

Sexual Dimorphisms in Aggressive Signal Structure and Use by a Polygynous Lizard, *Anolis carolinensis*

THOMAS A. JENSSEN, KIMBERLY S. ORRELL, AND MATTHEW B. LOVERN

Unlike many polygynous species, we found that females of the lizard, *Anolis carolinensis*, have the same repertoire of aggressive signals as males. These shared signals included three stereotyped headbob display patterns (types A, B, and C) that were performed with no significant intersexual difference in amplitude displacement. However, we did find the following sexual dimorphisms in signal structure and use. Females (1) had a smaller average extendable throat fan (i.e., dewlap) area (0.22 cm^2) than males (1.52 cm^2), (2) never displayed when alone (0/h), whereas males frequently did (18/h), (3) displayed 10-fold less during consensual encounters (17/h) than males (168/h), (4) lacked the ritualized intermale combat scheme of circling, jaw-sparring, and jaw-locking, (5) infrequently used physical contact in consensual encounters, whereas males frequently did, and (6) did not employ a shifting use of signals with decreasing interfemale approach distance, whereas contesting males did by decreasing the frequency of C displays in favor of A and B displays, decreasing the use of the dewlap during displays, and decreasing the sequencing of displays in volleys. These results are in accord with field studies, which report limited interfemale territoriality (i.e., low consensual threat) and short display broadcast distances, whereas male territorial behavior is well developed (i.e., high consensual threat), with frequent long-distance displaying between consensuels. We suggest that these displays, which function in competitive interference, have been less directionally selected in females than in males because the outcomes of consensual contests carry fewer reproductive consequences for females than for males.

INTRASPECIFIC communication functions to coordinate social interactions (e.g., parental care, mate choice, territorial contests), and as such, the number, design, and use of signals should vary with particular mating systems (e.g., Andersson, 1994; Bradbury and Vehrencamp, 1998). For example, in polygynous species where social roles can be sexually dimorphic, the signals associated with those roles should also reflect intersexual differentiation. Typically, the signals and signaling structures of polygynous males are enhanced for consensual competition to attract or to directly gain access to mates. In the extreme where the function of a signal resides solely with the male, the female may lack the analogous signal altogether (e.g., Hauser, 1996; Bradbury and Vehrencamp, 1998).

In our study, we use a polygynous lizard, *Anolis carolinensis*, to make an intersexual comparison of signal structure and use during consensual interactions. *Anolis carolinensis* is an intrasexually selected species (Jenssen and Nunez, 1998), and we expected contesting males to signal differently from contesting females in ways consistent with the species' mating system. The *A. carolinensis* mating system is driven by the outcome of intermale territorial aggression. Winners achieve and maintain direct mating access

to varying numbers of females (Ruby, 1984; Jenssen et al., 1995a; Jenssen and Nunez, 1998) because females are relatively sedentary and clustered in small contiguous home ranges (Nunez et al., 1997; Jenssen and Nunez, 1998). In addition, male competitive interference behavior is pushed to an endurance rivalry (sensu Andersson, 1994:10) due to a four-month breeding period during which females produce single-egg clutches at approximately weekly intervals (Andrews, 1985; Jenssen and Nunez, 1998). Unencumbered by parental care constraints, *A. carolinensis* breeding behavior is predictably associated with a dramatic divergence in intersexual activity profiles (Jenssen et al., 1995a; Nunez et al., 1997).

The signal repertoire which facilitates *A. carolinensis* polygyny features conspicuous headbobbing displays, previously characterized for males (DeCourcy and Jenssen, 1994; Lovorn et al., 1999) but undocumented for females. The general features of the display behavior are similar to most anoline species, consisting of vertical movements of the head or body (Jenssen, 1977, 1978; Carpenter, 1986). An extendable and brightly colored dewlap (e.g., Bels, 1990; Font and Rome, 1990) also amplifies the display visibility (Fleishman, 1988a, 1988b, 1992). The headbob displays are augmented by a number

of optional postures and movements which modify the appearance of the display or the display and sometimes have signal status independent of the headbob displays (e.g., Jenssen, 1979).

Given the *A. carolinensis* life-history traits and breeding structure, we expected the species' aggressive signals to reflect two intersexual relationships. First, both sexes should share a common repertoire of aggressive signals because males aggressively interact to monopolize mates, whereas females should also signal aggressively to other females to control resources for egg production. Second, signal design and manner of signaling, nevertheless, should show intersexual asymmetries due to sexual selection. This is because intermale contests associated with aggressive signaling largely determine male potential reproductive rates (Ruby, 1984; Jensen and Nunez, 1998), whereas interfemale aggression appears to have minimal observable effect on female potential reproductive rates (Nunez et al., 1997; Jenssen and Nunez, 1998). To deductively test our expectations for *A. carolinensis*, we used its aggressive signaling behavior to intersexually describe and compare (1) kinds of signals (including displays), (2) variance in temporal pattern and head amplitude of displays, (3) dewlap size, and (4) the differential use (i.e., relative frequency) of signals under different social contexts and interindividual separation distances (i.e., threat intensity).

MATERIALS AND METHODS

We collected 22 females [mean snout-vent length (SVL) $54.15 \pm \text{SE } 1.14$ mm] and eight males (mean SVL $65.5 \pm \text{SE } 1.05$ mm) near Augusta, Georgia. We then followed the same protocol used by DeCourcy and Jenssen (1994) for their study of display behavior by male *A. carolinensis* from Florida. Our database partially repeats that of DeCourcy and Jenssen (1994) because we wanted our female data to be compared with males from the same population.

We housed lizards singly in large, green painted plywood holding cages ($0.6 \times 0.6 \times 0.7$ m) containing a tree bark/mulch substratum, small stumps, branches, and artificial plants. Each cage was illuminated on a 14L:10D cycle, using a 150 W incandescent and double 40 W fluorescent lamps. Peak daytime temperature gradients within the cages ranged from 30–35 C directly under the incandescent lamps; night temperatures dropped to 24 C. Water was available in shallow earthenware dishes situated in the litter and by daily misting of the leafy habitat. The lizards were fed crickets dusted with

calcium lactate powder and vitamins. After the study was concluded, the lizards were returned to the same field site where they were collected.

Behavioral observations were made on consensual pairs within a green painted plywood chamber ($0.6 \times 0.8 \times 2.4$ m) with a screened top. One wall was of slanted glass to permit surveillance and videotaping, while reducing the likelihood that subjects could see their own reflections. An opaque, removable partition divided the chamber into halves and separated the two subjects. Temperature, light, and habitat characteristics were the same as in the holding cages. Each subject in the divided chamber had a similar habitat cluster in which the most frequented perches were at the far ends of the chamber. Thus, when the partition was removed, subjects were generally at initial separation distances ≥ 1.5 m.

We conducted 15 consensual trials (11 female and 4 male pairings), with no individual used more than once. To begin a trial, a pair of size-matched subjects was moved to the observation chamber and allowed 2–3 days to acclimate. A videotape recording was then made within two contexts: (1) 30 min of each subject with the partition in place (subject-alone context); and (2) a subject-determined duration with the partition removed (consensual aggressive context). The female-female or male-male interaction began with the removal of the partition and continued until one of the subjects repeatedly retreated from the advances of the other (criterion for a "winner/loser" relationship).

We videotaped trials from a separate, darkened room through a small window 1.5 m from the observation chamber. Two Panasonic cameras (Model-WV 1550, with 16-160 mm zoom lenses), one trained on each subject, were used to continuously record the subjects' behaviors. A split-screen generator (Vicon Model V270SP P8) juxtaposed both lizard images on the same screen. A time/date generator (Odetics Model G-77) superimposed elapsed time in increments of 0.01 sec. A Panasonic video cassette recorder (Model AG-7300) recorded at a rate of 30 frames/sec, thereby allowing for frame-by-frame analysis of signal behavior in 0.03-sec increments. Commentary and intersubject separation distances were dictated onto the audio track of the videotape. A metric measuring tape mounted outside the observation chamber facilitated estimates of intersubject distances.

We divided headbob displays into naturally occurring units of bobs (odd numbered units) and interbob pauses (even numbered units). Using frame-by-frame measurements, the relative head amplitude and duration of each bob

and interbob pause were plotted, with amplitude on the y-axis and duration on the x-axis. The resulting plots, referred to as "display-action-pattern" graphs (DAP graphs, sensu Carpenter, 1961), were examined for reoccurring (i.e., stereotyped) headbob patterns. Each unique, stereotyped pattern was considered a structurally separate signal and is referred to as a "display type."

The variables recorded for each videotaped display were (1) identity of displayer, (2) social context, (3) display type, (4) unit durations, (5) presence or absence of dewlap extension and unit of appearance if dewlap was extended, (6) distance separating the subjects during the display, and (7) sequential position of the display (i.e., first, second, third, etc.) if the display was a part of a "volley" of rapidly sequenced displays (i.e., displays < 2 sec apart).

Intersexual measurements were also made on the area of the extended dewlap and the relative amplitude of head movements during display. Dewlap area for live lizards of known size was quantified with a Numonics digitizer (Model 274-167) by tracing the outline of the extended dewlap (sensu Fitch and Hillis, 1984). For each dewlap, we measured the area three times and recorded the average value. We measured head amplitude from videotapes, but quantitative comparisons were complicated by the following factors. Amplitude can vary due to camera angle and distance to the displayer, the body size of the displayer, the specific bob and display pattern being performed, and the displayer's motivational state. The last factor by itself can largely confound an attempt to quantify head amplitude for a class of lizards. This is because the same individual can perform the same display pattern with an interdisplay amplitude variance ranging from less than the thickness of the head (appearance of "nodding," analogous to a whispered message) to exaggerated amplitude effected by both forelimb and neck flexure (appearance of "pushups," analogous to a shouted message). Thus, amplitude has a graded expression between display performances (i.e., a display modifier sensu Jenssen, 1979) but does not alter the display cadence pattern.

Despite the intraindividual variance in bob amplitude, we looked for an intersexual difference to head amplitude by controlling as many variables as possible. We selected only videotape sequences in which displayers were perpendicular to the camera and were engaged in the same social context at a similar intersubject distance (i.e., long range encounter > 60 cm in 2.4 m cage). Then we measured the same bob of a specific display pattern (i.e., unit 5 of the

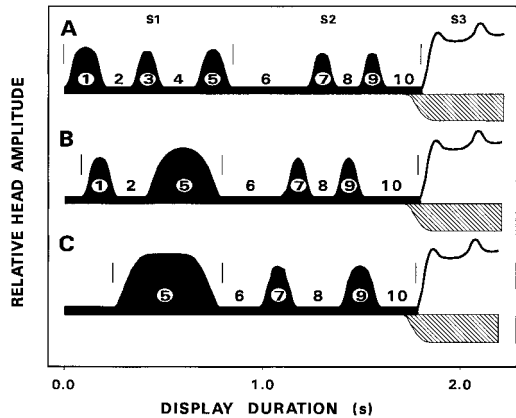


Fig. 1. Generalized Display-Action-Pattern (DAP) graphs for type A, B, and C patterns of *Anolis carolinensis*, based on 159 DAP-graphed displays from 22 females and 172 DAP-graphed displays from eight males collected near Augusta, Georgia. The x-axis is elapsed time (sec) for the durations of bob and interbob units (1–10). The y-axis depicts up and down head amplitude relative to elapsed time (but is quite variable). Relative dewlap extension (when present) is depicted with a downward vector (area of hash lines). Number of bobs after unit 10 varied (1–9) among display performances.

type C display, see Fig. 1). Placing a transparent overlay on a 50 cm video monitor, we plotted and measured the distance between the lizard's nose when (1) at its maximum height during the bob and (2) at its lowest amplitude going into the subsequent interbob pause. To compensate for camera distance and lizard size, we divided the bob amplitude's maximum to minimum distance by the nose tip to mideye distance; this dimensionless ratio related bob amplitude to the displayer's head size. Although males tend to have larger heads than females, the sex-biased dimorphism appears isometric, proportionally reflecting the "male-larger" scale of SVLs between the sexes (Jenssen et al., 1995b).

Descriptive statistics are reported as means (\bar{x}) \pm standard error of the means (SE). Statistical comparisons of display structure used intraindividual means as single datum to eliminate sample bias resulting from unequal number of displays from different individuals. SAS (Statistical Analysis Systems, vers. 6, Cary, NC, 1987, unpubl.) software provided the statistical procedures for tests of comparisons.

RESULTS

Display types.—From 132 female and 172 male displays, we isolated three distinct headbob pat-

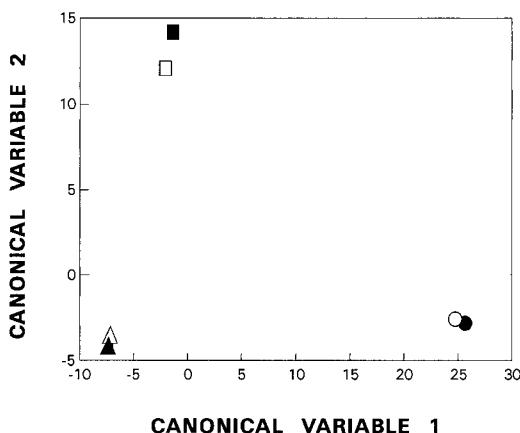


Fig. 2. Plots of the first two canonical variables from a discriminant analysis of units 1–10 for 159 displays by 22 female and 172 displays by eight male *Anolis carolinensis* for display types A (circles: females solid, males open), B (triangles: females solid, males open), and C (squares: females solid, males open).

terns (i.e., display types) which were intersexually homologous (Fig. 1). Following the convention of DeCourcy and Jenssen (1994), we first labeled the display types as A, B, and C, the intradisplay units as 1 through 10, and secondarily divided the displays into 3 sections (S_1 , S_2 , and S_3) to analyze and categorize the three display types (Fig. 1). Section one (S_1) was largely diagnostic for display type because S_1 of type A displays contained five units, type B displays three, and type C displays only one. The units in S_2 and S_3 were shared across the three display types, where S_2 comprised the four units from a pair of bobs and their intervening pauses, and S_3 contained a variable number of bobs (1–9) not included in our analysis (Fig. 1).

Dewlap use during headbob displays was the same for both males and females. Both sexes performed type A, B, and C displays with and without dewlap extension. Dewlap behavior, whether extended or withheld, had no effect on the bob cadence of the three display patterns (i.e., no statistical difference in unit durations). When the dewlap was extended, it invariably appeared at the end of unit 10 of all three display types. But when displays were closely sequenced (i.e., in a volley), the dewlap could remain extended from a previous display.

The uniqueness between the three display types and the intersexual similarity within each display type are graphically demonstrated using a Canonical Discriminant Analysis based on units 1–10 (Fig. 2). There was virtually no overlap in plotted data between the display types, but within display types, there was extensive

overlap for male and female data. Seventy-five percent of the total model variance was explained by the first canonical axis (eigenvalue 148.58) and 24% by the second axis (eigenvalue 48.25).

Display stereotypy.—There was relatively little temporal variability for each display unit (Table 1). As a measure of relative unit stereotypy, values for the coefficient of variation ($CV = \text{standard deviation} \times 100/\bar{x}$) < 35% were used to indicate highly stereotyped behaviors (Barlow, 1968). Nineteen of 24 female units for the three display types had CV values < 35%, and 23 of 24 male units were < 35% (Table 1).

The relatively small amount of temporal variance occurring in the three display types was partitioned by display unit according to display type, sex, among individuals, and within individuals using a nested ANOVA. Display type explained the greatest proportion of variance for units 1–6, 8, and 10 (Table 2). These eight units, then, primarily established the distinctiveness of the three discrete signal structures. In contrast, sex as a source of variance had little effect on display cadence. Except for unit 7 (17%), sex accounted for little (< 7%) of the total variance in all unit durations, including total display duration. For the two remaining units (7 and 9) and for total display duration, the intraindividual component was the greatest source of variance. However, we placed little functional significance to this because units 7 and 9 are both quick bobs (0.132–0.209 sec), with little opportunity for expressing much range in intraindividual expression. The same is true for entire display performances, for which CV values were < 8%.

Intersexual display comparisons.—Unit durations were very similar for homologous units within display types for male and female *A. carolinensis* (see also previous variance analysis). Only one unit duration significantly differed intersexually for type A, two for type B, and one for type C (Table 1). Total display duration was also intersexually similar, with only type B duration showing a significant difference (Table 1). The species' sexual size dimorphism (Jenssen et al., 1995b) appeared to have little impact on female/male display durations. Female subjects, who averaged 17% shorter SVLs than male subjects, had total display durations (units 1–10) similar to those of males (female/male comparisons of 1.52/1.53 sec for type A, 1.38/1.49 sec for type B, and 1.34/1.38 sec for type C displays; Table 1). Given that males have a similar or potentially greater head amplitude than females

TABLE 1. INTERSEXUAL COMPARISON (MEAN, STANDARD ERROR, COEFFICIENT OF VARIATION, AND KRUSKAL-WALLIS TEST, H AND P VALUES) FOR TYPE A, B, AND C DISPLAY UNIT DURATIONS FROM 22 FEMALE AND 8 MALE *Anolis carolinensis* COLLECTED NEAR AUGUSTA, GEORGIA. Sample sizes were seven type A, 20 type B, and 105 type C female displays and 47 type A, 49 type B, and 76 type C male displays.

Type	Unit	Unit statistics						H	P
		♀-♀ Context			♂-♂ Context				
		Mean	SE	CV	Mean	SE	CV		
A	U1	0.217	0.009	12.9	0.193	0.012	17.1	2.13	0.145
	U2	0.057	0.014	56.0	0.076	0.007	27.6	0.15	0.700
	U3	0.140	0.006	13.6	0.138	0.002	4.3	0.09	0.770
	U4	0.150	0.014	27.3	0.131	0.007	14.5	0.04	0.846
	U5	0.179	0.014	22.9	0.161	0.006	11.2	0.34	0.562
	U6	0.287	0.021	22.0	0.363	0.017	13.5	6.04	0.014
	U7	0.136	0.014	30.1	0.132	0.005	10.6	0.34	0.562
	U8	0.056	0.008	41.1	0.058	0.006	31.0	0.40	0.529
	U9	0.148	0.006	12.2	0.134	0.005	9.7	2.12	0.146
	U10	0.129	0.019	45.0	0.140	0.010	20.7	0.06	0.809
	U1-10	1.517	0.029	5.8	1.525	0.031	5.7	0.23	0.631
B	U1	0.190	0.013	16.3	0.172	0.004	7.6	2.82	0.093
	U2	0.122	0.005	9.8	0.104	0.008	23.1	1.37	0.243
	U5	0.339	0.009	6.2	0.389	0.015	11.3	4.83	0.028
	U6	0.175	0.013	18.4	0.240	0.020	23.8	4.01	0.045
	U7	0.160	0.011	16.3	0.149	0.008	14.8	0.15	0.698
	U8	0.048	0.010	52.1	0.057	0.007	35.1	0.02	0.897
	U9	0.158	0.013	19.6	0.157	0.007	12.1	0.51	0.477
	U10	0.188	0.019	23.8	0.225	0.015	18.7	1.68	0.195
	U1-10	1.380	0.031	5.5	1.492	0.027	5.2	5.40	0.020
C	U5	0.509	0.009	8.4	0.509	0.012	6.5	0.07	0.796
	U6	0.169	0.013	36.7	0.202	0.020	28.7	1.73	0.189
	U7	0.184	0.007	17.4	0.159	0.005	8.2	4.27	0.039
	U8	0.133	0.008	27.1	0.147	0.007	14.3	2.47	0.116
	U9	0.206	0.007	16.0	0.209	0.010	12.9	0.01	0.907
	U10	0.138	0.008	28.3	0.151	0.009	17.2	0.64	0.425
		U5-10	1.339	0.018	6.4	1.377	0.036	7.4	1.16

(see below), males must be using a greater head velocity (head distance traveled/unit of time) than females during display performance.

Dewlap area and bob amplitude.—At any given SVL for adult lizards (50–70 mm SVL), the female dewlap area was approximately two-thirds smaller than that of the male dewlap (Fig. 3). Even exceptionally large females (>63 mm SVL) did not have the dewlap area of a small adult male (50 mm SVL).

The vertical displacement of the head during the bobbing movements of a display was quantified for five males and six females. For this sample we were able to control for camera distance, SVL, social context, display type, and particular bob within a display (see Materials and Methods). We focused the analysis on unit 5 of the type C display, and found the average male and female headbob amplitudes (i.e., head am-

plitude/snout tip-to-eye ratio for males: $0.84 \pm \text{SE } 0.101$; for females: $0.71 \pm \text{SE } 0.097$) were not significantly different (Kruskal-Wallis test, $df = 1$, $H = 1.20$, $P = 0.27$).

Signal use (subject-alone context).—None of the 22 female subjects displayed during 11 h of “female-alone” videotaped sessions. In contrast, solitary males under identical conditions displayed at a mean rate of 18 displays/h, extending their dewlaps with almost every display (Table 3). By definition, the displays of a solitary lizard are nondirected and may reflect an advertisement function (i.e., assertion context). The male displays during the assertion context were a mixture of the three display types, with type C comprising the majority (50%; Table 3).

Signal use (consensual context).—During the initial phase of consensual contact (i.e., challenge con-

TABLE 2. PROPORTION (%) OF VARIANCE FOUND IN UNIT DURATIONS OF SEVEN TYPE A, 20 TYPE B, AND 105 TYPE C DISPLAYS BY 22 FEMALE AND 47 TYPE A, 49 TYPE B, AND 76 TYPE C DISPLAYS BY 8 MALE *Anolis carolinensis* ATTRIBUTED TO DISPLAY TYPE, SEX, AMONG-INDIVIDUAL, AND WITHIN-INDIVIDUAL COMPONENTS OF A NESTED ANOVA.

Unit	Variance component (%)			
	Display type	Sex	Among individuals	Within individuals
1	97.7	0.4	0.9	1.0
2	93.7	0.0	2.8	3.5
3	99.1	0.1	0.0	0.8
4	97.7	0.0	1.6	0.7
5	87.3	0.8	2.4	9.5
6	51.6	5.3	18.5	24.6
7	12.2	17.2	25.3	45.3
8	59.0	6.9	3.1	31.0
9	45.5	1.1	7.7	45.7
10	40.3	1.8	35.3	22.6
All (1-10)	32.2	2.5	9.7	55.6

text), while pairs were still at long separation distances (> 60 cm), the sexes tended to have a similar signal use profile (Table 3). Males and females showed no significant difference in signal rate (Wilcoxon-Mann-Whitney test, $W = 308, P > 0.05$), nor in the proportion of displays grouped into volleys (Wilcoxon-Mann-Whitney test, $W = 295, P > 0.05$). Although both sexes primarily performed type C displays at long separation distances (80%, females; 90%, males), there was a small but significant intersexual difference in the proportion of A, B, and C displays (chi-square test, $\chi^2 = 6.9, P = 0.04$). The largest intersexual difference occurred when comparing dewlap use during long distance dis-

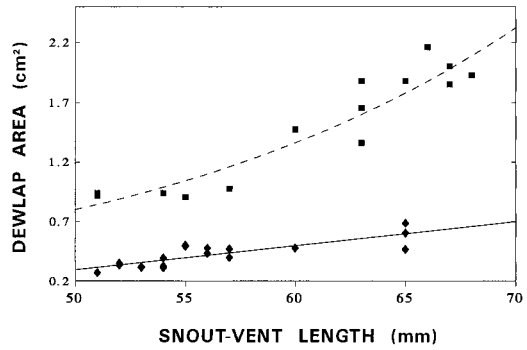


Fig. 3. Intersexual comparison of the extended *Anolis carolinensis* dewlap area by body size, where female (diamonds) and male (squares) data are fitted to solid and dashed lines, respectively.

play exchanges. Only 49% of female displays were accompanied by dewlap extension as compared with 86% of male displays (Wilcoxon-Mann-Whitney test, $W = 274, P = 0.01$)

The intersexual signaling profiles, however, dramatically diverged as subjects approached within lunging and biting distance (< 20 cm apart) of one another. Although the female signaling profile did not significantly change for any variable ($P > 0.05$) with decreased separation distance, the male signaling profile shifted significantly for all measured variables. The male display rate increased fourfold (Wilcoxon signed rank test, $Z = 34, P = 0.02$), type A and B displays increased sixfold and C displays decreased by half (chi-square test, $\chi^2 = 288, P = 0.0005$), displays in volleys decreased 10-fold (Wilcoxon signed rank test, $Z = 21, P = 0.03$), and displays with dewlap extension decreased sixfold (Wilcoxon signed rank test, $Z = 21, P =$

TABLE 3. INTERSEXUAL COMPARISON OF *Anolis carolinensis* SIGNAL USE IN SOLITARY AND CONSEXUAL CONTEXTS AND AT LONG (> 60 cm) AND SHORT (< 20 cm) INTERINDIVIDUAL DISTANCES. Data are based on 132 displays by 22 females and 172 displays by eight males. * These data are from DeCourcy and Jenssen (1994).

Signal variable	Solitary		Female-Female		Male-Male	
	♀	♂*	Long	Short	Long	Short
Display Rate (per min)	0.0	0.3	0.3	0.2	1.1	4.0
Display Types						
Type A	N/A	20%	5%	10%	5%	25%
Type B	N/A	30%	15%	15%	5%	35%
Type C	N/A	50%	80%	75%	90%	40%
Displays With Dewlap	NA	97%	49%	41%	86%	15%
Display Bouts In Volleys	NA	46%	73%	47%	80%	8%

TABLE 4. INTERSEXUAL COMPARISON OF *Anolis carolinensis* SIGNAL VARIABLES RECORDED DURING CONSEXUAL ENCOUNTERS BY 22 FEMALES AND EIGHT MALES. * See Greenberg (1977) or Jenssen (1979) for definitions of display modifiers.

Variables	Females	Males
Body size (SLV)	54.2 mm	65.5 mm
Dewlap size	0.22 cm ²	1.52 cm ²
Display pattern		
Stereotypic types	A, B, C	A, B, C
Dewlap extension	with or without	with or without
Display modifiers*		
Raised crest	Yes	Yes
Lowered throat	Yes	Yes
Sagittal flattening	Yes	Yes
Mouth gape	Yes	Yes
Mouth gape/tongue out	Yes	Yes
Color change	Yes	Yes
Display orientation*		
Lateral presentation	Yes	Yes

0.03). Over the course of the challenge encounter (long and short range phases combined), the intermale display rate (\bar{x} = 168 displays/h) was 14 times greater than that for interfemale encounters (\bar{x} = 17 displays/h).

In their respective consensual encounters, males and females employed very different tactics for conflict resolution. Male subjects followed a ritual common to males of their species, as well as to males of many *Anolis* species (e.g., Jenssen, 1979). Succinctly described, all pairs of contesting subjects circled head-to-head, then "jaw sparred" and finally "jaw locked." The reciprocal mouth-to-head hold was used to twist the opponent from the perch, with a male winning when the other declined to reengage. In contrast, the interfemale encounters were less ritualized, less intense, and much less likely to lead to escalated fighting than were intermale encounters. Females did not circle, jaw spar, or jaw lock, nor did interfemale contests pose any apparent injury to the contestants. Some encounters concluded with one female voluntarily moving away, but most concluded with a non-contact lunge and/or short chase. Only one encounter was settled by a quick bite to the nearest limb of the opponent. Nevertheless, during consensual contacts, females used the same three display types and all the display modifiers as observed during intermale encounters (Table 4).

DISCUSSION

Signal number and structure.—Our intersexual analysis of the aggressive signals of *A. carolinensis* documented a common repertoire. Included in this shared complement of signals were the same three headbob display patterns (types A, B, and C) which DeCourcy and Jenssen (1994) found males to use in both territorial advertisement (assertion context) and territorial defense (challenge context). For males, the temporal pattern of each display type is extremely stable, showing very little variation between individuals, whether captive or free-ranging, and between geographic populations (Lovern et al., 1999). We found that female *A. carolinensis* are also "precise" displayers, sharing the same high level of stereotypy observed in male displays. Within the limited temporal variation between display performances, sex contributed very little as a source of variance.

The anecdotal perception that displaying females "head-nod," while displaying males "head-bob" or "pushup," can be attributed to the male-larger body size dimorphism and the seemingly smaller range of amplitude that females use while performing any one of the three display patterns. Nevertheless, when controlling for body size and display type, extensive intraindividual variability in amplitude between display performances swamped any significant effect due to sex. The amplitude analysis also indicated that lizards were modulating the velocity of their head movement as they chose to perform an exaggerated or dampened version of a display pattern. Despite an almost threefold range in amplitude/head size ratios (0.41–1.10), the total time to move the head through units 1–10 showed little variance.

An obvious intersexual difference in signal structure was the size of the extended dewlap. Females have only one-third the dewlap area of similar sized males. Given the added effect of body size dimorphism, our average-sized male (65 mm SVL) had a dewlap area (1.52 cm²) seven times that of our average-sized female (54 mm SVL, 0.22 cm²; Table 4). The large size of the male dewlap distinctly amplifies the conspicuousness and potential broadcast distance of male displays over those of females. Given the manner in which the male dewlap is used, it can be inferred that its large size reflects prominent intrasexual selection. Field observations during the breeding season record males spending 37% of their time displaying in non-directed contexts and in long distance (> 3.5 m) consensual exchanges, whereas only 4% of their time was directed to the relatively short

distance heterosexual exchanges with resident females (Jenssen et al., 1995a). In contrast, the display exchanges between free-ranging females were infrequent (0.3% of daily activity period) and at short distances (< 2 m; Nunez et al., 1997).

Signal use.—The frequency-related use of aggressive signals showed pronounced intersexual differences. In making functional inferences for these differences, we assumed signal behavior during the subject alone context reflected territory advertisement (the assertion context), and signaling during the consensual context reflected territorial contests (challenge context). Our solitary females failed to display, whereas solitary males gave A, B, and C displays in similar proportions at an average rate of 18/h (DeCourcy and Jenssen, 1994; present study). This intersexual difference is even more dramatic for free-ranging *A. carolinensis*. Nondirected displaying by perched females and males averaged 1/h and 46/h, respectively, and when moving between perch localities diverged to 6/h and 209/h, respectively (Jenssen et al., 1995a; Nunez et al., 1997). Therefore, unlike males, females do not advertise their presence or their territories by displaying.

In our consensual context, the aggressive intensity between paired females was much less than between paired males. Females displayed less, did not adjust their aggressive signals to increasing threat, and resolved their conflict with much less ritualized interactions or escalated fighting. Display rate of interacting females (\bar{x} = 17/h) was 14 times less than that of interacting males (\bar{x} = 240/h). For males, approaching within lunging and biting distance (< 20 cm apart) created a fourfold increase in display rate, almost an eightfold increase in displays without dewlap extension, a 10-fold shift away from multidisplay volleys to separate displays, and an increase of A and B display types by five and sevenfold, respectively (DeCourcy and Jensen, 1994; present study). These frequency transitions, based on decreasing separation distances (i.e., increasing risk), can be interpreted as evidence of a bluff system for intimidation and assessment or as the outcome of heightened flight-fight conflict (reviewed in Bradbury and Vehrencamp, 1998). In contrast, the signal frequency profile for females showed little change as opponents came within physical threat distance of each other. If females have a contingent intimidation or assessment strategy or if they experience a growing conflicted arousal state, there were no obvious signal transitions to suggest such potentials.

Conflict resolution between paired males under various protocols (e.g., Greenberg and Noble, 1944; McMann, 1993; Leuck, 1995), including our own, follows a ritual which begins with shifts in body color (a flush of brown turning to green with a black eyespot), size-enhancing changes in body proportions (sagittal flattening, lowered throat, raised nuchal crest), and volleys of displays (featuring dewlap extension and type C cadence pattern). When close, opponents circle, display rates more than triple, and dewlaps are rarely extended (DeCourcy and Jenssen, 1994; present study). All display modifiers (see Table 4) are now employed. Circling progresses to a head-to-head proximity, then to "jaw sparring," and finally to "jaw locking" (Jenssen, 1979, for further description). Though other opportunities exist, males restrict their mouth holds to their opponent's head or jaw. Escalated fighting culminates in one or a series of protracted jaw locks, testing each other's strength, endurance, and willingness to risk injury. In laboratory-staged fights between size-matched males, encounters are intense, can last over an hour, and may result in exhaustion and bleeding wounds (unpubl. data; Leuck, 1995, pers. comm.). In contrast, our size-matched females lacked the male combat ritual (though they did exhibit the size-enhancing modifiers), never jaw sparred or jaw locked, and only once bit in 11 encounters. Free-ranging females corroborate our laboratory observations. Nunez et al. (1997) found that interfemale aggression between neighbors was infrequent (\bar{x} = 1/7 h), brief (\bar{x} = 1.6 min) and involved little ritual or likelihood of physical contact. In summary, agonistic females showed no dramatic shift in kinds of signals, rate of signaling, or proportion of signals with increased threat, nor did they participate in ritualized, high-risk physical struggles which are characteristic of males.

Overview.—The intersexual asymmetries that we found in dewlap size and consensual signal use (both territorial advertising and defense contexts) of *A. carolinensis* should reflect the selected consequences which consensual contests have on female and male potential reproductive rates (PRR). For free-ranging females, consensual competition for resources appeared to have a negligible effect on female PRR (Nunez et al., 1997; Jenssen and Nunez, 1998). Therefore, the female pattern of aggressive signal use should be under minimal intrasexual selection. As a consequence of the small risk involved in interfemale aggressive encounters, we suggest that females do not benefit from buffering their territories through advertisement displaying.

When intrusion does occur, females can afford to signal simply and "honestly" (sensu Bradbury and Vehrencamp, 1998).

For free-ranging males, however, consensual contests largely determine male PRR (Ruby, 1984; Jenssen and Nunez, 1998). Therefore, intermale signaling should be significantly affected by intrasexual selection, as reflected by sexual dimorphisms in territorial behavior. Field observations confirm that males have eightfold larger territories (69 m³) than females (8 m³), invest sixfold more patrol distance (27 m/h) than females (4 m/h), and produce nondirected displays at far greater rates than females while perched (46 and 1 displays/h, respectively) and moving (\bar{x} = 209 and 6 displays/h, respectively; Jenssen et al., 1995a; Nunez et al., 1997). The large male dewlap, used consistently during solitary displaying (DeCourcy and Jenssen, 1994; present study), presumably has selective advantage for greater broadcast distance and could function to intimidate males from entering the patrolled habitat. The large dewlap is also extended with the initial displays of male-male exchanges (DeCourcy and Jenssen, 1994; present study) and could function as a reliable assessment criterion for signaler body size (sensu Maynard Smith and Harper, 1988; present study). Finally, the intermale encounters used deceptive, size-enhancement signals (i.e., modifiers) and a shifting pattern of signal use when the risk from escalated fighting increased (e.g., DeCourcy and Jenssen, 1994; present study). This ritualized combat by male *A. carolinensis* is evidence for an evolved manipulative system of some complexity, perhaps as a game of sequential assessment (sensu Bradbury and Vehrencamp, 1998).

ACKNOWLEDGMENTS

We wish to thank D. Cunningham, K. DeCourcy, C. Miller, B. Sponseller, and L. Wemmer for their assistance; R. Andrews, J. Congdon, and B. Leuck for their comments on the manuscript and E. Smith as consultant from the Virginia Tech Statistical Consulting Center. Animals were collected under a Georgia Department of Natural Resources collecting permit (33714) and maintained following the approved protocol by the Virginia Tech Animal Care and Use Committee.

LITERATURE CITED

ANDERSSON, M. B. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

- ANDREWS, R. M. 1985. Oviposition frequency of *Anolis carolinensis*. *Copeia* 1985:259–262.
- BARLOW, G. W. 1968. Ethological units of behaviour, p. 217–232. *In*: Central nervous system and dish behaviour. D. Ingle (ed.). Univ. of Chicago Press, Chicago.
- BELS, V. 1990. The mechanism of dewlap extension in *Anolis carolinensis* (Reptilia: Iguanidae) with histological analysis of the hyoid apparatus. *J. Morphol.* 206:225–244.
- BRADBURY, J. W., AND S. L. VEHRENCAMP. 1998. Principles of animal communication. Sinauer Associates, Sunderland, MA.
- CARPENTER, C. C. 1961. Pattern of social behavior of Merriam's canyon lizard (*Sceloporus m. merriami*)—Iguanidae). *Southwest. Nat.* 6:138–148.
- . 1986. An inventory of the display-action-patterns in lizards. *Smiths. Herpetol. Info. Serv.* 68:1–18.
- DECOURCY, K. R., AND T. A. JENSSEN. 1994. Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Anim. Behav.* 47:251–262.
- FITCH, H. S., AND D. M. HILLIS. 1984. The *Anolis* dewlap: interspecific variability and morphological associations with habitat. *Copeia* 1984:315–323.
- FLEISHMAN, L. J. 1988a. Sensory and environmental influences on display form in *Anolis aeneus*, a grass anole from Panama. *Behav. Ecol. Sociobiol.* 22:309–316.
- . 1988b. Sensory influences in physical design of a visual display. *Anim. Behav.* 36:1420–1424.
- . 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.* 139:S36–S61.
- FONT, E., AND L. ROME. 1990. Functional morphology of dewlap extension in the lizard *Anolis equestris* (Iguanidae). *J. Morphol.* 206:245–258.
- GREENBERG, B., AND G. K. NOBLE. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Voigt). *Physiol. Zool.* 17:392–439.
- GREENBERG, N. 1977. A neurological study of display behavior in the lizard *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). *Am. Zool.* 17:191–201.
- HAUSER, M. D. 1996. The evolution of communication. MIT Press, Cambridge, MA.
- JENSSEN, T. A. 1977. Evolution of anoline lizard display behavior. *Am. Zool.* 17:203–215.
- . 1978. Display diversity in anoline lizards and problems of interpretation, p. 269–285. *In*: Behavior and neurology of lizards: an interdisciplinary conference. N. Greenberg and P. D. MacLean (eds.). National Institutes of Mental Health, Rockville, MD.
- . 1979. Display modifiers of *Anolis opalinus*. *Herpetologica* 35:21–30.
- , AND S. C. NUNEZ. 1998. Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intrasexual selection. *Behaviour* 135:981–1003.
- , N. GREENBERG, AND K. A. HOVDE. 1995a. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetol. Monogr.* 9:41–62.

- , J. D. CONGDON, R. U. FISCHER, R. ESTES, D. KLING, AND S. EDMANDS. 1995b. Morphological characteristics of the lizard, *Anolis carolinensis*, from South Carolina. *Herpetologica* 51:401–411.
- LEUCK, B. 1995. Territorial defense by male green anoles: an experimental test of the roles of residency and resource quality. *Herpetol. Monogr.* 9:63–74.
- LOVERN, M. B., T. A. JENSSEN, K. S. ORRELL, AND T. TUCHAK. 1999. Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis*: signal stability or lability? *Herpetologica* 55:222–234.
- MAYNARD SMITH, J., AND D. HARPER. 1988. The evolution of aggression: can selection generate variability? *Philo. Trans. R. Soc. B Biol. Sci.* 319:557–570.
- McMANN, S. 1993. Contextual signalling and the structure of dyadic encounters in *Anolis carolinensis*. *Anim. Behav.* 46:657–668.
- NUNEZ, S. C., T. A. JENSSEN, AND K. ERSLAND. 1997. Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. *Behaviour* 134:205–223.
- RUBY, D. 1984. Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica* 40:272–280.

BIOLOGY DEPARTMENT, VIRGINIA TECH, BLACKSBURG, VIRGINIA 24061. E-mail: (TAJ) tjenssen@vt.edu. Send reprint requests to TAJ. Submitted: 8 May 1998. Accepted: 8 July 1999. Section editor: S. T. Ross.