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FEMALE ACTIVITY PROFILE OF A POLYGYNOUS LIZARD (ANOLIS CAROLINENSIS): EVIDENCE OF INTERSEXUAL ASYMMETRY

by

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Summary

1. The activity profile of free-ranging individuals should reflect how females and males are optimizing their respective reproductive efforts. By using the polygynous, sexually dimorphic lizard, *Anolis carolinensis*, we expected to find an example of pronounced intersexual asymmetry in daily activity patterns.

2. In contrast to males who should focus on blocking consexual access to resident females, we expected females to strategically facilitate egg production by minimizing conspicuous and unnecessary behavior, while feeding frequently from a defended food resource optimal to their needs.

3. During a 56 day period, we made a 90 h record of focal animal observations on 22 unmanipulated, reproductive females; then we compared this activity profile to a known profile for males. We found the following.

4. Females were 1.6 times more stationary (82% of day), moved 1/7th the distance (< 40 m/day), displayed at 1/8th the overall rate (< 14 displays/h), and used $< 1/35$th the number of displays in non-directed advertisement (1.6 displays/h) as males.

5. Females spent 1/30th the time (0.3% of day) in overt defense of territories 1/9th the volume (8 m^3) as males.

6. However, both females and males had equivalent feeding rates (1.2 times/h), suggesting that the energetic needs of female egg production and male territorial maintenance are comparable.

7. The small, lightly defended territories and low feeding rates of females (along with their reptilian metabolism and insectivorous diet) indicate that females have a wide latitude in which to meet their energetic costs.

8. As expected, the proportion of intersexual contacts was similar between female and male profiles. Courtship and copulations occupied 3.2% and 3.9% of the females' day, respectively, with copula averaging 26 min in duration.

9. In a female activity profile which de-emphasized conspicuousness, we found little evidence for a pheromone-based alternative to visual signalling.

10. Predation, as an immediate threat to lizard activities, was not seen during three months of observations. We noted only four instances of avoidance behavior.

Introduction

Sexual dimorphism is a curious phenomenon, and its causation has been the topic of a number of hypotheses (*e.g.* Schoener, 1977; Stamps, 1983, 1995; Hedrick & Temeles, 1989; Shine, 1989, 1990). Of these hypotheses, Darwin's (1871) concept of sexual selection has been the dominant explanation for the occurrence of sexual dimorphisms within particular mating systems. According to this hypothesis, sexually selected traits should be most apparent in species with a pronounced intersexual divergence in potential reproductive rates (Clutton-Brock & Parker, 1992), a condition found in polygamous mating systems (Andersson, 1994). The function, as well as the structure, of sexually selected traits may be expected to diverge between the sexes, directly or indirectly influencing the respective reproductive success of each sex (*e.g.* Trivers, 1972; Emlen & Oring, 1977).

From an ethological perspective, intersexual asymmetries in structure and function should have observable behavioral correlates and find expression in sexually unique reproductive tactics. Thus, within polygynous species, the behavioral asymmetries between the sexes should be pronounced: females generally strive to increase reproductive quality and males generally attempt to increase mating opportunities by attracting more females, by inter-male contests for greater access to females, or a combination of the two (Andersson, 1994). However, the reproductive tactics of males are largely dependent upon the behavior, spatial relations, and reproductive characteristics of conspecific females (*e.g.* Trivers, 1972; Emlen & Oring, 1977; Partridge & Endler, 1987; Cockburn, 1988; Ims, 1988). Conse-

quently, the female response to reproduction places primary constraints on the potential expression of a species' mating system, while the contrast between the behavioral profiles of the sexes characterizes the mating system and provides inferences for the mode of selection.

As a likely model for sexually selected traits, we chose the lizard, *Anolis carolinensis*. The species exhibits territorial-based polygyny, with individual male territories enveloping an average of three female home ranges, and shows prominent sexually dimorphic traits (Fitch, 1976; Ruby, 1984; Nunez, 1994; Jenssen *et al.*, 1995a, b). If *A. carolinensis* has been influenced by sexual selection as current evidence suggests (Ruby, 1984; Jenssen *et al.*, 1995b), the naturally occurring behavior of the species should be concordant with the predictions of sexual selection theory. By simply observing the daily activity of unmanipulated, free-ranging individuals, we can establish which activities of the lizards' daily profile are sexually dimorphic, their degree of dimorphism, and their accord with predictions based on sexual selection.

Male and female *A. carolinensis* are predicted to optimize their respective reproductive potentials in much different ways. In general terms, females should invest a majority of their energy in egg production, while males should devote most of their energy toward territorial maintenance. Indeed, breeding males are found to exhibit intense inter-male intolerance as manifest by large exclusive territories, long nearest neighbor separation distances, high rates of territorial displaying, and continuous monitoring and patrolling behavior (Jenssen *et al.*, 1995a). Conversely, females should avoid the cost of unnecessary social behavior, prolong reproductive output by minimizing conspicuous behavior to avoid predation, and protect a food resource from which to forage frequently in support of egg production.

To examine the above predictions, we qualitatively and quantitatively described the female activity profile, then compared our results with a study of male activity (Jenssen *et al.*, 1995a). The female behaviors we recorded include: (1) inter-female relationships; (2) courtship responses; (3) foraging methods and their success rates; (4) predator avoidance behaviors and their frequencies; (5) general locomotion characteristics; and (6) the use and frequency of potential communication behavior. After comparing this data set with that of males, we discuss the intersexual differences in light of sexual selection theory.

Methods

Data were collected along the Augusta Canal in a bottomland hardwood forest (Workman & McLeod, 1990) 12 km north west of Augusta, Georgia from early May to the end of July 1993, well within the *A. carolinensis* breeding season (Licht, 1967; Jenssen *et al.*, 1995a). The configuration of the canal provided an excellent study site for extended observations of individual lizards. Within an abundant population of *A. carolinensis* along the canal, many males and females maintained home ranges in a narrow strip of riparian vegetation (approx. 3-5 m wide) growing on the bermed shoulder of the canal. From atop the 3-4 m high berm, an observer was provided an elevated vantage point for following the three-dimensional movements of a lizard, whether it moved laterally along the canal, vertically in a tree, or toward the canal side of its home range.

A total of 22 females (snout-vent length $\bar{x} = 50.0 \pm 0.8$ SE mm) were observed within the territories of seven males. Each male's territory represented an individual study site for observing the behavior of resident females. The male territories were chosen because the immediate habitat was not so dense as to preclude extended observations on individual lizards, but was complex enough (*e.g.* containing one or more trees) to be representative of the *A. carolinensis* habitat in the area.

Each of the seven male territories was observed for eight consecutive days. Before initiating observations at a study site, all spatially associated lizards were noosed, beginning with the resident male. Each lizard was measured for snout-vent length (SVL), received a unique identification paint mark on its tail, toe-clipped for permanent identification, and released at its point of capture. Daily observations were made between 08:30 to 18:30 h during which time we made 30 min focal animal samples (*sensu* Altmann, 1974) of individual females. All observed females were adults (SVL > 45 mm; Michaud, 1990).

Following the methods of Jenssen *et al.* (1995a), the behavioral data were divided into contextual variables, called 'events' (Table 1), and transitory variables, called 'occurrences' (Table 2). Event variables described broad operationally defined contexts, such as female-female interactions. Within an event were embedded the occurrence variables which were more ephemeral behaviors, such as displays. Events were maintained over long durations, ranging from several minutes to over an hour. In contrast, occurrences were of such short durations that they were simply counted. We used a multiple-function stopwatch to measure the durations of event variables and preprinted data sheets to facilitate the frequency records for occurrence variables.

Types of movement and distance travelled by females were also tallied during each event. Types of movement recorded were creeping, walking, running, and jumping. Distance travelled was estimated to the nearest 0.1 m by either counting short moves in terms of lizard body lengths or by using a 20 m measuring tape extended along the canal berm as a reference for longer moves.

During the period of behavioral observations, we measured air temperature and relative cloud cover every 30 min. A quick reading thermometer held 1.0 m above the ground in the shade provided an estimate of ambient temperature. Relative sun coverage was ranked by estimating the amount of time direct sunlight was blocked by clouds as follows: (1) clear — direct sunlight obstructed < 5 min/30 min, (2) partly cloudy — direct sunlight obstructed 5-25 min/30 min, and (3) cloudy — direct sunlight obstructed > 25 min/30 min.

Data were compared using nonparametric statistics (Hollander & Wolfe, 1973); using two tailed tests, the null hypothesis was rejected at $p \leqslant 0.05$. Means and their standard

TABLE 1. *Definitions of activity modes (Events) which compose the daily activity profile of female Anolis carolinensis*

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	Duration of locomotion activity, beginning with the initiation of a perch locality shift, and ending when the female initiates another event.
Female-Female	Duration of a female-female encounter, beginning with initial approach, and ending when one or both lizards move apart.
Male-Female	Duration of a male and female encounter, beginning with initial approach and ending with one or both lizards moving apart.
Coitus	Duration beginning with hemipenis insertion and ending with removal. Post copulation is defined as 1.5 min period after a copulation event.
Context-Unknown	Duration of a female response to a possible recipient (but unverified), beginning with two or more displays within a 30 s period, and ending when the female initiates another event.
Forage	Duration beginning with indications of prey detection and ending with ingestion of prey.

errors ($\bar{x} \pm$ SE) were calculated by: (1) summing data from all individuals and dividing by total observation time for all individuals and (2) summing individual means and dividing by the number of individuals. Although the two methods produced nearly identical results, the latter method is not biased by unbalanced contributions from individual lizards, and is reported in brackets. All data were analyzed using SAS statistical programs (SAS, 1988). Statistical analyses were only conducted on individuals with > 1.0 h of observation time (18 females).

The statistical comparison of female activity (our study) with a previous study of male activity (Jenssen *et al.*, 1995a) relies on the comparison of standard errors as the criterion of significance. Standard errors were derived from a sample size of 18 females and 10 males. When there were non-overlapping confidence intervals (CI = 2 SE on either side of the mean) between two means, the statistical probability level (*p*) was assumed to be significant ($\leqslant 0.05$).

TABLE 2. *Definitions of behaviors (Occurrences) which may occur within the context of an activity mode (Event) by female Anolis carolinensis*

Behaviors	Definition
Headbobbing w/o dewlap	Up and down head movement in species specific, stereotyped pattern without the extension of the dewlap. Shared by both male and females (DeCourcy & Jenssen, 1994; Jenssen, unpubl. data).
Headbobbing w/ dewlap	The same headbobbing patterns as above, but with dewlap extension included.
Neck Bend	Cocking the head downward into a held, neck-high posture.
Tail Undulation	Repetitious lateral movements of the tail.
Mouth Wipe	Wiping the lateral portion of the mouth against the substrate, alternately using both sides of the mouth.
Body Drag	Using the forearms, only, to drag the venter along the substrate.
Cloacal Drag	Dragging the cloacal region along the substrate, usually after defecation.
Substrate Lick	Rapid dabbing of the extended tongue to the substrate.
Aerial Lick	Rapid extension/retraction of the tongue out of the mouth.
Smack	A rapid opening and closing of the mouth.
Yawn	Large, prolonged gaping of the mouth.
Body Lick	Licking a conspecific or one's self.

Results and discussion

Environmental conditions

The daily average air temperature for the 56 days of the study was 29.0°C (0.16 SE). Mean air temperature at the beginning of each observation day (08:30 h) was 23.0°C (0.50 SE), reaching a mean daily maximum (13:00-14:00 h) of 32.7°C (0.48 SE). Most observation hours (86%) were cloudless or had only partial cloud cover. The first part of the day (08:30-14:00 h) had significantly less cloud cover (rank $\bar{x} = 1.60$) than the afternoon period (14:00-18:30 h) (rank $\bar{x} = 1.74$) (Kruskal Wallis test, $Z = 6.31$, $p = 0.04$).

There was a positive linear correlation of air temperature by time of day (Spearman, $r = 0.54$, $p = 0.0001$). Rising air temperatures negatively affected the number of observation hours collected on lizards in the after-
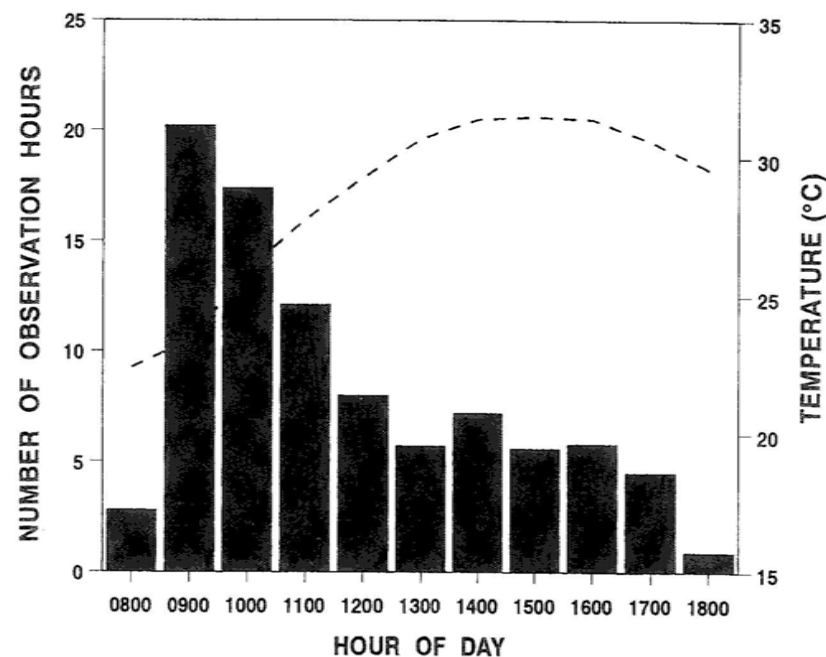
Fig. 1. Distribution of 90 h of observations (bars) for female *Anolis carolinensis* and concomitant mean air temperature (dotted line) by time of day at the Augusta Canal during May-July.

noon (Fig. 1; Spearman, $r = -0.78$, $p = 0.01$). At about 13:00 h each day, as ambient temperature approached the maximum 'preferred' body temperature of *A. carolinensis* (33°C, Clark & Kroll, 1974), females often moved into shadier, less exposed portions of the foliage, hindering their observability during that portion of the day.

Shifts in daily ambient conditions could conceivably affect the activity profile. To determine if female activities noticeably change with time of day, the daily observation period (08:30-18:00 h) was divided into three nearly equal portions: morning (08:30-11:00 h), mid-afternoon (11:00-14:00 h), and late-afternoon (14:00-18:30 h). These time periods were associated with obvious shifts in air temperature (Fig. 1) and/or cloud cover. Frequency of activities was compared across time periods using both an independent and dependent design. In the independent method (Wilcoxon Rank Sum (WRS) test; $N = 18$ females), data from individual females

are represented in only one time period, thus diminishing the potential bias due to inter-individual differences. In the dependent design (Wilcoxon Sign Rank (WSR) test; $N = 10$ females), we only used the data from individual females who were represented in two or more time periods. We found no significant differences in the relative frequencies of any activity events across any time periods, regardless of the method of analysis (WSR, all tests, $p > 0.10$; WRS, all tests, $p > 0.10$). Thus, female activities were not obviously associated with time of day.

There was also the possibility that an 'early season/late season' effect might influence the activity profile. Therefore, the data set was chronologically divided in half. No event activity was found to significantly vary across the two subseason data sets (WRS, all tests, $p > 0.08$, $N = 18$).

Female events

Stationary

The vast majority of the female day was spent in a stationary mode (82.6% (80.4 ± 2.5 SE, $N = 18$)) (Fig. 2). During stationary events, females were not totally motionless, but frequently re-oriented their body position and direction ($\bar{x} = 13.5$ body shifts/h (14.5 ± 1.7 SE, $N = 18$)). Little distance was actually travelled with each body shift, averaging only 5.6 cm/move (0.04 SE, $N = 997$).

Occurrence behaviors were rarely initiated while females were stationary (Table 3). All displays occurring within this event context were infrequent ($\bar{x} = 1.3$ times/h (1.2 ± 0.4 SE, $N = 99$)), solitary (*i.e.* not sequenced in rapid succession), non-directed (*i.e.* not specifically directed at a particular conspecific), and rarely performed with dewlap extension (11% of non-directed displays).

Travel

Travelling (*i.e.* moving several body lengths or more) was the second most common event category, but accounted for just 7.8% (9.2 ± 1.4 SE, $N = 18$) of the activity period (Fig. 2). When in a travel mode, females did not move continuously, but used a series of starts and stops which produced an average rate of 167 moves/h (195 ± 17.2 SE, $N = 18$) and 20.8 cm/movement (1.0 SE, $N = 1,150$). When actually moving, females averaged 34.7 m/h. Females mostly walked (48%) and crept (29%), or

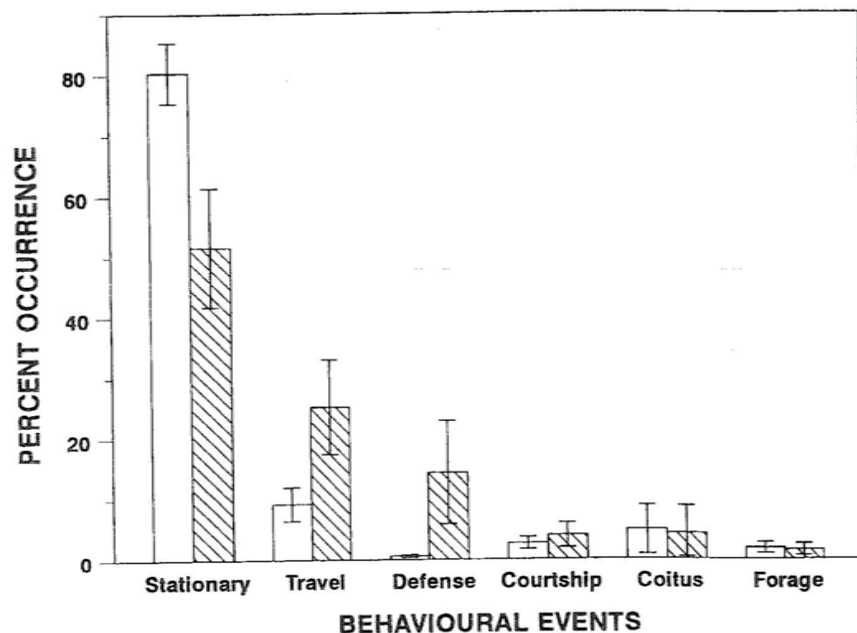
Fig. 2. Mean proportion of daily activity (± 2 SE) spent in six events (activity modes) for 22 female (white bars) and 10 male (striped bars) *Anolis carolinensis* at the Augusta Canal during May-July. Male data from Jenssen *et al.* (1995a).

more infrequently jumped (17%) and ran (6%). When female *A. carolinensis* jumped, they were capable of leaping up to 2 m (*e.g.* when jumping from an elevated perch to a lower substrate).

The respective occurrence of tail undulating and displaying when travelling was double (6.1 times/h (8.6 ± 2.2 SE, $N = 18$)) and quadruple (7.2 times/h) respective rates during stationary events (Table 3). Females rarely interrupted a travel event to display, but did use headbob displays to initiate and conclude a travel event.

Female-female encounters

Consexual encounters only occupied 0.3% (0.3 ± 0.11 SE, $N = 18$) of the female activity profile (Fig. 2); these interactions appeared agonistic in nature, and were interpreted as evidence of territorial behavior. The female-female interactions were infrequent and brief, averaging 0.12 times/h and 1.6 min (0.6 SE, $N = 11$) in duration. Residents quickly responded to in-

TABLE 3. *Mean rates ($\bar{x}$ occurrences/h), with sample sizes in parentheses, of 12 types of behaviors by 22 female Anolis carolinensis during eight activity modes (Events) as recorded from 90 h of observation during May-July at the Augusta Canal, Augusta, Georgia*

Behavior	Event							
	Male-Female $\bar{x}$ (N)	Coitus $\bar{x}$ (N)	Post coitus $\bar{x}$ (N)	Female-Female $\bar{x}$ (N)	Female-Unknown $\bar{x}$ (N)	Stationary $\bar{x}$ (N)	Travel $\bar{x}$ (N)	Forage $\bar{x}$ (N)
Headbob Display (w/o Dewlap)	87.5 (252)	137.5 (484)	45.5 (15)	13.8 (4)	38.0 (27)	1.3 (99)	6.1 (43)	1.5 (2)
Headbob Display (w/ Dewlap)	1.4 (4)	11.1 (39)	0.0	20.7 (6)	107.0 (76)	0.2 (11)	1.0 (7)	0.0
Neck Bend	2.8 (8)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tail Undulation	0.3 (1)	0.0	0.0	0.0	1.4 (1)	0.2 (18)	4.8 (33)	0.0
Mouth Wipe	1.0 (3)	0.0	0.0	0.0	0.0	2.1 (153)	2.5 (17)	5.4 (7)
Body Drag	0.0	0.0	0.0	0.0	0.0	0.2 (17)	0.0	0.0
Cloacal Drag	0.0	0.0	0.0	0.0	0.0	0.1 (6)	0.0	0.0
Substrate Lick	0.0	0.0	0.0	0.0	0.0	0.2 (15)	0.6 (4)	0.0
Aerial Lick	0.0	0.0	0.0	0.0	0.0	0.1 (8)	0.0	0.0
Smack	0.3 (1)	0.0	0.0	0.0	0.0	0.6 (45)	13.0 (9)	194.0 (260)
Yawn	0.0	0.0	0.0	0.0	0.0	0.1 (9)	0.0	0.0
Body Lick	0.0	0.0	0.0	0.0	0.0	0.1 (10)	0.0	0.0

trusions from neighboring females with displays and active pursuit. When separation distances were > 1 m, resident females usually displayed with dewlap extension (rate $\bar{x}$ = 20.7 displays/h), and less frequently without dewlap extension (rate $\bar{x}$ = 13.8 displays/h). Only one aggressive encounter ended in physical contact. The resident female lunged and grabbed the intruder's neck and head in her jaws. The intruder quickly broke free of the resident's grip and retreated by jumping to the ground.

Male-female encounters

Male-female encounters (*i.e.* courtship) averaged 3.2% (2.6±0.5 SE, N = 18) of the activity period (Fig. 2). Courting occurred about once an hour ($\bar{x}$ = 1.3 times/h), with a mean duration of 1.5 min (0.19 SE, N = 116). Females often responded to a male's courtship with many displays (rate $\bar{x}$ = 88.9 displays/h); 98% of these displays were without dewlap extension (Table 3). From laboratory data (Crews, 1973) and outcomes of the present observations, sexually receptive females performed volleys of headbob displays, remained relatively stationary (*i.e.* passive), presented their backs to the males, and then assumed a bent neck posture. If a female was not receptive, she headbobbed, but did not turn her back to the approaching male nor neck bend. If the male continued the approach toward the female, she would run away. No attempts to force a copulation were observed.

Coitus

When coitus occurred, it was of long duration ($\bar{x}$ coital duration = 26.4 min ± 6.7 SE; range 16-34 min; N = 8) and produced the third longest event in the female activity profile (3.9% (4.8±2.0 SE, N = 18)) (Fig. 2). Males always took a neck grip before and usually throughout coitus. Once the hemipenis was inserted, females did not appear able to break free of the male's grip, possibly due to hemipenile tumescence (Crews, 1973). However, females would occasionally try to free themselves by jerking, shaking, and dragging the male. When copulations were initiated in direct sunlight and/or in relatively open areas of the foliage, the female frequently dragged the male up to 2 m to a more secluded and/or shaded area.

During copulation, females headbobbed throughout, averaging 61 displays/copulation ($\bar{x}$ rate = 148.6 displays/h) (Table 3). Very rarely (7.5% of all headbobs) did the female extend her dewlap during copulation. After copulation, both sexes left the immediate site. The male usually returned

to a travel mode, while the female moved a short distance ($\bar{x} = 0.5 \pm 0.14$ SE m, $N = 14$) before entering a stationary mode. Immediately after copulation, females displayed ($\bar{x}$ rate $= 45.5$ displays/h, Table 3), but these displays did not appear to be directed at any lizard.

Context unknown

This event appeared to be a social context because by definition (Table 1) it was initiated when a female gave a series of displays. However, due to the density of the immediate vegetation, we could not verify the presence or absence of another lizard. Thus, the context remained unknown. Because of its criteria (Table 1), the context-unknown event was characterized by a high rate of display ($\bar{x} = 107$ displays/h, Table 3) and did not last long ($\bar{x} = 57 \pm 14$ SE s, $N = 31$). Consequently, this event only composed 0.8% (0.5 ± 0.16 SE, $N = 18$) of the activity period.

For unknown reasons, perhaps due to the sex of the potential recipient, there were several consistent patterns to these bouts of displaying. Of the 29 context-unknown events, nine events (31%) were entirely composed of headbob displays without dewlap extension, 17 (59%) entirely composed of headbob displays with dewlap extension, and in only three instances (10%) was there a combination of displays with and without dewlap extension.

Forage

Female foraging composed 1.5% (1.8 ± 0.45 SE, $N = 18$) of the activity period (Fig. 2). Females averaged 1.2 forage attempts/h (1.7 ± 0.5 SE, $N = 18$). Prey capture attempts were evenly distributed throughout the day from early in the morning (08:30) until later in the evening (18:30) (calculated from hourly intervals; $\chi^2 = 10.4$, df $= 9$, $p > 0.05$).

Females used three methods to capture prey: (1) prey detection when female is in a stationary mode ('sit-and-wait'); (2) prey detection when female is in a travel mode, then female diverts from her original path to attempt a prey capture ('on-the-run'); and (3) prey detection when female is creeping about the foliage, presumably in search of prey ('active search'). The frequency with which a method was used was positively related to its respective prey capture success (*i.e.* percent of attempts resulting in an ingested prey). Sit-and-wait was most frequent (83%) and successful (89%), on-the-run next most frequent (13%) and successful (71%), and active search was least used (4%) and least successful (60%).

Rare occurrences

Chemosensory

Some occurrence variables have potential chemosensory transmission and reception functions. However, those behaviors which might deposit odors (Mouth Wipe, Body Drag, and Cloacal Drag; Table 2) were rare. Mouth wipes, the most frequent ($\bar{x} = 2.0$ times/h), could serve to deposit saliva at a perch site. Cloacal and Body Dragging, which could potentially deposit cloacal exudates, were almost never observed ($\bar{x} = 0.07$ and 0.19 times/h respectively) (Table 3).

The potential chemoreceptive behaviors (Substrate Lick, Aerial Lick, Mouth Smack, Yawn, and Body Lick; Table 2) were nearly as infrequent as those with a suggested depository function (Table 3). Mouth Smacking was observed within most events ($\bar{x} = 3.5$ times/h), but they primarily concluded successful foraging attempts (Table 3). The remaining behaviors were each observed at rates of < 0.3 times/h (Table 3). Male *A. carolinensis* had a similar low frequency profile for these behaviors of potential chemosensory transmission and reception (Jenssen *et al.*, 1995a).

Predator avoidance

During three months of observation and approximately 1,120 observer hours in the field, only four instances of avoidance behavior were recorded. One was in response to a snake (*Coluber constrictor*) climbing the limb on which a male was perched, and the other three were in response to solitary crows (*Corvus brachyrhynchos*) flying 2-3 m overhead. Likewise Jenssen *et al.* (1995a) found little evidence of predation pressure during a five month study of male *A. carolinensis* (approx. 675 observer hours in the field).

Comparison of female/male profiles

In the following comparisons of female-male variables, all but rates of perch shift and foraging met the conditions of statistical significance as detailed in the Methods.

Locomotion and display behavior

Females, in comparison with males (Jenssen *et al.*, 1995a), conserved energy and averted visual detection by exhibiting a restricted pattern of loco

motion and display. Females were 1.6 times as likely to be stationary (82% of day) than males (51% of day) (Fig. 2). Stationary females rarely drew attention to themselves by visual signalling, having a mean rate 1/35th that of stationary males (1.6 ± 0.5 SE and 57.0 ± 9.7 SE displays/h, respectively). Females were 37% less likely to shift their perch sites, having longer mean stationary durations (4.7 ± 0.7 SE min) than males (3.3 ± 0.2 SE min). When females did shift perches, the mean distance travelled (0.2 ± 0.01 SE m) was 1/10 as far as males (2.3 ± 0.1 SE m). Over an average hour of the activity profile, mean total distance moved by females (3.6 ± 0.5 SE m) was 1/7th that of males (25.7 ± 5.1 SE m). When females did travel, they were much less likely to signal their presence by display behavior; the mean rate of female displaying (7.7 ± 2.2 SE displays/h) was 1/30th that of travelling males (238.6 ± 25.9 SE displays/h). Over an average hour of the activity profile, the mean display rate of females (13.6 ± 4.0 SE displays/h) was 1/8th that of males (107 ± 10 SE displays/h).

Territorial behavior

Direct consexual interactions to control territory showed pronounced intersexual differences in volume of defended space, distances between adjacent territories, and frequency and duration of defense. These behaviorally driven parameters indicate that females have a much greater tolerance of consexual neighbors than males. Females of our study averaged small (8 ± 1.3 SE m^3), contiguous (18% overlap) territories (Nunez, 1994); corresponding male territories were 9 times larger (69 ± 20.0 SE m^3) (Nunez, 1994), unshared with any other male, and clearly separated ($\bar{x} = 3.6$ m) from the next nearest male territory (Nunez, 1994; Jenssen et al., 1995a). Females were undoubtedly monitoring their small territories, but for their purposes, spent little daily activity time (0.3%) in aggressive interactions with consexual neighbors, being 1/30th that reported for males (9.2%; Jenssen et al., 1995a) (Fig. 2). When bouts of inter-female aggression occurred, they averaged 1/9th the frequency (0.14 ± 0.08 SE bouts/h) and lasted 1/4th the duration (1.6 ± 0.34 SE min) as inter-male encounters (1.3 ± 0.3 SE bouts/h, 5.6 ± 0.9 SE min, respectively) (Jenssen et al., 1995a). Furthermore, as indicated above by their low pattern of locomotion and display activity, females exhibit much less potential for either patrolling or conspicuously advertising their territories as observed for males.

Foraging behavior

Females and males foraged with almost identical frequency ($\bar{x} = 1.$ times/h) (present study; Jenssen et al., 1995a). There was an intersexua difference, however, in the frequency of method used to forage (Fig. 3) An explanation comes from Fig. 2 which depicts the proportion of tim females and males spent in a stationary or travel mode. Females and males stationary for 82 and 51% of their respective day, likewise used the sit and-wait method to forage 83 and 58% of the time, respectively. Males spending three times more of their day travelling (27%) than females (8%) likewise used the on-the-run method three times more often (42%) than females (13%) (Fig. 3). The active search method of foraging (i.e. creeping in the foliage) was little used by females and never seen in breeding males However, males frequently used active search (22%) and rarely on-the-rur (4%) methods when territorial behavior (e.g. travelling) subsided after the breeding season (Jenssen et al., 1995a).
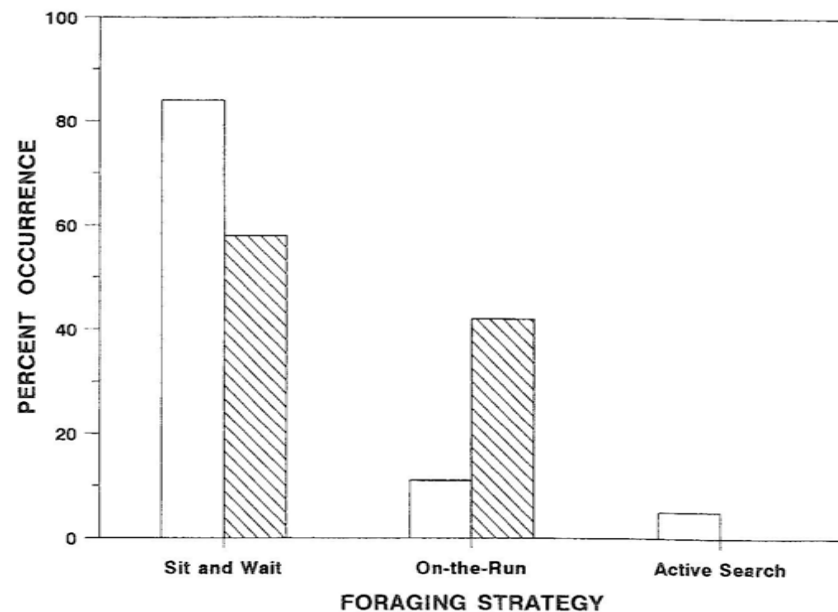

Fig. 3. Percent occurrence of three foraging methods used by 22 female (white bars) and 10 male (striped bars) Anolis carolinensis at the Augusta Canal during May-July. Male data from Jenssen et al. (1995a).

Overview

Based on sexual selection theory, one would expect males and females of a polygynous species to exhibit very different activity profiles as a reflection of differing reproductive stategies (see Introduction). This expectation was unequivocally supported in our study of *A. carolinensis*. Males are known to be polygynous. From field observations, up to six resident females may be mated by a single territorial male (Nunez, 1994), while census data of the general population showed a 1 : 1 adult sex ratio (Jenssen *et al.*, 1995b). Therefore, many males may be expected to have few or no females within their home ranges, while other have numerous resident females. This broad variance in potential reproductive rate among males creates a condition for intense male-male competition.

The distribution and availability of reproductive females in space and time should influence the structure and intensity of intra-male competition within *A. carolinensis*. Females have small, stable home ranges (Nunez, 1994). Thus, a male can use territorial behavior to exclude access of other males to females residing within his territory. Furthermore, because females lay a single-egg clutch every 4-10 days (Andrews, 1985a) over a four month period (Licht, 1971, 1973), the reproductive success of males is associated with long term maintenance of exclusive access to resident females. An activity profile of breeding males indicated that the majority of a breeding male's daily behavior appeared functionally directed at outside male threat, being composed of extensive advertisement displaying, territorial monitoring and patrol, and territorial defense (Jenssen *et al.*, 1995a).

Individual *A. carolinensis* females, who have a more assured but also a more limited potential reproductive rate than individual males, are predicted to optimize their reproductive success in a much different manner than males. Because neonates require no parental care and evidence for female choice of mates is equivocal (Sigmund, 1983; Andrews, 1985b), female options to enhance fitness are simplified. Individual females can improve their reproductive success by increased egg size and clutch number in a breeding season (Congdon, 1989; Michaud & Echternacht, 1995), avoidance of mortality to extend reproduction over more than one breeding season, and protection of a food resource for themselves and their offspring. To affect these ends, the females should: 1) conserve energy and avoid predation by minimizing unnecessary and conspicuous behavio 2) use consexual aggression to control some portion of a food resourc and 3) feed frequently to support egg production. To what extent, and t what contrast with male activities, did females meet these expectations?

As contrasted with males, female movement and display behavior cor formed to expectation. Females were largely sedentary, moved only sho distances, and displayed infrequently (almost never without an immediat recipient). This restricted pattern of behaviors would certainly conserv energy and be less conspicuous to a motion-oriented predator. As a cavea however, we observed little evidence on our study area that predation pres sure was much of a factor for either females or males.

From a territorial perspective, the low level of movement and displa by females would be unexpected if competitive interference were a majo requirement for reproductive success. Indeed, females were much more to erant of consexual neighbors than that exhibited by males. The infrequei inter-female aggression and small, overlapping female territories indicate minimal need for exclusive control of spatially distributed resources. Thes resources are generally considered to be shelter, mates, and food (Stamp 1977). The inference from female territories, which were neither larg nor vigorously defended, is that resources, including food, were not crit cally limiting to female *A. carolinensis* of our study. Because the speci is insectivorous, point sources of potential food for egg development ar subsequent neonate growth are probably broadly distributed and abunda in the microhabitat.

Though it was predicted that females should forage frequently, the was no intersexual difference. Using feeding rate as a crude index of lizard's energy requirements, the similar feeding frequencies for the sex suggest an equivalent cost to female egg production and male territori maintenance. Furthermore, the low feeding frequency, combined with th modest metabolic rate of reptilian physiology (Nagy, 1983; Jenssen *et a* 1996) and the general abundance of insects, indicates a considerable scop within which both females and males can adjust their feeding rates to me energetic needs. Thus, in conjunction with female territorial characteristic female foraging behavior also indicates that food is not a critically limitir resource for female reproductive success, per se; nevertheless, an energ conserving strategy remains reproductively adaptive.

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