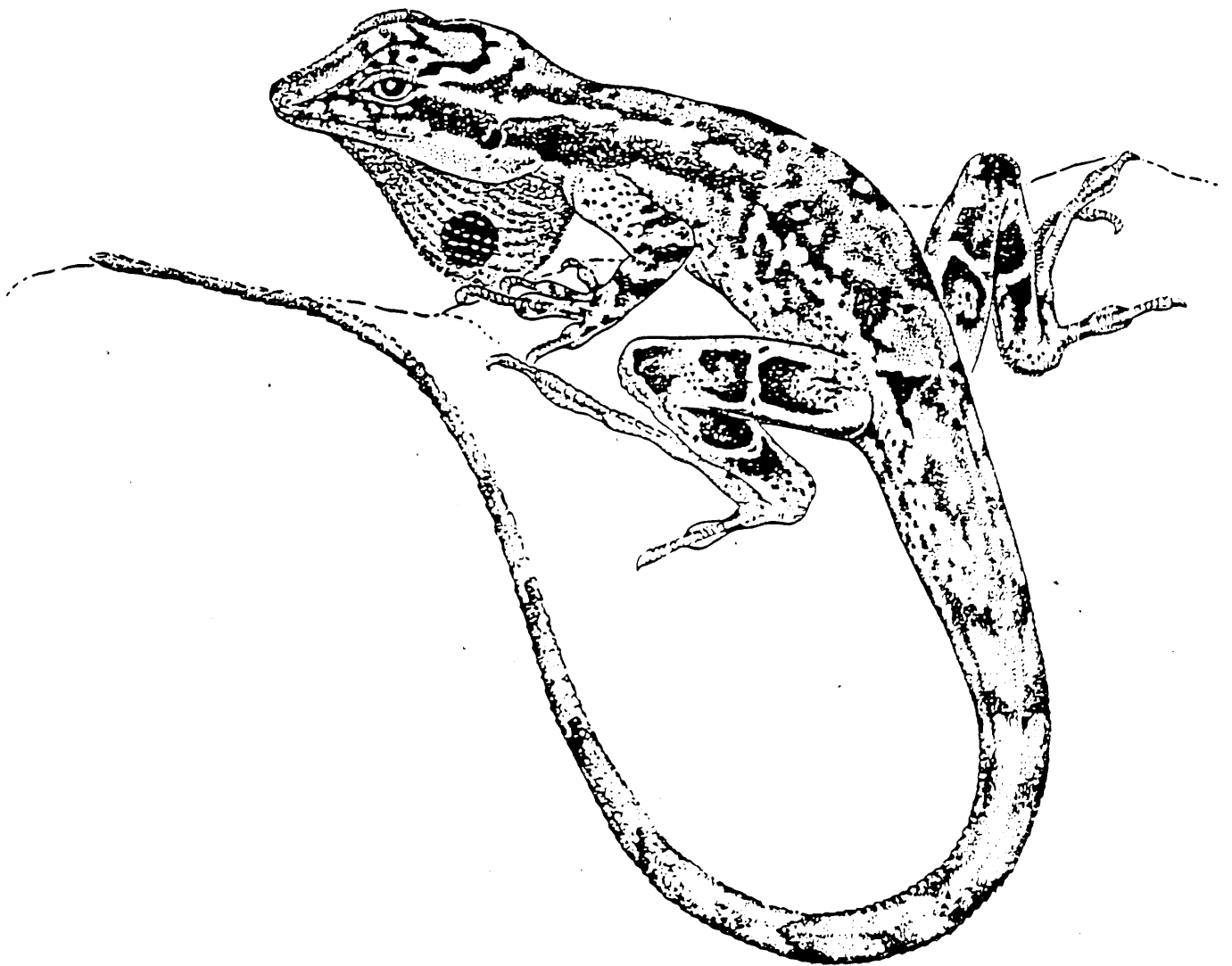


ANOLIS
NEWSLETTER
IV



EDITED BY:
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and
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Jonathan B. P.
September 3, 1991

On the cover:
An undescribed Ecuadorean anole, drawn by Laszlo Meszoly.

1991
Division of Amphibians and Reptiles
National Museum of Natural History
Smithsonian Institution
Washington, D.C.

Foreword

A symposium on Anolis biology, which we organized, was held at the 69th annual meeting of the American Society of Ichthyologists and Herpetologists, June 17-23, 1989, in San Francisco. The reasons for the symposium are discussed in Mayer's opening remarks to the symposium, which are reprinted here. In conjunction with the symposium, we felt it would be worthwhile to publish a fourth Anolis newsletter, particularly since it had been 12 years since the third newsletter. All those asked to participate in the symposium, as well as others active in Anolis research, were invited to contribute to the newsletter. In addition, several contributors learned of the newsletter from other sources.

As with previous installments, the newsletter is meant to be an informal forum for the presentation of data and discussion of theory pertinent to anoles. In particular, the newsletter serves three functions: 1. to allow investigators to inform others about their current research programs and future plans; 2. to provide an outlet for speculation and theorization perhaps inappropriate for publication in more formal arena; and 3. to present an opportunity for the presentation of data, in whatever format or state of analysis, that otherwise might be lost in the fog of time, never to see the light of day. As in previous newsletters, there is a general request that nothing said herein be quoted without the authors' express permission.

Other than basic guidelines concerning margin size, spacing, etc., format and style are entirely the authors' discretion, as the heterogeneity of the contributions will attest. The newsletter is divided into two parts. First, we have included the opening and concluding remarks of the Anolis biology symposium, along with its schedule. The second, and heftier, portion is comprised of the contributions.

We are extremely grateful to the Division of Amphibians and Reptiles, National Museum of Natural History, and Dr. George Zug for producing the newsletter. Thanks also to Dr. Sandy Echternacht for organizational assistance and advice.

Newsletters have been sent to the contributors. Others interested in obtaining it should contact one of the editors or the Division of Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560.

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Contents

Biology of <u>Anolis</u> Lizards Symposium	3
Adolph, S.C.	5
Andrews, R.	9
Bels, V.	13
Brown, P.R. & A.C. Echternacht	21
d'Orgeix, C.	31
Fleishman, L.J.	33
Gerber, G.P.	49
Greenberg, N.	54
Greene, H.W.	59
Jenssen, T.A.	63
Kramer, M. & E. Font	76
Losos, J.B.	81
MacDonald, D. & A.C. Echternacht	92
Mayer, G.C.	101
Michaud, E.J.	104
Minesky, J.J. & A.C. Echternacht	113
Schneider, C.	124
Schwenk, K. & G.C. Mayer	131
Stamps, J.	141

Biology of Anolis Lizards Symposium
69th Annual Meeting
American Society of Ichthyologists and Herpetologists
1989

Part 1--Systematics, Geographic Variation, and Biogeography

Sunday Morning, June 18th

Greg Mayer--Opening remarks

George Gorman--The classification of Anolis--needed: new research
not new names

Carl Lieb--Systematics of Mexican Anolis lizards: progress and prospects

Kurt Schwenk and Ernest Williams--Iguanian tongue morphology and the
phylogenetic relationships of anoloid lizards: are anoles agamids?

Jonathan Roughgarden--Geologic origin of the eastern Caribbean:
utility of data from Anolis

Chris Schneider--Mitochondrial DNA relationships among subspecies of
Anolis marmoratus

Brian Bock--Interdemic variation in dewlap pigmentation of Anolis limifrons
in Panama

Julian Lee--Anolis sagrei in Florida: phenetics of a colonizing species--
the Florida-Caribbean comparison

Ernest Williams--A crisis of expectations

Part 2--Ecology and Morphology

Sunday Afternoon

Tim Moermond and Julie Moran--Comparative habitat use behavior of
Lesser Antillean Anolis

Greg Mayer--Morphological convergence in Greater Antillean Anolis faunas.

Jonathan Losos--Ecomorphological evolution in West Indian Anolis

Stan Rand and Ernest Williams--Anoles of Soroa: a test of the ecomorph concept

Jane Peterson--Scaling and interspecific variation in the subdigital
morphology of six Puerto Rican Anolis species

Robin Andrews--Population dynamics of Anolis lizards

Craig Guyer--Seasonal patterns of demography in a tropical mainland anole,
Norops humilis

Tom Schoener--Effect of anoles on lower food-web levels

Jim Minesky and Sandy Echternacht--Microhabitat use by Anolis carolinensis
in East Tennessee

Part 3--Behavior and Physiology

Monday Morning, June 19th

Neil Greenberg (presented by Tom Jenssen)--Hormones and aggression

Mark Wilson--Anaerobiosis in Anolis carolinensis during territorial encounters staged in the laboratory

Tom Jenssen--Review of Anolis lizard communication behavior

Chris d'Orgeix--Individual and familiar/stranger recognition in the lizard Anolis limifrons

Richard Tokarz--Anolis copulatory behavior

Judy Stamps and Robin Andrews--Sexual size dimorphism in Anolis

Ed Michaud--Anolis carolinensis in Tennessee: bigger is better

Ray Huey--Thermal physiology, ecology, and evolution of Anolis

Paul Hertz--Effect of structural habitat on operative environmental temperatures for trunk-ground anoles of Puerto Rico

Harry Greene--Symposium conclusions

**Some Natural History Observations on *Anolis cupreus* in Costa Rica:
Thermal Ecology, Structural Habitat, and a Male-Biased Sex Ratio**

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Until the pioneering research by Cowles and Bogert (e.g., 1944), most biologists did not recognize that many lizards actively thermoregulate. Several decades (and several hundred studies) later, a new paradigm had emerged: the lizard as a careful, precise thermoregulator. However, an increasing number of studies are drawing attention to those lizard species that do not fit this paradigm, including nocturnal and crepuscular species as well as some diurnal species that are thermally passive (*sensu* Hertz 1974; Huey and Slatkin 1976).

Along with the thermal environment, microhabitat use is an important aspect of lizard ecology (e.g., Schoener 1977). However, relatively little attention has been paid to the relationship between these two. In open habitats (where sunlight readily penetrates, as in deserts and other xeric environments), microhabitats and thermal microclimates can be strongly interdependent (e.g., Adolph 1987, MS), whereas in closed habitats (dense forests), they are often essentially uncoupled. Lizards in closed habitats, including many *Anolis* species, often do not thermoregulate with the precision of, say, a desert lizard.

Here, I present some pilot data on the thermal ecology and microhabitat use by *Anolis cupreus* in a dry-deciduous tropical forest in Costa Rica. Because this habitat is intermediate in its degree of openness, I suspected that the anoles could thermoregulate more precisely than species in closed forests, and that microhabitat choice might be a mechanism of temperature regulation.

Methods

I collected these data while taking a tropical biology course offered by the Organization for Tropical Studies. The study area was located in Dr. Rafael Lucas Rodriguez Caballero Wildlife Refuge and Palo Verde National Park, Guanacaste Province, Costa Rica. I collected lizards from January 30 to February 2, 1984 (the dry season), in the forest behind the hacienda that serves as park headquarters, and along surrounding trails. Lizards were collected by hand or by noose. Upon capture, and using standard precautions, I measured the lizard's body temperature (T_b , measured cloacally) with an electronic thermometer (Bailey BAT-12) and small thermocouple probe. I also recorded the sex, snout-vent length (SVL), and mass of the lizard, along with the following characteristics of the perch where it was first seen: substrate type; height above ground; diameter of perch (where relevant), and illumination (lizard's body in full sun, partial sun, or shade).

I also measured the environmental temperature (T_e) of the lizard's perch using a physical model (see also Tsuji et al. 1982). The T_e of a particular microhabitat is defined as the equilibrium temperature reached by an inanimate object of approximately the same size, shape and reflectivity of the animal in question. Hence, T_e is similar in concept to the operative environmental temperature (Bakken and Gates 1975) and to the grey-body temperature index (Roughgarden et al. 1981). The object I used was a section of cylindrical PVC tubing 90 mm long, 20 mm in diameter, painted grey and sealed at both ends with corks. The temperature of the model's interior was measured with a thermocouple probe inserted through one of the corks. T_e is a more appropriate measure

of a lizard's thermal environment than is air temperature (T_a), because T_e accounts for solar heat gain and convective and conductive heat loss or gain in addition to air temperature.

Results and Discussion

General observations. In three and one-half days of collecting, only 31 lizards were collected; most *A. cupreus* I saw were caught. This is a very low encounter rate for *Anolis*, based on my experience elsewhere in Costa Rica and in the Lesser Antilles. Almost all lizards were found in the deep forest directly behind the hacienda, where very little direct sunlight penetrated, rather than in the more openly forested areas. Basic data are summarized below (Table 1).

Table 1. Sizes, perch heights and body temperatures (T_b) of *Anolis cupreus*. Mean values (± 1 s.d.) are given.

	T_b	Perch height (cm)	SVL (mm)	mass (g)	N
females	29.3 (1.74)	8.3 (13.24)	36.3 (3.3)	1.01 (0.21)	6
males	29.1 (1.56)	38.6 (55.4)	40.6 (3.1)	1.46 (0.32)	25

Structural habitat and sex ratio. As in many (most?) anoles (e.g., Schoener and Schoener 1980), males and females differed in their structural habitat use; however, these differences were not statistically significant. Four of the six females were seen on the ground, compared to just seven of 25 males, and males chose higher perches than did females (Table 1).

Of the 31 individuals collected, 25 (80.6 %) were males; this sex ratio differs significantly from 1:1 ($P < .0005$, binomial test). This is unusual for anoles; adult sex ratios are usually near 1:1, or are biased in favor of females (Schoener and Schoener 1980). Because I did not mark individuals, I cannot be certain that my data reflect the true sex ratio. For example, males may have been more active, or more conspicuous in their arboreal perches, and hence overrepresented in my sample.

Another possibility is that females may have abandoned my study area for isolated, relatively mesic patches of forest. Fleming and Hooker (1975) found this sort of clumping by both sexes in a population of *A. cupreus* at La Pacifica, 30 km northeast of Palo Verde. In addition, they observed (i) sex ratios near 1:1, and (ii) a high degree of structural habitat partitioning (males vs. females) in the wet season but not in the dry season. These between-population differences in several ecological aspects of *A. cupreus* deserve further attention.

Thermal ecology. Lizard body temperatures increased throughout the day (Fig. 1), and were highly correlated with the environmental temperature of their perch (Fig. 2). Males and females did not differ in T_b (Table 1; $t = .3453$, $P > 0.5$), and T_b was uncorrelated with perch height ($r^2 = .004$, NS), suggesting that the between-sex differences in structural habitat do not have a thermal basis. Most lizards were perched in the shade (25, vs. 5 in partial sun and only 1 in full sunlight). In fact, most lizards were found where they had little or no access to direct or even filtered sunlight. Thus, T_b appeared to passively follow environmental temperatures.

Tsuji et al. (1982) obtained similar results for *A. cupreus* at Santa Rosa National Park,

65 km northwest of Palo Verde. In addition, they measured the range of T_e 's available to the lizards over the course of the day, and found that lizard T_b 's were similar to the highest measured T_e for a given time of day. Hence, the anoles may have been thermoregulating in a more restricted sense, by maintaining the highest body temperature available, which increased over the course of the day (as ambient temperature increased).

van Berkum (1986) measured the thermal sensitivity of sprint speed in *A. cupreus*, and estimated that the optimal temperature for sprinting is around 30.2°C. Although most of the T_b 's I recorded were below this value, *A. cupreus*' sprint performance curve (as a function of temperature) has a fairly broad peak: van Berkum (1986) estimated that *A. cupreus* would be able to sprint at or above 80% of its maximum speed at T_b 's above 24.5°C. At least from the standpoint of locomotor performance, thermal passivity in *A. cupreus* may have relatively minor consequences for organismal fitness.

Since these lizards live in relatively closed parts of the deciduous forest, there appears to be little opportunity for them to obtain their preferred T_b until the afternoon. For other apparently thermally passive lizards, particularly some *Anolis*, it has been proposed that in closed habitats the cost of locating and moving to patches of sunlight is too high, and that these lizards therefore do not try to maintain a constant T_b (Hertz 1974; Huey 1974; Huey and Slatkin 1976). This is likely to be true for *Anolis cupreus* at Palo Verde, because the anoles live in parts of the forest where little sunlight penetrates. For some reason, *A. cupreus* appears to avoid the more open edges of the deciduous forest, where careful thermoregulation would be more economical. Perhaps, as Fleming and Hooker (1975) observed, this choice of habitat on a large scale is a seasonal phenomenon which helps the anoles avoid water loss during the dry season. This potential benefit may outweigh the apparently minor decrement in locomotor ability resulting from reduced T_b .

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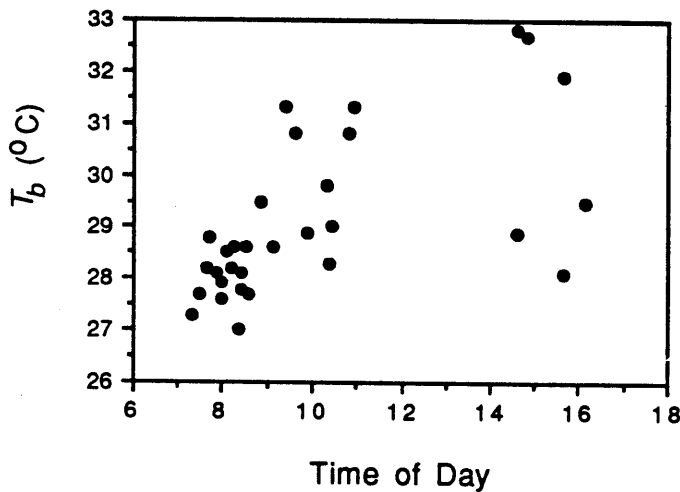


Fig. 1. Relationship between body temperature (T_b) of *Anolis cupreus* and time of day. T_b increased significantly over the course of the day ($r^2 = .371$, $P < .05$).

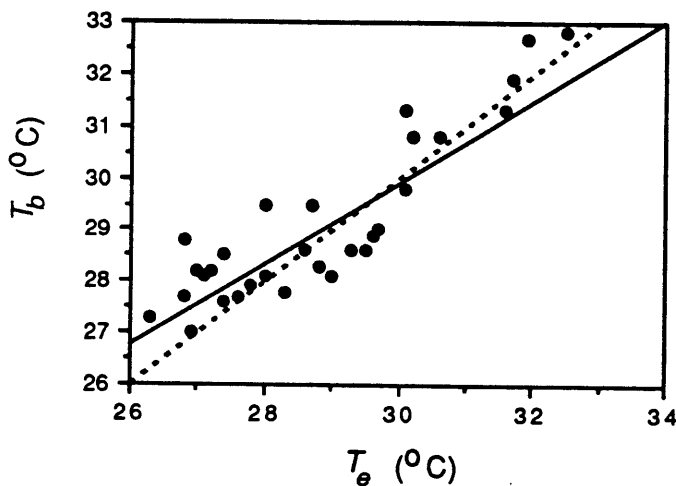


Fig. 2. Relationship between body temperature (T_b) of *Anolis cupreus* and environmental temperature (T_e) of the perch where the lizard was first seen. T_b and T_e are positively correlated [regression equation: $T_b = 5.21 + 0.83 * T_e$, $r^2 = 0.79$, $P < 0.01$; regression slope (solid line) differs significantly from 1; dashed line represents $T_b = T_e$].

ROBIN ANDREWS (Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Va 24061) continues her work in Panama on the population biology of *Anolis limifrons*:

1. I have recently completed two projects on survival patterns of *Anolis limifrons*: one of these involved eggs and the other, post-hatching individuals. One important result of these studies is information on means and variances of survival. Variability in survival overall and relative variability of survival of young vs. adult stages have been implicated as important life history variables (Pianka 1970, Schaffer 1974, Stearns 1976). Thus, these two projects provide information that is of conceptual interest although comparative data for other reptiles is limited.

Survival of adults at two sites, Lutz and AVA, at Barro Colorado Island (BCI) was evaluated using modified Jolly-Seber models (Andrews and Nichols, in prep.). Results of these analyses show that survival varies considerably on both temporal and microgeographic scales (but not as a function of size or sex). Adult survival was significantly higher at Lutz site during 1971-1976 than during 1976-1979 with a five-fold difference in annual survival (0.042 - 0.008). Survival was higher at AVA than at Lutz site during 1976-1979 with an eleven-fold difference in annual survival (0.087-0.008).

Spatial variation in survival exhibited by *A. limifrons* populations can be compared with that exhibited by populations of *Anolis* in the Bahamas. The coefficient of variation (CV) of annual survival for ten sites in central Panama (Lutz and Ava plus eight sites of Wright et al. 1984) is 122%. Survival of the Bahamian populations is much less variable. For example, the CV's of annual survival for female and male *A. sagrei* (n = 5, four forested sites, two years at one site) were 22 and 52%, respectively (Schoener and Schoener 1982). Moreover, survival rates of female and male *A. sagrei* at their short-blackland site in 1970 were within 5% of survival rates measured in 1973. Thus, *A. limifrons* populations are characterized by highly variable survival, at least in comparison to one set of West Indian species.

Survival of eggs was measured at six sites in central Panama (Andrews 1988). Survival averaged 0.35 over the 44 d incubation period and the CV for these observations was 40.9% (Andrews 1988). Annual adult survival at ten sites (as above) averaged 0.62 over 44 d and the CV for these observations was 13.2% (note CV here is based on survival over 44 d, in the previous paragraph CVs were calculated on the basis of survival over 365d). Thus, egg survival of *A. limifrons* is lower and more variable than lizard survival.

2. I am still working with demographic models of *A. limifrons* populations. This project was neglected for years because I did not have good data on the egg survival. With the completion of the projects discussed above, this project has moved off the back burner. Relatively complete information on survival and fecundity have facilitated construction of demographic models of populations at Lutz and AVA sites. These models were validated by comparing age distributions projected by the model with age distributions observed at the two sites. At present, I am using the models to test some hypotheses about demographic events associated with year to year variation in population density.

3. S. J. Wright (Smithsonian Tropical Research Institute) and I have been collaborating on a project designed, in part, to determine the impact of seasonal rainfall on *A. limifrons* populations. Two four-hectare plots at BCI were irrigated during the dry seasons of 1986, 1987, and 1988. Two four-hectare plots were used as controls. *Anolis limifrons* populations were sampled on two 30x30m areas within each of the four plots every six-seven weeks between December 1985 and April 1988.

The most obvious effect of irrigation was an increase in adult population density on the irrigated relative to the control plots. There are two intriguing features of this response: 1) higher density on the irrigated than the control plots is most apparent during the wet season not during the dry season when irrigation took place and 2) the response in 1986 was considerably stronger than in 1987. These features suggest that increased population density on the irrigated plots was not a simple consequence of irrigation facilitating egg production during the dry season when it is normally reduced or curtailed. Rather, irrigation must result in environmental perturbations that affect future population dynamics. Moreover, the strength of these perturbations is apparently modified by environmental conditions that change from year to year.

Potential factors that would increase population density on the irrigated relative to the control plots are 1) increased survival of eggs or lizards or both, 2) increased fecundity, and 3) a longer reproductive season. Survival of adult lizards did not differ among plots. However, egg survival was higher on the irrigated than the control plots (Andrews 1988). Improved egg survival thus is implicated in the increased population density on the irrigated plots, at least in 1986 when observations on eggs were made.

Fecundity was not measured directly. However, an index of condition ($IC = Mass^{0.3}/SVL$) is positively correlated with oogenesis in females (Andrews et al. 1983). Thus, relatively high values of IC should indicate relatively high egg production. Comparisons of IC do not support the idea that egg production was higher on the irrigated than the control plots. Rather, IC's for females (and males) were significantly higher in 1986 than 1987 on all plots irrespective of treatment. Because IC is also correlated with food intake, the IC data further suggest that irrigation did not affect the availability of food to lizards.

Recruitment patterns differed between treatments and between years. Normally, recruitment in *A. limifrons* populations is highly seasonal with low numbers of juveniles in the dry season and a strong peak in July and August. The effect of irrigation was to dampen this seasonal pattern. On the irrigated plots, hatchlings reached slightly higher levels (about 20% of the populations) in the wet season than the dry season. On the control plots, hatchlings were much more abundant from June-October (peaking at 40% of the populations) than in the dry season.

In 1986, the proportion of hatchlings increased sharply in March on the irrigated plots but did not represent an appreciable fraction of the populations on the control plots until June. In contrast, in 1987 the representation of hatchlings on all plots was very similar during the dry season and treatment differences were not apparent until June and July. These between year differences in recruitment are in accord with the between year differences in adult population density.

Why did responses to irrigation differ between 1986 and 1987? One explanation is that environment conditions in 1986 and 1987 were different enough to alter responses to irrigation. *Anolis limifrons* populations appear to be more abundant in years when annual rainfall is relatively low (Andrews and Rand, in press). Annual rainfall in 1986 was lower (2166mm) than in 1987 (2953mm). Thus, in 1986 when conditions should have been favorable for *A. limifrons* populations, irrigation appears to have strongly facilitated population growth. Populations on the irrigated plots reached much higher densities in part because they started increasing sooner than populations on the control plots; populations peaked on the irrigated plots 4-5 months sooner than on the control plots. This lag corresponds to the 4 month period between oviposition and growth of the hatchling to 36mm SVL, the size they are counted as adults. This suggests that egg laying during the dry season as facilitated by irrigation or that adults were more successfully recruited into the population on the irrigated plots than on the non-irrigated controls or both. However, if irrigation facilitated recruitment during the dry season in 1986, it is not clear why the same response was not observed in 1987. The weak population response in 1987, a year when rainfall conditions were less favorable to population growth, suggest that conditions during the wet season disrupted affects of irrigation.

4. Jim Karr (Dept. of Biology, VPI & SU) and I have just initiated a study of community level interactions between *Anolis*, birds, arthropods, and fruit in forest understory habitats in Panama. We will establish a series of bird exclosures and controls so that we can monitor populations of lizards, fruits, and arthropods that are protected from and exposed to birds. My interest in this project is related to the observation that survival rates of adult *A. limifrons* are independent of the numbers and abundance of birds that prey on and compete with anoles (Wright et al. 1984). This result is puzzling because survival of *Anolis* is inversely related to avian species density in the Bahamas (Schoener and Schoener 1978, 1980). Our study will provide a direct test of the null hypothesis that birds do not affect populations of *A. limifrons*. Both survival and body growth will be evaluated in an attempt to tease apart the effects of predation and competition.

We constructed one 10 x 10 m exclosure out of bird netting and PVC pipe in August 1988. This exclosure has been monitored weekly over the past few months to determine if a bird exclosure in tropical rainforest understory is actually feasible. Constant leaf fall has necessitated weekly roof clearing but we are working on a roof that will allow leaves to fall through and still keep birds out. Experimental exclosures and controls will be established this summer (1989) and monitored for approximately one year.

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The feeding behavior of *Anolis* remains unexplored. Some analyses have studied its role in the ecological adaptation of the *Anolis* lizards. Since four years, I was interested by the movements of the hyoid apparatus in variable functions (i.e., display, drinking, feeding, respiration). In a comparative point of view, several technics were used to compare the movements of the tongue, the whole hyoid and its elements. Here I only present the studies in progress for the feeding behavior. In the Laboratory of Functional Morphology, Isabelle Baltus, Véronique Goosse and myself have worked on the feeding mechanism of *Anolis*.

Methods.- Kinematic data were obtained from feeding cycles in *Anolis equestris*, *Anolis carolinensis* and *Anolis chlorocyanus*. The primary goal of our analysis was to determine the influence of food types on the feeding activities. Almost 3180 jaw cycles in *A. equestris* and 500 in *A. carolinensis* were filmed and statistically analyzed.

In the mean time, characteristics of the types of cyclic movements were measured and compared for different food items.

The kinematic of the gape, hyoid movements and forelimb displacements were studied in different cyclic activities of feeding locusts in *A. equestris*. In *A. carolinensis*, cyclic movements during feeding of variable species of living preys were analyzed. Table 1 summarizes the variables measured to construct the kinetics of tongue projection during prey capture and movements of the tongue-hyoid complex during mechanical reduction and transport of the prey to the esophagus. The horizontal (X) and vertical (Y) coordinates were plotted against time (frames) using a basic program developed by V. Bels in the Laboratory of Functional Morphology (with the help of M. Rinné, Institute of Physics, University of Liège). The physical characteristics (velocity and acceleration) of each movement may be calculated from the coordinates.

Results

1. Feeding sequence

After recognition and approach of the prey, the feeding behavior may be divided in four steps: (1) prey capture, (2) mechanical reduction of the prey, (3) transport to esophagus and (4) cleaning (Fig. 1). Cleaning seems to correspond to the passage of the prey through the pharynx (Bels and Baltus, 1986, *Copeia* 1986:479-481).

2. Influence of food items on feeding cycles

The mechanical resistance of the food items influences the number of cyclic movements of the gape combined to the tongue-hyoid apparatus (Fig. 2). The food item then have to influence the behavioral response of feeding in *Anolis* lizards (Bels and Baltus, 1986, *Copeia* 1986:479-481). The cyclic movements (i.e., mechanical reduction and transport to the esophagus) are separated by plateaued phase that may be very long when the lizard is stressed by presence of an observer or a predator (Fig. 3).

3. Kinematics of feeding cycles

We only here report some data on the feeding cycles in *Anolis* lizards.

3.1. Prey capture

The prey capture (adult locust) of *A. equestris* consists of a typical tongue projection to the prey. The gape cycle presents the characteristic pattern of the four stages : (1) slow open, (2) fast open, (3) fast close and (4) slow close (Fig. 4). The vertical movements of the upper and lower jaws produce the gape angle (Fig. 4). The tongue protraction begins during the slow open and reaches its greater velocity during the fast open. The gape

angle still increases during the first milliseconds of the tongue retraction. When the tongue is protracted to the prey, it rotates on its transversal axis so that the prey is touched by its dorsal surface (Fig. 5). The movement of the forelimbs are very important during the tongue cycle (protraction- retraction) : they drive the open mouth to the prey when the tongue and the prey is backward in the buccal cavity.

3.2. Other feeding steps

The mechanical reduction and transport of the prey to the esophagus have been described elsewhere (Bels and Baltus, Fortschritt der Zoologie 35, in press). Figure 6 presents the data of gape and hyoid-tongue movements during the transport of the prey within the buccal cavity (a) and cleaning (b and c) of *A. equestris* fed with adult locusts. The gape angle increases by combined movements of the lower and upper jaws. The movements of the hyoid apparatus are estimated from the high speed cinematographic frames. It is evident that the skin is not well attached on the hyoid and then intrinsic movements of the hyoid are not visible on the cinematographic films. However, the skin seems to be attached on the hyoid body firmly enough to allow a first analysis of the kinematics of the tongue-hyoid complex during the feeding cycles. The presented data are a first steps of the comparative analysis of the hyoid movements during all the functions performed by an *Anolis* lizard.

We begin an extensive analysis of the relative movements of the hyoid elements in collaboration with F. De Vree (I.U.A., Antwerpen, Belgium) and S. Renous and J.P. Gasc (Museum National d'Histoire Naturelle, Paris, France). During the tongue projection of the prey capture and the tongue forward movement during mechanical reduction, it seems that the ceratobranchials I and the ceratohyals are protracted (Fig. 7). The protraction of the ceratobranchials II seems to be delayed (Fig. 7). The ceratobranchials I are more protracted than the ceratohyals and may act on the tongue protraction. The ceratobranchials I and the ceratohyals are protracted during the SO and FO stages and retracts drastically during the FC and SC stages. The difference between both stages during gape close is very difficult to see. Backward movement consists of retraction of the hyoid elements.

A kinetic model may be constructed from kinematic curves and effects of the stimulation of the muscles. The tongue cyclic movement of prey capture seems to be produced by a combined action of relative movements of the hyoid apparatus and the tongue muscles divided in (1) extrinsics and (2) intrinsics. We present here some results on the stimulation of these muscles. The stimulation of the m. ceratomandibularis (= mandibulohyoidei) produces a protraction of the hyoid apparatus and then protraction of the tongue. The stimulation of the muscles of the tongue shows that extrinsic muscles of the tongue may be divided in two groups : protractive and retractive muscles. The m. hyoglossus retracts the tongue on the ceratobranchial I of the hyoid apparatus. The m. genioglossus protracts the tongue. The m. ceratohyoideus, inserted on the ceratobranchial I and the ceratohyal, protracts the ceratobranchials I against the ceratohyals. Figure 8 shows a first analysis of the tongue movements produced by relative movements of the hyoid elements during mechanical reduction.

4. Future researches

Two directions of research have to be generated:

- 1) the kinetic model constructed by combination of the stimulations and the kinematics has to be tested by several experimental procedures (removing the force vectors) and quantitative electromyography,
- 2) the model has to be tested with variable food items and different iguanid lizards to attempt to obtain the motor pattern of feeding in arboreal insectivorous species and

compare it with terrestrial species. The adaptive value of the feeding activities to the niche would be then discussed.

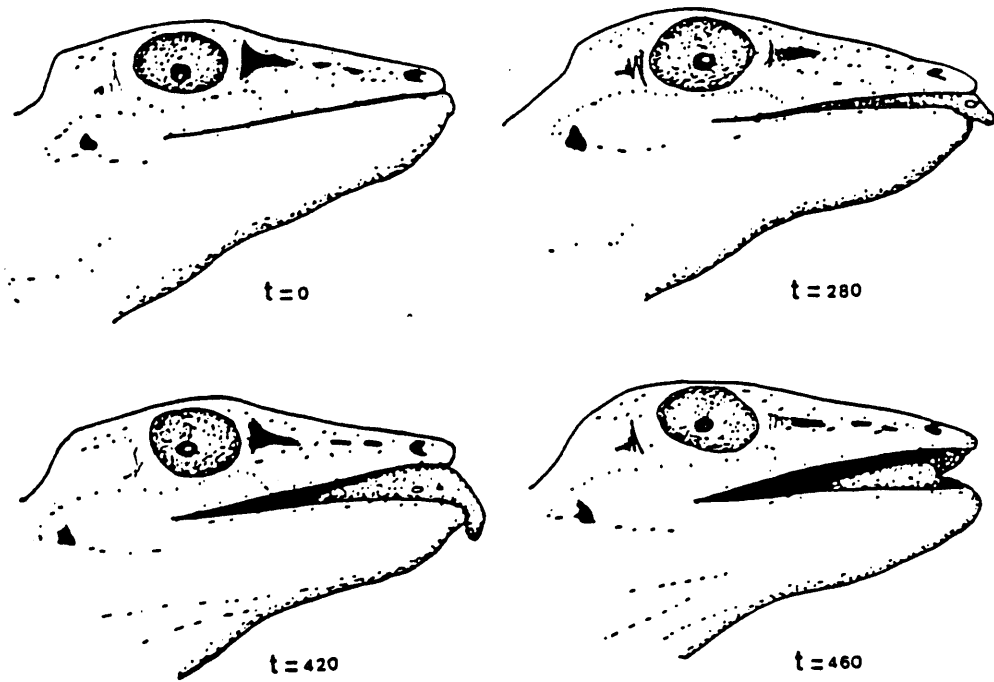


Fig. 1: Typical sequence of a cleaning movement in *A. equestris*.

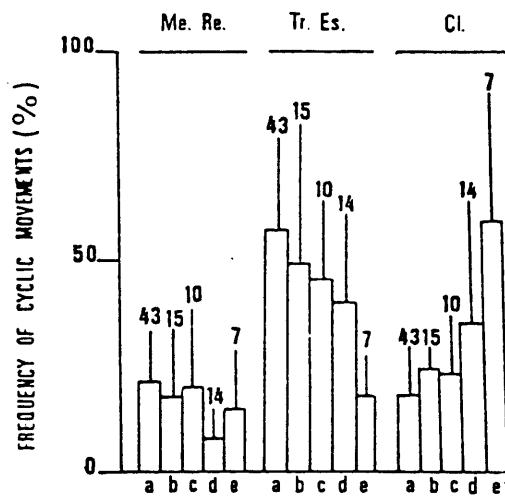


Fig. 2: Mean percentage of the jaw cycles in mechanical reduction (Me. Re.), transport of the esophagus (Tr. Es.) and cleaning (Cl.). a: adult locust; b: larva locust; c: cricket; d: young mouse and e: fruit.

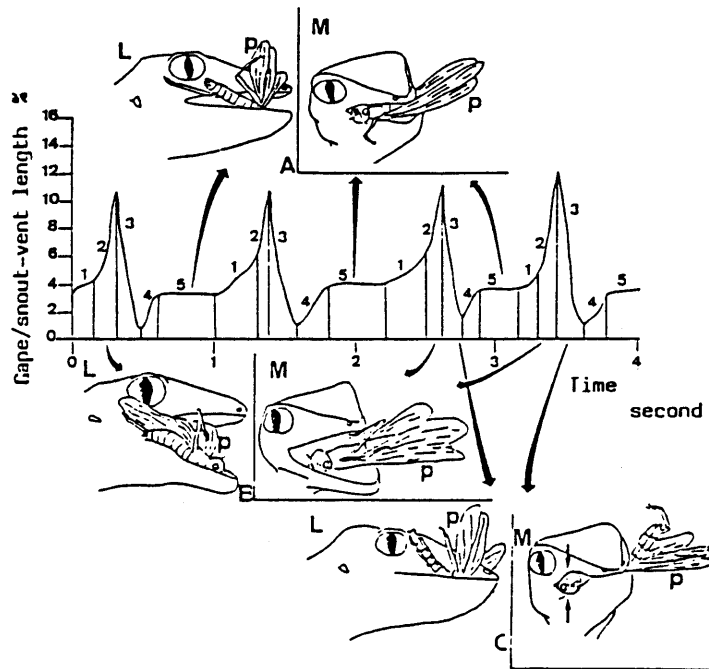


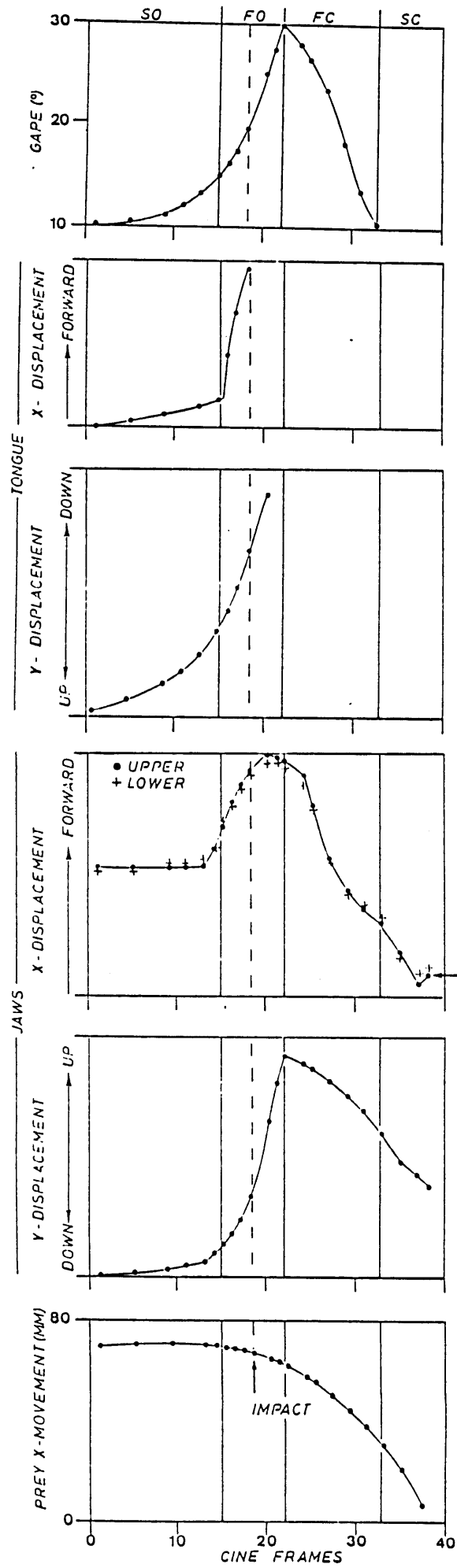
Fig. 3: Plateaued phase between the jaw cycles in *Anolis equestris*.

- A, B and C: three drawings of stages
- 1: SO stage (slow open)
 - 2: FO stage (fast open)
 - 3: FC-SC stage (fast close and slow close)
 - 4: O2: Open 2 of the mouth
 - 5: plateaued phase
- L: lateral view; M: mirror

Fig. 4: Kinematic profiles of selected cranial components during the prey capture by *Anolis equestris* as determined by high-speed cinematography (200 frames/s). The gape is in degree and prey movement is in mm. The other points are only presented as displacements against time. The broken line is the impact time. The horizontal arrows in the fourth graph shows the beginning of the first cycle of the mechanical reduction.

see next page

Figure 4



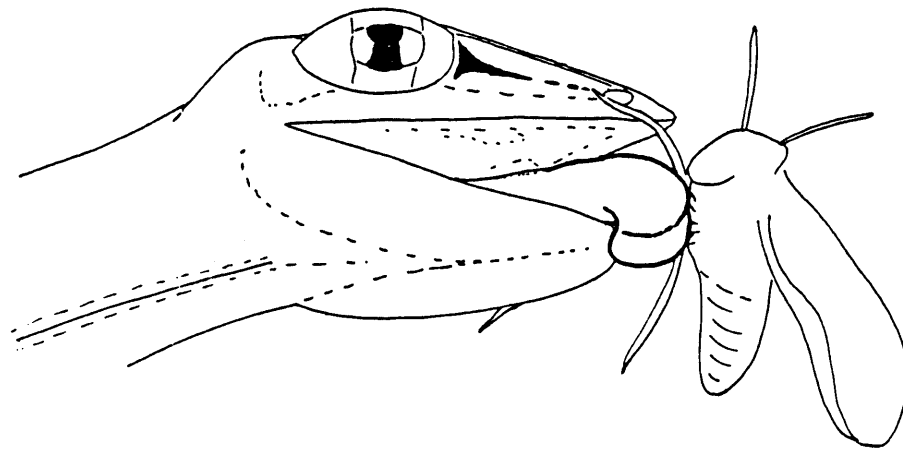


Fig. 5: Impact on a locust by the tongue of *Anolis equestris*.

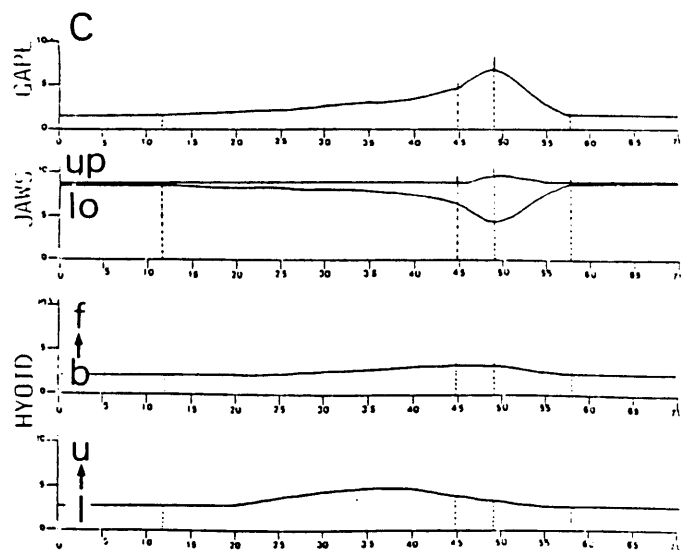
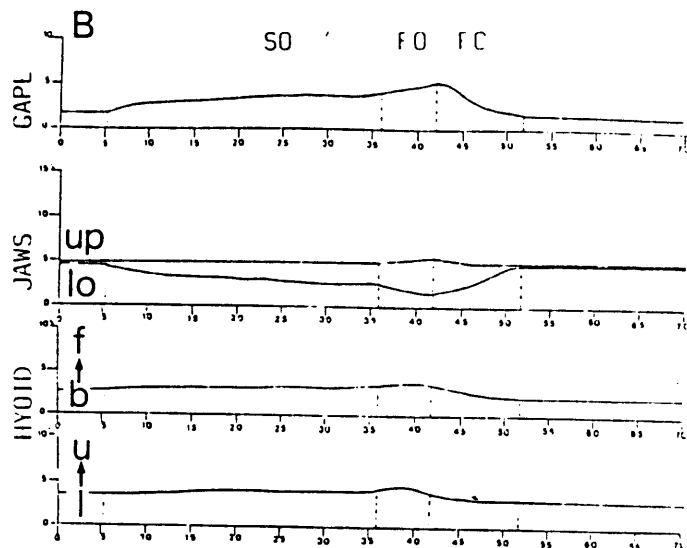
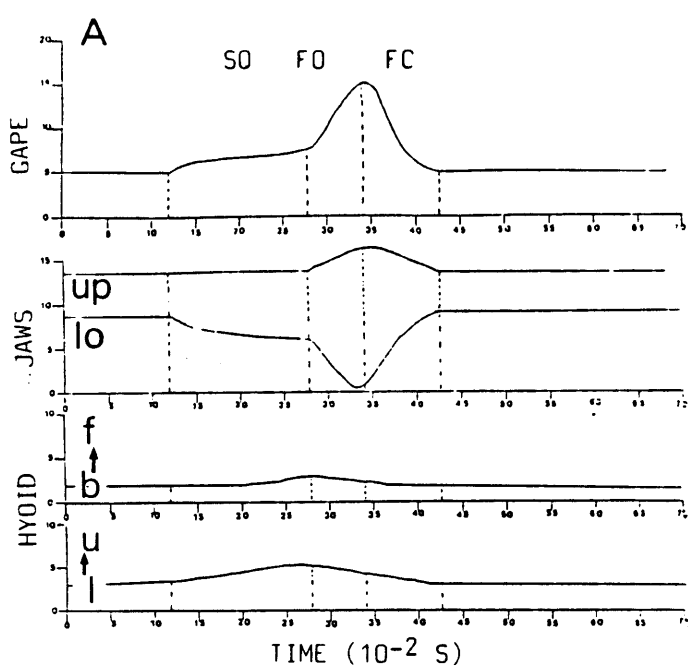


Fig. 6: Kinematic curves of cyclic movements during (A) movement of the prey within the buccal cavity, (B) cleaning with tongue protusion (see Fig. 1) and (C) cleaning without tongue protusion. All the curves are expressed as a percentage of the snout-vent length of the filmed lizards. b f: backward to forward movement; l u: lower to upper movement; SO: slow open; FO: fast open; FC: fast close (combined with slow close).

TIME (10⁻²S)

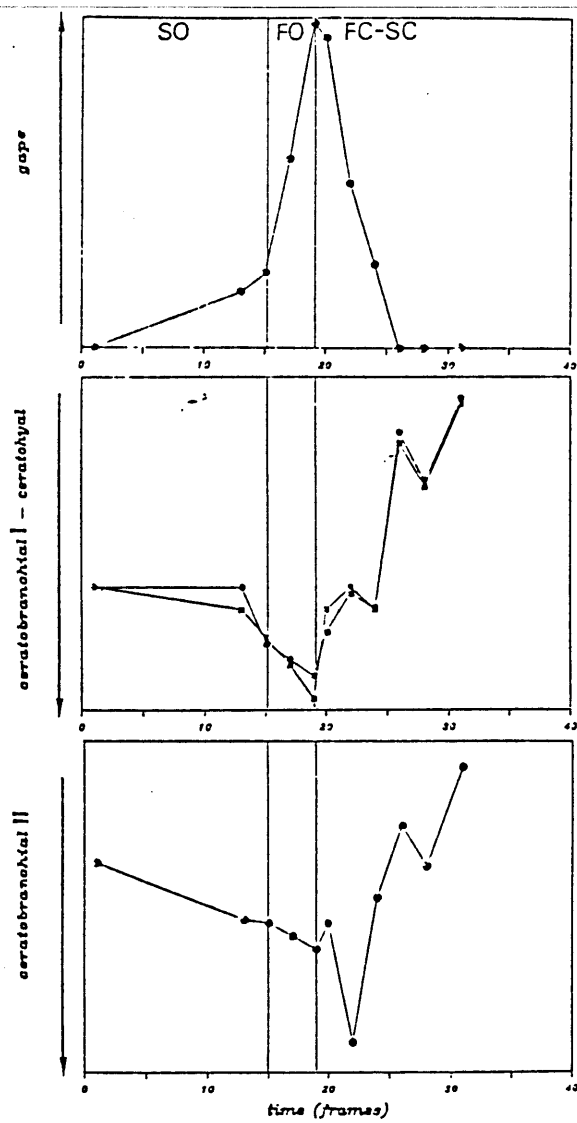


Fig. 7: Kinematic curves of the movements of the ceratobranchials I and the ceratohyals during the mechanical reduction of the prey in *Anolis equestris*.

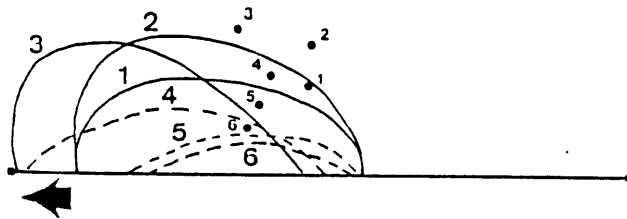


Fig. 8: Tongue movements against the lower jaw during the mechanical reduction of a larva locust traced from cinefluoroscopic films. The points (a lead mark in the prey) show the movements of the prey within the buccal cavity. The numbers of the tongue movements correspond to the numbers of the prey movements. The dashed lines correspond to fast-close stage. The arrow shows the postero-anterior direction of the lower jaw.

INTERSPECIFIC BEHAVIORAL INTERACTION OF ADULT MALE ANOLIS SAGREI
AND GRAY-THROATED ANOLIS CAROLINENSIS (SAURIA: IGUANIDAE):
A PRELIMINARY FIELD STUDY

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Members of the Anolis carolinensis (Sauria: Iguanidae) complex co-occur with Anolis sagrei on many Caribbean islands. Where the two species occur together, A. carolinensis occupies a trunk-crown niche, whereas A. sagrei is considered a trunk-ground species (Schoener 1968, Williams 1969). Prior to the introduction and subsequent dispersal of A. sagrei in Florida, A. carolinensis was the only member of the genus in North America and it exhibited ecological release, occupying a ground-trunk-crown niche. It still occupies this expanded niche in areas within its range presently unoccupied by A. sagrei. With the spread of A. sagrei in peninsular Florida (Godley et al., 1981, Lee 1985), A. carolinensis has been excluded from disturbed habitats it once occupied, or has exhibited population declines. In coastal areas of southwestern Florida, however, the two species appear to coexist without dramatic reductions in the density of A. carolinensis. Here, male A. carolinensis have a gray throat (= dewlap) in contrast to the red dewlap characteristic of the species elsewhere. These morphs may differ behaviorally as well. Tokarz and Beck (1987) report that, under laboratory conditions, adult male red-throated A. carolinensis interact very little with adult male A. sagrei. Our own laboratory studies (to be reported elsewhere) of intraspecific and interspecific encounters between adult male gray-throated A. carolinensis and adult male A. sagrei tend to confirm the findings of Tokarz and Beck (1987). These laboratory results, however, are counter to our field observations in southwestern Florida, where aggressive encounters between adult males of the two species are often observed. This seems paradoxical inasmuch as adult males of the two species are often found holding overlapping territories in the same tree in apparent peaceful coexistence. Our purpose here is to report (very) preliminary observations on naturally occurring interactions between adult male gray-throated A. carolinensis and adult male A. sagrei, and on the results of field experiments in which adult male A. sagrei (intruders) were released into the territories of adult male A. carolinensis.

METHODS

Field studies were conducted from 11 July to 4 August 1989 at Delnor-Wiggins Pass State Recreation Area near Bonita Springs, Lee Co., Florida. Observations were made in a ca. 1.5 km strip of vegetation between an extensive sand beach and a mangrove swamp. Lizards were found on sea grape (Coccoloba unifera), cabbage palm (Sabal palmetto), and Australian pine (Casuarina equisetifolia), and on the picket fences, picnic tables, elevated boardwalks, and bath houses interspersed among the trees. Behavioral observations were made between 0800 hr and sunset (ca. 2030 hr), the span over which the park was open to the public.

Naturally occurring interspecific interactions between adult males were made opportunistically. Because the frequency of these interactions was unknown, a combination of focal animal and scan sampling methods was employed.

Data were taken on 10 interactions which escalated beyond headbob-dewlap exchanges. These occurred in two contexts: those already in progress at the time the observer arrived at the site, and those encouraged by the observer by gently prodding one of the lizards to move within sight of the other. In neither context were the lizards actually handled by the observer. Although 10 encounters escalated beyond a display exchange, the actual number of individuals involved is not certain. Five encounters took place on one marked tree, and the others occurred at different sites throughout the study area. Therefore, the locations of the encounters suggest that a minimum of at least six A. carolinensis and six A. sagrei were involved (i.e., a minimum of six different A. carolinensis/A. sagrei pairs).

Eleven intruder-release trials were conducted. In each, a different adult male A. sagrei of known snout-vent length and mass was released within 2 m of a resident A. carolinensis. Care was taken to use intruders that were captured some distance from the territory of the resident, but the previous history of each animal was unknown, so it is not possible to know whether or not they had previous knowledge of one another. If no aggression occurred, the lizards were observed for a maximum of 15 min. and, if aggressive behavior was observed, the animals were observed for a maximum of about 60 min.

A record of aggressive behavioral encounters was made as they occurred using a cassette tape recorder. The following behaviors were noted: Headbob (HB), dewlap extension (DW), display (DP), approach (AP), extended throat (ET), crest erection (CR), sagittal expansion (SE), chase (CH), attack (AT), circling (CI), jaw sparring (JS), jaw locking (JL), retreat (RT), tail movement (TM), protruding tongue (PT), air lick (AL), tongue touch (TT), color change to black (BLACK), and eye spot (ES). Neither BLACK nor ES are included in the repertoire of A. sagrei. Definitions of these behavior appear in the Appendix.

RESULTS

Natural Encounters. The majority of observed encounters were nonaggressive and involved either (1) adult male A. carolinensis and A. sagrei perching within a few cm of one another or (2) no escalation of aggression beyond a volley of headbobs and dewlaps by one or both individuals. Of the 10 interspecific encounters that escalated further, four occurred between 0900 and 1200 hrs, three at midday, and three between 1845 and 2030 hrs. The duration of these interactions varied from less than 10 min to ca. 75 min. Encounters generally proceeded in the following manner:

- (1) A. carolinensis approached A. sagrei;
- (2) A. carolinensis turned a dark brown to black color and began exhibiting any or all of the following: CR, ET, SE, ES;
- (3) a volley of HB and DW by one or both individuals;
- (4) A. carolinensis exhibited AT, CH, and pursued A. sagrei repeatedly, with A. sagrei exhibiting RT;
- (5) several bouts of (4) often occurred with pursuit up into the trees and down onto the ground;
- (6) after being repeatedly attacked and chased by A. carolinensis, A. sagrei responded defensively with CR, ET, SE, or AT (CI, JS, or JL occurred occasionally);

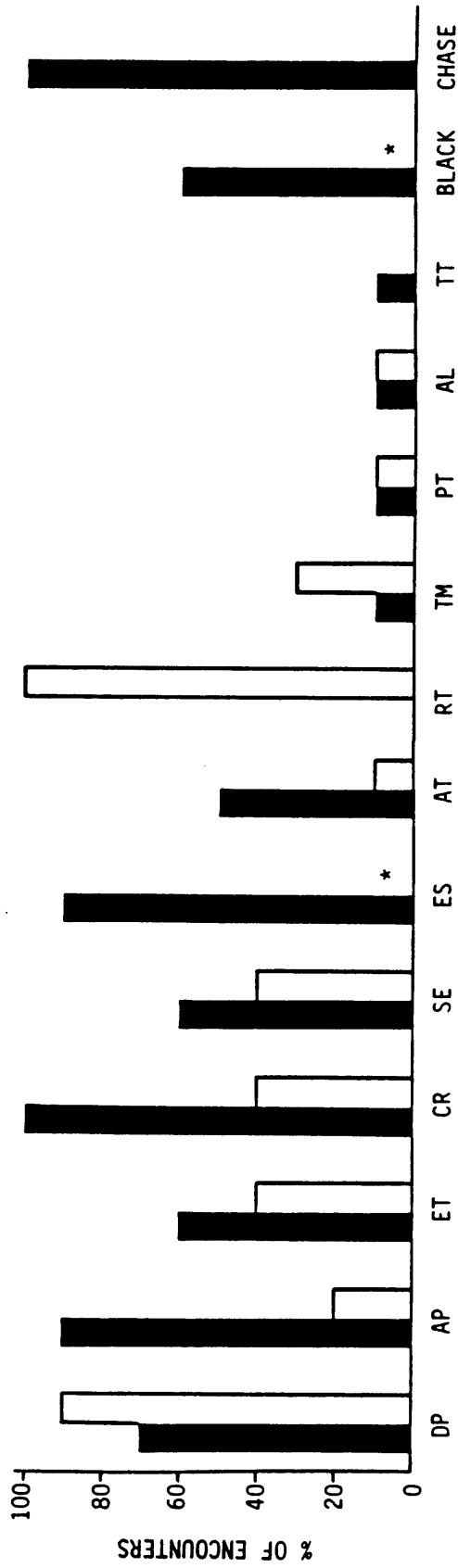


Figure 1. Percentage of naturally-occurring interspecific field encounters in which adult male gray-throated *Anolis carolinensis* and adult male *A. sagrei* exhibited Display (DP), Approach (AP), Extended Throat (ET), Crest Erection (CR), Sagittal Expansion (SE), Eye Spot (ES; exhibited by *A. carolinensis* only), Attack (AT), Retreat (RT), Tail Movement (TM), Protruded Tongue (PT), Air Lick (AL), Tongue Touch (TT), Black Color Change (BLACK; exhibited by *A. carolinensis* only), and Chase (CHASE). Black bars represent *A. carolinensis*; white bars represent *A. sagrei*.

Table 1. Behaviors performed by resident adult male Anolis carolinensis during intruder-release trials in southwestern Florida; intruders were adult male A. sagrei.

Behavior	Trial Number										
	1	2	3	4	5	6	7	8	9	10	11
Display	0	0	+	0	+	+	+	+	+	+	+
Approach	0	+	0	0	+	0	0	0	+	+	+
Extended Throat	0	+	0	0	+	0	0	0	0	+	0
Crest Erection	0	0	0	0	+	0	0	0	0	+	0
Sagittal Expansion	0	0	0	0	+	0	0	0	0	+	0
Eye Spot	0	0	0	0	+	0	0	0	0	0	0
Attack	0	+	0	0	+	0	0	0	0	+	0
Retreat	0	0	0	0	0	0	0	0	0	0	0
Black Color Change	0	0	0	0	+	0	0	0	0	+	0
Chase	0	+	0	0	+	0	0	0	0	+	0

+ = behavior present; 0 = behavior absent

Table 2. Behaviors performed by intruder adult male Anolis sagrei during intruder-release trials in southwestern Florida; residents were adult male A. carolinensis.

Behavior	Trial Number										
	1	2	3	4	5	6	7	8	9	10	11
Display	0	0	+	+	+	+	+	+	+	0	+
Approach	0	0	0	0	0	0	+	+	0	+	+
Extended Throat	0	0	0	0	+	0	0	0	0	+	0
Crest Erection	0	0	0	0	0	0	0	0	0	0	0
Sagittal Expansion	0	0	0	0	+	0	0	0	0	0	0
Attack	0	0	0	0	0	0	0	0	0	0	0
Retreat	0	+	0	0	+	0	0	0	0	+	0
Chase	0	0	0	0	0	0	0	0	0	0	0

+ = behavior present; 0 = behavior absent

- (7) if A. carolinensis attacked, it often bit the entire rostrum of the A. sagrei, thereby preventing A. sagrei from opening its mouth;
- (8) if A. sagrei attacked, it bit the flank of A. carolinensis and toss it from the tree (A. carolinensis would repeatedly return to the tree);
- (9) A. carolinensis was never seen to retreat during an aggressive encounter;
- (10) the interaction continued until A. sagrei was driven from the area, until A. sagrei moved out of the field of vision of A. carolinensis, or until sunset.

The percentage of interspecific encounters (N = 10) in which adult male A. carolinensis and A. sagrei exhibited each behavior is indicated in Figure 1. These observations may not be complete because lizards occasionally moved out of view of the observer and may have performed behaviors which were not recorded. Every effort was made, however, to follow the lizards and record a complete interaction.

In all aggressive field interactions, A. carolinensis was clearly the aggressor. In 50% or more of the encounters, A. carolinensis performed behaviors associated with escalated aggression: DP (70%), AP (90%), ET (60%), CR (100%), SE (60%), ES (90%), AT (50%), BLACK (60%), and CH (100%). Anolis sagrei exhibited behaviors associated with escalated aggression in less than 50% of the encounters. The repertoire of A. sagrei during naturally occurring aggressive encounters included primarily DP (90%) and RT (100%). Anolis sagrei approached A. carolinensis in only 20% of the encounters, and exhibited ET, CR, and SE in 40% of the encounters. CH was never performed by A. sagrei, and AT was exhibited in only 10% of the encounters. Other behaviors (Fig. 1) were exhibited relatively infrequently by either species. Color changes by both occurred, but only BLACK was recorded. No nonaggressive contacts were observed (i.e., one individual actually touching another). During staged encounters in a laboratory setting, A. sagrei occasionally exhibits Sagittal Expansion Display (SED) (Brown and Echternacht, in prep.) in which the body is laterally compressed and the limbs simultaneously extended in a rapid motion that appears to lift the lizard entirely off of the ground. The display may be accompanied by dewlapping. Anolis carolinensis was never seen to perform this display in the laboratory, and neither species did so during the field interactions reported here.

Staged Encounters. A summary of the behaviors performed by all A. carolinensis during intruder-release trials appears in Table 1, and the those performed by A. sagrei in Table 2. Of the 11 intruder-release trials, three resulted in levels of aggression which escalated above display exchange: trials 2, 5, and 10. These three interactions took place in trees where naturally occurring aggressive encounters had previously been observed. During these three trials, A. carolinensis was the aggressor and performed CH and AT, whereas A. sagrei repeatedly exhibited RT and never exhibited CH or AT.

DISCUSSION

Laboratory investigations of interspecific and intraspecific interactions of adult male A. carolinensis and A. sagrei (e.g., Sigmund 1978, Tokarz and Beck 1987, Brown and Echternacht, in prep.) agree that levels of interspecific aggression are lower than those of intraspecific encounters. The consensus

seems to be that A. sagrei should be the more aggressive species in interspecific encounters and should "dominate" A. carolinensis. Sigmund (1978), for example, found that when he paired adult male red-throated A. carolinensis from Louisiana with A. sagrei from Florida, A. sagrei seemed "...dominant, though it does not actively dominate or act aggressively towards A. carolinensis" (p. 24). In his study, A. carolinensis was found to relinquish perches or prey upon the approach of A. sagrei. He also found that the two species would nonaggressively share the same perch. These behaviors led him to suggest that this "...apparent dominance of A. sagrei..." (p. 25) might provide more insight into why A. sagrei has been able to displace A. carolinensis in areas of sympatry in southern Florida.

Behavioral observations made in the field tend to support laboratory findings, with one notable exception: when aggression was observed, it was instigated and sustained by A. carolinensis. Anolis sagrei was never seen as the aggressor in field encounters and demonstrated aggressive behaviors only in defensive situations after repeated attacks by A. carolinensis. This is all the more surprising because adult male gray-throated A. carolinensis tend to weigh less than adult male A. sagrei. Although there is no comparable data on interspecific matches, Tokarz (1985) found that larger male A. sagrei were more successful in defending their perches against smaller males, and Andrews (1985) found that dominance was correlated with body size in A. carolinensis, larger animals dominating smaller ones.

It is not immediately apparent why gray-throated A. carolinensis exhibit aggression towards A. sagrei, whereas A. sagrei exhibits little, if any, aggression towards A. carolinensis. To our knowledge, no observations of interspecific aggression have been made on islands on which members of the A. carolinensis group and A. sagrei occur in sympatry. With respect to A. porcatus, the putative ancestor of A. carolinensis, and A. sagrei on Cuba, however, Williams (1969, p. 364) states that "...they are well adjusted to one another." One might predict successful coexistence in Florida.

One possible explanation for interspecific aggression is misidentification (Nishikawa 1987). An individual of one species may direct aggression towards an individual of another, morphologically similar, species if it "misidentifies" the individual as a conspecific. Ortiz and Jenssen (1982) discount misidentification as the cause of the interspecific aggression which occurs between A. cooki and A. cristatellus, two morphologically similar species on Puerto Rico. Because neither species acts aggressively toward other morphologically similar ("look-alike") species, Ortiz and Jenssen propose that the two species are able to recognize each other as interspecific competitors. Since laboratory studies agree that interspecific encounters involving A. carolinensis and A. sagrei result in lower levels of aggression than do intraspecific encounters, it does not seem likely that misidentification is a factor. The species differ in body color, dewlap color, overall body shape and head shape. The generalized anoline body plan, however, may be identified as that of a "competitor," thereby eliciting aggression in some individuals in a population.

In studies of damselfish, Myrberg and Thresher (1974) suggest that interspecies recognition (of competitors) may be based on form, whereas Losey (1981) suggests that animals may respond aggressively toward heterospecifics on the basis of ecological cues, such as method of feeding. The possibility

exists that A. carolinensis retains an inherent or innate system of competitor recognition involving morphology or ecology that leads to its identification of A. sagrei as a competitor. This does not, however, explain why A. sagrei fails to act aggressively towards A. carolinensis, nor why the majority of gray-throated A. carolinensis seen in association with A. sagrei seem to be doing so in apparent nonaggressive coexistence.

Orians and Willson (1964, p. 737) state that, when two species of birds come into contact for the first time, "Initial aggression may be expected ... for any new intruder might profitably be considered to be a potential competitor. However, if the species are so different that the effort required for their mutual exclusion is not compensated by increased access to resources, interspecific aggression should, in time, decrease and disappear." Since interspecific aggression requires considerable time and energy, they contend that natural selection should favor ecological divergence and that, if this divergence is not apparent, that time may have been insufficient for the process to be completed. These suggestions may apply to the interaction of A. carolinensis and A. sagrei in Florida.

Anolis sagrei has only recently been introduced into Florida (Lee 1985), and has been known in the vicinity of Bonita Springs for less than 25 years (Collette 1961). The source of A. sagrei introduction on the west coast of Florida is thought to be Cuba and, to use the terminology of Williams (1969, p. 368), "...it is ecologically Cuban, hence adjusted to coexistence with carolinensis." Conversely, A. carolinensis has apparently existed in the United States without congeneric competition since the Pleistocene and may no longer be "ecologically Cuban". Although A. carolinensis may have recognized A. sagrei as a potential competitor when the two species first encountered one another in peninsular Florida, and exerted a great deal of energy in territorial defense, the effort required may not have been "compensated by increased access to resources" (Orians and Willson 1964, p. 737). This uncompensated effort and the lack of aggressive response by A. sagrei may have resulted, over a period of time, in a decline in the number of A. carolinensis exhibiting interspecific aggression. The nonaggressive coexistence of the two species often seen in southwestern Florida may reflect this decline.

Tokarz and Beck (1987) suggest that behavioral interference between adult males is not the most probable cause for the decline in population density of A. carolinensis observed in areas where they occur sympatrically with A. sagrei. They state that (p. 733) "...competitive resource exploitation may be the primary factor in the apparent competition between these two species." Our study does not address the question of resource exploitation, but our findings suggest that at this time and in this particular area (southwestern Florida), interspecific aggressive behavioral interference between adult males may very well have played a major role in an ongoing process of niche divergence, and may still be doing so. Clearly, these preliminary field studies suggest that the levels of interspecific aggression exhibited by these two species in laboratory situations underestimate those observed in the field, and more extensive field studies are warranted. The studies should include the reciprocal responses of both gray-throated and red-throated A. carolinensis to A. sagrei.

Acknowledgements. We would like to thank Drs. G. M. Burghardt, N. Greenberg, and R. A. Saudargas for comments on an earlier version of this paper, and Drs. T. A. Jenssen and A. S. Rand for their suggestions and interest in the study. We would also like to thank the staff of Koreshan State Historic Site, Estero, Florida for years of assistance and hospitality afforded the UTK Green Anole Outgroup, and the senior author would like to express her gratitude to Ed Higgins and his staff at Delnor-Wiggins Pass State Recreation Area, Naples, Florida.

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APPENDIX

PARTIAL ETHOGRAM

This partial ethogram was compiled utilizing the agonistic behavioral repertoire of A. carolinensis as described in Crews (1975) and Greenberg (1977), the repertoire of A. sagrei as described by Scott (1984), the repertoire of other Anolis species (Ortiz and Jenssen, 1982), and observations of a combination of 20 intra- and interspecific encounters which were conducted in April and May, 1986, using animals which were not used in this study. Behaviors which are indicative of agonistic encounters were chosen. Others (Crews, 1975; Greenberg, 1977) have described distinctive displays such as the Assertion, Challenge, Subordinate, and Courtship displays of A. carolinensis. These displays are defined on the basis of the appearance of morphological changes such as sagittal expansion, extended throat, etc., in conjunction with a headbob and/or dewlap extension. Since we recorded each of these morphological changes (= behaviors) separately, in this study no attempt was made to differentiate between display types. The Headbob portion of a display was recorded as such, and each extension of the dewlap was recorded as a separate behavior.

Air Lick (AL): tongue is rapidly passed over the lips, out of the mouth, and is immediately retracted; tongue does not come in contact with any object.

Approach (AP): one lizard decreases the distance between itself and another with no attempt to bite.

Attack (AT): one lizard exhibits a sudden rapid movement (lunge) directly toward another; mouth may be opened; may attempt to bite other lizard; occurs over short distances.

Black Color Change (BLACK): the skin color of A. carolinensis becomes a dark brown or black during aggressive encounters (personal observation); not frequently seen in laboratory settings.

Chase (CH): one animal rapidly pursues the other animal over long distances, the latter animal repeatedly retreating.

Crest Erection (CR): elevation of a ridge of tissue extending from the base of the head posteriorly along the spine to the base of tail.

Dewlap Extension (DW): a partial to complete extension of the gular flap; dewlap color is visible.

Display (DP): general term for the performance of either HB or DW; used in the final statistical analyses.

Extended Throat (ET): extension of one component of the hyoid apparatus providing an enlarged profile of the throat; color of the dewlap is not visible.

Eye Spot (ES): a darkening of the scales in the post-orbital region of A. carolinensis (does not occur in A. sagrei).

Headbob (HB): vertical movements of the head in a stereotyped manner; may be accompanied by raising and lowering the body by flexing the forelimbs; may or may not be accompanied by DW.

Jaw Locking (JL): one lizard bites the jaw of another while the second animal bites the rostrum of the first animal; may be accompanied by mutual twisting movements of the body.

Jaw Sparring (JS): two lizards with open mouths, each attempting to bite the jaw or rostrum of the other.

Protruded Tongue (PT): tongue is engorged and pushed forward so that it is visible between the slightly opened jaws.

Retreat (RT): one lizard rapidly increases the distance between itself and another lizard.

Sagittal Expansion (SE): lateral compression of the body; results in an enlarged sagittal profile.

Tail Movement (TM): distal portion of the tail is moved in a slow sinuous or curling motion.

Tongue Touch (TT): placing the tongue in contact with an object such as the substrate or perch.

INDIVIDUAL AND FAMILIAR/STRANGER RECOGNITION
IN ANOLIS LIMIFRONS

The ability of individuals in a species to recognize other members as individuals or as familiars and strangers is considered an important factor affecting decisions of mate choice, social status, territorial defense, and cues to spatial location in the environment. My Master's thesis research focused on the ability of Anolis limifrons females to discriminate between familiar and stranger males and whether they recognize males as individuals. Males were tested for the ability to distinguish between familiar and stranger males. This study was conducted at the Smithsonian Tropical Research Institution's laboratory on Barro Colorado Island, Panama, during the wet season from May through September, 1985.

I found females were capable of recognizing individual males. Males were able to differentiate between familiars and strangers and acted more aggressively toward strangers. In both cases visual cues were the presumed basis for recognition.

Many of the criteria I used to choose A. limifrons for testing hypotheses of individual recognition are shared by other species of anoles. These include:

- (1) Female home ranges occur within a male's home range.
- (2) Females lay eggs throughout the year. This could provide repeated opportunities for contact (courtship behavior and copulation) between a pair.
- (3) Anoles use visual cues in much of their social behavior which suggests that vision may be one of the means by which individuals recognize other individuals
- (4) Male aggressive behavior consists of highly visual displays which can be quantified.

I expect to find the capability of individual and familiar/stranger recognition widespread in anoles and other territorial species of lizards. Andrews (1985) reports that female A. carolinensis recognize males as individuals. Glinski and Krekorian's study on the lizard Dipsosaurus dorsalis (1985) documents male recognition of other males as individuals. The benefits in energy conservation accrued by distinguishing between territorial threats (strangers) and nonthreats (familiars) alone should warrant this ability. The finding that females recognize and prefer to associate with individual males reinforces hypotheses of sexual selection and/or hypotheses of

using individuals as cues to home territory or territory quality (Kiester 1979; Stamps 1987a, 1987b).

My future research interests include:

- (1) Determining the cues used by males and females to recognize individuals.
- (2) Testing male preference between previously mated females and non-mated females. This information would be relevant in evaluating sociobiological hypotheses on male fitness strategies.
- (3) Testing females for individual recognition of other females and how this influences their social structure and behavior.
- (4) Possible behavioral mechanisms effecting speciation using males of different dewlap color morphs.

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DESIGN FEATURES OF THE DISPLAYS OF ANOLINE LIZARDS

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The study of animal communication, particularly in the auditory modality, has been revolutionized by the application of an "engineer-like" approach to the physical design of signals. By studying (1) the sensory system of the receiver, (2) the transmission and noise properties of the habitat through which the signal must pass, and (3) the relationship between the information being transferred to the physical structure of the signal, many features of auditory signals have been explained. A similar approach has been used in a number of other sensory modalities. Surprisingly, vision has been largely left out (notable exceptions are the studies of firefly flashing (Case 1983) and John Endler's recent work on guppy coloration). I believe that such an approach has a great deal to tell us about the displays of iguanid lizards.

I will focus on two distinct display contexts. The "challenge" display is given at close range and directed at a specific second individual. It is the display used to challenge an intruder of either sex, and also the display used during agonistic interactions. The "assertion" display is given spontaneously by territorial males from elevated or conspicuous perches. It does not appear to be directed specifically at any one individual. It appears to function to attract females into the territory, and probably to warn other males that the territory is occupied. Both display types consist, at least in part, of a particular species-, and sometimes individual-specific pattern of head bobs and dewlap pulses, known as the "signature bob." The "challenge" display may also include behavioral and postural modifiers, usually associated with agonistic interactions.

What follows is an attempt to assess the impact of a number of sensory and environmental factors on the physical design of anoline displays. I will attempt to explain why anoline displays, in general, look like they do. I will then examine results from my work on the displays of *Anolis auratus* to illustrate how these principles can be applied.

I. WHY ANOLIS LIZARDS BOB

The first question to answer is why lizards communicate with funny little up-and-down head and dewlap movements in the first place. Jenssen (1977) has addressed this from the motor output point of view: he suggests that the movements evolved from motor capabilities already available to the animal. The movements became ritualized and were used to communicate information such as species identity, and perhaps individual identity and motivational state.

Most workers in the field believe that species recognition is the principle function of the stereotyped movements making up iguanid displays. The film playback experiments of Jenssen (1970) support this view. Not everyone agrees, however. In particular I have heard a number of variants of the following argument: "why do they need a complicated pattern of head bobs to identify the species? They're not blind. Why don't they just look and see what the species is?" Losos (1985) presents a more moderated version of this argument: "Given that there are at least two species recognition signals. . . there may be a hierarchical structure of signal examination. . . At a great distance, body shape is the easiest signal to see. . . As lizards approach and display, dewlap color can be observed. At close proximity, the head bobbing pattern can be discerned."

The idea that body shape offers the easiest and quickest cue for species identification is based on the way the human visual system works. Humans are very good at looking at a complex scene, dividing it up into discrete objects and identifying them. It is important to realize that this process is a fantastic feat of brain function, and in reality is not simple at all. There is good evidence that lower vertebrates do not analyze the visual world in the same way, relying much more heavily on motion patterns to identify objects.

One way to assess the objective difficulty in analyzing the world through shape (as opposed to motion) is to consider the progress of workers in artificial intelligence in their attempts to build vision machines. Marr (1982) reviews these efforts. While machines that analyze motion patterns have been commercially available for some time, machines that can look at objects and identify them by their shape are still being worked on.

Consider the problems involved in designing a "vision machine" that views a scene and identifies the objects in it based on their shape. The first step is to sample the brightness and color of every point in the visual field. It turns out that true brightness and color vary widely over a typical scene, highly influenced by shadowing, reflection, spectral quality of the light source, distance and direction to the light source, and illumination by reflected light sources, whose spectral quality differs from the primary light source. Often the brightness gradient over the width of an object is much greater than the change in brightness as one crosses the edge of the object. The edge of a shadow often results in a sharper break in color and brightness than the actual edge of an object does. The machine must also distinguish actual edges from pattern variation on the object itself.

If we want to design a machine that can identify a particular object (e.g. a lizard) the complexity of the problem increases. After somehow determining where the edges of objects in the scene are, it must compare each shape it "sees" with an internal template, for identification. Unfortunately the apparent size of objects varies with their distance away, so the template must be able to change sizes. The shape of an object also changes with the angle at which it is viewed. Rather than a single template, a large number must be available, appropriate to every angle.

In contrast, suppose we want to build a machine that identifies a precisely timed set of movements. It scans the scene and finds any moving edge or object. It then keeps track of the time between changes in direction of the movement. If we program the machine to look for a set of movements whose temporal pattern is a lizard's signature display, it will have little trouble locating the lizard. Only a single template would be required, since the time between changes in direction of head movement are invariant, regardless of distance, light source, angle of view, etc.

What we know of anoline vision strongly suggests that anoles are much better at motion analysis than at stationary scene analysis. The most convincing evidence is that most anoles eat only moving prey, and will generally ignore the same prey if it remains stationary. The anatomy of the anoline retina also suggests that it is designed for motion analysis.

I am suggesting that, in its evolution, the anoline visual system has foregone the complex and difficult task of stationary form analysis. Instead the anoles have become "experts" at analysis of motion patterns, identifying important parts of their world by the way they move. I am not suggesting that anoles are completely incapable of seeing stationary objects, merely that they are much better at detecting and analyzing moving ones.

I argue that, to an anole, a precisely patterned set of head movements is a much less ambiguous, more immediately recognizable cue for species identity than body shape or color. It is not affected by distance to the

viewer, by ambient light conditions, or by angle of view.

Finally, motion patterns have one other advantage as a signal. On theoretical and experimental grounds (see Davson 1980) motion acuity is approximately twice as good as stationary acuity. This means that the details of a motion pattern can be distinguished at a distance where features like body shape and color are not distinguishable.

I do not mean to say that anoles are incapable of identifying conspecifics by other cues (and Losos 1985 convincingly showed that they do), but I believe that a species-specific movement pattern is the quickest, least ambiguous, and most easily detected way to transmit

species identity, especially at a long distance. This is true for other types of information as well.

II. FACTORS AFFECTING MOTION PATTERNS IN ANOLINE DISPLAYS

A. Visual Acuity

The anoline eye is of high optical quality and clearly designed for high acuity vision. The broad retina and large lens provide a wide field of view. Anoles possess a pure cone retina. There are two foveal regions where cone densities are very high: the central fovea, associated with monocular fixation, and the temporal fovea, associated with binocular fixation. In the peripheral retina cone densities are much lower.

Visual acuity has never been measured in an anole. In other animals, visual acuity correlates well with cone density and eye size (a larger eye projects a larger image on the retina, allowing it to be spread over more photoreceptors). Makaretz and Levine (1980) measured cone densities in *Anolis carolinensis*. Based on these densities and making certain reasonable assumptions about the optics of anoline eyes (I used the eyeball pictured in Makaretz and Levine, p.681, and assumed that the nodal point of the eye is at the center of the lens), I have calculated the minimum resolveable angle to be 0.04° in the visual periphery and 0.003° for the central fovea. These, however, are optimum values based on receptor spacing. A small pupil induces diffraction errors which can reduce acuity substantially. Another factor which tends to reduce acuity is chromatic aberration. Many iguanids lessen this problem by filtering out blue light (which causes the worst problems of chromatic aberration) with yellow oil droplets in their photoreceptors. In motion detection experiments on *A. auratus*, which I will describe later, I found a threshold for response to moving objects presented in the visual periphery, of about 0.20° visual angle. Based on that value, at a distance of 2 m a movement of about 7 mm will be just detectable in the visual periphery. For an attentive animal, using foveal vision, this value should improve by a factor of about 10.

The central fovea has an extremely small field of view. The peripheral retina samples a broad visual field at lower acuity. When something of importance is detected in the periphery, a reflex shift of eye position brings the important image onto the fovea. This is referred to as the "visual grasp" reflex. Motion in the periphery is the strongest stimulus for the "visual grasp" reflex.

B. The viewer of the display.

Two important variables concerning the intended viewer of the display will influence display design: the distance from the viewer to the display, and whether or not the viewer has its attention directed toward the display. Displays break down into two general categories. Close

range displays (challenge displays, appeasement, pre-mating) and long range (the assertion display). In the close range displays, the displayer fills a large portion of the viewer's visual field, and often preceeds the display by a direct approach. It is likely in such cases that the attention of the viewer will be directed at the displayer. The assertion display probably functions to attract females from outside the territory, and to warn other males that the territory is occupied. In either case, the intended viewer of the display is a long distance away, and often does not have its attention directed at the displayer.

The effect of distance is straightforward. The movements in the display must exceed the detection threshold. The further the displayer is from the viewer, the higher the amplitude of the movements must be. Stamps and Barlow (1973) report, in *A. aeneus*, an increase in the height of display movements when the lizard eliciting the display is at a greater distance. In general, assertion displays are of higher amplitude than challenge displays.

If the intended viewer is inattentive, then the display will be perceived by the peripheral retina, rather than the fovea. If it is to be seen, the movements must be of substantially greater amplitude. Equally important, information in the periphery is probably not analyzed in detail by the brain (i.e. foveation is associated with attention). The display movements must drive the "visual grasp" reflex, which directs the viewer's attention and gaze toward the displaying individual.

C. Effectiveness of different patterns of motion in drawing attention.

I studied the effectiveness of different patterns of motion in driving the "visual grasp" reflex of *Anolis auratus*, a grass anole from Panama (Fleishman 1986a,b). In each experiment I placed a lizard in a cage and diverted its gaze to a particular point in space (see Fig.1). I then presented a moving stimulus in the visual periphery. The stimulus was a small black sphere suspended on a clear monofilament, which could be moved up and down, periodically, in any pattern. In each case I gradually increased the peak to peak amplitude of the lure motion until the lizard responded by shifting its gaze to the moving lure. In successive tests the pattern of movement of the stimulus was changed. In this way I tested the relative effectiveness of different motion patterns in eliciting attention.

Interestingly, when the lizards responded to the motion, they did so at approximately the same peak to peak amplitude, regardless of the pattern. Whether they responded at all, however, depended on the nature of the stimulus movement pattern. The probability of response was highest for motion patterns which combined high acceleration plus high velocity. Increases in either factor alone did not increase response probability. I tested sinusoidal stimuli of a range of frequencies. I found no difference in response probability between 0.5 and 6 Hz. Above 6 Hz response probability fell off rapidly. The flicker fusion frequency of *A. auratus* is much higher than this (Jenssen and Swenson 1974). It appears that at a critical threshold amplitude a "decision" is made whether or not to direct the gaze toward the moving object. This decision is based on the pattern of motion of the stimulus.

As far as I know, no comparable studies have been carried out for any other animal, so I will assume that these results are true for other anoles.

D. Habitat Effects

There are several ways in which the habitat can influence display design. For most anolines, the habitat is characterized by the most

common vegetation. The first effect I will discuss follows from the preceding discussion of motion detection.

Motion in the visual periphery is the strongest stimulus for the "visual grasp" reflex. Unfortunately, the world is full of irrelevant motion, mainly in the form of windblown vegetation. If an anole responded with the "visual grasp" reflex every time a leaf or blade of grass, moved in the wind, the reflex would quickly be swamped into uselessness. The visual system must somehow filter relevant (predators, prey, conspecifics) from irrelevant environmental motion. We have just seen that the reflex responds preferentially to certain motion patterns. Windblown vegetation tends to move in simple oscillations, with relatively low acceleration and velocity. In contrast, animals, with their relatively quick stops and starts, move with high acceleration and velocity (consider how often we detect lizards and other animals in the field when they start moving).

I took the motion detection experiments described in the previous section a step further. In all the experiments, I used artificial vegetation as the backdrop for the stimulus lure. In this next set of experiments I moved the vegetation backdrop up and down in simple oscillatory patterns during stimulus presentation (interference). In another set of experiments I moved the background vegetation up and down in simple oscillation for several minutes prior to stimulus presentation, but stopped the vegetation movement just prior to stimulus lure presentation (habituation). The result was the same in both cases. If the motion pattern of the stimulus lure was similar to the motion of the background vegetation, the probability of response to the moving lure was greatly reduced. If the stimulus motion differed substantially in frequency, or in sinusoidal frequency composition (e.g. square motion versus sine wave motion) from the motion of the background, the probability of response was essentially unaffected.

Thus, if display movements are designed to attract attention (i.e. drive the "visual grasp" reflex), their effectiveness can, potentially, be drastically reduced by vegetation movement. To avoid this problem the movements in the display must be different than the patterns of windblown vegetation movement.

A second potential habitat influence is ambient light quality. Jenssen and Swenson (1974) demonstrated that Flicker Fusion Frequency is correlated with average intensity of ambient light in the habitat for different species. FFF is essentially a measure of how quickly the visual system samples the world. In measuring the details of movement the higher the FFF the greater the detail discernible. This means that anoles from darker habitats may have to make do with less rapid and subtle movements in the display.

An interesting and important feature of a communication signal is its "active space," or the volume of space over which it can be functionally perceived. The ultimate limitation on active space is the distance at which movements can be resolved. Another component for a visual display is the average distance of unobstructed lines of sight. It would seem that a display in an arboreal habitat will, on average, have a much smaller active space than one in an open habitat, since as the distance to the viewer increases, the probability of the view being blocked by a branch or a leaf increases. Assuming that there are costs to displaying at high amplitude (see below), then assertion display amplitude might be expected to be lower for forest anoles, than for grass anoles, since the active space over which the display is likely to be effective is restricted in the forest case. Males improve the active space of their signals by choosing appropriate display perches. Many species in open habitats display from elevated positions. It is less clear, and would be interesting to study, how active space can be improved by choice of perch in arboreal species.

E. Dewlap Coloration

Dewlap coloration has received considerable attention. Williams and Rand (1977) demonstrated a relationship between numbers of sympatric species and complexity of color. Losos (1985) demonstrated that dewlap color can be used by at least one species to discriminate between its own and a very similar (except for dewlap color) sympatric species. Color is somewhat ambiguous as a cue, because perceived color can change with light conditions, but distinct differences in dewlap color can no doubt help an anole to avoid mistaking another species for its own.

It has been suggested that dewlap color may enhance visibility (Williams and Rand 1977; Sigmund 1983). To humans the most conspicuous color against a colored background is the complimentary color. Thus, red stands out maximally against green, yellow against blue, etc. At present, there is no way to know if this rule holds for anoles as well. It appears to be based on the fact that at the neuronal level, primate color vision is organized into color-opponent fields, in which one color stimulates a neuron and its complement inhibits the same neuron. Most of these fields show red-green or blue-yellow opponency. A similar organization is present in many vertebrates, and with a leap of faith we can guess that the same principle operates in anoles. Since most anoles live in habitats with green backgrounds, in general, the most easily visible color should be red, or possibly orange.

There is, however, another level of visual contrast: brightness contrast. If the background is generally dark, a bright object will stand out against it, and vice versa. The two contrast effects (color and brightness) interact. The color white reflects all spectral hues. Any other color absorbs some portion of the spectrum, reducing to some extent the brightness of the dewlap.

In habitats with a dense canopy, the amount of light is greatly reduced, and there is selective color filtering. Green and yellow light are most abundant. Red and other colors are relatively reduced in intensity. Under these conditions, a red dewlap will not be very bright, because there is too little red in the ambient spectrum to illuminate it. Under very dark conditions white may well be the most conspicuous color because it reflects all available downwelling light and stands out against the dark backdrop of the forest. If any color is to be used under deep shade conditions, it should probably be yellow. Green will not stand out against the green background. Yellow is a compromise between color and brightness contrast. It stands out to some extent against green, and is relatively well lit by the ambient spectrum.

I predict, then, that as one moves from very densely vegetated habitats to more and more open ones there will be a general transition from white to yellow to orange to red dewlaps. Under extremely bright conditions the most conspicuous color may be one which reflects little or no light (i.e., black, brown, or dark blue) in contrast to the brightly lit backdrop.

The most common anoles of Panama fit this prediction nicely. The deep forest *A. frenatus* has a white dewlap, *A. limifrons*, which occupies the forest and occasionally ventures into forest edge, has a white and yellow dewlap (this varies somewhat between individuals), the edge and second growth species, *A. tropidogaster*, has an orange dewlap, and the grass anole *A. auratus* has a dark blue (almost black) dewlap.

To test this idea more widely, I sought the assistance of A.S. Rand and E.E. Williams. I reviewed the color plates of anoline dewlaps in Schwartz and Henderson (1985) and categorized them by dominant color. Rand and Williams, independently categorized them by general habitat types. We lumped closely related species to avoid over-representation of certain

phylogenetic lines. The results are summarized in Table 1. The trends are in the general direction predicted, although with more overlap than I had expected.

Fitch and Hillis (1984) analyzed dewlap color in a number of North and Central American species. They made a distinction between "seasonal" and "aseasonal" habitats as follows: "'Aseasonal' localities were those occupied by cloud forest or tropical rain forest; 'seasonal' localities were those occupied by desert, thorn-scrub, deciduous forest, or dry coniferous forest." From the point of view of light conditions it seems to me that what they defined as "seasonal" localities are generally bright and well-lit, while the "aseasonal" localities are likely to be dense and poorly lit. They found that the anoles from "seasonal" habitats nearly all had brightly colored dewlaps (usually red or orange), and none had white dewlaps. Many of the anoles (about 25%) from the "aseasonal" localities had white dewlaps. This is in good agreement with my hypothesis. They also reported however, a fairly large number of aseasonal locality species with red or orange dewlaps. I am not sufficiently familiar with microhabitat preferences of these species to say if this might explain some of these. It is also possible that some dense forest species have behavioral specializations which allow them to have red or orange dewlaps under generally light-poor conditions. If they display preferentially in light flecks, for example, the spectrally rich downwelling light will illuminate their red dewlaps, and they would stand out brilliantly against the spectrally poor forest backdrop.

My only disagreement with the interpretation of Fitch and Hillis (1984) is their claim that white dewlaps are less visible than colored ones. As outlined above white dewlaps may be maximally visible under certain conditions. Further, what appear to be dull, white dewlaps are sometimes translucent (*A. frenatus* is an example). When viewed from the side or from below, the downwelling light makes such a dewlap appear to glow and it becomes very visible.

A puzzle in both data sets is the presence of a few deep forest anoles with dark brown dewlaps. My guess is that these species do not use a long distance assertion display, and the brown color is actually designed to be visible only at very short range.

The dewlap color story is made more complicated by the fact that some species appear to use dewlap color as a species recognition cue when sympatric species are present. This appears to result in color divergence when several species are present. There may also be historical, phylogenetic considerations. A species which recently invaded a habitat may have a dewlap color more appropriate for its old habitat.

In summary, it is clear that dewlap color serves more than one function. To the extent that the function of dewlap color is to enhance the visibility of the display, habitat brightness and color-richness appear to exert some influence on the possible colors a dewlap may have. This question obviously needs further study.

F. Information Content

A display presumably serves to broadcast some type of information. Jenssen (1977) reviewed the relationship between display variability (at the population and individual level) and information content. A single display may broadcast several distinct pieces of information, and, in fact, different portions of displays show different levels of stereotypy. In brief, where species identity is being transmitted, low between-individual and low within-individual variability is expected. Where individual identity is being broadcast, one expects high between-individual variability, and low within-individual variability (as of yet, there is no

convincing proof that individual recognition exists in anoles, although there is anecdotal evidence that it does). Where motivational state is being broadcast, high within-individual variability is expected. The first two conditions can be found in the temporal pattern of the signature bob of several species. The last condition is met by the various dynamic and static modifiers which are added to the display.

I will add only one point to Jenssen's overall analysis. Where information cannot be accurately transmitted, there may be very little selective pressure for stereotypy. I am referring specifically to the amplitude of movements in head-bobbing displays. Since apparent amplitude changes with distance and angle of view, a viewer cannot accurately assess true amplitude of movements. As we will see shortly, amplitude in *A. auratus* shows high within-individual variability. I believe that this variability reflects the inherent ambiguity of amplitude as an information source, leading to little selection pressure for stereotyped amplitude. While amplitude of movements may be influenced by emotional state, I do not believe it is being used to communicate this information.

G. Counter-selective pressures

The two principle counter selection forces are energy expenditure and predator risk. I have little to say about energy. The higher the amplitude of movements, the higher the acceleration, or the higher the frequency, the more the energy required. Where possible, anoles may be expected to reduce these. I do not know of any examples where these costs have been measured, so it is difficult to assess the impact of energy limitations.

There is little doubt that predation is a potent selection force on anoles. The principle predators for most anoles are birds and snakes. Most of the birds and many of the snakes are visual predators and probably rely heavily on motion to detect the presence of their cryptically colored prey. I have observed the hunting behavior of several arboreal snakes, and they seem to rely almost exclusively on prey movement for its detection and location. This suggests that display movements are risky. I do not know of any studies which have directly tested the conspicuousness of different movement patterns to predators, but it seems likely that the same features that make a display conspicuous to a conspecific will make it conspicuous to a predator.

The net effect is that lizards will, whenever possible, limit the conspicuousness of their displays. Thus, close range displays to attentive conspecifics should be of low amplitude, and also of low acceleration and velocity. In the case of assertion displays, where high amplitude, conspicuous movements are needed to draw the attention of inattentive conspecifics, these should be restricted to the early part of the display. Once attention is gained, less conspicuous movements can be used.

There are several famous (non lizard) cases in which predators actually use the communication signals of males to detect their prey (e.g., Ryan 1985). There is no experimental evidence that this occurs in anoles, but I have an impressive anecdote to relate. Near the end of my studies on *A. auratus* in Panama, I decided I needed a good photograph of a male displaying. I located a large male whose territory included a pile of cement blocks from which he frequently displayed. I set up my camera, and had an assistant place another male about 1 m away. The large male went into a beautiful display. I took one photograph, but before I could get a second, a vine snake (*Oxybelis aeneus*), dropped from an overhanging tree and snatched up the still displaying male. *Oxybelis* is a highly visual *Anolis* specialist, and it would not surprise me if they rely on detecting displays as a way of locating prey.

It is possible that males take special steps to reduce the risks

associated with displaying. J. Wright (pers. comm.) claimed that displaying *A. limifrons* are much harder to catch than non-displaying ones. Non-displaying individuals seem to rely on crypsis to avoid detection, and therefore remain motionless as a person approaches. A male that has just displayed behaves as though it is aware its strategy of crypsis has been compromised and flees much sooner as one approaches. Male *A. auratus* display from tops of grass stalks and other elevated locations. It has generally been assumed that this makes them more visible to conspecifics, but it may also allow them to "scout the area" for predators before displaying.

III. THE DISPLAYS OF *A. AURATUS*

I will now describe, in some detail, the displays of *A. auratus* and in doing so illustrate some of the principles outlined above. I studied displays in two contexts. In order to film spontaneous, assertion displays, I housed several individuals in large (4 x 4 m) outdoor enclosures. After several days in such enclosures one male would begin giving assertion displays every few minutes. I filmed these displays from an elevated blind overlooking the enclosure. I then captured the displaying male and moved him to a small cage. After several days I introduced a second male to the cage, and filmed the ensuing challenge display by the resident. This was repeated a number of times (only the first display in each encounter was used). I completed these steps for a number of males. Filming was done at either 18 or 54 frames/s, using a Nizo super-8 camera. Displays were analyzed by digitizing the films with a Zenith personal computer. The only methodological improvement over other studies of anoline display was that I recorded, on each individual, the distance from the bottom of the upper jaw to the top of the eye. Since this measurement is in the same plane as the movements used in the displays, it can be used to correct for camera angle and distance and allowed me to calculate true amplitude of display movements.

A. General Description

Examples of repeated displays by the same individual *A. auratus* are shown in Fig. 2. The temporal pattern is consistent between displays of the same individual. Assertion and challenge displays have the same temporal pattern but show differences in amplitude (the challenge display also differs in that it is often repeated a number of times in continuous succession, and is often accompanied by postural modifications like those described in Jenssen 1977). Fig. 3 shows displays by several different individuals. There are striking differences between the displays of different individuals.

For descriptive purposes, I divided the displays into Parts I and II. The head movements in Part II are quite similar in displays of all individuals. The head movements in Part I, and the dewlap movements in Part II show obvious individual differences.

B. Sources of Variability

I divided the displays into distinct recognizable temporal components present in displays of all individuals (shown in Fig. 3, see Fleishman 1986b for details). I calculated between- and within-individual coefficients of variation for each of these temporal units. The averages for Part I and Part II are shown in Table 2. I also calculated the coefficients of variation for the amplitude of each head movement, and averages for each Part also appear in the table.

The greatest between-individual variation appears in the head movements of Part I. Also note, in Fig.3, that there are differences between individuals in the number of head bobs in Part I. Part II dewlap movements also show high between individual variability. It is possible, therefore, that one, or both of these components allows for the identification of individuals. These displays show a higher degree of individual uniqueness than has been described in other anoline species. *Anolis auratus* is the only species studied in which dominant males allow breeding age subordinates to remain within the territory during the breeding season. Dominance is settled by a single agonistic encounter (Fleishman 1988a). It is possible that a high degree of individual uniqueness is necessary to continuously remind defeated subordinates that the dominant male is still present.

The head movements of Part II show much more between-individual stereotypy. This portion of the display may be critical for species identification.

Amplitude shows a great deal of within-individual variability. As discussed earlier I believe that this arises from the inherent ambiguity of amplitude as a source of information. There is little selective pressure for high levels of stereotypy in amplitude of displays. This is not to say that there is not selective pressure on amplitude (see below), simply that amplitude can be allowed to vary without destroying the message carried by the display.

C. Challenge Versus Assertion Display

Challenge displays are usually given at close range to an attentive viewer. Assertion displays are given at long range to potential viewers that may not be attentive. Based on the principles outlined earlier, I made several predictions about differences between the two types of displays: 1) the assertion display must be of greater amplitude to be resolvable at a greater distance; 2) the initial portion of the assertion display should contain movements of high acceleration and high velocity to effectively elicit the attention of inattentive conspecifics; 3) the initial portion of the assertion display should be of higher amplitude than the latter portion since the initial portion will be viewed in the low acuity visual periphery, 4) the latter portion of the assertion display, though of higher amplitude than the challenge display (see prediction 1), should be of lower amplitude, and lower acceleration and velocity than the initial portion of the assertion display to avoid unnecessary risk of attracting predators, after the attention of the conspecific has already been drawn early in the display.

Comparisons of Part I and Part II of assertion and challenge display amplitude, acceleration, and velocity are summarized in Fig. 4 (see Fleishman 1988b). The predictions are borne out quite nicely.

Wiley and Richards (1982) analyzed the structure of bird songs and observed that complex calls are often preceded by a loud, simple, easily locatable "alerting" signal. They suggest that this serves to alert potential listeners to an incoming signal of greater complexity (i.e. it draws their attention). They also state that the alerting signal (1) should not contain critical information, since before attention is gained information might be lost, and (2) that it should bear a precise temporal relationship to the remainder of the signal. It seemed to me that the initial portion of the *A. auratus* assertion display was serving a similar, alerting, role. It is easily locatable, and simple and consists of movements of high acceleration and velocity which effectively draw attention. On the other hand it appears to violate the last two rules mentioned. The fact that the length of Part I differs between individuals

means that the "alerting" portion of the display does not bear a precise temporal relationship to the rest of the signal. This may be a much less critical requirement for a visual signal than for an auditory one. Once an animal is foveally fixated at a point in space it will see with full attention all that follows. The same is not necessarily true for audition.

The other provision --that the alerting signal not contain critical information-- may be violated. If individual identity is contained in the variable number and timing of head bobs of Part I, then it seems odd that this should be placed at the beginning of the display where much of the information is likely to be missed by an inattentive viewer. An interesting possibility is that the individual variability at the beginning of the assertion display actually enhances its ability to draw the attention of females. Kiester (1979) showed that *A. auratus* females tend to approach conspecifics regardless of their breeding condition or the identity of the conspecific. Thus if a male can repeatedly catch the attention of a female, she will tend to approach his territory. I showed earlier that the motion detection response habituates to commonly present motion patterns. The females may habituate to frequently seen display movements. Thus, a male whose alerting signal differs from other males may be more successful at eliciting the attention of females. In this way there may be selection for individually unique display patterns in the initial portion of the assertion display.

Stamps and Barlow (1973) presented territorial male *A. aeneus* with conspecifics at various distances away. At longer distances males actually added an introduction to their signature bob which consisted of several simple, jerky, square-wave like movements of the head. These high acceleration, high velocity movements, added to the beginning of the display almost certainly represent an alerting signal.

D. The Effect of Background Movement

I have discussed this problem at length elsewhere (Fleishman 1988c), and will briefly review the results here. Vegetation movement tends to be sinusoidal in nature. I have shown experimentally that if movements differ in sinusoidal frequency composition from the background movement no habituation or interference will occur. I recorded the pattern of motion of windblown vegetation typical of the *A. auratus* habitat. Using Fourier analysis I characterized the full range of amplitude present at each sinusoidal frequency. Amplitude is high through 3 Hz and drops off quickly at higher frequencies. I analyzed the initial portion of the assertion display (during attention elicitation the problem of habituation and interference is most critical) using Fourier analysis, and found it to generate amplitude in the 4-7 Hz range several times greater than that present in the background motion. These frequencies are generated by short duration bobs whose fundamental frequency is either 4-5 Hz, or by square-wave-like bobs of 2 Hz whose harmonic at 6 Hz is of high amplitude. Thus, the attention-gaining portion of the display will not suffer reduced effectiveness due to background motion.

I have not yet studied vegetation movement in the habitats of other species and its relationship to display form. I should note that for this analysis it is necessary to know the amplitude of display movements and to record the display at a high sampling rate. Unfortunately most display analyses in the literature do not meet these criteria, so that, at this time, I cannot determine a relationship between habitat types and display form. I suspect that some differences in display form will be turn out to be attributable to differences in the nature of vegetation in the habitats of different species.

E. Active Space

The amplitude of the head movements in the initial portion of the *A. auratus* assertion display are about 15 mm peak to peak. This amplitude falls just below 0.20^0 (the experimentally determined threshold for elicitation of the "visual grasp" motion detection reflex) at a distance of 4.3 m. The average territory size for *A. auratus* males is 7.9 m^2 (Fleishman 1986b). From the center of a territory a male can display effectively, roughly to the edge of the next territory. If the animal viewing the display has its attention focused on the displayer (i.e., it is viewing the display with foveal portion of the retina) the distance at which the movements can be resolved will increase approximately ten-fold, based on the difference in photoreceptor densities in the periphery versus the fovea.

Other factors may function to reduce the active space of the signal. Line of sight may be blocked after a shorter distance. As distance increases so does the apparent velocity and acceleration of the display, which probably decreases its effectiveness in drawing attention.

IV. CONCLUSIONS

I hope by now I have convinced the reader that an "engineering design" approach has a lot to tell us about anoline displays. Most of the ideas given here remain to be put to rigorous tests, and it is my sincere hope that someday this will be done.

ACKNOWLEDGMENTS

The work on dewlap color was done in collaboration with A.S. Rand and E.E. Williams, although I, alone, take blame for the hypothesis. Many of the ideas contained herein were discussed with, inspired by, or unintentionally stolen from A.S. Rand. J.B. Losos made suggestions for improvements in the manuscript.

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Table 1. Dewlap color and habitat type for west indian anoles.

habitat	dewlap color (% of total species from each habitat type)				n*
	<u>white</u>	<u>yellow</u>	<u>orange or red</u>	<u>dark(brown or blue)</u>	
dark forest	46%	38%	0%	15%	13
edge or canopy	38%	46%	7%	8%	26
open	14%	14 %	43%	29%	7

 *n represents the number of species (or closely related species groups) on which the percentages are based for each habitat.

Table 2. Average coefficients of variation for *A. auratus* displays.*

Temporal Intervals:

	<u>Part I</u> <u>Head Movements</u>	<u>Part II</u> <u>Head Movements</u>	<u>Dewlap</u> <u>Movements</u>
between-individual	60%	32%	26%
within-individual	21%	16%	9%

Head Bob Amplitude:

	<u>Assertion display</u>		<u>Challenge Display</u>	
	<u>Part I</u>	<u>Part II</u>	<u>Part I</u>	<u>Part II</u>
within-individual	38%	36%	34%	19%
between-individual	7%	55%	24%	13%

 * Based on 12 displays each by 3 individuals. For details see Fleishman(1986b)

Figure Legends

Figure 1. Side (A) and top (B) views of experimental cage used in motion detection experiments: (a) glass at front of cage through which experimenter observes lizard's eye, (b) stimulus lure, (c) artificial vegetation background mounted on a clear plexiglass rectangle (d) which can be rotated about a pivot. Motion of background and stimulus lure are controlled by oscillograph pen motors attached to the moving object by a clear monofilament. The lizard gazes in direction (i) as experiment begins. A positive response involves a shift to direction (j). From Fleishman (1986a).

Figure 2. Display action pattern graphs of challenge and assertion displays by a single individual *Anolis auratus*. Letters indicate bobs on which amplitude calculations are based. From Fleishman (1986b).

Figure 3. Examples of assertion displays by four different individuals. Displays are divided into Parts I and II. For analysis of temporal patterns displays are divided up into components (lower case letters and numbers) which are present in displays of all individuals. From Fleishman (1986b).

Figure 4. Means and standard deviation of amplitude, velocity, and acceleration for the displays of three individuals, pooled. Part I and Part II for each display type are plotted separately. Each bar represents 15 values (five each by three individuals). From Fleishman (1988b).

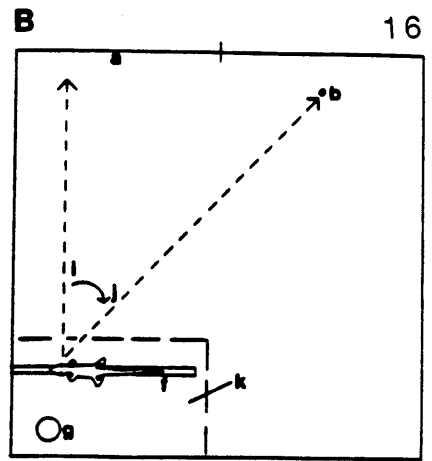
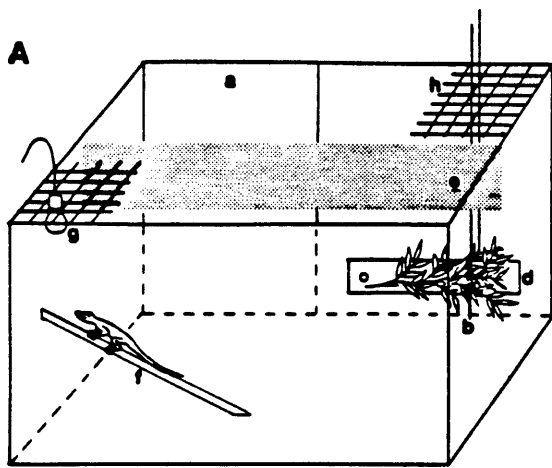


FIGURE 1

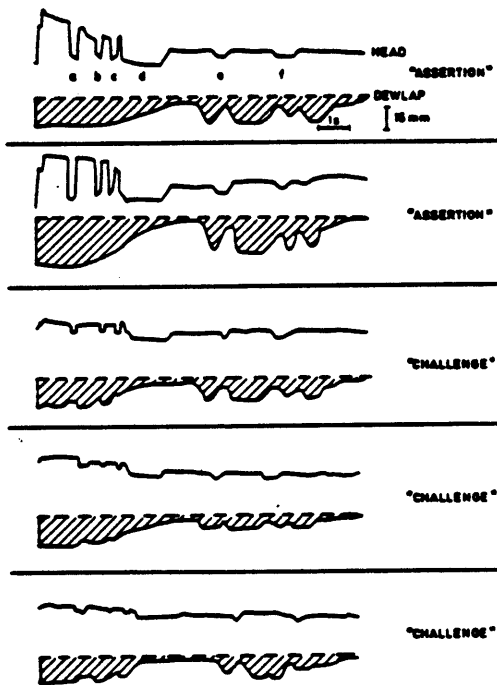


FIGURE 2

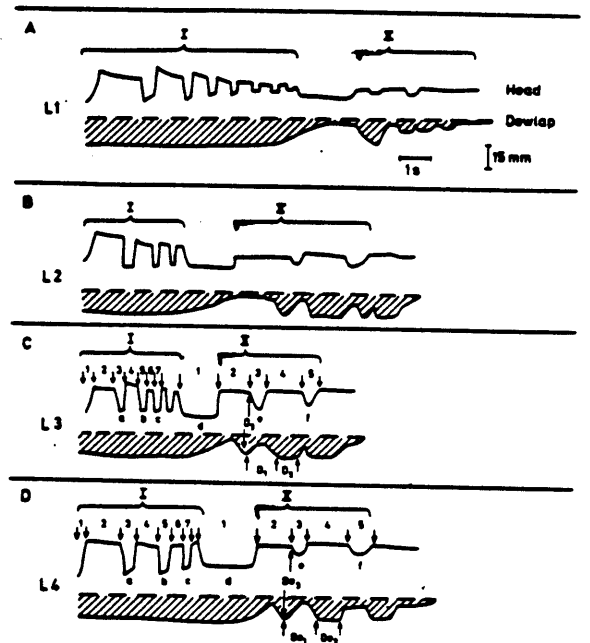


FIGURE 3

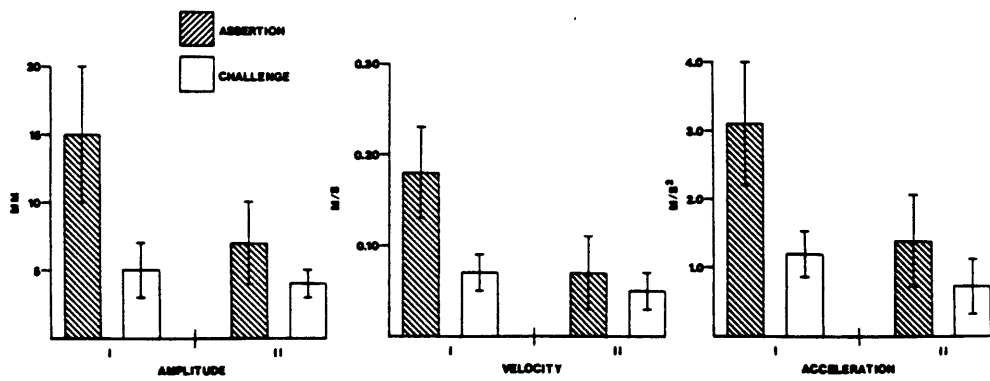


FIGURE 4

***Anolis sagrei* and *Anolis carolinensis* in Florida: evidence for interspecific predation.**

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In recent decades many exotic species of *Anolis* have been introduced into south Florida. Most of these species survive only in localized populations near their site(s) of introduction. However, one species, *A. sagrei*, has been extremely successful in colonizing new areas. Introduced approximately fifty years ago, *A. sagrei* has now colonized most of peninsular Florida (reviewed in Lee, 1985). The success of *A. sagrei* in Florida can be attributed to both repeated and widespread introductions and the affinity of the species for disturbed habitats. Florida, with one of the fastest growing human populations in the United States, has an increasing number of disturbed areas.

Florida populations of *Anolis carolinensis*, the only species of *Anolis* native to the United States, have experienced density reductions in areas colonized by *A. sagrei*. A pattern of partial or complete replacement has been reported for several localities (e.g., Tokarz and Beck, 1987) and interspecific competition has been hypothesized to explain the observed change in species abundance.

These two species (or close relatives in the case of *Anolis carolinensis*) coexist in sympatry on Cuba and on many of the smaller islands in the Greater Antillies (see Williams, 1969, for a review). Where they co-occur in the Greater Antillies, *A. sagrei* has been described as a "trunk-ground" lizard and *A. carolinensis* as a "trunk-crown" lizard (Williams, 1969). Such differences in habitat use between species should reduce interspecific competition and may be the result of more intense competition in the past. Schoener (1975) compared the perch characteristics of these species on islands where they occur sympatrically with islands where either *A. sagrei* or *A. carolinensis* occurs allopatrically. He found their structural niches more similar in allopatry than in sympatry, providing indirect evidence for interspecific competition.

Populations of *Anolis carolinensis* in Florida appear to occupy a broader niche than has been reported for island populations. Using Williams' (1969) terminology, *A. carolinensis* in Florida is a crown-trunk-ground lizard (personal observation). Ecological release, resulting from reduced congeneric competition, may explain the expanded niche of *A. carolinensis* in Florida.

If *Anolis carolinensis* has undergone ecological release in Florida, then contact with introduced populations of *A. sagrei* may result in more intense competition between these species than where they have a long history of sympatry. Competition, presumably for limited resources, can be manifested through behavioral interference or resource exploitation. Behavioral interference frequently results from competition for space. In *Anolis* lizards, this often involves male-male aggression, as males tend to be more over-dispersed and territorial than females. If spatial overlap between species is extensive, behavioral interference may result in interspecific male aggression similar in intensity to intraspecific male aggression (Ortiz and Jenssen, 1982; Jenssen et al., 1984). Several researchers have recently investigated the role of interspecific male aggression between *A. sagrei* and *A. carolinensis* (Tokarz and Beck, 1987; Brown, 1988). Although these studies are not in complete agreement, and results of laboratory studies differ somewhat from field studies (see Brown and Echternacht, this newsletter), interspecific aggression generally appears to be less intense and less frequent than intraspecific aggression, suggesting that male-male aggression is not the primary mechanism of competition between *A. sagrei* and *A. carolinensis*.

My observations of *Anolis sagrei* and *A. carolinensis* in Florida suggest that adult *A. sagrei* are largely syntopic with hatchling and juvenile *A. carolinensis*. If large *A. sagrei* include small *A. carolinensis* in their diets, interspecific predation, an extreme form of interference competition, may explain the decreases in *A. carolinensis* populations.

In July and August of 1988 I conducted behavioral tests to determine if *Anolis sagrei* and/or *A. carolinensis* adults would prey on hatchlings. In these tests adult males served as predators and hatchlings as prey.

Adult male and hatchling anoles were collected from areas in south Florida where the two species are sympatric. Twenty adult males of each species were tested for intraspecific and interspecific predation. Each male was individually housed in a four liter jar fitted with a screen top and provisioned with a wooden perch and a water dish. Males were not fed for three days prior to testing to ensure equal hunger levels. On the fourth day a single hatchling was introduced into the container of each male. Uneaten hatchlings were removed one day later. Each male was tested twice, once for intraspecific predation and once for interspecific predation; the order of presentation was determined randomly and heterospecific hatchling pairs were matched by weight. Hatchlings

used in this study were usually between 0.10 and 0.30 g and were never larger than 0.50 g. Large males were matched with large (older) hatchlings and vice versa. Differences in predation frequencies were analyzed for statistical significance in 2 x 2 contingency tables using a G-test with William's correction ($\alpha = 0.05$). Adult male *A. sagrei* ate significantly more heterospecific than conspecific hatchlings ($G = 7.357, P < 0.01$); adult male *A. carolinensis* did not ($G = 0.941, P > 0.25$) (Table 1).

To test directly for species discrimination, 11 adult male *Anolis carolinensis* and 13 adult male *A. sagrei* were simultaneously presented with two hatchlings, one of each species, matched by weight to within 0.01 g. Males were individually housed as before, but in larger (40 liter) terraria. Trials were conducted as described above. Again, adult male *A. sagrei* ate significantly more heterospecific than conspecific hatchlings ($G = 5.796, P < 0.025$). No adult male *A. carolinensis* ate hatchlings (Table 2). These results suggest that adult male *A. sagrei* selectively prey on hatchling *A. carolinensis*.

Following behavioral tests, adult anoles were morphometrically compared using snout-vent length (SVL), weight and head width (Table 3) to determine if these characters might explain the behavioral results. SVL and weight were used to determine if anoles differed significantly in body size. Head width was used because of its relationship to the maximum size of prey which can be handled. Species did not differ significantly (t-test, $\alpha = 0.05$) in SVL ($t = 0.597, P > 0.50$), weight ($t = 1.760, P > 0.05$) or head width ($t = 0.284, P > 0.50$), suggesting that *Anolis carolinensis* is not morphologically constrained, relative to *A. sagrei*, from preying on hatchlings. Furthermore, the SVL (weight and head width are highly correlated with SVL within species) of saurophagous *A. sagrei* ($n = 19$) did not differ significantly from non-saurophagous *A. sagrei* ($n = 14$) ($t = 0.093, P > 0.90$). In fact, both the largest (SVL = 65 mm) and the smallest (SVL = 53 mm) individuals tested were saurophagous. These results suggest that most, if not all, adult male anoles of these species are capable of preying on hatchlings and that differences in saurophagy are the result of behavioral, not morphological, differences between individuals and species.

In sum, the evidence accumulated thus far is consistent with the hypothesis that interspecific (congeneric) predation is important in reducing *A. carolinensis* populations sympatric with *A. sagrei* in Florida. The behavioral basis of saurophagy, and the importance of predation under more natural experimental conditions are currently being investigated.

Acknowledgments

I wish to thank Arthur C. Echternacht for originally suggesting this research and for his assistance in the field. Chris Samblanet also provided valuable assistance in the field. A portion of this research was conducted at the Archbold Biological Station in Lake Placid, Florida. Funding was provided by the Department of Zoology and the Graduate Program in Ethology at the University of Tennessee, Knoxville.

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Table 1. Predation of hatchling *Anolis sagrei* (AS) and *A. carolinensis* (AC) by adult males during intraspecific and interspecific predation trials. Each male was tested twice, once with a conspecific hatchling and once with a heterospecific hatchling.

<u>Adult</u>	<u>Hatchlings Eaten</u>			
	<u>AS only</u>	<u>AC only</u>	<u>Both</u>	<u>Neither</u>
AS	0/20	7/20	1/20	12/20
AC	1/20	0/20	0/20	19/20

Table 2. Intraspecific and interspecific predation of hatchling *Anolis sagrei* (AS) and *A. carolinensis* (AC) by adult males during species discrimination trials. Each male was tested once with two hatchlings, one conspecific and one heterospecific.

<u>Adult</u>	<u>Hatchlings Eaten</u>			
	<u>AS only</u>	<u>AC only</u>	<u>Both</u>	<u>Neither</u>
AS	2/13	8/13	2/13	1/13
AC	0/11	0/11	0/11	11/11

Table 3. Snout-vent length (SVL), weight (WT) and head width (HW) of adult male *Anolis sagrei* (n = 33) and *A. carolinensis* (n = 31) used in predation trials. Values expressed as means and standard deviations.

<u>Species</u>	<u>SVL (mm)</u>	<u>WT (g)</u>	<u>HW (mm)</u>
<i>A. sagrei</i>	60.1 ± 2.4	6.26 ± 0.83	10.00 ± 0.42
<i>A. carolinensis</i>	61.7 ± 4.0	4.61 ± 1.03	9.84 ± 0.68

PHYSIOLOGICAL ETHOLOGY OF SOCIAL DOMINANCE

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Anolis carolinensis is the animal model of choice for most of the research conducted in the Laboratory of Physiological Ethology at the University of Tennessee. Here I provide an overview of several recent and current Anoli-centric projects.

1. Reciprocal Influences of Physiological Stress and Reproductive Behavior.

The manner in which the physiological stress response can influence reproduction in many taxa was reviewed by Greenberg and Wingfield, (1987), who felt that stress cannot be presumed to be invariably deleterious. Indeed, the physiological responses to environmental challenges to homeostasis can be a constitutitional part of a much more complex ensemble of traits--behavioral as well as physiological.

A particularly useful manifestation of the incorporation of the physiological stress response into a stereotyped behavioral system may be the mutual influences of the social environment and stress endocrinology in the social dominance relationships of Anolis carolinensis (Greenberg and Crews, 1983). Because the hormones involved in the physiological stress response also affect body color and have psychoactive properties, it appears that the body color changes seen in agonistic Anolis carolinensis, well known in the field and easily reproduced in the laboratory, can help us examine several hypotheses about stress physiology and other autonomic aspects of aggression and status. Interestingly, non-specific exploratory activity is also stress-sensitive in A. carolinensis (Greenberg, 1985).

A. carolinensis may be unique among reptiles in that its dermal chromatophores are known to be free of sympathetic innervation (Kleinholz, 1938). Thus, body color is under the exclusive influence of circulating hormones: epinephrine (E), norepinephrine (NE) and melanotropin (melanocyte-stimulating hormone, MSH) MSH or relatively low levels of E will cause darkening of melanophores, while NE or high levels of E will cause its lightening. The hormone associated with a chronic stress response, the glucocorticoid corticosterone (CS), does not usually affect color directly but can alter the rate of synthesis of E from NE by facilitating a key enzyme in the synthetic pathway. Further, because one site on the body (the "eye spot") is specifically devoid of hormone receptors that might balance or mask the effect of E, we possess a specific in situ "bioassay" of adrenal "medullary" (chromaffin cell) activation.

In the laboratory as in the field, aggressive interactions of males cause rapid shifts in color, with losers frequently appearing brown at the conclusion of a fight. If formerly isolated individuals are required to continue to cohabit a single vivarium after an aggressive encounter, changes indicative of social dominance are apparent and typical body color generally shifts: those that had become socially dominant developed a slightly lighter (more green) color, while subordinates generally become darker (more brown).

These associations of body color and social status with the hormones of the physiological stress response, suggest that subordinates might be chronically stressed. To test this, the circulating levels of the corticosterone were determined for dominants and subordinates by radioimmunoassay. The data indicate that CS, which is classically associated with chronic stress, was significantly elevated in subordinates (Greenberg, Chen, and Crews, 1984).

Androgens are generally regarded as crucial to the agonistic behavior that structures social status. Recently, however, the stress hormones of the pituitary-adrenal axis have been implicated in its control (reviewed by Leshner, 1978). To examine the possible interactions of these two endocrine systems in dominance phenomena, pairs were constituted in which one or both animals were castrated. Although aggressive, castrates become subordinate to intact, but do not exhibit darker body color (Greenberg, Chen, and Crews, 1984). If darkening is in fact associated with chronic stress we would not expect elevated blood CS in castrated subordinates, and indeed, radioimmunoassay indicates that this is the case.

These data indicate that stress endocrinology is deeply involved in the aggressive and status relationships seen in A. carolinensis, that reproductive status can alter the stress response, and that body color may prove to be a valuable in vivo bioassay of these physiological aspects of their social behavior. In a complementary fashion, the androgen reduction that is associated with reduced status (Greenberg and Crews, 1988) may function, at least in part, to ameliorate the deleterious effects of chronic stress. The elevation of MSH, a hormone associated with restorative actions, may contribute, along with such a "protective" action of reduced androgen, to the future availability of dominant males, recruited from the ranks of healthy subordinates. In this regard, a hypothesis I am concerned with, is that as animals gradually shift from the acute (agonistic) phase in the etiology of subordination to the chronic (stable) phase during which a dominance hierarchy is manifested, the conversion of a key prohormone, pro-opiomelanocortin (POMC), is shifted from one end-product, ACTH, to another, MSH.

2. Functions of the Basal Forebrain.

The reptilian basal forebrain, with its characteristic level of representation of vertebrate neural structures, may provide insight into higher neural influences on behavior and its dysfunctions in other taxa, with all the attendant implications for the evolution of behavior.

Anolis carolinensis has been useful for the study of the role of higher neural structures in behavior. In these early studies, the highly stereotyped, species-typical aggressive displays provided robust data to illuminate striatal function in the proper expression of the species-typical challenge display response to conspecific males (Greenberg, MacLean, and Ferguson, 1979). These studies showed a specific effect on aggression without an impairment of general arousal (feeding and non-specific activity) or of displays that were under less specific stimulus-control than challenge, such as courtship (Greenberg, Scott, and Crews, 1984). The behavioral profile of lizards showing such an inability to recognize appropriate stimulus input is sometimes characterized as "social agnosia" (Greenberg, 1977)

More recent studies utilizing analyses of neurocytological structure and chemistry to explore neural correspondences with other taxa were conducted with Robert Switzer and Enrique Font. We found, for example, indications that the ventral portion of the striatum could, in part, be homologized to mammalian caudate-putamen on the basis of their similar distribution of acetylcholinesterase and catecholamine activity (Greenberg, Font, and Switzer, 1986). This hypothesis is further supported by the projection indicated by terminal degeneration seen after treatment with a dopaminergic neurotoxin: the resulting cell damage is seen to largely overlap the histofluorescent, cholinesterase-sensitive areas. These areas probably correspond to the terminus of the mesostriatal pathway in mammals, the caudate and putamen.

In conjunction with this and related work, the atlas of the anoline forebrain (Greenberg, 1984) is being extended to the cervical cord, albeit on A. equestris instead of the much smaller A. carolinensis.

3. Central Dopamine.

Several effects recalling Parkinson's disease were observed in lizards following administration of a dopaminergic neurotoxin, MPTP. While the primary site of cell death is the pars compacta of the substantia nigra (SN), the adjacent ventral tegmental area and other sites are also often affected.

Following administration of MPTP to Anolis, the cupric silver method of de Olmos (et al. 1981) was used to detect neuronal degeneration and thereby construct maps of the sites of toxic damage. This procedure revealed cytopathological changes were noted at several loci ranging from the forebrain to the cervical cord. Degenerative changes in striatal terminals occur in areas that also show catecholamine histofluorescence and AChE reactivity (Greenberg, Font, and Switzer, 1986), thus supporting the putative homology of the reptilian striatal afferents and the mammalian mesostriatal pathway.

4. Neural Control of Dewlapping.

Another important dimension of the neural influences on social behavior was provided by Enrique Font's doctoral research into efferent control (Font, 1988). Font conducted detailed dissections and electromyographic analyses on the giant relative of the green anole, A. equestris, in order to determine the precise mechanism of dewlap extension: the ceratohyoid muscle generates the force that causes the second ceratobranchials to move forward. Font then determined the brainstem influences on that system by applying horseradish peroxidase (HRP) to the cut end of the nerve supplying that muscle.

Histological analyses of HRP-treated animals revealed responsive motoneurons localized primarily in a columnar nucleus in the caudal rhombencephalon ipsilateral to the nerve treated with HRP. This nucleus apparently corresponds to nucleus ambiguus. HRP-labeled neurons are also seen in another nucleus dorsal and medial to nucleus ambiguus (Font, Greenberg, and Switzer, 1986).

5. Birth and Early Behavior.

With honors student Laura Hake, the conditions of maintenance and appearance of eggs collected from field-fresh A. carolinensis were correlated with hatching success, sex, size, and behavior of neonates. Time of hatching provided evidence of hatching synchrony. Distinct prenatal movements and neonate behavior during and subsequent to emergence were documented by closed-circuit television. Most interesting were assertion ("signature") displays

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and challenge displays in an agonistic context. Exploratory and predatory behavior were observed within the first hour post-hatching. Perch-sites selected were significantly lower than those selected by adults. Observations of body color indicates that most neonates manifest adrenal epinephrine activity at birth, possibly related to mobilizing metabolic resources for the energetic demands of hatching and the attendant physiological stress.

6. Spontaneous Sociality and Dominance Relationships.

Science Alliance Summer Research Fellow, Rochell Webster, helped provide useful documentation of the possible presence, extent, and dynamics of sociality in the diurnal lizard, Anolis carolinensis, in naturalistic laboratory habitats (Webster and Greenberg, 1988). Our findings indicate that this species may not be strictly territorial.

Known territorial males were isolated in naturalistic laboratory habitats for 9 days and then allowed free movement between their home cage and two comparable adjacent habitats by means of an opening near the bottom of the opaque dividers that separated them. The opening was such that it constituted an effective visual barrier, allowing subjects to move freely between habitats but not see each other.

The average site fidelity was 52%. Movements to adjacent cages could not always be attributed to attempts to extend social dominance; in each triad of habitats, low site fidelity was associated with low social dominance scores, but many individuals dominant in their home tank would voluntarily associate with males in alien tanks where they apparently relinquished their dominance.

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ACKNOWLEDGMENTS

Recent work on the neural control of social behavior was made possible by a University of Tennessee Faculty Research Grant to Neil Greenberg and a Cole Neuroscience Foundation grant to Robert Switzer; behavioral endocrinology was supported largely by NSF grant BNS-8406028 to Neil Greenberg.

Most of the material presented here is freely adapted from Greenberg, N. et al. Animal Models in Biomedical Research, Volume I, edited by Avril D. (CRC Press), and from Font, Greenberg, and Switzer (1986), Greenberg and Crews (1988), Webster and Greenberg (1988), and Greenberg, Chen, and Vaughan, (1986).

"Concluding Remarks" for the 1989 Anolis Symposium

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Thirty years or so have elapsed since research on Anolis blossomed, with a burst of publications on Caribbean species (Underwood 1959, Underwood and Williams 1959) and Etheridge's (1961) dissertation on osteology of the genus. Shortly thereafter, Collette (1961), Ruibal (1961), and Rand (1964)--all students of Ernest Williams--published their ecological work, and anoles have been prominent in the literature on evolution and ecology throughout the ensuing decades. Hutchinson's famous "Concluding Remarks" (1957) were published just over 30 years ago as well, and I certainly hope the comments that follow--slightly revised from my oral presentation--will be as frequently cited!

No doubt some participants in this symposium wonder why, having never studied these lizards in any direct way, I am in the role of commentator. Perhaps others correctly suspect a sort of reverse nepotism, involving one of the impetuous young conference organizers. From a research perspective, I see anoles as small creatures of the understory and forest floor, eaten by everything from ctenid spiders to frogs, birds, and especially snakes--and it really doesn't matter whether a limifrons disappearing down the gullet of an eyelash pit viper is assigned to Anolis or Norops! In any case, rather than summarize speakers in the symposium, I'll offer some parting shots from the point of view of an interested bystander.

The history of research on anoles is clearly going to provide fascinating material for those interested in the sociology of science. One obvious topic is the role of a central figure in shaping a field. G. Evelyn Hutchinson's impact on ecology was once depicted as a large-crowned, symmetrically spreading tree, with him as the trunk. Each limb was one of Hutchinson's graduate students, each branch one of theirs, and so on. I toyed with producing a similar tree for Ernest Williams and his academic descendants, and constrained the design such that only those working on anoles were included. Unfortunately, the result was something like a baobab because most of the students of Williams' students have not continued to work on those lizards! This business of a tree metaphor shouldn't be taken very far, but Ernest's role in our understanding of this wonderful radiation of lizards is profound and thought-provoking.

Beyond the central figure, the role of competing personalities, goals, and tactics deserves study. Hull (1988) concluded that such conflicts actually aid the progress of a field, if not always the emotional lives of its practitioners. Anole biologists seem thus far to have been spared the extreme acrimony that characterizes some other, more New York City-based branches of evolutionary biology. However, some reviews of grant applications and manuscripts I've seen, the complexion of certain interactions in the symposium, and even published remarks (Lazell 1972) suggest that there is rich material here as well. Maybe it's too early for an exhaustive review of the human side of anole research, but I hope someone does that soon and we all get to read it!

As Jonathan Losos mentioned, the application of phylogenetic approaches to problems that traditionally have been seen strictly as ecological processes seems to be a growth industry. On the one hand, some workers have reacted with rigid and undue skepticism, preferring to take it on faith that reversals and convergence for traits like body size are so common that parsimony algorithms are irrelevant. On the other hand, Gauthier et al. (1988) demonstrated significant effects of excluding fossil taxa in assessing the relationships of and character evolution among major tetrapod lineages, a sobering result for those of us studying non-fossilizable characters among extant taxa. At the very least, utilization of phylogenetic approaches will require attention to new developments in this dynamic field.

The early measurement of morphological variables in ecological studies on anoles was necessarily somewhat naive--we still don't know too much about structural constraints on what a lizard can swallow, but head width is probably more important than jaw length (Schoener and Gorman 1968, see DeMarco et al. 1985). Even today, much of what is called "morphology" by anole ecologists is pretty simplistic. Surely there are more differences among anoles than just four or five external measurements, and most things I can see on these lizards are not yet mentioned in ecomorphological studies (but see Williams 1983). It's not realistic to expect ecologists to become practicing morphologists (nor the reverse, which in any case is even rarer), but Jane Peterson and Kurt Schwenk can't do it all! This group of animals cries out for more attention from functional and evolutionary morphologists.

Beyond the problem of what to measure and describe, there is the matter of theory. Evolutionary biology has the exciting prospect in the next decade or so of merging population and macroevolutionary perspectives into a new, more robust synthesis (e.g., Wake and Larson 1987, Levinton 1988). I expect that because of Ernest Williams' exceptionally broad vision in its formative stages, and because, for all the gaps, we still will understand more kinds of topics for anoles than is true for most organisms, the study of these lizards will play a major role in that synthesis. Obvious questions for the future include has there been parallel phylogenesis of those island ecomorphs, and if so, why would one expect that pattern instead of diverse trajectories to similar end-points? Why does the ecomorph concept fail when applied to mainland anoles?

Several speakers portrayed the "island" anoles, as a group, as different from "mainland" congeners, and yet there is at least one important respect in which those on the two largest Caribbean islands might be substantially different from the smaller islands on which most work has been done: Hispaniola and Cuba have much richer snake faunas, and many of those snakes eat anoles (Henderson et al. 1988). Does existing knowledge predict any consequences for that difference among the island radiations?

With respect to the last point, emphasis seems to have been on demographic responses to predation on anoles (but see Williams 1983:Table 15.1), yet many other lizards have a variety of antipredator specializations (Greene 1988). Beyond hiding, leaping, and squeaking, don't anoles ever threaten or fight in the face of imminent death? Jonathan Losos leads his hockey league in aggressive fouls, so he might argue they're just the ultimate macho animals, but the situation remains to be analyzed. If anoles generally don't stress behavioral defenses against predators, why not?

We now know a lot about the neurobiology of intraspecific communication and aggression in anoles (e.g., Greenberg and Crews 1983, Thomas Jenssen's symposium talk). My casual observations while handling these lizards suggest that many displays are used in both social and antipredator contexts, thus providing rich possibilities for investigating common underlying processes of these seemingly separate motivational systems--a topic that is poorly understood for vertebrates in general (Archer 1988) and reptiles in particular (Greene 1988).

Finally, which anoles are going to make it well into the 21st century, and which ones are already threatened or extinct?

Williams (1983) discussed several large island forms that are rare or possibly extinct, and Pregill (1986) documented Holocene dwarfism in certain Caribbean anoles that might result from human-related factors. Carl Lieb's ongoing studies (summarized in the symposium) indicate several Mexican taxa are extremely localized or already gone, and several South American species are so poorly known that their ranges cannot even be estimated. Do endangered anoles warrant specific recovery programs, or will ecosystem-level efforts suffice to save a reasonable fraction of this radiation? How might anoles contribute to conservation biology, a field that suffers chronically from a need for fast answers to problems that require long-term study?

In fact, the theory of Pleistocene refugia that has inspired much controversy regarding management design was spawned in part by Vanzolini and Williams' (1970) work on geographic variation in Anolis chrysolepis. And obviously the population biologies of these lizards in diverse habitats stand as models for more poorly studied and unstudiable organisms, thanks to extensive field studies by Andrews, Guyer, Roughgarden, Schoener, Sexton, and others. Another opportunity lies in the implementation of priorities for management, an unhappy but inevitable prospect: given their relatively well-studied diversity and occupancy of a wide variety of habitats, anoles are well-suited for exploring the utility of Colwell's (in press) "principle of relative replaceability" (see also Greene and Losos 1988).

Several participants commented that the 1989 symposium on Anolis biology provided opportunities to reconsider old data, recharge intellectual batteries, and consider some new problems. Hopefully this gathering will renew enthusiasm among those already studying anoles, convince others to join in the fray, and lead to the confrontation of an even broader range of questions using these nimble, big-headed, and sometimes beautiful lizards.

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has sent in the following.

Since the Third Anolis Newsletter much time has passed. Therefore, it seems appropriate to selectively present some subsequent, but published data as well as unpublished research in progress. The following is a synopsis of some prior studies on Anolis.

Prior Studies. The vocalizations that a limited number of Anolis produce when captured or during aggressive social encounters was studied in A. grahami (Milton & Jenssen, 1979, *Copeia* 1979:481-489). They are capable of producing a variety of sounds within aggressive and life-threatening contexts; oscilloscope analysis indicated these sounds are produced by a vibratory structure. However, histological examination of the entire respiratory tract produced no likely agent. The "squeaks" made during male-male attacks are produced by the attacker, yet during playback experiments, subjects showed no indication of response, even though conditioning experiments showed that A. grahami can hear sounds of like frequency (Rothblum, et al., 1979, *Copeia* 1979:490-494). We concluded the sounds most likely function to startle predators (anti-predator device), and are preadapted, but still ineffective in a social communication role.

The Anolis brevirostris complex in Haiti was a large topic in the 3rd Anolis Newsletter. Webster and Burns had reported on three parapatric populations of unique allozyme profiles which have since been recognized as full species; Arnold named them A. websteri, A. caudalis, and A. brevirostris. A behavioral analysis was made of the complex to first see if there were display differences between the populations (Jenssen & Gladson, 1984, *J. Herpetol.* 18:217-230), and if so, whether females in and around the contact zone were selecting against non-conspecific males (unpubl. results, see below). Results of the display analysis showed that all three sibling species have a multiple display repertoire, and that there were distinct interspecific differences which could serve as a potential behavioral isolating mechanism.

[The following has never been published.] The next step was to test female choice. Within the contact zone between A. websteri and A. caudalis (2 km south of Montrouis), I selected a moderate-sized acacia tree (lacey, scant leaves) surrounded by a wide stretch of sand (lizard barrier) as an event enclosure. On the tree were placed a group of lizards (consisting of one male and three females) from each of the two

sibling species. The males were kept under constant surveillance, and a record made of the females with whom the males engaged in courtship attempts and copulations. The trial lasted three days, and a total of five trials were run, each time with new individuals. The results showed that male A. websteri and A. caudalis show no significant discrimination between sibling species females; they courted females of both species with similar frequency. Furthermore, of 24 observed copulations (11 by male A. caudalis and 13 by A. websteri), all were with female A. websteri. Though frequently courted by males, no female A. caudalis was seen to copulate. Without the latter observations, I could not support or reject the hypothesis of female selection against conspecific males. The data did show that males of both species and websteri females were "non-choosy". However, the question remained open whether or not caudalis females may be acting as an agent for reproductive isolation.

Floyd & Jenssen (1983, *Copeia* 1983:319-331) used A. opalinus on Jamaica to test for food partitioning among different size classes of lizards, and to test whether insular species appear to be food limited, as might especially be true during the dry season. The results showed no partitioning. They also found no change in food volume among wet and dry months, though lizards ate fewer and larger items in the wet season and more but smaller items in the dry season.

Growth rates of the above A. opalinus population were also analyzed (Jenssen & Andrews, 1984, *J. Herpetol.* 18:338-341). Extensive recapture data across a 12-month period indicated reduced growth during the dry season. Given the constant ingested food volume between wet and dry seasons, we concluded that reduced available water to the the lizards' diets may be a primary factor for the lower growth rates, a conclusion also reached by Stamps & Tanaka (1981, *Ecology* 62:33-40) for Anolis aeneus

Competitive interference between Anolis cooki and Anolis cristatellus of Puerto Rico was verified by several studies (Ortiz & Jenssen, 1982, *Z. Tierpsychol.* 60:227-238; Jenssen, et al., 1984, *Copeia* 1984:853-862). Under lab-staged encounters, A. Cooki and A. cristatellus males engaged in as intense interspecific combat as during intraspecific matches. In every case during these symmetrical encounters (males matched for size), A. cristatellus dominated A. cooki. Because A. cooki and A. cristatellus may have been mistaking each other as conspecifics, additional experiments were run where both species were pitted against look-alike congeners (Anolis gundlachi and Anolis monensis); there was almost no

interspecific response, thus eliminating the possibility that the cooki-cristatellus aggression was due to mis-identification.

In the field, male A. cristatellus intruders were released into the territories of similar sized A. cooki. Intense aggression ensued, with resident A. cooki able to repel only 40% of the intruding A. cristatellus. This is a very low figure when considering the advantage a resident has over an intruder, and when most A. cristatellus in the population were heavier and longer than A. cooki. We also field-tested A. cooki tendency toward interspecific aggression by releasing a sympatric congener, Anolis poncensis, into cooki territories; no response resulted from resident A. cooki. Thus in lab and field, A. cooki recognized A. cristatellus as a competitor, but were over-matched.

Field data showed that A. cooki were displaced in the habitat where sympatric with A. cristatellus by being shifted from large clumps of vegetation (e.g., trees and large bushes) to smaller structured vegetation (e.g., small bushes, dead plants, and fence posts). Yet untested is the distinct possibility that A. cooki fitness is lowered in the sparse, more exposed microhabitat (e.g., lower rate of egg survival, lower food availability, higher mortality rates). Contrary to expectations, hundreds of cloacal and site temperatures, ordered by hour of day from both allopatric and sympatric areas, indicated no significant difference in cooki-cristatellus temperature profiles. Thus local populations of A. cristatellus appeared just as able to tolerate the hot, arid habitat of the restricted area of A. cooki distribution as A. cooki. Therefore, there is now good evidence for Williams' belief that A. cooki is an endangered species due to congeneric competition.

Jenssen et al. (1988, J. Herpetol. 22:266-274) looked at spacial distributions of species and sex classes for A. cybotes and A. caudalis across seasons on a sympatric study area in Haiti. As predicted, there was a vertical stratification according to species and sex, with males higher than females within species. The highest perch sites were taken by male A. caudalis ($\bar{x} = 3$ m), and the lowest by female A. cybotes ($\bar{x} = 1$ m). Perch diameter reflected microhabitat preference, with A. Caudalis and male A. cybotes frequenting large trees, while female A. cybotes were randomly using available vegetation at low elevations. These trends did not shift with season (June vs. Nov.). When degree of structural habitat separation was quantitatively compared among classes, overlap coefficients were very high (.90-.99), and a discriminant analysis produced few significant differences. Habitat partitioning was more evident at a qualitative than quantitative level. Other data on class sizes and nearest neighbor distances indicated stable population sizes and sex ratios for A. caudalis across seasons. However, there were marked seasonal shifts in male A.

cybotes; in June, during the breeding season, we found fewer males and at greater separation distances than in November, a possible result of strong territorial interactions.

Studies in Progress. In my lab, Kristi Decourcy, Lauren Wemmer, and Pat Feely are assisting with a description of the kinds and use of male and female Anolis carolinensis social signals. Male-male and Male-female contexts have been run, and the female-female context is in the planning stage.

Methods - male-male. For the male-male portion, males from northern Florida were housed separately (each with a female) in large cages (1.3 x .6 x .6 m) fitted with simulated habitat. For each trial, a pair of males were transferred to a 2.6 x .6 x .6 observation chamber of like habitat, with a male placed on each side of a middle divider. From a blind 1.5 m away, each male was watched during irregularly spaced catch trials until both were showing spontaneous, non-directed displays (1-3 days). These displays were also videotaped (non-directed displaying was a criterion for territorial behavior). When both subjects appeared territorial (acting like residents), the divider was lifted and the ensuing behavior videotaped for 60 min. Two cameras were used, one for each subject, to provide a good close-up of each male. The two signals were juxtapositioned onto a common tape using a split-screen generator. Also a time generator provided a record of elapsed time in .01 s intervals. Distance between subjects was dictated onto the audio portion of the tape. Ten trials were run using a subject once (20 males). Each pair was matched within a mm SVL of each other (symmetrical contests). A second experiment was run with the identical protocol in which paired subjects were much different in size (2-7 mm SVL)(asymmetrical contests). We hoped to: (1) quantitatively describe the headbob patterns, (2) their frequency of use under different conditions (e.g. distance between males), (3) find predictable and possibly hierarchical use of displays and their modifiers (e.g., color changes, erected crest, dewlap use, sagittal flattening, etc.), (4) find predictors for eventual winners, and (5) look for deviations in sequence of signal use between symmetrical and asymmetrical encounters involving two "resident" males.

Methods - male-female. The male-female data were gathered upon a female introduction into a male's cage; four treatment effects were used : 1) 1 h separation, with familiar female returned to male; (2) 24 h separation, with familiar female returned; 3) 1 h separation, with an unfamiliar female returned; and 4) 24 h separation, with an unfamiliar female returned.

Taking two pairs at a time, the coupled male-female pairs housed together in the male-male protocol were moved to each side of the event chamber described above (each side is the same size as their home cage). After three days the female of each pair was removed then replaced after a 1-h absence, using a

remote-controlled release box. The male and female responses to one another were videotaped for 30 min with the 2-camera system outlined above. The next treatment called for the removal of the resident female for 24 h and then returning her to her familiar male, with the ensuing behaviors of each lizard videotaped for 30 min. In the next treatment the females of the two cages were removed and switched between cages to produce unfamiliar females for the two males. The unfamiliar females were introduced after the resident females had been absent for 1 h. The last treatment was to remove the unfamiliar females, hold them for 24 h, and place them back with their respective, unfamiliar males. We hoped to show that the intensity of courtship would increase with longer periods of abstinence and increase with unfamiliar females (evidence for individual recognition). These 4 treatments were applied to 10 pairs of A. carolinensis.

Results - male-male. Three distinct headbob patterns, labelled A, B, and C, have been identified for a north Florida population (Fig. 1). These three patterns can be performed with or without dewlap extensions. In other studied anoles, there is a single bob pattern which is performed during non-directed displays (i.e. displayer does not necessarily see another conspecific, but is simply advertising its presence); this is the "assertion" context and the display pattern appearing in this context by definition is the species' "signature" display. When male A. carolinensis were videotaped during the period before the partition was raised (male alone - assertion context), they did not perform a single pattern (signature display) as other species have done, but they produced all three bob patterns.

When the partition was raised, males were at a separation distance of 2.0 - 2.5 m apart (Fig. 2). As they approached each other, three separation distances (phases I-III) were defined which indicated increasing risk of physical attack (Fig. 2). The kinds and frequencies of behaviors which occurred within and between these phases were examined. This analysis was made for both 10 symmetrical and 10 asymmetrical encounters.

All three display patterns were performed with similar frequency in the assertion context (male-alone)(Fig.3). The dewlap was extended in almost all of these 108 displays. After the partition was raised, C displays predominated; again the dewlap was extended with almost all displays. As the males approached one another, the type of displays shifted toward A and B patterns, but more dramatically, dewlap extension sharply dropped off with decreasing distance (Fig. 3). Presumably, the dewlap is vulnerable to injury. If displays were performed in volleys, it was most likely that subsequent displays of a volley would be pattern C (Fig. 4).

Other aggressive behaviors were performed in a somewhat progressive manner. Each male was watched for the first appearance of 8 kinds of aggressive signals listed in Table 1. Each behavior was ranked as to the first to appear to the last to appear for the 20 males used in the experiments. After averaging the rank position of each behavior, a loose hierarchy resulted (Table 1) in which antagonists usually advanced toward each other, started changing their color, or gave a headbob display upon initial exposure to each other.

Comparisons of symmetrical and asymmetrical encounters provided few differences. It was hypothesized that asymmetrical encounters would be truncated, because the smaller lizard would assess that it could not win in a physical contest, and so would withdraw during the ritualized portion of the match. Such mismatches might also highlight cues during ritualized aggression by which the ultimate winner could be predicted.

We found little to support these expectations.

Similar durations were spent in the three distance categories, regardless of symmetrical or asymmetrical contests (Fig. 5). As the animals got closer, they spent more time displaying, but there were no significant differences between ultimate winners and losers or between matched and mismatched antagonists (Fig. 6). In both symmetrical and asymmetrical encounters, the first male to invade the other's territory tended to eventually lose the match (Table 2). Finally, contrary to prediction, small males in asymmetrical matches did not pull out early, but actually showed a greater inclination to escalate to physical fighting (Table 3). In fact, the smaller male tended to be the initial aggressor by being the first to pass into the other male's territory (Table 4). The only variable which predicted ultimate winner of in 8 of 9 asymmetrical matches (there was one 60 min fight without dominance - a draw) was size; the larger male dominated the smaller opponent. Dominance was recognized by the male who chased and supplanted, while the subordinate attempted to escape and/or hide.

These data are to be updated and modified.

Results - male-female. Data analysis for this study are still too preliminary for tabulation. However, current trends are as follows. During a combined 20 h of videotaping the 4-30 min experiments for 10 pairs of males and females, 771 male and 249 female displays were recorded. Over 90% of the male displays were pattern C. Female display patterns appear to be much more variable than those of males, and to date there

is too much variability to reveal a repertoire of discrete patterns. Perhaps when the female-female encounters are run a consistency will emerge.

There was a wide variance in courtship behavior between males. One male performed 221 displays in his 4-30 min trials, while another male only displayed 8 times. This variance has so far obscured any indication that males may be courting strange females more intensely than familiar or "resident" females. The same is true of the effect of increasing separation periods.

The experiments were conducted with freshly captured males and females during April-June when both sexes should be in full reproductive condition. However, during these various 30 min trials, no copulations were observed. Furthermore, the interactive sequences between males and females were so variable (females which hid to females which appeared to "court" uninterested males), there may be little potential for portraying "typical" courtship behavior sequences and signal exchanges.

Figure Legends

Figure 1. Mean headbob patterns of Anolis carolinensis from northern Florida; black contours show amplitude-motion for consistently appearing bobs and grey contours indicate optional bobs and dewlap extension.

Figure 2. Observation chamber, showing central partition, positioning of habitat, and three categories of separation distance (Phases I-III, where I = > 100 cm, II = 99-20 cm, and III = < 20 cm).

Figure 3. Proportion of the 3 display patterns (A-C) performed within the 3 separation distances (Phases I-III) of the aggressive context and during the assertion context (male alone). Sample sizes appear over bars.

Figure 4. Proportion of the 3 display patterns (A-C) given by their position within a potential volley of displays. Sample sizes appear over bars.

Figure 5. Mean proportion of time males spent within the 3 categories of separation distance (Phases I-III) during 60 min aggressive encounters. S identifies symmetrical matches and A the asymmetrical matches. Vertical lines indicate 95% confidence intervals.

Figure 6. Mean percent of time spent displaying by males within the 3 categories of separation distance (Phases I-III) during 60 min aggressive encounters, and during the assertion context (Phase IV). S identifies the ultimate winner and loser of symmetrical matches and A those in asymmetrical matches.

Table 1.

Ranked Aggressive Behaviors

Behaviors	Average Rank	Overall Rank
Advance	3.1	1
Color Change	3.2	2
Head Bob Display	3.3	3
Lateral Compression	3.9	4
Lateral Presentation	4.6	5
Raised Nuchal Crest	4.8	6
Gular Expansion	6.1	7
Eye Spot	7.1	8

Table 2.

Fate of the initial aggressor during 10 symmetrical and 10 asymmetrical encounters.

Fate	Encounters	
	Symmetrical*	Asymmetrical**
Winner	3	3
Loser	6	6
No Decision	1	1

* 0-1 mm SVL differential

** 2-7 mm SVL differential

Table 3.

Percent occurrence of jaw sparring and jaw locking by paired males during 10 symmetrical and 10 asymmetrical encounters.

	Encounters	
	Symmetrical*	Asymmetrical**
Jaw Sparring	60	80
Jaw Locking	30	50

* 0-1 mm SVL differential

** 2-7 mm SVL differential

Table 4.

Relative size of initial aggressor and eventual winner of encounters between pairs of asymmetrically matched males

Relative Size	Aggressor	Winner
Larger	2 (2)	8
Smaller	7 (1)	1

(n) number who also were winners

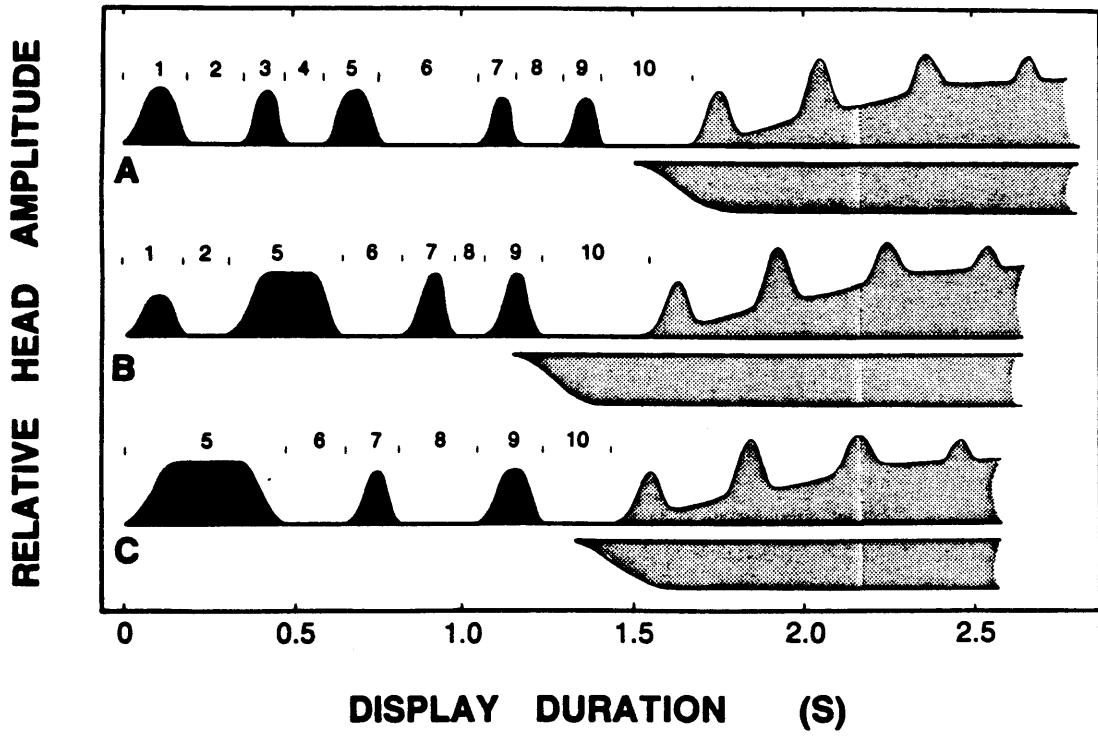


Fig. 1

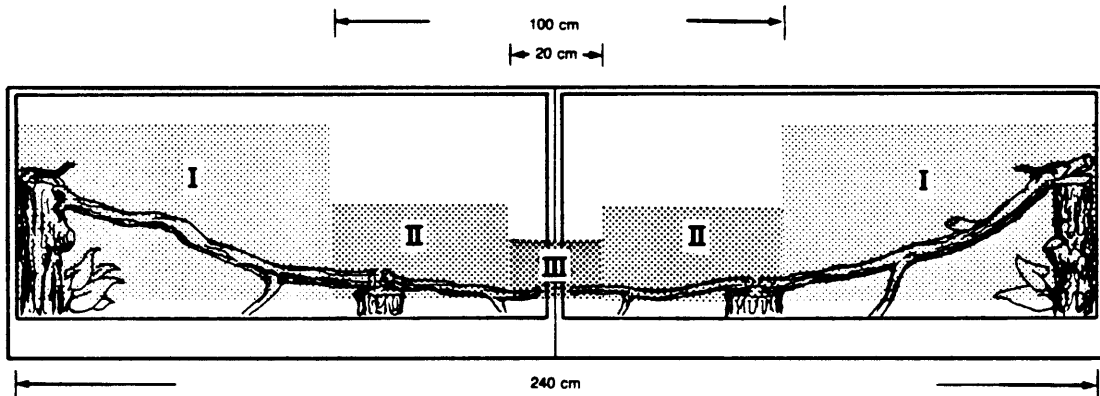


Fig. 2

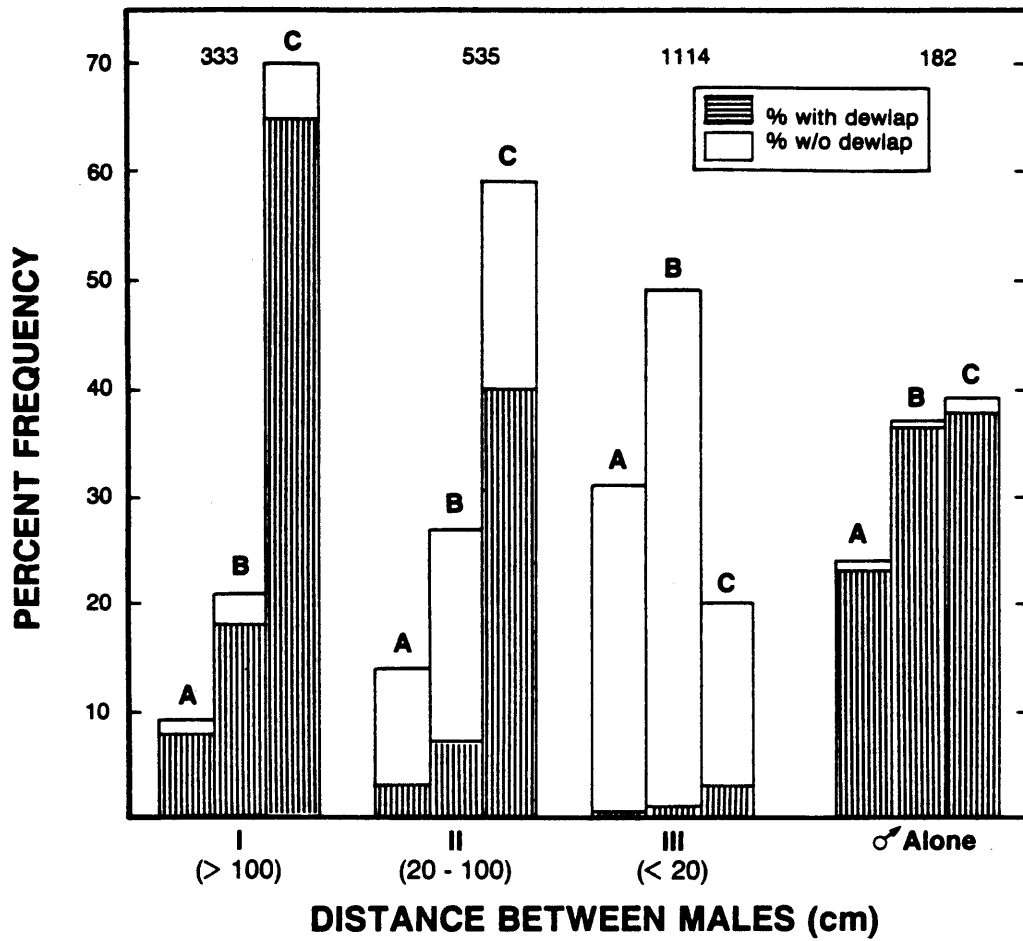


Fig. 3

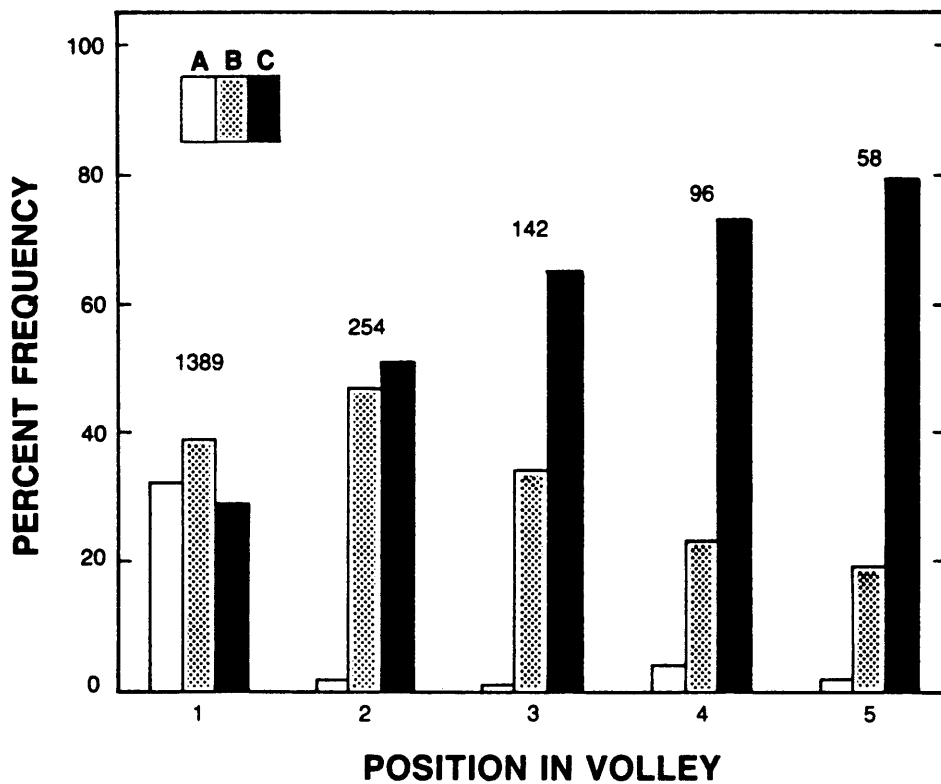


Fig. 4

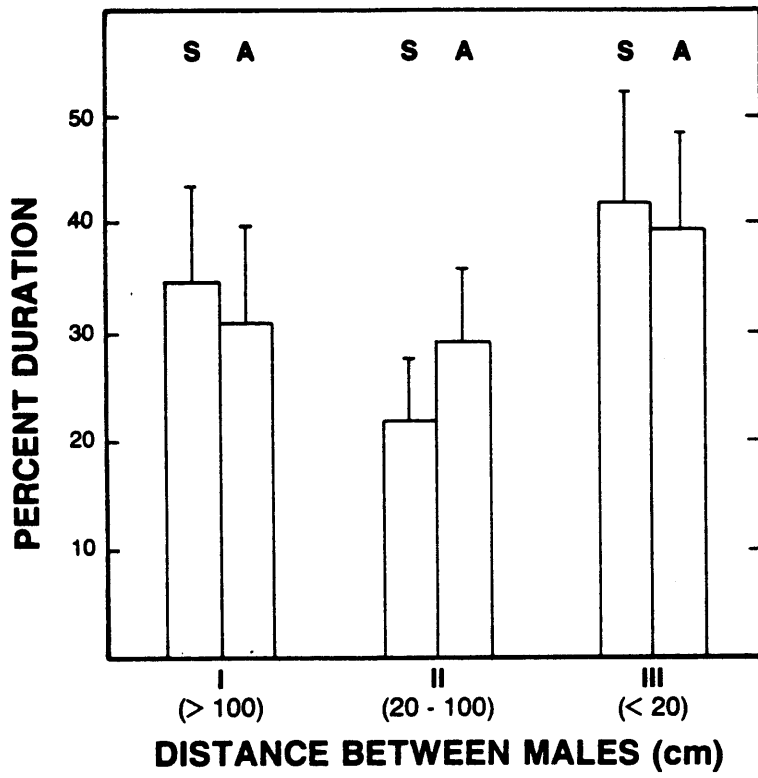


Fig. 5

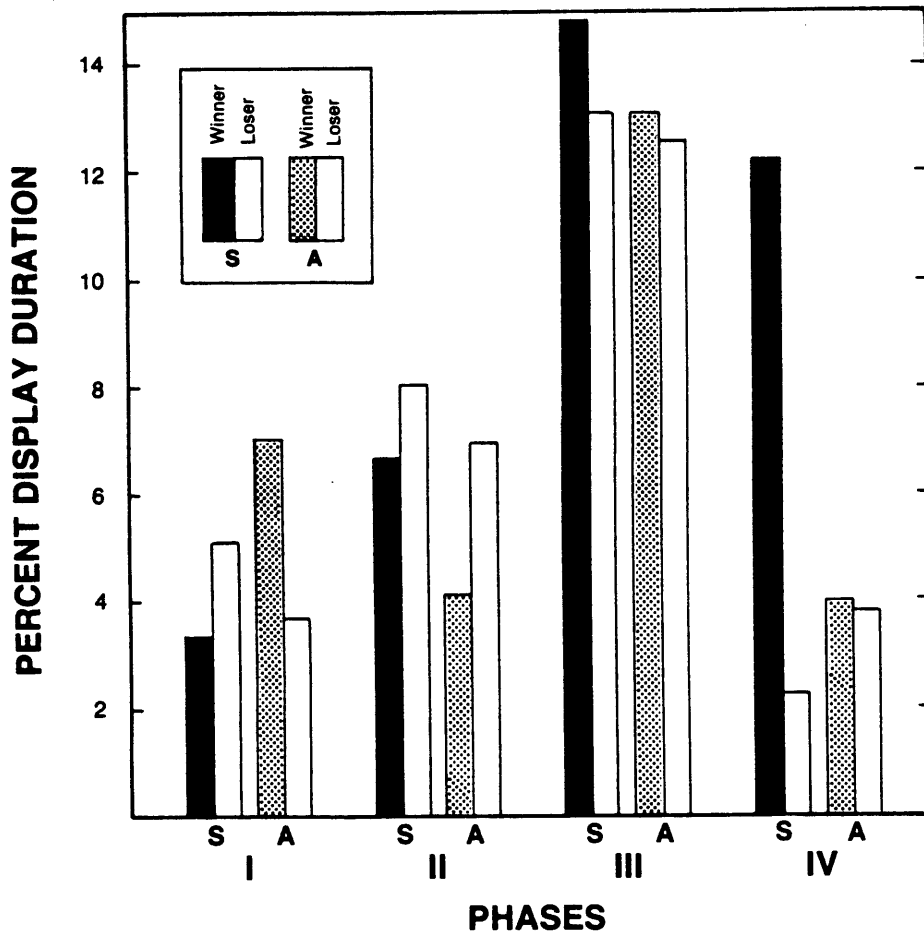


Fig. 6

AN ANALYSIS OF THE HEADBOBBING DISPLAYS OF *ANOLIS CAROLINENSIS*

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The analysis of a communication system relies on understanding the signals used, particularly the criteria an organism uses to discriminate among these signals (Green and Marler, 1979). The visual signals of *Anolis* have proven useful in investigating communication systems. Reasons for this include the feasibility of analyzing visual displays rather than those using other sensory modalities, and the relative stereotypy of many of the displays. A consequence of the apparent ease of analyzing visual displays is that a rigorous methodology to classify *Anolis* displays has only recently been developed (Font and Kramer, in press). This method best serves to guide the researcher in cases where several classification schemes are plausible. Subjective classifications introduce researchers' biases and deal ineffectively with species possessing variable display patterns.

Font and Kramer (in press) suggest the use of cluster analysis to initially classify *Anolis* displays followed by a discriminant analysis to verify that resulting clusters are composed of similar displays and that there are large differences between displays from different clusters. Cluster analysis groups observations (in this case, displays) based on the degree of their similarity using the variables entered. While no guarantee exists that cluster, or any other statistical analysis, will group displays using the same criteria as lizards, this could later be determined experimentally (Jenssen, 1970; Sigmund, 1978).

Here we apply techniques suggested by Font and Kramer (in press), developed to classify *Anolis equestris* displays, to classify the displays of *A. carolinensis*. We find that the technique works poorly for analyzing this lizard's display patterns, and discuss a possible reason for the difference.

Headbobbing displays of *Anolis carolinensis* are readily elicited in the laboratory by introducing conspecifics. We used Super-8 films at 18 frames/s of captive animals (24 males, 5 females) from a Louisiana population and filmed by N. Greenberg, videotapes from a single male from Tennessee, and filmed displays of a single male from Florida (gray-throated morph). A total of 97 displays (all but 9 from males) were used in the analysis from a variety of contexts (but, to the best of our knowledge, excluding courtship sequences). Displays were graphed by projecting the film (frame by frame) or videotape (every fourth frame) on graph paper, as described by Jenssen (1978). For some individuals we had only one or two displays, for others many were

available. The number of displays per individual, however, should not adversely affect the clustering technique. If an individual's displays are similar, the clustering technique should reflect this by grouping these displays.

Headbobbing displays consist of vertical up-and-down movements of the forepart of the body (i.e., headbobs), with or without concurrent dewlap extension. Variables used by Font and Kramer (in press) were measured from these displays (Table 1), with the exception that bob duration could fall into one of three categories, rather than two. This was because bob duration in this species appears to follow a normal distribution after log transforming the data, rather than the bimodal distribution observed in *A. equestris*. A small bob (< 0.11 s) was one having a duration at least one standard deviation below the mean, and a large one (> 0.33 s), at least one standard deviation above. Thus, there are nine possible sequences of two bobs; large-large, large-medium, large-small, etc. We did not include the duration of dewlap extension because preliminary results suggested that this variable was more closely associated with the number of previous displays performed in a bout than with the form of a particular display (but see Crews, 1975). Dewlaps often remained extended between consecutive displays.

Table 1. Variables used for the cluster analysis of headbobbing displays of *Anolis carolinensis*.

	Variable	Definition
1)	TOTDUR	Total number of frames of the headbobbing display, standardized to 18 frames/s.
2)	NUMBOBS	Number of headbobs in display.
3-12)	LL - SS	Number of large (> 0.33 s)-large, large-medium (0.11 - 0.33 s), large-small (< 0.11 s), medium-large, etc. sequential pairs of headbobs in a display.
13-28)	BOI-0 - BOI-14	Bob onset intervals (see text for details).

Since temporal patterning of headbobs is likely used by animals to discriminate among display types, we wanted to include variables that reflected the cadence of a display. However, we felt that a bob-by-bob comparison was not warranted because two otherwise identical displays might be categorized separately if one was missing a bob at the beginning of a display. This would result in overestimating display repertoire size. To construct variables largely independent of bob order while preserving features of the display's cadence, we developed bob onset intervals

(BOI's)(Font and Kramer, in press). BOI's were constructed by first calculating the time elapsed between the onsets of all combinations of bobs in a display. This distribution was then partitioned into categories of 0.1 to 1.5 s duration in 0.1 s increments. BOI-0 refers to the number of bob onset intervals of 0 to 0.1 s in a display, BOI-1 to the number of bob onset intervals of 0.1 to 0.2 s, and so forth.

We used 11 different algorithms for forming clusters available in Statistical Analysis System (SAS Institute, 1982; Proc Cluster). Unlike results of Font and Kramer (in press) for *Anolis equestris*, these displays gave little evidence of separation into distinct and different clusters. In fact, the groupings given by the cluster analyses (these results are not included) contradicted our expectation that displays would be categorized by what appeared to us as the most obvious feature; the pattern of the first few bobs. Prior to performing the cluster analysis, we had tentatively assigned 76 of the displays to one of two forms. One started with a large bob, followed by a medium or small and then followed by another large or medium bob (Fig. 1, A, C, and Table 2). The second form was similar but an additional small or medium bob was inserted at the beginning of the display (Fig. 1, B, D, and Table 2). The remaining displays were variable, some lacked large bobs, others appeared similar to the second form, but with an additional bob inserted near the beginning of the display.

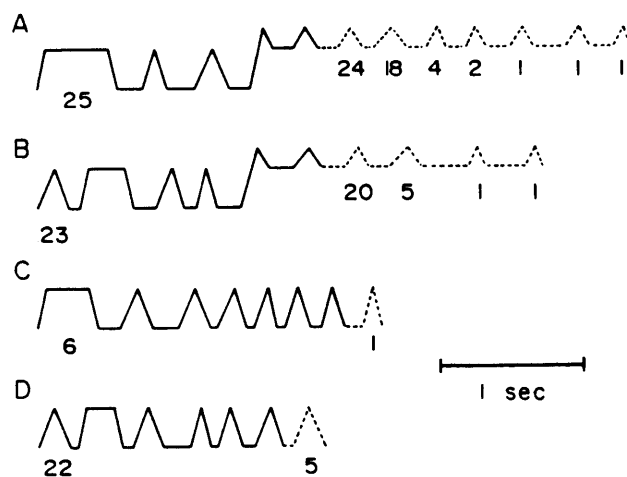


Figure 1. Composite displays of *Anolis carolinensis*. A. First common display form starting with a bob of long duration (not included are displays of the Florida gray-throated male). B. The second common form starting with a small or medium bob. C. Form A given by the Florida gray-throated male. D. Form B given by the Florida gray-throated male. The cartoons are based on the mean values from several displays (n = the first numeral under the display). The numeral below the dotted portion gives the number of displays with these additional bobs. Displays of the gray-throated male were performed slightly more quickly than those of other subjects and, for most bobs, from the same starting posture. Other subjects often elevated themselves during the 4th, 5th or 6th bob.

Table 2. Standard deviation of the duration (s) of each bob and between bob interval in the composite *Anolis carolinensis* headbobbing displays in Fig. 1. The mean coefficients of variation for the display units of each display are: A, 34.04; B, 35.88; C, 48.10; D, 53.77.

Unit	A	B	C	D
Bob 1	0.1395	0.1122	0.1361	0.1056
Interval 1	0.1272	0.0990	0.1092	0.1336
Bob 2	0.0740	0.1082	0.0907	0.1411
Interval 2	0.0806	0.1158	0.1859	0.1147
Bob 3	0.0934	0.1133	0.0836	0.1336
Interval 3	0.0806	0.0875	0.0836	0.1220
Bob 4	0.0667	0.0546	0.0930	0.0718
Interval 4	0.0914	0.0765	0.1346	0.1008
Bob 5	0.0584	0.0870	0.0703	0.0835
Interval 5	0.0973	0.1022	0.1721	0.1066
Bob 6	0.0862	0.1273	0.0836	0.0949
Interval 6	0.1277	0.1190	0.0907	0.1217
Bob 7	0.2374	0.1739	0.0454	0.1267
Interval 7	0.1398	0.1859		
Bob 8	0.0642	0.1925		
Interval 8	0.2357			
Bob 9	0.0786			

After carefully examining the results of the cluster analyses, we realized that by removing the effect of the exact order of bobs there was little difference among displays. The clustering algorithms, since they were not provided with variables by which bob-by-bob comparisons could be made, grouped displays by other criteria. These largely reflected display duration differences, since long displays typically have many bobs and contain many pairs of small-small bob transitions. As in Font and Kramer (in press), displays were not grouped by individual. This does not imply that displays could not be used for individual discrimination, only that an individual's displays are variable, some resembling displays of others.

Our results are consistent with those of Sigmund (1978) (see his Fig. 2), who labels these displays as species typical ("assertive-aggressive headbobbing", p. 29) and describes no other

headbobbing displays used in male-male aggressive encounters. Crews (1975) further divides this category into assertion and challenge displays based on context, but does not provide other criteria to distinguish them. We examined our output from the cluster analysis to determine if grouped displays occurred in the same context (solitary males, male to male, male to female, female to male, male to male *Anolis sagrei*). All but the smallest groups contained displays from all contexts.

We conclude that the display repertoire of *Anolis carolinensis* appears limited when compared to that of *A. equestris*. While our clustering procedure was unable to satisfactorily group displays, the analysis was nevertheless instructive. Clustering algorithms are best suited to multimodal distributions, not continuous ones. Since we agree with Sigmund (1978) that this species has only one type of assertive-aggressive display, used in both assertive and challenge contexts, we suggest that the variation observed should best be viewed as continuous rather than coming from a multimodal distribution. Thus, it is not surprising that the clustering algorithms performed poorly. We attribute the observed variation to both within-fight factors, such as changes in intensity or fatigue, and individual variation.

Acknowledgements. We thank N. Greenberg for use of the films, T.A. Jenssen for graphing some of the displays, and A.C. Echternacht and M.E. Gompper for critically reading the manuscript.

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My dissertation research focuses on the evolution of ecomorphs in the Greater Antilles. As most readers of this newsletter are probably aware, the work of Williams, Rand, Schoener, and others established that a series of ecomorphs (species that are morphologically, ecologically, and behaviorally similar) exists on each of the Greater Antillean islands. For example, the long-legged "trunk-ground" anoles from Jamaica, Puerto Rico, Hispaniola, and Cuba are morphologically very similar, occupy the same microhabitat, and behave similarly. Further, members of the same ecomorph category (there are five basic ecomorphs, defined by the microhabitat occupied: "trunk," "trunk-ground," "trunk-crown," "crown-giant," "twig," and "grass-bush") are similar due to convergence rather than recent ancestry. Jamaica and Puerto Rico have experienced essentially independent evolutionary radiations; Hispaniola and Cuba have been colonized several times, but much of the radiation has been *in situ*. Ecological theory predicts that communities in similar environments should evolve the same structure; however, they do not predict that the community convergence should extend to the evolution of a series of convergent ecologies and morphologies. Greater Antillean *Anolis* are the only well-documented example of such a situation.

I chose to work on this case for two reasons. First, the repeated convergence, producing species with similar morphology and behavior in similar environments, strongly suggests that the evolution has been adaptive. I doubt that anyone would question this case as an example of adaptive radiation. Consequently, these anoles present an unparalleled opportunity to develop a methodology to investigate and attempt to understand the patterns and processes involved in adaptive radiation. Paradoxically, the *Anolis* story is not well-enough known and appreciated outside of the circle of anologists. This results in part because, although copious amounts of data have been collected on the ecology, morphology, behavior of these animals, no one, with the recent exception of Greg Mayer's dissertation, has quantitatively demonstrated that the ecomorphs are real phenomena.

The term "ecomorph" was coined in 1972 (*Evolutionary Biology* 6: 47-89) by Ernest Williams (not Karr and James in Cody and Diamond, Eds., *Ecology and Evolution of Communities*, Belknap Press, 1975). Since that time, ecomorphological studies have mushroomed, dealing with all kinds of animals. Some studies simply document morphological differences among members of a clade or community and infer ecological differences; others attempt to correlate morphology and ecology. However, ecomorphological studies are implicitly about adaptation. Two further approaches can be taken to more convincingly argue that adaptive evolution has occurred:

1. What is the link between morphology and ecology? Presumably, morphological differences among species result in functional differences; in turn, differences in the animals' capabilities affect what they actually do in nature and where they do it. In other words, performance capability is the link between morphology, on one hand, and behavior and ecology on the other. This can be studied at two levels. First, I have measured performance capability at three ecologically relevant tasks: maximum sprinting speed, jumping distance, and clinging ability on a smooth surface. I have

attempted to correlate morphology, performance ability, and ecology and behavior. A more detailed biomechanical analysis is necessary to understand how and why morphological differences result in different capabilities.

2. Studies of adaptation are about evolutionary history and make specific historical predictions. In this case, if particular morphologies have evolved for new "niches," then one would predict that morphology and ecology have evolved simultaneously. If morphology evolved prior to ecology, then it did not evolve as an adaptation (in the narrow, evolutionary sense, following Williams (Adaptation and Natural Selection, Princeton Univ. Press, 1966) and Gould and Vrba (Paleobiology 8: 4-15, 1982) for that environment. Alternatively, if the morphology evolved subsequent to the move into a new niche, then it may be an adaptation, but the ecomorphological hypothesis that morphology and ecology are strictly associated is incorrect. Fossil anoles are extremely rare (except in recent cave deposits); fossilized anole ecologies are even scarcer. Consequently, these hypotheses cannot be directly examined. However, phylogenetic techniques, assuming parsimony, are now available to infer at what point on a phylogeny evolutionary changes occurred. Using these techniques, one can investigate whether morphology, performance capability, and ecology have evolved concordantly, as the ecomorphological adaptation hypothesis predicts. This approach, however, requires an established phylogenetic hypothesis. For my studies of Jamaican and Puerto Rican anoles, an established phylogeny exists. To extend my evolutionary analyses to other Caribbean anoles, and perhaps to the mainland fauna, will require the resolution of current disputes and uncertainties concerning anole relationships. I have begun to learn molecular techniques for DNA sequencing in order to attempt to resolve some of these questions.

I have conducted my field studies on the anoles of Jamaica, Puerto Rico, and the Dominican Republic during the last three summers. This fall I will go to the U.S. Naval Base at Guantanamo Bay, Cuba. I have not yet analyzed the data from this past summer in the Dominican Republic, so I will limit this summary of my results to Jamaica and Puerto Rico. From my observations in the D.R., I do not expect many surprises from the data analysis.

On each of the islands, I have gathered three types of data. First, I captured 15-20 adult males of each species (I limited my studies to adult males to avoid the confounding effects of intraspecific allometry and sexual dimorphism). I took a series of morphometric measurements from each live animal (e.g., limb span, svl, mass) and added data on mean lamellae number from Mayer's dissertation (courtesy of G.C. Mayer). "Rand census data" were taken for 50-100 adult males of each species. With the aid of assistants, I measured height at which the lizard was first observed, diameter of the object it was upon, and distance to the nearest object to which it could jump (modified from Pounds' work on Costa Rican anoles). Lastly, I observed 20-30 adult males of each species for 20 minutes (or until they disappeared). I recorded how often they moved, what type of movements were made (run, walk, or jump), how much time was spent displaying, and how far they jumped.

Figure 1 shows the position of the species in a 3-dimensional morphospace defined by principal components analysis of the morphological data. The effect of size (represented by svl) was removed from all variables prior to the analysis. The different symbols represent the different ecomorphs (open triangle: trunk-ground; enclosed star: trunk-crown; square: grass-bush; asterisk: twig; inverted and filled

triangle: crown-giant). Although some species are closer to members of another ecomorph category, the ecomorph categories themselves are distinct entities, confirmed by MANOVA, using each PC axis as a variate. For those not convinced, I include a UPGMA phenogram based on these data (Fig. 2). The species are distributed exactly according to ecomorph category.

Figure 3 shows the distribution of species in a 3-dimensional space based on the ecological and behavioral data. I have no data for *A. occultus* or *A. cuvieri*. Again, despite some incongruences, the ecomorph category centroids are distinct, as confirmed by MANOVA. I have investigated the relationship between morphology and behavior in greater detail. My analyses support the predictions of Moermond and Pounds: 1. longer-legged species jump more frequently; 2. crawling is inversely related to hindlimb length; 3. species with long hindlimbs relative to their forelimbs jump more often, whereas species with their fore- and hindlimbs of more equal length tend to run more often (this makes sense because jumping is a bipedal action whereas running in anoles is almost always quadrupedal). Further, my analyses indicate that ecomorphs differ behaviorally in ways unrelated to locomotor mode. Specifically, ecomorphs differ in how often they move and display. Further, the rate of rapid (i.e., runs or jumps) movements and display rate are correlated. This is partly because the Jamaican twig anole, *A. valencienni*, which is an active forager, rarely moves rapidly or displays. Even among sit-and-wait anoles (i.e., when *valencienni* is excluded), however, the relationship holds.

Figure 4 displays the position of species in a 2-dimensional performance space based on running, jumping, and clinging capability. *Anolis occultus* is excluded because they refused to perform on the lizard racetrack. Again, the species cluster by ecomorph, with some exceptions and confirmed by MANOVA. Running and jumping ability are tightly linked. I analyzed this relationship in greater detail. Predictions based on biomechanical models were generally confirmed. Performance capability is related to body size; bigger species run faster and jump farther. With the effect of size removed, species with greater hindlimb length perform better. Forelimb length appears to negatively affect performance. The affect of mass and tail length are unclear.

I used canonical correlation analysis to investigate whether position in morphological, performance, and ecobehavioral spaces are correlated. In all cases, a significant relationship exists. Thus, performance ability appears to be the link relating morphology to ecology. One surprise from this analysis is that clinging ability is related to neither morphology (in particular, lamellae number, the relevant morphological parameter investigated) nor ecology and behavior. Several explanations are possible. First, my measure of clinging ability may be faulty. I slowly pulled the lizards with a noose around their waist attached to a pesola scale, and measured the force necessary to dislodge the lizard. Alternatively, I may have measured the wrong variables. Clinging ability on a smooth surface might be more related to pad area (and, more directly, number of subdigital setal hairs); lamellae number is perhaps more relevant to the ability of the lizards to mold their pads to irregular or rugose surfaces. Similarly, clinging ability on a smooth surface may relate more to the smooth leaves the lizards can cling to while they sleep. The ecological variables I measured may be more related to the ability to cling to surfaces with different contours and shapes.

I used phylogenetic techniques to question whether all of the results previously presented represent evolutionary patterns. A correlation of two variables among

extant species might result from adaptation. Species in different environments (measured by variable 1) might always evolve the same adaptation (variable 2). Alternatively, species may be similar in both variables solely because they share a recent common ancestor. For example, if all primates have vestigial appendices (I don't know if this is true), then one might suggest that large brain size is an adaptation for coping with vestigial appendices. However, a more likely explanation is that the ancestral primate had a relatively large brain and a vestigial appendix and has passed it along to all its descendant species. If, however, cetaceans also have vestigial appendices, then the adaptive argument is stronger, because in this case two taxa have convergently evolved the same response to a common condition (i.e., vestigial appendices; of course, the causality could go the other way). Thus, using these phylogenetic techniques allows one to determine whether two variables change in concert, as adaptive hypotheses predicts. It also avoids the problems arising because species are not statistically independent points.

In collaboration with Barry Sinervo at Berkeley, I investigated the performance-ecology relationship in greater depth. We started with the observed correlation between hindlimb length and mean perch size. Short-legged species live on twigs, long-legged ones on trunks. We hypothesized that species may be adapted to perform maximally on substrates of the width they most commonly use. This prediction was only partially confirmed (Fig. 5). The longer-legged species did perform best on the broad surfaces, and were greatly affected by narrower perches. However, the twig anole also performed slightly better on the broader surfaces. It is clear why the longer-legged species occur on broad surfaces; they are greatly incapacitated on narrow surfaces. But why should the twig anole A. valencienni have evolved short legs to utilize twigs? The long-legged species can run as fast on the narrow surfaces, without giving up their capability on the broader surfaces, as valencienni has. The answer lies in a second measure of performance. We also scored the ability of each lizard to move effectively on each surface. On the narrow surfaces, the long-legged species A. gundlachi had difficulty moving in @ 80% of the trials. In contrast, valencienni had relatively little difficulty on these surfaces. We concluded that short legs are an adaptation for the ability to move effectively, rather than quickly, on narrow surfaces.

In Bob Full's laboratory at Berkeley, I have begun using high-speed video cameras to more fully understand the mechanics of movement. We have not proceeded very far, but one interesting lead has emerged. Sinervo and I found that, among populations of Sceloporus occidentalis (the Western Fence Lizard), a relationship opposite to that just reported holds; shorter-legged species suffer a greater decline in sprinting performance and effective movement capability on narrower surfaces. We filmed both Anolis and Sceloporus moving on surfaces of different diameters. Although the films have not yet been analyzed in detail, the answer seems obvious. Running lizards rotate their girdles to increase stride length. The lizards' center of gravity moves laterally; on narrow surfaces, it moves off the support, and the lizard must actively maintain balance and prevent toppling. The films suggest that in stockier animals, the center of gravity moves further off the support, whereas in slender animals, less of the animal's mass is near the pelvic girdle and, consequently, the center of mass moves less and the animal is better able to maintain its balance. Thus, A. valencienni's ability to move effectively on narrow surfaces may result more from its slender body than its short legs. In Sceloporus, by contrast, it is the longer-legged populations which are more slender.

Lastly, I have been working in the Evolutionary Genetics Laboratory at the Museum of Vertebrate Zoology to learn DNA sequencing techniques. I have been using the Polymerase Chain Reaction to amplify certain regions of the mitochondrial genome, which are subsequently sequenced. I have only just begun this project, which I hope will be the major focus of my post-doctoral work. I have extremely preliminary data, 160-180 base pairs from the 12sRNA region of the mitochondrial genome. So far, I have sequence information from one individual of five species, selected solely on the basis of tissue availability (though note that Chris Schneider has been able to extract and sequence data from formalin preserved museum specimens of Anolis!). Phylogenetic analysis of the data with PAUP, using each base as a character, gives two unrooted trees with branch length of 79, one of 80, and 0 of 81. Figure 6 presents the three best trees. Numbers above the branches are the branch lengths (means of the different possible optimizations). As one would expect, all three trees indicate that A. frenatus, a member of the latifrons group, is the most primitive. However, all three trees reveal a relationship between bimaculatus and carolinensis, which I do not think any one would have predicted. I do not know how much confidence, if any, to place in these results as yet, though I expect that future work will be very interesting.

Fig 1

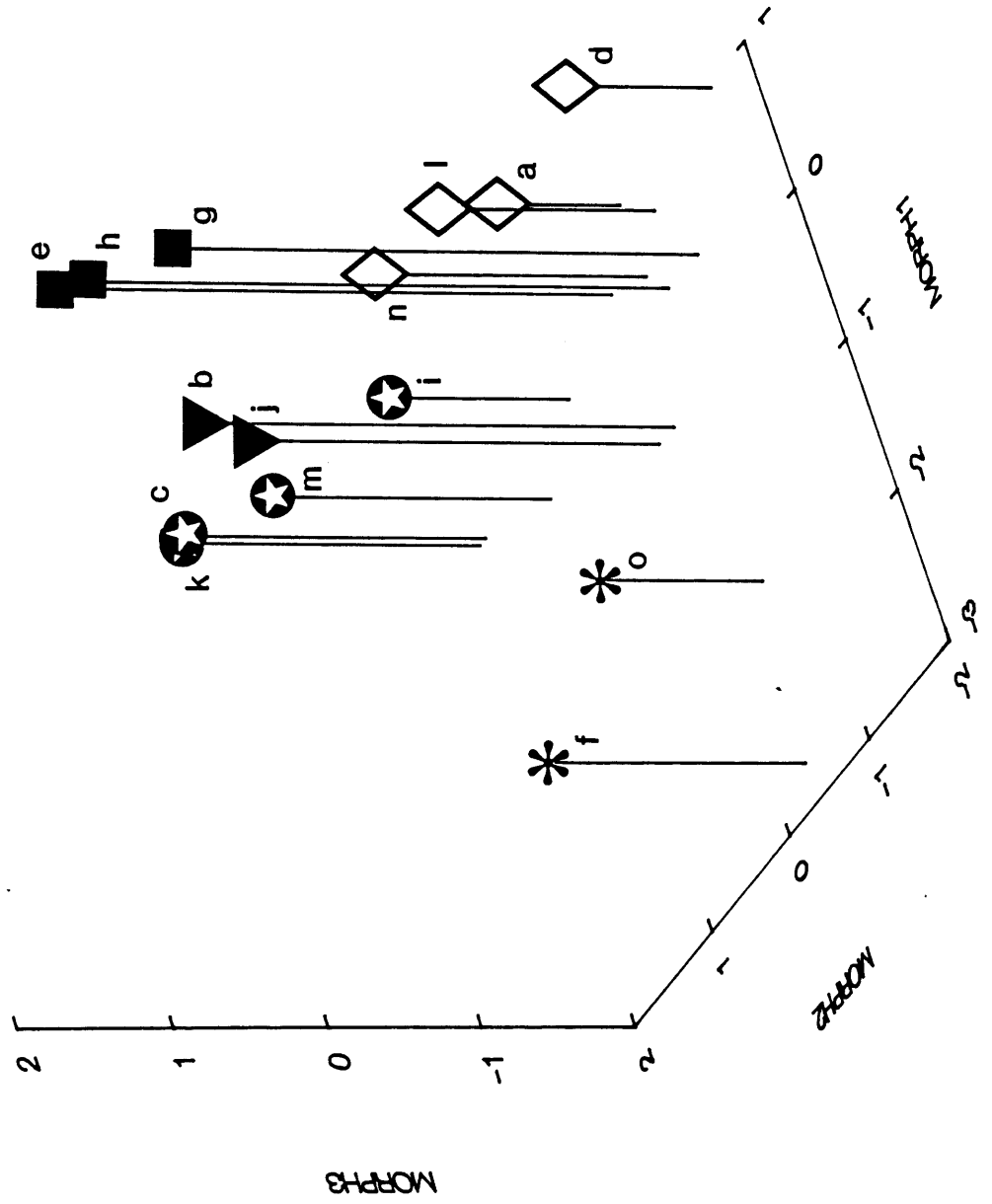
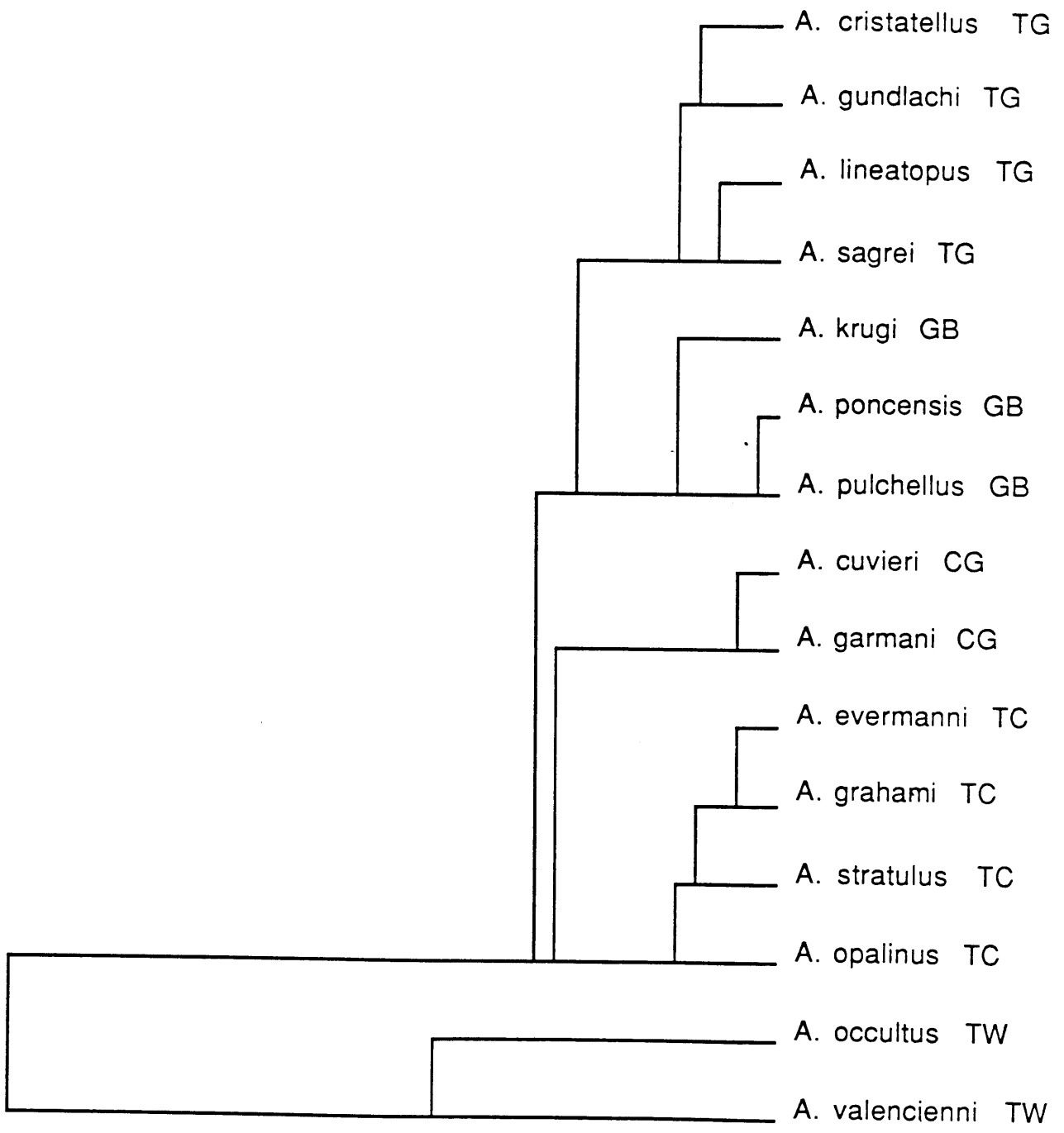
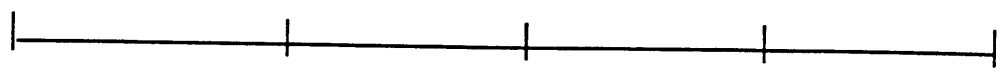


Fig 2



1.00 0.75 0.50 0.25 0.00



Average Taxonomic Distance

Fig 3

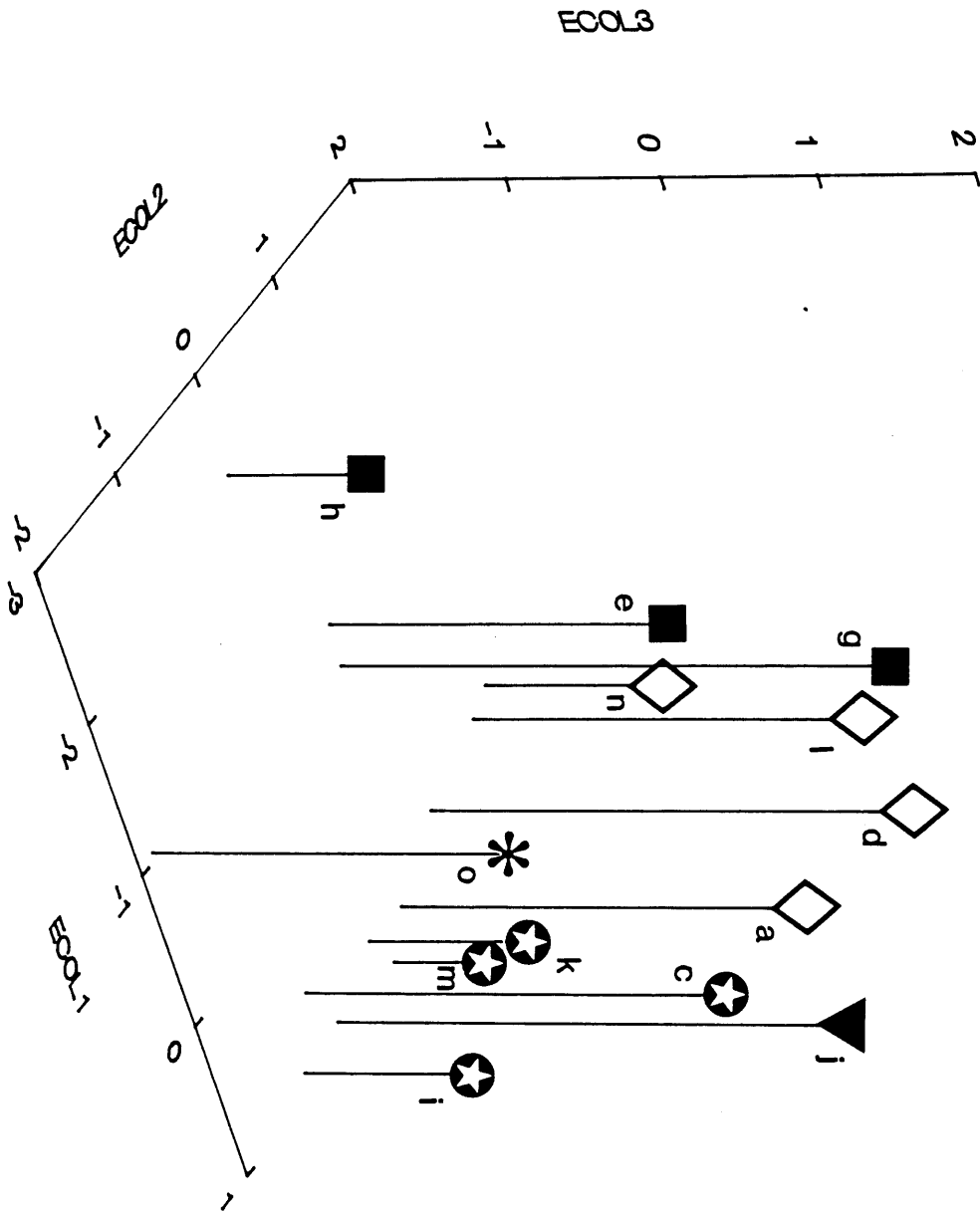


Fig 4

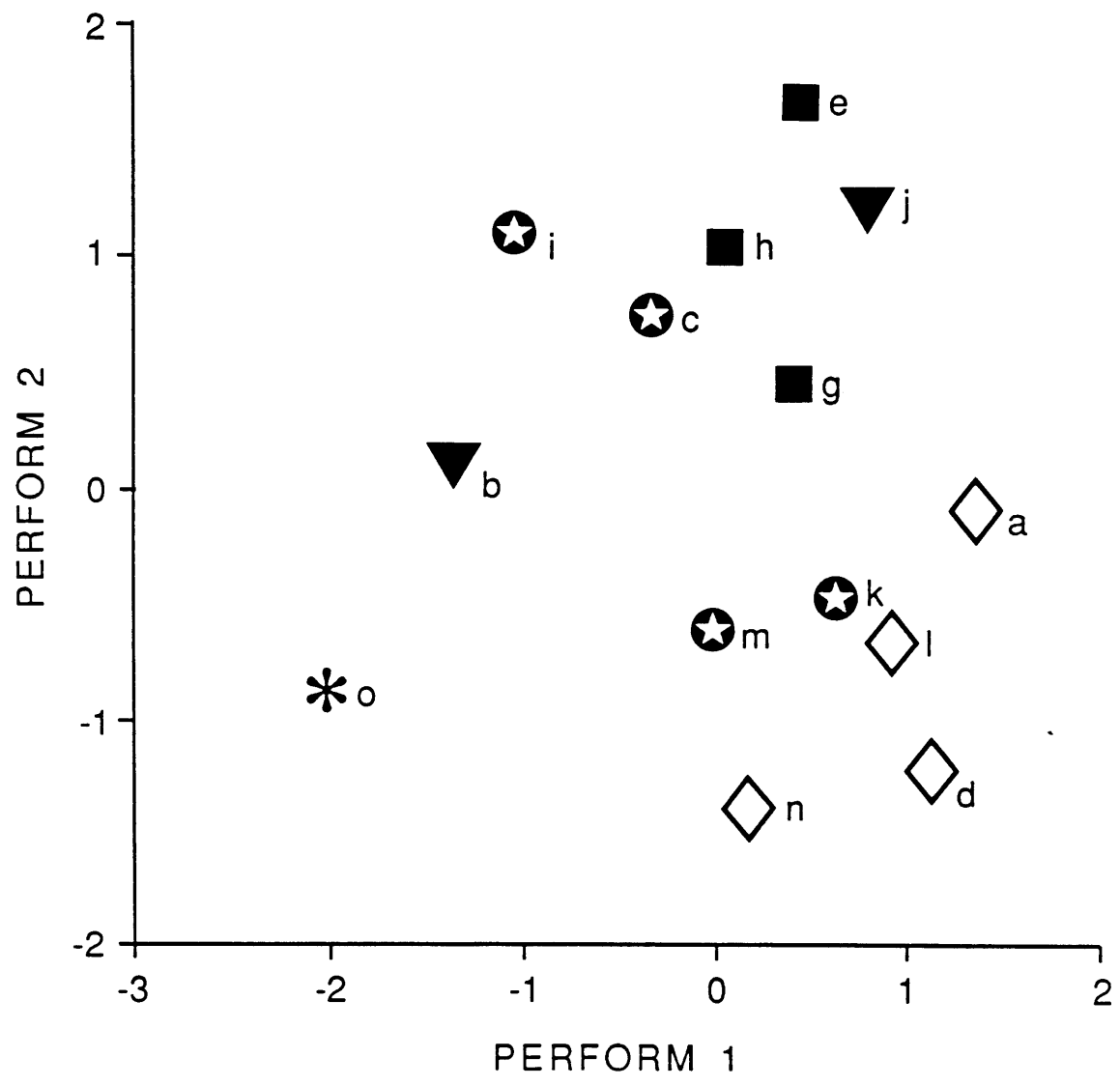


Fig 5

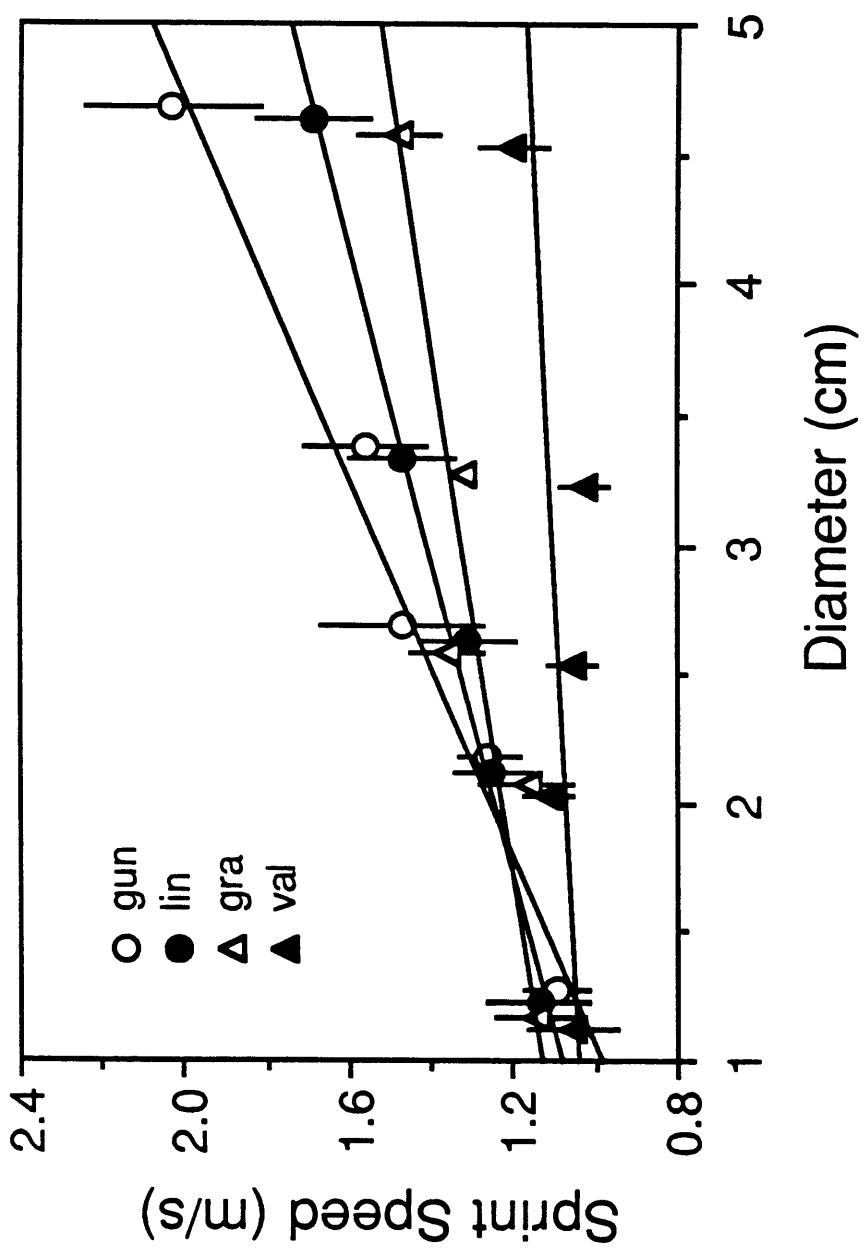
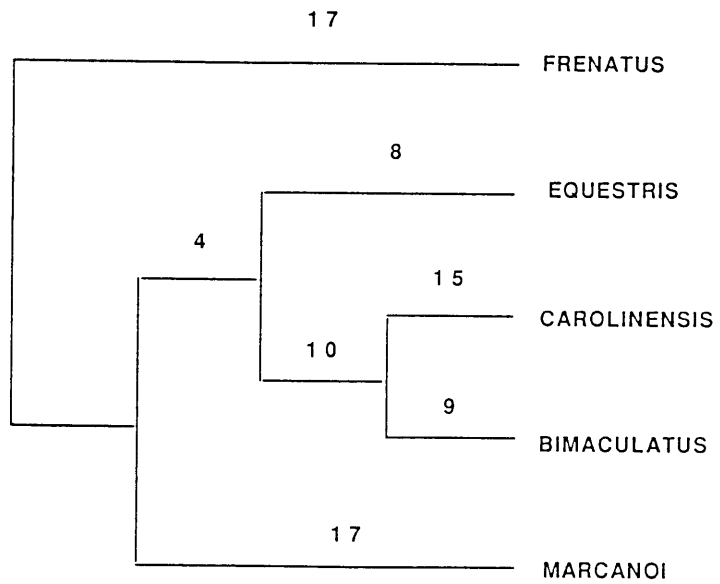
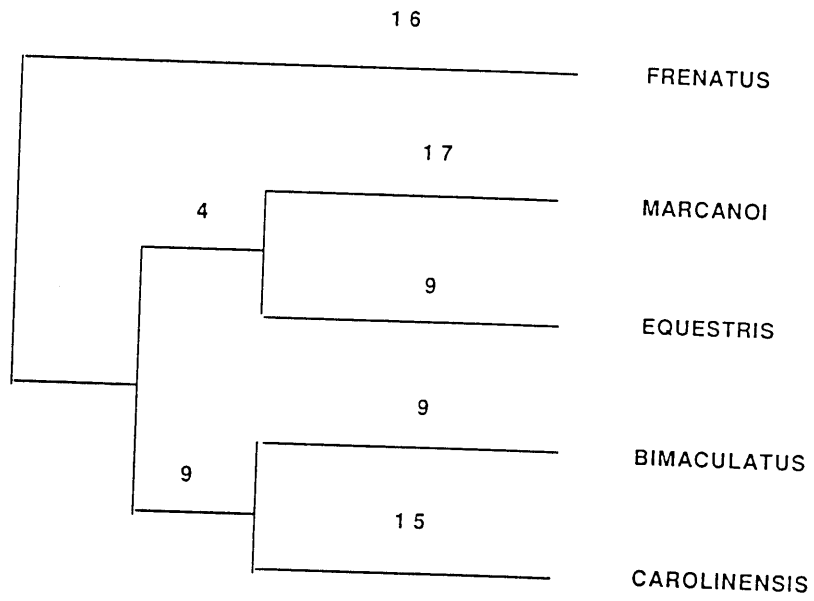
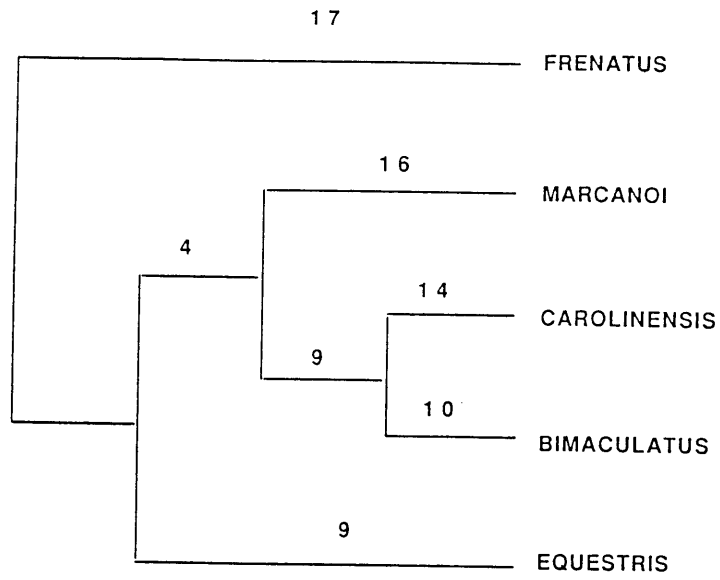


Fig 6



RED-THROATED AND GRAY-THROATED *ANOLIS CAROLINENSIS*:
DO FEMALES KNOW THE DIFFERENCE?

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INTRODUCTION

For many years studies of male-male intraspecific competition have occupied a wide berth in the literature. Only recently has mate choice, especially mate choice by females, begun to receive the proportional scrutiny it deserves.

Teasing out the effects of a given factor upon an animal's choice of mate can be an extremely difficult task. The very existence of mate choice may be difficult to determine. Halliday (1983) says mate choice may assume a "very subtle form". He distinguishes female courtship from that of males:

By contrast, female courtship behavior is often not in the form of stereotyped displays, but simply involves the adoption or non-adoption of receptive postures or movements. When a female is courted by more than one male at a time, she may exercise choice simply by moving towards a particular male. However, the observer may not be able to tell whether such a movement represents a positive female response, or whether she was moving in that direction for other reasons. (Halliday, T.R. 1983: p. 19)

Our study focused upon a distinct population of *Anolis carolinensis* from southwest Florida in which the males lack the typical red coloration of the dewlap. This form, first described by Duellman and Schwartz (1958), has been referred to as the "gray-throated" *A. carolinensis*, although males from various localities in southwest Florida have exhibited gray, magenta, or in a few instances, yellow dewlaps (Christman, 1980).

Christman (1980) suggested that the gray-throated form of *A. carolinensis* may warrant subspecies recognition on the basis of several morphological and behavioral characteristics. These factors, which included differences in habitat preferences, predator avoidance behavior, head shape, and relative tail and hind leg length, have yet to be quantified and published. Christman could find no present predator or prey animal distribution or plant distribution which correlated in any way with the present range of the gray-throated *A. carolinensis*. Its origins are obscure, but Wade, et al. (1983) suggest the possibility that the gray-throated *A. carolinensis* may be a second invader from Cuban *Anolis porcatius* stock, rather than a derivative of mainland *A. carolinensis* stock.

The specific objectives of the present study were (1) to determine whether female gray-throated *A. carolinensis* exercised any form of mate selection when given the option of gray-throated vs. red-throated males, (2) to determine whether female red-throated *A. carolinensis* exercised any form of mate selection when given the same option, and (3) to determine the dominance relationship between each of the red-gray pairs of male *A. carolinensis* used in the experiment and whether that relationship correlates in any way

with female choice. Our study was essentially an application of the same testing procedure (outlined in detail in Materials and Methods) used by Andrews (1985) to determine whether red-throated female *A. carolinensis* preferred larger or smaller red-throated males. Our primary question, however, was not whether the individual female would pick the larger of two males, as it was in Andrew's study, but whether or not she would pick the male appropriate to the population from which she was derived (i.e., pure red-throat or pure gray-throat).

Crews found that the "critical factor in courtship-facilitated OR in *A. carolinensis* is the ability of the male to change his body shape and not the red colour of the dewlap" (Crews, 1975). Sigmund (1979) demonstrated that red-throated females showed no preference for color of dewlaps in males visible at distances of 1 m or less. In a later study, however, Sigmund (1983) found male dewlap color to be a significant factor at distances of 2m.

Sigmund carefully delineates what he believes Crew's study says:

While his results show that dewlap color at close range is unimportant in the physiological stimulation of courtship readiness, Crews did not examine female *preference* for dewlap color. Indeed, the dewlap color does seem to be a factor in attracting a female's choice of mate: (in the Sigmund study) she preferred the normal, red-dewlapped male to a green-dewlapped male. Even if the main function of color is visibility, it is still a factor relevant to female choice. (Sigmund, 1983: p.141)

A choice for a particular male in this study may or may not be a choice simply for the color of his dewlap; it may in fact be a choice for a package of characteristics which accompany (and possibly include) the dewlap color.

MATERIALS AND METHODS

Males and females of the gray-throated form of *A. carolinensis* were collected from Vanderbilt Beach, Collier Co., Florida, and from Bonita Beach, Lee Co., Florida. Red-throated *A. carolinensis* were collected from Belle Glade and South Bay, Palm Beach Co., Florida. Both red-throat sites are within a few miles of the range boundaries for gray-throated *A. carolinensis*.

Ten cages, each measuring 84 cm x 45 cm x 45 cm, were used in the experiments. Each cage was divided into three compartments of equal size, following the general design used by Andrews (1985). A live plant, *Kalanchoe blossfeldiana* cvs. (Poelln), was placed in each cage compartment to provide cover, thermal gradients and an area for male displays.

In each test, or "run", one gray-throated or one red-throated female *A. carolinensis* was placed in the center compartment of each of the mate-choice cages. Each of the two outer compartments was occupied by single male *A. carolinensis*; a red-throated individual was on one side, a gray on the other. As in Andrews experiment, "access to the outer compartment was such that the female could enter an outer compartment through a plastic tube entry port but neither the female nor a male could move from an outer to the central

compartment" (Andrews, 1985). Each experiment was comprised of a series of ten-day runs. One experiment was conducted in June-July 1985, another in August, 1985, and a third in July-September, 1986.

The position of each female was checked twice daily, at 900-1100h and again at 1600-1800 h. Any change of position by a female was recorded and the female returned to the center compartment.

Ten days after each female's first "choice", the males in her cage had their positions reversed such that the red-throated male occupied the cage previously occupied by the gray-throated male and vice-versa. To negate the potential effects of size upon dominance and mate choice the males of each test cage were matched as closely as possible by weight and snout-vent length. Since male red-throats collected for the tests were, on average, nearly 4 mm longer (snout-vent length) and a gram heavier than their gray-throated counterparts, exact matching was impossible; in all but three of the pairings the red male was the larger of the pair.

Male-female pairs found together in the field were labeled in the record as such and never reintroduced to one another in the experiments. The cages were maintained in a greenhouse which provided a full natural light spectrum and normal (Tennessee) photoperiod. The test anoles were subjected to a temperature cycle approximating that of their natural habitat in Florida.

After each experiment was completed the males of each selection cage were placed together to determine which was dominant. "Winners" and "losers" were scored in a manner similar to that used by Neil Greenberg, Dept. of Zoology, the University of Tennessee:

Winners and losers of agonistic encounters were identified only in those encounters in which both individuals manifested displays which included a postural modifier unique to aggression: sagittal expansion. Losers were identified by their cessation of display, supplantation from their perch site, and the adoption of a head-down or cryptic posture. (Greenberg, in prep.)

RESULTS

As a group, gray females demonstrated no preference for either morph (Table 1, Wilcoxon's Signed Rank Test). Red females as a group also demonstrated no preference for either morph (Table 2, Wilcoxon's Signed Rank Test). Gray females exhibited no left-right compartment bias. Red females exhibited a bias toward the left compartments of their test boxes, but that statistical bias may be an artifact caused by one female who appeared to strongly favor one male and then, upon the reversal of the males, ceased "choosing" altogether.

Group statistics tend to mask behavior at the individual level, however. Five (three gray, two red) of the 21 females tested demonstrated highly significant preferences for a specific male (Table 3). Of the gray females, two picked gray males and one picked a red male. Of the red females, one picked a red male and the other a gray male. The highest G

Table 1. Preference by gray-throated female *Anolis carolinensis* for red or gray males as determined by Wilcoxon's Signed Rank Test. ^a

Female Number	Number of Associations With Red Male	Number of Associations With Gray Male
VB9	9	4
VB10	11	11
VB13	11	17
VB12	12	17
VB8	13	15
VB18	6	6
VB32	23	6
VB38	7	22
VB42	12	44
VB43	13	10
Totals	117	152

^aThe test was applied to data from the first experiment of 1985 and the experiment of 1986, both of which used previously untested males and females. The number of associations with red vs. gray males are not significantly different from each other ($T = 12.5$, $P > .05$, Sokal and Rohlf, 1981; Wilcoxon and Wilcox, 1964).

Table 2. Preference by red-throated female *Anolis carolinensis* for red or gray males as determined by Wilcoxon's Signed Rank Test. ^a

Female Number	Number of Associations With Red Male	Number of Associations With Gray Male
BG54	17	20
BG56	5	13
BG58	12	23
BG66	14	12
BG68	16	13
SB1	14	15
BG4	10	31
SB3	30	11
BG6	12	20
SB10	17	9
Totals	147	167

^aThe test was applied to data from the first experiment of 1985 and the experiment of 1986, both of which used previously untested males and females. The number of associations with red vs. gray males are not significantly different from each other ($T = 20.17$, $P > .05$, Sokal and Rohlf, 1981; Wilcoxon and Wilcox, 1964).

Table 3. The five *Anolis carolinensis* females exhibiting significant preferences for males.^a

Female No.	Female's Color Dewlap	Color Dew-lap of Male Chosen	Chosen Male Dom. or Sub.	Chosen Male Larger or Smaller	Left-Right Bias(G)	Mate Choice (G)
VB32	Gray	Red	Sub.	L	1.48	10.45
VB38	Gray	Gray	Sub.	S	0.22	8.00
VB42	Gray	Gray	Sub.	S	0.00	9.63
BG4	Red	Gray	Sub.	S	1.97	11.15
SB3	Red	Red	Dom.	L	0.22	9.04

^a G test results of 3.84 and above are significant ($P < .05$).

statistics recorded in the experiments were for the two females who picked males of the opposite throat color.

While all five females demonstrating significant preferences did lay eggs, many egg-laying females did not show preferences. None of the five exhibited significant left-right compartment bias. The total visits to outer compartments by the five preferring females was significantly larger than the total visits to outer compartments by non-preferring females (t-test, $P < .05$).

In Andrews' (1985) study, a trend "for females to prefer the larger of a pair of males (was) also present in the number of visits by all females regardless of statistical significance." Andrews states that females visited the larger male most frequently in 12 experiments and the smaller most frequently in 9 experiments. In this study the trend was in the opposite direction: 18 females picked the smaller male most frequently and 10 picked the larger (two ties were recorded). Red females "preferred" the smaller male on 11 occasions, the larger on 4. Gray females "preferred" the smaller male on 7 occasions, the larger on 6. Andrews also used a "more conservative test" of preference by counting only those experiments involving the first testing of individual females and individual males. By this test (which eliminates one of our experiments) the result for this study is 11-7 in favor of the smaller males of all pairs, with two tie scores.

By any method of evaluation used by Andrews, the smaller males of this study were chosen more often. In total moves to compartments, regardless of statistical significance, gray females picked the smaller males 179-144 over the larger males. Red females picked the smaller males 207-174 over the larger males. Of the five females who exhibited significant preferences, three preferred the smaller male. Of those three, one (BG4) was a red female who picked a gray male (31-10, $G = 11.15$) over a red male 10 mm longer and 2.03g heavier than the gray male. This discrepancy in size had occurred only because the

particular pair of males had been matched toward the end of the matching process for that experiment and the available supply of gray males of sufficient size had been exhausted filling the previous test cages.

Andrews (1985) found dominance to be correlated with larger body size in all male pairs used in her experiments. Out of 30 pairs of males used in this study, 17 larger males were dominant, 9 smaller males were dominant and there were four ties. Since females demonstrated a tendency (disregarding statistical significance) to pick the larger male in Andrews' study, there was an equal tendency to pick the dominant male of the pairs. In this study, also disregarding statistical significance, the dominant male was picked in 11 of the 24 male pairs in which dominance could be determined. Of those 11, 6 were gray-throats. All 6 gray-throats were smaller than their red counterparts. The submissive male was picked 13 times. Of those submissive 13, 10 were gray-throated males.

DISCUSSION

While both red-throated and gray-throated female *A. carolinensis* show no significant group preference for either male morph, the strong preference demonstrated by five of the females creates a suspicion that those five, rather than the non-preferring females, may in fact be demonstrating natural behavior for females of their populations. It is the behavior of those five females which causes us to reexamine assumptions about *A. carolinensis* female mate choice in general. Our original mate-choice question shifts from "Do females care about dewlap color?" to the new problem: "Do females practice a greater degree of individual mate recognition and selection than previously assessed?"

Within Andrews' (1985) study and ours, if an individual female shows any preference at all, it tends to be a rather astoundingly strong preference, with a G-test score so high as to leave no reasonable doubt she has selected one male over the other. In our study such females could not be deceived by reversing males from one compartment to the other, by reversing the plants in the males' cages, or by washing cages to eliminate residual odor of the originally preferred male. The preference of these females does not appear to be any sort of artifact of captivity or test design.

Andrews (1985) seems to accept at face value that the non-preference of 2/3 of her red-throated females is indicative of what their behavior would be in the field. She hypothesizes several reasons why they may not demonstrate such a preference in nature (Andrews, 1985: p. 288). One of Andrews' explanations was that her females might be demonstrating a natural variation in preference. This seems unlikely. Within the context of evolutionary stable strategies it is difficult to develop a natural selection/sexual selection scenario involving a species extant since at least the close of the Pleistocene (Williams, 1969) or, according to Buth et al. (1980), as far back as the late Pliocene, in which 1/3 or 1/4 of the females of all populations exhibit intense mate selection and the remainder show no preference at all.

In light of the tremendously strong mate selection of certain females in both this and Andrews' study, we think the *non-preference* of many captive females may be an artifact of captivity. The significantly greater overall movement of "preferring" females in our

study supports this hypothesis. There were nearly identical reductions in movement over time for all females in the tests of 1985 and 1986, despite a 30-day variation in the starting dates of the studies of '85 and '86. This decline in movement further supports the conclusion that captivity seriously affects the behavior of some female *A. carolinensis*.

For lack of a better term, we've labeled the preference demonstrated by some captive females as a "fidelity factor" which may be present in some natural *A. carolinensis* populations. If the "fidelity factor" does exist in natural populations of *A. carolinensis*, there are factual conflicts to resolve and questions to consider. There would seem to be a selective advantage to a female's ability to recognize her preferred male and remain with him. If she has selected him first by virtue of the resources he held and secondly by virtue of his superior individual characteristics, her offspring should benefit from his genetic contribution. The chances of a wandering, territoriless male having genes equal or superior to her mate's are remote.

But a "fidelity factor" would seem useless in the population studied by Gordon (1956). He cites evidence of frequent "raiding" of females in his New Orleans study site: females were often bred by several males, including some who appeared to be wandering, non-territorial mavericks of the population.

This paradox might be explained by the relative population and resource levels of the sites studied. The New Orleans site supports many more *A. carolinensis* per unit area than do either our sites or those of Andrews. Precise comparisons aren't available, but from our own experience with all three areas, the *A. carolinensis* of the New Orleans site appear to outnumber those of the other two areas by a factor of at least 3 to 1. If this greater population level reflects a superior habitat resource for *A. carolinensis* in New Orleans, then individual females there may have less to lose from the standpoint of their offspring's competitiveness if they are raided by wandering males. Even offspring of a mediocre male might survive.

In contrast, *A. carolinensis* in Vanderbilt Beach, Fla., are usually segregated into one pair per tree, with considerable high-risk, relatively open space between trees. Optimum habitat is scattered and discontinuous. Males and females are frequently caught in pairs, with few "odd" males to be seen. In the Vanderbilt Beach habitat, to be "raided" by a wandering male would seem to be a considerable risk for a female *A. carolinensis* to incur and summarily bestow upon her offspring, if territorial males are assumed to be in some way superior.

Gray-throated males seem to disturb the normal scale of dominance and mate selection as previously observed in red-to-red interactions of *A. carolinensis*. The introduction of natural dewlap color as a variable into the mate-choice experiment first conducted by Andrews (1985) skews the results in favor of gray-throated males, and, consequently, in favor of smaller males.

There is the possibility that a rare male effect could have influenced the initial decisions of our test females since they were each presented with one male morph which was unfamiliar to them, but gray-throated females also demonstrated the shift toward gray-throated, and, hence, smaller males. The presence or absence of a rare male effect would not conflict with our hypothesis of a "fidelity factor" unless we considered a rather bizarre alternative theory: that a rare male effect could trigger a fidelity not otherwise exercised in nature. Other, correlating results of our study, however, seem to eliminate the possibility of any rare male effect:

In Andrews study, the larger male of *every* male pair was dominant and females picked (numerically) the larger male a slight (12-9) majority of the time. By comparison, were any smaller males to be dominant in this study it would be a departure from the strong trends established in the studies of Andrews (1985) and Greenberg and Noble (1944). Nearly one third (9 of 30) of the smaller males in this study were dominant. That 18 of 30 females in this study visited the smaller male more often is a departure from the trend in the red-to-red encounters recorded in Andrews' study. With regard to both dominance and female mate selection, gray males appear to carry more influence per unit of body size than do red males.

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Lizards of the genus Anolis are vastly interesting animals. Over the past several decades, students of behavior, physiology, ecology, zoogeography and evolution have often found that they, and their close relatives, have provided favorable material for the investigation of problems within their discipline. Anoles have been the subject of studies on the behavioral and physiological control of reproduction, the effects of competition on community structure, the comparative demography of island and mainland populations, the correlation of habitat use with thermal physiology, the ecological factors promoting colonization, the evolutionary consequences of such colonization, the structuring of populations by territories, and the signaling behaviors used to maintain these territories, to mention but a small sample of the problems for which anoles have been found useful study organisms. They range from questions of the proximate causes of individual behavior and physiology, to the ultimate causes of adaptive radiation. Indeed, there is scarcely a problem in organismic and evolutionary biology to the solution of which anoles have not, or will not, contribute.

What is it about anoles that has made them such useful objects of study? I suggest that it is their diversity, in several aspects. First, is their diversity of species. The species richness of anoles is such that as long as 50 years ago Thomas Barbour thought it "wicked" to describe any more, yet he did, and many more have been described since his time. Although no one knows for sure, I suppose there are about 250 species, about equally divided between the islands and the mainland. Second, is their diversity of individuals, the vast numbers in which they can swarm in certain localities. This is especially notable in the West Indies, where, as Skip Lazell has remarked, the anoles aren't really abundant unless you can catch ten without having to move your feet. Third, is their diversity of form, physiology, behavior, and ecology. Although anoles can be fairly described as being diurnal, arboreal insectivores, some species are terrestrial, while others are aquatic; most eat insects, while some eat fruit and small vertebrates; some live in rainforests, others in deserts; some sit and wait for their prey, others pursue it; and some live at the edges of tree crowns, some in the centers, and others at the base of the trunk. Even the most characteristic features of anoles, their dewlaps and expanded subdigital lamellae, are lacking in some

species. Third is their geographic diversity, occurring across the Central and South American mainland, up through the West Indian Archipelago into the United States, and on a few scattered islands in the eastern Pacific. This range provides a wealth of habitats and geographic circumstances. And finally, their diversity of lineage, the many sub-groups within the anoles, combined with their wide distribution, allowing hypotheses based on particular lineages or locations to be tested by the "natural experiments" of other lineages and other locations. Overall, the rich diversity of anoles allows for the recognition of repeated patterns and the testing of evolutionary hypotheses.

Study of anoles began seriously in the last century, with the systematic work Dumeril, Bibron, Boulenger, Cope and Garman. Stejneger (1904), while an unsurpassed systematist, provided some of the first analyses of an anole fauna, noting vertical zonation in Puerto Rico. This analysis was furthered by Schmidt (1928), who realized the zonation on Puerto Rico was by climatic habitat, regardless of elevation, presaging what Williams (1972) would eventually term "climatic vicariants." Barbour (1930, 1934) continued the description of anole diversity, noting the important fact that a knowledge of the animals alive and in the field greatly facilitated systematic work. Noble (Greenberg and Noble, 1944) pioneered in the analysis of behavior using a species that was to become a favorite of many experimentalists, Anolis carolinensis.

In the 1960s and 1970s there was a flowering of anole studies as Ernest Williams at the MCZ, Henry Fitch at Kansas, and Albert Schwartz, along with their numerous students and collaborators, to name but a few, contributed greatly to our knowledge of anoles. There then seemed to be something of a lull, but not for long could such vastly interesting animals remain unattended to. The purpose of this symposium is to bring together younger workers with those who are established in order to stimulate further studies on anoles, to reevaluate what has been done, to see where we are, and to see where we might go. Despite all that has been done, and all that anole studies have contributed, the biology of Anolis must still be considered a relatively dark field, with only scattered points of illumination to light our way.

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The evolution of size in a temperate zone *Anolis* (Sauria: Iguanidae).

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Anolis carolinensis is an inhabitant of the southeastern United States, and is the only species of anoline lizard indigenous to this area (Fig. 1). *Anolis carolinensis* is similar to all other anoles in that it originated in the tropics (*Anolis porcatius* of Cuba is the putative ancestor of *A. carolinensis* [Williams, 1969]), but it is unique in having a decidedly temperate distribution. The range of *A. carolinensis* represents the northern limit for the distribution of the genus.

In the southern portion of its range, the green anole occurs in a variety of habitats ranging from landscaped areas around hotel swimming pools in large cities, to pristine, freshwater swamps. The availability of permanent bodies of water (or abundant rainfall), and arboreal perch sites in "edge" situations are two features in common to all habitats. Habitat use by lizards of any single population does not appear to change markedly during the course of the year. This may be explained by the relatively equable environment experienced by lizards in this subtropical region (e.g., mean winter [November - February] temperature in Orlando, Florida is 16.8° C).

With increasing latitude and decreasing winter temperatures, habitat use by *A. carolinensis* begins to shift seasonally. Lizards in the north require more specific features in the habitat that permit successful overwintering. In east Tennessee, where the mean winter temperature is 6.5° C and snowfall averages 35 cm, *A. carolinensis* occurs only in areas with south-facing cliffs adjacent to permanent bodies of water.

In the spring and summer, these lizards are typical trunk-crown dwellers on vegetation along waterways. Reproduction, egg laying, and the emergence of hatchlings occurs during this time. In the fall, lizards begin to move to the cliff faces and become predominantly saxicolous. The cohort of juveniles present at the end of the fall must first survive a relatively severe winter before they reach sexual maturity and have the opportunity to reproduce the following spring. Adults and juveniles overwinter in rock crevices of the cliffs, but continue to emerge and bask during the winter. Basking is facilitated by the extended exposure to the sun received by these south-facing cliffs, and the resulting elevation of the surface temperature of the rock relative to the air temperature. However, lizards do not venture far from their crevices when basking. This may be due to the diminished capacity of these Tennessee anoles to power locomotion anaerobically following exposure to cold winter temperatures (Gatten et al., 1988). By restricting

activity to areas close to the winter crevices, lizards may escape predators without having to rely on prolonged movement or sprint speed. Restricting activity in the winter is also important for conserving lipid reserves in fat bodies that will be used for winter maintenance (Dessauer, 1955).

I assumed that such marked variation among populations with respect to latitude and seasonal use of habitat might also result in the variation of certain basic life history characteristics. I wanted to know how increases in latitude affect female body size, and concomitantly, their egg and offspring sizes. To quantify these relationships I established a latitudinal transect ranging from east Tennessee to central Florida and sampled six populations over a three year period (Fig. 1).

Gravid females were collected in the field, brought into the laboratory, housed individually, and closely monitored until eggs were laid. Weights and lengths of females and eggs were recorded following oviposition. Each egg was placed in a small plastic container on a mixture of 20 g of vermiculite and 20 ml of water. Containers were placed in an illuminated incubator at 30° C and given a 12 hour light/dark photoperiod. Upon hatching, each neonate's weight and snout-vent length were recorded.

The results of these investigations revealed that the weights and lengths of females, eggs, and hatchlings of *Anolis carolinensis* increase significantly with increasing latitude (Fig. 2). Latitudinally related increases in egg and hatchling size are partially explained by the fact that eggs and hatchlings scale allometrically with female body size; as females become larger, so do their eggs and offspring. However, in addition to the allometric relationship, some variable(s) associated with latitude (presumably temperature) explains a significant amount of the variation in egg and offspring size.

This becomes clear when we examine the relationship between hatchling weight and female weight within and among each of the six populations (Fig. 3). There is a positive relationship (of varying degree) between hatchling weight and female weight in all populations, but this relationship is most pronounced in the three northernmost populations (TN, SC, and GA). Female weight explains 32-41% of the variation observed in hatchling weight in these three populations (square r to obtain these values); the biggest females have the biggest offspring. In the three southernmost populations, female weight is not a good predictor of hatchling weight; all females have approximately the same size offspring, regardless of the female's weight. In one of these southern populations (Seminole Co., Florida), however, the sample size is large enough so that this weak relationship between hatchling weight and female weight in the south is detected at a significant level. Even

so, female weight accounts for only 17% of the variability in hatchling weight in this population.

The important point here is that the females in the north are the largest, and on average, produce eggs and offspring that are proportionately larger than those of females in the south. It appears that there is some selective pressure for large size that exists for individuals occupying the more northern latitudes, and that no such pressure is present in the southern populations.

The following hypothesis is proposed to explain the size differences observed among the individuals that comprise the six populations of this investigation. In the northern populations, only the largest hatchlings are able to survive the harsh winters, whereas hatchlings of all sizes have an equal probability of surviving the mild winters of the southern latitudes. If large hatchling size increases the probability of hatchling survival in the northern populations, ultimately increasing the fitness of the female, then large hatchling size should be selected for in these populations. There is a strong positive relationship between egg and hatchling size; large eggs produce large hatchlings ($F = 344.60$; $df = 1,136$; $P < 0.00001$). So a female can maximize offspring size by maximizing egg size. This is what we observe for females in the northern populations. If, on the other hand, hatchling survival is not as greatly affected by size in the southern populations, then I would not expect there to be any selective pressure for these females to produce large eggs. Females of all sizes should lay approximately the same sized eggs, and this is what we observe.

How might hatchling size affect survivorship of *A. carolinensis* living at the northern edge of its distribution? These lizards rely on lipids stored in fat bodies for maintenance energy during the winter (Dessauer, 1955). I assume that there is a critical minimum size that these lizards must attain in order to have enough lipid reserves to survive a long winter (see Vitt, 1974). Lizards at this latitude ($35^{\circ} 34' N$) also have a shorter activity period in which to harvest resources before the onset of winter. Counter to intuition, the largest eggs hatch in the shortest period of time ($F = 12.67$; $df = 1,131$; $P < 0.001$). This may be the result of embryos in larger eggs reaching a more advanced stage of development before the eggs are oviposited (pers. comm., R. Huey). These one or two "extra" days may be important additional time for resource acquisition, resulting in larger hatchling size and greater lipid reserves before overwintering. Larger neonates may also have increased room for the storage of yolk to provide the energy needed to secure the first prey items after hatching (Congdon et al., 1978). Bigger hatchlings may be able to capture and eat larger prey (see Schoener and Gorman, 1968; and Roughgarden, 1974), which would be an energetically efficient

strategy. Larger prey would presumably provide more energy than smaller prey, and less time and energy expenditure would be required to capture an equivalent total mass of prey per foraging bout. Large hatchlings that have the ability to eat large prey may also avoid competition with other small predators for the smaller classes of prey (Congdon et al., 1978). Assuming that resource abundance diminishes in higher latitudes as winter approaches, larger hatchlings may be competitively superior to smaller conspecifics in obtaining these limited resources (Vitt, 1974). Even if invertebrate prey abundance is uniform throughout the year, prey may not be as accessible to these lizards during the winter because the lizards do not forage far from the crevices in which they overwinter. Lizards may have to rely predominantly on the lipid reserves that were accumulated before the onset of winter. Finally, when lizards emerge in the spring they have already reached sexual maturity, or will soon do so. Females do not grow much during the reproductive season (personal observation). If larger hatchlings grow quicker, or even if growth rates are similar among all hatchlings relative to their body size, then the largest hatchlings should grow to become the largest adults. Therefore, the larger the size that a juvenile can attain before the onset of winter, the larger it will be when it begins reproducing in the spring, and in the case of females, will have the ability to lay the largest eggs.

The ecology of *A. carolinensis* that inhabit the southern portion of the distribution of the species is quite different. Winter temperatures are mild, prey appear to be abundant and accessible throughout the year, and lizards in the south do not need to overwinter. The size of these hatchlings at the onset of winter may have relatively little to do with their ability to survive until springtime. The selective pressure for females to produce large eggs does not appear to be as strong in the southern populations as it is for those in the north. As a result, hatchlings and adults are not as large either.

Males were not included in this study, but I think a word or two about them is appropriate here. The males also increase in size with increasing latitude, and males are on average larger than the females, both in weight and snout-vent length.

I have presented what I believe may be a general explanation for the diversification of size observed in *A. carolinensis* along a latitudinal gradient. The hypothesis seems plausible given the tropical origin of this species, and its present-day, temperate zone distribution. Just as the distribution of *A. carolinensis* is unique for *Anolis*, this explanation for body size differences may be too. Roughgarden and Fuentes (1977) demonstrated that size in solitary populations of *A. aeneus* and *A. oculatus* in the West Indies is correlated with prey abundance.

Undoubtedly, the selective regime acting on the individuals in any single population changes from one location to the next and may have unique consequences depending on the genetic diversity among individuals and the environmental conditions under which these genotypes express themselves.

ACKNOWLEDGMENTS

My sincere thanks to Arthur C. Echternacht for his continued support and valuable advice during all phases of this research. I am grateful to Pam Brown, Sandy Echternacht, Dan MacDonald, Susan Michaud, Jim Minesky, and Mark Wilson for their assistance in the field. This study was funded by the Department of Zoology at The University of Tennessee.

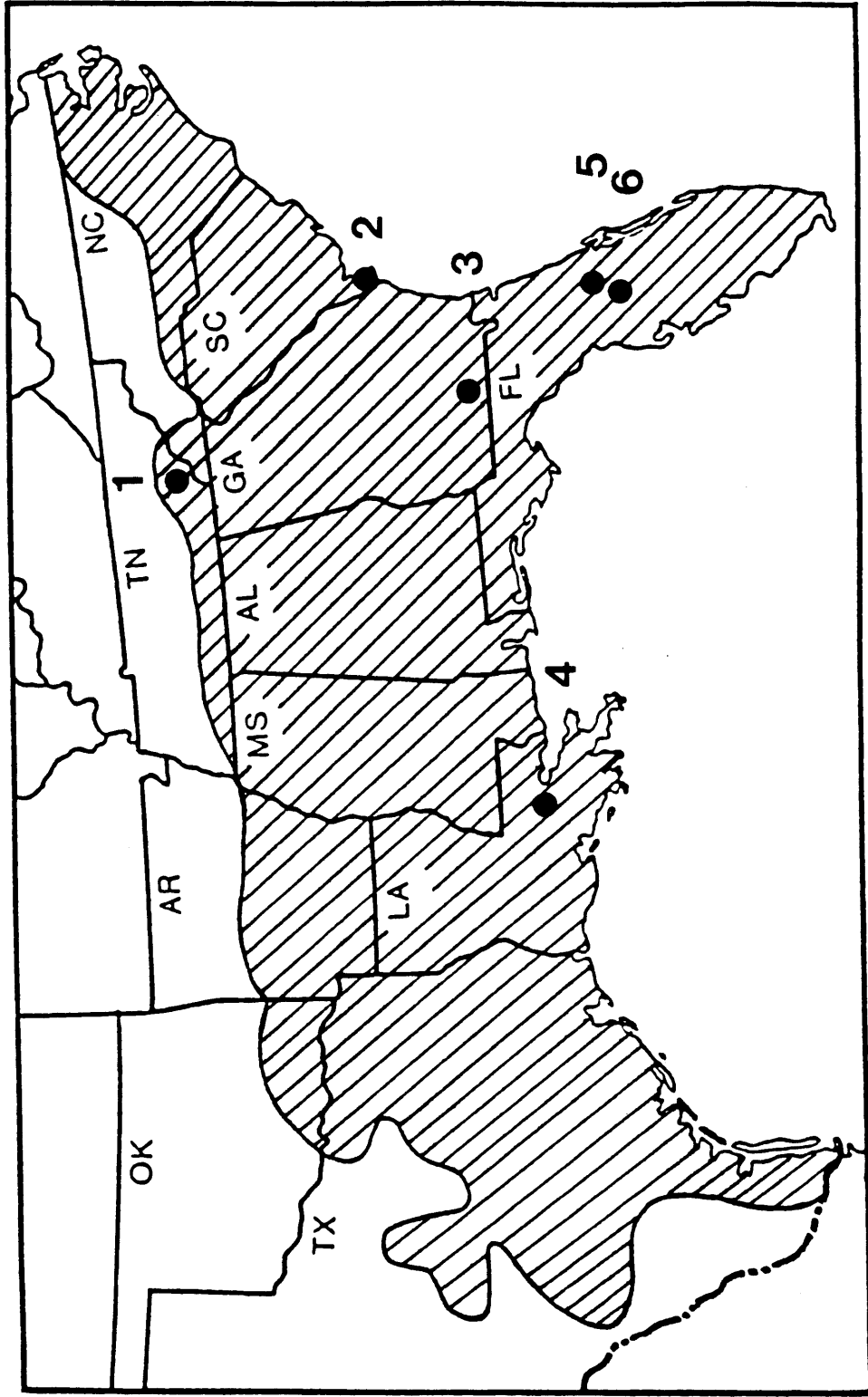


Fig. 1. Geographic distribution of *Anolis carolinensis* (cross-hatched area) in the southeastern United States (Conant, 1975; Dixon, 1987). Closed circles indicate the locations of the lizard populations in this investigation: 1 = Blount County, Tennessee; 2 = Beaufort County, South Carolina; 3 = Lowndes County, Georgia; 4 = St. John the Baptist Parish, Louisiana; 5 = Seminole County, Florida; 6 = Orange County, Florida.

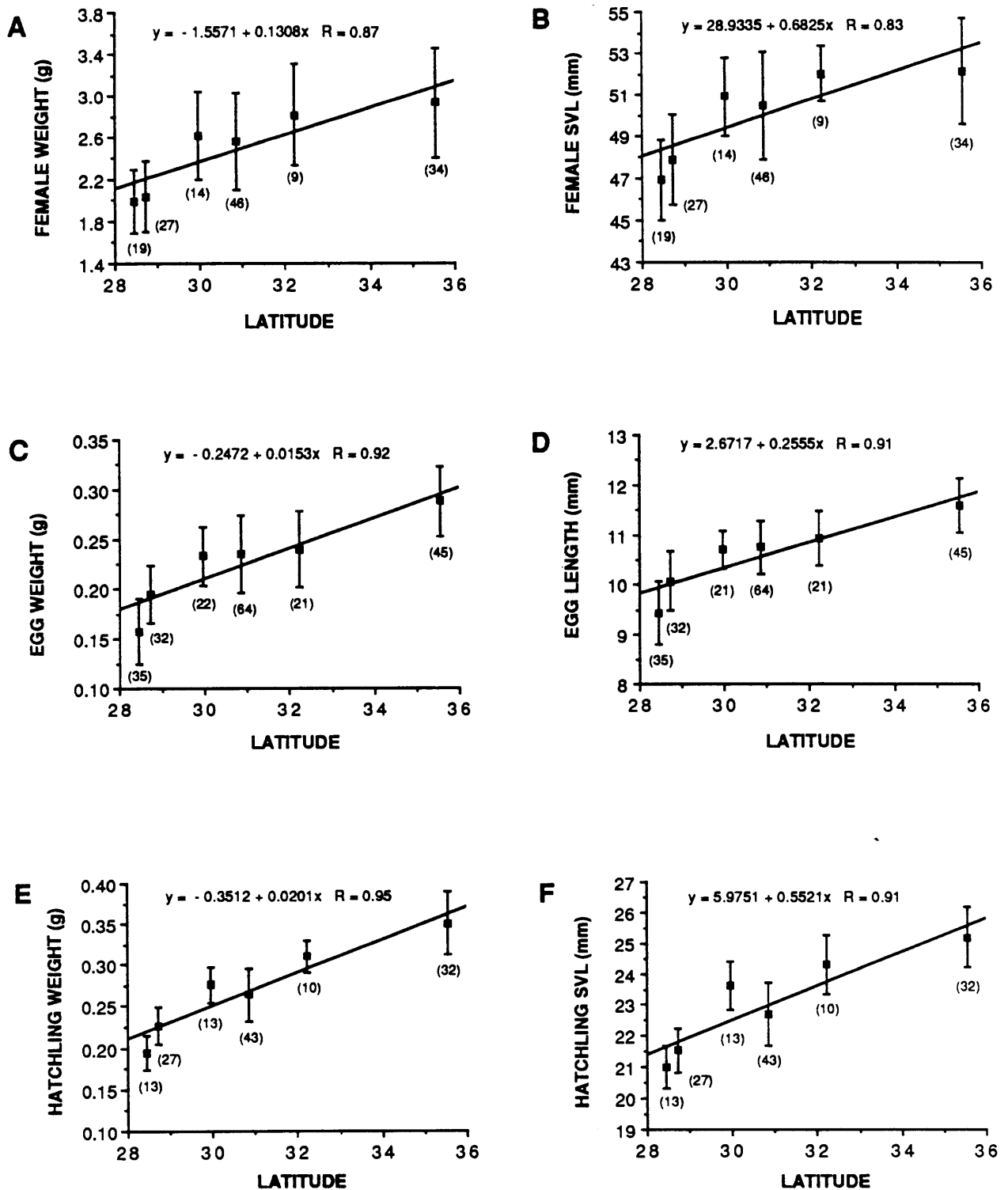


Fig. 2. Relationship between: A - Female weight, B - Female snout-vent length (SVL), C - Egg weight, D - Egg length, E - Hatchling weight, F - Hatchling SVL; and latitude for six populations of *Anolis carolinensis* ($P < 0.05$ for A-F). Each square represents one population mean and the vertical bars are one standard deviation about the mean. Sample sizes for each population are shown in parentheses.

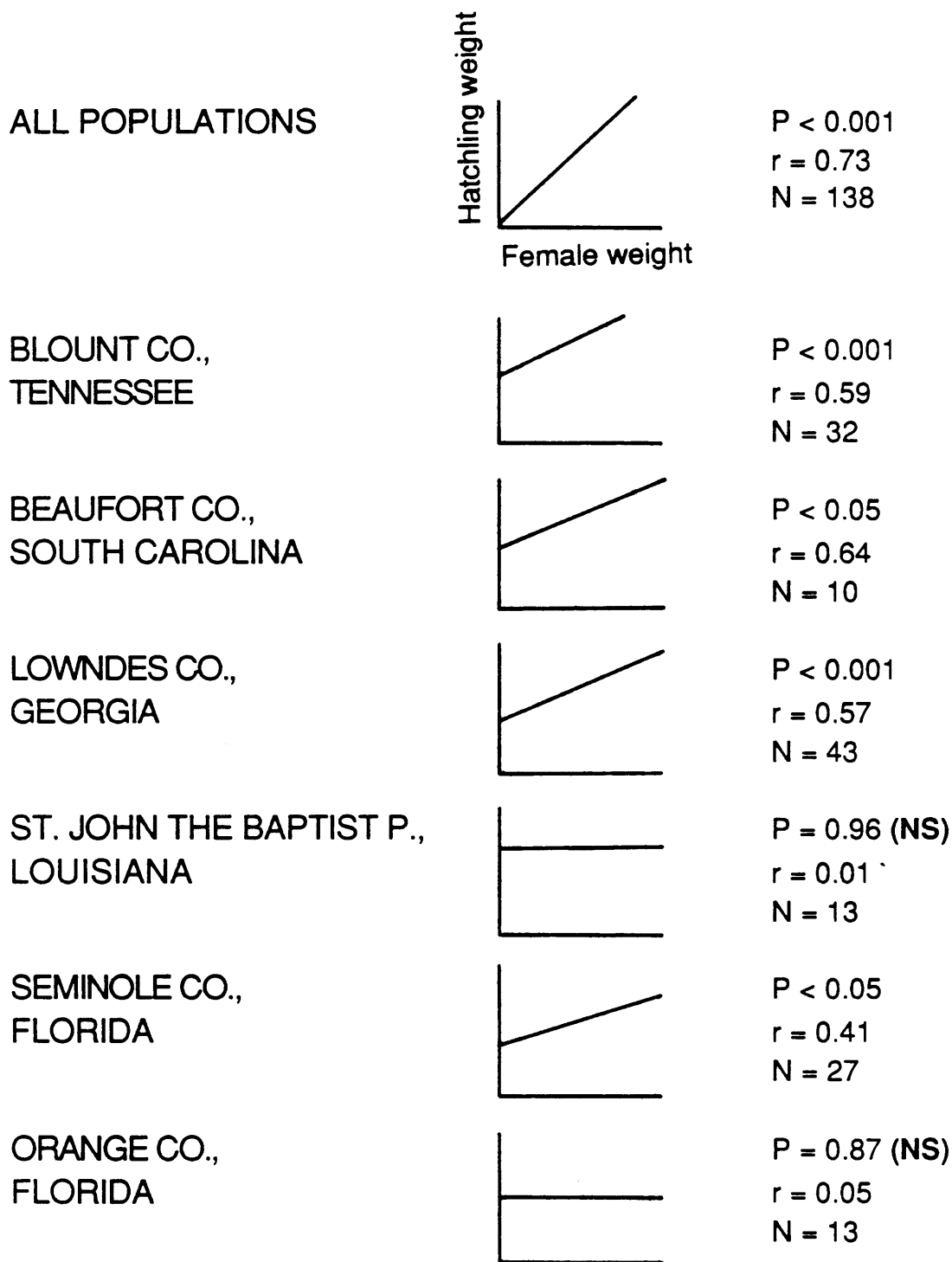


Fig. 3. Relationship between hatchling weight and female weight of *Anolis carolinensis* for all populations combined, and within each of the six populations under investigation (NS = not significant). The ordinate and abscissa are standardized for all graphs to facilitate direct comparison of slopes among each population.

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HEATING AND COOLING RATES IN
ANOLIS CAROLINENSIS AND *ANOLIS SAGREI*
(SAURIA: IGUANIDAE)

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Introduction

It is well known that many reptiles can exert some regulation over body temperature through behavioral mechanisms. In addition, some reptiles exhibit physiological mechanisms of control over body temperature (Bartholomew, 1982).

Demonstration of the ability of an ectothermic reptile to control body temperature by physiological means has come from two different approaches. One approach is to determine whether or not a particular reptile possesses any physiological mechanism known to alter thermal exchanges with the environment (such as changes in peripheral blood flow or in metabolic rate and endogenous heat production). Another approach is to simply determine whether or not the species exhibits differences between heating and cooling rates under controlled conditions. Specifically, if an animal cools more slowly than it heats, then it is inferred that the animal has some physiological means of controlling heat loss (Bartholomew, 1982).

Many studies have shown that medium to large lizards (>30 g) possess the ability to physiologically control thermal exchange rates, as demonstrated either by determining differences in heating and cooling rates (Bartholomew and Tucker, 1963, 1964; Bartholomew and Lasiewski, 1965; Weathers, 1970) or by determining specific physiological mechanisms known to alter rates of change in body temperature (see Bartholomew, 1982). However, only a few studies have measured heating and cooling rates for small (< 15 g) lizards (Spellerberg, 1972; McKenna and Packard, 1975; Claussen and Art, 1981).

The present study measured heating and cooling rates for the iguanid lizards *Anolis carolinensis* (both the red-throat and gray-throat morphs) and *Anolis sagrei* with two purposes in mind. The first purpose was to determine whether or not these small lizards (< 7 g) exert any physiological control over body temperature by simply examining for differences in cooling and heating rates within each of the three groups. The second purpose was to compare the heating and cooling rates of the three groups to determine any possible intra- and interspecific differences in these rates.

Materials and Methods

All of the *A. sagrei* and the gray-throat *A. carolinensis* were collected in Lee County, Florida, while the red-throat *A. carolinensis* were collected in Palm Beach County, Florida and Lowndes County, Georgia. Only males lizards were captured and used in this study. All anoles were captured between 12 and 18 July 1987, transported to Knoxville, Tennessee on 18 July 1987, and housed in the Herpetology Lab at the University of Tennessee.

Lizards were housed individually, fed crickets three times per week, and supplied with water. For the four week period prior to the experimental runs the photoperiod was maintained at 10 - 11 h light and 13 - 14 h dark, while lab temperatures ranged from 21.0 - 25.5°C for the lows and from 25.0 - 31.5°C for the highs. Heating and cooling rates were conducted in late November and early December 1987.

The step transfer method for heating and cooling was chosen since many other studies on lizards have used this method. The step transfer method involves cooling a lizard down to about 20°C, transferring it then to a constant 40°C chamber in order to heat the lizard, and then finally transferring it to a constant 20°C cooling chamber in order to cool the lizard down to about 20°C. Two Precision Scientific incubators (GCA Precision Scientific, Chicago, IL) were used as heating and cooling chambers. The heating chamber was set at 40°C and the cooling chamber was set at about 20°C. Freas 818 temperature control units (GCA Precision Scientific, Chicago, IL) were used to set and control chamber temperatures. Since the chambers were large in volume (about 1 cubic meter), paper was taped across most of the front inside portion of the chambers in order to minimize air exchange with the room when the door was opened or closed. Inside each chamber was a block of styrofoam on which a paper tube, about 12 cm in diameter and constructed of typing paper, was placed. Since air flow blowing from fans in the chambers could not be controlled, lizards were placed inside these tubes to prevent any air from flowing across the lizard's body. Thus, these experiments were essentially performed in still air.

Experiments were performed between 1100 and 1400 h EST and lizards were fasted 48 - 96 h before a run. Each lizard was weighed to the nearest 0.01 g before and after a run and SVL was measured to the nearest mm. Lizard body temperatures and chamber temperatures were measured with 30 gauge copper-constantan thermocouple wires and portable Micromite digital temperature indicators (Thermo Electric Company, Inc. Saddle Brook, NJ). A thermocouple was taped inside each paper tube (above the lizard's position) in order to measure the chamber temperature to which the lizard was exposed. A thermocouple was inserted about 5 mm into the cloaca of the lizard and the trailing wire was taped to the lizard's tail to prevent the wire from slipping out. The lizard was then taped near its pectoral and pelvic girdles to a rectangular strip of styrofoam. The tape used was clear, air-vented, first aid tape (Johnson and Johnson, New Brunswick, NJ).

Each chamber was maintained dark so that lizards would remain undisturbed and quiet. Each lizard was placed in a 19.5°C chamber to cool it down to a body temperature between 19.5 and 20.0°C. Then the lizard was transferred to the 40°C chamber and placed inside the paper tube. When the body temperature was between 38.0 and 39.0°C the lizard was transferred to the cooling chamber, placed inside the tube, and cooled to a body temperature of about 21°C. Body and chamber (tube) temperatures were recorded every 30 s. At the completion of each heating and cooling run, relative humidity was measured in the chambers using a Cole Parmer Psychro-Dyne, battery driven psychrometer. Relative humidity in the heating chamber was 5-12 % and that of the cooling chamber was 10-24%.

Calculation of heating and cooling rates followed a method similar to that of Bartholomew and Tucker (1963). Data were plotted as $\log \Delta T$ vs. time, where ΔT equals the difference between the lizard's body temperature and the chamber temperature. According to Bartholomew and Tucker (1963), heating and cooling rates (in °C per min) can be calculated for step transfer data using the following formula:

$$\text{Rate of temperature change} = 2.303(m) \Delta T,$$

where m is the slope of the straight line from the plot of $\log \Delta T$ vs. time. For all cases, ΔT would be 10°C because a lizard with a body temperature of 30°C represents a temperature at the mid-point (or half-step) between 20 and 40°C. The rate of temperature change is thus calculated as an instantaneous rate at the 30°C mid-point.

Some modifications were made to the method of Bartholomew and Tucker (1963). First, only body and chamber temperature data between 25 and 35°C (inclusive) body temperature were used in the calculation of ΔT because that data seemed to be the most linear portion of the log plot. Also, by using this portion of the data set, initial data were avoided where temperatures were biased due to fluctuations in the chamber temperatures due to opening and closing the chamber door. Chamber temperatures fluctuated about 2 - 3°C during the first three minutes and about 1 - 1.5°C during the remainder of each run. Second, ΔT was calculated as the difference between the median chamber temperature and lizard body temperature rather than the actual chamber temperature minus body temperature for each 30 s

reading. Median chamber temperature was used in the belief that this temperature was more representative of the overall chamber temperature than the temperature at each 30 s reading due to the fluctuations in chamber temperatures. Third, the slope for each heating and cooling curve was obtained from least-squares linear regression analysis. Bartholomew and Tucker (1963) simply state that the slope is obtained from the best fit line.

Least-squares linear regression analysis was used to determine the relationship between initial body weight and heating and cooling rates for each of the three groups of anoles. A repeated measures ANOVA, using initial body weight as a covariate, was performed to determine inter- and intraspecific differences in both heating and cooling rates, as well as to determine any differences between heating and cooling rates within each lizard group. A paired t-test was calculated for the entire sample to compare initial and final body weights. Statistical analyses were computed using SAS (Statistical Analysis System, SAS Institute, Inc., Version 5 edition). The significance level used for all statistical tests was 0.05. Means are reported with \pm one standard error.

Results

A total of 15 *Anolis sagrei*, 7 *A. carolinensis* gray-throat morphs (GT), and 7 *A. carolinensis* red-throat morphs (RT) were run in the heating and cooling experiments. Least-squares linear regression analysis of the log ΔT vs. time relationship produced r^2 values between 0.9800 and 0.9998. Thus, the curves were extremely linear and slopes of the lines could be easily obtained in order to calculate heating and cooling rates.

The regression functions for both heating and cooling rates vs. initial body weight are shown for each group in Figure 1. The general inverse relationship between rate of change of body temperature and initial body weight can be seen for all six cases. The slopes for all regression functions are similar in magnitude, with the exception that heating slope for *A. carolinensis* GT is more negative than the other slopes (Table 1). Only heating in *A. carolinensis* RT and cooling in *A. carolinensis* GT showed non-significant relationships (Table 1), although a trend can be seen and sample sizes were small.

Using repeated measures ANOVA, no significant differences were found between heating and cooling rates within any group ($F=0.35$, $P>0.5584$, Table 2A). No significant interaction effects were found for either rate-lizard group or rate-initial body weight interactions (Table 2A). However, the small P value of 0.0547 for rate-lizard group interaction suggests a potential interaction here. For the between-subjects effects no significant differences were found between lizard groups for either heating rate ($F=2.57$, $P>0.096$) or cooling rate ($F=1.06$, $P>0.362$, Table 2B). Body weight was significant in explaining much of the variation between lizard groups with respect to both heating and cooling rates (Table 2B).

The adjusted means of heating and cooling rates (using initial body weight as the covariate in ANOVA), as well as the unadjusted means, for each group are shown in Table 3. The difference between adjusted mean heating and cooling rates is greater in *A. carolinensis* GT than in the other two groups. It appears that *A. carolinensis* GT may be heating more slowly, but cooling more rapidly than the other groups (Table 3), although no significant differences were found. However, these differences between *A. carolinensis* GT and the other groups may be a contributing factor to the nearly significant rate-group interaction seen in the within-subjects effects (Table 2A). A larger sample size might permit a better exploration of this possible interaction.

Mean initial weight was significantly greater than mean final weight as determined for the entire sample ($t=2.86$, $P<0.0041$, $n=27$). Mean initial weight was 4.65 ± 0.18 g and mean final weight was 4.58 ± 0.18 g, with an average difference of 0.07 ± 0.03 g.

Discussion

This study examined heating and cooling rates in *Anolis sagrei*, *A. carolinensis* GT, and *A. carolinensis* RT in order to determine whether or not these small lizards cool at a different rate than they heat and if any intra- or interspecific differences existed in terms of either heating or cooling rates. Heating and cooling rates are not different within each group, thus indicating that, under the conditions of these experiments, these anoles show no ability to physiologically control rate of heat loss. Though the differences are not significant, the trend in the present study shows that each individual anole's cooling rate is greater than its heating rate. Other studies on small lizards have suggested that such lizards can exert physiological control over heat loss because those species studied showed lower cooling than heating rates Spellerberg, 1972; McKenna and Packard, 1975; Claussen and Art, 1981).

Several factors may explain the differences in the results and their interpretation among these different studies. First, chamber relative humidities differed among the studies:

	<u>Heating Relative Humidity</u>	<u>Cooling Relative Humidity</u>
Present study	5 - 12%	10 - 24%
Spellerberg (1972)	72 - 80%	75 - 80%
McKenna and Packard (1975)	25%	42%
Claussen and Art (1981)	26%	59%

Relative humidities were calculated from water vapor pressures given by McKenna and Packard (1975). Weathers (1972) found that heating rates increased in an exponential fashion as water vapor pressure (and thus, relative humidity) increased, but cooling rates showed little change within a certain range. He also noted that the ratio of cooling to heating will show greater departures from 1.0 as the humidity of the heating chamber is increased. This suggests that comparisons among the studies mentioned above might be difficult to make and that even within a species, artificial differences might occur between heating and cooling rates if relative humidities in heating chambers are higher than those of cooling chambers.

Second, statistical analyses differed among these studies. The present study used a repeated measures ANOVA approach and factored out the differences in rates due to differences in body weight. This type of analysis was used to examine both within and among species (group) differences in terms of both heating and cooling rates. Spellerberg (1972) did not perform any statistical analyses to determine within and among species differences. Claussen and Art (1981) also did not perform any statistical analysis to compare heating and cooling rates, but simply calculated the ratio of heating to cooling rate. McKenna and Packard (1975) did use paired t-tests to analyze the differences within species, but did not test for any differences between the two species in their study. Third, as mentioned by Bartholomew (1972) concerning such comparisons, experimental methodology often varies among studies. All of the studies mentioned above used the step transfer method, but some differences still occurred.

Why were cooling rates observed in this study greater than heating rates? As previously, the chamber humidities here were lower than those of the other studies. Weathers (1972) indicated that heating and cooling rates can be influenced by water vapor pressure by means of creating condensation of water on the body surface and/or by affecting the rate of evaporative water loss. If the relative humidity in the heating chamber (40°C) is 31.8% (water vapor pressure of 17.5 mm Hg), then water will condense on the lizard's surface, eventually evaporate, and increase the rate of heating (Weathers, 1972). Claussen and Art (1981) found this to be the reason why heating rate for *A. carolinensis* at 95% relative humidity was greater than heating rate at 26% relative humidity.

Condensation could not influence heating rates in this study because relative humidity was well below 31.8% in the heating chamber. Instead, an increase in evaporative water loss at low humidity (large saturation deficit between chamber air and lizard's evaporating surface) could decrease heating rate and increase cooling rate as suggested by Weathers (1972). Several factors in this study suggest that this may indeed be the case. First, relative humidity in the heating chamber was low enough to create a large

saturation deficit between chamber air and respiratory surfaces. Second, low humidities in the cooling chamber (< 25% RH) would permit considerable evaporative water loss and increase the cooling rate. Third, body weight at the end of the experiment was, on the average, less than that immediately prior to the experiment. This decrease in body weight could be due to evaporative water loss. Claussen (1967) measured water loss for *A. carolinensis* at 30°C and found average rates of water loss for a 4.5 g lizard were 2.82 mg water per g body weight per hour. Over a 30 min period at 30° C a 4.5 g *A. carolinensis* would thus lose 0.06345 g of water, which is very close in value to the average body weight loss of 0.07 g found for the anoles in the present study.

It is interesting to note that for *A. carolinensis* RT, Claussen and Art (1981) calculated a heating rate of 1.04°C/min, whereas in this study heating rate was found to be 0.976°C/min. Any differences between these two studies are probably due to differences in chamber humidities.

As for the differences among groups, no differences among the three groups were found in either heating or cooling rates. However, considering the adjusted means, *A. carolinensis* GT seems to be heating more slowly, but cooling more rapidly, than the other two groups. Larger sample sizes for the RT and GT morphs would certainly aid in a more powerful test of among group differences, as well as the interaction between rate and lizard group.

In conclusion, *Anolis sagrei* and *Anolis carolinensis* do not appear to reduce the rate of heat loss by physiological mechanisms. If anything, these anoles increased their heat loss by means of evaporative water loss, but this needs more experimentation to be fully resolved. McKenna and Packard (1975) ruled out evaporative water loss and some other factors to demonstrate that *Cnemidophorus sexlineatus* (Sauria:Teiidae) may indeed possess physiological means to help reduce heat loss. Other laboratory studies on small (< 15 g) lizards may have found lower cooling than heating rates due to humidity effects and not physiological control by the lizards. Comparison of different studies is often difficult due to differences in chamber humidities, statistical analyses, and experimental methods. It seems that additional studies are needed to examine the relationship between heat loss and factors such as humidity, evaporative water loss, and species differences before any generalities can be made about the physiological control of heat loss in small lizards.

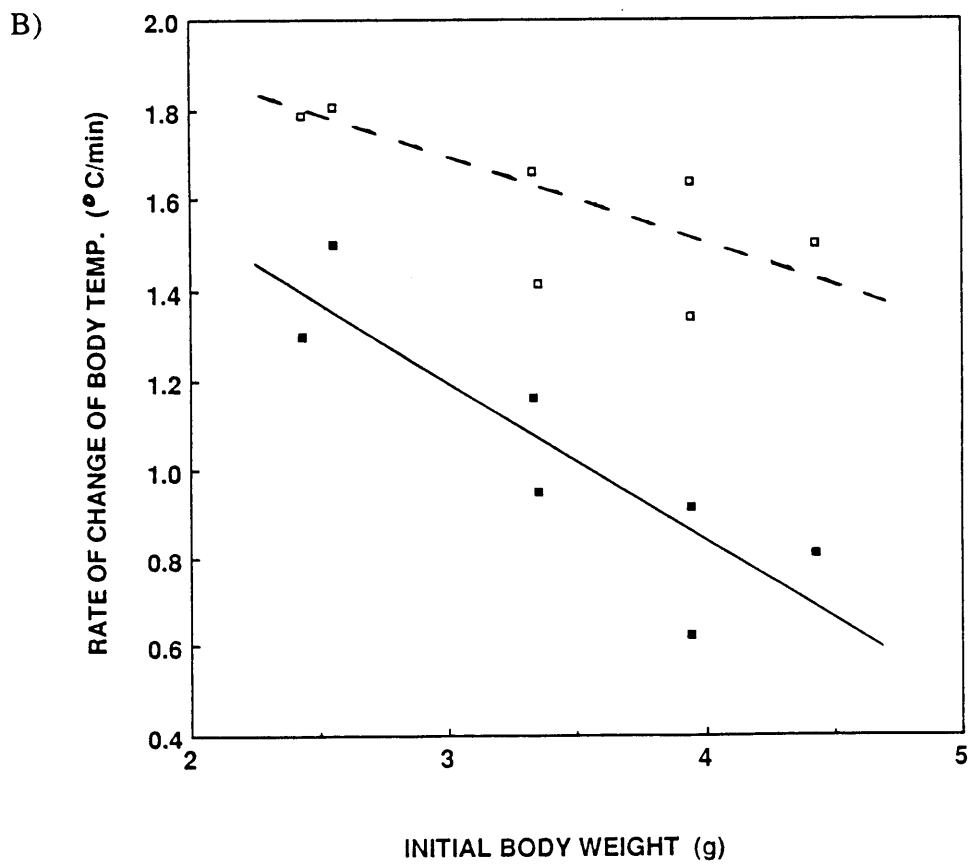
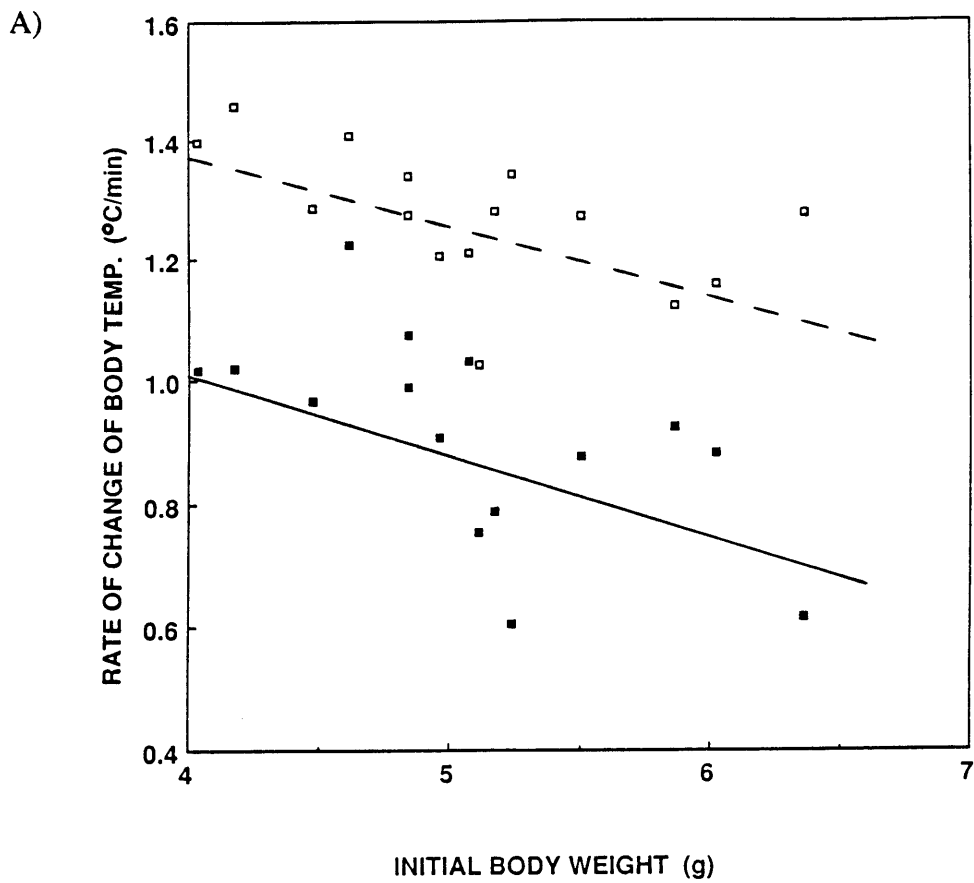
Acknowledgements

Thanks goes to Ed Michaud for helping in the collection of anoles in Florida and Georgia, and to Ed's mother, Mary Michaud, for graciously housing and feeding the authors on the return trip to Knoxville. Dr. Dewey Bunting kindly provided use of the incubators. Paula Goetting-Minesky assisted with some of the data collection and her help is greatly appreciated. Special thanks goes to Dr. Jim Schmidhammer for his advice on statistical analysis.

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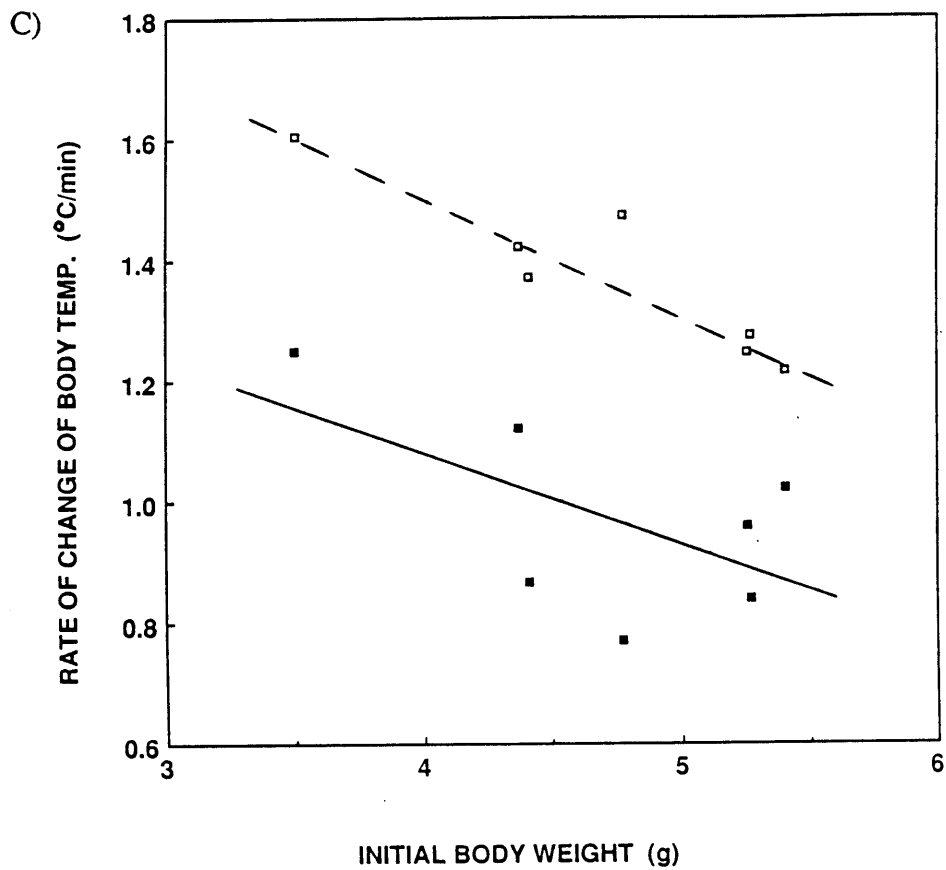


Fig. 1. Least-squares linear regression lines for rate of change of body temperature vs. initial body weight for A) *Anolis sagrei*, B) gray-throated *A. carolinensis*, and C) red-throated *A. carolinensis*. Open squares and dashed line show cooling curve, while solid squares and solid line show heating curve.

HEATING

<u>GROUP</u>	<u>PARAMETER ESTIMATE</u>	<u>STD. ERROR</u>	<u>P</u>	<u>R²</u>
<i>Anolis sagrei</i>	-0.153	0.0567	0.018	0.3596
<i>A. carolinensis</i> gray-throats	-0.355	0.0877	0.010	0.7663
<i>A. carolinensis</i> red-throats	-0.149	0.0885	0.154	0.3604

COOLING

<i>Anolis sagrei</i>	-0.100	0.0400	0.027	0.3229
<i>A. carolinensis</i> gray-throats	-0.172	0.0759	0.073	0.5068
<i>A. carolinensis</i> red-throats	-0.189	0.0354	0.003	0.8515

Table 1. Regression slopes and r-squared values for regression functions for *A. sagrei*, gray-throated *A. carolinensis*, and red-throated *A. carolinensis*, as shown in Fig. 1. Initial body weight is independent variable and heating and cooling rates are dependent variables. P value is associated with hypothesis test that a given slope=0.

A)

WITHIN-SUBJECT EFFECTSSOURCE: RATE

<u>df</u>	<u>Mean Square</u>	<u>F value</u>	<u>P</u>
1	0.00589	0.35	0.5584

SOURCE: RATE*GROUP

<u>df</u>	<u>Mean Square</u>	<u>F value</u>	<u>P</u>
2	0.05482	3.27	0.0547

SOURCE: RATE*INITIAL WEIGHT

<u>df</u>	<u>Mean Square</u>	<u>F value</u>	<u>P</u>
1	0.02756	1.64	0.2114

SOURCE: ERROR (RATE)

<u>df</u>	<u>Mean Square</u>
25	0.01676

B)

BETWEEN SUBJECTS EFFECTS

HEATRATE:

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F value</u>	<u>P</u>
GROUP	2	0.1206	2.57	0.0966
WEIGHT	1	0.5206	22.18	0.0001

COOLRATE:

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F value</u>	<u>P</u>
GROUP	2	0.0217	1.06	0.3624
WEIGHT	1	0.2369	23.04	0.0001

Table 2. A) Repeated measures ANOVA (using initial body weight as covariate) for within group effects. Three hypotheses tested here are that within *A. sagrei*, gray-throated *A. carolinensis*, or red-throated *A. carolinensis*: 1) heat rate and cool rate are equal, 2) heat rate and cool rate interactions with group are equal, and 3) heat rate and cool rate interactions with initial body weight are equal. B) Repeated measures ANOVA tests for differences in both heating rates and cooling rates among *A. sagrei*, gray-throated *A. carolinensis*, and red-throated *A. carolinensis*. Group differences were not significant for either rate, but initial weight for each group was significant in explaining the differences between groups.

A)

<u>GROUP</u>	<u>HEATING</u>	<u>COOLING</u>
BROWN ANOLES	1.015 (0.0451)	1.340 (0.0298)
RED-THROATS	1.001 (0.0581)	1.390 (0.0385)
GRAY-THROATS	0.796 (0.0775)	1.429 (0.0513)

B)

<u>GROUP</u>	<u>HEATRATE</u>	<u>COOLRATE</u>
BROWN ANOLES	0.913 (0.0432)	1.27 (0.0296)
RED-THROATS	0.976 (0.0637)	1.37 (0.0528)
GRAY-THROATS	1.038 (0.1139)	1.593 (0.0678)

Table 3. Heating and cooling rate means ($^{\circ}\text{C}/\text{min}$) \pm one SE for *A. sagrei*, gray-throated *A. carolinensis*, and red-throated *A. carolinensis* : A) Adjusted means from ANOVA using initial body weight as covariate and B) Unadjusted means.

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GEOGRAPHIC VARIATION IN LESSER ANTILLEAN ANOLES.

The study of geographic variation in polytypic species is a central theme in evolutionary biology with two important goals: 1) to elucidate causal factors responsible for spatial patterns of phenotypic and/or genotypic variation, and 2) to identify microevolutionary processes by which species arise. I am studying the geographic variation in Lesser Antillean solitary anole species with these two broad questions in mind.

After the initial step of describing spatial patterns of differentiation, it is important to ask whether spatial patterns of variation are congruent with spatial patterns of environmental variation or with the phylogenetic patterns of the entities under study (Cracraft, 1989). If patterns of morphological variation are congruent with phylogenetic patterns, this suggests a strong historical component related to differentiation following population vicariance. If patterns of variation exhibit congruence with environmental patterns but not with phylogenetic history, then adaptive or other determinants of variation might be more important (Cracraft, 1989; Straney and Patton, 1980). The standard explanation of geographic variation in Lesser Antillean anoles is one of adaptive divergence in response to varying selective regimes in different habitats (Lazell, 1972). Additionally, Lande (1982) has developed a model showing how sexual selection can promote divergence along a morphological character cline and has suggested that this may explain the extreme differentiation in male morphology in A. marmoratus.

Many currently recognized, solitary anole species in the Lesser Antilles are polytypic (see Lazell, 1972). In some species, variation lies in the differences between allopatric groups on separate islands within island banks; in others, variation exists within single islands where contiguous populations are geographically differentiated over small spatial scales. It is the latter group of species in which I am interested. Three species in the Lesser Antilles show a high degree of intra-island differentiation; A. marmoratus from Guadeloupe (5 subspecies on Basse Terre), A. oculatus from Dominica (4 subspecies), and A. roquet from Martinique (6 subspecies).

PATTERNS OF MORPHOLOGICAL VARIATION

Lazell (1972) has described in broad terms the patterns of morphological variation in A. marmoratus, A. roquet and A. oculatus. It would be informative to reanalyze his data set in more detail to

clearly define patterns of character congruence, incongruence and clinal variation. Unfortunately, the raw data is not published, so I have begun to collect data on many of the characters he analyzed as well as others, focusing initially on A. marmoratus.

PHYLOGENETIC ANALYSIS

An historical analysis of geographic variation in morphology requires a phylogenetic hypothesis derived from information independent of morphology. Mitochondrial DNA (mtDNA) has become a widely used molecule for phylogeny construction due to its non-recombining, maternal mode of inheritance (Wilson et al. 1985, Avise et al. 1987). Because of the rapid evolution of portions of the molecule, it has been particularly useful for exploring the geographic patterns and causes of genetic divisions among populations; what Avise and co-workers have called intraspecific phylogeography (see Avise et al. 1987 for review). Additionally, techniques have recently been developed for measuring gene flow among populations using mitochondrial gene phylogenies (Slatkin, 1989; Slatkin and Maddison, 1989).

As part of a pilot study I visited Guadeloupe in July and August of 1988 and collected a series of animals from thirty-five localities on the main islands of Grande Terre and Basse Terre as well as Marie Galante. I have been using the recently developed Polymerase Chain Reaction which allows for detailed examination of mtDNA through amplification and direct sequencing of specific portions of the molecule (Kocher et al. 1989). Very small amounts of tissue are required and even shed skin (<2 mg) or dried tail tip (2-3 mm) have provided sufficient starting material for subsequent amplification and sequencing. In addition, I have recently obtained good amplification from formalin fixed tissue, though neither simply nor consistently, which may make museum collections available for this type of analysis. I am amplifying a roughly 300 base pair region of the cytochrome-b gene. A preliminary analysis of a 50 base pair section of this area shows that there is phylogenetically informative variation in this region of the genome among the subspecies of A. marmoratus. This is fortunate since primers necessary for the amplification of the desired fragment have already been developed for this region. I am working now on completing the sequencing of the 300 base pair region of cyt-b for all of the sampled populations.

The most interesting finding so far is that the montane subspecies, A. m. alliaceus, is highly divergent from the other subspecies. Sequences compared among mainland subspecies and A. m. ferreus vary at about 6% of the sites and do not differ in the amino acid sequence of the translated products (since cyt-b is a

protein coding region, it offers two levels of comparison). Of 220 sites compared between A. m. alliaceus and A. m. ferreus, 61 sites varied (28% sequence divergence) resulting in 16 amino acid substitutions in the translated product. Assuming a 2% per million years rate of divergence, A. m. ferreus and A. m. alliaceus shared a most recent common ancestor 14 million years ago. A. m. alliaceus may be a distinct species and apparent intergrade zones between A. m. alliaceus and other subspecies of A. marmoratus may be stable hybrid zones. The presence of two disparate mtDNA haplotypes in Guadeloupe also suggests that there have been at least two colonization events. Further analysis of mtDNA from other species in the bimaculatus group should further clarify phylogenetic relationships in the Lesser Antilles. The construction of a relatively robust phylogeny through the combination of morphological and biochemical data sets will not only be intrinsically valuable, but will almost certainly be valuable in testing hypotheses of Caribbean biogeography and taxon cycles recently advanced by Roughgarden (1987) and co-workers (Roughgarden and Pacala, 1989).

The depth of the differences among populations on Basse Terre suggests that A. marmoratus is strongly divided genetically. The genetic subdivisions within A. marmoratus - though incompletely mapped - correspond roughly with an area cladogram of Basse Terre. Basse Terre was formed through a series of volcanic eruptions beginning about a million years ago (Lasserre, 1975). The oldest part of the island is the northwest tip. Subsequently, other portions of the island were formed, initially as separate islands, as the center of volcanism moved south. The sequence of eruptions and emergence of land masses is such that lizards could have colonized the northwest portion of the current island and subsequently colonized other portions of the island as they were formed. The last portion of the island likely to be colonized would be the volcanically active highlands (the central mountain chains of the current islands). This hypothesis is testable since the population phylogeny should correspond closely with the area cladogram. The amount of genetic information currently at hand is inadequate to construct a complete phylogeny of the populations on Basse Terre, but I hope to resolve this problem in the next month and begin work on A. oculatus and A. roquet. This process of sequential colonization of emerging landmasses may be a general one in the Lesser Antilles, promoting divergence in anoles on other volcanic islands. Though the role of volcanism in promoting divergence remains unclear, it is an eminently testable hypothesis.

ADAPTATION TO LOCAL HABITAT TYPES

Adaptation to local habitat types involves physiological and morphological changes that increase some relevant performance parameter that is directly related to important features of the habitat (Losos, pers. comm. and in prep.; Greene, 1986). Additionally, it is necessary to map the origins of the character(s) of interest onto a robust phylogeny in order to differentiate between aptation, exaptation and adaptation (Greene, 1987; Gould and Vrba, 1982). Habitat types on Guadeloupe, Dominica and Martinique are defined by rainfall patterns produced by interaction of moisture laden easterly trade winds with the islands' mountainous terrain. Subspecific ranges as defined by Lazell (1972) map roughly onto different habitat types, but the fit is by no means perfect. Since temperature and humidity vary greatly from the hot, dry leeward coasts to the cool, moist upland forest, one would expect to find differences among Anolis populations in voluntary thermal preference, critical thermal minima and maxima, and desiccation tolerance. Hertz (1983) states that "Morphological differentiation within the solitary anoles of the Lesser Antilles appears not to be related to their thermal ecology (Hertz, 1977; Ruibal and Philibosian 1970), and these species exhibit relatively little physiological differentiation among populations (Hertz 1977, 1980, 1981; Hilman et al., 1979)"; suggesting that there has been little if any adaptation (at least in observed thermal ecology) to local habitats. This is certainly in line with Huey and Webster's (1975) observations of A. marmoratus, though a more detailed analysis of between population variation is warranted. Hertz (1980) also found that desiccation tolerance did not vary among sampled populations of A. roquet along an altitudinal gradient from the windward northeast coast to the more humid uplands. He attributed this to selection for desiccation tolerance even in the high altitude, moist habitats because lizards must bask more to maintain a favorable body temperature. It is unclear whether differences exist in critical thermal minima and maxima and desiccation tolerance among populations inhabiting the very dry leeward coasts and the more humid uplands and windward lowlands. I am planning on exploring the variation in thermal biology during my next field season. In addition, since habitat types vary greatly in physical characteristics (perch height, diameter and availability for example), one might expect to find morphological differences related to habitat structure. A detailed morphological analysis of limb and body proportions should illuminate any differences that might be related to habitat structure. Field measurements of habitat structure and analysis of animal's behavior

could then be done to assess the functional roles of any such differences.

In conclusion, I must say that the biology of Anolis still has a lot to offer in the way of providing answers to fundamental evolutionary and ecological questions and that I look forward to contributing to the knowledge of the group.

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TONGUE DISPLAY IN ANOLES AND ITS EVOLUTIONARY BASIS

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Use of the tongue as a component of visual display has been reported for several lizards (e.g. Carpenter & Murphy, 1978; Murphy et al., 1978), but is particularly widespread among anoles (Kastle, 1963, 1965; Rand, 1967; Ruibal, 1967; Echelle et al., 1971a,b; Greenberg, 1977; Hover & Jenssen, 1976; Jenssen & Hover, 1976; Jenssen & Rothblum, 1977; Jenssen, 1979; Ortiz & Jenssen, 1982; Losos, 1985). It is likely, however, that tongue display in some form is characteristic of many taxa, given the ubiquity of gaping as a threat display among lizards (see Carpenter & Ferguson, 1977).

In this preliminary report we review information about tongue display in anoline lizards (true anoles, *sensu* Etheridge & de Queiroz, 1988) and clarify some ambiguities in the literature regarding its form and content. We emphasize that there are two different lingual displays exhibited by anoles and argue that these have been evolutionarily derived from two different, more fundamental, patterns of tongue use that are primitive for squamates generally.

Tongue display in anoles. Although some form of tongue display has been described for a variety of species (references above), our own observations and some literature accounts indicate that there are two distinctly different displays that have been erroneously equated in some cases. The distinction is not a trivial one because it is likely that the two displays have inherently different signal contents and separate evolutionary histories. They are easily confused, however, particularly in the field, because they share certain similar features of form and context.

The first display we call "tongue-bunch" (after Losos, 1985). This behavior is almost certainly equivalent to Greenberg's (1977) "tongue-gorge," may be partly synonymous with Carpenter & Ferguson's (1977) "protrude tongue" in that this designation very likely includes both tongue displays described herein, and may also be partly synonymous with Jenssen & Hover's (1976) "open mouth" in which the tongue is said to usually be clearly

exposed. During tongue-bunch the mandible is depressed to a greater or lesser extent, revealing the tongue within the oral cavity. The tongue is moved anteriorly between the mandibular rami, the tongue tip is curled ventrally and sometimes posteriorly so that the tip is hidden from view, and the tongue dorsum is steeply arched anteroposteriorly (Fig. 1A). Salient features of this display are: a. the arched or "bunched" form of the tongue body; b. the tongue is protruded only slightly, or not at all, beyond the jaws; c. if the tongue is protruded, it is protruded with the dorsal surface, not the tip, as its leading edge, due to the curled conformation of the tongue.

The second display we call "tongue-protrude" (after Jenssen, 1979). This behavior is probably equivalent to Greenberg's (1977) "tongue-out" and Ruibal's (1967) "tongue everted," although the equivalency of the latter is somewhat problematic (see below). During tongue-protrude, the jaws are parted as in the tongue-bunch, but usually to a lesser degree so that the gape angle remains small. The tongue is protruded beyond the jaws with the tip directed anteriorly (Fig. 1B). The tongue is usually engorged with blood. Salient features of this display that distinguish it from tongue-bunch are: a. most of the lingual dorsum remains more or less flat anteroposteriorly; b. the tongue is always protruded beyond the jaws; c. during protrusion the tongue tip remains pointed anteriorly, although it may bend somewhat ventrally, so that the ventral surface of the tongue touches the mental scale (see Fig. 3 in Jenssen, 1979:25); in any case, the tongue tip is never tucked completely ventrally or posteroventrally, resulting in an arched tongue as in tongue-bunch.

Both tongue-bunch and tongue-protrude can be exhibited by the same individual at different times, making careful observation and description necessary to distinguish them. To highlight this point, we note the case of Anolis lineatopus. Rand (1967:41) described clearly a tongue-bunch display in this species: "Frequently the mouth is opened slightly and the tongue, which is short and broad, is raised and pushed forward so that the tip appears as a small ball between the ends of the jaws." In describing the threat display of the same species, Ruibal (1967:129) noted only, "The tongue is sometimes everted," a description we interpret as probably meaning the tongue is protruded. Both descriptions are equated by Jenssen (1979) with each other and with "protruded tongue" in A. opalinus. We, however, equate unequivocally Jenssen's (1979) "protruded tongue" with our "tongue-protrude." Distinguishing between the two displays is made particularly difficult given that tongue-bunch can involve some protrusion. Only careful note of the form of the tongue during display can unambiguously distinguish. For example, Losos (1985) observed tongue-bunch in A. marcanoi, but noted that tongue protrusion sensu Jenssen (1979), never occurred in this species.

Display context and signal content. Tongue-bunch in anoles and other iguanian lizards in which it occurs is always a component of threat or defensive display. It often precedes a bite, or sometimes an attack without a bite (e.g. Losos, 1985;

KS & GCM, pers. obs.). Tongue-bunch is often observed when a lizard is directly threatened by an observer's hand or finger, particularly if the lizard is restrained (KS & GCM, pers. obs.). In general, tongue-bunch seems to be a component of high-level agonistic behavior and is similarly used in defensive behavior, indicating that an attack or bite is imminent.

Tongue-protrude remains more difficult to characterize. It is most likely a "static modifier," as suggested by Jenssen (1979), that serves to boost, or in some way alter, an agonistic behavior. As such, it is always associated with some other more prevalent behavior, and occurs only during some fraction of these (Jenssen, 1978). Jenssen (1979) noted that such static modifiers are used by A. opalinus principally during male-male agonistic encounters and are invoked in an "additive heirarchy" apparently associated with increasing arousal.

It is worth noting herethat color may be an important element of the signal content of tongue display in anoles. Anole tongues are unusual among iguanian lizards in a number of aspects of their microscopic structure (Schwenk, 1988; Schwenk & Williams, in prep.) For example, they exhibit a distinct zonation of papillar morphology along the length of the tongue (Rabinowitz & Tandler, 1986; Schwenk, unpublished data). This zonation appears to be associated with the distribution of melanophores and other chromatophores, as well as differences in vascular and epithelial structure that might relate to blood engorgement and its consequent red coloration of the tongue. Thus, there is the potential for species-specific pattern and color in the anole tongue. One of us (GCM) has observed in the field tongue-bunch displays in which contrasting coloration of the anterior half of the tongue seems to be a result of dermal chromatophores. Gordon Burghardt has long noted the variety of color and pattern in the squamate tongues and thinks it likely that such patterns are related to the signal content of lingual displays, particularly in some snakes (Burghardt, unpublished data, pers. comm.). Jenssen (1977:206) noted that "signal markings and colors would be most beneficial if they appeared on structures normally out of sight, but which became visible during lateral area enlargement." This observation, relating to the evolution of anoline dewlaps and sceloporine belly and throat patches, could easily be applied to tongue displays as well.

Finally, we note in this context that the principal difference between tongue-bunch and tongue-protrude is in the form and display of the tongue tip. In tongue-bunch the tip is tucked ventrally or curled under the tongue. It is hidden beneath the body of the tongue and/or beneath the level of the sublingual plicae (containing the sublingual glands). Our very preliminary observations suggest that it is the tongue tip that is most brightly colored during engorgement. Therefore, hiding the tip during tongue-bunch, as opposed to displaying and engorging it during tongue-protrude, could relate to differences in the signal content of the displays. Alternatively, these differences might relate only to the different behavioral substrates from which they evolved (see below).

Evolution of tongue displays in anoles. It is generally thought that species-specific, stereotyped displays evolve by exploitation of pre-existing "source" behaviors that have no communicative function (Barlow, 1977; Jenssen, 1977). This is the behavioral equivalent to the classical concept of pre-adaptation (or exaptation, sensu Gould & Vrba, 1982). Such exploitation of pre-existing, non-communicative behaviors has the advantage of economy in its use of already available structures and motor patterns. Therefore, elaborate displays need not be viewed as having arisen de novo without behavioral precedent. We believe that we have identified the source behaviors for tongue display in anoline lizards. Our observations are appealing because they not only elucidate the origin of tongue display generally, but also provide an historical basis for the presence of two distinct displays in anoles.

The source behaviors for tongue-bunch and tongue-protrude are lingual feeding and chemosensory tongue protrusion, respectively. Feeding and chemoreception are the two fundamental functions of the tongue in squamate reptiles. These two functions have been viewed as competing evolutionary demands that have shaped the morphology of the tongue (e.g. McDowell, 1972; Schwenk, 1982), although this has been disputed by Smith (1986). In any case, these behaviors are widely distributed among squamates.

Use of the tongue during feeding characterizes all lepidosaurs (Sphenodon + squamates) except varanid lizards and snakes. However, salient to this discussion is the fact that use of the tongue as a prehensile organ during the initial, or ingestion, stage of feeding is limited to the Iguania (Iguanidae, Agamidae, Chamaeleontidae), including anoles (Schwenk, 1988; Schwenk and Throckmorton, 1989). During a prey capture sequence, the jaws are parted and the tongue is moved forward in the mouth. As soon as it is visible, the tongue is seen to be curled with the tip tucked ventroposteriorly and the dorsal surface arched anteroposteriorly (Fig. 1C). The tongue continues to move anteriorly until it is protruded beyond the jaws, dorsal surface foremost. It is the arched, dorsal surface of the tongue that contacts and apprehends the prey item, rapidly drawing it back into the mouth (Schwenk & Throckmorton, 1989). The same pattern of tongue movement is used when a large object, such as an observer's finger, is attacked and bitten. The resemblance between the display tongue-bunch and the morphology of the tongue in the early stages of a lingual ingestion sequence is striking (compare Figs. 1A and C; also Fig. 3 with Figs. 7, 8 and 12 in Kastle [1965]; see also plates and figures in Schwenk & Throckmorton [1989]). Furthermore, the behavior in both cases can indicate an imminent attack or bite. It is significant that the extra-oral component of anterior tongue movement during lingual feeding is not a fait accompli; rather, the feeding sequence is often aborted at an early stage, with the tongue "bunched" within the mouth, depending on the status and movement of the prey item. Aborted feeding attempts, which sometimes last several seconds owing to ambiguous prey signals, are indistinguishable from tongue-bunch displays.

Tongue-mediated chemosensory behavior is a derived feature of squamate reptiles (Schwenk, 1986, 1989). Such chemosensory tongue protrusion is universal among squamates (see reviews by Burghardt, 1970, 1980; Simon, 1983; also Gove, 1979) and is usually called "tongue-flicking." Tongue-flicking is presumed to stimulate the vomeronasal organs, as has been clearly demonstrated for snakes (e.g. Kubie & Halpern, 1979), although gustation may also be used in some cases (Schwenk, 1985). Two types of tongue-flick occur: those in which the tongue touches the substrate (tongue-touch or substrate-lick) and those in which only the air is sampled (tongue-flick proper, or air-flick). These comprise either a single tongue extension, or multiple dorsoventral oscillations of the tongue before its withdrawal into the mouth. Multiple oscillation is characteristic of most scleroglossan squamates, whereas iguanians (including anoles) have never been observed to use more than a simple extension (Gove, 1979; Schwenk, 1988).

Among iguanians, the rapidity and relatively short distance of tongue protrusion sometimes makes tongue touches difficult to distinguish from air-flicks; however, some workers have done this successfully (e.g. Greenberg, 1985; Burghardt et al., 1986). Such differences in the kinematics of tongue-flicking seem to relate to different aspects of exploratory behavior (Greenberg, 1985; Burghardt et al., 1986) and might be associated with stimulation of different sensory modalities (Schwenk, 1985). However, both tongue-touches and air-flicks are initially similar in form and are distinctly different from tongue protrusion associated with feeding. Chemosensory tongue protrusion in iguanids always begins with a small gape angle and a relatively flat (unarched) tongue. Most important, the tongue is protruded with its tip foremost (Fig. 1D). Some downward deflection of the tip occurs at the end of the flick. The form of the tongue during a tongue-flick appears very similar to the anole tongue-protrude display (compare Figs. 1B and D; also see Jenssen [1979] Figs. 1 and 3).

We suggest that the fundamental iguanian behaviors of lingual feeding and chemosensory tongue protrusion were exploited by anoline lizards in their evolution of complex visual displays. These source behaviors are phylogenetically primitive for squamates and have no communicative function. They continue to exist in all iguanian lizards, including anoles, and were ideally preadapted in form, function and context for signal value in displays associated with agonistic and assertive behavior. Furthermore, the presence of two distinct lingual source behaviors helps to explain the presence of two distinct displays in anoline lizards. We note that tongue protrusion during feeding and chemosensory behavior are not only different in superficial form, but result from fundamentally different mechanisms of movement, hyoid protraction and hydrostatic deformation, respectively (Smith, 1984; Schwenk & Throckmorton, 1989; Schwenk, unpublished data). These mechanisms rely on different muscles for their action, and therefore involve different motor patterns. Thus, differences between these displays are not merely subtle modifications of a single basic

pattern, but have evolved from separate neural substrates. This putative dichotomy in CNS patterning underscores our assertion that tongue-bunch and tongue-protrude are indeed separate "units" of behavior (see Barlow, 1977), an hypothesis testable by electromyographic and electrophysiological techniques.

An observation, a solicitation, and a plea. At the Anolis symposium at the ASIH meetings in San Francisco, we noted with interest that many of the slides used to illustrate talks on a variety of topics showed anoles exhibiting tongue displays, both tongue-bunch and tongue-protrude. Since speakers usually choose photographs with the most impact, this informal observation highlights the fact that tongue display adds a dramatic visual addendum to an anole's usual repertoire, sufficient at least to catch the eye of a human observer. We believe that tongue displays are more widespread among anoles than has been reported (see Jenssen, 1979) and solicit unpublished observations on the presence (and absence) of such displays in anoles and other lizards. We urge workers to consider the differences in displays we have outlined here in order to test their consistency and generality with additional observations. We are continuing this work, and would appreciate greatly hearing about all such observations, old and new. Correspondence should be addressed to the senior author. All such data will be credited to its source.

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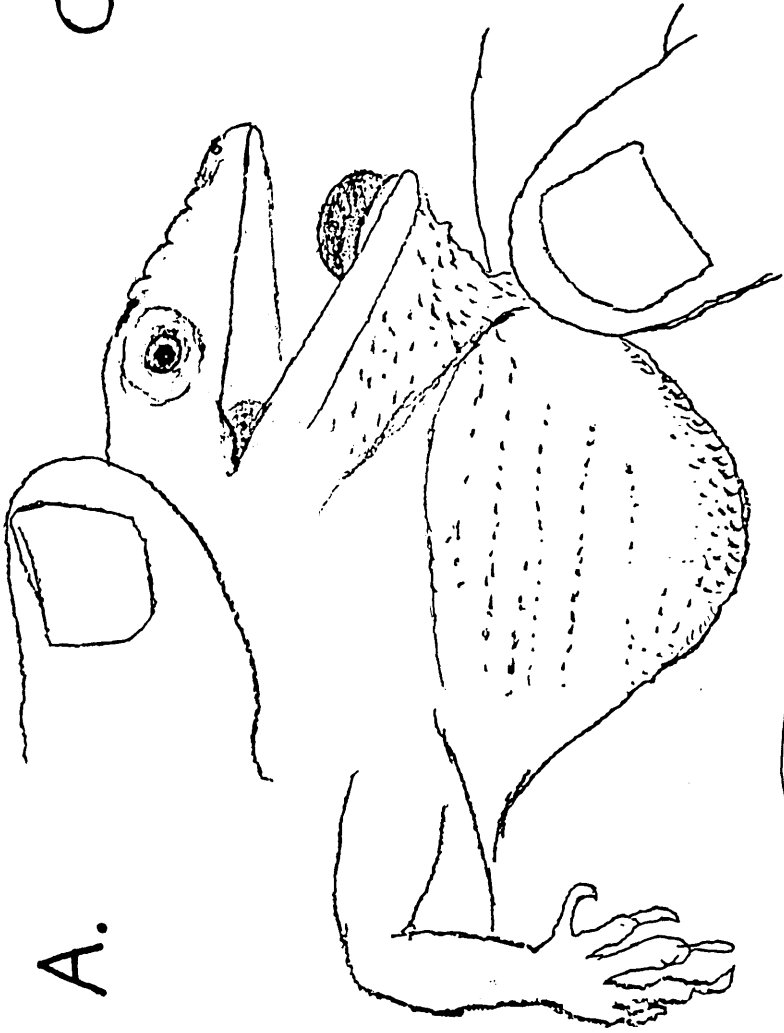
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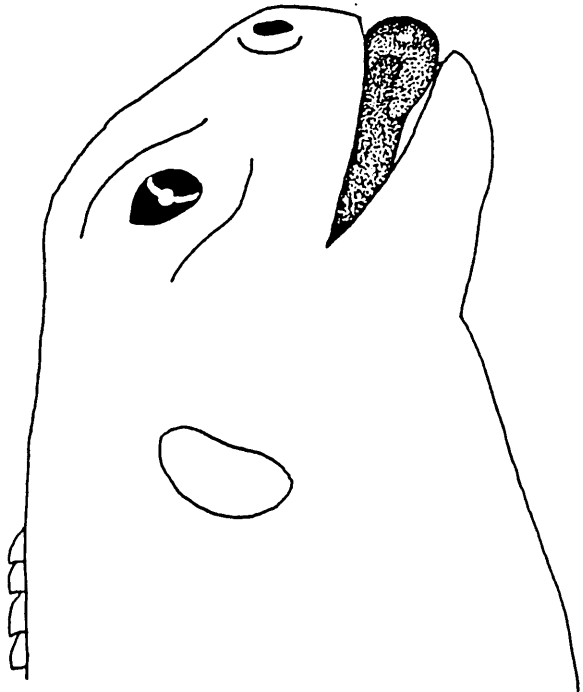
Figure 1. A. Tongue-bunch exhibited by Anolis barahonae from Isla Saona, Dominican Republic, while being held by hand. The tongue is not engorged with blood. Traced from a transparency by Roy McDiarmid. B. Tongue-protrude exhibited by Anolis stratulus from Guana Island, British Virgin Islands, while engaged in male-male agonistic display. The tongue is engorged and reddened with blood. This lizard is at a very high level of arousal, with dewlap extended, nuchal and dorsal crests erected, skin around eye darkened, and body raised on all four limbs. Traced from a Kodachrome transparency. C. Lingual feeding by Dipsosaurus dorsalis (see Schwenk & Throckmorton, 1989). Traced from 16 mm cine film. D. Chemosensory tongue protrusion by Dipsosaurus dorsalis. Traced from 16 mm cine film.

Erratum: "Anolis barahonae" should be "Anolis baleatus".

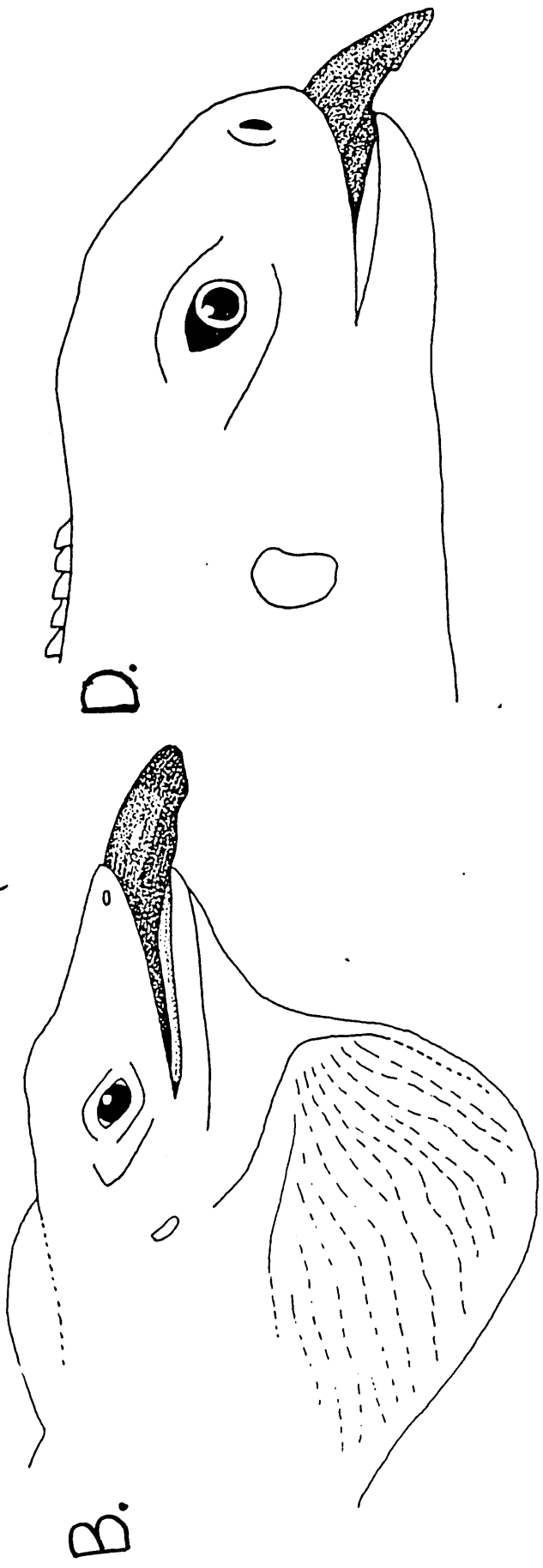
A.



C.



D.



In the last few years, my research has focused on general questions about territorial behavior, using Anolis aeneus juveniles as experimental subjects. Anoles in general, and juvenile anoles in particular, are opportune subjects for field experiments on territorial behavior, because their territories are usually much smaller than those of birds and mammals, and because their behavior is more easily observed than that of other poikilothermic vertebrates, such as fish or salamanders. Hence, they can be used to test assumptions and hypotheses about territorial behavior originally proposed with other vertebrates or invertebrate taxa in mind.

I. Relationships between social and spacing parameters and growth rates.

One current project deals with relationships between behavioral parameters (e.g. territory size, territory overlap) and territory "payoff" (e.g. juvenile growth rates). Juveniles were introduced to a series of patches of high quality, homogeneous habitat in the field and allowed to set up territories. Juvenile growth rates were related to two factors, one reflecting temporal fluctuations in food level and the other reflecting social and spacing patterns; together these factors accounted for 43% of the variance of the growth rates of these free living lizards.

Temporal (daily) fluctuations in prey level, as measured by sticky traps, had a threshold relationship with juvenile growth rates; juvenile growth rates were restricted only on days when prey availability fell below a certain level. Given the small gut sizes of juveniles 22 mm snout-vent length, and the normal abundance of small prey items, this relationship was not too surprising. It cautions that one would not always expect a linear relationship between prey abundance and measures of territory payoff such as growth, survival, or reproductive effort, and suggests that other Anolis may only be food limited when food falls below some threshold level. Something similar has recently been suggested for birds (Pulliam and Dunning 1987). Juveniles made no attempt to "track" daily fluctuations in prey abundance by altering their social and spacing behavior, and neither territory size nor territory overlap were related to average prey levels during the period when juveniles were defending their territories.

The only behavioral factor related to juvenile growth rates was the distance each individual traveled per hour. This variable had a hyperbolic relationship with growth, with maximal growth for juveniles moving 400 cm per hour and lower growth rates for juveniles moving farther and shorter distances (Figure 1). Travel distance incorporated two types of behavior: foraging activity (as juveniles moved from perch to perch in their home ranges and jumped or ran after prey) and social activity (as juveniles engaged in chases or fights). Social and spacing variables such as territory size, territory overlap, dominance rank and aggressive rate appeared to affect growth indirectly, by displacing travel distances above or below optimal levels. For example, high status juveniles generally achieved relatively exclusive territories about 0.5 m² in size, had travel distances of about 400 cm per hour and relatively high growth rates; exceptions were very aggressive dominants that continually chased smaller neighbors, had large territories, extensive overlap, high travel distances and relatively low growth rates. In

contrast, most low ranking juveniles fell into two groups. Subordinates tended to hide within the territories of more dominant individuals, and they rarely moved (often being attacked when they did so!). They had small territories, moderate degrees of overlap, low travel distances and relatively low growth rates. On the other hand, floaters were low ranking individuals with home ranges overlapping those of several higher ranking lizards. They foraged in territories ranges until detected and expelled by each owner in turn, had large home ranges, extensive overlap, high travel distances and low growth rates. A few low ranking juveniles managed to find a territory of reasonable size with moderate overlap; they had travel distances near the optimum and grew at rates comparable to those of higher ranking juveniles in the same patch.

Thus, this study suggests that the effect of spacing and social parameters on growth is complex. The variable "travel distance" may reflect a rate of movement compatible with efficient foraging and a moderate amount of social activity. In that case, behavioral factors such as territory size, overlap and social rank may affect growth indirectly, by influencing an animal's ability to use its home range in an efficient fashion.

II. Contender pressure and spacing patterns

The territorial literature has suggested for many years that the number of individuals competing for territories at the time of establishment affects territory sizes (and/or overlap) in the subsequent territorial season. A key point is that contender pressure theoretically could vary independently of the quality of a particular patch of habitat. For example, heavy density-independent mortality in the nonterritorial season could result in fewer individuals competing for territories at the onset of the next territorial season. Thus, contender pressure could affect territory sizes, territory overlap and related factors such as population density independently of factors such as food levels or rates of predation on territory residents.

Surprisingly, despite the long interest in this hypothesis there are very few empirical studies showing that contender pressure can affect spacing patterns under natural conditions. Juvenile Anolis aeneus were used for an experimental study of contender pressure, because juveniles could be introduced to patches of suitable habitat surrounded by a "permeable" boundary, e.g. a zone that juveniles could traverse if they wanted to. The same patch of habitat could then be used for successive trials with different numbers of introduced individuals (= contenders). If the number of juveniles simultaneously released in a patch affected territory size and territory overlap, then one would expect more settlers, smaller territories and more extensive territory overlap when contender numbers were high than when they were lower. Conversely, if patch quality determined densities and spacing patterns, then a given patch should always end up with the same number of settlers, territory sizes and territory overlap, regardless of how many juveniles were originally introduced to it.

The results of a series of experiments with different patches strongly supported the hypothesis that contender pressure can affect spacing patterns. Juveniles were free to emigrate from the patches, and many did so. Even so, the number of patch residents was higher when more individuals were released into each patch than when fewer individuals were released, and a measure

reflecting both territory size and territory overlap (net territory size) was significantly smaller when contender numbers were high than when they were low in the same patch.

Among other things, the results of this experiment caution against using local density, territory size or degree of territory overlap as an index of "habitat quality." A particular area may have higher contender pressure (leading to higher densities and smaller territories) for reasons unrelated to the quality of that particular habitat for territorial residents. For example, if we compare two patches with different adult densities, the temptation is to assume that the patch with smaller territories and more territory owners is "better" for adults of that species. However, a given patch may have more adult lizards because of a) favorable conditions for egg survival, b) low rates of predation on juveniles and subadults or c) the availability of microhabitats suitable for the growth and survival of juveniles and subadults. None of these factors would necessarily be correlated to food levels, interspecific competition or predation on adults, yet they could increase the number of individuals eventually competing for adult territories, and hence increase adult densities and decrease adult territory sizes. Discrepancies between contender pressure and habitat quality may be especially pronounced in poikilotherms with continuous growth, because the size differences between hatchlings and adults lead to substantial differences in the niches of different age classes within the same species.

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Figure 1. Relationship between distance moved (cm/hr) and juvenile growth rates (mm/day) for the 37 individuals in the study.

