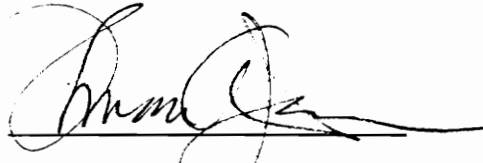BEHAVIORAL, TEMPORAL, AND SPATIAL RELATIONSHIPS

IN FREE-RANGING FEMALE *ANOLIS CAROLINENSIS*

(SAURIA: POLYCHRIDAE)

by

Steven C. Nunez

Thesis submitted to the faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree of
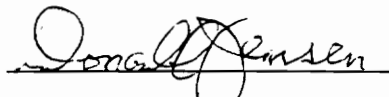
MASTER OF SCIENCE in Biology

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(ABSTRACT)

The behavior and spatial relationships of 7 male and 22 females were described from 56 days of observation from focal and scan samples made between 0830 and 1830 h during May-July, 1993 at the Augusta Canal near Augusta, Georgia. Behavioral observations indicated that females primarily remain stationary (82.6%), while dividing the remainder of their time into travelling (7.7%), overt foraging (1.5%), and social interactions (8.2%). Though territorial, inter-female contacts were rare (0.3%) with more of a female's time spent interacting with the resident male (3.2%) or in copula (3.9%). Females used three methods to capture prey: (1) sit-and-wait (84%), (2) opportunistic prey captures (11%), and (3) active search (5%). Dewlap extension is primarily used during aggressive interactions with females (60%), but rarely during courtship (2%) or copula (7%). Predation pressure was minimal as only four predator avoidances were observed.

Home range volume and area for males averaged 68.5 m^3 and 50.5 m^2, respectively. For females, home range volume and area were considerable smaller than males,

averaging 7.8 m^3 and 8.2 m^2, respectively. Intra-sexual overlap averaged 0% for males and 18% for females. Male snout-vent length (SVL) was positively correlated with male home range area and number of females overlapped. Female SVL did not correlate with either volume or area of territory. However, within a male's territory, the largest female usually controlled the largest home range volume, perched highest, and maintained a green body color most often. Females tended to perch on smaller diameter limbs and to perch higher than males.

ACKNOWLEDGEMENTS

This study would have never been completed if it were not for the knowledge, experience, patience, and skill of many people to which I am indebted. First, I wish to thank my advisor Dr. Thomas Jenssen, who through his wise leadership eventually saw the completion of this project. Secondly, I wish to thank my other committee members, Drs. Jack Cranford and Donald Jensen for their critical readings, long discussions, and helpful suggestions. There are many people who I wish to thank for their support during the field season of 1993 including Kim Orrell, Kasey Ersland, and Travis Tuchak. Without their support this project would have never made it past the proposal stages.

Finally, I would like to thank my parents, relatives, and friends for their continuous monitoring and maintenance of my mental state during these two years.

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GENERAL INTRODUCTION

CHAPTER I

Anolis carolinensis (green anole) is a small, arboreal, insectivorous lizard found in the semi-tropical environments of the south eastern United States and Bahamas. Anolis carolinensis is the only anole endemic to the United States, making it the most northerly distributed anole of the genus, with some populations located as far north as Tennessee (Conant, 1975). The lizard seems to be a habitat generalist, found over a broad geographic distribution, many diverse habitats, and experiencing a wide range of environmental conditions.

Anolis carolinensis is one of the most studied of anoles (Crews, 1977), with over a hundred papers published on its life history, reproduction, behavior, distribution, morphological characteristics, and endocrinology, yet surprisingly most of the data were collected on laboratory populations and not free-ranging subjects. Also, much of the data were collected specifically from males, leaving a male-biased record for many topics.

The research was initiated to thoroughly study and characterize the structural niche and behavior of females from a free-ranging A. carolinensis population. Specifically, a thorough time budget analysis was conducted on female A. carolinensis that provides for the first time a field level control that can be used as a comparison with laboratory studies. Home range size and structural niche components (perch heights and diameters)

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for male and female $\underline{A}$. $\underline{carolinensis}$ were also estimated to help quantify and clarify intra and intersexual relationships in the species.

LITERATURE REVIEW

CHAPTER II

In the early 1940's, Greenberg and Noble conducted a set of experiments that were meticulous and so well conceived as to be of great use some 50 years later. The subsequent paper released (Greenberg and Noble, 1944) explained in great scientific detail the many behaviors and activities of the carolina anole, <u>A</u>. <u>carolinensis</u>. While primarily descriptive in nature, the observations revealed many unique behaviors and other unique phenomena. These observations permitted Greenberg and Noble to expound on something as broad as territoriality as or unique as specific gestures that the lizards make. Since that period, hundreds of additional papers have expanded our knowledge of the lizard <u>A</u>. <u>carolinensis</u>.

Male <u>A</u>. <u>carolinensis</u> are sexually dimorphic, territorial, and polygynous (Greenberg and Noble, 1944; Ruby, 1984). Males have larger territories than females in order to maximize overlap with neighboring female home ranges (female defense polygyny) (Hickon, 1987). By guarding against male intruders, the male territory owner could increase the number of offspring potentially sired by minimizing the risk of another male copulating with the females in his territory, practically guaranteeing that the female will bear his young. If male and female territories remain relatively fixed and stable throughout the breeding season, then this strategy would guarantee a large number of

offspring sired by the territorial male.

It is possible for a male territory owner to maximize his reproductive success by increasing the number of females within his territory, to guard those females from any intruding males, and to only copulate with the female at the moment of oestrus. Any unnecessary copulations with the female would waste valuable energy and time that could be better utilized by the male to patrol his territory, search for food, and/or mate.

Sexual selection theory predicts that in species in which males invest nothing in their offspring other than sperm (little parental investment), that males be selected to maximize their reproductive success by fertilizing as many eggs as possible, and therefore, maximizing his number of copulations with females (Trivers, 1976; Darwin, 1871). The only limitation to the fertilization rate is the number of available fertilizable females (Emlen and Oring, 1977).

However, there is now accumulating evidence that ejaculates are not as cheap as once thought, and this limitation can impose a constraint on the numbers of females a male can inseminate and consequently the number of eggs he can fertilize (Dewsbury, 1982). Therefore, unnecessary copulations could easily increase the potential costs of reproduction by lowering the sperm count of individual males in subsequent copulations (Dewsbury, 1982).

Other costs of reproduction could include decreased survival and increased energy expenditure to males that must patrol their territorial boundaries and expose themselves more often to predation than females (Parker and Pianka, 1973). Ruby (1984) showed

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that male A. carolinensis lost weight in the peak reproductive months, possibly due to increased energy expenditures. Unnecessary copulations would expose both males and females to increased predation (Crews, 1973b; Trivers, 1976). This is especially true for A. carolinensis which copulate in the open for long periods of time (Ruby, 1984), for periods of up to 28 minutes (Jenssen, pers. comm.). This is probably due to the fact that sperm transfer to the female only occurs late in the copulatory event (Conner and Crews, 1980).

All female anoles exhibit a unique pattern of reproduction in which two ovaries alternate in the production of a single ova throughout the reproductive season (Licht, 1973). Since female reproduction is limited to producing only one egg a reproductive cycle (8-10 days for A. carolinensis; Andrews, 1985; Licht, 1973), and because the breeding season in A. carolinensis is limited to a maximum of five months (19-20 eggs total per breeding season maximum), then it is important that the matings are successful in producing fertile ova. Hence, it seems plausible that males would copulate with the available females at least once per egg cycle to guarantee the fertility of the eggs.

Anolis females can store sperm for later use if males are unavailable for direct insemination (Cuellar, 1966; Fox, 1963), as sperm has been shown to be viable for long periods of time (up to four months) (Cuellar, 1966). Fox (1963) suggested that sperm storage was primarily used to lengthen the breeding season, and could be used in two ways: (1) use the stored sperm early in the reproductive season before mating actually began or (2) use the stored sperm when males were experiencing testicular regression

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later that same year.

While male behavior and social structure of lizards has been extensively studied, female lizards have been studied less or have been ignored totally in many species of lizards (e.g., Fleishman, 1988). Many generalizations are made about female behavior from male behavior studies, but it is necessary to study female behaviors in detail as well if a more rigorous understanding of the organism is to be achieved. While female behavior studies are lacking, those that have been conducted give a greater understanding of female behavior in Anolis lizards (Hicks and Trivers, 1983; Stamps, 1973; Jenssen, 1970). Behavioral studies on female A. carolinensis are also lacking and an extensive study would contribute to a greater understanding of female behavior.

The studies that have been conducted on Anolis females have shown that female behaviors are rather diverse in their expression. Anolis females can be highly aggressive toward other females as in Anolis aeneus (Stamps, 1973) or quite tolerant as in Anolis valencienni (Hicks and Trivers, 1983). Aggressiveness is highly correlated with whether the females exhibit some territoriality or if the females are free ranging. There are some very good studies on female social relationships (Greenberg and Noble, 1944; Stamps, 1973), but they are lacking in number in contrast to male lizards probably because males have more conspicuous displays and behavior than females (Stamps, 1977).

Male and female Anolis form dominance hierarchies or tyrant-subordinate relationships under laboratory conditions, usually when the lizards are at high conspecific densities (e.g., Greenberg and Noble, 1944). However, while many possible dominant-

subordinate relationships have been described for male Anolis species in free-ranging populations (Stamps, 1977), only one free-ranging female Anolis species has been described as having dominant relationships (A. aeneus; Stamps, 1973).

Female Anolis show considerable more overlap in their home ranges than their male counterparts, but still typically fight amongst themselves (Stamps, 1977). Central portions of the home range may be defended vigorously while intrusion into the periphery may be tolerated (Stamps, 1977). Territoriality occurs during the breeding season with only a few exceptions (e.g., Anolis opalinus, Jenssen unpubl. data). Male and female A. carolinensis are considered territorial with the male often including three to five females in his territory (Greenberg and Noble, 1944). Few studies have been conducted on a truly arboreal lizard species (e.g., A. carolinensis) that adequately explained the expanse of an individual territory. Obviously, the typical method (estimating area; Rose, 1982) of calculating home range or territory size cannot be used for an arboreal species because the species is partitioning the environment in three dimensions, and new methods must be devised to more adequately describe the home range volume of a species.

To quantify the relationship of the lizard with its habitat and to look at the interactions between lizards, investigators often looked at different aspects of the lizard's daily life. Variables could include displays between lizards, typical perch heights and perch diameters for arboreal species, copulation rates, site fidelity, and so on. These variables mean very little by themselves, but combined can piece together the life history of the species. Many investigators have studied A. carolinensis, and there is a large

collection of life history information available (Fox, 1963; Crews et al., 1974) including social behavior (Greenberg and Noble, 1944; Ruby 1984). While many of the behavior studies are of use, some may be suspect in their results and conclusions because they were conducted in the laboratory and/or under unnatural conditions (Greenberg and Noble, 1944; Andrews, 1985).

HABITAT DESCRIPTION

AND

GENERAL METHODS

CHAPTER III

Data were collected along the Augusta Canal in a bottomland hardwood forest (Workman and McLeod, 1990), 12 km NW of Augusta, Georgia from the beginning of May to the end of July 1993. After July, breeding subsides, dramatically affecting many behaviors (Licht, 1967; Michuad, 1990; Jenssen et al., 1995). The configuration of the canal provided an excellent study site for extended focal animal observations (Altmann, 1974). Between the canal and a tow path was a strip of habitat (Fig. 1) in which males and females established home ranges, and which greatly facilitated observation of lizard behavior. The tow path, approximately 3-4 m above the ground, provided an elevated platform to facilitate the observation of A. carolinensis as they moved vertically within their habitat. The observer could also parallel any lateral movements of a lizard by transversing the length of the tow path. Last, the narrowness of the habitat, rarely extending beyond 4 m deep, insured visual contact when a lizard moved to the backside of its territory.

Choosing subjects for study was based on several conditions: (1) females were found associated within a habitat cluster patrolled by a male; (2) this habitat cluster could not be too dense so as to preclude extended observation periods of individual lizards; and (3)

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the habitat cluster should be complex enough (containing at least one tree) to reflect representative lizard densities. Each habitat cluster observed was a consistent subset of all available habitat, but may not be completely representative of a more complex, contiguous habitat found in the surrounding geographic areas in which $\underline{A}$. carolinensis is also found.

After a habitat cluster was chosen, the resident male was noosed, his Snout-Vent Length (SVL) measured to the nearest 1.0 mm, and a unique visual identification pattern placed on his neck and tail with waterproof acrylic paint. After being toe-clipped for permanent identification, a released male would quickly resume normal activity (within minutes). Observations were then initiated to determine the extent of a male's territory, and the females residing within his patrol area. Females were captured by hand or noose as they were observed and processed as described for males. No behavioral observations were taken from females for at least 5 hours after capture to insure their return to normal activity. Data were only taken from adult females (SVL >45 mm, Michuad, 1990). Each male's territory was observed from 0830 to 1830 h for eight consecutive days. Observation was facilitated by 8X binoculars, with data recorded onto preprinted data sheets. The resulting sample was seven adult males and the 22 associated adult females.

Climatological variables, measured every 30 min on site, were air temperature (using a shaded quick reading thermometer at breast height), relative humidity (using a slinging cyclometer), and relative sun coverage. The later was estimated for a 30 min period by determining the amount of time direct sunlight was blocked as follows: 1) clear - direct

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sunlight >25 min, 2) partly cloudy - direct sunlight between 5 - 25 min, and 3) cloudy - direct sunlight <5 min. Climatological conditions during the study favored uninterrupted lizard activity; only one day of observation was shortened for longer than one hour due to rain storms.

BEHAVIOR AND TIME BUDGET OF FREE-RANGING

FEMALE *ANOLIS CAROLINENSIS*

CHAPTER IV

INTRODUCTION

The social behavior of female anoline lizards has been largely neglected, except as an adjunct to male courtship behavior (e.g., Crews, 1973b, 1981; Ruby, 1984; Fleishman, 1988). Perhaps the male-biased record is due to the more sedentary and inconspicuous nature of females (Stamps, 1977). However, the possibility exists that investigators have underestimated the range of expression of female social organization and influence. Where data are available, there appear to be considerable interspecific differences between females as well as intersexual differences within species. For example, Anolis nebulosus (Jenssen, 1970) and Anolis aeneus (Stamps, 1973) females are very aggressive toward consexuals, while female Anolis valencienni are quite tolerant of one another (Hicks and Trivers, 1983). Within species, time budget analyses of Anolis polylepis and Anolis humilis have shown that females spend much less of their time in social encounters and more time foraging than conspecific males (Andrews, 1971; Talbot, 1979).

For Anolis carolinensis, the most studied of anoles (Crews, 1977), there are few data

from free-ranging females (e.g., Gordon, 1956; Ruby, 1984). Perhaps because the species is easily obtained through dealers, what is known about female A. carolinensis social behavior has been derived from captive-held subjects (e.g., Crews, 1973a, b; Evans, 1936a b, 1938; Greenberg and Noble, 1944), and is largely anecdotal or inferential as it relates to natural populations. Without validation from the field, the accuracy and relevance of lab studies to natural systems remain open to question, partly because of intrinsic problems associated with the response of lizards to captivity (Moore et al., 1991; Jenssen et al., 1995).

The present study was initiated to quantify basic activities and relationships of female A. carolinensis to their habitat and nearest neighbors, using free-ranging subjects and naturally occurring social groups. My specific objectives were to describe the activity profile of female A. carolinensis including: (1) territoriality and female-female relationships, (2) male-female courtship, (3) foraging methods and success rates, (4) predator avoidance techniques and frequencies, and (5) general locomotion characteristics.

METHODS AND MATERIALS

Over a 56 day period, the seven groups of females were each observed for eight consecutive days. Each day, females of a group were located in the morning and observed by 1-3 observers from 0830 to 1830. When spotted, a female was watched for 30 min or until she moved out of sight. After a 30 min focal animal sample (Altmann, 1974), observations were shifted to another female within the male's territory for the next 30 min sample.

Observed behaviors were divided into the categories of activities and acts. The first category, called "events", was comprised of seven modes of activities which could be operationally defined (see Table 1) and established a contextual disposition in which more ephemeral behaviors were embedded. These latter behaviors comprised the second category, called "occurrences", and numbered 12 kinds of acts (Table 2). Event and occurrence variables differed temporally. Events, such as the activity disposition of being stationary had temporal significance, and were maintained over long durations, ranging from most of a minute to an hour. A multiple function stopwatch permitted the observer the flexibility of stopping the timing of one event, while continuing to time other events simultaneously. Occurrences, such as the act of displaying or tongue touching, were of very short durations and had more significance as frequency data.

Types of movement and distance travelled were also tallied during each event. Types of movement recorded were creeping, walking, running, and jumping. Distance travelled

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was determined by either estimating the number of body lengths moved and/or by using a tape measure extended along the tow path. Estimated distance travelled is fairly accurate because females rarely travelled distances greater than 1 m and often travelled at a slow pace.

Nonparametric statistics were used to quantify results (Hollander and Wolfe, 1973). All descriptive statistics are given as means ($\bar{x}$) with standard errors (SE).

RESULTS

Subjects

The behaviors of 22 females ($\bar{x}$ SVL=50.0 mm, SE 0.8 mm) were recorded for an average of 4.1 h/subject (SE 0.8 h) over all times of the day, with an abundance of data during the morning (Fig. 2). The decreasing hours of observation in the afternoon directly reflected a change of perch sites from those on exposed positions to those in more dense foliage where females were less conspicuous.

Environmental Conditions

Air Temperature.-- Air temperatures at 1000 h averaged 25.9°C (SE 0.11), which is close to the minimum "preferred" body temperature reported for A. carolinensis (Clark and Kroll, 1974); behavioral observations also indicated that females appeared to increase activity levels at this time. The daily average air temperature for our observational period was 29°C (SE 0.16), with a mean starting temperature of 23.0°C (SE 0.50) and a daily maximum air temperature averaging 32.7°C (SE 0.48) (Fig. 3). During periods in the afternoon when air temperature was >35°C, females tended to move down into shadier portions of the foliage (canal side), hindering observation (Fig. 2).

Cloud Cover.-- Most observation hours (approx. 86%) were cloudless or had only minimal cloud cover. Cloud density was initially high in the morning, tapering off by 1100, but again increasing in density by late afternoon (Fig. 4). The late afternoon also brought increased chances for rain, as some days were briefly interrupted (< 30 min)

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by rain storms.

Time of Day.-- Emergence was variable among females because tree canopies to the east could delay basking opportunities early in the morning; typically lizards emerged by 0900 h. By 1000 h, lizard behavior had shifted from sedentary basking to more active behaviors. By early evening (1800 h), female movement decreased, with lizards being less responsive to events around them. Shade patterns changed as the day progressed, and as air temperature increased during the later fraction of the day (1200-1400 h; Fig. 3), lizards would move with these shade patterns to avoid direct sunlight.

Relative Humidity.-- Relative humidity averaged 65.7% (SE 0.42) and ranged from 100% (rain) to a low of 20%. Relative humidity was negatively correlated with air temperature (Spearman, r= -0.62, P= 0.0001).

Events

Stationary.-- Females were in a stationary mode for 82.6% of the time (Fig. 5). During the stationary event, females frequently reoriented their body position and direction, averaging 13.5 body shifts/h. The distance actually travelled per movement, however, averaged only 5.6 cm/move (SE 0.04).

Occurrence behaviors initiated while females were stationary were rare (Table 3). Mouth wipes ($\bar{x}$=2.1 times/h) mostly occurred when females were shedding and seemed to facilitate skin removal from the head. Mouth smacking ($\bar{x}$=0.6 times/h) was infrequent, and may have concluded unobserved foraging attempts. Solitary, nondirected headbob displays were infrequent ($\bar{x}$=1.3/h), and were rarely performed with dewlap

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extension ($\bar{x}=0.1$ displays/h).

Travel.-- Travelling only accounted for 7.8% of the female daily activity profile (Fig. 5), averaging 167 moves/h and 20.8 cm/movement (SE 1.0) during the travelling event (Fig. 6). Females frequently walked (48%) and creeped (29%), yet were rarely seen to either jump (17%) or run (6%) during travelling. The frequency of mean headbob displays during bouts of travelling was only 6.1 times/h (Table 3). Females rarely stopped and displayed during their travels, but instead used headbobs to initiate and conclude a travel event. Tail undulations also increased from 0.24 times/h while stationary to 4.8 times/h when travelling (Table 3).

Forage.-- Females overtly foraged during only 1.5% of their daily activity profile (Fig. 5), averaging 1.2 attempts /h. Females made about the same number of prey capture attempts during all activity hours of the day (Chi Square, $P > 0.05$).

Females used three methods to capture prey: (1) a sit-and-wait strategy in which the lizard remained nearly motionless until an insect came within range of capture; (2) an active search in which the female creeped about the foliage in search of prey, and (3) opportunistic prey detection while travelling during which a female would divert from her original path to make a foraging attempt. These three methods were used in differing frequencies and success rates, with sit-and-wait the most frequent and successful (Fig. 7).

Female unknown.-- Activities for which the purpose was not clear were brief ($\bar{x}=$ 57 s, SE 14), yet the display rates for this event were high, averaging 107.0 displays/h

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with dewlap extended and 38.0 displays/h without dewlap extended (Table 3). Specific recipients of these displays could not be seen, resulting in the uncertain context or possible function for the behavior. I made no attempt to distinguish individual bob patterns for females as has been described for males (DeCourcy and Jenssen, 1994). However, of the 29 female-unknown events observed, nine events were entirely composed of volleys of headbobs without dewlap extension, 17 entirely composed of volleys of headbobs with dewlap extension, and in only three instances was there a combination of headbobs with and without dewlap extension during a volley.

Social Encounters.-- The remaining 8.2% of an average female day was composed of identifiable social encounters (female-female, male-female, and copulation) (Fig. 5). Thus, an accumulation of one hour each day (for a 10-11 hour activity period) was devoted to social interactions.

Female-female encounters were rare and brief, lasting an average of 1.6 min (SE 36 s). Female $\underline{A}$. carolinensis are territorial (Chapter V), and if a female intruded into the territory of an adjacent female, the resident quickly responded with displays and a chase (27.6 m/h). Resident females were seen using headbob displays with dewlap extension ($\bar{x}$ rate =20.7 displays/h) presumably to intimidate the female intruders at a distance, but would occasionally headbob without dewlap extension ($\bar{x}$ rate =13.8 displays/h). Female-female encounters usually were limited to individuals interacting across home range boundaries using ritualized aggressive behavior. However, in nine aggressive encounters in which both females were positively identified, the largest female always

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chased the smaller female from the immediate area. One encounter was seen in which a resident female lunged at an intruding female, and then grabbed the intruder's neck and head in her jaws. The intruder quickly broke free of the resident's grip and retreated by jumping 2 m to the ground.

Females often responded to a male's courtship with a display rate of 88.9 displays/h; 98% of these displays were without dewlap extension (Table 3). If the female was receptive toward the male's advances, she would continuously headbob, remain relatively motionless, turn her back to the approaching male, and then neck bend. If the female was not receptive, she would still headbob, but she would not turn her back to the approaching male. If the male continued the approach toward the unreceptive female, the female would run away.

In 43 observed copulations, females were almost always passive and neck bent for the male. A neck grip by the male preceded all copulations. Copulatory duration ranged from 4.0 to 51.5 min and averaged 23.7 min (SE 1.35) and the neck hold was usually maintained for the extent of the copulation. Once the hemipenis was inserted, it appeared impossible for the female to break free of the male's grip, possibly due to hemipenile tumescence (Crews, 1973b). Females would occasionally try to free themselves by jerking, shaking, and dragging the male, but a female was never seen to succeed in breaking the male's hold. In 50% of the copulations initiated in direct sunlight and/or in relatively open areas of the foliage, the female dragged the male for up to two meters from the original spot of hemipenial insertion to a more secluded,

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shaded area.

During copulation, females headbobbed for the duration of the encounter, averaging 61 displays/copulation (137.5 headbobs/h) (Table 3). Very rarely (one out of eight copulations observed for this data set), did the female extend her dewlap during copulation.

Post-copulatory behavior was observed after 14 copulations. Both the male and female would leave the immediate site of copulation; the male usually returned to territorial patrol, and the female returned to the stationary context after moving 0.5 m (SE 0.14). During the immediate post-copulatory period, females registered a mean display rate of 45.5 displays/h (Table 3), but these displays did not appear to be directed at any lizard.

Locomotion

General Movement.-- Air temperature, humidity, cloud cover, or time of day did not appear to affect distance travelled by females, as females moved similar distances/h over all environmental and temporal conditions recorded (Regression analysis, $P > 0.05$). Females moved a mean total of 40 m for every 10 h observation period (Fig. 6). Females averaged more than 12 creeps/h, but the majority of the distance moved was conducted when the female was walking (10 walks/h). Bouts of running were rare (1.4/h), but the distance covered during a run was > 1 m. Female A. carolinensis were capable of some extraordinary jumps (> 2 m), even though jumping was used little (3.1/h). A female's longest jumps were associated with female-female chases.

Predator Avoidance.-- In over 2000 observation hours, only four instances were observed in which either a male or a female A. carolinensis were seen to avoid a potential predator. One instance was in response to a snake (Coluber constrictor) climbing the limb on which a male was perched, and three instances involved lizards avoiding a crow (Corvus brachyrhynchos) that was in flight 2-3 m overhead.

DISCUSSION

My study documents for the first time the behavior of female $\underline{A}$. carolinensis within natural environmental and social conditions. The study showed that females have a wide diversity of behaviors, some contradictory to previous laboratory evidence, and some undescribed for females of this species.

Locomotion/Distance Travelled.-- Females remained stationary and inconspicuous during most of the day. Only 7.8% of the activity period was spent travelling, in part due to the small female home range volume ($\bar{x}=7.8$ m^3; Chapter V), with an overall daily mean distance of 40 m. Females rarely ran or jumped, primarily relying on creeping and walking to move throughout the habitat. In contrast, male $\underline{A}$. carolinensis spend a quarter of each day travelling, and are much more conspicuous than the sedentary females due to the larger number of displays and frequent long-distance moves (Jenssen et al., 1995). Males travel an average of 4 (Nunez, unpubl. data) to 7 times further per day (Jenssen et al., 1995) than an average female.

Only one paper has reported distance travelled data on female anoles (Lister and Aguayo, 1992). They found that female $\underline{A}$. nebulosus moved only 1.4 m/h, or almost three times less distance/h than female $\underline{A}$. carolinensis. However, in studies in which sex was unspecified (Bennett and Gormon, 1979; Moermond, 1979), $\underline{A}$. carolinensis females still travelled more distance/h than six of eight anoles reported in those studies. So while female $\underline{A}$. carolinensis has often been characterized as sedentary in comparison

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to the male, in many instances, female $\underline{A}$. carolinensis often travel more distance than other anoles, making it one of the most active female anole for its size.

Foraging.-- Essentially, Anolis species have been deemed "pure pursuers" (MacArthur and Levins, 1964) in which they remain relatively motionless and locate prey by scanning the area around their perch. However, this terminology oversimplifies what for most lizards is a complex set of foraging techniques. Other anoles, while primarily sit and wait predators, have the ability to switch to active search methods when necessary (e.g., Anolis polylepis; Andrews, 1971; $\underline{A}$. chlorocyanus, Rand, 1962). Both male (Jenssen et al., 1995) and female $\underline{A}$. carolinensis used "sit-and-wait", "opportunistic", and "active search" methods of foraging. While the first strategy was the most successful (89%) and most used (82%) (Fig. 7), lizards should only continue the sit-and-wait strategy when prey is uniformly distributed (Krebs, 1978), and should switch to active searching when prey densities become clumped. However, there may be a greater cost to being either an opportunistic or an active searcher because: (1) both methods are used rarely by male or female $\underline{A}$. carolinensis; and (2) successful prey captures for both opportunistic and active search techniques were lower than the sit-and-wait method (Fig. 7).

The "survey posture" has been described in many species as a foraging-related behavior of anoles. It consists of perching vertically with head down and arched at a 45° angle to the body (Rand, 1962, 1967; Andrews, 1971; Scott et al., 1976), facilitating the lizard to visually scan the ground for prey (Rand, 1962, 1967). For $\underline{A}$. carolinensis,

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neither males (Jenssen et al., 1995) nor females in the present study made much use of this posture. Instead, A. carolinensis were more inclined to be horizontally perched and infrequently attempted prey captures on the ground.

Female-Female Aggression.-- Females are territorial, yet within nearest neighbor aggregations, show indications of dominant-subordinate relationships (Chapter V). However, dominant-subordinate expressions are subtle because female interactions were infrequent (1 interaction/5h), brief ($\bar{x}=1.6$ min), and occupied only 0.3% of the time budget of a female. If, however, a female crossed territorial boundaries (intruder), then the neighbor (resident) would upon spotting the intrusion, display (34.5 displays/h) with the dewlap sometimes extended (60%), and quickly chase the intruder (27.6 m/h) from the territory. The low encounter rate suggests that unlike conspecific males, there is a tolerance for the near proximity of consexuals. Is this a tolerance based on a non-invasive policy of a defended habitat volume, or a minimum individual distance phenomenon? Data support the former because home ranges are small and generally non-overlapping (Chapter V). Previous laboratory studies in which subjects were at unnatural densities suggest that female-female encounters are quite frequent and violent. For example Greenberg and Noble (1944) saw high encounter rates and highly aggressive females in their laboratory population where 10 females fought 218 times in three months; this is contradictory to our findings.

Advertisement.-- Traditionally, Anolis females are portrayed as displaying only during immediate social encounters. In fact, female territorial advertisement has only

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been documented in one other anole, the highly aggressive A. aeneus (Stamps, 1973). In A. carolinensis, advertisement displays, as described for the male (DeCourcy and Jenssen, 1994), are yet undescribed and unquantified for females. Our observations suggest for the first time that free-ranging female A. carolinensis perform nondirected advertisement displays. Single nondirected displays were given at low frequencies during the stationary phase ($\leq$ 1.3 /h). However, during female-unknown events seemingly nondirected displaying increased dramatically, with 74% of the displays with dewlap extension (Table 3). Searches failed to reveal any other conspecifics near the serial displaying females. In one case, a female was seen to transverse a limb, pausing every 10 cm to headbob with dewlap extended. Her behavior was so similar to a patrolling male that she was recaptured to confirm her sex.

Dewlap Function.-- Female A. carolinensis seemed to be using their display repertoire much differently than males. Male A. carolinensis display types have been described and consist of three patterns of headbob signals, labelled the type A, B, and C displays (DeCourcy and Jenssen, 1994). These three patterns are shared by females as well (Jenssen et al., in prep.). Males performing each display type can either include or exclude dewlap extension. Our study suggests that females also display with or without the dewlap extended. Females withhold the dewlap during courtship (90 displays/h, 1.6% with dewlap) and copulatory displaying (148.6 displays/h, 7% with dewlap), yet often extend it in the presence of females (34.5 displays/h, 60% with dewlap). In laboratory studies, females were also seen to use the dewlap approximately

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60% of the time during female-female encounters (Kim Orrell, unpubl. data). The dewlap may function as an added aggressive component to the normal repertoire of a female's A,B, or C displays (Orrell, personal communication).

Response to Environmental Conditions.-- Female A. carolinensis responded to increasing air temperatures and lower humidity by decreasing perch heights (Chapter V). Females are probably moving away from areas with direct sunlight in the upper canopy to areas that are more shaded in the lower canopy in order to maintain preferred body temperatures. Also, lizards would typically move to the west facing side portion of their habitat later in the day in conjunction with the movement of sun. Movement into more dense habitat hindered observation, and resulted in less accumulated data during the later portions of each observation day (Fig. 2).

Reagan (1992) indicated that ground level scan sampling may be inadequate when gathering data on arboreal species because many lizards could be unobserved in the upper canopy, possibly leading to erroneous density calculations. Our observations indicate that scan sample accuracy is also highly dependent on the time of day, as lizards were seen to decrease perch heights with increased temperatures (Chapter V), setting up a situation where afternoon censuses might under estimate population densities.

Predator Avoidance.-- Female lizards usually remain stationary to increase crypticity and decrease energetic demands (Rose, 1982). Male lizards are usually more active (Andrews, 1971; Nunez and Jenssen, pers. observ.) and more conspicuous than females (Parker and Pianka, 1973), accounting for greater injury rates for many male lizards

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(Parker and Pianka, 1973; Schoener and Schoener, 1980). Male A. carolinensis were much more conspicuous than females because of the high movement and display rates of males (Jenssen et al., 1995). However, there are no data to quantify whether males are more preyed upon at our study site than females. Schoener and Schoener (1980) found evidence to suggest that in some populations, male A. carolinensis had higher injury rates than females (i.e., tail breaks), yet the overall injury rate was still very low for both sexes. On our study site, predation appeared low as only four instances of predator avoidance were recorded in over 2000 hours of observation. While the lizards on our study site seemed to be less preyed upon than other A. carolinensis populations (e.g., Crews, 1981), a more detailed study is needed since most of the data on predation pressure is largely anecdotal.

Summary and Conclusion

The few previous studies conducted on female Anolis behavior have shown that their behavior can be quite diverse in its expression and much different than males and between species (Stamps, 1973; Jenssen, 1970; Hicks and Trivers, 1983; Andrews, 1971; Talbot, 1979). In contrast to males, female A. carolinensis spend over 80% of each day remaining stationary, primarily as a sit-and-wait predator. While only 1.5% of each day was devoted to overt foraging, females had high overall success rates in capturing prey (89%), eating an average of 13 times/day. Females had three prey capture methods: sit-and-wait, opportunistic, and active searching. If prey becomes clumped, females presumably switched from sit-and-wait predators, to active searchers. Less than 10% of

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each day was devoted to social interactions. Even though females are territorial and can form dominant-subordinate relationships (Chapter V), females rarely encountered one another. However, female-female encounters could be very violent. Females used the dewlap as an aggressive component in their normal display behavior, especially during female-female encounters. Females were also seen to have nondirected displays, perhaps serving as territorial advertisement.

SPATIAL AND SOCIAL RELATIONSHIPS

OF FREE-RANGING *ANOLIS CAROLINENSIS*:

Evidence for Inter-Female Dominance

CHAPTER V

INTRODUCTION

Aggregation and its consequences have been discussed for many years (Allee et al.,

1949; Darling, 1952; Fisher 1954) and have been studied in birds (Darling, 1952; Fisher,

1954), fish (Phillips, 1974), and lizards (Kiester, 1979). Kiester et al. (1975) reported

that three species of <u>Anolis</u> lizards often use high perches to observe the quality of the

surrounding habitat before establishing territories ("post-vantage behavior"); it was also

suggested (Kiester, 1979; Kiester and Slatken, 1974) that lizards might indirectly track

resource levels (i.e., food items) within a habitat by observing the presence and/or

behavior of conspecifics. Individuals might also use conspecifics as a cue to habitat

quality where minimal quality is guaranteed by the mere presence of a long-term resident

on a homesite ("minimal quality" hypothesis; Stamps, 1987a). If habitat quality is

patchy, some individuals might prefer territories of lower quality that are adjacent to high

quality territories, leading to a short term disadvantage, but which increases the

probability of acquiring a high quality territory in the future ("future advantage"

hypothesis; Stamps, 1987b). Others have suggested that aggregating improves and/or accelerates breeding performance (Darling, 1952; Fisher, 1954), or improves defense against intruders and/or competitors ("competitor defense" hypothesis; Burger, 1981; Getty, 1981).

Besides naturally occurring aggregations, artificial aggregations are created in laboratories and zoos, by restricting inter-individual distances. Animals of captive aggregations often form social hierarchies, which in turn become the subjects of social studies (e.g., Evans, 1936 a,b; Greenberg and Noble, 1944; Crews, 1973b). However, an argument persists whether dominance structures in captivity reflect naturally occurring populations or are an artifact of sustained crowding (Gartlan, 1968; Rowell, 1974; Jenssen et al., 1995). To make the issue more convoluted, investigators have had difficulty in defining variables that consistently correlate with dominance, as variables differ not only between species, but populations as well (Bernstein, 1981).

As has been described for many iguanians (Carpenter, 1967), male <u>Anolis</u> <u>carolinensis</u> form dominant/subordinate relationships in captivity (Evans, 1936a; Greenberg and Noble, 1944). Previous laboratory studies (e.g., Greenberg et al., 1984; Greenberg and Crews, 1990) have indicated that dominant males are significantly greener, perch higher, and had higher levels of circulating androgens than subordinate males, while the latter appeared to have increased levels of stress (greater corticosterone levels) and reduced courtship rates. Yet, laboratory studies as well as field observations have indicated that both male and female <u>A</u>. <u>carolinensis</u> are territorial (Evans, 1936b;

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Greenberg and Noble, 1944; Ruby, 1984; Jenssen et al., 1995).

Thus, the perceptions from available laboratory studies concerning the social structure of male and female $\underline{A}$. carolinensis are contradictory and unreconciled with the social behavior of natural populations. Both sexes are described as being territorial, while also prone to dominant/subordinate relationships when involuntarily crowded. Fundamental to the solution of the schismatic view of $\underline{A}$. carolinensis is an observational record for the spatial and social relationships of naturally occurring lizard aggregations. Our specific objectives were to: (1) determine home range size of both males and females; (2) determine the spatial overlap between neighboring females and between territorial males; (3) describe the social organization of aggregated females (e.g., hierarchical, despotic, or rank neutral); and (4) describe female micro-habitat utilization (i.e., perch heights and diameters).

METHODS AND MATERIALS

Scan samples (Altmann, 1974) of each female's perch diameter, perch height, general location within the habitat (see below), and body color were made at intervals $\geq$ 30 min. These variables for males appear elsewhere (Jenssen et al., 1995). Female perch diameters were estimated to the nearest 5 mm. Perch height estimates were facilitated by a 7 m pole marked in 0.5 m increments with fluorescent orange paint and placed against the base of the tallest tree in the territory. Female body color was categorized as either green, olive, or brown.

To estimate the volume of female home ranges, an X, Y, Z coordinate system was developed to describe the general location of the lizard within the habitat. The X coordinate (width) was estimated ($\pm$ 0.3 m) from a tape measure that was placed along the tow path and paralleled the width of the territory. The Y coordinate (depth) was taken with a range finder (Ranging, model 120); accuracy decreased with distance, and at 7 m (maximum home range depth) was $\pm$ 0.2 m. The Z coordinate (height) was estimated ($\pm$ 0.3 m) by the vertical pole mentioned previously. Scan samples of spatial locations (X, Y, Z) for each female in the habitat were accumulated over an eight day period to be transformed into a three-dimensional scatter diagram describing her home range volume. However, the portion of a female's home range volume which was defended (i.e., territory volume) could not be strictly determined as few female interactions were observed.

To derive female home range volumes, the sets of X, Y, Z vectors for each female

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were first plotted (Proc Plot, SAS Institute, 1988) using X-Y (width-depth) coordinates at one meter height increments (Z coordinate). From each scatter diagram, at each 1 m slice, a minimum convex polygon (Rose, 1982) was manually scribed with a Numonics (Model 605-1A) digitizer to give a resultant area. This area was considered a volume, or a 1 m thick slice of a female's home range. Summation of the series of 1 m "slices" produced the total home range volume (m^3) for each female.

Amount of overlap between resident females and also between resident females and the resident male were calculated for each individual from the following formula;

$$Overlap = (\sum_{n=0}^{s} AO)/TV$$

where n is equal to the ranges of 1 m slices in which individual lizards coexist; where s is equal to the total number of 1 m slices in which lizards coexist; where AO is equal to the amount of overlap between individuals at each 1 m slice; and TV which is equal to the total volume of the home range for the individual in which overlap computations are being made.

The convex polygon method was also used to calculate the total area (m^2) of each resident female home range. The data for each lizard were plotted once more, but without regard to the Z coordinate. The area of the resulting convex polygon was derived with a digitizer, including overlap between female home range areas, and

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between the resident male home range area (see below) with respective resident females.

The calculations of home range volume and area for each male followed the same methods as the female data, with one exception. During each eight day observation period, the male was seen to use all parts of his specific habitat. Therefore, vectored perch sites were not necessary to calculate male home ranges; instead, each male's home range could be depicted by vectoring the outer edges of the clumps of vegetation which he was seen to visit. This was not the case with female home ranges as females partitioned a vegetational continuum.

Nonparametric statistics were used to quantify results (Hollander and Wolfe, 1973). All descriptive statistics are given as means ($\bar{x}$) with standard errors (SE). The calculated P values used during Backward Elimination Stepwise linear regression are conditionally given due to the regressors eliminated previously and must be cautiously interpreted.

RESULTS

Home range Size

Male Home Range Size.-- For the home ranges of 7 males, 851 vectors (X,Y,Z coordinates) were measured ($\bar{x}$=122.3 vectors, SE 6.6). Male home range volume and area averaged 68 m^3 and 51 m^2, respectively (Table 4). No observed male shared his home range with another male; therefore, there was no overlap between male home ranges. Most of a male's territorial volume was unoccupied by females and averaged only a 10% overlap with the combined resident female home ranges.

Male size (SVL) was significantly correlated with area of territory (Spearman, r=0.82, P=0.02), but not significantly correlated with his territorial volume (Spearman, r=0.73, P=0.06). Because home range depth was limited by the tow path and canal for all males, no significant correlation occurred between SVL and home range depth (Spearman, r=0.67, P=0.10). However, SVL was correlated with home range width (Spearman, r=0.82, P=0.02). Larger males also overlapped more females than smaller males (Spearman, r=0.94, P=0.001).

Female Home Range Size.-- Adult females were seen to aggregate near trees with some underlying brush, often within the confines of a tree's canopy. Less suitable habitats (i.e., without trees) were sometimes visited by females, but infrequently.

Home ranges of 22 females were calculated from 480 vectors ($\bar{x}$=23.7 vectors, SE 0.6). Mean female home range volume and area were 7.8 m^3 and 8.2 m^2, respectively

(Table 4). There were no significant correlations between SVL and home range volume or SVL and home range area (Spearman, r=0.17, P=0.47; r=0.08, P=0.72, respectively).

Using home range area, female-female overlap averaged 50% (Table 4). However, when using volumetric data, average overlap between females was only 18%.

As female home range volume increased, the amount of female-female overlap also increased (Spearman, r=0.62, P=0.002). Female distance travelled/h (data from Chapter 2) increased as female-female overlap increased (Spearman, r=0.59, P=0.01), but female distance travelled/h was not significantly correlated with either territorial volume (Spearman, r=0.36, P=0.15) or area (Spearman, r=0.30, P=0.10). Volumetric and area measurements indicate that male overlap with female territories were 50% and 83% respectively (Table 4).

<div align="center">Female Perch Niche and Body Color</div>

Perch Diameter.-- Perch diameter data indicates that males and females used all available perch diameters, from the smallest limb to the largest trunk (Fig. 8). Females, however, primarily inhabit perches of mean distribution (1.0 - 8.0 mm), while males have a more uniform distribution across all perch diameters, frequenting larger tree trunks (16.0 - 32.0 mm) and smaller limbs (0.5 - 1.0 mm) (Fig. 8). As sample size varied between individuals, average mean perch diameters were computed for males and females to reduce any individual bias on statistical procedures. Males were found on average to perch on larger diameter limbs than females ($\bar{x}$=5.31 cm, SE 0.57; $\bar{x}$=3.44

cm, SE 0.62; respectively; Wilcoxon Rank Sum, P= 0.006). There was no significant regression between perch diameter and hour of day, air temperature, relative humidity, cloud cover, or time of year (Backward Elimination Stepwise linear regression, P> 0.05).

Perch Height.-- The asymmetric female perch height distribution was more uniformly distributed than the male's asymmetric distribution (Fig. 9). Females tend to distribute themselves uniformly throughout the habitat (Fig. 9), possibly reflecting a repulsive distribution among resident females, while males tend to perch below 2 m. However, when average means were computed for males and females to reduce individual bias, perch height means were not significantly different between males and females ($\bar{x}$=2.27 m, SE 0.29; $\bar{x}$=2.43 m, SE 0.25; respectively; Wilcoxon Rank Sum, P=0.87). Females were found to inhabit the entire available vertical range of habitat, perching as high as 7 m. However, there were no trends with maximum available perches and the mean perch heights of females (Spearman, r=0.24, P=0.54).

There was a significant regression between perch heights and month of observation and air temperature; however, the decreases in perch height were not correlated with time of day, relative humidity or amount of sun coverage (Backward Elimination Stepwise linear regression, r^2=0.23, P< 0.0001). The strong seasonal effect can possibly be explained by the strong correlation between air temperature and month of observation as there were significant increases in mean air temperature during the three months of observation (Kruskal-Wallis Test, P=0.0001).

Female Color.-- Scan samples (N=200) of body color for 15 resident females within four male territories indicated that females were twice as likely to be green (62%) as brown (31%), and rarely intermediate or olive (7%). On an individual basis, however, some females within a male's territory tended to be consistently green, while others were consistently more brown (Chi Square, P$\leq$ 0.025). There was no correlation between female SVL and percentage time green (%) for the pooled sample (Spearman, r=0.01, P= 0.91). However, when comparing among females aggregated within a male's territory (i.e., overlapping home ranges), the largest female of the aggregate was the most consistently green (Fig. 10a), usually perched higher (Fig. 10b), and controlled larger home ranges (Fig. 11).

DISCUSSION

Our observations and those of Jenssen et al. (1995) and Ruby (1984) indicate that male A. carolinensis are territorial, have larger home ranges than females, and tolerate little overlap with other territorial males. Females also appeared territorial, tolerating little overlap with other females. Nevertheless, females were seen to aggregate in habitat clusters centered about a tree. This aggregation of females was curious because adjacent habitat without trees was available for expansion or dispersal of home ranges, but went unused by adult females. Thus in our sample, small female aggregations (2-4 females) appeared to be voluntary, long-term, and subject to the formation of female dominant-subordinate relationships (see below).

Structural Niche

Male Home Range.-- Male lizards typically have larger home ranges than females, even in cases where adult females are on average larger than adult males (Rose, 1982). Anolis carolinensis is no exception as male mean territorial volume (69 m^3) is one of the largest reported for Anolis species of similar size (Table 5), and is about nine times greater in size than the average female home range (8 m^3). In the present study and those of Ruby (1984) and Jenssen et al. (1995), male A. carolinensis were known to be polygynous and have been described as expanding their territorial boundaries to maximize overlap with female home ranges (Schoener and Schoener, 1982; Hickon, 1987). Larger males appear more successful at initially expanding territory size and defending

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boundaries during the breeding season as our data showed a positive relationship both between male size (SVL) and territorial areas and between male size and the number of females overlapped by a male.

Schoener and Schoener (1982) indicated that male lizards may not necessarily be maximizing the size of their territory, but only the number of females overlapped. Our data only partially supported this hypothesis as male size was not significantly correlated with male territorial volume, but did correlate with basal area and maximum width of territories. Therefore, it is impossible to determine whether the male is maximizing the size of his territory or whether the male is directly maximizing the number of resident females overlapped (e.g., Anolis sagrei, Schoener and Schoener, 1982).

Male-Male Overlap.-- Anolis carolinensis males overlap very little with other territorial males, a characteristic of many other anoline males (e.g., A. lineatopus, Rand 1967; A. garmani, Trivers 1976; A. cuperus, Fleming and Hooker, 1975). However, during our observations there were three small males (< 60 mm SVL) who occasionally entered the peripheries of resident male territories. The three small males displayed or moved little, presumably to remain hidden from the actual territorial holders. The territorial male would, upon spotting an intruder, quickly chase the intruder out of his territory into either an unclaimed area or into an adjacent male's territory, yet the same intruder was continuously seen in the same general location every day in which we observed.

Male-Male Relationships.-- How might one classify male A. carolinensis

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relationships, particularly in light of contradictory data that indicate that aggregated males can not only form dominant-subordinate hierarchies, but can also be territorial? Several types of social systems have been described for free-ranging males: (1) the "dominant-subordinate" relationship where large males tolerate (low aggression) the presence of smaller males within their territories (e.g., A. lineatopus, Rand, 1967; A. nebulosus, Jenssen, 1970); (2) the "floater" which has a large undefended home range that interdigitates with the territories of more than one male (e.g., A. cupreus, Fleming and Hooker, 1975; A. cristatellus, Philibosian, 1972); and (3) the "nearest territorial neighbor" which is the typical condition between territorial males exhibiting similar aggressive status. On our site, the relationship of male A. carolinensis who intruded into the territories of our observed males did not exactly fit any of the above types for three reasons. First, the intruders did not appear to be vestiges of a dominant-subordinate hierarchy because the intruders occupied predictable areas outside the resident's territory, and were consistently driven from the territory by an intolerant resident. Second, because the intruders were predictably seen in the same general locations adjacent to those territories under observation, these potential interlopers were not considered floaters. Last, the intruders did not demonstrate the equal status of a neighboring territorial owner because the intruders did not appear to have females within the confines of their home ranges or to give frequent advertisement displays (Nunez, unpubl. data). Perhaps the intruders represent a fourth type of relationship, the "destitute neighbor". It is likely that these "destitute" intruders are subadult males who are trying to expand

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their territorial boundaries from areas without females to areas where females are located. Removal experiments conducted with A. cristatellus indicated that once the territorial resident was removed from an area with females, the vacated territory would immediately be occupied by a male from a peripheral reservoir of males without females (Philibosian, 1972).

Male-Female Overlap.-- Female A. carolinensis home ranges were rarely 100% overlapped by males, and so females have the ability to remain in areas that were essentially unpatrolled by the resident male. Females could use these areas as "sanctuaries", essentially removing themselves from areas of encounter with the resident male when they were sexually nonreceptive. Trivers (1976) first described this phenomenon in A. garmani, where females became more conspicuous to patrolling males when receptive. Anolis carolinensis females often went unobserved by the patrolling male for days, yet when obviously receptive (i.e., did not run from the male and neck bent; Greenberg and Noble, 1944), were seen to inhabit a resident male's travelling perch (Nunez, unpubl. data).

Female Home Range.-- Home range volumes varied widely among female A. carolinensis (1.4 - 23 m^3), with no correlation between female SVL and female home range size for the pooled data. A similar lack of covariance has been reported for some lizard species (Rose, 1982); Schoener and Schoener (1982) even found a negative correlation for some anolines. Therefore, females are often considered to have home range sizes based on energetic demands only, while the correlation between male SVL

and home range size is attributed to increasing male reproductive success in polygynous species (Rose, 1982; Schoener and Schoener, 1982). Schoener and Schoener (1982) discussed the possibility that larger females could be finding and defending areas with richer resources, and therefore, need less area (volume) to support themselves. They also discussed the possibility that larger individuals are able to select a greater range of sizes of prey items in their home ranges than smaller individuals. As female $\underline{A}$. carolinensis is normally a sit-and-wait predator (Chapter IV), the first possibility that large females could be actively searching and defending areas with greater resources is probably not realistic. However, the second hypothesis is much more likely as larger females could be selecting from larger prey than smaller females.

Female-Female Overlap.-- Considering that the home ranges of aggregated females were positioned within shared clusters of micro habitat, there is surprisingly little overlap among female home ranges within a male's territory ($\bar{x}=18\%$). Females with larger home ranges had larger overlap values, and females with high overlap values travelled greater distances/h. These relationships could be an indication that females with larger home ranges may be more likely to patrol their home ranges as a means to monitor for consexual intruders.

The relative exclusiveness of female home ranges can be masked by the particular measure of home range. When using area only, mean overlap approached 50%, suggesting an absence of habitat defense among females. However, with a volumetric measure of home range, overlap values were dramatically less ($\bar{x}=18\%$), now suggesting

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the likelihood of female territoriality. Investigators studying arboreal species should be particularly alert to the potential impact of their methods on a study's conclusions.

Perch Diameter.-- While the range of perch diameters were very similar between males and females, females were on average seen on smaller diameter substrates than those reported for males (Fig. 8). Males continuously patrolled their territories and were seen more often than females on large diameter limbs that allowed easy and quick access to other portions of their habitat. As concluded for males (Jenssen et al, 1995), female A. carolinensis can be considered as a perch generalist because they utilized all perch substrates from large diameter limbs to small diameter limbs, as well as leaves, rocks and barren ground.

Perch Height.-- The taking of high perches by male anoles is thought to facilitate observation of and interaction with consexuals (Scott et al., 1976). In contrast, female anoles are less socially oriented in many species, and spend a greater amount of time searching for prey on the ground (e.g., A. polylepis, Andrews, 1971; A. humilis, Talbot, 1979), and hence, perch lower than males on average (Scott et al., 1976). In our study, female A. carolinensis typically perch higher than males (Fig. 3). Females, however, do not forage more than males and also spend less time in social interactions (Jenssen et al., 1995; Chapter IV). Female A. carolinensis rarely forage on the ground; most prey capture attempts were in the upper canopy, where females spent a great portion of their time (Nunez, pers. observ.).

Perch heights of all females decreased as temperature increased and relative humidity

decreased. During many days, when air temperatures approached 38°C and relative humidity decreased to below 55%, lizards were seen to seek shade early in the day. The voluntarily preferred thermal maximum for A. carolinensis is 35°C (Licht, 1968, Wilson and Echternacht, 1990), and as body temperatures increased close to the thermal maxima of the lizards, the lizards could be moving to shadier portions of the habitat to avoid thermal stress and increased desiccation rates (Fleming and Hooker, 1975).

Summary.-- During the breeding season, Jenssen et al. (1995) found that A. carolinensis males criss-cross their territories, averaging 27 m/h; much of this movement was in a horizontal direction. Although males transversed their vertical habitat, they remained below 2 m over 60% of the time (Jenssen et al., 1995). In contrast, we found female territories to be more vertically oriented with home range height often greater than home range width, and females perching higher than males on average (Fig. 9). This sexually dimorphic tendency in habitat utilization may reflect divergent social roles between the sexes. Female home ranges exhibit: (1) lateral compression of home range due to territorial effects of adjacent females within the habitat cluster; (2) a strong arboreal component; yet containing (3) access to the ground for ovipositing. In contrast, males accentuate horizontal movements to optimize the monitoring and aggressive advertisement of their territorial borders toward potential consexual intruders, while continuing to transect some portion of all resident female home ranges (Fig. 12).

Social Dominance

Dominance Defined.-- When an observer labels a subject "dominant", the observer

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is essentially making a prediction about the course of future interactions or the outcome of competitive situations (Rowell, 1974). The "loser" or subordinate individual should experience decreased motivation for further aggression against the "winner" or dominant individual (Bernstein, 1981), reducing the risk of injury due to conspecific conflict (Richards, 1974).

Social Dominance in A. carolinensis.-- To our knowledge, no data exist on Anolis female dominant-subordinate relationships except for A. carolinensis (Greenberg and Noble, 1944) and A. aeneus (Stamps, 1973). In the Greenberg and Noble (1944) study, female A. carolinensis were housed under high densities, and females responded by forming dominance-subordinate relationships. Our observations of free-ranging A. carolinensis females indicate that females were not only territorial, while reflecting dominance relationship within their respective aggregate groups. In a habitat clump shared by two or more females, one female would appear to dominate the others by initiating aggressive chases. These aggressive females often had the largest SVL (Chapter IV), were the most conspicuous (easier to observe), controlled the largest home range (Fig. 11), perched the highest (Fig. 10a), and were more frequently green in body color (Fig. 10b). Previous laboratory studies have documented that artificially confined aggregations of male A. carolinensis will also produce a dominant-subordinate hierarchical structure (Greenberg and Noble, 1944), often with larger males dominating smaller males (Evans, 1936a), and with the dominant male perching highest and remaining significantly greener (Greenberg et al., 1984; Greenberg and Crews, 1990).

Skin color in A. carolinensis is under the control of adrenergic endocrines (Vaughan and Greenberg, 1987), as well as those associated with physiological stress (Greenberg and Crews, 1983). In a study of chronically stressed male A. carolinensis, pairs of males housed together for up to a week in 20 L containers differentiated into a green dominant and a brown subordinate (Greenberg et al., 1984; Greenberg and Crews, 1990). The latter class of lizards had the highest levels of corticosterone (Greenberg and Crews, 1983) which has been shown to facilitate the production of epinephrine (Wurtman et al., 1967). Increased epinephrine levels are directly associated with darkening of skin color in A. carolinensis (Hadley and Goldman, 1969). While caution must be taken in extrapolating laboratory data onto free-ranging subjects, the laboratory data do suggest that our subordinate females (which remained brown more often) could be experiencing significantly higher levels of circulating corticosterone. However, only endocrine studies on free-ranging subjects can possibly clarify whether present laboratory studies are applicable to free-ranging populations.

Benefits/Costs.-- The benefits and costs associated with dominant-subordinate relationships have been thoroughly discussed for many species. Commonly, dominant males benefit by increasing their reproductive success by copulating more frequently (Appleby, 1982, Howard, 1978) or by guarding and monopolizing copulations with estrus females (McCann, 1981). However, dominant females are usually associated with gaining increases in resources (i.e., food and nesting sites). For both sexes in gregarious mammal species, subordinate individuals have been found to have higher levels of

cortical hormones, which in turn reduces inflammatory responses, levels of antigen anti-body, and reproductive hormones (Christian and Davis, 1964).

The benefits of being a dominant Anolis female have not been previously described. However, dominant females are probably receiving increased or higher quality resources, as dominant females in our population often controlled the largest home range volume. Other benefits of being dominant could include better oviposition sites, safer and/or more productive foraging sites (e.g., male acorn woodpeckers; Ekman, 1987). Subordinate females are possibly experiencing increased levels of cortical hormones, while decreasing a female's reproductive potential (< reproductive hormones), yet remain within the aggregate to possibly gain high quality territories or resources in the future (see below).

Summary.-- The actual social structure of female A. carolinensis is nearly impossible to discern from our study. We cannot conclusively state that the female social system is despotic or whether a rank hierarchy forms when >2 individuals are present within the same habitat clump. Nonetheless, it can be stated that this social system is unique; females form dominant-subordinate relationships, and they are simultaneously territorial. However, possible explanations for this dominant-subordinate territorial system remain unclear at this time.

Aggregation

Hypotheses. Lizard aggregations have rarely been documented under natural conditions (e.g., A. aeneus juveniles; Stamps, 1988). Unlike the repulsive distribution of male A. carolinensis (Jenssen et al., 1995; this study), female distribution on our

study site appeared clustered within habitat configurations containing at least one tree with low surrounding brushes. Other habitat, including areas with sparse foliage and/or not including a tree were left either partially or totally vacated. If this perception of female clumping is correct, such a distribution may be explained by one or more of the following three hypotheses.

The "competitor defense" hypothesis (Burger, 1981; Getty, 1981) states that during territorial establishment, settlers should choose adjacent territories with contiguous boundaries, and cooperatively prevent a late arrival from inserting between previously established territories; thus the overall cost for individual defense would be lowered (Getty, 1987). However, if high quality habitat is clumped, territorial settlers would only have to form contiguous boundaries around these clumps of habitat.

The "minimal quality" hypothesis (Stamps, 1988) suggests that conspecific cuing could be advantageous both during initial settlement of individuals as well as during territorial ownership. Relatively young individuals, with little or no previous experience with the habitat, might use more experienced individuals as cues to initial habitat quality, but only if habitat quality did not fluctuate spatially between breeding seasons. Minimal quality territories are, therefore, guaranteed by the mere presence of a previous territorial owner. As some species increase advertisement displays when resource quality increases on their territory (Stamps, 1987a; Ewald and Orians, 1983; Tamm, 1985), conspecifics could be using this as a cue for minimum quality of habitat.

The "future advantage" hypothesis (Kiester and Slatkin, 1974; Stamps, 1988)

explains that inexperienced individuals could also be using neighbors as cues to habitat quality, and hence, acquire better territories in the future. Opportunities to acquire a better territory are when a territory becomes vacant during the breeding season due to predation of the original territorial holder or during territorial establishment in future breeding seasons.

Summary.-- Field data that describe territorial establishment and the aggregation process in anoles are sorely lacking, with most of our knowledge only from theory, speculation, and anecdotal evidence. No field data on territorial establishment in either male or female A. carolinensis exist, and without actual data, none of the three above hypotheses can be argued effectively, nor can the possibility be ruled out that the aggregations are due to clumping of usable habitat, and not due to an active choice by the females.

Summary and Conclusion

Many perceptions of A. carolinensis have until recently been solely based on anecdotal evidence, laboratory studies conducted on challenged subjects, or from generalizations made from other anoles. Our study concurs with previous studies of polygynous Anolis males in many ways including that males have larger home ranges than females, that males transverse larger perch substrates, and that larger males often overlap more adult females. However, females were also found to perch higher than males on average, contradictory to previous findings and theory. We have also documented evidence for a fourth type of male-male relationship- the "destitute" intruder.

Previous laboratory studies have also documented how females were territorial, yet when placed in unnatural artificial aggregations would form dominant-subordinate relationships. Our study has documented that both social structures are occurring simultaneously under natural, voluntary, long-term aggregate groups. This phenomenon of dominant-subordinate territoriality has not previously been described for any species.

However, this study has revealed many questions that cannot be effectively answered at this time including: (1) why do females aggregate; (2) what benefits do dominant females acquire and what costs do subordinates incur; and (3) why do subordinate females remain within the aggregation if there is a cost from the association with an aggregate neighbor? These questions can only be answered by conducting carefully controlled experiments on free-ranging subjects.

Table 1. General categories of activity modes (durational events) and their definitions which compose the daily activity profile of female <u>Anolis</u> <u>carolinensis</u>.

Events	Definition
Stationary	Duration when a female maintains her perch site. May include non-locomotion movements as when shedding or shifting body orientation at perch site.
Travel	Deliberate locomotion involving a change in perch location beginning with overt movement and ending when the female has commenced another event.
Forage	Duration beginning with overt detection and ending with ingestion of prey.
Female-Unknown	Duration of a female social response to an unknown recipient, beginning with two or more nondirected displays within a 30 s period, and ending when the female has commenced with another event.
Female-Female	Duration of a female-female encounter, beginning with initial approach and ending with one or both individuals moving apart.

Male-Female	Duration of a male and female encounter, beginning with initial approach and ending with one or both lizards moving apart.
Copulation	Duration beginning with hemipenis insertion and ending with removal. Post copulation is defined as 1.5 min period after a copulation event.

Table 2. Categories of behaviors and their definitions which may occur within event durations (See Table 1), represented by frequencies and rates, for female <u>Anolis</u> <u>carolinensis</u>.

Behaviors	Definition
Smack	A rapid opening and closing of the mouth
Yawn	Large, prolonged gaping of the mouth
Mouth Wipe	Wiping the lateral portion of the mouth, against the substrate, and usually repeated on both sides of the mouth
Body Drag	Dragging the body, using only the forearms, along the substrate
Cloacal Drag	Dragging the cloacal region along the substrate, usually after defecation
Aerial Lick	Quickly extending the tongue into the air
Substrate Lick	Quickly extending the tongue to touch a substrate
Neck Bend	Movement of the head in a downward angle
Headbobbing	Up and down head movement, one of several species specific, stereotyped headbob patterns shared by both male and females (DeCourcy and Jenssen, 1994; Jenssen, et al., 1995)

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Headbobbing w/dewlap	A headbob display in which the dewlap (throat with dewlap fan) is extended and contracted as part of a stereotyped display
Tail Undulation	Lateral movement of the tail
Body Lick	Substrate licking on a conspecific or one's self

Table 3. The rates of occurrence (as symbolically depicted*) of 11 types of behaviors of 22 female <u>Anolis</u> <u>carolinensis</u> during 8 activity modes (Events) as recorded from 90 h of observation during May - July at the Augusta Canal, Augusta, Georgia.

Event / Behavior	Male - Female Interaction	Copulation	Post - Copulation	Female- Female Interaction	Female- Unknown	Stationary	Travel	Forage
Head Bob	>59	>59	>59	12.1-59	12.1-59	0.1-2	2.1-12	0.1-2
Head Bob w/ Dewlap	2.1-12	2.1-12	0	12.1-59	>59	0.1-2	0.1-2	0
Neck Bend	2.1-12	0	0	0	0	0	0	0
Tail Undulation	0.1-2	0	0	0	0.1-2	0.1-2	2.1-12	0
Mouth Wipe	0.1-2	0	0	0	0	2.1-12	2.1-12	2.1-12
Substrate Lick	0	0	0	0	0	0.1-2	0.1-2	0
Smack	0.1-2	0	0	0	0	0.1-2	0.1-2	>59
Yawn	0	0	0	0	0	0.1-2	0	0
Body Lick	0	0	0	0	0	0.1-2	0	0
Body Drag	0	0	0	0	0	0.1-2	0	0
Cloacal Drag	0	0	0	0	0	0.1-2	0	0

* frequency/hour where:

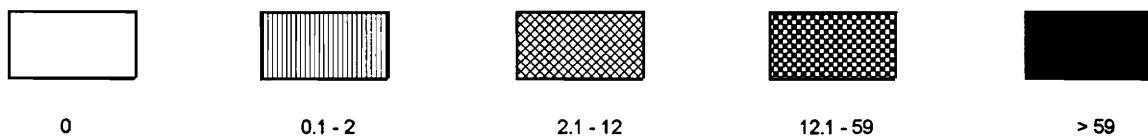|				
0	0.1 - 2	2.1 - 12	12.1 - 59	> 59

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Table 4. The mean home range volumes (m³) and areas (m²) with their respective standard errors and percentage overlap values in male and female <u>Anolis</u> <u>carolinensis</u>.

Variable	Male (N=7)	Female (N=22)
Volume		
Territory Size (m³)	68.5 ± 20.0	7.8 ± 1.3
Percent Overlap (%)		
Intrasexual	0.0	18.0
Intersexual	9.6	48.0
Area		
Territory Size (m²)	50.5 ± 11.1	8.2 ± 1.0
Percent Overlap (%)		
Intrasexual	0.0	49.0
Intersexual	23.3	83.0

Table 5. Comparison of adult male and female home range sizes of <u>Anolis</u> species (adults 74mm $>$ SVL $>$ 44mm) with their respective method of home range estimation and citations.

Anolis sp.	Home Range Size	Source
carolinensis		
male[b1]	29.1 m²	Schoener and Schoener, 1982
female[b1]	18.6 m²	Schoener and Schoener, 1982
female[c1]	2.8 m²	Schoener and Schoener, 1982
male[d2]	173.6 m³	Jenssen et al., 1995
male[g5]	8.3 m²	Gordon, 1956
female[g5]	5.9 m²	Gordon, 1956
acutus		
male[e3]	1.2 m²	Philibosian, 1972
female[e3]	0.5 m²	Philibosian, 1972
angusticeps		
male[b1]	15.8 m²	Schoener and Schoener (1982)
female[b1]	5.3 m²	Schoener and Schoener (1982)

cristatellus

male[e3]	19.0 m^2	Philibosian, 1972
female[e3]	1.2 m^2	Philibosian, 1972

lineatopus

male[j7]	2.5-16.7 m^2	Rand, 1967
female[j7]	0.5- 3.3 m^2	Rand, 1967

sagrei

male[a1]	10.1 m^2	Schoener and Schoener (1982)
female[a1]	4.0 m^2	Schoener and Schoener (1982)
male[b1]	16.1 m^2	Schoener and Schoener (1982)
female[b1]	3.2 m^2	Schoener and Schoener (1982)
male[c1]	2.8 m^2	Schoener and Schoener (1982)
female[c1]	2.0 m^2	Schoener and Schoener (1982)

stratulus

adults[h6]	6.2 m	Reagan, 1992

tropidonotus

males[i4]	63.2 m^2	Jackson, 1973
females[i4]	11.3 m^2	Jackson, 1973

a Abaco Island

b Bimini

c Andros Island

d Augusta, GA

e Virgin Islands

f Tepic, Mexico

 New Orleans, LA

h Puerto Rico

i Honduras

j Jamaica

1 Schoener method (1981)

2 Jenssen et al., 1995 method

3 Philibosian, 1972 method

4 Minimum Polygon method

5 Diameter, recapture method

        Carpenter, 1952

6 Ellipsoid method

        Koeppl, et al., 1977

7 undefined
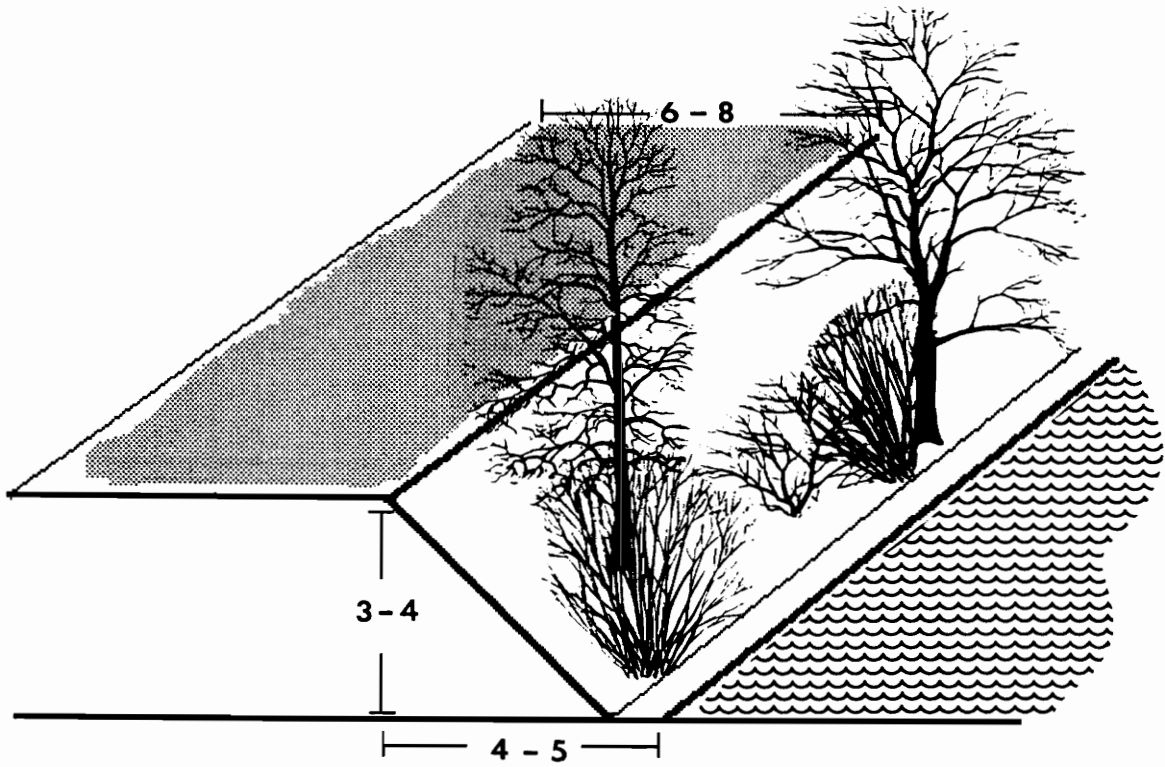
Figure 1. Strip of riparian habitat between the elevated tow path (stippled) and water (wavy lines) of the Augusta Canal near Augusta, Georgia, in which 56 days of observation were made of <u>Anolis</u> <u>carolinensis</u>. Measurements are in meters.
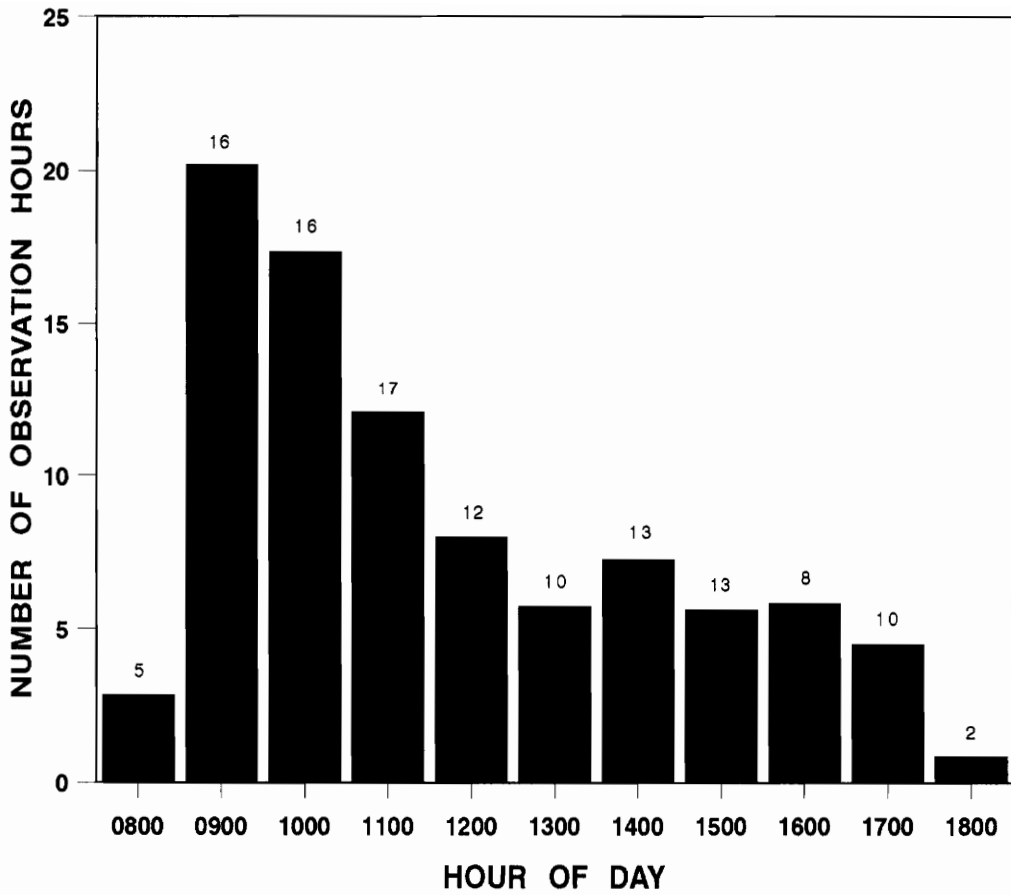
Figure 2. Illustrates the skewed relationship with time of day and the number of observation hours obtained on female <u>Anolis carolinensis</u> at the Augusta Canal in Augusta, Georgia during May - July, 1993. The number above each bar indicates the number of separate females that were observed during each hour of day (N=22 females, 90 hours of observation).
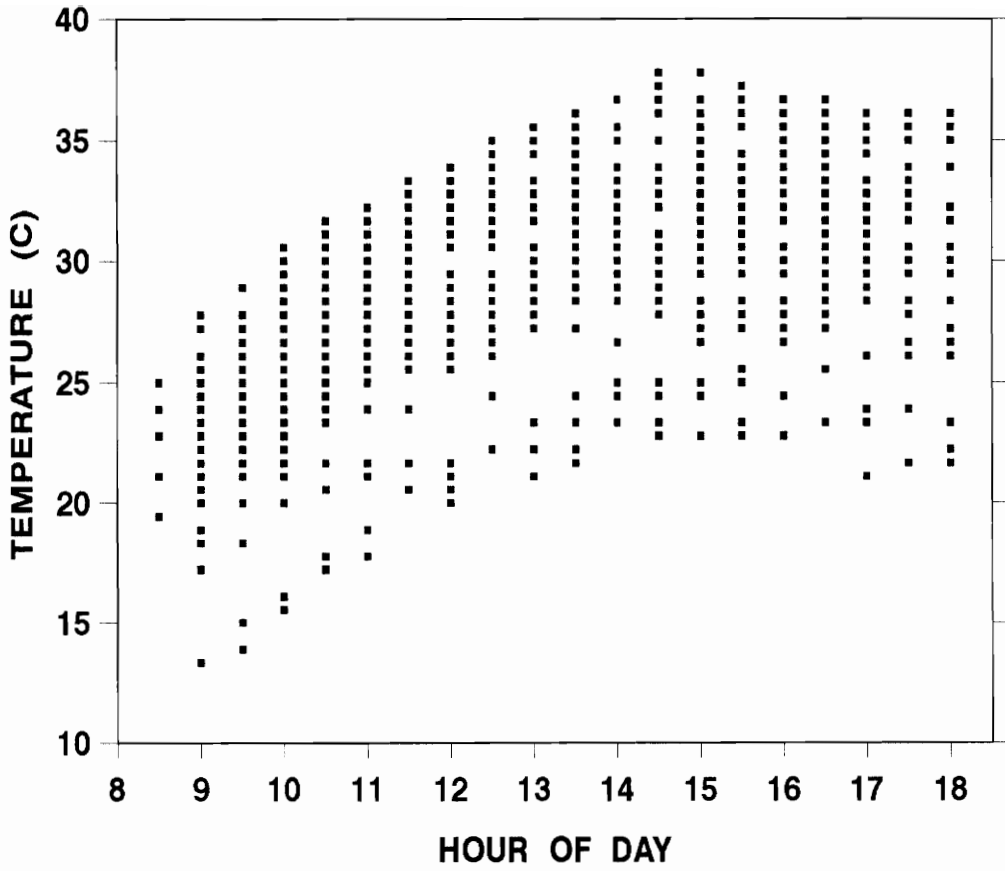
Figure 3. Air temperatures, taken during 30 min intervals from 0830 until 1800, during daily observations of female <u>Anolis</u> <u>carolinensis</u>, at the Augusta Canal near Augusta, Georgia during May - July, 1993.
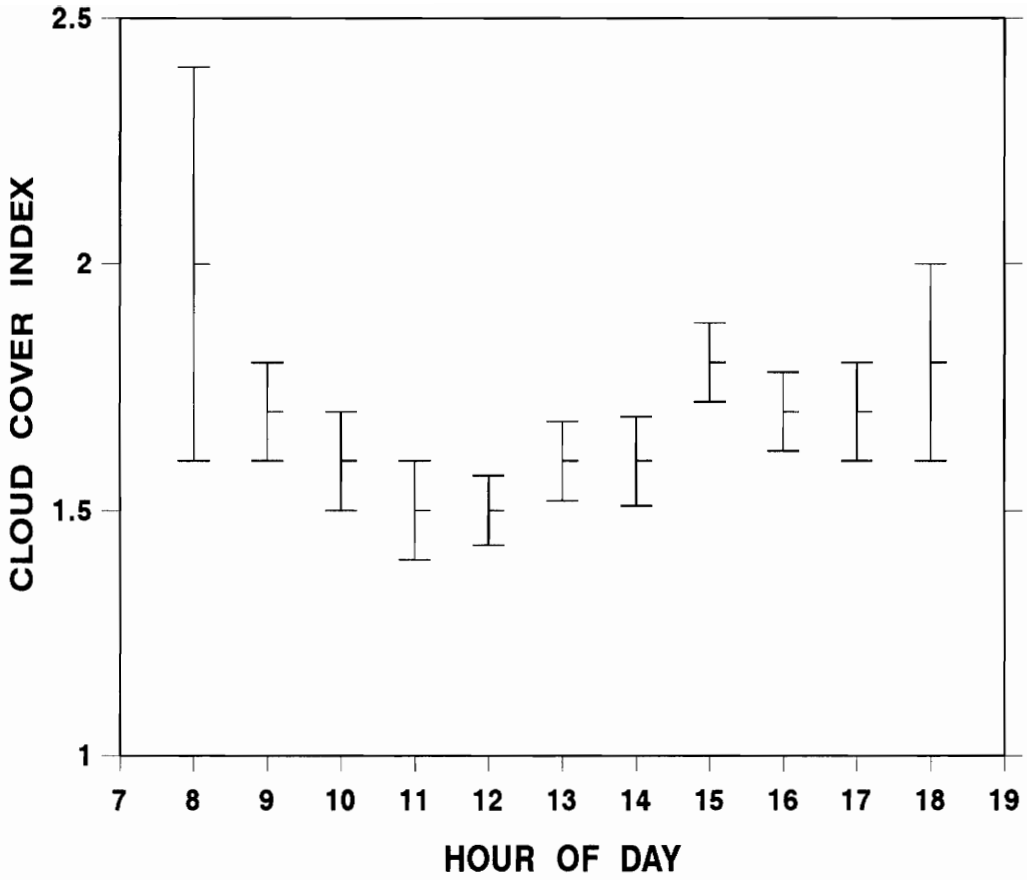
Figure 4. Mean cloud cover ($\pm$ SE) of direct sunlight with samples taken at 30 min intervals from 0830 until 1800, during daily observations of female <u>Anolis</u> <u>carolinensis</u> at the Augusta Canal near Augusta, Georgia during May - July, 1993.
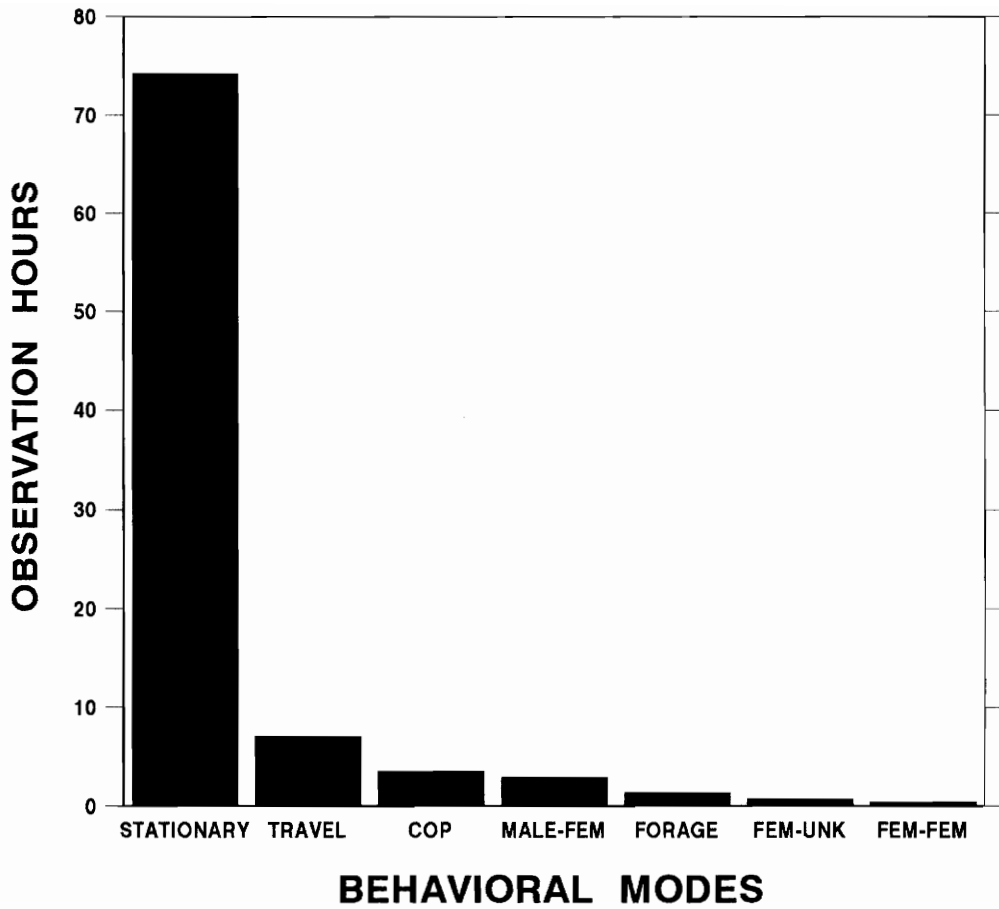
Figure 5. The number of observation hours accumulated for each behavioral mode (event) for 22 female <u>Anolis</u> <u>carolinensis</u> at the Augusta Canal near Augusta, Georgia during May - July, 1993.
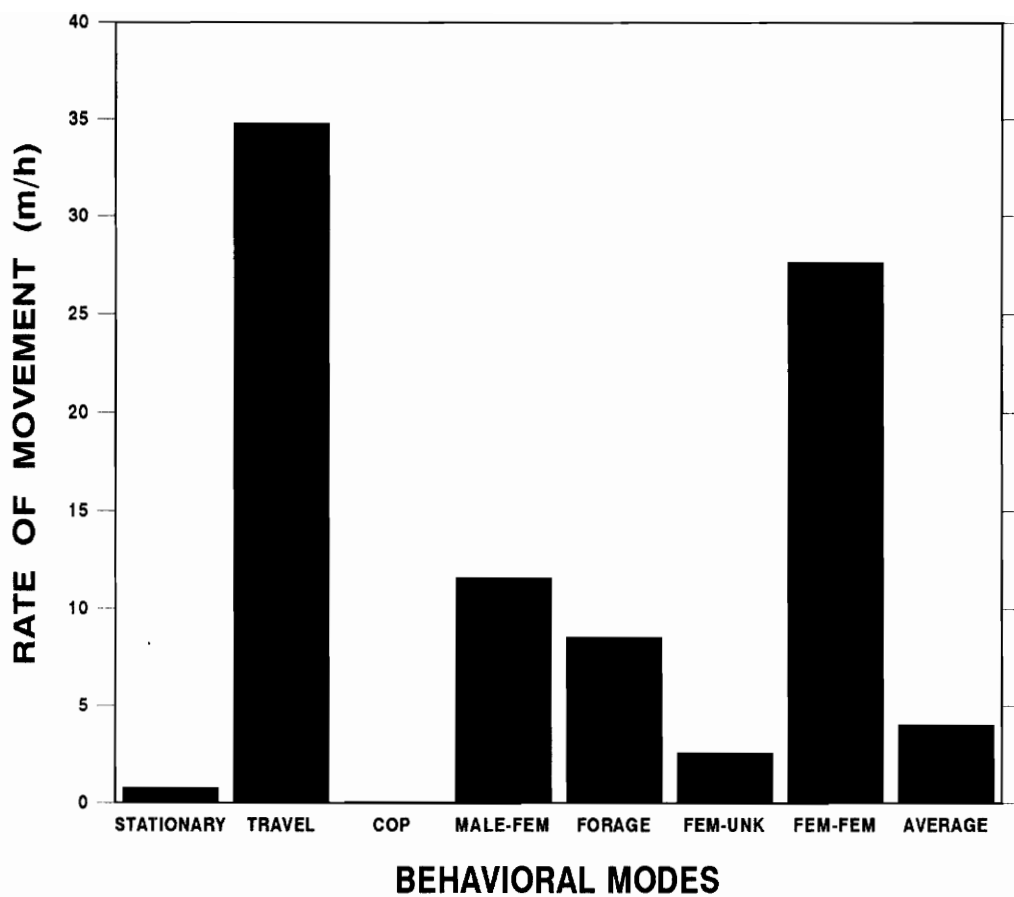
Figure 6. Mean distance travelled per hour during specific behavioral modes (events) of 22 female <u>Anolis</u> <u>carolinensis</u> at the Augusta Canal near August, Georgia during May - July, 1993.

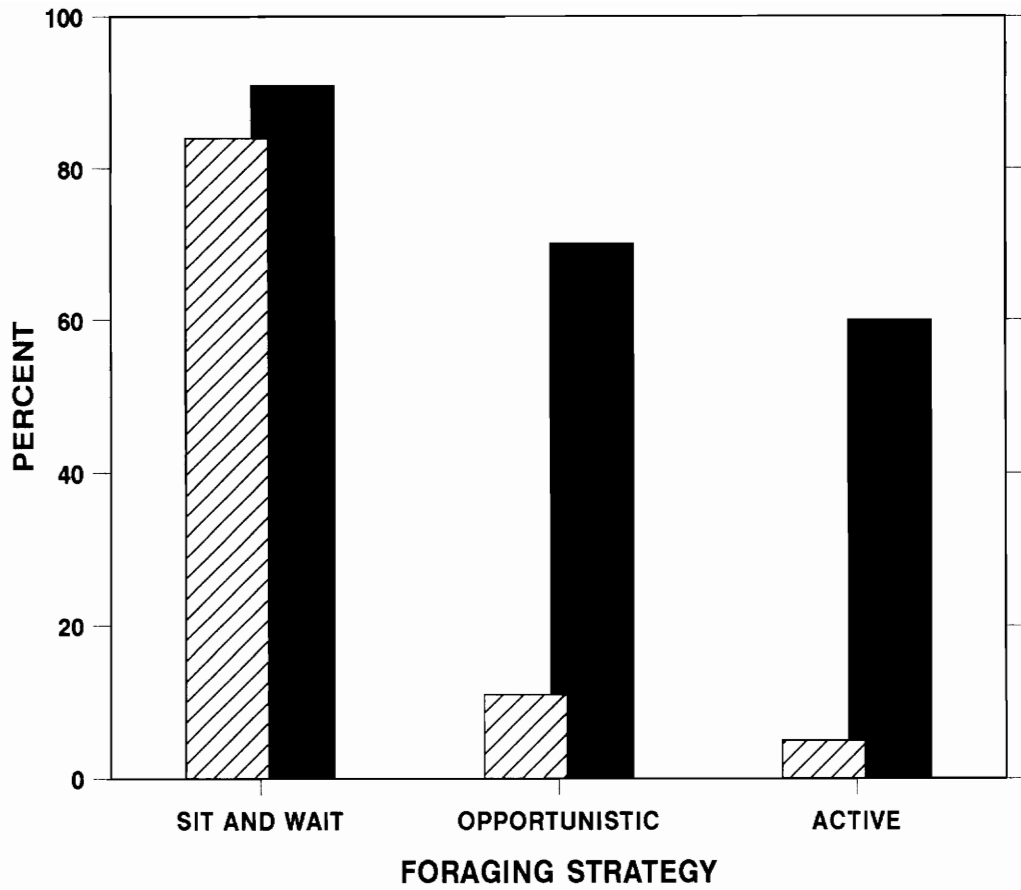Figure 7. Proportion of three observed foraging strategies (striped bars) and their respective success rates (black bars) used by female <u>Anolis</u> <u>carolinensis</u>.
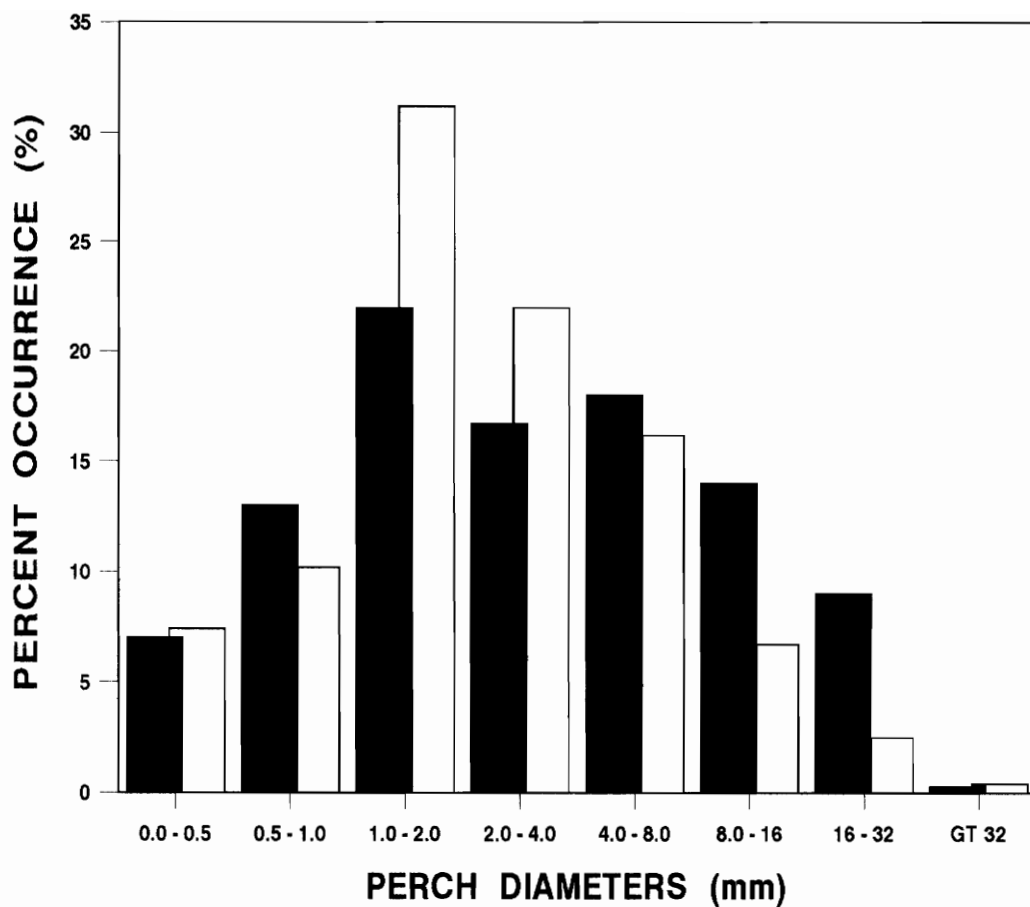
Figure 8. Distribution of perch diameter classes collected during May-July. Female distribution (white bars) obtained from 30 min focal observations of 22 female Anolis carolinensis at the Augusta Canal near Augusta, Georgia. Male data (black bars) from the same study site during May-July, but a separate study (Jenssen et al., 1995).
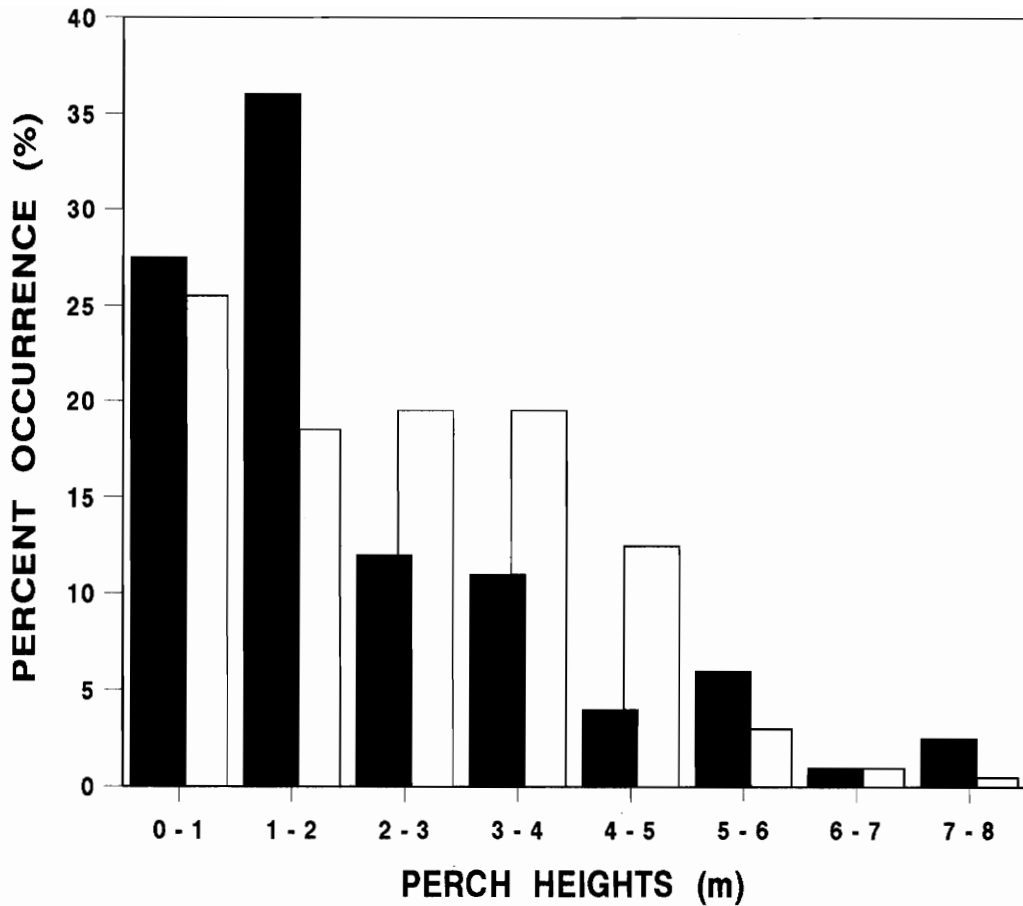
Figure 9. Distribution of perch height classes collected during May-July. Female distribution (white bars) obtained from 30 min focal observations of 22 female Anolis carolinensis at the Augusta Canal near Augusta, Georgia. Male data from the same study site during May-July, but a separate study (Jenssen et al., 1995).
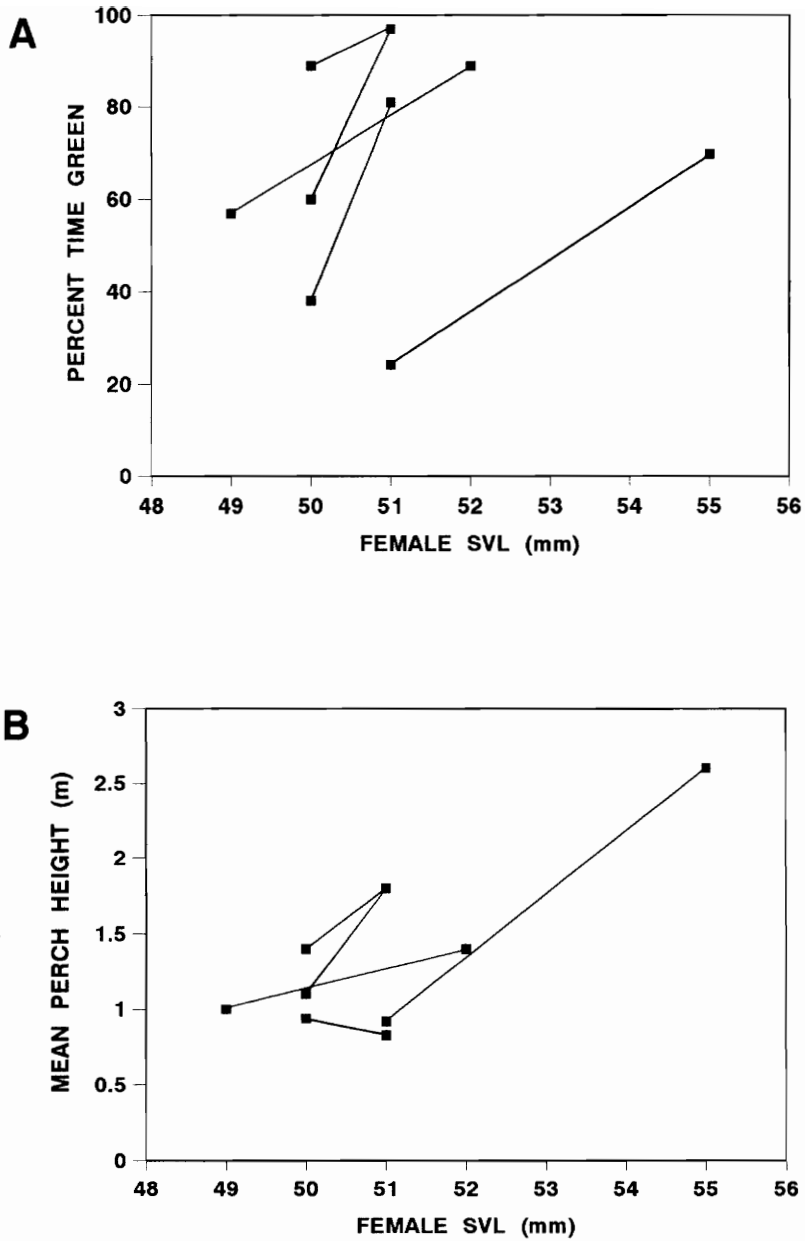
Figure 10. Relationship between (A) body color (% green) and body size (mm) and (B) mean perch height (m) and body size (mm) for female <u>Anolis</u> <u>carolinensis</u> during May - July at the Augusta Canal near Augusta, Georgia. Points connected by lines indicate spatially associated females.

Figure 11. Relationship between home range volume (m³) and body color (% green) for female <u>Anolis</u> <u>carolinensis</u> during May - July at the Augusta Canal near Augusta, Georgia. Points connected by lines indicate spatially associated females.
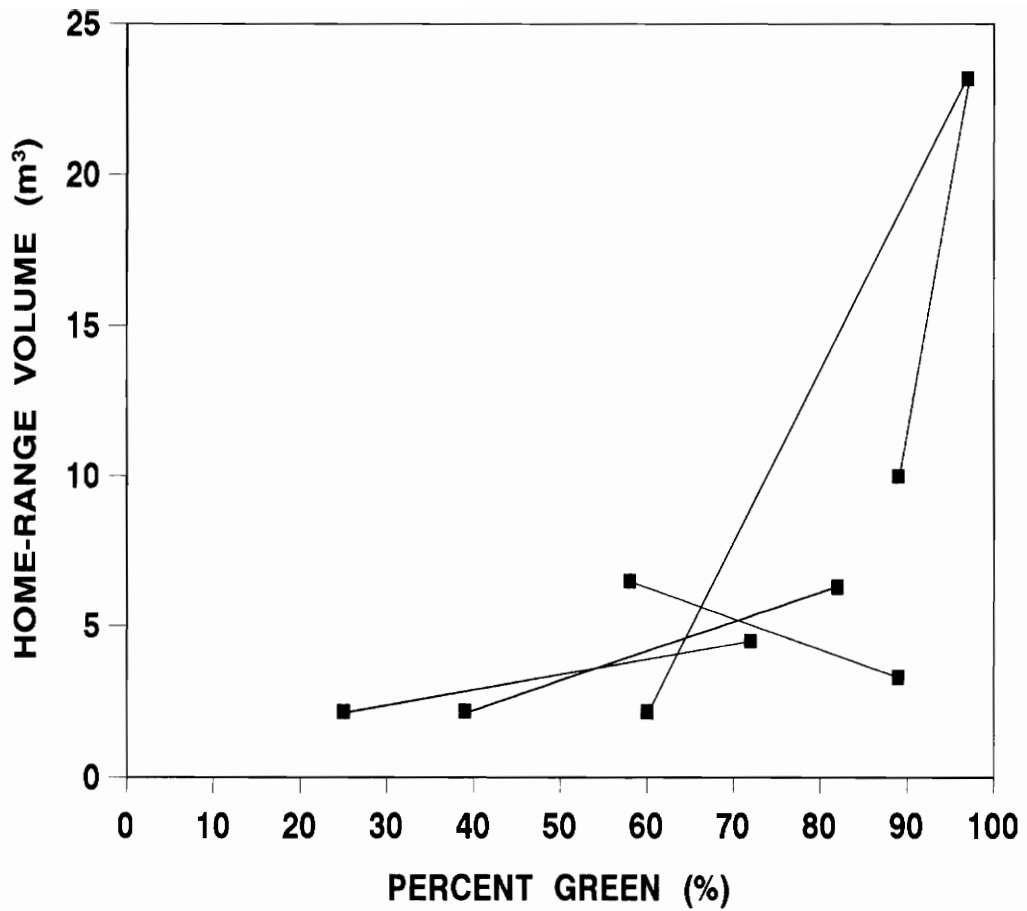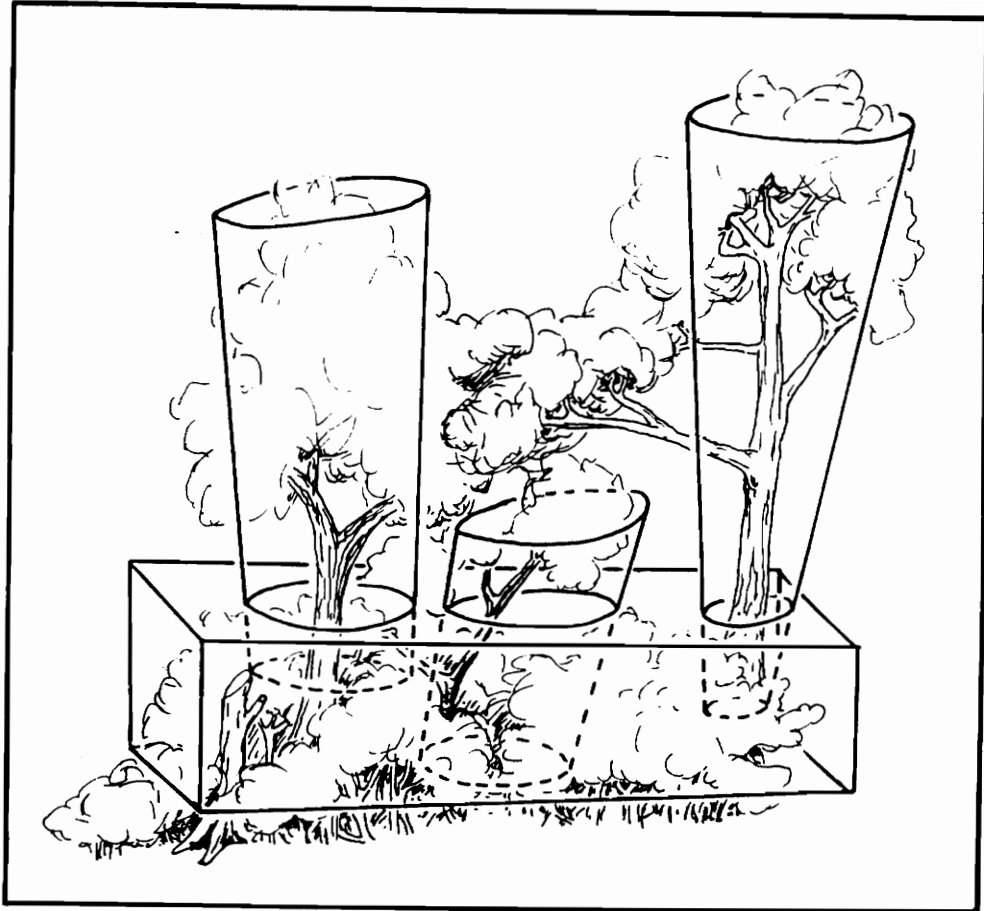
Figure 12.   Theorectical spatial relationship between male and female <u>Anolis</u> <u>carolinensis</u> home ranges at the Augusta Canal near Augusta, Georgia.   The male home range is typically more horizontally distributed than the vertically distributed female home range.

LITERATURE CITED

Allee, W. C., O. Park, A. E. Emerson, T. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders, Philadelphia.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49: 227-267.

Andrews, R. M. 1971. Structural habitat and time budget of a tropical lizard. Comp. Biochem. Physiol. 58: 57-62.

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

Appleby, M. C. 1982. The consequences and causes of high social rank in red deer stags. Behaviour 80: 259-282.

Bennett, A. F., and G. C. Gorman. 1979. Population density and energetics of lizards on a tropical island. Oecologia 42: 339-358.

Bernstein, I. S. 1981. Dominance: the baby and the bathwater. Behav. Brain Sci. 4:

74

419-457.

Burger, J. 1981. Super territories: a comment. Amer. Natur. 118: 578-580.

Carpenter, C. C. 1952. Comparative ecology of the common garter snake (Thamnophis sirtalis), the ribbon snake (Thamnophis s. sauritus), and Butler's garter snake (Thamnophis butleri) in mixed populations. Ecol. Monogr., 22: 235-258.

Carpenter, C. C. 1967. Aggression and social structure of iguanid lizards. Pp. 87-105. In W. W. Milstead (Ed.), Lizard Ecology: a Symposium. Univ. Missouri Press, Columbia, Missouri.

Christian, J. J., and D. E. Davis. 1964. Endocrines, behavior, and population. Science 146: 1550-1560.

Conant, R. 1975. A Field Guide to Reptiles and Amphibians of Eastern and Central North America. Houghton Mifflin Company, Boston, Massachusetts.

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

Crews, D. 1973a. Behavioral correlates to gonadal state in the lizard, <u>Anolis</u> <u>carolinensis</u>. Horm. Behav. 4: 307-313.

Crews, D. 1973b. Coition-induced inhibition os sexual receptivity in female lizards (<u>Anolis</u> <u>carolinensis</u>). Physiol. Behav. 11: 463-468.

Crews, D. 1977. The annotated anole: studies on the control of lizard reproduction. Amer. Sci. 65: 428-434.

Crews, D. 1981. Interrelationships among ecological, behavioral, and neuroendocrine processes in the reproductive cycle of <u>Anolis</u> <u>carolinensis</u> and other reptiles. Pp. 1-74. <u>In</u> J. S. Rosenblatt, R. A. Hinde, C. Beer, and M-C Busnel (Eds.), Advances in the Study of Behavior. Academic Press, New York, New York.

Crews, D., and J. S. Rosenblatt, and D. S. Lehrman. 1974. Effects of unseasonal environmental regime, group presence, group composition, and male physiological state on ovarian recrudescence in the lizard, <u>Anolis</u> <u>carolinensis</u>. Endocrin. 94: 541-547.

Cuellar, O. 1966. Oviductal anatomy and sperm storage structures in lizards. J. Morph. 119: 7-20.

Darling, F. F. 1952. Social behavior and survival. Auk 69: 183-191.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. Appleton, New York, New York.

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

Dewsbury, D. A. 1982. Ejaculate cost and male choice. Amer. Nat. 119: 601-110.

Ekman, J. 1987. Exposure and time use in willow tit flocks: the cost of subordination. Anim. Behav. 35: 445-452.

Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197: 215-223.

Evans, L. T. 1936a. A study of a social hierarchy in the lizard, Anolis carolinensis. J. Genet. Psychol. 48: 88-111.

Evans, L. T. 1936b. Territorial behavior of normal and castrated females of Anolis carolinensis. J. Genet. Psychol. 49: 49-60.

Evans, L. T. 1938. Courtship behavior and sexual selection of <u>Anolis</u>. J. Comp. Psychol. 26: 475-497.

Ewald, P. W., and G. H. Orians. 1983. Effects of resource depression on use of inexpensive and escalated aggressive behavior: experimental tests using Anna hummingbirds. Behav. Ecol. Sociobiol. 12: 95-102.

Fisher, J. 1954. Evolution and bird sociality. Pp 71-83. <u>In</u> J. Huxley, A. C. Hardy, and E. B. Ford, (Eds.), Evolution as a Process. Allen and Unwin, London.

Fleishman, L. J. 1988. The social behavior of <u>Anolis</u> <u>auratus</u>, a grass anole from Panama. J. Herpetol. 22: 13-23.

Fleming, T. H., and R. S. Hooker. 1975. <u>Anolis</u> <u>cupreus</u>: the response of a lizard to tropical seasonality. Ecology 56: 1243-1261.

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

Gartlan, J. S. 1968. Structure and function in primate society. Folia Primatol. 8: 89-120.

Getty, T. 1981. Competitive collusion: the preemption of competition during the sequential establishment of territories. Amer. Natur. 118: 426-431.

Getty, T. 1987. Dear enemies and the prisoner's dilemma: why should territorial neighbors form defensive coalitions? Amer. Zool. 27: 327-336.

Gordon, R. E. 1956. The biology and biodemography of Anolis carolinensis carolinensis, Voigt. Ph.D. diss., Tulane Univ., New Orleans, LA.

Greenberg, B., and G. K. Noble. 1944. Social behavior of the american chameleon (Anolis carolinensis voigt). Phys. Zool. 1944:392-439.

Greenberg, N., and D. Crews. 1983. Physiological ethology of aggression in amphibians and reptiles. Pp. 469-506. In B. Svare (Ed.), Hormones and Aggression. Plenum, New York.

Greenberg, N., and D. Crews. 1990. Endocrine and behavioral responses to aggression and social dominance in the green anole lizard, Anolis carolinensis. Gen. Comp. Endocrinol. 77: 246-255.

Greenberg, N., T. Chen, and D. Crews. 1984. Social status, gonadal state, and the

adrenal stress response in the lizard, <u>Anolis</u> <u>carolinensis</u>. Hor. and Behav. 18: 1-11.

Hadley, M. E., and J. M. Goldman. 1969. Physiological color changes in reptiles. Amer. Zool. 9: 489-504.

Hickon, Mark A. 1987. Territory area as a determinant of mating systems. Amer. Zool. 27: 229-247.

Hicks, R. A., and R. L. Trivers. 1983. The social behavior of <u>Anolis</u> <u>valencienni</u>. Pp. 570-575. <u>In</u> G. J. Rhodin and K. Miyata (Eds.), Advances in Herpetology and Evolutionary Biology. Mus. Comp. Zool., Harvard Univ., Cambridge, Massachusetts.

Hollander, M., and D. Wolfe. 1973. Nonparametric Statistical Methods. Wiley, New York, New York.

Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, <u>Rana</u> <u>catesbiana</u>. Evolution 32: 850-871.

Jackson, J. F. 1973. Notes on the population biology of <u>Anolis</u> <u>tropidonotus</u> in a Honduran highland pine forest. J. of Herp. 7: 309-311.

Jenssen, T. A. 1970. The ethoecology of <u>Anolis</u> <u>nebulosus</u> (Sauria, Iguanidae). J. of Herpetol. 4: 1-38.

Jenssen, T. A., K. Orrell, D. Cunningham, and B. Sponseller. Structure and use of headbob signals by female <u>Anolis</u> <u>carolinensis</u> lizards: a comparison with males. (<u>In</u> prep.).

Jenssen, T. A., N. Greenberg, and K. A. Hovde. 1995. Behavioral profile of free-ranging male lizards, <u>Anolis</u> <u>carolinensis</u>, across breeding and post-breeding seasons. Herpetol. Monogr. <u>In</u> <u>Press</u>.

Kiester, A. R. 1979. Conspecifics as cues: a mechanism for habitat selection in the panamanian grass anole (<u>Anolis</u> <u>auratus</u>). Behav. Ecol. Sociobiol. 5: 323-331.

Kiester, A. R. and M. Slatkin. 1974. A strategy of movement and resource utilization. Theoret. Populat. Biol. 6: 1-20.

Kiester, A. R., G. C. Gorman, and D. C. Arroyo. 1975. Habitat selection behavior of three species of <u>Anolis</u> lizards. Ecology 56: 220-225.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. Pp. 23-63. <u>In</u> J.

R. Krebs and N. B. Davies (Eds.) Behavioural Ecology: an Evolutionary Approach. Sinauer Assoc., Suderland, Massachusetts.

Licht, P. 1967. Environmental control of annual testicular cycles in the lizard <u>Anolis</u> <u>carolinensis</u>. II. Seasonal variations in the effects of photoperiod and temperature on testicular recrudescence. J. Expt. Zool. 166: 243-253.

Licht, P. 1968. Response of the thermal preferendum an heat resistance to thermal acclimation under different photoperiods in the lizard <u>Anolis</u> <u>carolinensis</u>. Amer. Midland Nat. 79: 149-158.

Licht, P. 1973. Influence of temperature and photoperiod on the annual ovarian cycle in the lizard <u>Anolis</u> <u>carolinensis</u>. Copeia 1973: 465-472.

Lister, B. C., and A. G. Aguayo. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. J. Anim. Ecol. 61: 717-733.

MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection, and character displacement in patchy environments. Nat. Acad. Sci. Proc. 51: 1207-1210.

McCann, T. S. 1981. Aggression and sexual activity of male southern elephant seals,

Mirounga leonina. J. of Zool. 195: 295-310.

Michuad, E. J. 1990. Demographic variation of life history traits in the lizard, Anolis carolinensis. Ph.D. diss., Univ. Tennessee, Knoxville, Tennessee.

Moermond, T. C. 1979. The influence of habitat structure on Anolis foraging behavior. Behaviour 70: 147-167.

Moore, M. C., C. W. Thompson, and C. A. Marler. 1991. Reciprocal changes in corticosterone and testosterone levels following acute and chronic handling stress in the tree lizard Urosaurus ornatus. Gen. Comp. Endocrin. 81: 217-226.

Parker, W. S., and E. R. Pianka. 1973. Notes on the ecology of the iguanid lizard, Sceloporus magister. Herpetol. 29: 143-152.

Phillips, R. R. 1974. The relationship between social behaviour and the use of space in the benthic fish Chasmodes bosquianus Lacepede (Teleostei, Blenniidae). III. The interactions between attraction-repulsion and prior social experience. Behaviour 49: 205-226.

Philibosian, R. 1972. Territorial behavior and population regulation in anoline lizards.

Ph.D. diss., Univ. Calif., Riverside, CA.

Rand, A. S. 1962. Notes on hispaniola herpetology. The natural history of three sympatric species of <u>Anolis</u>. Breviora 154: 1-15.

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

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

Richards, S. M. 1974. The concept of dominance and methods of assessment. Anim. Behav. 22: 914-930.

Rose, B. 1982. Lizard home ranges: methodology and functions. J. Herpetol. 16: 253-269.

Rowell, T. E. 1974. The concept of social dominance. Behav. Biol. 11: 131-154.

Ruby, D. E. 1984. Male breeding success and differential access to females in <u>Anolis carolinensis</u>. Herpetologica. 40: 272-280.

SAS. 1988. User's Guide: Statistics. Release 6.03. SAS Institute Inc., Cary, North Carolina.

Schoener, T. W. 1981. An empirically based estimate of home range. Theoret. Populat. Biol. 20: 281-325.

Schoener, T. W., and A. Schoener. 1980. Ecological and demographic correlates of injury rates in some Bahamian Anolis lizards. Copeia 1980: 839-850.

Schoener, T. W., and A. Schoener. 1982. Intraspecific variation in home-range size in some Anolis lizards. Ecology 63: 809-823.

Scott, N. J., D. E. Wilson, C. Jones, and R. M. Andrews. 1976. The choice of perch dimensions by lizards of the genus Anolis (Reptilia, Lacertilia, Iguanidae). J. Herpotol. 10: 75-84.

Stamps, J. A. 1973. Displays and social organization in female Anolis aeneus. Copeia 1973: 264-272.

Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. Pp. 265-334. In C. Gans and D. W. Tinkle (Eds.), Biology of the Reptilia, vol. 7: Ecology and

Behaviour. Academic Press, New York, New York.

Stamps, J. A. 1987a. Conspecifics as cues to territory quality: a preference of juvenile lizards (Anolis aeneus) for previously used territories. Amer. Natur. 129: 629-642.

Stamps, J. A. 1987b. The effect of familiarity with a neighborhood on territory acquisition. Behav. Ecol. Sociobiol. 21: 273-277.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. Amer. Nat. 131: 329-347.

Talbot, J. J. 1979. Time budget, niche overlap, inter- and intraspecific aggression in Anolis humilis and A. limifrons from Costa Rica. Copeia 1979: 472-481.

Tamm, S. 1985. Breeding territory quality and agonistic behavior: effects of energy availability and intruder pressure in hummingbirds. Behav. Ecol. Sociobiol. 16: 203-207.

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in Anolis garmani. Evolution 30: 253-269.

Vaughan, G. L., and N. Greenberg. 1987. Propranolol, A beta-adrenergic antagonist, retards response to MSH in skin of <u>Anolis</u> <u>carolinensis</u>. Physiol. Behav. 40: 555-558.

Wilson, M. A., and A. C. Echternacht. 1990. A comparison of heat and cold tolerance of two morhps of <u>Anolis</u> <u>carolinensis</u> (Iguanidae) from southern Florida. J. Herpotol. 24: 330-333.

Workman, S. W., and K. W. McLeod. 1990. Vegetation of the Savannah River site: major community types. Publ. Savannah River Site Nat. Environ. Res. Park Progr., SREL, Drawer E, Aiken, South Carolina.

Wurtman, R. J., J. Axelrod, and J. Tramezzani. 1967. Adrenalin synthesis: control by the pituitary gland and adrenal glucocorticoids. Science 150: 1464-146.

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