collective picture of attributes frequently overlooked in studies addressing larger systematic and/or evolutionary questions.

Diet

We have examined the diets of *Anolis armouri* (Lenart et al. 1994 [1995]), *A. barahonae* (Bowersox et al. 1994b), *A. barbouri* (Howard et al. 1999), *A. barkeri* (Birt et al., in review), *A. brevirostris* (Moster et al. 1992), *A. cybotes* (Fobes et al. 1992), *A. distichus* (Burns et al. 1992, Cullen and Powell 1994), *A. olssoni* (Smith et al. 1994), and *A. whitemani* (Carr et al. 1989, Burns et al. 1992). Although the sample is far too small to make accurate generalizations for all anoles, the species examined all appeared to be dietary generalists and, even when one food item (usually ants) dominated the diet, it appeared to reflect availability of prey rather than any selectivity on the part of the lizards.

Reproduction

Pflanz et al. (1991) examined reproduction in *Anolis whitemani*, Allen et al. (1994 [1995]) in *A. barahonae*, and Birt et al. (in review) in *A. barkeri*. Although the data generally supported the contention that the monoallochronic pattern of ovideposition is typical of anoles (Smith et al. 1972), a large percentage of females in these stocky species were carrying two shelled eggs.

Parasitism

Coccidian parasites have been described from *Anolis armouri (Eimeria schwartzi*, *Isospora hendersoni*, Cisper et al. 1995), *A. bahorucoensis* (*I. reui*, Cisper et al. 1995), *A. cybotes* (*I. hendersoni*, Cisper et al. 1995), *A. distichus* (*I. guarocuyai*, Bui et al. 1991), and *A. olssoni* (*E. avilae*, Cisper et al. 1995).

Nematodes (*Skrjabinoptera leiocephalorum*) were recorded in *Anolis armouri* (Lenart et al. 1994 [1995]), *A. brevirostris* (Moster et al. 1991), and *A. cybotes* (Fobes et al. 1992). Birt et al. (1997) recorded immature anisakine ascarids, probably *Terranova* sp., in *A. barkeri*, a semi-aquatic anole from southern México. *Terranova caballeroi* has been found in *A. barbouri* (Howard et al. 1999) and syntopic *Eleutherodactylus* frogs (Powell et al. 1998) from Hispaniola. They proposed a life cycle for *T. caballeroi* in which the lizard or frog consumes an arthropod, probably an insect vector, and are, in turn, eaten by a snake (e.g., *Antillophis parvifrons*, from which adult *T. caballeroi* have been described; Powell et al. 1991), which serves as the definitive host.

Zippel et al. (1996) examined the distribution of larval mites (*Eutrombicula alfreddugesi*) in *Anolis coelestinus*, *A. cybotes*, and *A. olssoni* from montane and lowland areas.

Spatial Relationships and General Natural History

Powell et al. (1992) recorded *Anolis pogus* at sea level on St. Maarten, in contrast with the prevailing view that populations were restricted to higher elevations. Powell et al. (1996) included *A. brevirostris* and *A. whitemani* in a study of spatial partitioning by a lizard community in xeric habitat in the Dominican Republic. Vertical stratification and microhabitat use was examined in an anoline guild including *A. bahorucoensis*, *A. barahonae*, *A. coelestinus*, *A. cybotes*, and *A. distichus* (Lenart and Sowell 1996, Lenart et al. 1997), and density compensation was noted in increasingly disturbed areas in which some forest characteristics (e.g., upper canopy or shade) were missing. Birt et al. (in review) studied *A. barkeri* along a heavily shaded stream in southern México. Howard et al. (1999) provided data suggesting that *A. barbouri*, an unusual leaf-litter specialist, is ecologically much more similar to syntopic *Eleutherodactylus* frogs than to sympatric congeners. Powell (1999) included preliminary natural history data on the extremely euryoecious *A. longiceps* from Navassa Island.

On several occasions, we have focused on anoles in habitats altered by human activity, on the assumption that such data often are lacking and are more representative of modern realities than studies in the few remaining pristine habitats of the West Indies. These studies have examined *Anolis brevirostris* (Moster et al. 1992), *A. cybotes* (Fobes et al. 1992), and *A. olssoni* (Smith et al. 1994, Queral et al. 1995). Queral et al. (1995) also recorded agonistic behavioral responses by male *A. olssoni* to conspecifics.

Range Expansion

Williams (1977) had reported the presence of Cuban *Anolis porcatus* in Santo Domingo, Dominican Republic, but a subsequent study like that addressing Puerto Rican *A. cristatellus* in La Romana (Fitch et al. 1989) had been lacking. Powell et al. (1990) found that, like *A. cristatellus*, *A. porcatus* had extended its distribution throughout most of the highly modified habitats in the city, but was apparently limited from further expansion by the presence of a native ecological counterpart (*A. chlorocyanus*). Powell (1990) subsequently documented the species east of the Río Ozama, and Powell and Parmerlee (1991a) reported a disjunct population at the international airport 20 km to the east. Recent surveys (through 1999) indicated that all of these populations are still extant, but have revealed no additional range expansion.

Powell et al. (1991) recorded the presence of *Anolis chlorocyanus*, a North Paleoisland endemic, near Barahona. Subsequently, Garcia et al. (1994) documented hybridization between *A. chlorocyanus* and *A. coelestinus*, its South Paleoisland counterpart.

Anecdotal Observations

Cusumano et al. (1991) related low frequencies of tail autotomy in *Anolis whitemani* to low densities of lizards and predators in xeric habitats. Powell and Parmerlee (1991b) described agonistic behavior between *A. chlorocyanus* and introduced *A. cristatellus*. P. A. Zani (unpubl. data) found that critical thermal maxima were higher in lowland populations of *A. coelestinus*, *A. cybotes*, and *A. distichus* than in cooler montane habitats. Parmerlee et al. (1992) reported male displacement during copulation in *A. porcatus*. Nocturnal activity around lights was reported for *A. brevirostris* in the Dominican Republic (Bowersox et al. 1994a) and *A. gingivinus* on St. Maarten (Powell and Henderson 1992). Bowersox et al. (1994a) also recorded infanticide by *A. chlorocyanus*, predation by chickens on *A. coelestinus* and *A. cybotes*, and used the frequency of jaw lesions on male *A. cybotes* as an indicator of intraspecific combat.

Systematics

Zani et al. (1993) demonstrated a closer affinity of introduced Dominican *Anolis cristatellus* with a native population from Río Piedras, Puerto Rico, than with a population from the more geographically proximate Mayagüez. Powell (1993) listed 16 currently recognized subspecies of Hispaniolan *Anolis* that might warrant recognition as full species.

Plans for future studies, some beginning as early as this summer (1999), include natural history surveys and focal animal studies of some little known Hispaniolan anoles (e.g., *Anolis longitibialis*, *A. sheplani*, *A. singularis*) and some additional work on the response of a Hispaniolan herpetofaunal community to the clearcutting of their montane forest habitat. I also hope to examine more species on small islands and to collaborate in systematic and biogeographic studies of several large species complexes, including the *A. cybotes* and *A. distichus* complexes. In addition, pursuing an interest in aquatic anoles triggered by recent studies of *A. barkeri*, I have begun an examination of limb, toe, and claw morphology of these habitat specialists.

Literature Cited

Allen, A. L., M. K. Albright, and R. Powell. 1994 (1995). Notes on the reproductive biology of *Anolis barahonae* (Lacertilia: Polychrotidae), a crown-dwelling giant anole from Hispaniola. Herpetol. Nat. Hist. 2(2): 93–95.

Birt, R. A., J. H. Greve, and R. Powell. 1997. *Anolis barkeri*. Parasitism. Herpetol. Rev. 28: 201.

—, R. Powell, and B. D. Greene. In review. Natural history of *Anolis barkeri*, a semi-aquatic lizard from southern México.

Bowersox, S. R., S. Calderón, G. Cisper, R. S. Garcia, C. Huntington, A. Lathrop, L. Lenart, J. S. Parmerlee, Jr., R. Powell, A. Queral, D. D. Smith, S. P. Sowell, and K. C. Zippel. 1994a. Miscellaneous natural history notes on amphibians and reptiles from the Dominican Republic. Bull. Chicago Herpetol. Soc. 29: 54–55.

—, —, R. Powell, J. S. Parmerlee, Jr., D. D. Smith, and A. Lathrop. 1994b. Nahrung eines Riesenanolis, *Anolis barahonae*, von Hispaniola, mit einer Zusammenfassung des Nahrungsspektrums westindischer Riesenanolis-Arten. Salamandra 30: 155–160.

Bui, H. T., R. Powell, D. D. Smith, J. S. Parmerlee, Jr., and A. Lathrop. 1992. A new coccidian parasite (Apicomplexa: Eimeriorina) from *Anolis distichus* (Sauria: Polychridae) in the Dominican Republic. J. Parasitol. 78: 784–785.

Burns, J. K., C. A. Cunningham, R. A. Dupuis, M. N. Trask, J. S. Tulloch, R. Powell, J. S. Parmerlee, Jr., K. L. Kopecky, and M. L. Jolley. 1992. Lizards of the Cayos Siete Hermanos, Dominican Republic, Hispaniola. Bull. Chicago Herpetol. Soc. 27: 225–232.

Carr, D. K., R. Powell, J. S. Parmerlee, Jr., and D. D. Smith. 1989. *Anolis whitemani whitemani*. Food habits. Herpetol. Rev. 20: 49, 53.

Cisper, G. L., C. Huntington, D. D. Smith, R. Powell, J. S. Parmerlee, Jr., and A. Lathrop. 1995. Four new Coccidia (Apicomplexa: Eimeriidae) from anoles (Lacertilia: Polychrotidae) in the Dominican Republic. J. Parasitol. 81: 252–255.

Cullen, D. J. and R. Powell. 1994. A comparison of food habits of a montane and a lowland population of *Anolis distichus* (Lacertilia: Polychrotidae) from the Dominican Republic. Bull. Maryland Herpetol. Soc. 30: 62–66.

Cusumano, M. A., D. J. Pflanz, R. Powell, and D. D. Smith. 1991. *Anolis whitemani*. Tail autotomy. Herpetol. Rev. 22: 58.

Fitch, H. S., R. W. Henderson, and H. Guarisco. 1989. Aspects of the ecology of an introduced anole: *Anolis cristatellus* in the Dominican Republic. Amphibia-Reptilia 10: 307–320.

Fobes, T. M., R. Powell, J. S. Parmerlee, Jr., A. Lathrop, and D. D. Smith. 1992. Natural history of *Anolis cybotes* (Sauria: Polychridae) in a disturbed habitat in Barahona, Dominican Republic. Carib. J. Sci. 28: 200–207.

Garcia, R., A. Queral, R. Powell, J. S. Parmerlee, Jr., D. D. Smith, and A. Lathrop. 1994. Evidence of hybridization among green anoles (Lacertilia: Polychrotidae) from Hispaniola. Carib. J. Sci. 30: 279–281.

Howard, A. K., J. D. Forester, J. M. Ruder, J. S. Parmerlee, Jr., and R. Powell. 1999. Natural history of a terrestrial Hispaniolan anole: *Anolis barbouri* (Squamata: Polychrotidae). J. Herpetol. 33: in press.

Lenart, L. A., R. Powell, J. S. Parmerlee, Jr., D. D. Smith, and A. Lathrop. 1994 (1995). The diet and a gastric parasite of *Anolis armouri*, a cybotoid anole from montane pine forests in southern Hispaniola. Herpetol. Nat. Hist. 2(2): 97–100.

—, —, —, A. Lathrop, and D. D. Smith. 1997. Anoline diversity in three differentially altered habitats in the Sierra de Baoruco, República Dominicana, Hispaniola. Biotropica 29: 117–123.

— and S. P. Sowell. 1996. Anoline diversity in three differentially altered habitats in the Sierra de Baoruco, Dominican Republic, Hispaniola (abstracts in English, Spanish, and French), p. 442–443. *In* R. Powell and R. W. Henderson (eds.), Contributions to West Indian Herpetology: A Tribute to Albert Schwartz. Soc. Study Amphib. Rept. Contrib. Herpetol., vol. 12. Ithaca, NY.

Moster, J. A., R. Powell, J. S. Parmerlee, Jr., D. D. Smith, and A. Lathrop. 1992. Natural history notes on a small population of *Anolis brevirostris* (Sauria: Polychridae) from altered habitat in the Dominican Republic. Bull. Maryland Herpetol. Soc. 28: 150–161.

Parmerlee, J. S., Jr., R. Powell, D. D. Smith, and A. Lathrop. 1992. Unusual behavior in the Cuban Green Anole, *Anolis porcatus* (Sauria: Polychridae). Bull. Chicago Herpetol. Soc. 27: 118.

Pflanz, D. J., M. A. Cusumano, and R. Powell. 1991. Notes on reproduction in a xeric-adapted anole, *Anolis whitemani* (Sauria: Polychridae) from Hispaniola. J. Herpetol. 25: 491–493.

Powell, R. 1990. Geographic distribution: *Anolis porcatus*. Herpetol. Rev. 21: 96.

—. 1993. Comments on the taxonomic arrangement of some Hispaniolan amphibians and reptiles. Herpetol. Rev. 24: 135–137.

—. 1999. Herpetology of Navassa Island, West Indies. Carib. J. Sci. 35: in press.

—, J. H. Greve, and A. K. Howard. 1998. Hispaniolan *Eleutherodactylus* (Anura: Leptodactylidae) as hosts of immature *Terranova* (Nematoda: Ascarididae), with notes on additional nematodes. Carib. J. Sci. 34: 155–157.

— and R. W. Henderson. 1992. *Anolis gingivinus*. Nocturnal behavior. Herpetol. Rev. 23: 117.

—, S. A. Maxey, and J. H. Greve. 1990. The occurrence of *Terranova caballeroi* (Nematoda: Ascarididae) in *Antillophis parvifrons protenus* (Serpentes: Colubridae) from Hispaniola. Carib. J. Sci. 26: 72.

— and J. S. Parmerlee, Jr. 1991a. Geographic distribution: *Anolis porcatus*. Herpetol. Rev. 22: 65.

— and —. 1991b. *Anolis chlorocyanus*. Behavior. Herpetol. Rev. 22:130.

—, —, and D. D. Smith. 1991. Geographic distribution: *Anolis chlorocyanus*. Herpetol. Rev. 22: 134–135.

—, —, and —. 1996. Evidence of spatial niche partitioning by a Hispaniolan lizard community in a xeric habitat, p. 317–326. *In* R. Powell and R.W. Henderson (eds.), Contributions to West Indian Herpetology: A Tribute to Albert Schwartz. Soc. Study Amphib. Rept. Contrib. Herpetol., vol. 12. Ithaca, NY.

—, R. J. Passaro, and R. W. Henderson. 1992. Noteworthy herpetological records from Saint [sic] Maarten, Netherlands Antilles. Carib. J. Sci. 28: 234–235.

—, D. D. Smith, J. S. Parmerlee, Jr., C. V. Taylor, Jr., and M. L. Jolley. 1990. Range expansion by an introduced anole: *Anolis porcatus* in the Dominican Republic. Amphibia-Reptilia 11: 421–425.

Queral, A., R. Garcia, R. Powell, J. S. Parmerlee, Jr., D. D. Smith, and A. Lathrop. 1995. Agonistic responses by a grass anole, *Anolis olssoni* from the Dominican Republic, to male conspecifics. Amphibia-Reptilia 16: 313–321.

Schwartz, A. and R. W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. Univ. Florida Press, Gainesville.

Smith, H. M., G. Sinelnik, J. D. Fawcett, and R. E. Jones. 1972. A unique reproductive cycle in *Anolis* and its relatives. Bull. Philadelphia Herpetol. Soc. 20: 28–30.

Smith, J. W., R. Powell, J. S. Parmerlee, Jr., D. D. Smith, and A. Lathrop. 1994. Natural history notes on a population of *Anolis olssoni* (Sauria: Polychrotidae) from the Dominican Republic. Bull. Maryland Herpetol. Soc. 30: 67–75.

Williams, E. E. 1977. Anoles out of place: introduced anoles, p. 110–118. *In* E. E. Williams (ed.), The Third *Anolis* Newsletter. Mus. Comp. Zool., Harvard University, Cambridge, MA.

Zani, P. A., S. I. Guttman, and R. Powell. 1993. The genetic relations of *Anolis cristatellus* (Sauria: Polychridae) from Hispaniola and Puerto Rico. Carib. J. Sci. 29: 250–253.

Zippel, K. C., R. Powell, J. S. Parmerlee, Jr., S. Monks, A. Lathrop, and D. D. Smith. 1996. The distribution of larval *Eutrombicula alfreddugesi* (Acari: Trombiculidae) infesting *Anolis* lizards (Lacertilia: Polychrotidae) from different habitats on Hispaniola. Carib. J. Sci. 32: 43–49.

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Studies of Puerto Rican Fauna

Permit me to give a 'plug' for research in the Caribbean. Living year-round in Puerto Rico is an obvious advantage for students wishing to pursue investigations with neotropical species. The Department of Biology of the University of Puerto Rico grants master's and Ph.D.degrees and has 46 faculty members (31 are research oriented). There are additional biologists in Puerto Rico associated with the Institute of Tropical Forestry, NSF's program of Long Term Ecological Research, the Department of Natural and Environmental Resources, the US Forest Service, and the US Fish and Wildlife Service. My research at the University of Puerto Rico deals with terrestrial ecology, ecological physiology, and constraints to organismal performance that can potentially influence the evolution of life histories. My students and I have pursued studies of *Anolis* species, the Puerto Rican Boa, *Eleutherodactylus* frogs, birds, beetles, and small mammals. The remainder of this note describes some of our work with anoles.

In studies of two anole species, *A. cristatellus* and *A. gundlachi*, we have shown that conspecifics at different altitudes and latitudes do not exhibit differences in standard metabolic rate, SMR (after adjusting for mass). We find no evidence of local adaptation of SMR by conspecifics in different environments other than that related to body size (the largest *A. gundlachi*, which occur at the highest elevations, have the highest SMR). Other work in our laboratory has indicated that anoles lack a capacity for thermal acclimation of metabolism, i.e., SMR at a given test temperature does not change after one or two weeks of exposure to a cold or warm acclimation temperature. If you are interested in these questions, see Journal of Thermal Biology (1996, 21:11-14) and Copeia (1996:535-542).

We have also conducted comparative studies of anoles which reveal species differences in energy expenditure (in prep.). In a study of six anoles (*A. pulchellus, A. krugi, A. cristatellus, A. gundlachi, A. evermanni*, and *A. stratulus*), we have found that the grassland species *A. pulchellus* and *A. krugi* have a rather high SMR, whereas the rainforest species *A. gundlachi* has a comparatively low SMR. We have yet to determine why this difference in energy expenditure occurs and whether it is adaptive. Could a higher SMR evolve to increase readiness for activity?

One of the species we plan to work with in the future is the giant anole, *Anolis cuvieri,* a rather slow moving lizard that seems chameleon-like. We are planning studies of its locomotor performance, habitat use, and energy expenditures. This would make a nice thesis project for someone, so if you are interested, let me know. Puerto Rico is perhaps best known for its coquies, small frogs with amazing vocal abilities. My students and I have examined the reproduction, habitat use, locomotion, and physiological abilities of these frogs (e.g., Copeia 1999:40-48; J. Comp. Physiol. B, in press). It is noteworthy that *Anolis* lizards and *Eleutherodactylus* frogs share the same habitats and often consume similar foods, yet there is a temporal partitioning of resources, because the anoles are day-active and the frogs are mostly nocturnal. This is another topic that merits further consideration.

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Colonization and Extinction of *Anolis* Populations on Small Bahamian Islands

In October 1993 we began an experimental study of interspecific competition between *A. sagrei* and *A. carolinensis*. The study had 3 major objectives: 1) examine the ecological effects that two common lizard species, *A. sagrei* and *A. carolinensis*, have on each other, 2) investigate whether the presence of congeners leads to predictable evolution in morphology for both species, and 3) compare the top-down effect of lizards on food-web dynamics when each species is present alone to the effect when both are present together. To meet these objectives, we conducted a field experiment in which we introduced lizards onto small islands in the vicinity of Great Exuma, Bahamas. The experiment was monitored annually in October until 1996 when Hurricane Lili extirpated most of the lizards populations. Although the hurricane precluded our analysis of long-term evolutionary effects on the lizards, we obtained significant data on ecological processes (Losos and Spiller 1999). Moreover, we were on site when the hurricane struck and had just completed our annual census of the island populations. During the following week, we were able to recensus the populations on the study islands. This unique situation resulted in an unprecedented study of the impact of a catastrophic hurricane on insular populations (Spiller et al. 1998). We first summarize the experimental study and then describe the impact of the hurricane on lizards.

Prior to the experiment, lizards were absent on all of the 19 study islands. The experimental design was a 2x2 factorial with the following 4 treatments: 1) control islands – no lizard introductions, 2) only *A. sagrei* introduced (allopatric islands), 3) only *A. carolinensis* introduced (allopatric islands), and 4) both introduced (sympatric islands). Islands were divided into blocks, according to vegetation structure and location, and treatments were randomized within blocks. The first treatment had 4 replicate islands and the other treatments had 5. *Anolis sagrei* populations thrived on almost all islands, whereas within three years, many *A. carolinensis* populations had gone extinct and most others were very small. Thus, *A. sagrei* was a more successful colonist, probably because they are better adapted for the habitat on the small islands. *Anolis carolinensis* was not more likely to become extinct on islands containing *A. sagrei*, but population densities of *A. carolinensis,* averaged over 1994-96, were lower on sympatric islands compared to allopatric islands. In addition, *A. carolinensis* tended to perch higher, relative to available vegetation, on sympatric islands than they did on allopatric islands. Conversely, the presence of *A. carolinensis* had no significant effect on average densities or perch heights of *A. sagrei* populations. However, inspection of population changes through time suggests that *A. carolinensis* may have initially had an effect on *A. sagrei*, but this effect decreased as *A. carolinensis* populations declined. Overall the species interaction was asymmetrical; the effect of *A. sagrei* on *A. carolinensis* was greater than vice versa.

At the end of the experiment, numbers of web spiders and leaf damage was lower on islands with *A. sagrei* than controls, as found in another introduction experiment (Schoener and Spiller in press) conducted on small islands in a different region of the Bahamas (Abaco) and in experimental enclosures (Spiller and Schoener 1994) located on a relatively large island (Staniel Cay). Thus, these effects by *A. sagrei* on different components of the food web appear to be a general phenomenon. Dial and Roughgarden (1994) documented similar food-web effects by *Anolis* lizards in a Puerto Rican rainforest. *Anolis carolinensis* had no significant effect on web spiders or leaf damage because they failed to colonize most islands.

In the early morning of October 19, 1996, Hurricane Lili, the first major hurricane to strike anywhere in the Exumas since 1932, passed directly over our study site with sustained winds of 90 knots and a storm surge of nearly 5 m. We had just finished a census of lizard and spider populations on the experimental islands. The small experimental islands were located on both sides of the very large island of Great Exuma. Because Lili's approach was westerly, islands on the southwest side were exposed to the full force of the storm surge, whereas islands on the northeast side were protected from this aspect of the hurricane. The next day, as soon as the storm subsided, and for three days thereafter, we recensused populations on all the islands. All populations were again censused approximately one and two years later. On the protected side, although effects were marked, a moderate number of individuals survived: mean number of lizard individuals per island was 34% lower immediately after than before the hurricane. One year later, mean number of lizards remained at about the same level as immediately after the hurricane. Two years after, numbers of lizards rebounded to about the same level they were before the hurricane. On the exposed side, all lizards were exterminated on the study islands, even though some populations were quite large. No lizard was found on the experimental islands 1 and 2 years after the hurricane.

Bahamian lizards have been experimentally introduced, repeatedly and successfully, onto small islands where they do not occur (Schoener and Schoener 1983). Because these islands were united with much larger ones when sea levels were lower 8-10,000 years ago, it is reasonable to conclude that they did, at one time, have lizard populations. Schoener and Schoener (1983) suggested that infrequent catastrophic hurricanes exterminated lizards on such islands. We now have an actual demonstration of the hypothesized mechanism. Immediately after the hurricane, lizards were found on an exposed island that was much larger than the experimental islands, but only in the highest area of that island. Hence, catastrophic extinction of lizards may have occurred only on islands small enough to be inundated completely during the hurricane. Thus, given the poor dispersal abilities of lizards, their absence from most small islands may literally represent the high-water mark of previous hurricanes.

References

Dial, R., and J. Roughgarden. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. Ecology 76:1821-1834.

Losos, J. B. and D. A. Spiller. 1999. Differential colonization success and asymmetrical interspecific interactions in two lizard species. Ecology 80:252-258.

Schoener T.W. and A. Schoener. 1983. Time to extinction of a lizard propagule is related to island size. Nature 302: 332-334.

Schoener, T. W. and D. A. Spiller. 1999. Indirect effects in an experimentally staged invasion by a major predator. American Naturalist 153:347-358.

Spiller, D. A., and T. W. Schoener. 1994. Effects of top and intermediate predators in a terrestrial food web. Ecology 75:182-196.

Spiller, D. A., J. B. Losos and T. W. Schoener. 1998. Impact of a catastrophic hurricane on island populations. Science 281:695-697.

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The Competitive Impact of *Anolis sagrei* (Sauria: Polychrotidae) on the Reproductive Output of *Anolis carolinensis*: An Enclosure Study

Introduction

Anolis carolinensis is the only member of its genus that is native to the United States. It is a trunk-crown ecomorph whose range encompasses the southeastern United States and occupies a variety of habitats from freshwater swamps to upland forest and mangrove islands. It is generally recognized that populations of *A. carolinensis* have suffered serious declines in density in areas colonized by *A. sagrei*, a trunk-ground ecomorph that was introduced into the Florida keys approximately 60 years ago (Williams, 1969). The range of this invader continues to expand, reaching most of Florida and spreading across the gulf coast (Campbell, 1996; Echternacht et al. 1995; Thomas et al., 1990). The decline of *A. carolinensis* has been attributed anecdotally to competitive pressure from *A. sagrei* (e.g., King and Krakauer, 1966; Tokarz and Beck, 1987; Case and Bolger, 1991; Echternacht and Harris, 1993).

Tokarz and Beck (1987), Brown (1988) and Brown and Echternacht (1991) performed laboratory and/or field experiments to determine whether behavioral interference between adult males is an important component of the interaction between these two species. They all found significantly lower levels of aggression in heterospecific encounters than conspecific encounters. These findings suggest that for adult male *A. sagrei* and *A. carolinensis,* intraspecific interactions are more important than interspecific interactions.

Instead of focusing upon adult male territoriality, I conducted an outdoor enclosure experiment with the intention of determining whether the decline of *A. carolinensis* in Florida could be attributed to a competitive impact of *A. sagrei* upon the reproductive output of *A. carolinensis*. I maintained adult pairs of the two species in different allopatric and sympatric densities during their breeding season, collected the eggs of the females as they were laid, recorded their masses and analyzed them for the amount of non-polar lipids, which are the main source of energy for the developing embryo.

Methods

The experiment consisted of five treatments in a balanced design intended to measure both allopatric density effects (intraspecific competition) and sympatric density effects (interspecific competition [Figure 1]). There were 23 enclosures: 5 enclosures each for treatments 2 - 4, and 4 enclosures each for treatments 1 and 5. The enclosures were erected within the confines of a series of chain link dog kennels with gravel floors with an enclosure size of 1.8 (h) X 1.6 (w) X 1.6 (d) meters. The enclosures were constructed of a nylon mesh material that was sewn into a tent shape with four walls and a roof with a velcro lined vertical slit for an entrance. The experiment was conducted during the summers of 1996 and 1997. The subject animals for each year were hand-captured in and around Gainesville, Florida and immediately transported to Knoxville for placement in the enclosures.

During the course of the study, the enclosures were supplemented with a combination of large (1.25cm) and small (0.66cm) crickets twice weekly. The nature of the enclosure interiors allowed for the crickets to find refugia, therefore maintaining a supply of food for the foraging lizards. In addition to the supplemental crickets, the mesh walls of the enclosures allowed for a variety of arthropod prey to enter the enclosures and provide an additional food source. In order to ensure an adequate supply of water for the lizards, the enclosures were sprayed with a garden hose if there had not been rain for 2 consecutive days. As they were collected, the eggs were cleaned with a soft bristled toothbrush, weighed, and measured for length and width with calipers. The eggs were then stored in an ultracold freezer (-80º C) until they could be analyzed for nonpolar lipid content.

The eggs collected from cages in treatment 3 were identified to species by distinctive differences in their shell surface morphologies (see T.C. Vincent, this issue). Dry mass was recorded for all the eggs (freeze-dried to a constant mass) and the nonpolar lipids were extracted using a petroleum ether wash. After the nonpolar lipids were extracted, a final dry mass was measured and used to calculate the dry mass of the nonpolar lipids of each egg.

Figure 1 Experimental design for the enclosure experiment.

	Treatment				
	1	**2**	**3**	**4**	**5**
A. carolinensis	1 pair	2 pair	1 pair		
A. sagrei			1 pair	2 pair	1 pair

Results

Regardless of treatment or year, on average *A. carolinensis* eggs are more massive than those of *A. sagrei* (Figures 2 and 3). In both years, *A. sagrei* laid significantly more eggs than *A. carolinensis*, and both species show patterns of egg output that strongly indicate intraspecific competitive effects upon reproduction (Table 1). Comparisons of treatments 1 to 3 and 5 to 3 show that reproductive output by *A. carolinensis* is severely curtailed in the presence of *A. sagrei*, although the reproductive output of all treatments (and *A. carolinensis* in particular) was depressed in 1997 (Table 1).

In 1996, *A. carolinensis* and *A. sagrei* both showed increases in egg dry mass from early season eggs to late season eggs (Table 2). This also held for 1997, although not as strongly. In 1996, *A. sagrei* eggs tended to have a higher lipid dry mass in late season eggs than early season eggs, although the relationship did not appear in 1997 (Table 3). Comparisons of egg lipid proportion show that in 1996 and 1997, *A. carolinensis* eggs tended to decrease in quality (as measured by proportion of the egg that is lipid) from early season to late, while *A. sagrei* eggs tended to retain their quality in 1996, but not in 1997 (Table 4).

Discussion

Given that there is a finite amount of energy that a female anole can dedicate to reproduction, she can either lay more eggs of a minimum quality, fewer eggs of a high quality, or an optimization of the two strategies. If the resources that are available to reproduction become constrained due to competition (either intraspecific or interspecific), a reduction in the quantity of eggs, quality of eggs, or both would be expected. My data indicate that female *A. carolinensis* and female *A. sagrei* respond to competition primarily through the reduction in the number of eggs produced during the reproductive season. This can be very clearly seen in the intraspecific comparisons of mean number of eggs produced per female in Table 1. The interspecific comparisons also show that the number of eggs produced per female by *A. carolinensis* drops drastically when in the presence of *A. sagrei*. This drop in reproductive output, if it holds true in natural situations, could be one of the primary mechanisms by which *A. sagrei* is causing reductions in populations of *A. carolinensis*.

The data in Tables 2-4 are inconclusive as to whether the females respond to competition by reducing egg quality. What is much more interesting are the seasonal dynamics in egg quality that differ between the two species. *Anolis carolinensis* females in this experiment tended to lay larger eggs (as measured by total egg dry mass [Table 2]) as the reproductive season progressed. However, they did not exhibit equivalent increases in lipid content (Table 3). *Anolis sagrei* females showed the same pattern of egg dry mass increase, but they also showed an equivalent increase in lipid dry mass (Tables 2, 3). As a result, the pattern seen is that *A. carolinensis* females produced larger eggs of lower quality (as measured by percent of egg that is non-polar lipid) as the reproductive season progressed, whereas *A. sagrei* females produced larger eggs while maintaining quality. This assumes that egg quality is only dependent upon the proportion of non-polar lipids. There will be a minimum absolute quantity of lipid in an egg that will guarantee a viable offspring, regardless of total egg size. If that is the case, the late season eggs of *A. carolinensis* in this experiment may not be "lower quality" than the early season eggs, just larger. Given that these patterns of egg quality for the two species are exhibited across all treatments in both years, they are not likely to be due to competition.

Acknowledgments

I would like to thank Sandy Echternacht for his support and for everything he does as an advisor. I would also like to acknowledge the graduate and undergraduate students who helped me a great deal in the construction of these enclosures. The analysis of the egg lipid content was only possible through the generosity of Justin Congdon and his laboratory at the Savannah River Ecology Lab. Last, but not least, I recognize my wife Beth who makes all this possible.

Literature Cited

Brown, P.R. 1988. Intraspecific and interspecific behavioral interactions in adult male *Anolis sagrei* and grey-throated *Anolis carolinensis* (Sauria, Iguanidae). Unpubl. M.S. Thesis, University of Tennessee, Knoxville. 115p.

Brown, P.R. and A.C. Echternacht. 1991. Interspecific behavioral interaction of adult male *Anolis sagrei* and grey-throated *Anolis carolinensis* (Sauria, Iguanidae): A preliminary field study. *Anolis* Newsl. 4:21-30.

Campbell, T.C. 1996. Northern range expansion of the brown anole (*Anolis sagrei*) in Florida and Georgia. Herp. Rev. 27:155-157.

Case, T.J. and D.T. Bolger. 1991. The role of interspecific competition in the biogeography of island lizards. TREE 6:135-139.

Echternacht, A.C. and L.D. Harris. 1993. The fauna and wildlife of the southeastern United States. In: Biodiversity of the Southeastern United States / Lowland Terrestrial Communities. (Martin, W.H., Boyce, S.G., and Echternacht, A.C. eds.) pp. 81-115. John Wiley and Sons, Inc., New York.

Echternacht, A.C., M.A. Wilson, E.J. Michaud, and D.M. MacDonald. 1995. Geographic distribution: *Anolis sagrei*. Herp. Rev. 26:107.

King, F.W. and T. Krakauer. 1966. The exotic herpetofauna of southeast Florida. Quart. J. Fla. Acad. Sci. 29:144-154.

Thomas, R.A., P.J. Thomas, J.O. Coulson, and T. Coulson. 1990. Geographic distribution: *Anolis sagrei sagrei*. Herp. Review. 21:22.

Tokarz, R.R. and J.W. Beck 1987. Behaviour of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*: an experimental test for behavioural interference. Anim. Behav. 35:722-734.

Williams, E.E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quart. Rev. Biol. 44:345-389.

Figure 2 Mean egg dry masses per treatment per year. Refer to Figure 1 for a description of the treatments. For treatment 3, 3c refers to the *A. carolinensis* and 3s refers to the *A. sagrei.*

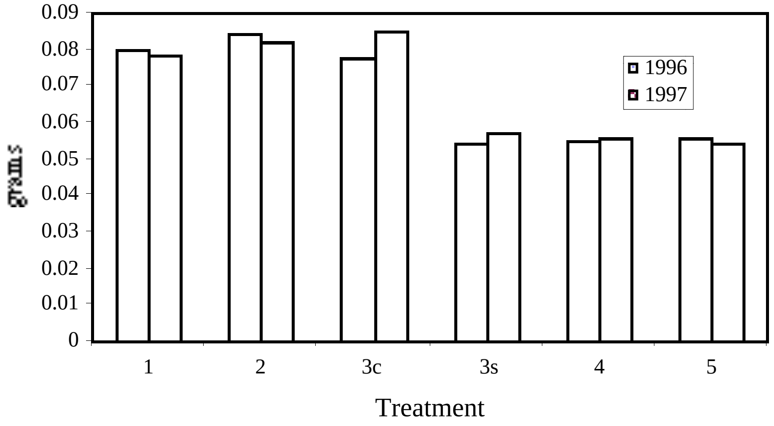

Figure 3 Mean lipid dry masses per treatment per year. Refer to Figure 1 for a description of the treatments. For treatment 3, 3c refers to the *A. carolinensis* and 3s refers to the *A. sagrei*.

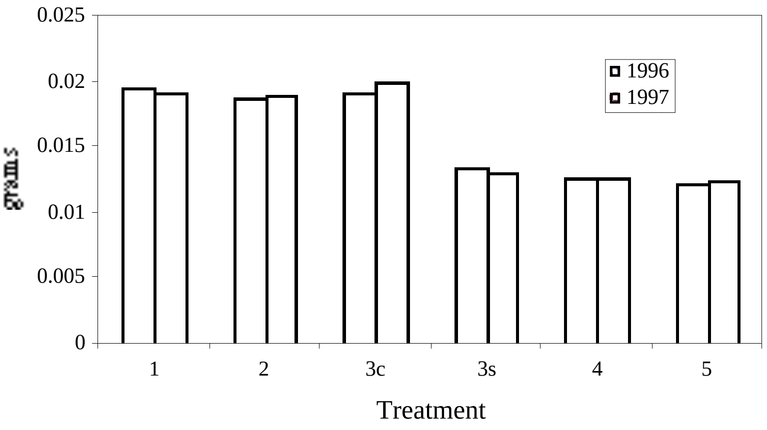

Table 1 Total number of eggs and the mean number of eggs produced per female (in parentheses) per treatment during the 1996 and 1997 enclosure studies. Period 1 = days 0-43, Period 2 = days 44-86, Period 3 = days 87-97. Periods 1 and 2 represent the duration of the reproductive period common to both species. Period 3 represents any portion of the reproductive period of *A. sagrei* that extended beyond that of *A. carolinensis*.

1996

Treatment	**Period 1**	**Period 2**	**Period 3**	**Total Eggs**
1	17 (4.25)	20 (5.0)	0	37 (9.25)
2	25 (2.5)	27 (2.7)	0	52 (5.2)
3 *A. carolinensis*	6 (1.2)	8 (1.6)	0	14 (2.8)
A. sagrei	19 (3.8)	37 (7.4)	7	63 (12.6)
4	33 (3.3)	52 (5.2)	13	98 (9.8)
5	19 (4.75)	31 (7.75)	4	54 (13.5)

1997

Treatment	**Period 1**	**Period 2**	**Period 3**	**Total Eggs**
1	4 (1.0)	5 (1.25)	0	9 (2.24)
2	8 (0.8)	12 (1.2)	0	20 (2.0)
3 *A. carolinensis*	6 (1.2)	8 (1.6)	0	14 (2.8)
A. sagrei	14 (2.8)	21 (4.2)	0	35 (7.0)
4	24 (2.4)	28 (2.8)	0	52 (5.2)
5	13 (3.25)	15 (3.0)	0	28 (7.0)

Table 2 Mean egg dry mass per treatment in the first and second halves of the reproductive season common to *Anolis carolinensis* and *A. sagrei* within outdoor enclosures. Mass values are in grams. Period 1 = days 0-43, Period 2 = days 44-86. Due to differences between 1996 and 1997, no statistical comparison was performed for the combined values. For a description of the treatments refer to Figure 1.

1996

Treatment	**Period 1**	**n 1**	**Period 2**	**n2**	**t-Test p value**
1	0.0754	13	0.0832	17	0.0064
2	0.0769	20	0.0887	25	0.0016
3 *A. carolinensis*	0.0765	5	0.0782	8	0.8522
A. sagrei	0.0506	17	0.0547	36	0.0071
4	0.0535	32	0.0558	46	0.1297
5	0.0511	18	0.0578	25	0.0012

1997

Treatment	**Period 1**	**n 1**	**Period 2**	**n 2**	**t-Test p value**
1	0.0806	3	0.0793	5	0.8210
2	0.0721	7	0.0837	12	0.0137
3 *A. carolinensis*	0.0805	6	0.0878	8	0.2972
A. sagrei	0.0574	14	0.0570	21	0.8926
4	0.0542	24	0.0569	28	0.0756
5	0.0543	13	0.0553	15	0.7076

Combined 1996 and 1997

Treatment	**Period 1**	**n 1**	**Period 2**	**n 2**
1	0.0764	16	0.0823	22
2	0.0773	28	0.0875	37
3 *A. carolinensis*	0.0787	11	0.0830	16
A. sagrei	0.0536	30	0.0562	63
4	0.0538	56	0.0561	87
5	0.0524	31	0.0567	45

Table 3 Mean lipid dry mass per treatment in the first and second halves of the reproductive season common to *Anolis carolinensis* and *A. sagrei* within outdoor enclosures. Mass values are in grams. Period 1 = days 0-43, Period 2 = days 44-86. Due to differences between 1996 and 1997, no statistical comparison was performed for the combined values. For a description of the treatments refer to Figure 1.

1996

Treatment	**Period 1**	**n 1**	**Period 2**	**n 2**	**t-Test p value**
1	0.0191	13	0.0197	17	0.2509
2	0.0182	20	0.0188	25	0.5519
3 *A. carolinensis*	0.0174	5	0.0202	8	0.3097
A. sagrei	0.0123	17	0.0135	36	0.0159
4	0.0116	32	0.0130	46	0.0029
5	0.0113	18	0.0125	25	0.0333

1997

Treatment	**Period 1**	**n 1**	**Period 2**	**n2**	**t-Test p value**
1	0.0194	3	0.0189	5	0.7635
2	0.0187	7	0.0189	12	0.8882
3 *A. carolinensis*	0.0194	6	0.0203	8	0.6565
A. sagrei	0.0135	14	0.0125	21	0.2901
4	0.0127	24	0.0125	28	0.6625
5	0.0129	13	0.0117	15	0.1556

Combined 1996 and 1997

Treatment	**Period 1**	**n 1**	**Period 2**	**n 2**
1	0.0191	16	0.0195	22
2	0.0183	28	0.0189	37
3 *A. carolinensis*	0.0185	11	0.0202	16
A. sagrei	0.0128	30	0.0134	63
4	0.121	56	0.0128	87
5	0.0120	31	0.0124	45

Table 4 Mean lipid proportion per treatment in the first and second halves of the reproductive season common to *Anolis carolinensis* and *A. sagrei* within outdoor enclosures. Values represent the proportion of the eggs composed of non-polar lipids. Period 1 = days 0-43, Period 2 = days 44-86. Due to differences between 1996 and 1997, no statistical comparison was performed for the combined values. For a description of the treatments refer to Figure 1.

1996

Treatment	Period 1	n1	Period 2	n2	t-Test p value
1	0.2545	13	0.2381	17	0.0499
2	0.2377	20	0.2046	25	0.0064
3 *A. carolinensis*	0.2280	5	0.2549	8	0.1611
A. sagrei	0.2430	17	0.2479	36	0.5019
4	0.2194	32	0.2335	46	0.0187
5	0.2200	18	0.2172	25	0.9425

1997

Treatment	Period 1	n1	Period 2	n2	t-Test p value
1	0.2405	3	0.2396	5	0.9127
2	0.2610	7	0.2255	12	0.0017
3 *A. carolinensis*	0.2422	6	0.2302	8	0.4099
A. sagrei	0.2362	14	0.2197	21	0.1273
4	0.2361	24	0.2207	28	0.0313
5	0.2385	13	0.2192	15	0.0249

Combined 1996 and 1997

Treatment	Period 1	n 1	Period 2	n 2
1	0.2519	16	0.2384	22
2	0.2404	28	0.2156	37
3 *A. carolinensis*	0.2357	11	0.2448	16
A. sagrei	0.2406	30	0.2397	63
4	0.2266	56	0.2293	87

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A Method for the Visual Discrimination of the Eggs of Two Sympatric Species of *Anolis* Lizards - a Short Note

During the course of a study of the ecological interactions between *Anolis carolinensis* and *A. sagrei* (Sauria: Polychrotidae), it became necessary to find a non-destructive method for discriminating between the eggs of the two species (see T.C. Vincent, this issue). Preliminary evidence (Pers. obs.; A. Echternacht, pers. comm.) had indicated that *A. carolinensis* eggs are larger (length, width) than those of *A. sagrei*. My data indicate that although *A. carolinensis* eggs are generally larger, there is enough overlap that a simple size comparison is inadequate for accurate species identification (Fig. 1).

Visual inspection of the shells of freshly laid intact eggs of the two species (103 *A. carolinensis* and 219 *A. sagrei*) reveal them to be distinguishable on the basis of their respective shell surface morphologies (Fig. 2). The egg shell surface of *A. sagrei* is characterized by shallow, but distinct, longitudinal fissures that uniformly cover the entire surface of the egg. *Anolis carolinensis* eggs lack this feature: the egg surface is predominantly smooth with a loose covering of flaking shell material. These differences are apparent in freshly laid, intact eggs, as well as those which have been held for up to 7 months in an ultracold (-80° C) freezer. Three volunteers who had each been given about 5 minutes to visually inspect known eggs from each species through a dissecting microscope were then asked to identify 20 unknown eggs (10 of each species drawn randomly). This test resulted in an average 90% accuracy rate (range: 85-95%) for identification of unknown eggs. All three volunteers stated that the accuracy would be improved with a longer familiarity period.

There is evidence to suggest a strong ecological interaction between these two species in Florida (King and Krakauer, 1966; Tokarz and Beck, 1987; Case and Bolger, 1991; Echternacht and Harris, 1993; Campbell and Gerber, 1996). Field and lab investigations into this interaction would benefit from the ability to identify the species affiliation of unknown eggs. Given that potential investigators take the necessary time to familiarize themselves with the features of the eggs of each species, I believe that this is a valid method for non-destructive, fast, and inexpensive egg identification. Plans are underway to collect eggs from additional anole species to see if egg surface morphology is phylogenetically correlated.

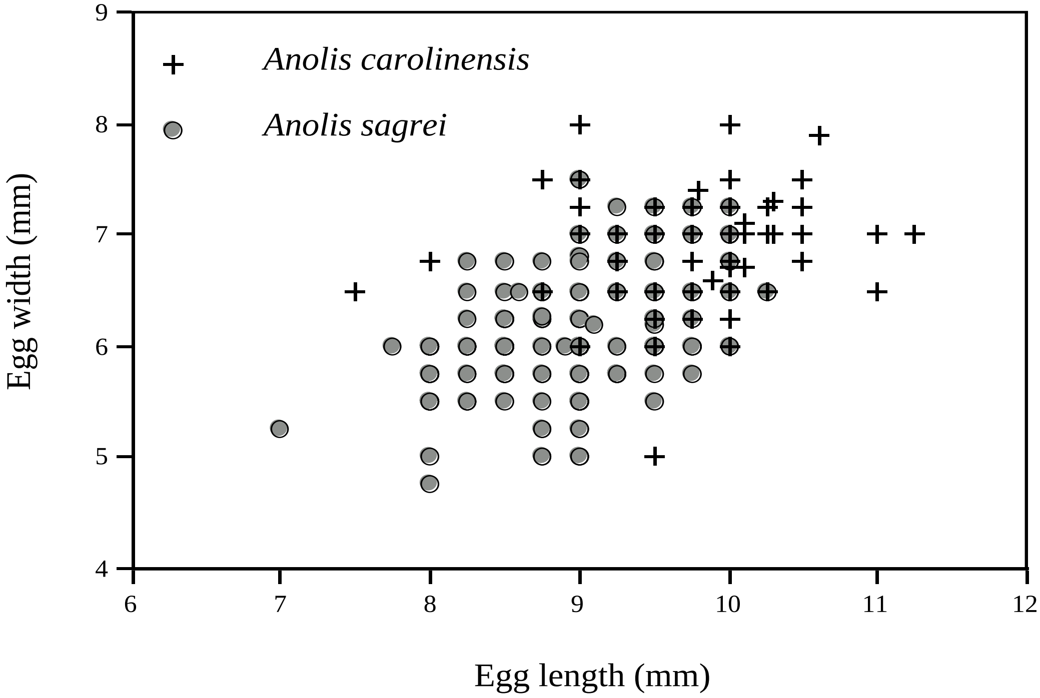

Figure 1 A graph of egg length plotted against egg width for *Anolis carolinensis* (n=103) and *A. sagrei*.(n=219). All egg dimensions were recorded within 3 hours of collection.

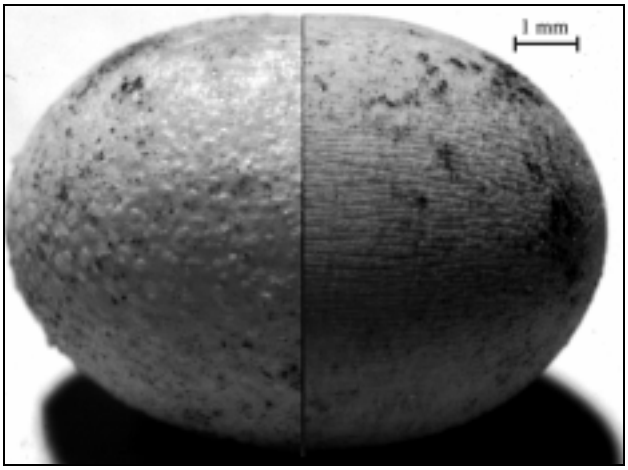

Figure 2 Egg surface morphology of *Anolis carolinensis* (left) and *A. sagrei* (right). Photographs by Todd Campbell.

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I would like to thank Paul Andreadis for turning on the lightbulb, Todd Campbell for the photographic expertise, and my advisor Sandy Echternacht for all the things he does.

Literature Cited

Campbell, T.C. and G. P. Gerber. 1996. Natural history notes: *Anolis sagrei*: Saurophagy. Herp. Rev. 27:200.

Case, T.J. and D.T. Bolger. 1991. The role of interspecific competition in the biogeography of island lizards. TREE 6:135-139.

Echternacht, A.C. and L.D. Harris. 1993. The fauna and wildlife of the southeastern United States. In: Biodiversity of the Southeastern United States / Lowland Terrestrial Communities. (Martin, W.H., Boyce, S.G., and Echternacht, A.C. eds.) pp. 81-115. John Wiley and Sons, Inc.

King, F.W. and T. Krakauer. 1966. The exotic herpetofauna of southeast Florida. Quart. J. Fla. Acad. Sci. 29:144-154.

Tokarz, R.R. and J.W. Beck 1987. Behaviour of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*: an experimental test for behavioural interference. Anim. Behav. 35:722-734.


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