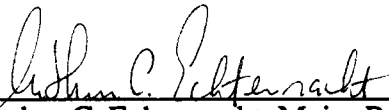
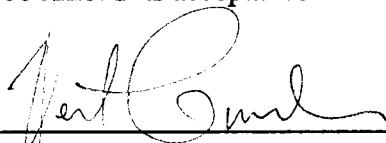
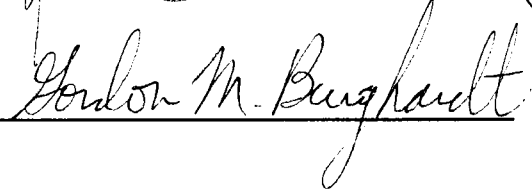


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I am submitting herewith a thesis written by Dan M. MacDonald entitled "The Significance of Male Dewlap Color in Female Mate Selection of *Anolis carolinensis* (Iguanidae) from South Florida". I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Zoology.


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THE SIGNIFICANCE OF MALE DEWLAP COLOR IN FEMALE MATE SELECTION
OF ANOLIS CAROLINENSIS (IGUANIDAE) FROM SOUTH FLORIDA

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Dan M. MacDonald
December 1987

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I hereby acknowledge with thanks the permission granted by Steven P. Christman to reprint the range map and caption from page 13 of his study published in Volume 8 of the Florida Field Naturalist, 1980.

ABSTRACT

The gray-throated form of the lizard *Anolis carolinensis* (Iguanidae) occupies a small range on the southwest margin of Florida, a range that adjoins and overlaps that of the typical red-throated *Anolis carolinensis*. Very little is known of how the two forms interact with one another.

This study sought to determine whether either red or gray-throated females, when given the choice between red and gray-throated males, would prefer males of their own or the alternative throat color.

Within throat-color groups, neither red-throated nor gray-throated females exhibited significant preference for either throat color morph. Some individual females of either dewlap color, however, exhibited a strong preference for a certain male, but the male selected did not necessarily have the throat color characteristic of the population from which the female was drawn.

Five (3 gray, 2 red) of 21 females tested exhibited highly significant preferences. A female "fidelity factor" is identified for females which exhibit strong preference for a given male. In an additional and unexpected result, gray-throated males often exhibited dominance over red-throated males and were selected by females despite being smaller than their red-throated counterparts. A possible explanation for the "fidelity factor" is proposed and placed in evolutionary and ecological context. The gray-throated male superiority is also placed within this context and both it and the "fidelity factor" are discussed as possible means by which the boundary between the two color morphs is maintained.

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I. 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.

Wittenberger emphasized this gap in the ongoing research:

While a great many studies have focused on tactics of male competition and why they evolve, relatively few studies have focused on the tactics of mate choice. Indeed, mate choice has typically been viewed as an essentially non-tactical acceptance or rejection of prospective mates who happen to present themselves to the choosing individuals, rather than as a potentially complex set of tactics that are designed to find the most suitable mate available given existing constraints. (Wittenberger, J.F. 1983: p. 436)

Enormous obstacles may be encountered in any attempt to tease out the effects of a given factor upon an animal's choice of mate. In his study "Evolution of anoline lizard display behavior", Jenssen states that "virtually all biological phenomena could have an influence upon any one behavior under investigation. It is a humbling experience to attempt to isolate causal agents of behavior" (Jenssen, 1977: p. 203). The very existence of mate choice may be difficult to determine. Halliday (1983: p.19) 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)

This study is focused upon female mate choice in the lizard *Anolis carolinensis*

(Iguanidae). Male-male competition, the function of social displays, and the effects of male behavior upon the physiology of females of this species have been the subjects of extensive study, collectively involving decades of work by many researchers (see Crews, 1980; Crews and Greenberg, 1981, for an introduction to this literature), but relatively few studies have directly addressed the topic of female mate choice.

In a study in which female *Anolis carolinensis* were allowed to choose from pairs of red-throated males, Andrews (1985) determined that, although some females demonstrated marked preferences for individual males, females in general did not prefer larger or dominant males. Two-thirds of her test females demonstrated no statistically significant preference. Andrews' study was one of the few to examine female mate choice in its entirety; that is, she looked for female selection between alternative males rather than female response to various components of the behavior of all males.

Crews (1977) believes the lizards of the genus *Anolis* satisfy all the major criteria for the ideal experimental animal: they are easily observable in nature, they have a short generation time, they have a "social system that can be manipulated in the field and, better yet, a social organization and behavioral repertoire that will be retained in captivity. . ." (Crews, 1977: pp. 428-429)

Anolis carolinensis occupies a wide range in the southeastern United States and several islands in the Bahamas. The species exhibits considerable genetic and morphological variation within its range (Wade, et al., 1983). This study is focused on 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" *Anolis 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 *Anolis 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's suggestion of subspecies recognition was given further credence in the genetic studies conducted by Wade, et al. (1983) in which the gray-throated form was found to have unique alleles at three of eight polymorphic loci studied and was nearly as distinct from New Orleans *Anolis carolinensis* (for the loci studied) as the species in general is from its putative ancestor, *Anolis porcatius*. Christman (1980) 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 *Anolis carolinensis*. Its origins are obscure, but Wade, et al. (1983) suggested the possibility that the gray-throated *Anolis carolinensis* may be a second invader from Cuban *A. porcatius* stock, rather than a derivative of mainland *Anolis carolinensis* stock.

The specific objectives of the present study were (1) to determine whether female gray-throated *Anolis 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 *Anolis 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 *Anolis carolinensis* used in the experiment and whether that relationship correlates in any way with female choice. My study is essentially an application of the same testing procedure (outlined in greater detail in the Materials and Methods section) used by Andrews (1985). The primary question to be answered, however, is not whether the individual female will pick the larger of two males, as it was in Andrews' study, but whether or not she will pick the male of her own throat color.

In addition to contributing to an understanding of the mechanics of mate choice in general, and to the role of dewlap color in mate choice by female *Anolis*, answers to

these questions might be expected to clarify the taxonomic status of the two color morphs of *Anolis carolinensis*. Species status for the gray morph would be suggested if females showed a marked preference for males with dewlap colors appropriate to the population from which the females were collected.

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: p. 354, OR= ovarian recrudescence). Several years later, in a general review of his long-term research on *Anolis carolinensis*, Crews refined a hypothesis dating back to his 1975 study:

In view of the circumstantial evidence, the seeming lack of effect when dewlap color is changed in *A. carolinensis* is curious. One possible reason is that *A. carolinensis* is allopatric throughout most of its range in the continental United States and never comes into contact with other anoles. In such single-species situations, it may be that the change in body shape of the displaying animal, rather than the dewlap color, is the sexual signal. (Crews, 1977: p. 430)

It follows that if the present experiment were to demonstrate that females do distinguish between gray and red-throated males it would not necessarily mean the difference in dewlap color was the deciding factor. There is the possibility, albeit remote, that female *Anolis carolinensis* in southwest Florida could choose mates primarily on the basis of dewlap color since, for that factor, the red and gray-throated populations are different morphs, if not different subspecies, and their ranges do meet and overlap with or without intergradation. Christman (1980), however, cited several works in progress which indicated that gray and red-throated *Anolis carolinensis* differed in behavioral characteristics and several additional morphological characteristics. A choice for a particular male in the present 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. This study was designed to

determine the females' choice of mates; it does not attempt to identify precisely which factors influenced the decisions.

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 2 m.

At first glance, the conclusions of Crews (1977) and Sigmund (1979) seem to undermine the design of the present study. In my study, cages much smaller than 1 m in size are used to test mate choice in female *Anolis carolinensis* on the basis of a natural difference in throat color despite Crews' finding that throat color may not be relevant to mate choice and Sigmund's qualification that throat color may be important, but only at distances greater than 1 m. Sigmund, however, is careful to delineate precisely what he believes Crews' 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)

If dewlap color is relevant to female mate choice, even at distances of less than 1 m, then the present study seems to be the ideal natural experiment to test just how important that color is to female *Anolis carolinensis*. Previously, investigators tested the effects of dewlap color by injecting the dewlaps of the test males with India ink (Crews, 1975: p. 350), an alteration which was necessarily accompanied by some stress in handling the test males. In this experiment, nature has done the "injecting" of the dewlaps. All possible effects of stress which were involved in handling the males to alter

their color have been removed. It appears to be the acid test for the effects of dewlap color in the mate choice of *Anolis carolinensis*, but, as is often the case, there are other factors at play which may complicate the picture. As previously mentioned, those factors include a variety of morphological and behavioral characteristics which appear to distinguish gray-throated *Anolis carolinensis* from the red-throated morph of the species.

II. MATERIALS AND METHODS

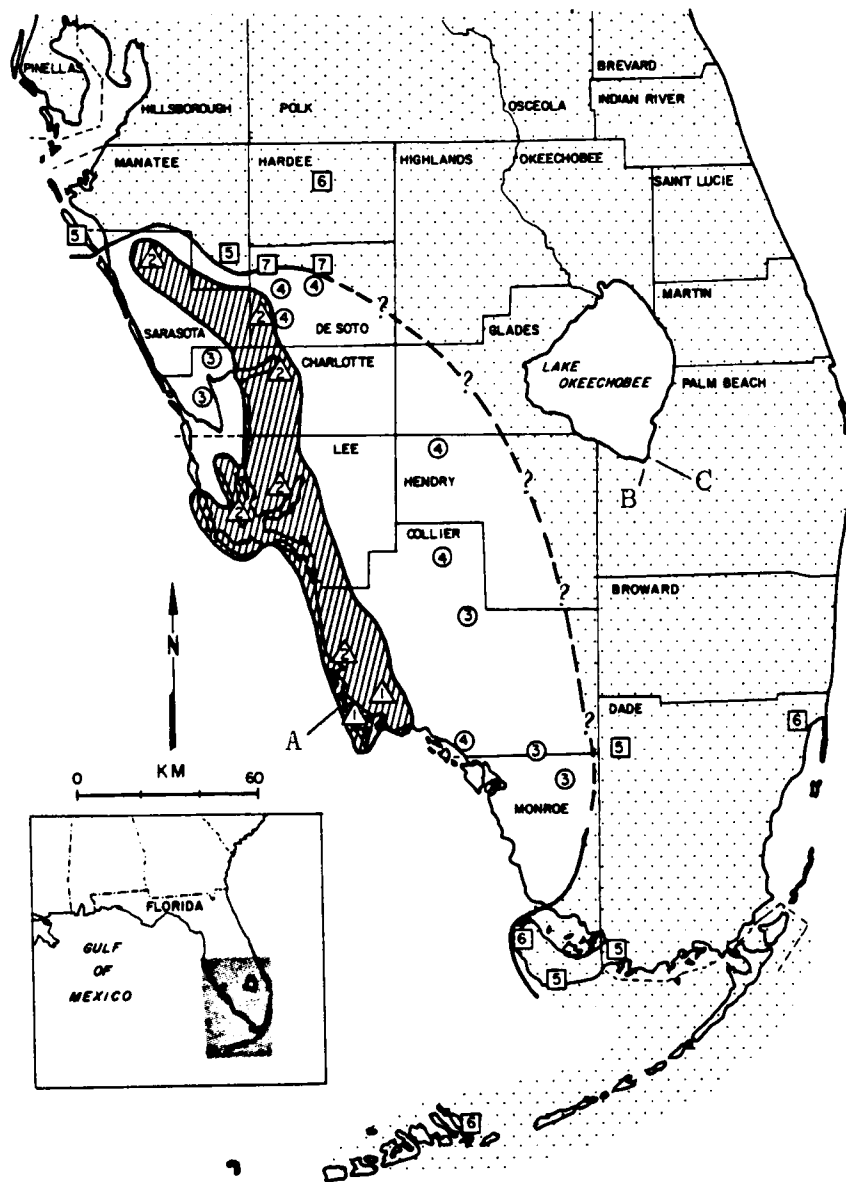
Males and females of the gray-throated form of *Anolis carolinensis* were collected from Vanderbilt Beach, Collier Co., Florida, and from Bonita Beach, Lee Co., Florida. Red-throated *Anolis carolinensis* were collected from Belle Glade and South Bay, Palm Beach Co., Florida. Both red-throat sites are within a few miles of the range boundaries for gray-throated *Anolis carolinensis* (Fig. 1).

Ten cages, each measuring 84 cm x 45 cm x 45 cm, were used in the experiments (Fig.2). 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 *Anolis 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 *Anolis carolinensis*; a red-throated individual was on one side, a gray on the other. As in Andrews experiment, access to the outer compartments 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) used this method to determine whether male size was correlated with female mate choice in *Anolis carolinensis*; this study was essentially an application of the same testing method to determine whether red and/or gray female *Anolis carolinensis* would prefer males of their own color morph when selecting mates.

Two experiments were conducted in 1985 and one in 1986 (Table 1). An additional experiment, begun in late March of 1986 and lasting some 15 days, was



Distribution of the gray-throated form of *Anolis carolinensis*. Hatching represents the minimal distribution of the gray-throated form and stippling the typical red-throated form. The unshaded area includes the zone of intergradation, the exact boundaries of which are not precisely known. Sampling localities are indicated by squares for red-throated populations, triangles for gray-throated populations and circles for populations with intermediated dewlap colors and/or both gray and red dewlaps. The numbers within the symbols refer to modal scores of dewlap colors based on samples ranging from three to 18 specimens.

Fig. 1. Collection sites for red and gray-throated *Anolis carolinensis* used in the female mate selection study. A. Vanderbilt Beach (gray-throats) B. South Bay (red-throats) C. Belle Glade (red-throats). Range map and caption above are from Christman (1980).

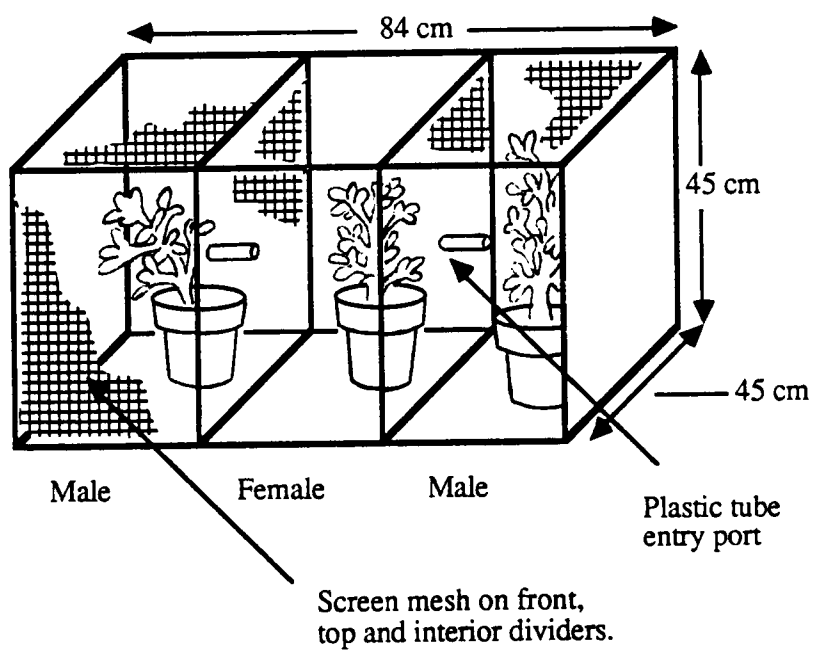


Fig. 2. Mate choice test cage for *Anolis carolinensis*.

discontinued when the females showed virtually no movement from their center compartments. Each experiment consisted of a series of ten-day runs.

Andrews (1985) encountered some variation in the time it took individual female *Anolis carolinensis* to begin moving to the outer boxes. To negate the effects of this period of adjustment in the present experiments the data recording for 10-day runs did not begin on a common date for all cages, but separately for each female upon the date of her first selection/ movement. When an individual female first visited an outside compartment, her run began.

Table 1. Schedule of *Anolis carolinensis* female mate choice experiments. ^a

Date Experiment Started ^b	10-day Runs	Changes Made At End Of Previous 10-day Run
6/26/85	6/26 - 7/9/85 7/7 - 7/21/85 7/19 - 7/31/85	males reversed plants reversed
8/3/85 ^c	8/3 - 8/21/85 8/22 - 8/31/85	males reversed
7/29/86	7/29 - 8/8/86 8/9 - 8/18/86 8/19 - 8/28/86 8/29 - 9/7/86	males reversed males reversed males reversed

^a Each experiment tested five red and five gray females.

^b Dates represent the span of time in which the 10 - day test was completed for all the females in the experiment.

^c With the exception of one female and one male, all lizards were the same as those used in the 6/26/85 experiment. Each female was moved to a new test box and exposed to a new pair of males.

The position of each female was checked twice daily, at 900-1100 h 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. The one exception to this pattern was the third run of the first experiment in 1985, in which the males were left in the same compartments as they were in the previous run, but the plants in their compartments were reversed to test whether the females were influenced by the plants rather than the males.

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 and in all but three of the pairings the red male was the larger of the pair.

If either male or the female in any test cage became ill or appeared to be in a weakened condition the experiment for that particular female was terminated. In Andrew's (1985) experiment with red-throated *Anolis carolinensis* one pair of lizards found copulating in the field were reintroduced in the mate-choice tests. That same pair was to become one of the nine significant preferences found in Andrew's results. For this study all such past associations were deliberately avoided; 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 that approximated that of their natural habitat in Florida: mean temperatures for 10 - day runs ranged from nighttime lows of 21.3 - 23.8 C to daytime highs of 32.8 - 37.5 C. The one exception to this range of temperature means was the

first run of the 7/29/86 test in which an air conditioning malfunction yielded an abnormally high mean low temperature of 27.5 C.

All test anoles were fed crickets 3-4 times a week. For one feeding each week, crickets were dusted with Theralin (Lambert-Kay Co.), a wide-spectrum vitamin supplement. Since the greenhouse facility provided enough sunlight for normal Vitamin D3 synthesis, the additional calcium-phosphorous supplement usually added for lizards in indoor terraria was not used. The anoles received their water from droplets left on the leaves of the *Kalanchoe* plants as they were watered each day.

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 Dr. Neil Greenberg:

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.)

Losers identified in the dominance tests of this study were usually, but not always, colored a dark brown or mottled green, while the winners were colored bright green. On a few occasions, males managed to defeat the design of the test cages and managed to enter the center (female) compartment and then pass on to the opposite male's compartment. On these occasions the "winners" and "losers" were clearly indicated. These accidental results were later repeated, always with the same winner and loser, when the encounter was deliberately reenacted in the dominance test.

III. RESULTS

The experiments of 1985 and 1986 tested mate choice in 10 red and 11 gray female *Anolis carolinensis*. All of the females laid eggs during the experiments and elicited courtship response from the males. Twenty red males and 21 gray males were used.

Gray-throats of both sexes were smaller in snout-vent length, weight, and weight to snout-vent length ratios (Table 2). This made precise matching of males by size impossible and, consequently, in all but three test cages the red male was larger than his gray counterpart. The difference in s-v length was, however, usually kept below 2 mm.

Table 2. Sizes for all *Anolis carolinensis* collected for mate choice project.

Color/Sex	n	Mean Snout-vent Length	Max.s-v Length	Mean Weight	Mean Wgt./Length
Gray Males	66	58.2 mm	65 mm	3.55 g	.061 g/mm
Red Males	43	61.9 mm	70 mm	4.57 g	.074 g/mm
Gray Females	36	48.1 mm	53 mm	2.10 g	.044 g/mm
Red Females	24	49.0 mm	57 mm	2.38 g	.049 g/mm

As a group, gray females demonstrated no preference for either color (Table 3, Wilcoxon's Signed Rank Test). Red females as a group also demonstrated no preference for either color (Table 4, Wilcoxon's Signed Rank Test). Gray females exhibited no left-right compartment bias (Table 5, Wilcoxon's Signed Rank Test). Red females exhibited a bias toward the left compartments of their test boxes (Table 6, Wilcoxon's

Table 3. Preference by female *Anolis carolinensis* for red or gray males as determined by Wilcoxon's Signed Rank Test (gray females).^a

Female Number	Number of Associations With Red Male	Number of Associations With Gray Male	Deviation	Signed Rank
VB9	9	4	-5	-3.5
VB10	11	11	-	-
VB13	11	17	+6	+5
VB12	12	17	+5	+3.5
VB8	13	15	+2	+1
VB18	6	6	-	-
VB32	23	6	-17	-7
VB38	7	22	+15	+6
VB42	12	44	+32	+8
VB43	13	10	-3	-2
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 4. Preference by female *Anolis carolinensis* for red or gray males as determined by Wilcoxon's Signed Rank Test (red females).^a

Female Number	Number of Associations With Red Male	Number of Associations With Gray Male	Deviation	Signed Rank
BG54	17	20	-3	-3.5
BG56	5	13	-8	-5.67
BG58	12	23	-11	-8
BG66	14	12	+2	+2
BG68	16	13	+3	+3.5
SB1	14	15	-1	-1
BG4	10	31	-21	-10
SB3	30	11	+19	+9
BG6	12	20	-8	-5.67
SB10	17	9	+8	+5.67
Totals	147	167		

^a The 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 5. *Anolis carolinensis* female bias for left or right compartments as determined by Wilcoxon's Signed Rank Test (gray females). ^a

Female Number	Number of Choices for Left Compartment	Number of Choices for Right Compartment	Deviation	Signed Rank
VB9	8	5	+3	+3.67
VB10	3	19	-16	-8
VB13	14	14	-	-
VB12	16	13	+3	+3.67
VB8	21	7	+14	+7
VB18	7	4	+3	+3.67
VB32	15	9	+6	+6
VB38	8	10	-2	-1.5
VB42	18	18	-	-
VB43	6	8	-2	-1.5
Totals	116	107		

^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. Differences in left-right compartment choices were not significant ($T = 11$, $P < .05$, Sokal and Rohlf, 1981; Wilcoxon and Wilcox, 1964).

Table 6. *Anolis carolinensis* female bias for left or right compartments as determined by Wilcoxon's Signed Rank Test (red females).^a

Female Number	Number of Choices for Left Compartment	Number of Choices for Right Compartment	Deviation	Signed Rank
BG54	19	13	+6	+5.67
BG56	14	3	+11	+10
BG58	17	9	+8	+8
BG66	11	7	+4	+4
BG68	15	9	+6	+5.67
SB1	16	13	+3	+1.5
BG4	16	25	-9	-9
SB3	22	19	+3	+1.5
BG6	19	13	+6	+5.67
SB10	12	14	-2	-1
Totals	161	125		

^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. There was a significant bias toward the left compartments ($T = 10$, $P < .05$, Sokal and Rohlf, 1981; Wilcoxon and Wilcox, 1964).

Signed Rank Test, $P < .05$) as a result of the strong left compartment bias of two females, BG056, who demonstrated a left compartment bias in both tests of 1985, and female BG066, who demonstrated a strong left bias in the second test of 1985. These two females further distorted the group left-right bias by moving more frequently than the other females in the second test of 1985, thus "weighting" the group data in favor of a left bias.

The 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 7). 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 statistics recorded in the experiments were for the two females who picked males of the opposite throat color.

Table 7. The five *Anolis carolinensis* females exhibiting significant preferences for males. ^a

Female No.	Female's Color Dewlap	Color Dewlap 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 ($P < .05$).

The five females who exhibited significant preferences visited their preferred males 77% of the time and the non-preferred males 23% of the time. Preferences were

independent of female body size, that is, the five varied considerably in weight and snout-vent length. 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 movement patterns of the five preferring females are shown in Figs. 3 and 4. For comparison, the movement patterns of the 8 non-preferring red females and of the 7 non-preferring gray females are averaged and represented in the graph in Fig. 5. 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 (Fig. 6, t-test, $p < .005$).

Three of the females demonstrating significant preferences (VB32, VB38 and VB42) were involved in both tests of 1985. The second test of 1985 provided the opportunity to test whether these females would pick from new pairs of males the same color (dewlap) of male. Gray female VB42, having demonstrated a strong preference for a gray male (44 gray : 12 red, $G = 9.63$) in the first experiment, died of a jaw injury which occurred after the first experiment ended and before the second was begun. Gray female VB32, having demonstrated a strong preference for a red male (23 red: 6 gray, $G = 10.45$) in the first experiment, demonstrated a numerical preference (12-5) for another red male in the second test. The third female, also a gray-throat, VB38, having shown strong preference for a gray male (22 gray : 7 red, $G = 8.00$) in the first experiment, demonstrated a very weak numerical preference (6-4) for a red male in the second experiment (Tables 8-13, Data Summary of Tests of Mate Selection).

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

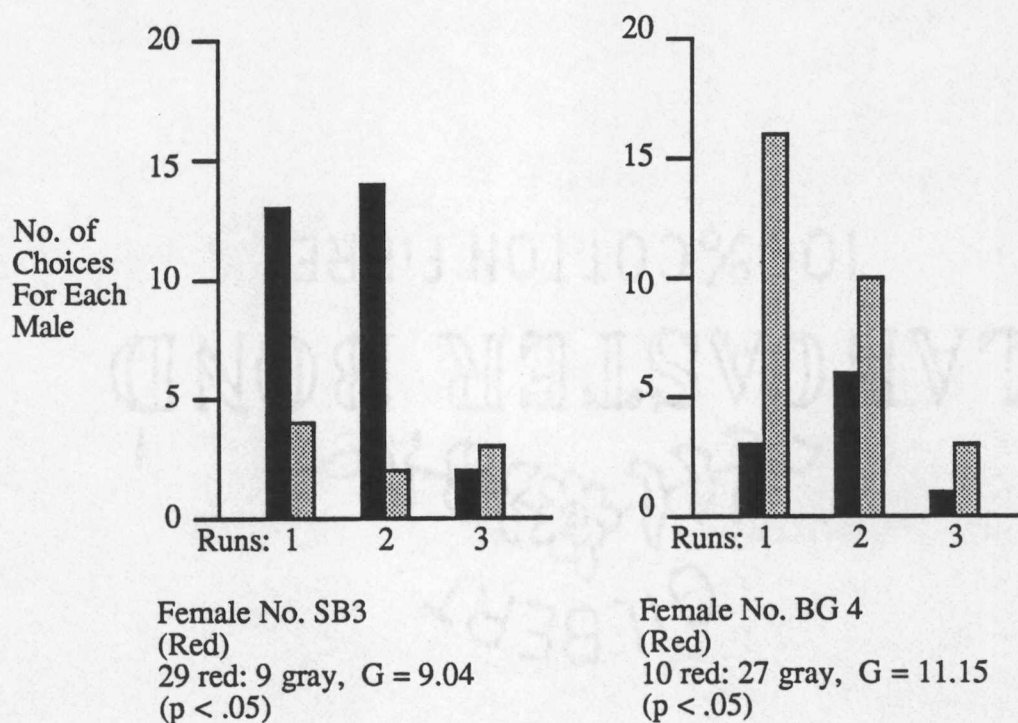


Fig. 3. Movement patterns of red females demonstrating significant preferences. Each pair of bars represents the choices the female made during one of the first three runs of the 1986 experiment.

Visits to red male: Visits to gray male:

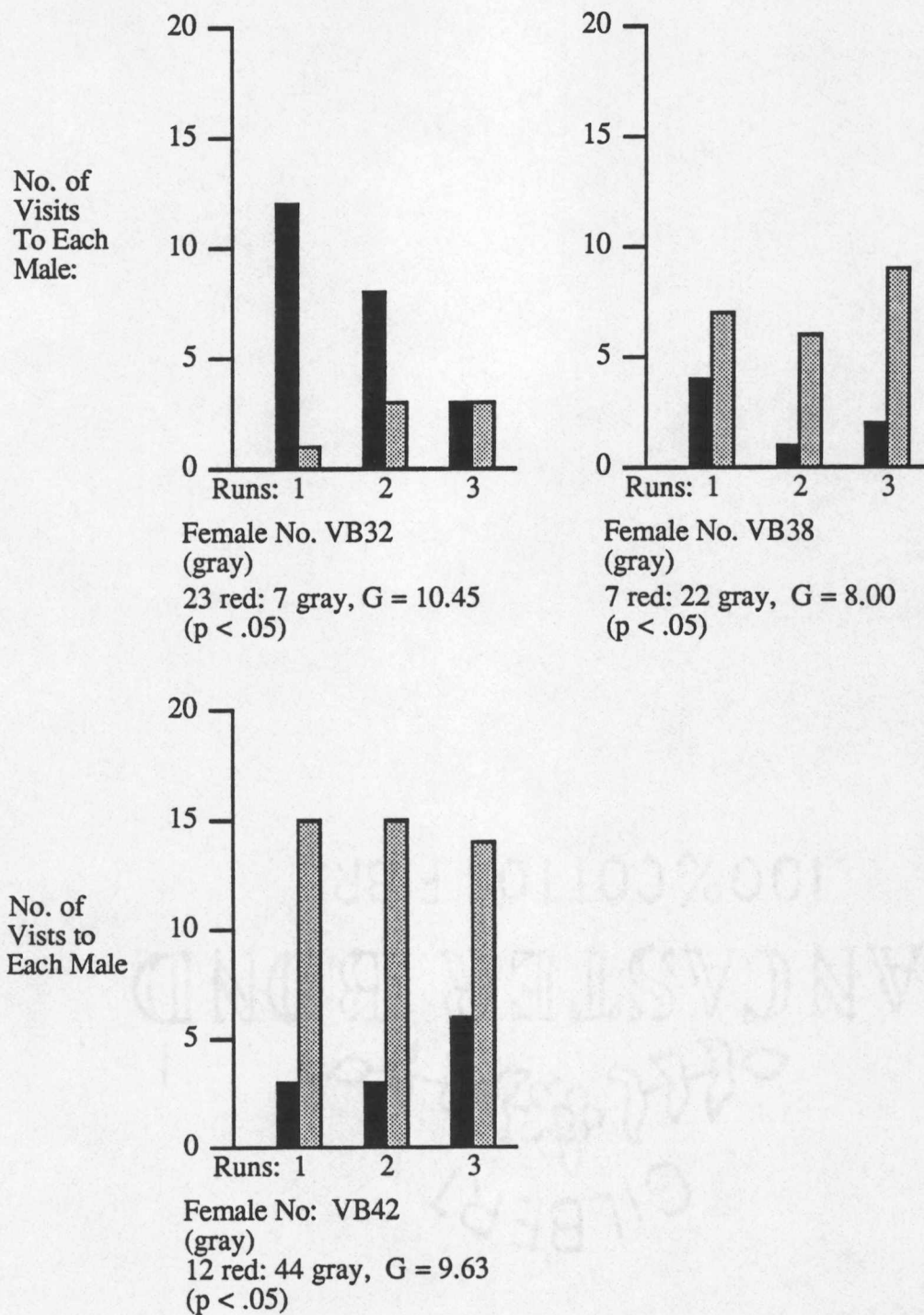


Fig. 4. Movement patterns of gray females demonstrating significant preferences. Each pair of bars represents the choices made in one of the runs of the first 1985 experiment. Visits to red male: Visits to gray male:

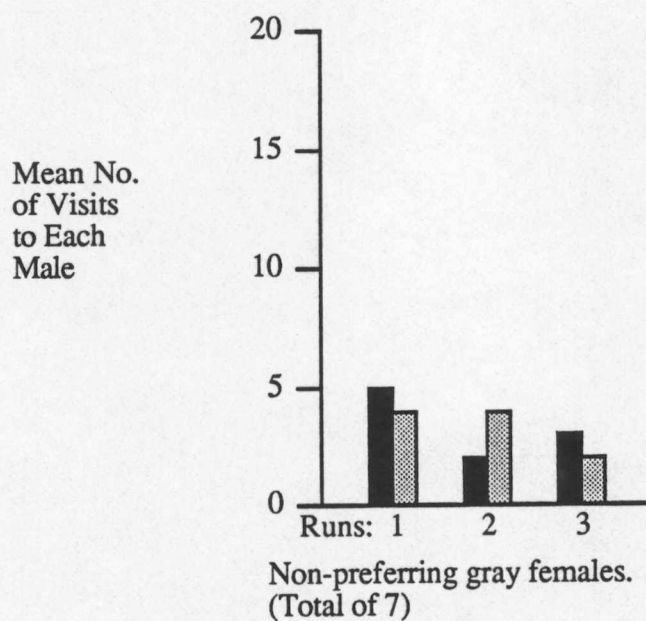
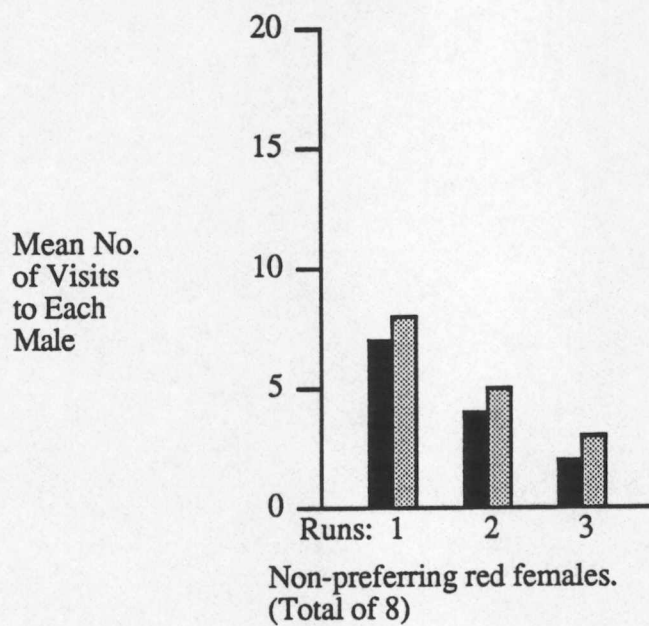


Fig. 5. Mean movement patterns of the 15 non-prefering females. The figures are based upon data from the first three runs of the first experiment of 1985 and the 1986 experiment. Visits to red males: Visits to gray males:

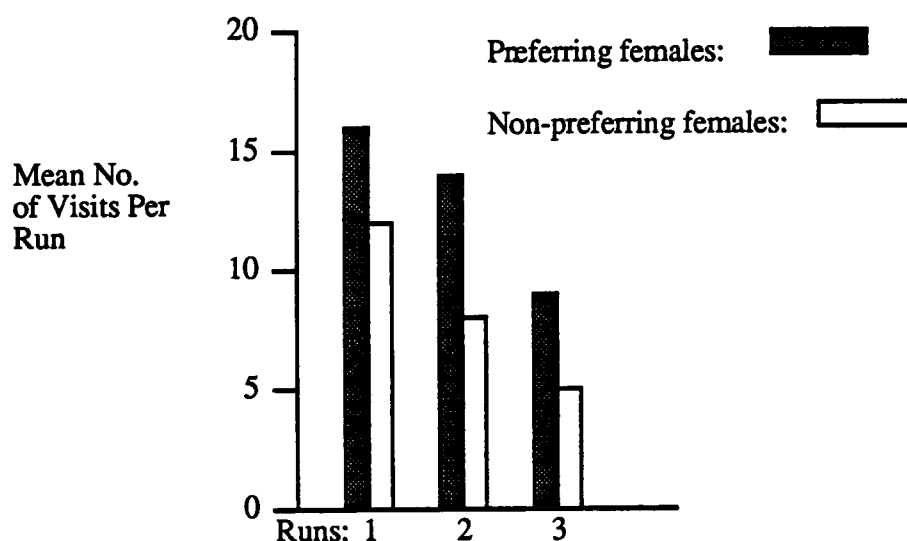


Fig. 6. Mean total movement of preferring females as compared to that of non-preferring females. Figures are based upon data taken from the first experiment of 1985 and the first three runs of the 1986 experiment. Each pair of bars represents one of the 3 runs of either experiment. Data from all 3 runs for every female were combined for evaluation by t-test. Movement of preferring females was significantly higher than that of non-preferring females ($p < .005$). For the three runs combined preferring females averaged 38.2 visits, non-preferring females averaged 24.5 visits.

Table 8. Data summary of tests of mate selection by female *Anolis carolinensis* (red-throated females, experiment beginning 6/26/85).^a

Female No.	Left-Right ^b				Dom./Sub.				Dewlap Color			
	L	R	N/C	G ^c	D	S	N/C	G	RD	GR	N/C	G
1. BG54	19	13	8	1.10	20	17	23	.24	17	20	23	.24
2. BG56	14	3	23	7.50	5	13	42	1.79	5	13	42	1.79
3. BG58	17	9	14	2.45	12	23	25	3.47	12	23	25	3.47
4. BG66	11	7	22	.87	14	12	34	.08	14	12	34	.08
5. BG68	15	9	16	1.49	13	16	31	.31	16	13	31	.31
Total:	76	41	83		64	81	155		64	81	155	
%Moves:	65	35	-		44	56	-		44	56	-	
%Options:	38	21.5	41.5		21	27	52		21	27	52	

^a (data from 3 10-day runs)

^b Left-Right data are taken from 1st 2 runs only.

^c G tests results of 3.84 and above are significant ($P < .05$, Sokal and Rohlf, 1981). All G tests are with Williams' Correction. In this test all red males were larger than their gray counterparts, so the data for size would be identical to that for Dewlap Color.

Table 9. Data summary of tests of mate selection by female *Anolis carolinensis* (red-throated females, experiment beginning 8/3/85).^a

Female No.	Left-Right			G ^b	Dom./Sub.			Dewlap Color ^c			
	L	R	N/C		D	S	N/C	GR	N/C	G	
1. BG54	8	7	25	.06	5	10	25	5	10	25	1.64
2. BG56	12	4	24	4.06	9	7	24	7	9	24	.24
3. BG58 ^d	4	1	35	-	2	3	35	2	3	35	-
4. BG66	17	3	20	10.55	8	12	20	8	12	20	.79
5. BG68	4	7	29	.79	-	-	-	5	6	29	.04
Total:	45	22	133		24	32	104	27	40	133	
%Moves:	67	33	-		43	57	-	40	60	-	
%Options:	22	11	67		15	20	65	13	20	67	

^a (data from two ten-day runs)

^b All G tests are with Williams' Correction. G tests results of 3.84 and above are significant ($P < .05$, Sokal and Rohlf, 1981).

^c In this test all red males were larger than their gray counterparts, so the data for size would be identical to that for Dewlap Color.

^d BG58 test did not yield sufficient moves for application of the G test.

Table 10. Data summary of tests of mate selection by female *Anolis carolinensis* (red-throated females, experiment beginning 7/29/86).^a

Female No. ^b	Left-Right			G ^c	Dom./Sub.			G	Dewlap Color ^d			
	L	R	N/C		D	S	N/C		RD	GR	N/C	G
1. SB1	16	13	51	.31	14	15	51	.03	14	15	51	.03
2. BG4	16	25	31	1.97	10	31	31	11.15	10	31	31	11.15
3. SB3	22	19	38	.22	30	11	38	9.04	30	11	38	9.04
4. BG6	19	13	46	1.10	12	20	46	1.99	12	20	46	1.99
5. SB10	12	14	43	.08	9	17	43	2.45	17	9	43	2.45
Total:	85	84	209		75	94	209		83	86	209	
%Moves:	50	50	-		45	55	-		49	51	-	
%Options:	22.5	22.5	55		20	25	55		22	23	55	

^a (data from 4 10-day runs)

^b SB1 is the only female in this test for which 4 complete runs (80 options) were recorded. SB3 (79 options) and BG6 (78 options) were nearly complete. BG4 (72 options) died near the end of her test and one of the males for SB10 (69 options) died during the last run.

^c All G tests are with Williams' Correction. G tests results of 3.84 and above are significant ($P < .05$, Sokal and Rohlf, 1981).

^d In this test all red males were larger than their gray counterparts, so the data for size would be identical to that for Dewlap Color.

Table 11. Data summary of tests of mate selection by female *Anolis carolinensis* (gray-throated females, experiment beginning 6/26/85).^a

Female No.	Left-Right ^b			G ^c	Dom./Sub.			Dewlap Color ^d				
	L	R	N/C		D	S	N/C	G	RD	GR	N/C	G
1. VB18	7	4	29	.79	6	6	48	0.00	6	6	48	0.00
2. VB32	15	9	16	1.48	6	23	31	10.45	23	6	31	10.45
3. VB38	8	10	22	.22	7	22	31	8.00	7	22	31	8.00
4. VB42	18	18	4	0.00	12	44	4	9.63	12	44	4	9.63
5. VB43	6	8	26	.28	-	-	-	-	13	10	37	.38
Total:	54	49	97		31	95	114		61	88	151	
%Moves:	52	48	-		24	76	-		41	59	-	
%Options:	27	24	49		13	40	47		20	30	50	

^a (data from three ten-day runs)

^b Left-Right data are taken from 1st 2 runs only.

^c G tests results of 3.84 and above are significant ($P < .05$, Sokal and Rohlf, 1981). All G tests are with Williams' Correction.

^d In this test all red males were larger than their gray counterparts, so the data for size would be identical to that for Dewlap Color.

Table 12. Data summary of tests of mate selection by female *Anolis carolinensis* (gray-throated females, experiment beginning 8/3/85).^a

Female No.	Left-Right			G ^b	Dom./Sub.			Dewlap Color ^c				
	L	R	N/C		D	S	N/C	G	RD	GR	N/C	G
1. VB18 ^d	3	5	12	-	5	3	12	-	3	5	12	-
2. VB32	7	10	23	.52	12	5	23	2.89	12	5	23	2.89
3. VB38	5	5	30	0.00	6	4	30	.38	6	4	30	.38
4. VB36 ^d	2	0	18	-	2	0	18	-	2	0	18	-
5. VB43	6	11	23	1.48	10	7	23	.52	7	10	23	.52
Total:	23	31	106		35	19	106		30	24	106	
%Moves:	43	57	-		65	35	-		56	44	-	
%Options:	14	19	67		22	12	66		19	15	66	

^a(data from 2 10-day runs)

^bG tests results of 3.84 and above are significant ($P < .05$, Sokal and Rohlf, 1981). All G tests are with Williams' Correction.

^cIn this test all red males were larger than their gray counterparts, so the data for size would be identical to that for Dewlap Color.

^dVB18 (20 options) and VB36 (20 options) did not complete 2 runs (40 options); males died during each of these tests. VB18 and VB36 tests did not yield a sufficient number of moves for application of the G test.

Table 13. Data summary of tests of mate selection by female *Anolis carolinensis* (gray-throated females, experiment beginning 7/29/86).^a

Female No.	Left-Right			Dom./Sub.			Dewlap Color		
	L	R	N/C	D	S	N/C	RD	GR	G
1. VB9	8	5	67	-	-	-	9	4	67
2. VB10 ^c	3	19	54	11	11	54	11	11	54
3. VB13	14	14	52	17	11	52	11	17	52
4. VB12	16	13	51	17	12	51	12	17	51
5. VB8	21	7	52	-	-	-	13	15	52
									1.90
									0.00
									1.27
									.85
									.14
Total:	62	58	276	45	34	157	56	64	276
%Moves:	52	48	-	57	43	-	47	53	-
%Options:	15	15	70	19	14	67	14	16	69

^a(data from 4 10-day runs)

^b All G tests are with William's Correction. G tests results of 3.84 and above are significant ($P < .05$, Sokal and Rohlf, 1981).

^cVB10 (76 options) is the only female in this test for which 4 complete runs (80 options) were not recorded; one of her males died during the last run.

Table 13 (continued) ^a

Female No.	Larger / Smaller Male ^b			
	L	S	N/C	G
1. VB9	* 4	9	67	1.90
2. VB10	*11	11	54	0.00
3. VB13	11	*17	52	1.27
4. VB12	12	*17	51	.85
5. VB8	*15	13	52	.14
Total:	53	67	276	
%Moves:	44	56	-	
%Options:	13	17	70	

* Indicates choices for a gray-throated male.

^aAll G tests are with Williams Correction. G tests results of 3.84 and above are significant ($P < .05$, Sokal and Rohlf, 1981).

^bThis was the only test in which some gray males were larger than their red counterparts. Gray males were the larger of the two males for females VB9, VB10 and VB8.

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 the first of individual males. By this test (which eliminates the second experiment of 1985) 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. The three red females who demonstrated left-right compartment bias in their choices did, as an apparent result of the bias, appear to pick the smaller males more often (34-20), but those figures are skewed by one of the three "biased" females, no. BG56, who severely altered her overall results by moving 10-1 in favor of a smaller gray male in her first 10 - day run and then moving a total of only seven times to either male during the following two 10-day runs. The "bias" for one compartment in this case may have been mate choice. If Andrew's more conservative evaluation (using only the first experiment for each animal) is applied to the red females of this study who did not show left-right compartment bias, five females picked the smaller male, four picked the larger.

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 gray: 10 red, $G = 11.15$) 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.

The size difference between these two males was one of the two largest recorded in the study, yet the smaller gray male was chosen.

Andrews (1985) found dominance to be correlated with 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. Two of the four ties occurred among the three pairs in which the gray male was the larger of the pair. 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 11 times. 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 13, 10 were submissive gray-throated males. Among the remaining 6 pairs of males in the study there were four pairs in which neither male was dominant and two pairs in which the female registered an equal number of visits to each male.

Four copulations were observed. In one instance, during the first 1985 experiment, copulation was observed between gray female VB32 and the red male for whom she demonstrated a very strong (23 red: 6 gray, $G=10.45$) preference. In the 1986 experiment, however, gray female NP12 copulated with red male SB16 despite her overall numerical choice (17 - 12) for gray male NP7. Closer examination of female NP12's behavior, however, appears to indicate that she "chose" the red male she copulated with during the first 10 - day run, in which she demonstrated a numerical (6 - 2) preference for him. When the males' positions were reversed, she went to the same compartment to discover the gray male, whom she had visited twice on only one previous day, in the compartment where the red was expected. She then developed a strong numerical preference (15 - 6) for the gray male, a preference which encompassed two additional male reversals. Red female SB10 copulated with red male SB15, for whom

she exhibited a numerical (17 - 9) preference. Red female BG66 copulated with red male BG46, for whom she demonstrated only a slight (14 - 12) numerical preference.

Three of the four females observed copulating continued to visit males in the days following the copulations. The fourth, female NP12, did not visit a male for 3 days after her observed copulation. The initial 2 - 3 visits following each copulation were to the same males with which the females had bred.

The three gray females exhibiting significant mate choice were all in the experiment of 6/26/85 and were all in adjoining cages on the east side of the test area, but they did not all choose in the same direction. Two of these females, VB032 and VB042, immediately demonstrated very high preferences for their males, one of which was in a left compartment, the other in a right compartment. After the males' positions were reversed the females continued their strong preferences for the originally selected males.

Movement to the outer compartments declined sharply after the first two ten - day runs of the experiments, irrespective of the time of year in which each experiment was begun. In the experiment of 6/26/85, for example, the first ten - day run registered 125 movements out of 200 possible moves, or 62.5%. In the second ten - day run females registered only 90 out of 200 possible moves, or 45%. Movement declined to 37.5% by the third ten - day run. The 8/3/85 experiment, which involved the same females used in the 6/26/85 experiment, females moved only 38% of the time during their first 10 - day run and 28% during the second run. Although the experiment of 7/29/86 began a full month later in the season than the experiment of 6/26/85, females demonstrated a similar pattern of declining movement, from 65% to 45% to 23% in the first 3 runs. The fourth run of the 7/29/86 experiment resulted in virtually no movement of the females.

Andrews (1985) referred to female movement to outer compartments in terms of the percentage of days of the experiments in which each female moved, rather than the percentage of total potential moves (two per day), which renders her figure of 72% (days

in which females moved) difficult to compare with the percentages here. To further complicate comparisons, the individual 10-day runs of this experiment did not begin until each female had moved to an outer compartment, which would tend to increase the percentages as compared to Andrews' figures. Also, this experiment was conducted in a greenhouse with no supplemental lighting; Andrews' experiments were conducted in a laboratory under artificial light with some natural supplementation. On extremely overcast days the females of this study exhibited virtually no movement. This factor tended to decrease movement relative to that recorded by Andrews.

Andrews (1985) recorded individual female movement on 29 - 97% of the days of her tests, with an overall average of 72%. If a similar movement - by - day evaluation of this study is done, with the fourth run of 1986 left out, females moved on 64% of the days of the experiments. For the first two runs of the experiments of 6/26/86, in which previously untested females were used, the females moved on 77% of the days of their experiments. An exact comparison cannot be made, but total movement as a percentage of options available appears to be slightly less than that recorded by Andrews. If severely overcast days, in which the most active females did not move, are deleted, movement is more frequent (by approximately 5-10 %) than that recorded by Andrews.

IV. DISCUSSION

Gray-throated males seem to disturb the normal scale of dominance and mate selection as previously observed in red-to-red interactions of *Anolis carolinensis*. The introduction of natural dewlap color as a variable into the experiment first conducted by Andrews (1985) skews the results in favor of gray-throated males, and, consequently, in favor of smaller males. In Andrews study, the larger male of *every* pair was dominant (Andrews, 1985, p. 287) 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: p. 411,412). 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' (1985) 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.

Hover (1985) found similar behavior in his study of dominance relationships between naturally occurring green and orange throat color morphs of male *Urosaurus ornatus* (Iguanidae). Green males were "more likely to dominate similarly sized orange males than (was) expected by chance" (Hover, 1985: p. 933). Green males in Hover's study lost their competitive advantage when their dewlaps were painted orange (Hover, 1985: p. 939), but, in an analysis which closely parallels my own assessment of gray-throat *Anolis carolinensis*, Hover states "there is some evidence, however, that there are inherent differences between orange and green males in aspects of behavior probably related to aggression" (Hover, 1985: p. 938).

Brown (work in progress), in a recent field study of interspecific encounters between gray-throated *Anolis carolinensis* and *Anolis sagrei*, observed on several occasions male gray-throats overwhelming and driving from their territories male *A. sagrei* which outweighed the *carolinensis* males by as much as two grams. Gray-throated *Anolis carolinensis* appears to be a more aggressive animal in both intra- and interspecific encounters than does its red-throated relative. These findings, coupled with the electrophoretic data presented by Wade, et al. (1983), the obvious size differences (Table 2), the additional behavioral differences cited by Christman (1980: p. 15) and, finally, the mate selection and dominance results of this study collectively give strong credence to the argument for (at least) subspecies recognition for gray-throated *Anolis carolinensis*.

Wade, et al. (1983) suggested that gray-throated *Anolis carolinensis* may be a second invader from Cuban *A. porcatius* stock, rather than a derivative of mainland *Anolis carolinensis* stock. The collective argument for subspecies recognition drawn from the studies previously listed would support that theory or, alternatively, a theory that the *Anolis carolinensis* population in southwest Florida became separated from the mainland population by rising sea levels and was subsequently reconnected after genetic drift and/or different selective pressures had rendered the gray throat population distinct from mainland *Anolis carolinensis*.

Williams recognized that *Anolis carolinensis* might not be a single species, noting "it certainly possesses a high variability" (Williams, 1969: p. 355). He does not entertain the possibility of more than one invasion of the mainland by *carolinensis* stock, however, and that premise is essential to a major theme Williams asserts for the *carolinensis* species group:

This group is nowhere known to have invaded an integrated complex of anoline species. . . . we know of no instance of capture of even the continental

margins in the presence of a resident anoline fauna. It has been a spectacular invader in the southeastern United States, but it is precisely there that it met no prior resident anole fauna. (Williams, 1969: p. 364)

Gray-throated *Anolis carolinensis* may in fact be the second invader which "captured the continental margins in the presence of a resident anoline fauna" and that fauna would have been the red-throated variety (or complex of varieties) of *Anolis carolinensis*. The gray-throats' range, however, puzzled Christman; he could find no correlation of that range with geological features or with ranges of extant plant or animal species.

Among alternate theories there remains a modified version of the "second invader" hypothesis of Wade et al. which must be considered: that gray-throated *Anolis carolinensis* stock, originating from Cuba, may have invaded their present range or a piece of it, but they did so when that region of Florida was not contiguous with the mainland, perhaps separated from the rest of Florida by higher sea levels of a period in the late Pleistocene or sub-Recent. If this were the case, the rejoining of the reef or island group to the mainland would have resulted in the *de facto* "invasion" of the red-throats' range by the gray-throats and, as such, could not be considered a true exception to Williams rule.

As a group, gray-throated females show no preference for either throat color; red-throated females as a group also show no preference. For individual females, whether red-throated or gray, the situation is obviously more complicated. A given female of either throat color may demonstrate a significant preference for a male of her own throat color or of the alternate color. This is consistent with Christman's (1980: p.15) observation that gray-throated males mounted both red and gray-throated females.

If the individual female *Anolis carolinensis* shows any preference at all, it tends to be a rather astoundingly strong preference, with G-test scores so high as to leave no

reasonable doubt she has selected one male over the other. Such females cannot 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. When these particular females are subjected to these "tricks" they may overcome the deception with an ease that makes the researcher's hours of effort in setting up the deception look rather foolish. Such was the case when female VB42 preferred male VB19 by 15-3 visits in her initial 10-day test. When her preferred male was switched to the opposite compartment she visited his original compartment three consecutive times, only to find another male, and then visited her preferred male fifteen consecutive times without once returning to the other male.

Andrews found a similar high fidelity among the females exhibiting significant preferences in her experiments. Among those nine females of Andrews' study there were G test scores as high as 18.49 and 19.46. The five females demonstrating significant preferences in this experiment had G scores as high as 11.15. One-third of Andrews' females exhibited a preference (Andrews, 1985, p.288); one-fourth of the females in this study preferred one male over the other.

The high G test scores of "preferring" females in the Andrews experiments and this study are intriguing, but perhaps equally puzzling are the scores of the females in both studies who did *not* show preferences. With very few exceptions, the scores of these females are far less than 2.0, that is, they failed to demonstrate so much as a strong trend, let alone a significant preference.

As previously mentioned, the numerical scores of these females seem to follow the same trend as the statistically significant findings with regard to mate selection as it relates to male dominance and size, that is, they demonstrate a tendency toward an unexpected, disproportionate preference for smaller and/or submissive males. But among the South Carolina females collected by Andrews and the females from three

different sites in Florida collected in this study, there seems to be very little middle ground: individuals show either dramatically strong mate preferences or comparatively weak numerical trends.

Andrews hypothesized "three nonexclusive explanations" for the reason why two-thirds of her females did not show significant preferences. In the first explanation, individual females exhibit different patterns of response. By this hypothesis, the females who did not prefer one male in the two studies did so because they would not have demonstrated a preference in the field; in this respect they would be behaviorally distinct from the "preferring" females.

The second explanation is that the females not discriminating between males "would do so if given more options for mate choice" (Andrews, 1985; p. 288). The third explanation given by Andrews is as follows:

Finally, discrimination between males by females may be weakly developed because, under natural conditions, females may seldom directly choose among males for mates. Instead, females may pick or compete for territories on the basis of food or other resources and males may compete with other males for territories that include females. If this is true, the association between females and particular males would be by default rather than by active mate choice. (Andrews, 1985; p. 288)

The first of these explanations, that the females of Andrews' study (and mine) are simply demonstrating different patterns of response, and would do so in the natural state, seems the least plausible of the three. 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; p. 358) or, according to Buth (1980: p. 282) 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. Were the phenomenon limited to one population, we could speculate that speciation might

be occurring at that site, but it occurs in three populations in south Florida and in Andrews' source population on Hilton Head Island in South Carolina.

The second explanation, that the females demonstrating no preference would do so if given more options, seems more plausible. Even the females in the smaller, more dispersed populations of this study, such as those inhabiting Vanderbilt Beach in Florida, could have been exposed to at least 2-3 males other than their apparent mates at time of their capture.

The third explanation, that females may choose their mates indirectly by first choosing food or other resources with the males' territories, also seems viable. The very existence of male dominance hierarchies implies some selective advantage to holding territories.

Andrews calls these explanations "nonexclusive". In my opinion, the second and third explanations may be the operative ones and may be sequential; females may indirectly select a group of males based on the resources of their combined territories and then select from the group an individual, based on his physical and behavioral characteristics.

As clearly demonstrated by this study and that of Andrews, once they have selected their mates, at least some females have a tremendous capacity to recognize and return to their preferred male. Andrews (1985) does not seem to separate this recognition factor and give it the attention it merits, perhaps because her focus was drawn to the 2/3 of the test animals who demonstrated no preference. The 1/3 that did show significant preference, and the 1/4 that did in my study, might be the true representatives of the natural behavior of *Anolis carolinensis* females in moderate to small natural populations inhabiting areas of limited resources.

The other 2/3 (or 3/4) may be thrown off their natural course in the experiments by factors relating to Andrews' second and third explanations, that is, that they haven't

enough males to choose from and cannot judge their males by the size or quality of their territories or by comparing the available food supplies. In both studies males were compelled to have territories that were virtually identical and females were never fed while in the males' compartments.

This discussion is necessarily limited to those factors which might sway the behavior of several or many females at a time; there is a virtually unlimited array of factors which might influence an individual female, of course, and those include her own sexual receptivity (although all females of my experiments did lay eggs and elicit courtship from their males) and the possibility that males may also have preferences and might not display to certain females.

Another possible explanation for the absence of mate selection behavior in 2/3 (or 3/4) of females could be added, that of the overall effects of captivity upon *Anolis carolinensis*. This factor could have the effect of reducing statistically significant preferences to numerical trends or to apparent random movement. The author's zoo and private collection experience with lizard species, though not published, is broad-based, involving at least 30 species in extensive breeding projects involving 20 individual animals or more, representing 7-8 of the lizard families. Of all of this diverse group, only a few species of Chamaeleonidae demonstrated as immediate and lasting a reaction to captivity as does *Anolis carolinensis*. Crews' assessment of *Anolis* as the perfect experimental reptile (Crews, 1977: p. 428-429) seems too all-encompassing; *Anolis carolinensis*, at least, is not a durable captive and does not necessarily retain "its social repertoire in captivity". *Anolis carolinensis* may retain primary behavior such as display action patterns for a considerable, if not indefinite period of time, but individual behavior which is in turn dependent upon layers of other behavior patterns in other individuals, as is mate selection, may quickly deteriorate in captivity. This phenomenon was inadvertently supported when the females of the two years of my study demonstrated

nearly identical declines in movement over time, although the 1985 animals began their tests four weeks earlier than did the 1986 animals. Moreover, the five females exhibiting significant preferences visited the outside compartments significantly more often (38:24) than did the non-preferring females. In Andrews (1985, p. 286) study, however, the same ratio was 32:31, for no significant difference.

In my zoo and private collection experience, many individuals of a variety of lizard species "crashed" when brought into captivity; that is, they temporarily went off feed and entered a state of general depression. Zoo curators are accustomed to these "crashes" and their patience is often rewarded with recoveries so dramatic as to yield an animal in far better condition than it was the day it was captured. Zoos and museums have conquered the mysteries of the environmental parameters, and, hence, the captive husbandry needs, for many formally "difficult" lizard genera to such an extent that these species are now readily bred and reared in captivity almost upon demand. These "success stories" involve a wide spectrum of genera and families [Behler and McCrystal, 1982 (Teiidae: *Ameiva* sp.); Bloxam, 1976 (Scincidae: *Leiolopisma* sp.); Bloxam, 1980 (Iguanidae: *Basiliscus* sp.); Bloxam and Vokins, 1978 (Gekkonidae: *Phelsuma* sp.); Conners, 1987 (Helodermatidae: *Heloderma horridum*); Demeter, 1976 (Gekkonidae: *Phelsuma* sp.); Demeter, 1981 (Agamidae: *Physignathus* sp.); Langerwerf, 1980 (Lacertidae: 17 *Lacerta* sp.); McKeown, 1981 (genera within Iguanidae, Scincidae and Gekkonidae); Montanucci, 1983 (Iguanidae: *Phrynosoma* sp.); Thorogood and Whimster, 1979 (Gekkonidae: *Eublepharis* sp.); Townsend, 1979 (Teiidae: *Cnemidophorus* sp.); Visser, 1984 (Agamidae: *Hydrosaurus* sp.); Wagner, 1974 (Gekkonidae: *Eublepharis* sp.);].

This is decidedly not the case for *Anolis carolinensis*. Although Crews (1980: p. 5) refers to it as a "hardy animal, living up to 3 years in captivity", the track record for captive husbandry of *Anolis carolinensis* simply cannot match that of most of the

"success stories" listed above. For many of those species, even the smaller ones with relatively short lifespans, to live only 3 years in captivity would be considered a disappointment. *Anolis carolinensis*, however, may only live 3-4 years in its natural state (Gordon, 1956: pp. 92, 252). To be fairly compared in this regard to the aforementioned "success story" species, however, captive *Anolis carolinensis* would have to exceed their expected natural lifespan on a fairly frequent basis.

If *carolinensis* "crash" in captivity it is usually a one-way phenomenon; they seldom recover to their original condition. The sheer number of *Anolis carolinensis* used in many laboratory experiments no doubt overwhelms the husbandry logistics on occasion, contributing to the poor track record for the species, but when all these external influences are taken into consideration *Anolis carolinensis* still emerges as a comparatively fragile captive species. This fragile nature is further emphasized by the extreme difficulties researchers have encountered in efforts to rear hatchling *Anolis carolinensis* in captivity (A.C. Echternacht, E. Michaud, pers. comm.). In many of the "success story" species previously mentioned, the authors could offer several, if not dozens, of second and third generation offspring in the form of healthy, viable adults as evidence of the captive hardiness or responsiveness of those species. There would be no sign of the deformities, vitamin/mineral deficiencies, and other growth related problems so prevalent in captive reared *carolinensis*. These offspring would be the rule, not the exception. In retrospect, it should be no surprise that such a small, short-lived and photosensitive species as *Anolis carolinensis* would be such a delicate captive.

It is in studies of the nature of my experiments and Andrews' tests that the dependability of the species might begin to break down, and that is why the behavior of the "preferring" females in Andrews study and my own should, in my opinion, carry even more weight than the data and statistical evaluation might suggest. Greenberg (1978), in a general review of "ethological constraints on the activity of captive reptiles",

outlined the many restrictions which captive lizard species might suffer, including the absence of seasonal fluctuation in temperature and photoperiod. For *Anolis carolinensis*, the complete set of behavioral data collected on a given captive group might grow less dependable as (1) the time since capture increases, especially after the first captive winter, or (2) the functional "distance" between the level of behavior studied and fundamental, primary behavior (e.g., display action patterns) increases, as it did in my study and that of Andrews, or (3) the captive setting becomes more unlike the natural setting in temperature regimen, photoperiod and physical characteristics or (4) when the individual's options for movement within thermal and light gradients are reduced. Any combination of these factors might cause a percentage, perhaps a majority, of the group to fail to perform as they would in nature.

If the 1/3 to 1/4 of female *Anolis carolinensis* in my study and Andrews' study who demonstrated male preference do in fact represent the behavior of most females in the natural state 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. The "fidelity factor" found in Andrews' study and my own would insure that most, if not all, of her offspring would receive the benefit of the genetic contribution of the most fit male. If the "fidelity factor" operated during 60-80% of her encounters with new males it would seem to be effective. The test results indicate the percentage may be higher, at least with some females. Since most chances for "raiding" a female would go to males holding neighboring territories, she would be relatively assured of not suffering the worst possible option, that of being bred by an inferior, wandering male.

From the size-dominance relationships found by Andrews (1985) and Greenberg and Noble (1944), it would seem that red-throated *Anolis carolinensis* would have long ago eliminated their gray-throated neighbors by virtue of the considerable size advantage the red-throated males would have over the gray-throated males. The "fidelity factor" of both red and gray-throated female *Anolis carolinensis* in Florida, coupled with the strong implications from both my study and that of Brown (in progress) that gray-throated males may be exceptionally aggressive, may partially explain how gray-throated *Anolis carolinensis* have maintained their range.

Crews and Greenberg (1981: p. 275) depict a seasonal sequence of events for *Anolis carolinensis* in which males emerge before females, establish territories through the use of assertion and challenge displays, and then maintain those territories through a pattern of relatively fewer challenges and more assertive displays. The males are generally in the maintenance phase by the time the females emerge. In regions where both color phases are in close proximity (Fig. 1, p. 8) gray males would, it seems from my study, have little problem in establishing and holding territories against red males during the early season before the emergence of the females. When gray females emerged, they would not necessarily be inclined to pick a male of their own color, but gray males would be holding most of the territories within the gray females' range. After both red and gray females along the zone of sympatry had selected mates, their "fidelity factor" would help insure that genes from either color phase would not leak across the zone. Such an influence might work in concert with differences (as yet unidentified) in the selective pressures between the ranges of the gray-throats and that of the red-throats; the combined effect of all of these factors would serve to maintain the gray-throats' range.

A "fidelity factor" as exemplified in the females of my study and in those of Andrews' study would seem useless in the population studied by Gordon (1956). He cites evidence of frequent "raiding" of females in his New Orleans study: females were

often bred by several males, including some who appeared to be wandering, territoriless mavericks of the population (Gordon, 1956: pp.122,127).

This paradox might be explained by the relative population and resource levels of the sites studied. From Gordon's collection figures (Gordon, 1956: pp.110, 111, 250) and from my own personal experience with both his and Andrews' study/collection sites it is apparent that the New Orleans site supports many more *Anolis carolinensis* per unit area than do either my sites or those of Andrews. Precise comparisons aren't available, but the difference must at least be a factor of 3 to 1. If this greater population level reflects a superior habitat resource for *Anolis 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. If mate selection operates at all in Gordon's population, it appears to operate by group rather than at the individual level: males holding territories, which often overlapped, were more aggressive and successful breeders than males who held no territories (Gordon, 1956: p.127). Selection may be operating at a different level or from a different angle altogether in the Louisiana populations: Gordon (1956: p.252) cites heavy rains followed by sudden temperature changes as a major cause of death in the New Orleans *carolinensis*.

In contrast, *Anolis 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, not continuous. Males and females are frequently caught in pairs, with few "odd" males or females to be seen. Even the unimaginative observer might sense an atmosphere of regimentation when looking at the community from a distance. In this community, to be "raided" by a wandering male would seem to be a considerable risk for a female to incur and summarily bestow upon her offspring.

If female *Anolis carolinensis* on Hilton Head Island, S.C., and those at

Vanderbilt Beach (Naples, Fla.) and Belle Glade, Fla., are limiting themselves primarily to one male and, in contrast, those in the New Orleans, La., area are not, there are independent means by which such a difference could be verified. The simplest method might be to run the experiment used in this study, using New Orleans females and males, but that simple application runs the risk of introducing extraneous factors which for some reason might discourage New Orleans females from demonstrating a "fidelity factor" that actually exists. For example, Andrews's second hypothesis for nonpreference, that females need more males to choose from, might be more relevant to New Orleans females. DNA "fingerprinting" of blood samples taken from successive offspring of females in each region should be the best method of revealing whether or not offspring of a given female are all of one father or of several fathers. If it can be shown conclusively that sperm remain viable for several months in the female, the DNA test could be easily done by capturing females in the height of their season and simply testing the succession of offspring obtained from each female while she remained captive. As many as 4 fertile eggs have been harvested from females held in isolation following capture (E.J. Michaud, pers. comm.). By the hypothesis presented here, one would expect offspring of New Orleans females to be of multiple fathers and those of Vanderbilt Beach and Belle Glade, Fla. or those of Hilton Head, S.C., to be of fewer fathers or, in many cases, of only one father.

If this is not the case, if females from all the collection sites of this study and that of Andrews have offspring fathered as randomly as those of New Orleans females, we will again be left to speculate why at least some *Anolis carolinensis* females demonstrate such a remarkable capacity to recognize and return to a specific male. Although its purpose in nature is not clear, the "fidelity factor" identified in my study and that of Andrews (1985) is, to my knowledge, one of the few instances in which individual mate recognition has been found in reptiles.

If *Anolis carolinensis* females do demonstrate a "fidelity factor" in the Hilton Head and south Florida populations and exhibit no such behavior in some Louisiana populations, then the Louisiana populations are either genetically incapable of the behavior through some divergence in the populations or the behavior is somehow inactivated under certain conditions which prevail in Louisiana. The fidelity factor discussed here may be a density-dependent or habitat related phenomenon which varies in its expression from population to population. Lande (1981,1982) produced models for the evolution of female choice which depicted geographical variation within a species for male traits and female preference for those traits. From information gathered from my study and that of Andrews (1985) we could modify Lande's hypothesis to say that geographical variation may exist in females' preferences, or in their ability or drive to reinforce their preferences through precise mate recognition and at least seasonal (and not necessarily complete) fidelity to the male preferred. That variation, if it does exist in nature, may have a genetic basis or it may simply be a variation in the expression of a trait omnipresent in the species. For species such as *Anolis carolinensis*, in which several matings occur per season, then, it is not simply a question of whether geographical variation exists in male traits and female preference for those traits, but also a question of whether females from separate populations differ in their expression and reinforcement of those preferences over time.

Hedrick (1987) and Wilson and Hedrick (1982) speak of the "economics of mate choice":

. . . time and energy costs or the risk of predation could limit travel by females between prospective mates, and restrict their ability to choose the most preferred males as mates. Considerations such as these (which we term the "economics" of mate choice) could be important in many species exhibiting female mate choice. . . (Hedrick, 1987: p. 46)

At Vanderbilt Beach, where resources are limited and interrupted by high-risk

predator zones, the "economics" of mate choice as described by Hedrick and Wilson may become very tight, indeed. The various environmental factors which combine to make mate choice economics "tight" for a female, however, might simultaneously make the risk of being fathered by a territoriless male very high to her offspring. A female paired with a territory-holding male encounters the potential costs of mate choice economics as she ventures in search of a superior male, whether in fact she finds a superior male or is "raided" by a territoriless male inferior to her original mate. Environmental factors such as predators and restricted resources make mate choice "economics" of a female's generation more severe, but if she should be bred by an inferior male those same environmental factors could be visited upon her offspring who are less fit to withstand the "economics" of their own generation. Thus, the fidelity factor in a given population might be the females' "answer" to selective pressures in both their own generation and that of their offspring.

V. CONCLUSION

The major findings of this study were (1) that females of some gray and red-throated populations of *Anolis carolinensis* possess an allegiance to specific males which I call a "fidelity factor", and (2) that male gray-throated *Anolis carolinensis* seem to be more aggressive for their size than male red-throats. DNA fingerprinting or electrophoretic study of offspring of females from south Florida and New Orleans should confirm or reject the presence of a fidelity factor or determine whether it exists in some populations and not in others. Brown's (work in progress) study of interspecific encounters between gray-throated *Anolis carolinensis* and *Anolis sagrei* should be repeated for red-throated male *Anolis carolinensis*. If red-throated males did not perform as aggressively against *Anolis sagrei* as did the gray-throats, my hypothesis of exceptional aggression in the gray-throated males would receive further confirmation.

The true relationship between gray-throated and red-throated *Anolis carolinensis* may never be fully revealed; the entire range of the gray-throats and that portion of the red-throats' range which is within south Florida are being overrun by enormous numbers of *Anolis sagrei*, which seems to be experiencing ecological release throughout the Florida peninsula. The exact competitive advantage is not known, but in those portions of south Florida which have been invaded by *Anolis sagrei* densities of *Anolis carolinensis* populations have been severely reduced.

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