

Laboratory and Field Test of the Functional Significance of the Male's Dewlap in the Lizard *Anolis sagrei*

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The extension and retraction of the throat fan or dewlap is one of the most conspicuous aspects of the display behavior of male *Anolis* lizards. We explored aspects of the functional significance of displaying the male's dewlap by surgically preventing male brown anoles (*Anolis sagrei*) from extending their dewlaps and comparing their behavior with controls that could extend their dewlaps. In 30-min laboratory contests, we compared the display behavior of untreated males paired with either experimental males or with sham-treated control males. In a subsequent field study, we tested what effect displaying the dewlap has on male residence time (days males remained at a site), visibility (number of sightings of males), maximum distance moved (from site of release), home range size, and body size during 18 censuses over a 47-day period. Untreated males paired with the two types of stimulus males in the laboratory study did not differ significantly in latency to display, number of dewlap extensions, number of bobbing displays, number of bobbing displays with dewlap extensions, or in proportion of males erecting crests in both short distance physical encounters (< 0.6 m) and in visual encounters at 1 m and 3 m. Thus, males did not modify their display behavior based on whether their opponents extended their dewlaps. In the field study, experimental and control males did not differ significantly in residence time, visibility, maximum distanced moved, and home-range size. In addition, males in the two treatment groups captured at the end of the study did not differ in snout–vent length or body mass. These results provide no evidence for a functional significance of the displaying of the male's dewlap in *A. sagrei*.

MALE display behaviors often provide insight into how sexual selection affects male reproductive success. One structure used in the display behavior of male anoles that may be subjected to strong sexual selection is the throat fan or dewlap (Fitch and Hillis, 1984; Losos and Chu, 1998; Fleishman, 2000). The dewlap, which is often brightly colored, is an area of throat skin made visible by the downward and forward movement of elements of the hyoid apparatus (Bels, 1990; Font and Rome, 1990). Although the dewlap can be displayed alone (either singly or in a series of pulses of extensions), it is frequently extended in conjunction with stereotyped and in some cases species-specific movements of the head and body (Jenssen, 1977, 1978; Fleishman, 1992).

Several nonexclusive hypotheses have been proposed for the function of dewlap extension. The display of the male's dewlap in *Anolis* lizards may play a key role in species recognition (Rand and Williams, 1970; Losos, 1985; Macedonia and Stamps, 1994), communication effectiveness (Fleishman, 1992, 2000), competition for territories (Greenberg and Noble, 1944; Cooper, 1977; DeCourcy and Jenssen, 1994), female choice of mates (Evans, 1938; Crews, 1975; Sigmund, 1983), and even predator defense

(Leal and Rodríguez-Robles, 1997). However, few studies have addressed directly the functional significance of dewlap extension by examining the consequences of removing or retaining dewlap extension in the display. In particular, it is unknown what effect the display of the dewlap has on the behavior of conspecifics during male-male interactions.

Furthermore, if the display of the male's dewlap in anoles is important in assessing or intimidating rivals (see Greenberg and Noble, 1944; DeCourcy and Jenssen, 1994; Jenssen et al., 2000), then it may play an important role in male territorial behavior.

Thus, the purpose of the present study was to examine what effect displaying of the male's dewlap has on the display behavior of opponents in staged male-male interactions in the laboratory and on the residence time, visibility, maximum distance moved, home-range size, and changes in body size of males in nature. We hypothesized that untreated males exposed in the laboratory to experimental males that are prevented from extending their dewlaps will behave differently than untreated males exposed to sham-treated control males. We also hypothesized that the residence time, visibility, maximum distance moved, home-range size, and fi-

nal body size of experimental males that are prevented from extending their dewlaps will differ significantly from that of sham-treated control males in the field. We elected to examine these particular variables for several reasons. First, animals that are unable to extend their dewlaps could lose their territories and be driven from their previous home ranges by rival males. Second, the inability of a male to extend its dewlap could also affect the size and location of its home range in one or more ways. Therefore, we determined each lizard's home range. Third, the inability of a male to extend its dewlap may make territory defense more costly. Such costs could cause mortality and reduced growth rate and/or loss of body mass. Alternatively, dewlap extension itself could be a handicap that enhances overall fitness but increases mortality, reduces growth, and/or causes weight loss (see Grafen, 1990). To quantify possible consequences of dewlap extension, we recorded the residence time of study males and measured two aspects of their body size at the start and end of the experiment.

MATERIALS AND METHODS

Subjects.—The study organism was the brown anole, *Anolis sagrei*. This anole is believed to have evolved in Cuba and to have then spread through the western Caribbean and into Florida (Williams, 1969; Lee, 1985). In terms of the ecomorph concept (Williams, 1983), *A. sagrei* is a "trunk-ground" species, denoting its habit of perching close to the ground and running to the ground to capture prey. It usually perches less than 1.8 m above the ground on bushes, post, and tree trunks (Schoener, 1968). *Anolis sagrei* is a sit-and-wait predator, feeding primarily on large insects, supplemented with a few fruits (Schoener and Schoener, 1980). Males are highly territorial and polygynous (Schoener and Schoener, 1982; Stamps, 1983). The sexual dimorphism in body size (male/female) as reported in Stamps (1983) is relatively high (i.e., 1.29). Adult males have exclusive home ranges, which overlap with female territories (Schoener and Schoener, 1980). According to Schoener and Schoener (1980), larger males occur in better habitats than do smaller males. Moreover, male body size is positively related to male home-range size and thus to the number of potential female mating partners (Schoener and Schoener, 1982). Schoener and Schoener (1980) have reported that a relatively large male may have as many as six females within its home range. The population densities of *A. sagrei* can be very high (Lister, 1976; Schoener and Schoe-

ner, 1982); for instance, Schoener and Schoener (1980) found a maximum population density of 0.97 individuals per square meter in islands of the Bahamas. In southern Florida, males and females are reproductively active from March through August (Lee et al., 1989; Tokarz et al., 1998), a period when males defend territories and court and mate with females (Tokarz, 1998).

Surgical procedures.—We prevented experimental males from extending their dewlaps by cutting across the subcutaneous cartilaginous rods (second ceratobranchials) where they meet the mineralized central mass of the hyoid body (see Bels, 1990; Font and Rome, 1990). This method, which does not affect headbob displays (Crews, 1975), has been successfully used to prevent dewlap extension in *Anolis carolinensis* (Crews, 1975) and in *A. sagrei* (Tokarz, 2002). In addition, the surgical procedure required to prevent dewlap extension does not affect the muscles (e.g., muscle branchiohyoideus) normally involved in dewlap extension (Bels, 1990); thus, much of the sensory feedback associated with normal dewlap extension should be preserved.

Prior to surgery, we applied xylocaine (5% ointment, Astra Pharmaceutical Products, Westborough, MA) to the throat of a male about to undergo surgery (laboratory experiments only), then placed the animal into crushed ice until it was insensitive to touch and could not right its body (3–5 min). Hypothermia is a method for anesthetizing small reptiles for minor surgical procedures (Frye, 1973) and was used to anesthetize male *A. carolinensis* for a similar procedure (see Crews, 1975). We placed the anesthetized male onto a platform, which rested on a dish of crushed ice. Using a StereoZoom microscope (Bausch & Lomb Instruments and Systems Division, Rochester, NY) to view the neck, we made an incision (approximately 5 mm long) parallel to the midline of the throat and exposed the subcutaneous second ceratobranchials. We then made a single transverse cut across the second ceratobranchials to separate them from the hyoid body, closed the incision with two sutures, and applied an antiseptic ointment (Povidone Iodine, Eckert Drug Co., Clearwater, FL) to the incision area. Males in the control group were treated in the same manner as experimental males with the important exception that the second ceratobranchials were not cut.

Statistics.—We used nonparametric tests to analyze the data. We used the Mann-Whitney *U*-test

to determine significant differences between two groups and the Kruskal-Wallis test when evaluating three or more groups. For simplicity, we report *Z*-values rather than the *U*-statistic for the Mann-Whitney tests. In situations where we compared matched pairs, we used the Wilcoxon-matched pairs test.

The Fisher exact probability test was employed for frequency data (2×2 contingency table).

We considered an alpha level of 0.05 in a two-tailed test to be significant. However, if a significant difference was detected after multiple comparisons, we used the sequential Bonferroni technique as described in Rice (1989) to maintain an experiment-wise error of 0.05 (see Sokal and Rohlf, 1981). Analyses were performed using StatView 4.0 software (SAS Institute Inc., Cary, NC).

Laboratory experiments.—We captured reproductively active males as needed in the Miami, Florida, area from April through June 2000 and brought them to our laboratory at the University of Miami. We housed males in animal rooms with environmental conditions similar to those that occur in the Miami area during the summer months (based on data from the U.S. Department of Commerce, National Climatic Data Center, Asheville, NC). During the 14-h light phase, rooms were illuminated from the ceiling by four, 122 cm long 40-W General Electric F40DX Deluxe Daylight fluorescent lamps. The temperature of the animal rooms ranged from 30 C during the light phase to 27 C during the 10-h dark phase. The relative humidity of the rooms varied from a low of 50% during the light phase to 70% during the dark phase as determined by a Cole-Parmer Instrument Co. hygrometer.

Males were housed individually in glass terraria (61 cm L \times 32 cm W \times 42 cm H) with screen tops until used in behavioral tests. Each terrarium was illuminated by a 46 cm long 15-W Vita-Lite® fluorescent lamp (Duro-Test, North Bergen, NJ) resting on the top of the cage. The luminance of a 20-W Vita-Light® at 30 cm from sensors is 452 lux (Gehrmann, 1997:44). Cages had a simulated natural habitat consisting of a bromeliad in a clay pot, twigs, and a prominent perching site (a wooden dowel 47 cm long and 1.8 cm in diameter). All cages contained a small dish of water. Lizards were fed on live crickets every other day.

In the first of two experiments, we examined the effects of displaying the male's dewlap on the display behavior of opponents in short-distance encounters (< 0.6 m) in which paired

males were able to interact physically. We paired one group of untreated males (untreated 1) with experimental males that were surgically prevented (see surgical procedures) from extending their dewlaps and another group of untreated males (untreated 2) with sham-treated control males. We sized-matched each pair of males to minimize the difference in their snout-vent lengths (SVLs) prior to staging encounters.

We staged encounters by placing an untreated male and either an experimental or a control male into adjacent sides of a testing cage with a removable plywood partition in place. Each compartment of the testing cage (30.5 cm L, 32 cm W, 42 cm H) was covered by a clear plastic lid and had a centrally placed wooden dowel (47 cm in length and 1.8 cm in diameter) as a perch site. Prior to placing an untreated male into the testing cage, we marked its back with a nontoxic paint marker (Speedball® painters marker, Hunt Manufacturing Co., Statesville, NC).

Twenty-four hours after placing males into a testing cage, we removed the partition that separated the two compartments of the cage and videotaped both males for 30 min using a JVC GF-700 video camera. We left the animal room while videotaping. Following encounters, we measured each male's SVL and determined its body mass to the nearest milligram. We then released animals into the field.

In the second experiment, we examined interactions at longer distances. Males were able to view each other at a distance of either 1 m or 3 m but could not interact physically. As in the first experiment, we paired untreated males with either experimental or control males. However, unlike in the first experiment, we placed males into separate testing cages (61 cm L \times 32 cm W \times 42 cm H) that were separated by removable wooden partitions. These cages were aligned end-to-end and were either 1 m or 3 m apart as measured from the center of each cage (location of perch); thus, males could be as close as 0.4 m or as far away as 1.6 m in the cages separated by 1 m and as close as 2.4 m or as far away as 3.6 m in cages separated by 3 m. We sized-matched paired males to minimize the difference in their SVLs. Twenty-four hours after placing paired males into adjoining cages, we removed the partition between the cages and videotaped the behavior of the untreated male of each pair for 30 min. We used each male in only one encounter. Following encounters, we measured each male's SVL, determined its body mass, and released it into the field.

We transcribed the videotapes of the encoun-

ters and recorded the latency period (min) to the first display (either a dewlap extension or bobbing display, see McMann, 2000), number of dewlap extensions, number of bobbing displays (total), and number of bobbing displays with dewlap extensions of untreated males and of their pair mates in short distance physical encounters (< 0.6 m). We also recorded the proportion of males in each group that erected a crest along the neck and back. In the visual contests at 1 and 3 m, we only recorded the aforementioned behaviors for the untreated males.

Field experiment.—We conducted the field experiment from 22 May to 14 July 2002 in a subtropical hardwood hammock at the Frank Smathers Jr. Biology Field Station located within Four Fillies Farm. The Four Fillies Farm, which is owned by the University of Miami, is 9.6 km south of the campus in Miami-Dade County. The vegetation of the hammock is similar to that found in other regions where *A. sagrei* is found (e.g., Snyder et al., 1990). The population density of *A. sagrei* at the study site is similar to the high densities that appear common in this species (Lister, 1976; Schoener and Schoener, 1980).

We collected 42 adult *A. sagrei* males during a four-day period (22–26 May) by walking throughout the hammock, sighting males and noosing them. After capturing a male, we placed it into a separate cloth bag and marked the site where it had been initially seen with a surveyor's flag. The date and the colors of the unique sequence of three colored beads that would subsequently be used to identify the captured lizard were noted on the flag. When choosing males to be used in the study, we selected males that were located approximately 10 m or more apart to reduce the possibility that study males would interact with each other when released.

We transported captured males to our laboratory, measured their SVL to the nearest millimeter, and determined their body mass to the nearest milligram. We assigned males to either an experimental or to a control treatment group by flipping a coin to determine the group assignment of the first captured male. Thereafter, we alternated in assigning the remaining males to the two treatment groups based on the group assignment of the first male and the chronological order in which males had been captured.

We surgically prevented experimental males ($n = 21$) from extending their dewlaps (see surgical procedures) and performed a sham-surgery on control males ($n = 21$). While males

were still anesthetized, we permanently marked each male by attaching a unique sequence of three colored beads to the tail as described in Fisher and Muth (1989). This method has been used previously in field studies of *A. sagrei* (e.g., Tokarz, 1998; McMann, 2000; Paterson, 2002) and other lizards (e.g., Knapp and Moore, 1996).

After males had recovered from surgery (approximately 30 min), we placed males into separate cloth bags and returned them to the field site and released each male where it had been first sighted (marked with a surveyor's flag). It was important to return study males to their territories as quickly as possible because neighboring nonfocal males over time may take over vacated territories (see Beletsky and Orians, 1987; Paterson, 2002).

We conducted the first census the day after all of the treated males had been returned to the field (i.e., 27 May). For each census, we visited the site where each male had been released and searched (within 10 m of the surveyor flag) for the male for a maximum of 10 min. When a male was sighted, we recorded its identity based on its bead tag, the time when it was sighted, whether it displayed its dewlap, gave a bobbing display, and/or a nodding display (see McMann, 2000). We also marked the location of the male when it was first spotted with a surveyor's flag. We then determined the relationship between the location of where the animal was sighted and its original site of release (marked by a labeled flag) by taking a compass bearing (to the nearest degree) and measuring the distance (to the nearest 0.01 m) between the two locations with a 30-m measuring tape. We used these measurements to calculate the Cartesian coordinates for each animal sighting. After sighting a marked male and recording its location (or after 10 min of searching and not finding the marked male), we moved to the next subject and so on until all of the 42 flagged sites where study males had been released were examined. We visited sites based on the chronological order of capture of study males. To avoid possible differences in the likelihood of sighting animals based on time of day effects, we did not start with the same male for each census but rather moved the starting point 10 males forward with each census. We visited the study site and took a census approximately three times a week for a total of 18 censuses over a 47-day period (27 May to 12 July). On the two days following the last census, we captured study males, measured their SVLs, and determined their body masses. Captured males were then released.

TABLE 1. THE DISPLAY BEHAVIOR OF UNTREATED MALES IN TWO EXPERIMENTS IN WHICH UNTREATED MALES WERE PAIRED FOR 30 MIN EITHER WITH EXPERIMENTAL MALES THAT COULD NOT EXTEND THEIR DEWLAPS OR WITH CONTROL MALES THAT COULD EXTEND THEIR DEWLAPS.

Experiment	Pair mate	n	Median display latency (min)	Mean (\pm SE) number			Males with crests (%)
				Dewlap extensions	Bobbing displays	Bobbing displays with dewlap extensions	
One	Experimental	16	3.22	57.75 \pm 9.55	4.63 \pm 1.70	2.00 \pm 0.67	18.75
	Control	16	3.67	54.31 \pm 9.68	4.13 \pm 1.61	2.00 \pm 0.65	37.50
Two							
1 m	Experimental	14	6.63	61.00 \pm 13.10	1.14 \pm 0.56	0.86 \pm 0.40	00.00
	Control	14	4.62	58.93 \pm 11.33	0.21 \pm 0.21	0.21 \pm 0.21	00.00
3 m	Experimental	10	11.15	11.30 \pm 5.95	1.10 \pm 0.72	0.10 \pm 0.10	00.00
	Control	10	14.63	9.80 \pm 4.81	0.20 \pm 0.20	0.00 \pm 0.00	00.00

We calculated the home-range area of males using the convex polygon method of the HomeRange program (vers. 2.1.4) authored by Robert Huber and Jack Bradbury. This program is freeware available at <http://caspar.bgsu.edu/~software>. We defined the residence time of males at sites as the number of days between the day when males were released and the last census day when males were observed.

We defined the visibility of males simply as the number of sightings of a male during the 18 censuses. We also calculated a conspicuousness index (visibility prior to disappearance), which we defined as the number of times a male was sighted divided by the number of censuses from the first census to the last census it was seen.

RESULTS

Laboratory experiments.—Untreated males in experiment 1 paired with either experimental males or control males in short distance physical encounters did not differ significantly either in latency to display ($Z = -0.0380$, $P = 0.9699$), number of dewlap extensions ($Z = -0.3580$, $P = 0.7202$), number of bobbing displays ($Z = -0.524$, $P = 0.6005$), number of bobbing displays with dewlap extensions ($Z = 0.000$, $P > 0.9999$), or in the proportion of males with crests ($P = 0.4331$; Table 1). Within contests, untreated males that were paired with experimental males differed significantly from their pair mates in number of dewlap extensions ($Z = -3.517$, $P = 0.0004$) and in number of bobbing displays with dewlap extensions ($Z = -2.673$, $P = 0.0075$). This result was expected because experimental males could not extend their dewlaps. However, untreated males did not differ significantly from their experimental pair mates in latency to display ($Z = -1.913$, P

$= 0.0557$) and in number of bobbing displays ($Z = -0.441$, $P = 0.6594$). Untreated males that were paired with control males did not differ significantly from their pair mates either in latency to display ($Z = -0.259$, $P = 0.7960$), number of dewlap extensions ($Z = -0.310$, $P = 0.7563$), number of bobbing displays ($Z = -1.227$, $P = 0.2198$), or in number of bobbing displays with dewlap extensions ($Z = -0.433$, $P = 0.6649$).

As expected none of the experimental males in any of the staged encounters extended their dewlaps either singly or in association with bobbing displays. In experimental males, the median latency to display was 4.77 min, the mean (\pm SE) number of bobbing displays was 5.50 \pm 1.18, and the percentage of males with crests was 25%. In control males, the median latency to display was 4.10 min, the mean (\pm SE) number of dewlap extensions was 43.88 \pm 7.96, the mean (\pm SE) number of bobbing displays was 8.19 \pm 1.97, the mean (\pm SE) number of bobbing displays with dewlap extensions was 2.69 \pm 1.00, and the percentage of males with crests was 43.75%.

Experimental males gave significantly fewer dewlap extensions ($Z = -5.158$, $P < 0.0001$) and bobbing displays with dewlap extensions ($Z = -3.424$, $P = 0.0006$) than did control males. However, experimental and control males did not differ significantly either in latency to display ($Z = -1.206$, $P = 0.2278$) or in number of bobbing displays ($Z = -0.721$, $P = 0.4707$). Thus, the only significant difference between the two types of stimulus males was that experimental males did not extend their dewlaps during encounters.

In experiment 2, untreated males paired with the two types of stimulus males in 1 m visual encounters did not differ significantly either in

TABLE 2. THE MEAN (\pm SE) RESIDENCE TIME, VISIBILITY (NUMBER OF SIGHTINGS), MAXIMUM DISTANCE MOVED, AND HOME-RANGE AREA OF EXPERIMENTAL MALES THAT WERE PREVENTED FROM EXTENDING THEIR DEWLAPS AND OF CONTROL MALES THAT WERE RELEASED AT THE SITES WHERE THEY HAD BEEN FIRST SIGHTED IN A NATURAL HARDWOOD HAMMOCK AND MONITORED IN 18 CENSUSES OVER A PERIOD OF 47 DAYS.

Treatment group	Residence time (days)	Sightings (n)	Maximum distance moved (m)	Home-range area (m ²)
Experimental	28.43 \pm 4.11 (n = 21)	7.57 \pm 1.17 (n = 21)	4.05 \pm 0.68 (n = 18)	8.37 \pm 2.32 (n = 5)
Control	33.24 \pm 3.68 (n = 21)	8.67 \pm 1.15 (n = 21)	3.86 \pm 0.66 (n = 20)	6.94 \pm 3.68 (n = 8)

latency to display ($Z = -0.505$, $P = 0.6133$), number of dewlap extensions ($Z = -0.046$, $P = 0.9633$), number of bobbing displays ($Z = -1.793$, $P = 0.0730$), number of bobbing displays with dewlap extensions ($Z = -1.729$, $P = 0.0838$), or in the proportion of males with crests (Table 1). Similarly, untreated males paired with the two types of stimulus males in 3 m encounters did not differ significantly either in latency to display ($Z = -1.161$, $P = 0.2456$), number of dewlap extensions ($Z = -0.079$, $P = 0.9368$), number of bobbing displays ($Z = -1.135$, $P = 0.2562$), number of bobbing displays with dewlap extensions ($Z = -1.000$, $P = 0.3173$), or in the proportion of males with crests (no crests were erected in either group).

There were no significant differences in SVL ($H = 1.406$, $P = 0.7042$) or in body mass ($H = 1.547$, $P = 0.6715$) among male groups in the laboratory experiments (data not shown).

Field experiment.—The residence time of experimental and of control males (Table 2) at their sites of release did not differ significantly ($Z = -0.857$, $P = 0.3912$). This calculation is based on the data for all of the 42 released males. There was also no significant ($Z = -0.381$, $P = 0.7031$) difference in residence time of experimental males (33.17 \pm 3.73 days, $n = 18$) or of control males (34.90 \pm 3.45 days, $n = 20$) when only the data from males that were observed at least once after release were considered. Moreover, there was no significant association between whether a male was subsequently seen after release and treatment group ($P = 0.6060$) based on the finding that three of the 21 released experimental males and one of the 21 released control males were not seen again after release.

The visibility of experimental and of control males as indicated by the total number of sightings (Table 2) did not differ significantly during the 18 censuses ($Z = -0.694$, $P = 0.4876$). Nor was there a significant difference ($Z = -0.498$,

$P = 0.6182$) in the conspicuousness index of experimental males (mean \pm SE = 0.68 \pm 0.24) and of control males (0.71 \pm 0.25).

There was no significant ($Z = -0.409$, $P = 0.6823$) difference in the maximum distance that experimental males and control males moved from their initial release sites (Table 2). Nor was there a significant difference between treatment groups in home-range area as estimated by the convex polygon method (Table 2). Because the convex polygon method of calculating home-range area is sensitive to sample size (i.e., sightings; Rose, 1982), we empirically determined the number of sightings that are required to estimate accurately home-range area as described in Rose (1982). We plotted the number of sightings against cumulative home range-area (as a percent of maximum area) for the two subjects (an experimental and a control male) that had the highest number of sightings (i.e., 18 sightings/male). As expected this analysis indicated that home-range area initially increased rapidly with number of sightings but as the number of sightings was increased the rate of increase in home-range area slowed and eventually reached an asymptote. Approximately 13 sightings were found to be sufficient to describe 80% of home-range area, and we used this number of sightings as the minimum number necessary to calculate home-range area in *A. sagrei*. There was no significant ($Z = -1.464$, $P = 0.1432$) difference in home range area of the five experimental males and the eight control males that were sighted 13 or more times (Table 2). There was also no significant difference ($Z = -0.033$, $P = 0.9737$) in home-range area between experimental males (mean \pm SE, 6.90 \pm 1.53 m²) and control males (5.37 \pm 1.79 m²) when home-range areas were calculated using data from the 17 experimental and 18 control males for which there were sufficient sightings (≥ 3) to calculate home ranges. The mean (\pm SE) number of sightings for the 17 experimental males (10.29 \pm 1.06) and the 18 control

TABLE 3. THE MEAN (\pm SE) INITIAL AND FINAL SNOUT-VENT LENGTH (SVL) AND BODY MASS AS WELL AS THE RATE OF CHANGE IN SVL AND BODY MASS OF THE EIGHT EXPERIMENTAL AND SIX CONTROL MALES THAT WERE RECAPTURED AT THE END OF THE STUDY.

Treatment group	SVL (mm)		Body mass (g)		Rate of change	
	Initial	Final	Initial	Final	SVL (mm/day)	Body mass (mg/day)
Experimental	58.1 \pm 0.9	58.6 \pm 1.0	5.72 \pm 0.31	5.43 \pm 0.23	0.010 \pm 0.006	-0.006 \pm 0.005
Control	57.2 \pm 0.7	57.5 \pm 0.6	5.09 \pm 0.16	5.03 \pm 0.13	0.007 \pm 0.004	-0.001 \pm 0.003

males (11.00 ± 1.04) did not differ significantly ($Z = -0.694$, $P = 0.4876$).

There was no significant difference at the beginning of the field experiment between treatment groups in the SVL ($Z = -0.381$, $P = 0.7031$) and body mass ($Z = -0.742$, $P = 0.4580$) of males. The mean (\pm SE) SVL of the 21 experimental males and of the 21 control males was 56.9 ± 0.51 mm and 56.8 ± 0.51 mm, respectively. The mean (\pm SE) body mass of experimental males and of control males was 5.45 ± 0.19 g and 5.29 ± 0.15 g, respectively. At the end of the experiment (two-day period following last census), we were able to capture eight experimental males and six control males. There were no significant differences between experimental and control males in their initial SVL ($Z = -0.983$, $P = 0.3254$; Table 3) or initial body mass ($Z = -1.551$, $P = 0.1209$). Experimental and control males also did not differ significantly in their final SVL ($Z = -1.117$, $P = 0.2639$), final body mass ($Z = -1.430$, $P = 0.1528$), or in their rate of change in SVL ($Z = 0.000$, $P > 0.9999$) or in body mass ($Z = -0.645$, $P = 0.5186$; Table 3).

All of the control males (20/20) that were observed after release displayed their dewlaps, whereas none of the experimental males (0/18) did, a significant difference ($P < 0.0001$). However, the proportion of experimental males (11/18) and of control males (11/20) that gave bobbing displays did not differ significantly ($P = 0.7521$). There was also no significant difference ($P > 0.9999$) in the proportion of experimental males (5/18) and of control males (5/20) that gave nodding displays. On separate occasions during the study, we observed a copulating experimental male and a copulating control male.

The mean (\pm SE) time from capture in the field to return of treated males to their original sites of capture at the beginning of the experiment was 5.09 ± 0.14 h (range = 2.95–6.68 h). The mean (\pm SE) minimum distance between nearest neighboring study males as measured at the end of the study was 16.25 ± 1.31 m (range = 7.33–33.23 m). Experimental and control

males did not differ significantly in minimum distance to nearest neighbor ($Z = -0.164$, $P = 0.8701$).

DISCUSSION

The hypothesis that display of the dewlap during male-male interactions in *A. sagrei* affects the display behavior of opponents was not supported. Responses of untreated males paired with experimental males that could not extend their dewlaps did not differ significantly from untreated males paired with sham-treated control males that could extend their dewlaps. In both short distance (< 0.6 m) physical encounters and in longer distance (1 m and 3 m) visual encounters, untreated males paired with the two types of stimulus males did not differ significantly in latency to display, number of dewlap extensions, number of bobbing displays, number of bobbing displays with dewlap extensions, or in the proportion of males that erected crests.

Because the dewlap is often extended early in male agonistic interactions in anoles (DeCourcy and Jenssen, 1994; Jenssen et al., 2000), the latency period to the first display in untreated males might differ between stimulus males. However, untreated males exposed to the two types of stimulus males did not differ significantly in latency to display. Thus, in *A. sagrei*, the timing of when a male first displays in a male-male interaction does not appear to be affected by when its opponent displays its dewlap.

The frequency of dewlap use in anoles often varies with the distance between displaying males (Stamps and Barlow, 1973; DeCourcy and Jenssen, 1994). In the present study, untreated males gave fewer dewlap extensions in the 3 m encounters than they did in either the 1 m or in the close range physical encounters (< 0.6 m). However, the display behavior of untreated males did not differ significantly based on whether they were paired with experimental or control males.

The extension of the dewlap may be of importance in how male anoles assess each other

because a male with its dewlap extended may appear larger to its opponent (DeCourcy and Jenssen, 1994; Jenssen et al., 2000), and body size often influences the outcome of male-male encounters (Andrews, 1985; Tokarz, 1985). However, we found no evidence that displaying the dewlap has a size enhancement effect because untreated males did not vary their display behavior based on whether their opponents extended their dewlaps.

Headbob displays as well as dewlap extensions are a conspicuous feature of male-male interactions in anoles (Jenssen, 1977, 1978; DeCourcy and Jenssen, 1994). In short distance (< 0.6 m) encounters, where bobbing displays were common, untreated males did not modify their number of headbob displays based on whether their opponents extended their dewlaps. A similar lack of difference occurred with long-distance encounters, although untreated males in these encounters performed relatively few headbob displays and headbob displays with dewlap extensions, a situation that makes it more difficult to detect possible treatment effects.

The erection of a crest along the neck and back is a display modifier that occurs only in aggressive interactions between sexually mature male anoles (Greenberg, 1977; Jenssen, 1979; Scott, 1984). The proportion of untreated males that erected crests in the present study did not differ significantly based upon whether untreated males were paired with males that could or could not extend their dewlaps. Thus, the displaying of the male's dewlap in *A. sagrei* does not appear to affect the tendency for males to exhibit aggressive behavior in male-male interactions. This finding is consistent with the speculation of Macedonia and Stamps (1994) that, under natural conditions, the displaying of the dewlap in anoles may function to acknowledge the presence of a displaying conspecific rather than as a signal to engage in an aggressive interaction.

We had hypothesized that free-ranging males in the field that were prevented from extending their dewlaps would differ from control males in residence time, visibility, maximum distance moved, home-range size, and/or in body size. However, our findings did not support this hypothesis because experimental males did not differ significantly from control males in any of these variables. Dewlap extension could be a handicap that could diminish survival or body condition while enhancing overall fitness. However, we found no evidence for this idea because experimental males did not differ significantly in residence time or in body size from control males. The dewlap might also be important in

the ability of male anoles to maintain territories. Greenberg and Noble (1944) and DeCourcy and Jenssen (1994), for example, suggested that the display of the dewlap as male anoles patrol their territories may serve to intimidate other males from entering their territories and thus prevent short-distance aggressive interactions. Moreover, some muted songbirds in comparison to sham-treated control birds lost their territories, had their territories diminish in size, and/or suffered higher intrusion rates into their territories (e.g., Smith, 1979; McDonald, 1989; Westcott, 1992). Although we did not directly measure territory size, territorial behavior, or intrusion rates by neighboring males in our field study of *A. sagrei*, our findings suggest that experimental males were just as successful as control males in defending territories. For example, experimental and control males did not differ significantly in home-range size. This is noteworthy because home-range size in lizards often reflects individual fitness (Stamps, 1983). Nor did we find evidence that experimental males may have been shifting the location of their home ranges more than control males because there was no significant difference between treatment groups in the maximum distance that males were sighted from their original sites of release. We also found no evidence that experimental males were experiencing greater mortality than were control males because there was no significant difference between treatment groups in how long males were observed at the study site. Taken together these findings suggest that experimental males were no more likely than control males to be displaced from their territories by intruding neighboring males, a phenomenon that can occur in *A. sagrei* (see Tokarz, 1998; Paterson, 2002). Moreover, experimental males appeared to be just as visible as control males based on the fact that there was no significant difference in how frequently males of both treatment groups were observed during the entire census period or during their tenure at a particular site. Although based on a relatively small sample size, experimental and control males did not differ significantly in SVL or body mass at the end of the experiment, a finding that further suggests that experimental males were not at a competitive disadvantage in comparison to control males.

Although we found no evidence for a functional role of dewlap display in male-male interactions, our field studies occurred when males had established territories. Displaying the dewlap may be of more importance early in the reproductive season when males are most likely

establishing their territories. Dufty (1986), for example, found that muting captive brown-headed cowbirds (a nonterritorial species) lowered dominance status when groups were first being established but not after establishment was complete. In addition, our focus on interactions between conspecific males did not address potential roles of display of the dewlap in male-female or interspecific interactions.

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