

BEHAVIORAL PROFILE OF FREE-RANGING MALE LIZARDS, *ANOLIS CAROLINENSIS*, ACROSS BREEDING AND POST-BREEDING SEASONS

THOMAS A. JENSSEN,¹ NEIL GREENBERG,² AND
KATHERYN A. HOVDE³

¹Biology Department, Virginia Tech, Blacksburg, VA 24061, USA

²Zoology Department, University of Tennessee,
Knoxville, TN 37916, USA

³Savannah River Ecology Laboratory, Aiken, SC 29802, USA

ABSTRACT: The behavior of 10 free-ranging male *Anolis carolinensis* was videotaped in a riparian habitat for 41 h during May–July of the breeding season; 8 of the original 10 males plus 1 substitute were videotaped for an additional 22 h during August–September of the post-breeding season. Comparisons of breeding versus non-breeding seasons showed dramatic shifts in the percentage of time spent in the following behavioral modes: (1) “stationary,” 51.1% versus 85.6% (with respective display rates of 46/h versus 2/h); (2) “travel,” 26.7% versus 2.6% (with respective distance rates of 73 m/h versus 106 m/h and display rates of 209/h versus 78/h); (3) “creep,” <1% versus 14.1% (with post-breeding distance rate of 17 m/h and display rate of 15/h); (4) “courtship,” 4.2% versus 0% (occurring 1/40 min with a display rate of 233/h); (5) “copulation,” 6.1% versus 0% (occurring 1/7 h, each averaging 15 min); (6) “male dispute,” 9.2% versus 0% (occurring 1/h, with a display rate of 73/h); (7) “foraging,” 1.0% versus 1.5% (occurring 1.2/h versus 3.6/h); and (8) “predator avoidance,” “drinking,” “defecation,” and “shedding,” total 1.5% versus 0.2%. Over all contexts, the respective breeding versus post-breeding season rates for distance moved and displaying were 26 m/h versus 8 m/h and 100 displays/h versus 6 displays/h.

Breeding males were polygynous and defended exclusive, closely monitored home ranges (\bar{x} = 174 m²) that overlapped an average of 2.8 resident females. Males used all available microhabitats and were considered perch generalists. Males spent two-thirds of their time between 0 and 2 m above the ground on perches 1–8 cm in diameter during the breeding season, but more often frequented higher and thinner perches in the post-breeding season, during which time much creeping and foraging occurred. Males exhibited a wide range of foraging behavior, reflecting a generalist's mode of prey capture. Feeding was initiated when stationary (sit-and-wait), traveling (eat-on-the-run), and creeping (active search); more feeding events were initiated from a stationary mode, but traveling (breeding season) and creeping (post-breeding season) produced more feeding attempts per unit of time. Males were bright green 75% (breeding season) and 87% (post-breeding season) of the time. Shifts between four categories of body colors (bright green to chocolate brown) averaged 4.7 (breeding season) and 1.0 changes/h (post-breeding season), with a bright green state maintained for significantly shorter durations during the breeding period than after the breeding period (\bar{x} = 27.1 and 89.6 min, respectively). There was no evidence that change in body color was matching substrate color; however, green-to-brown shifts in body color were usually associated with the initiation of social interactions. Behaviors possibly associated with pheromone reception or deposition were infrequent (<8 times/h), occurring most often in the post-breeding season when no social behavior was observed. Based on our results, the influence of captivity on lizard behavior is discussed.

Key words: *Anolis carolinensis*; Courtship; Display behavior; Foraging behavior; Habitat niche; Locomotion; Pheromone; Polychrotidae; Seasonality; Social behavior; Territoriality

ANOLIS CAROLINENSIS is common to a large geographic area of the United States (Conant, 1975) and easily available to pet stores and laboratories. As such, *A. carolinensis* has been the subject of hundreds of studies, many of which have made inferences about adaptations and/or behavioral characteristics of the species. With few exceptions (e.g., Gordon, 1956; King,

1966; Ruby, 1984), these investigations were conducted in controlled environments under a myriad of conditions, from observations of behavior in greenhouses (Greenberg and Noble, 1944) to studies of lizards in 38-L enclosures (McMann, 1993). However, animals held in captivity for exhibition or for behavioral/physiological investigation may suffer from stress, thus

compromising zoo or laboratory objectives (e.g., Chiszar et al., 1993; Greenberg, 1990; Moore et al., 1991). Lance (1990) suggested that behavior could be used as a non-intrusive criterion of stress. Kreger (1993) added that in order to identify what may be abnormal or stress-related behavior, one first needs to have species-specific behavioral and ecological data from field conditions.

To our knowledge, no study has validated (*sensu* Martin and Bateson, 1986: Chapter 6) the behavioral profile of free-ranging *A. carolinensis*. In providing these data, we had two primary objectives. First, the species' behavior in the field needed to be qualified and quantified. As the most northerly distributed anole of a tropical radiation (Williams, 1969), *A. carolinensis* exhibits unique life history and physiological adaptations for its temperate range extension (e.g., Jenssen et al., in press; Michaud, 1990; Wilson and Echternacht, 1987), and its behavior would be expected to reflect similar adaptive properties. Second, a "field level" control was needed for comparison with previously described captive behavior of *A. carolinensis* subjects. Our results can be used by investigators as a guide for normal species behavior. Knowledge of normal species behavior is important because aberrations in the behavioral profile of captive subjects may confound laboratory results.

MATERIALS AND METHODS

The Augusta Canal (northwest of Augusta, Georgia, latitude 33°N) was chosen as the study site because of unique characteristics favoring our objective to videotape free-ranging males on a continuous basis. Along the 16-km canal, a tow path cuts through the riparian vegetation growing between the canal and the Savannah River. On the canal side of the tow path is a 3–6-m-deep strip of trees and understory that supports a linear distribution of *A. carolinensis* home ranges. This thin slice of habitat greatly facilitated the videotaping of resident lizards. From the tow path, which is approximately 4 m above the canal, males could be kept on camera whether they moved to the base of their habitat,

climbed 6–8 m into the top of the canopy, or traveled to the back of their home ranges. The tow path also permitted repositioning the camera laterally as males traversed the length of their home ranges.

Observations were made in May–July 1992 during the male breeding season and continued into August–September after males stopped breeding. From 63 h of videotape, males were "on-camera" for 54.9 h. The average duration when males were "off-camera" was 3.6 min (SE 0.58, $n = 135$). The total of on-camera durations was greater for the breeding than non-breeding records, being 36.9 h and 18.0 h, respectively. We videotaped during days of partial or full sunlight when lizards were active, and we avoided periods of rain or excessive heat when activity was likely to be depressed (air temperature ≥ 35 C; Wilson and Echternacht, 1990). When videotaping was in progress, air temperatures were measured with a shaded quick-reading mercury thermometer every 15 min at 1.5 m above the ground. This procedure provided a record of the general thermal context in which our data were gathered across seasons (Fig. 1).

We attempted to videotape 10 individual males across the breeding and non-breeding seasons. However, because 2 of the original 10 males had disappeared by August, an additional male was added to the non-breeding sample. Each male was videotaped for an average of 3.1 h/season. Males were not captured until videotaping was completed. Then males were noosed, measured for snout–vent length (SVL), examined for unique body markings, and marked by painting if they had not been previously captured and marked. Because eight males and their home ranges were held in common between the breeding and post-breeding samples, inter-sample differences could most likely be attributed to seasonal effects rather than to differences in inter-male behavior or home range microhabitat.

Data were gathered with a team of two or three persons. One person used a tripod-supported Panasonic video camera (AG 460) fitted with a 2 \times magnified 84-mm zoom lens (comparable to a 672-mm lens

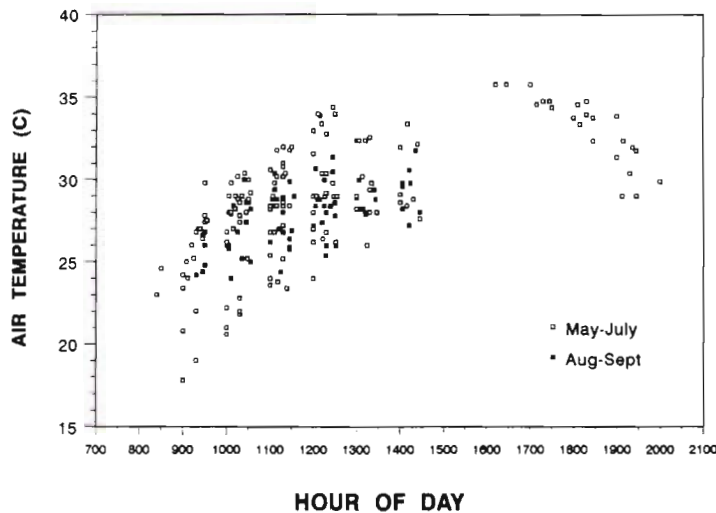


FIG. 1.—Air temperatures, taken at 15-min intervals, during videotaping sessions of *Anolis carolinensis* males near Augusta, Georgia, during May–July (breeding period) and August–September (post-breeding period).

for a 35-mm film format) to track a male. A time-data generator imposed the date and the time of day from hour to 0.1-s increments on the videotape. Camera-to-subject distance varied between 3 and 8 m, which gave excellent to adequate resolution of the subject. The camera's microphone recorded off-camera information dictated by other team members onto the audio track. These audio data included perch height estimates of the male, the behavior of the male when he temporarily moved behind vegetation out of view of the camera, and the behavior and separation distances of off-camera conspecifics with whom the male interacted during social events. Multiple batteries were used for the long video sessions, and a small umbrella was fitted to the camera to prevent the build-up of solar-generated heat from disabling the camera. Resulting videotapes were played back on Panasonic (AG 7300) editing cassette recorders, which provide multiple speed and frame-by-frame capabilities.

Thirty-four variables were taken from the analysis of videotapes and from notebooks of field-recorded data, and grouped within five categories (Table 1). Under the first category (General), the number of resident females in a male's home range was

based on the maximum number of females seen simultaneously during a taping session; this number is likely to be conservative because other females might have been present but out of view. Minimum distances between a male under observation and his nearest male neighbors represent either the closest that the male subject and an adjacent male were seen to approach one another or the minimal vegetational gap between the home ranges of the two males, whichever was smallest. Home range volume was approximated by summing a series of rectangular volumes, where each volume was calculated with x -, y -, and z -axes through the dominant vegetational components (e.g., tree, bush) that a subject was seen to occupy. The axes were approximated from a 2-m vertical reference for y -data and a meter tape on the tow path for x - and z -data. This method probably overestimated the total perch volume because the physiognomy of the vegetation was treated as cuboid, and the relatively small volumes of structures like tree trunks were not differentiated from their corresponding canopy volumes.

Behaviors were divided among two categories (Table 1): (1) those of durational significance, operationally defined, which provided a context (labeled "events"); and

TABLE 1.—Variables and their respective categories (general information, time variables associated with all other variables, status by periodic updates, events as behavioral contexts, and occurrences of behaviors within events) used to describe the behavioral profile of 11 male *Anolis carolinensis* along the Augusta Canal, Augusta, Georgia, during May–September.

Category	Variable (with definition)
General	Subject Identification
	Snout–Vent Length (mm)
	Territory Volume (m ³)
	Number of Resident Females
Time	Minimum Nearest Male Distance (m)
	Date
	Season (breeding/post-breeding)
	Hour of Day
Status	Elapsed Time of Video Session (to 0.1-s increments)
	Air Temperature (C) (at 15-min intervals)
	Perch Height (m) (at 5-min intervals)
	Perch Diameter (cm) (at 5-min intervals)
Event	Posture Rank (1–3) (where 1 = low, 2 = moderate, and 3 = high head position; at 5-min intervals)
	Body/Substrate Color Match (yes–no) (at 5-min intervals)
	Stationary (duration of holding a stationary perch for ≥ 60 s, without evidence of other event variables)
	Travel (duration of making a perch shift by walking/running, including pauses of ≤ 59 s, without evidence of other event variables)
	Creep (duration of making a perch shift by creeping, including pauses of ≤ 59 s, without evidence of other event variables)
	Forage (duration from prey detection to end of food handling)
	Drink (duration of one or a series of related drinking bouts)
	Defecate (duration from cloacal swing over side of perch to conclusion of post-defecation cloacal drag)
	Predator Avoidance (duration from initial avoidance movements to resumption of undisturbed behavior)
	Territorial Defense (duration from initial directed inter-male behavior to resumption of other non-male/male events)
	Courtship (duration during which male directed displays at, moved toward, and attended a female)
	Copula (duration while male and female were in copula)
	Unknown (duration when male was out of view of camera and other observers)

TABLE 1.—Continued.

Category	Variable (with definition)
Occurrence	Distance Moved (m) during each bout of an event
	Headbob/Dewlap Display number performed
	Body Color Change (shifting between a color rank, where 1 = bright green, 2 = mossy green, 3 = brown, and 4 = dark brown)
	Substrate Lick (head directed at substrate, tongue extended to substrate during brief, narrow-mouthed open/shut cycle)
	Aerial Lick (head up, tongue extended during brief, narrow-mouthed open/shut cycle)
	Mouth Smack (brief, narrow-mouthed open/shut cycle, no tongue extension)
	Yawn (prolonged, wide-mouthed open/shut cycle)
	Mouth Wipe (rubbing the length of the side of the mouth on the substrate, frequently repeating with opposite side of mouth)
	Cloacal Drag (pressing the cloaca to the substrate while slowing moving the body forward)
	Belly Drag (pressing length of venter to the substrate while slowly pulling the body forward with only the forelimbs)

(2) those of frequency significance, ethereal acts that were performed within a context (labeled “occurrences”). For example, courtship was an event that established the context within which the occurrence of displaying took place. The order and grouping of variables of Table 1 are followed in the presentation of results.

Descriptive statistics formed the basic level of analysis, given as mean (\bar{x}) and standard error (SE). Where data were compared between classes for statistical significance, nonparametric tests were used when possible (Siegel and Castellan, 1988); the null hypothesis was rejected at $P \leq 0.05$, unless stated otherwise. Data were analyzed using the SAS (1988) statistical software package.

RESULTS

General Variables

Subjects, home range, companions.—The 11 adult male *A. carolinensis* used as

subjects had a mean SVL of 62.3 mm (SE 1.5), a mean home range volume of 173.6 m³ (SE 37.9), and a highest mean available perch site of 7.4 m (SE 0.6). Male home ranges overlapped an average of 2.8 resident females (SE 0.44), ranging from 1 to 5. No significant probabilities resulted from applying Spearman's correlation procedure to: male SVL and male territorial volume ($r_s = 0.425$, $P = 0.221$); male SVL and number of resident females ($r_s = 0.576$, $P = 0.082$); and male territorial volume and number of resident females ($r_s = 0.045$, $P = 0.901$).

None of our focal males was seen to share his home range with other adult males. The mean minimum distances that separated the territorial boundaries of our observed males from those of their conspecific neighbors to the left and right were 3.4 m (SE 1.4) and 3.9 m (SE 1.0), respectively.

Time and Status Variables

Time/air temperature.—Videotaping took place between 0900 and 1900 h, when air temperatures were between 20 and 35 C (Fig. 1). Seasonal data were not biased by hour of observation or seasonally different air temperatures, as no significant correlation existed between season and either hour of day or air temperature (Spearman correlation; $r_s = 0.011$, $P = 0.86$; $r_s = -0.115$, $P = 0.071$, respectively).

Perch height/diameter.—Perch height and perch diameter, as measures of structural niche, should be influenced by the physiognomy of available habitat. Indeed, the males of our study were observed to use their entire vertical range of habitat, which included tree canopies in excess of 7 m high. During the sampling times, however, our males spent 64% and 60% of their time between 0 and 1.9 m above the ground during the breeding and post-breeding periods, respectively (Fig. 2). The remaining perch height localities were distributed from 2 to 8 m (Fig. 2).

Males also ranged over all available perch diameters, but the majority of utilized perch substrates during the breeding season (57%) and post-breeding season (67%) were of relatively small diameters (0.1–3.9 cm; Fig. 3). Using subject means

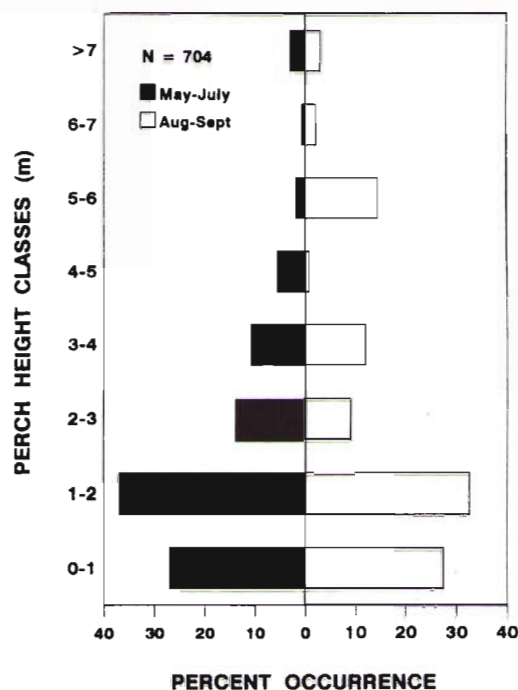


FIG. 2.—Distribution of perch height classes from observations made at 15-min intervals from a 63-h videotape record of 11 male *Anolis carolinensis* during May–July (breeding period) and August–September (post-breeding period) near Augusta, Georgia.

as individual observations, the average perch height and diameter for our 10 males during the breeding period were 2.3 m (SE 0.29) and 5.3 cm (SE 0.58), respectively, and for the nine post-breeding males the means were 2.9 m (SE 0.58) and 4.9 cm (SE 1.34), respectively.

During the post-breeding observations, males tended to spend more time occupying higher (≥ 5 m) and thinner (≤ 2 cm) perches than in the breeding season (Figs. 2, 3). The perch height data, analyzed with an ANOVA procedure (general linear model; SAS, 1988), indicated significant effects due to season ($F = 10.18$, $P < 0.002$) and subject ($F = 30.32$, $P < 0.001$), but not hour of day ($F = 1.49$, $P = 0.132$); perch diameter data were significant for the effects of subject ($F = 11.73$, $P < 0.001$), but not for season ($F = 1.89$, $P = 0.170$) or hour of day ($F = 0.66$, $P = 0.777$). Intermale differences had a significant effect on both perch height and diameter. To hold habitat and subject differences to a

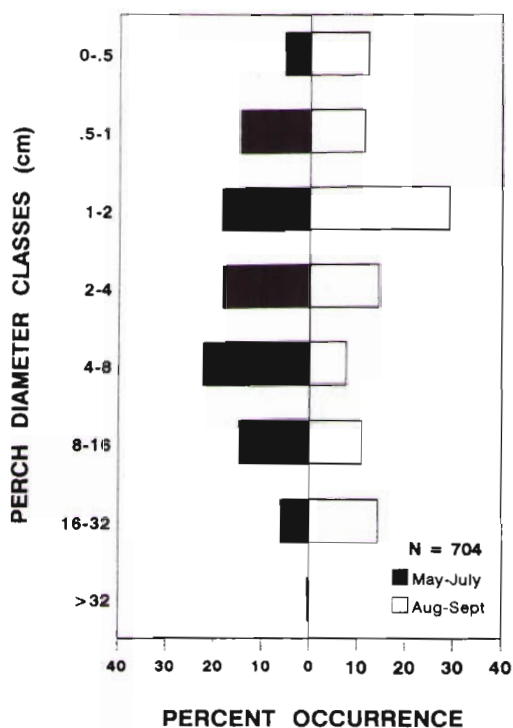


FIG. 3.—Distribution of perch diameter classes from observations made at 15-min intervals from a 63-h videotape record of 11 male *Anolis carolinensis* during May–July (breeding period) and August–September (post-breeding period) near Augusta, Georgia.

minimum, the habitat data of only the eight males common to both seasons were examined. Seven had their highest mean perch heights and six had their smallest mean perch diameters in the non-breeding season (sign test, $P = 0.035$ and 0.145 , respectively).

Body posture.—Relative head elevation (i.e., head posture) when a lizard was not moving varied with relative forelimb extension. This posture was ranked 1–3, with complete venter/substrate contact (head low) being 1, partial forelimb extension (head moderately up) being 2, and full forelimb extension (head high) being 3 (Table 1). Individual males had means between 1.4 to 2.6 for this 1–3 positional evaluation. An ANOVA (general linear model; SAS, 1988) indicated a significant effect due to season ($F = 25.57$, $P < 0.001$) and subject ($F = 2.78$, $P < 0.003$), but not

hour of day ($F = 1.14$, $P = 0.330$). Because inter-male differences significantly influenced posture, we used data from only the eight males observed across seasons; all had greater mean values for the breeding than for the post-breeding period (sign test; $P = 0.004$) (Fig. 4).

Body color.—Body color was also evaluated with a ranking system. *Anolis carolinensis* is capable of shifting its body color from bright green to very dark brown, the same general color range of the various substrates on which the lizards usually perch. We divided this color range into four categories: bright green, mossy green, brown, and dark brown/black. Our males were primarily bright green in both seasons (75.6% and 87.6% of the total breeding and post-breeding durations, respectively). Breeding males, however, shifted their body colors more frequently ($\bar{x} = 4.7$ times/h) than during the post-breeding period ($\bar{x} = 1.0$ times/h). The reduced likelihood of changing color during the post-breeding period meant that, on average, a male maintained his bright green color state for a period three times longer than in the breeding period (Wilcoxon 2-sample test; $Z = 3.001$, $P = 0.0027$) (Fig. 5). Inter-seasonal comparisons for each of the other three color states were not significantly different (Wilcoxon 2-sample test; $Z = 0.653$, $P > 0.071$). Within each season, the duration of the bright green state was significantly longer than for the three other color states. Conversely, there were no significant differences among the durations of the latter three color states (mossy green, brown, and dark brown) (ANOVA, with Duncan's multiple-range test; season 1: $df = 3$, $F = 13.39$, $P = 0.0001$; season 2: $df = 3$, $F = 7.54$, $P = 0.0016$) (Fig. 5).

The match between a male's body color and the color of his immediate substrate was determined at 5-min intervals. A simple match (brown-on-brown, green-on-green) or mismatch (green-on-brown, brown-on-green) criterion was used. If *A. carolinensis* is actively cryptic, the proportion of body/substrate color matches should approach 100%, whereas mismatches should approach 0%. If lizards are not actively matching their immediate

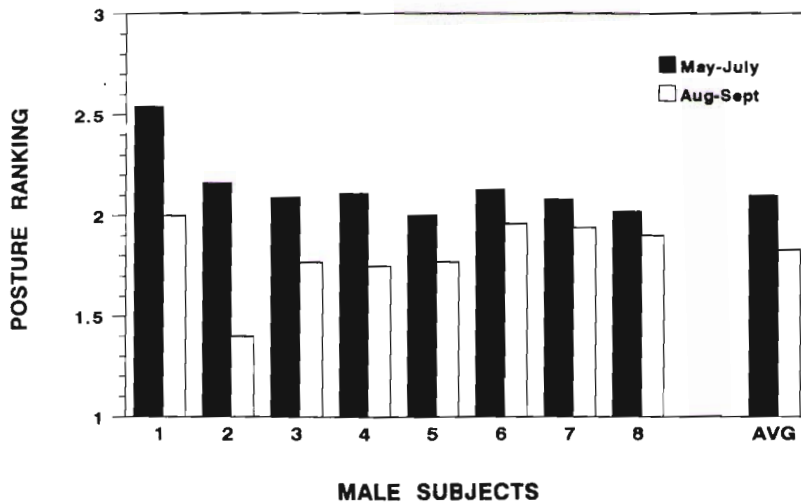


FIG. 4.—Mean posture rankings (1 = head low, 2 = head moderate, 3 = head high), noted at 15-min intervals, from a 63-h videotaped record of eight male *Anolis carolinensis* during May–July (breeding period) and August–September (post-breeding period) near Augusta, Georgia.

background, matches to mismatches should approach a random 50/50 split. For 704 samples, matches and mismatches were 36% and 64%, respectively. The deviation from random was significant ($\chi^2 = 28.98$, $P < 0.0001$). Clearly the trend was toward non-crypsis.

Event Variables

Stationary/travel/creep.—During the breeding season, males spent 51% of their time in a stationary mode and 28% traveling (walking/running/jumping; Fig. 6; Table 2). Mean durations of being station-

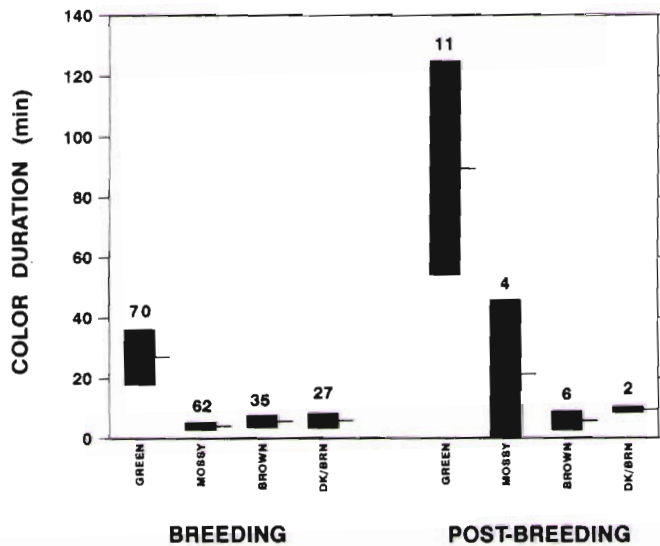


FIG. 5.—Mean duration of four body color states (green, mossy, brown, and dark brown) of 11 male *Anolis carolinensis* videotaped for 63 h during May–July (breeding period) and August–September (post-breeding period) near Augusta, Georgia. Mean, ± 2 standard errors, and sample size are represented by the horizontal line, ends of the bar, and number over the bar, respectively.

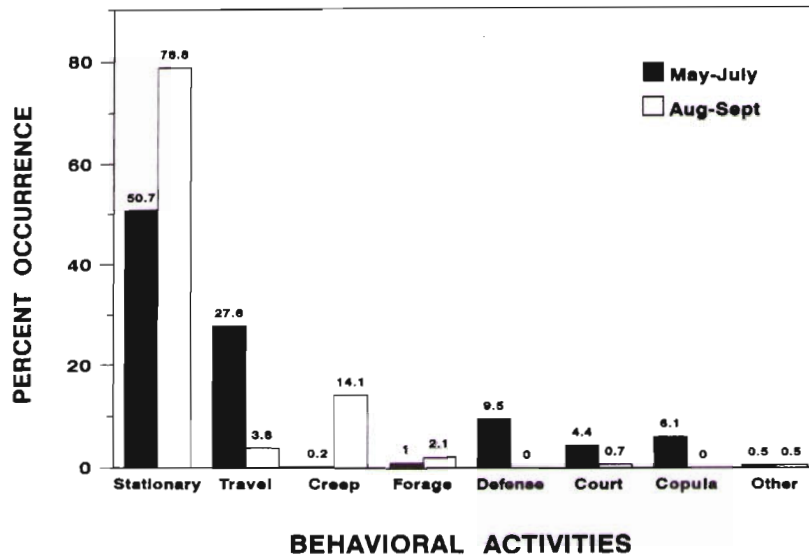


FIG. 6.—Activity profile of 11 male *Anolis carolinensis* videotaped for 63 h during May–July (breeding period) and August–September (post-breeding period) near Augusta, Georgia.

ary and traveling were 3.3 and 1.9 min, respectively (Table 2). Males frequently performed headbob/dewlap displays (sensu DeCourcy and Jenssen, 1994) while in a stationary mode, averaging 46 displays/h (Fig. 7). Of particular interest, however, was the high rate of display production, averaging 209 displays/h when moving

rapidly and conspicuously through their territories at a rate of 73 m/h (Fig. 8; Table 2). A bout of traveling, averaging 2.3 m/bout (Table 2), was generally composed of short bursts of locomotion interspersed with brief pauses during which the male would display before continuing on; all displays were given while the performer was sta-

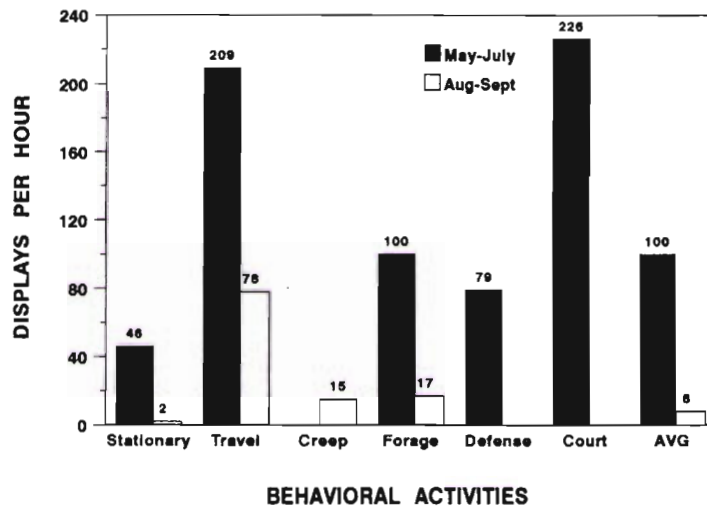


FIG. 7.—Display production per hour during specific activities by 11 male *Anolis carolinensis* videotaped for 63 h during May–July (breeding period) and August–September (post-breeding period) near Augusta, Georgia.

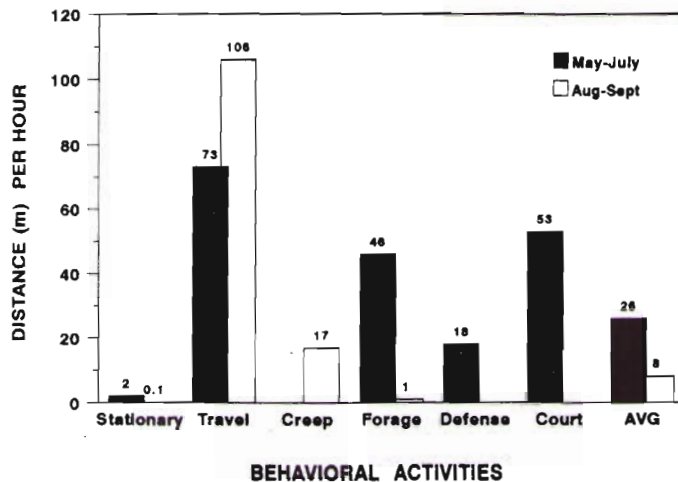


FIG. 8.—Distance moved per hour during specific activities by 11 male *Anolis carolinensis* videotaped for 63 h during May–July (breeding period) and August–September (post-breeding period) near Augusta, Georgia.

tionary. Travel speeds would have been higher if the pauses to display had not been part of the distance/time calculations.

Whereas breeding male behavior seemed to be socially motivated, post-breeding male behavior appeared to be directed by energetic considerations. Social interactions all but disappeared in the post-breeding period: display production during the stationary mode dropped 23-fold, social behaviors per se were absent (see below), and traveling (very likely a territorial patrol function) decreased by 7-fold after the breeding season (Fig. 6; Table 2). Post-breeding energy conservation and intake predominated in three ways: (1) more time was spent motionless, with more than three-quarters of the total time budget spent in a stationary mode (an increase of 28% over that of the breeding season); (2) when moving, more than three-quarters of the time was spent creeping (an appetitive expression of active foraging); and (3) instances of prey capture tripled over those of the breeding period (Fig. 6; Table 2).

Creeping behavior was unique to and pervasive (14% of time budget) during the post-breeding observations. Males were seen to move off the larger perches and onto the thin-diameter substrate of the tree canopies. Here they crept slowly along the

twigs, even investigating the undersides of leaves. Bouts of creeping averaged 1.3 min at a mean sustained rate of 17 m/h (Table 2).

Foraging.—Breeding/post-breeding foraging behavior differed in technique and frequency. Bouts of feeding were initiated from three modes: (1) eat-on-the-run, (2) sit-and-wait, and (3) active search. Breeding (i.e., territorial) males averaged 1.2 feeding events/h. In 42% of 45 feeding events, males ate on the run, capturing prey as they traveled rapidly through their territories. When feeding from this mode, a male would diverge from his path to lunge at an insect. After consuming the food item, the lizard would resume traveling. Food detection occurred opportunistically while a male was traveling, and was not the stimulus for the locomotion. The remaining foraging behavior (58%) was initiated while males were stationary, and as such could be labeled “sit-and-wait.” Mean feeding rate was greater while males were traveling ($\bar{x} = 1.8$ prey/h) than when stationary ($\bar{x} = 1.4$ prey/h). The means for distance moved from point of apparent detection of prey item to point of attack, foraging duration from detection to consumption, and display rate immediately after eating were 0.4 m, 0.5 min, and 100/h, respectively (Table 2).

TABLE 2.—Duration (min), distance moved (m), and headbob displays performed during bouts of primary activities (>1% of time budget) by 11 male *Anolis carolinensis* during the breeding (1) and post-breeding (2) seasons near Augusta, Georgia, derived from a 63-h videotape record. Rates/hour are set off in brackets.

Activity	Season 1			Season 2		
	Mean	SE	n	Mean	SE	n
Stationary (% of budget)	(51)			(79)		
Mean bout duration	3.3	0.18	339	3.7	0.51	244
Mean distance/bout	0.1	0.02	339	<0.1	<0.01	244
Distance/hour	[2]			[<0.1]		
Mean displays/bout	2.5	0.25	339	0.1	0.04	244
Displays/hour	[46]			[2]		
Travel (% of budget)	(28)			(4)		
Mean bout duration	1.9	0.11	328	0.5	0.05	92
Mean distance/bout	2.3	0.12	328	0.8	0.06	92
Distance/hour	[73]			[106]		
Mean displays/bout	6.5	0.35	328	0.6	0.13	92
Displays/hour	[209]			[78]		
Creep (% of budget)	(<1)			(14)		
Mean bout duration				1.3	0.14	123
Mean distance/bout				0.4	0.03	123
Distance/hour				[17]		
Mean displays/bout				0.3	0.08	123
Displays/hour				[15]		
Forage (% of budget)	(1)			(3)		
Mean bout duration	0.5	0.09	45	0.4	0.04	65
Mean distance/bout	0.4	0.06	45	0.4	0.05	65
Distance/hour	[46]			[71]		
Mean displays/bout	0.8	0.19	45	0.1	0.04	65
Displays/hour	[100]			[17]		
Defense (% of budget)	(10)			(0)		
Mean bout duration	5.6	0.93	38			
Mean distance/bout	1.7	0.25	38			
Distance/hour	[18]					
Mean displays/bout	7.3	1.32	38			
Displays/hour	[79]					
Courtship (% of budget)	(4)			(0)		
Mean bout duration	1.7	0.19	56			
Mean distance/bout	1.5	0.29	56			
Distance/hour	[53]					
Mean displays/bout	6.6	0.59	56			
Displays/hour	[226]					
Total (% of budget)	(100)			(100)		
Distance/hour	[26]			[8]		
Displays/hour	[100]			[8]		

Post-breeding foraging events, on average, occurred at a frequency ($\bar{x} = 3.6/h$) that was three times as great as during the breeding season, covered 0.4 m, and lasted 0.4 min (Table 2). In addition, individuals rarely displayed after eating (Table 2). Of 65 feeding events, few (4%) occurred while males were traveling (i.e., eating on the run), probably because males

had largely abandoned rapid locomotion in the post-breeding period. Instead, males opportunistically detected prey while creeping (i.e., active search) or while stationary (i.e., sit-and-wait). Creeping and stationary behaviors were associated with 22% and 74% of prey captures, respectively. Given that creeping and stationary modes of behavior occupied 14% and 79%,

respectively, of the post-breeding activity profile (Fig. 6), feeding during creeping yielded a slightly better rate of success.

Defense.—Territorial behavior was not observed after July; however, prior to August, males behaved as if there was great potential for a territorial takeover. Of the frequent displays and perch shifts by our males, most were directed at other males and relatively few were female-directed (see "Courtship/copulation" below). Yet, a close-range, male-male encounter was never observed for our males nor was an intruding or cohabiting male ever seen within their territories. In fact, after more than 1000 h of focal animal observations at the study site during two breeding seasons by several research teams from Virginia Tech, only one naturally occurring fight was seen. Though the threat of a takeover may be high, realization of that threat appeared low because: (1) actual fighting that could result in eviction was rare, and (2) the 8 of 10 males that were on the same territories over the course of several months indicate relatively stable and long-term residencies. The greatest possibility for resident turnover and unstable territories may be in the early part of the breeding period (e.g., April); current field observations did not include this period.

Of the total 38 male-male events recorded (10% of time budget; Fig. 6), aggression was limited to displaying at neighboring males. Interactions averaged 5.6 min in duration, with a mean of 7.3 displays performed per event (Table 2). Approximate inter-male separation distances during directed displaying ranged 2–6 m. The display rate was not especially high during these defense events (79/h; Table 2) because the interactions had large separation distances, with a few volleys of displays being interspersed by long periods of mutual staring. Males occasionally made short forays into the low vegetation between territories or, more frequently, they moved along the edge of their territory where the boundary neared a neighboring territory; such movements during aggressive encounters averaged 1.7 m (Table 2).

A curious resident response associated with border defense indicated that the res-

ident males may actually anticipate an aggressive exchange with a neighboring male. Forty-four percent of the green-to-brown body color shifts could be identified with a defense event (see "Color change" below). Approximately half of these color shifts were initiated as a male moved through his territory toward a boundary closest to a neighboring male; this pre-defense color shift was initiated before the neighboring male could be seen by the resident male and, in some instances, during episodes when the neighbor was never seen (e.g., located on the back side of a tree trunk). One observer, Eva Lacy, suggested the intriguing inference that resident males move with deliberate intent to the boundary of their territory to defend against expected antagonists.

Courtship/copulation.—With the exception of one occurrence in early August, all courtship events took place in the May–July observation period. Males devoted only 4% of their time during the breeding season to interactions with resident females (Fig. 6); these intersexual contacts averaged 1.7 min in duration, elicited the highest display rate of all events (226/h), and covered an average of 1.7 m per event (Table 2). During 41 h of observations, 6 of our 10 males copulated once with a resident female, for a mean copulatory rate of 1/7 h; given that a male is active for 7–9 h per day, the data suggest that males copulate about once a day. The copulatory duration ranged from 6.3 to 26.6 min ($\bar{x} = 15.8 \pm 3.0$ [SE] min). Though copulation was a relatively infrequent event, it nevertheless represented a large block of time (6.1% of time budget; Fig. 6).

Males ignored numerous opportunities to copulate with receptive resident females. There were 56 courtship events, with only 6 resulting in copulation. The 50 male-female contacts not leading to copulation were divided into two outcomes: (1) male approached female, but female moved off (female not interested), and (2) male approached female, female passive with bent neck (female receptive), but male moved off (male not interested). The latter category represented 62% (31) of courtship events. During ignored opportunities, the

male circled or brushed over the female before switching into a travel mode and moving off. With single-frame review of these videotaped encounters, we looked for evidence of pheromone transmission; although vegetation occasionally blocked a continuous view of a male's head, no substrate or aerial licking was evident.

Drinking/defecation/predator avoidance.—Drinking water, defecation, and predator avoidance were of such short duration and low frequency that, combined, they only occupied 0.5% of the overall time budget (Fig. 6, "Other"). Males were observed to lap from leaves the droplets of water left by dew and rain. Several males occasionally moved to the edge of the canal, and subsequent observations verified lizards drinking from the moving water (S. C. Nunez, personal communication).

When defecating, the lizard swung his tail and rear torso over the edge of his perch, dropped the pellet into midair, then realigned his body with the perch, and frequently dragged his cloaca for half a body length. The behavior suggests a health benefit from uncontaminated perches but precludes the use of the fecal pellet as a signpost agent. However, the post-defecation cloacal drag may function as a pheromone-depositing activity.

No predation was ever seen within the course of the present study. In addition, during more than 1000 h spent at the site by us and others outside of the present study, only one incident of predation was witnessed. A juvenile *A. carolinensis* was captured and wrapped in the web of an *Argiope aurantia*. The spider embedded its chelicerae into the rump of its prey and fed on the still living lizard. Predator avoidance behavior was observed once when a male "squirreled" to the underside of its perch in response to a bird's shadow. The lizards, however, did not seem particularly threatened by the presence of birds per se, as passerines frequented the canopies where lizards were perched and the behavior of nearby birds did not elicit a noticeable response. Too few instances of this kind occurred to determine if the males were reacting to particular bird behaviors, minimum lizard/bird separation

distances, shadow movement, or specific bird species.

Occurrence Variables

Distance.—The mean rates of distance traveled during the various contextual events (Fig. 8; Table 2) reflected seasonal shifts. Across all events, males had average traveling rates of 26 and 8 m/h during the breeding and post-breeding periods, respectively. The dramatic decrease in post-breeding travel distance was largely attributed to the cessation of territorial patrol (Fig. 6, "Travel"). Of interest is the difference in speed for traveling males in the breeding versus post-breeding periods (Fig. 8). When post-breeding males occasionally walked, ran, or jumped (i.e., traveled), they did not pause to display, leading to a faster estimated travel speed ($\bar{x} = 106$ m/h) than was the case in the breeding season ($\bar{x} = 73$ m/h). Creeping, the predominant form of post-breeding locomotion (Fig. 6), was more than five times slower ($\bar{x} = 20$ m/h) than other modes of traveling.

Territorial defense did not cover much distance (18 m/h; Fig. 8). Male aggression was generally restricted to moving along territorial edges while exchanging displays with nearest neighbors (see "Defense" above). High-speed locomotion was not observed in the defense event; much time was spent motionless at boundary perch sites.

Displays.—The headbob and throat fan displays of *A. carolinensis* (DeCourcy and Jenssen, 1994) were the most conspicuous behaviors exhibited by our males during the breeding season, averaging a rate of 100 displays/h across all events (Fig. 7). Not only did males display during obvious social contexts (i.e., an identifiable recipient of the displays), but much displaying also accompanied the stationary, travel, and forage events (Fig. 7), contexts when no conspecifics were observed in the immediate vicinity. This nondirected displaying demonstrated the continuous effort resident males put into advertisement.

Nonbreeding males almost never displayed, regardless of contextual event; the mean display rate across all events was 8/

h (Fig. 7). The lack of displaying during the post-breeding season strongly suggests the relative importance of the display behavior in social functions.

Color change.—A green body color was the apparent baseline condition, having the longest durations of the four color states for both seasons (Fig. 5). Social stimuli usually triggered the shift from green to mossy green or one of the shades of brown, and no male was seen to go from brown to green when initiating a social encounter. The contexts for green-to-brown shifts were classified as (1) defense (e.g., displaying from a territorial boundary toward a seen or unseen neighboring male, traveling toward an actively defended boundary), (2) courtship (e.g., almost always when a female ran from a male pursuit), (3) non-social (e.g., clouds passing over sun, after eating), and (4) undetermined.

We recorded 194 color shifts in the breeding season; many were intermediate stages as males slowly returned from one of the brown states to bright green after stimulus cessation. In contrast, color transitions from green to brown were usually rapid (a few seconds). There were 80 such episodes of green-to-brown: 35 from defense, 12 from courtship, and 4 from non-social occurrences, whereas the stimulus for 29 episodes could not be identified.

In the post-breeding sample, only 22 color shifts occurred, and of these, a mere 7 were in the green-to-brown direction. One such color shift occurred when an observed male interacted with a resident female, and the stimuli for the others were undetermined.

Summarizing both seasons, 60% of the 87 green-to-brown color shifts were identified with social interactions, and very few (5%) with possible nonsocial stimuli. Exogenous stimuli for the remaining 35 episodes of skin darkening were not obvious.

Chemosensory behavior.—In direct contrast with the high rate of visual displays performed during the breeding season ($\bar{x} = 100/h$; Fig. 7), the occurrence of any behavior that might be linked to pheromone reception or deposition was infrequent (Fig. 9). The most common behavior, substrate licking, averaged about once

per hour by territorial males. It is doubtful that pheromones are an important form of social signaling in *A. carolinensis*.

During the post-breeding period, five of the six behaviors potentially related to chemosensory behavior showed higher frequencies than during the breeding season (Fig. 9). Only cloacal dragging decreased; because this behavior was only seen after defecation and copulation, the post-breeding period offered fewer occasions for the appearance of cloacal dragging.

DISCUSSION

Our study of male *A. carolinensis* has documented significant behavioral changes corresponding to seasonality, the most striking of which occurred at the July/August boundary. At that time, males underwent a transformation from being socially oriented animals, with attendant social behaviors, to solitary animals focused on feeding and exhibiting little or no social activity. The seasonal shift in behavior most likely parallels endogenous events. Licht (1971), using Louisiana *A. carolinensis*, found testicular size to decrease in July, with a cessation of gametogenesis at the beginning of August. Dessauer (1955) and Licht (1971) also reported concomitant glycogen storage and enlarging fat bodies in August, a reflection of enhanced feeding and decreased activity levels.

Stationary/travel/creep.—Breeding males were primarily occupied with territorial patrol and advertisement. They spent a quarter of their day on the move, traversing their territories at a mean rate of 73 m/h, performing the second highest display rate (209/h) next to courting, and averaging more than 2 m and 6 displays per bout of locomotion (Table 2). This behavior makes males very conspicuous and is undoubtedly energetically expensive. For an average hour across all possible events, males moved 26 m and displayed 100 times. Compared with many other lizards, breeding male *A. carolinensis* registered high rates of locomotion and display. Data from 24 species of *Anolis* (Bennett and Gorman, 1979; Lister and Aguayo, 1992; Losos, 1990; Moermond, 1979) showed that *A. caroli-*

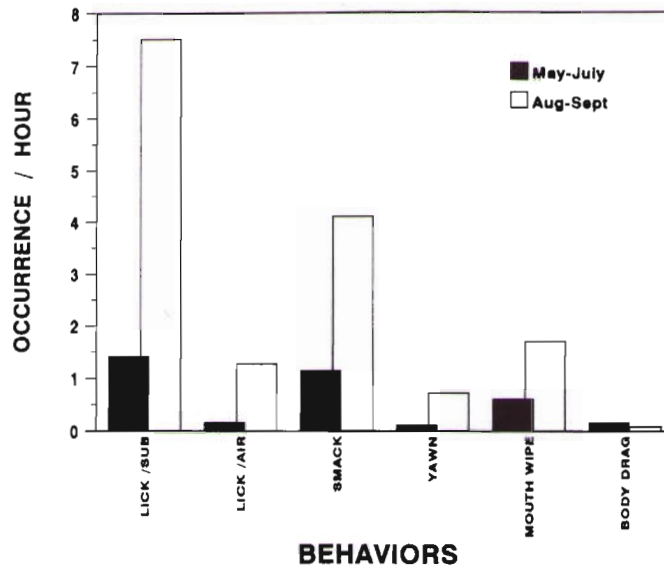


FIG. 9.—Frequency of occurrence per hour of behaviors possibly related to olfactory reception (substrate licking, aerial licking, smacking, and yawning) and scent deposition (mouth wiping and body dragging) by 11 male *Anolis carolinensis* videotaped for 63 h during May–July (breeding period) and August–September (post-breeding period) near Augusta, Georgia.

ensis traveled 3.4 times farther per hour than the most active anole (*Anolis bonaiensis*), and displayed 7 times as often as the highest rate (15 displays/h; *Anolis nebulosus*). Over an 8-h day, male *A. carolinensis* are estimated to travel 208 m (i.e., 26 m/h \times 8 h). This figure is greater than half of the total daily distances reported for 16 non-anolines, all of larger body size than *A. carolinensis* (Garland, 1993).

The proportion of time breeding male *A. carolinensis* spent in social behavior is difficult to quantify. However, it is clear that 20% was in defense, courtship, and copulation (Fig. 6). Of the 28% of the time spent traveling, most appeared devoted to territorial patrol and advertisement displaying. A large proportion of the time spent in the stationary mode was undoubtedly used to monitor neighboring male and resident female positions, as evidenced by frequent displaying (Fig. 7); however, nonsocial surveillance also occurred, as shown by the frequency of feeding events (1.2 times/h) initiated by stationary males. Conservatively, we estimate at least two-

thirds of daily male activity was socially motivated during the breeding season.

Comparison of the *A. carolinensis* activity profile with other breeding male anoles indicated similarities as well as broad congeneric differences. The activity profile of *Anolis cupreus* (Fleming and Hooker, 1975) is surprisingly similar to that of *A. carolinensis*. Examples of very different profiles are found for *Anolis humilis* and *Anolis limifrons* (Talbot, 1979), where more than three-quarters of the time budget was foraging, and *A. nebulosus* (Lister and Aguayo, 1992), where almost half (>40%) of the day was extended resting/hiding, a category not shared by *A. carolinensis*.

After July, male *A. carolinensis* moved at a slow rate (\bar{x} = 8 m/h), primarily using a creeping locomotion, and displayed infrequently (\bar{x} = 8 displays/h). These rates are similar to the range of means given for the 24 surveyed species of anoles by Bennett and Gorman (1979), Lister and Aguayo (1992), Losos (1990), and Moermond (1979). Courtship and traveling were absent or infrequent events after July, find-

ings that most likely reflect the decline in male motivation to breed and defend a territory. This post-breeding activity level decreased still further for emerged *A. carolinensis* during the winter (December–March; Jenssen et al., in press). The behavior profile of wintering *A. carolinensis* has been characterized as the most sedentary of anoles (Jenssen et al., in press). Thus, across seasons, male *A. carolinensis* range from an anoline with one of the greatest activity levels to one with the least.

Foraging/posture.—Anoles are generally considered sit-and-wait predators, with species practicing specific kinds of foraging behaviors depending on their morphology and habitat characteristics. However, *A. carolinensis* was a generalist in its hunting techniques. Of the four prey-capture methods differentially used by *Anolis* lizards (“approach-pause-strike,” “stationary-strike,” “jump-strike,” and “stalk-strike”; Moermond, 1981), *A. carolinensis* males employed all four. In addition, where food-searching patterns seen in other anoles corresponded to the spatial structure of a species’ microhabitat (Moermond, 1979), *A. carolinensis* males remained in the same microhabitat while shifting their foraging techniques between seasons (i.e., a July/August boundary). During the breeding season foraging was undoubtedly affected by territorial activities. Breeding males ate infrequently (\bar{x} = 1.2 times/h) and primarily initiated feeding from a stationary mode (using approach-pause-strike or stationary-strike methods) or ate on the run if they encountered prey while traveling through their territories (using the jump-strike method).

Post-breeding males foraged three times as often as during the breeding season, and frequently used an active search technique (i.e., creeping), during which the stalk-strike method was seen. These seasonal differences suggest a basic shift in motivation from territoriality to feeding. The involvement of an endocrine agent for such seasonal shifts in behavior was examined by Marler and Moore (1989). They induced a conflict between territorial defense and foraging by implanting male *Sceloporus jarrovi* with testosterone. Treated lizards

displayed more and fed less often than controls (testosterone implants versus controls: displays/h, 41 versus 23; feeding/h, 0.8 versus 1, respectively).

Another notable difference between *A. carolinensis* and other anoles was the infrequent use of the anoline “survey posture,” defined as a downward-facing lizard with raised head on a vertical tree trunk (Scott et al., 1976). This posture, characteristically associated with monitoring lizards, was found to facilitate prey detection (Stamps, 1977a) but was rarely used by stationary *A. carolinensis* males during either season. That *A. carolinensis* males were never seen leaving an elevated perch to make a prey capture on the ground might explain the relative absence of a downward-directed monitoring posture.

Although males did not regularly assume a head-down position when stationary, they did tend to hold their heads in an elevated attitude above the substrate. The degree to which the head was elevated (i.e., head-to-body posture) tended to be higher in the breeding season (Fig. 4). Scott et al. (1976) hypothesized that maintaining a high head posture and holding the eyes at an elevated distance from the perch would effectively increase the angle through which surveillance would be facilitated. They speculated that a high posture in *Anolis* was primarily functioning to enhance predator avoidance and foraging. However, the greatest occurrence of high posturing in our study of *A. carolinensis* was seen in the breeding period, when foraging was infrequent. Therefore, high head elevation, at least during the breeding season, may be related less to prey detection and more to conspecific monitoring.

Defense.—A large portion of a breeding male’s day was engaged in conspecific behavior such as a high display rate from key surveillance perches, consistent patrolling, and display exchanges with neighboring males at territorial boundaries. More intense aggressive behavior, such as close-quarter fights between males, was not observed in this study. Such fighting behavior in male anoles can be caused by: (1) the resident male invading a neighboring ter-

ritory, (2) a neighbor or unfamiliar "floater" male invading the resident's territory, or (3) the resident male encountering a cohabiting male within his territory. The first two possible reasons for escalated fighting are reasonable because neighboring males were not far away. That actual fights were not seen while we were in the field from May to September suggests that serious inter-male encounters may be more likely at the beginning of the breeding season when territorial boundaries are being established.

The third possible reason, aggression toward an inside threat, found no support by our observations. When male lizards are forced to cohabit under conditions of captivity, dominant-subordinate relationships usually result (e.g., Carpenter, 1960, 1961; Greenberg and Crews, 1990; Hunsaker and Burrage, 1969). However, anoles are typically territorial during the breeding season. Although certain combinations of ecological conditions may select for increased inter-male intolerance in some species (e.g., *Anolis auratus*, Fleishman, 1988; *Chamaelinorops barbouri*, Jenssen and Feely, 1991; and *Anolis agassizi*, Rand et al., 1975), no field data to date have indicated that adult male *A. carolinensis* share territories or establish social hierarchies during the breeding season. After the breeding season, however, male *A. carolinensis* become much more tolerant of one another and, on warm winter days, may congregate near refugia with almost no social interaction (Jenssen et al., in press).

Courtship/copulation.—Our analysis of the courtship behavior of *A. carolinensis* revealed some unexpected findings. Prevailing sexual selection theory would predict that males without parental care obligations should take advantage of every copulatory opportunity (e.g., Goodenough et al., 1993:471). However, breeding male *A. carolinensis* appeared "choosy." They spent only 4% of their time in female-directed behavior. Males copulated approximately once per day, even though there was opportunity for additional copulations if they had been motivated to copulate. In the majority of instances (31/37) when males encountered sexually recep-

tive females (i.e., stationary, neck-bending females; Crews, 1973), the males did not copulate, but moved away from the females.

We speculate that a male may be mating with resident females on a "round robin" schedule that reflects his choosing; subsequent field data for the same population have largely supported this hypothesis (Nunez, 1994). The cause for the economy of sexual activity may relate to long copulation durations (\bar{x} = 16 min, our study; 24 min, S. C. Nunez, T. A. Jenssen, and K. Ersland, Behavior and time budget of free-ranging female *Anolis carolinensis* (Sauria, Polychrotidae), in preparation), which require that males suspend territorial defense for an extended period. Considering that, on the average, males leave their stationary mode after 3–4 min to initiate a bout of traveling and displaying, a copulation duration of up to 52 min (Nunez et al., in preparation) is a significant portion of the day to be removed from the surveillance and advertisement routine. Copulatory durations may create an opportunity for other males to invade the copulating male's territory. If by copulating, a male does increase the likelihood of a territorial challenge by another male, then it may be too risky for a male to copulate multiple times per day. A low copulatory rate would not decrease a male's reproductive fitness among resident females because *A. carolinensis* females are known to store sperm for several months (Conner and Crews, 1980; Fox, 1963; Licht, 1973). Furthermore, the once-a-day copulation rate appears voluntary and not related to a post-copulatory refractory period in males. *Anolis sagrei* males, for example, are known to average a second copulation after 1.3 h under laboratory conditions (Tokarz, 1988). Considering sperm storage, the greatest threat to a territorial male's fitness, besides losing his territory, would be permitting another male temporary access to resident females, whether the male was an interloper from outside the territory or was a skulking male tolerated within the territory.

Color.—Early studies (e.g., Hadley, 1929; Kleinholz, 1938) indicated that *A.*

carolinensis matched its body color with its background (i.e., turned green on a light background and brown on a dark background), and background adaptation continues to be considered an important aspect of endocrine control of skin color changes (e.g., Dores et al., 1987). From field observation, Schoener (1975) also suggested that *A. carolinensis* populations vary their body color to match the general color of their respective microhabitats. More recently, Medvin (1990) examined *A. carolinensis* body color matching to substrate. She concluded that males were color matching, even though brown-on-green and green-on-brown mismatches occurred in almost half (42%) of her 48 observations. Medvin (1990) also suggested that male body color may signal sex and social status recognition to conspecifics.

Our data revealed no obvious substrate-matching component to male body color in either season. Males were mismatched on 64% of 704 scan samples. This was especially apparent in the post-breeding periods, when males were averaging moves every 4 min (Stationary duration, Table 2), bringing themselves onto a variety of perch colors, while body color remained green for mean durations of 90 min (Fig. 5).

Though various stimuli may evoke color change (e.g., predation), the most immediate cause for body color shifts in our study appeared to be social in nature. Social interactions that activate the adrenal stress response can result in rapid melanophore darkening (Cooper and Greenberg, 1992; Greenberg et al., 1984), causing green lizards to turn brown. None of our data support Medvin's (1990) speculation that brown male lizards, for instance, are signaling social status. First, our males were not involved in any apparent social hierarchy, so long-term differential social ranking is not an issue. Second, the contexts when green skin color shifted to brown ranged from displaying at a neighboring male to courtship with a resident female; no observed context threatened the territorial status of focal males. Further evidence that social stimuli were the primary cause for green-to-brown color shifts

comes from post-breeding, nonsocial males. Post-breeding males were consistently green (88% of scan samples) and made few green-to-brown shifts ($\bar{x} = 1/2.6$ h) as compared with their green-to-brown shift rate in the breeding season ($\bar{x} = 1/0.46$ h). Our data suggest that the green body color is a "baseline" condition. Although temperature and light intensity can affect melanosome activity (Cooper and Greenberg, 1992), our observations were made when these environmental effects were not pervasive.

Chemosensory behavior.—Neurologically, *A. carolinensis* has an extremely reduced olfactory/vomer nasal apparatus (Crews and Greenberg, 1981). In feeding experiments with *Anolis*, Curio and Mobius (1978) found no evidence that *Anolis lineatopus* used olfactory cues to select prey. Yet, in other contexts, anoles, including *A. carolinensis*, perform behaviors indicative of gathering olfactory cues from the substrate and air by tongue touching, aerial licks, and mouth smacking (Greenberg, 1977; Jenssen, personal observation). In enclosures, newly released *A. carolinensis* males employ a much higher rate of tongue touching than later when they have habituated to their cages (Greenberg, 1985). Again, in enclosures, aerial licks occurred at a higher rate when a breeze was initiated than before or after the air movement (Greenberg, 1985). In the field, we observed behavioral patterns that could possibly function to deposit pheromones (Mason, 1992). Male *A. carolinensis* mouth wipe (which could function to deposit saliva on their perches), cloacal drag following copulation and defecation (which could place glandular or excretory products on their perches), and belly drag (which could also rub exudates onto the substrate).

Contrary to expectation, our field record did not support the contention that pheromones are functioning as an obvious form of communication. Tongue touching, the most frequent of potential chemosensory behaviors, did not occur often ($\bar{x} = 7.5$ times/h; Fig. 9). As a comparison, free-ranging male *Dipsosaurus dorsalis* averaged a 10-fold greater rate of tongue touches (75/h) than observed in our *A.*

carolinensis males (Pedersen, 1992). Furthermore, potential *A. carolinensis* chemosensory behaviors were least common during the breeding period, when social communication would most likely occur (Fig. 5).

Perch.—Our *A. carolinensis* males were perch generalists. Males used every aspect of their microhabitat, from bare rocks to the highest stems of the tree canopy, and from large tree trunks to thin-stemmed annuals and vines. Perch height appeared limited only by the highest habitat structure. In old secondary growth near our study site, males were observed perching and displaying more than 30 m above the ground.

The structural niche characteristics of any particular population of *A. carolinensis*, however, appear to be influenced by season, habitat physiognomy, and congeneric associations. Our population of males showed a seasonal shift. During the breeding period, males primarily utilized low perch heights (<2 m) and moderate perch diameters (1–8 cm). In the post-breeding period, males tended to spend more time on higher and thinner perches (Figs. 2, 3), reflecting increased foraging in the canopy.

Inter-site variance in plant physiognomy is most likely reflected in the perch height differences between our Georgia population and those in the Bahamas. At various sites in the Bahamas, where tall trees were rare, *A. carolinensis* infrequently perched higher than 3 m (Schoener, 1975). On our study site, males spent more than 20% of their time over 3 m (Fig. 2).

Anolis carolinensis on our study area has no sympatric congeners. However, in complex anoline faunas, competitive interactions promote interspecific partitioning of the habitat (Schoener, 1988). There is some evidence that insular populations of *A. carolinensis* shift their perch characteristics in response to syntopic congeners (Schoener, 1975), as do some Florida *A. carolinensis* populations (King, 1966).

Captivity.—Seasonality profoundly influenced male *A. carolinensis* behaviors and their frequencies. These seasonally af-

ected behaviors may have strong endogenous roots that cannot be masked entirely by laboratory manipulation. For example, investigations of territorial behavior of male *A. carolinensis* after July could be seriously confounded. How much of the July/August seasonal shift in *A. carolinensis* behavior is influenced by endogenous rhythms remains an important question. For example, Licht (1976) found that with high ambient temperature (32 C) and long photoperiod (>13.5 h light) one can sustain the male *A. carolinensis* breeding state long after the breeding season. In contrast, observations of male–female interactions at the Animal Behavior Laboratory, Virginia Tech, have indicated that male subjects maintained on a 14:10 L:D cycle at 31 C still registered a post-July drop in courtship behavior (Orrell, unpublished data).

Naive protocols can subject lizards to environmental deprivations and aberrations. Even carefully considered capture, transport, and housing procedures have been shown to cause significant endocrine shifts within captive lizards (Moore et al., 1991). If research findings from studies of captive lizards are to provide insight into a species' **natural** behavior or ecology, then behavioral criteria should be established for laboratory subjects, so that critically stressful conditions can be identified and corrected before data are collected (Greenberg, 1995; Lance, 1990). From our experience, for example, holding and observation enclosures that are too small will depress almost all behavior. As captive lizards are provided more living space and improved habitat quality, an increase should also occur in the kinds and frequencies of behaviors characteristic of field conditions. DeCourcy and Jenssen (1994) reported that solitary male *A. carolinensis* averaged 18 displays/h in 500-L holding cages; this rate is below that seen in the field (46/h for stationary males), but the behavior was expressed and at a reasonable rate. When males were paired within a 1000-L test enclosure at a 2–2.5-m separation distance, a distance-dependent use of display signals was revealed during aggressive encounters (see also Hover and

Jenssen, 1976). Much of this information would have been missed if paired males had been matched within a smaller enclosure. Consider that it would take 4500 40-L terraria to equal the average territorial volume of one male *A. carolinensis* on our study site. Even within the most ideal laboratory facility for housing and observing *A. carolinensis*, crowding will always be a factor.

Along with normal living space, natural light intensity is extremely difficult to duplicate in the laboratory. The connection between light and the pineal organ in *A. carolinensis* is well established (e.g., Underwood and Calaban, 1987). The pineal organ responds as a photoendocrine transducer through its secreted hormone, melatonin, which in turn affects gonadal cycles and circadian locomotion rhythms (Underwood, 1992). In humans, short day-lengths and low ambient light conditions are associated with increased melatonin secretion, leading to behavioral depression (seasonal affective disorder, "SAD"; Rosenthal et al., 1984). Increasing the day-length for SAD patients is not sufficient, in itself, to treat their hypomania if the light source is of indoor intensity (approx. 400 lux). Phototherapy becomes effective when the light is also intense (approx. 10,000 lux) (Rosenthal and Wehr, 1987).

For *A. carolinensis*, light intensity may have an important behavioral effect, much in the same manner as observed in human SAD. General activity levels of lab-held lizards may be depressed by low light intensity, particularly for those species adapted to open habitats. In our experience, solitary male *A. carolinensis* housed under standard fluorescent lighting conditions exhibit little spontaneous displaying and perch shifting. When light intensity is increased (e.g., heat-filtered flood-lamps), spontaneous activities also increase. A lighting condition in the lab that supported a low level of spontaneous activity by solitary *A. carolinensis* males (Jenssen and Hovde, unpublished data) consisted of a bank of four 1.3-m-long 40-W fluorescent lamps, a 100-W halogen lamp, and a 150-W incandescent flood-lamp just above a 1.3-m-wide \times 1.3-m-

long \times 1-m-high enclosure. With this enhanced light intensity, a photometer registered $70 \mu\text{M m}^{-2} \text{s}^{-1}$ at the brightest spot on the cage floor; late in the afternoon (1530 h), the same photometer registered 42 and $400 \mu\text{M m}^{-2} \text{s}^{-1}$ in a closed canopy forest and under a clear sky, respectively. We suggest that most laboratory situations are poorly illuminated, regardless of photoperiod regimes, which may depress spontaneous activity levels of captive lizards.

Studies of animals under captive social conditions may also lead to a distorted view of their evolved social systems unless the results from such studies are validated by field observations. Most lizards, including anoles, are known to be territorial, with field data for a few species demonstrating inter-male dominance or tolerance (Stamps, 1977b). However, it is also well documented for lizards that groups of two or more captive males will create a despotic inter-male relationship (e.g., Carpenter, 1960; Greenberg and Noble, 1944; Hunsaker and Burrage, 1969). In the field, an abnormally high lizard density may temporarily form where an episodic decrease in habitat or resources has occurred; this population concentration may lead to male dominance relationships (Evans, 1951). Thus, nonvoluntary crowding will alter social systems. To further cloud the representation of a species' social structure, the common terminology describing social relationships has become ambiguous (Bernstein, 1981). For example, the terms dominant and subordinate encompass a range of interpretation. They can refer to a temporary winner/loser relationship during a territorial dispute (before the loser leaves the territory) or to a long-term relationship involving social rank. In the application of the dominant/subordinate concept to *A. carolinensis* male relationships, the former interpretation is appropriate and the latter remains unsupported by field observations. If a long-term dominance relationship exists for *A. carolinensis* under field conditions, it will most likely involve the females within a male's territory.

In summary, we met an objective of the

present study by providing baseline data from the field for comparison with captive animal observations. The resulting overview of free-ranging male *A. carolinensis* shows that they are very active during the breeding season, moving and displaying frequently and traveling long distances. Males are polygynous, defend closely monitored and stable territories, and devote large blocks of time and energy on territory maintenance. Males direct only a small percentage of their attention to resident females, and ignore many potential mating opportunities with resident females. Foraging is infrequent, largely opportunistic, and occurs during territorial patrol and social monitoring from display perches. Then months before weather changes would alter the lizards' thermoregulatory requirements, food availability, or egg/juvenile survival, male behavior changes radically. Males become nonterritorial, asocial, and sedentary, and forage purposefully.

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