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Importance of Dewlap Display in Male Mating Success in Free-Ranging Brown Anoles (*Anolis sagrei*)

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Abstract.—Extension and retraction of the throat fan or dewlap is one of the most conspicuous aspects of display behavior of male *Anolis* lizards. Although dewlap display plays a role in species recognition, signal detection, and even predator defense, the importance of the male dewlap in male mating success in nature has not been established. The present study tested whether the display of the dewlap by males of *Anolis sagrei* affected the mating success of free-ranging males. We compared the number of males that copulated and their copulation rates between two groups: experimental males that were surgically prevented from extending their dewlaps and control males that were sham treated. Experimental and control groups did not differ significantly in the proportion of males that copulated or in copulation rate. These results do not support the hypothesis that the male dewlap affects male mating success in *A. sagrei*. If the male dewlap does have an effect on male mating success in this species, then the effect was too subtle to be detected by our study.

Male anoles are noted for the extension and retraction of a throat fan or dewlap (Carpenter and Ferguson, 1977; Jenssen, 1977). The dewlap is believed to have many functions in *Anolis* lizards (Losos and Chu, 1998), and there is good experimental evidence that the male dewlap plays a role in species recognition (Losos, 1985), detecting a displaying animal (Fleishman, 1992, 2000), and even in predator defense (Leal and Rodgríguez-Robles, 1997). However, evidence that the male dewlap influences female mate choice of conspecific males is equivocal (for a review, see Tokarz, 1995).

In a laboratory study, Tokarz (2002) found no evidence that the male dewlap affected male copulation success or female sexual receptivity of Brown Anoles (*Anolis sagrei*) when males and females were relatively close to each other in laboratory cages. Males that were surgically prevented from extending and retracting their dewlaps were just as successful as control males in obtaining copulations, and females that were courted by experimental males were judged as sexually receptive as those courted by control males (Tokarz, 2002). These laboratory findings suggest that the displaying of the male dewlap does not affect the ability of males to obtain mating partners. However, it is important to conduct a field study to test the external validity of these laboratory findings (see Nelson, 1998). For example, a positive effect of dewlap extension on male mating success might only occur under natural conditions. Thus, the purpose of this study was to test the hypothesis that dewlap extension affects mating success in free-ranging male Brown Anoles. We reasoned that if the hypothesis were correct, then males that were prevented from extending their dewlaps would differ significantly from control males in the proportion of males that obtained copulations or in copulation rate or both. To our knowledge, this is the first study to directly test the hypothesis that dewlap extension in a male anole affects male mating success in nature. A failure to find evidence for such an effect on mating success in at least one species of anole is of interest because the male dewlap in *Anolis* lizards is believed to be a sexually selected trait (see Fitch and Hillis, 1984).

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Materials and Methods

The subjects were adult male Brown Anoles (*A. sagrei*), a species that evolved in Cuba and subsequently spread through the western Caribbean and Florida (Williams, 1969; Lee, 1985). Based on the ecomorph concept of Williams (1983), *A. sagrei* is a "trunk-ground" species, which usually inhabits low vegetation ranging from the under storey of forest to barren scrub (Schoener and Schoener, 1980). It feeds primarily on large insects, and individuals are sit-and-wait predators that passively search for food (Schoener and Schoener, 1980). *Anolis sagrei* is a highly territorial and polygynous species (Schoener and Schoener, 1980, 1982; Stamps, 1983. Tokarz, 1988). It is sexually dimorphic: Mature males are larger than mature females (Stamps, 1983). Number of females in the home range of a male is significantly related to home-range area and to male body size (Schoener and Schoener, 1982). Schoener and Schoener (1980) found that a relatively large male may have up to six females within its home range. *Anolis sagrei* breeds seasonally, and in southern Florida males and females are reproductively active from approximately March through August (Lee et al., 1989; Tokarz et al., 1998).

Our study site was a subtropical hardwood hammock at the Frank Smathers Jr. Biology Field Station located within Four Fillies Farm. This Farm, which is owned by the University of Miami, is located 9.6 km south of Coral Gables campus in Miami-Dade County, Florida. The hardwood hammock has a population of *A. sagrei*, and the vegetation of the hammock is similar to that described for regions of the Caribbean where this species occurs (e.g., Snyder et al., 1990). The population density of *A. sagrei* in the hammock appears to be comparable to the high densities that are common in this species (Lister, 1976; Schoener and Schoener, 1980).

Our study ran from 26 May to 22 June 2004, which was well within the breeding season. We selected males to be used in the study by walking through the hammock. After selecting males, we captured them via noosing and marked their site of capture with surveyor's flags. Because the protocol was for each of the three observers (RRT, AVP, and SMcM) to watch a study male for up to a maximum of five days, we captured, treated, and released new study males on approximately a weekly basis. During the course of the study, we captured and released a total of 12 experimental and eight control males. We transported captured males individually in cloth bags to our laboratory at the University of Miami, measured their snout–vent length (SVL) to the nearest millimeter and determined their body mass to the nearest milligram. Prior to surgery, we lined up the bags containing captured males and flipped a coin to determine whether the male in the first bag would be assigned to the experimental or control group. Thereafter, we alternated the group assignment for the remaining males captured that day.

Experimental males were surgically prevented from extending their dewlaps and control males were sham operated in a way that did not affect dewlap extension. Males were anesthetized prior to surgery with an intraperitoneal injection of Pentothal® (thiopental sodium, Abbott Laboratories, North Chicago, IL; 15 mg/kg) and hypothermia (crushed ice). Using a Stereo Zoom microscope (Bausch and Lomb Instruments and Systems Division, Rochester, NY) to view the throat area of anesthetized males, we made an incision (about 5 mm long) parallel to the midline of the throat to expose the second ceratobranchials. The second ceratobranchials are paired cartilaginous rods that play a key role in extending and retracting the male dewlap in *Anolis* lizards (Bels, 1990; Font and Rome, 1990). For experimental males, we cut transversely across the second ceratobranchials separating them from the hyoid body and then removed them. For control males, we performed a sham surgery by only making an incision parallel to the midline of the throat. Incisions in both experimental and control males were closed with a suture. An antiseptic ointment (Povidine Iodine, Eckert Drug Co., Clearwater, FL) was applied to the incision area. These surgical procedures have been successfully used to prevent dewlap extension in *Anolis carolinensis* (Crews, 1975) and in *A. sagrei* (Tokarz, 2002; Tokarz et al., 2003). After surgery, we marked each male on its sides (using a white Painters® nontoxic opaque marker, Hunt Corporation, Statesville, NC) with a number that corresponded to its capture location at the study site. This method of marking animals has been successfully used in previous field studies of *A. sagrei* (e.g., Tokarz, 1998; Paterson and McMann, 2004).

After males had recovered from surgery (usually from 3–4 h), we placed them in separate cloth bags and returned them to their site of capture. We returned all treated males to their territories on the day of capture. Returning males to their territories as quickly as possible reduced the risk of neighboring, nonstudy males taking over a vacated territory (see Paterson, 2002). We began looking for released males the following morning. We observed each study male for a 3-h period between 0700 and 1100 h. Copulation frequency in *A. sagrei* has been found to be relatively high in the early morning (Tokarz, 1988). At the beginning of an observation period, each observer would go to the location of their assigned male and look for the marked male. If the assigned male was sighted, the observer recorded the time when it was in view during the 3-h observation period. This process was repeated for up to a maximum of five different days. If a newly assigned study male could not be found on its territory during the entire 3-h observation period and at the start of following day's observation period, the observer selected a new study male to observe. We recorded all copulations by study males as long as they occurred during the 3-h observation periods in the morning (for a description of copulation in *A. sagrei*, see Scott, 1984; Tokarz, 1988). We did not attempt to determine how many different female-mating partners each male obtained because it would have been too difficult to capture and mark all of the females within the territory of each male. While watching study males for copulations, we also recorded their number of dewlap extensions. To reduce the impact of any observer differences on the results, each of the three observers was assigned both experimental and control males to observe during the study.

We observed and acquired data from eight experimental males and six control males. To accurately calculate copulation rates, we used males that were observed on their territories on three or more days. When males lost their old skin, or appeared to be in the process of shedding their skin, they were recaptured, remarked (in the field), and released. Two control males and two experimental males were remarked during the study.

We analyzed the data statistically using nonparametric tests. We used a 2×2 test of independence with Yates correction to test whether the proportion of males that copulated was independent of treatment group (see Sokal and Rohlf, 1981). We used the Mann-Whitney U-test to determine significant differences between the two treatment groups. For simplicity, we report Z-values rather than the U-statistic for this test. An alpha level of 0.05 in a two-tailed test was considered significant. We performed analyses using StatView 4.0 software (SAS Institute Inc., Cary, NC).

Results

We observed a total of 20 copulations while observing the eight experimental males and six control males. Nine of these copulations were by experimental males and 11 copulations by control males. Five of the eight experimental males (62.5%) and four of the six control males (66.67%) copulated during the study. Treatment group did not significantly affect the proportion of males that copulated ($G_{adj} = 0.16148$, df = 1, $P > 0.50$). The range in number of copulations per male was 0–3 copulations for experimental males and 0–4 for control males. Only one male, an experimental male, was observed to copulate twice during a 3-h morning observation period. All other males that were observed to copulate copulated only once during the 3-h observation period.

Males in the experimental and control groups did not differ significantly in copulation rate ($Z = -0.740$, $P = 0.4592$) based on a comparison of the average copulation rate in those study males that were seen and continuously watched or searched for during the daily 3-h observation periods for at least three days. The mean (± SE) copulation rate (copulations/hours male viewed) for the five experimental males and for the five control males that were observed for at least three days was 0.11 ± 0.048 and 0.18 ± 0.066, respectively. The amount of time that these experimental males and control males were visible to an observer did not differ significantly ($Z = -0.522$, $P = 0.6015$). The mean (± SE) number of hours that experimental males and control males were visible was 12.1 ± 0.45 and 11.6 ± 1.02, respectively. When considered on a daily basis rather than on an hourly basis there was still no significant difference in copulation rate between the treatment and control groups ($Z = -0.967$, $P = 0.3337$). The mean (± SE) copulation rate (copulations per day) for the five experimental males and five control males that were observed for at least three days was 0.28 ± 0.120 and 0.44 ± 0.147, respectively.

There was no significant difference between treatment groups in the number of days (out of a maximum of five days) males were observed ($Z = -0.243$, $P = 0.8080$). The mean (± SE) number of days the eight experimental and six control males were observed was 4.125 ± 0.581 and 4.167 ± 0.654, respectively. In addition, experimental and control males did not differ significantly in SVL ($Z = -0.135$, $P = 0.8929$) or in body mass ($Z = -0.516$, $P = 0.6056$). The mean (± SE) SVL for the eight experimental males and six control males was 59.1 ± 0.72 mm and 58.8 ± 0.95 mm, respectively. The mean (± SE) body mass for experimental males and control males was 5.97 ± 0.150 g and 5.96 ± 0.202 g, respectively.

As expected none of the experimental males extended their dewlaps during the study; thus, it was impossible to count dewlap extension in these males. In addition, we did not observe any dewlap color or change in throat shape in experimental males. In contrast, all of the control males were observed to extend their dewlaps. The mean (± SE) rate of dewlap extensions (extensions/hours male viewed) for the five control males that were observed for at least three days was 79.138 ± 10.111. This frequency of dewlap extensions was similar to that observed in untreated males under seminatural conditions (Paterson, 2002).

Discussion

The results of this study do not support the hypothesis that the display of the male dewlap affects male mating success in free-ranging *A. sagrei* in nature. Males that were experimentally prevented from extending and retracting their dewlaps did not differ significantly from sham-treated control males in the proportion of males that achieved copulations or in copulation rate. Thus, this study documents that females of *A. sagrei* in nature will copulate with experimentally manipulated males that do not extend their dewlaps. The finding that the proportions of experimental and control males that obtained copulations did not differ significantly is in agreement with results obtained from a previous laboratory study (Tokarz, 2002).

Tokarz (2002) suggested three possible ways the displaying of the male dewlap in *A. sagrei* might still affect male mating success in nature even though dewlap extension was unnecessary for males to obtain copulations under laboratory conditions. First, the male dewlap in nature might increase the likelihood of recruiting additional females for mating, some of which may be relatively distant from the displaying male. Sigmund (1983), in a laboratory study of *A. carolinensis*, found evidence that male dewlap color and its contrast with the background was important in attracting females when displaying males were at least 2 m from females (but see Greenberg and Noble, 1944; Crews, 1975; MacDonald and Echternacht, 1991), a distance that Sigmund believes is similar to the distance that females would typically view males in adjacent territories. Second, the display of the male dewlap may increase male mating success by causing females to have shorter time intervals between their periods of sexual receptivity. This idea is based largely on the finding of Crews (1975) that females of *Anolis carolinensis* under laboratory conditions reached sexual maturity sooner when exposed to males that could display their dewlaps than when exposed to males that were unable to display their dewlaps. Finally, the extension and retraction of the male dewlap may not only attract the attention of females but also serve to make the displaying male more conspicuous to other males (see Jenssen et al., 2000; Orrell and Jenssen, 2003). This could act to increase the mating success of a displaying male if the displaying of the dewlap prevents other males in adjacent territories from interfering with the courtship of the displaying male (Orrell and Jenssen, 2003).

In the present field study, treated males had the opportunity to attract females at a distance, to court females for an extended period (up to a week in some cases), and to interact with neighboring males. Nonetheless, experimental males did not differ significantly from control males in the proportion of males that copulated and in copulation rate. Although these results, based upon relatively small sample sizes, do not prove that the display of the male dewlap plays no role in male mating success in *A. sagrei*, they do suggest that any effect of the dewlap, if present, may be relatively weak and thus difficult to demonstrate. It is also possible that, if the study had been conducted for a longer period of time, an effect of dewlap extension on female sexual receptivity, if present, might have affected male copulation rate. Finally, we cannot discount the possibility that the displaying of the male dewlap might affect the number of different mating partners a male obtains because we made no attempt to determine how many different females mated with each study male.

In a field study that addressed the role of the male dewlap in intrasexual interactions in *A. sagrei*, Tokarz et al. (2003) found that experimental and control males did not differ significantly in a number of variables related to the ability of males to maintain residency on a territory. Similarly in this study, there was no significant difference between experimental and control groups in the number of days that males were observed on their territories or in the number of hours that males were visible to an observer. Thus, both laboratory and field experiments have failed to detect any negative fitness consequences of preventing males of *A. sagrei* from extending and retracting their dewlaps (Tokarz, 2002; Tokarz et al., 2003).

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Literature Cited

Bels, V. L. 1990. The mechanism of dewlap extension in *Anolis carolinensis* (Reptilia: Iguanidae) with histological analysis of the hyoid apparatus. Journal of Morphology 206:225–244.

Carpenter, C. C., and G. W. Ferguson. 1977. Variation and evolution of stereotyped behavior in reptiles. *In* C. Gans and D. W. Tinkle (eds.), Biology of the Reptilia: Ecology and Behavior. Vol. 7, pp. 335–554. Academic Press, London.

Crews, D. 1975. Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. Animal Behaviour 23:349–356.

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. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. American Naturalist 139:S36–S61.

———. 2000. Signal function, signal efficiency and the evolution of anoline lizard dewlap color. *In* Y. Espmark, T. Amundsen, and G. Rosenqvist (eds.), Animal Signals: Signalling and Signal Design in Animal Communication, pp. 209–236. Tapir Academic Press, Trondheim, Norway.

Font, E., and L. C. Rome. 1990. Functional morphology of dewlap extension in the lizard *Anolis equestris* (Iguanidae). Journal of Morphology 206:245–258.

Greenberg, B., and G. K. Noble. 1944. Social behavior of the American Chameleon (*Anolis carolinensis* Voigt). Physiological Zoology 17:392–439.

Jenssen, T. A. 1977. Evolution of anoline lizard display behavior. American Zoologist 17:203–215.

Jenssen, T. A., K. S. Orrell, and M. B. Lovern. 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. Copeia 2000:140–149.

Leal, M., and J. A. Rodríguez-Robles. 1997. Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. Animal Behaviour. 54:1147–1154.

Lee, J. C. 1985. *Anolis sagrei* in Florida: phenetics of a colonizing species. I. meristic characters. Copeia 1985:182–194.

Lee, J. C., D. Clayton, S. Eisenstein, and I. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. Copeia 1989:930–937.

Lister, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. Evolution 30:659–676.

Losos, J. B. 1985. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. Copeia 1985:905–910.

Losos, J. B., and L.-R. Chu. 1998. Examination of factors potentially affecting dewlap size in Caribbean anoles. Copeia 1998:430–438.

MacDonald, D., and A. C. Echternacht. 1991. Red-throated and gray-throated *Anolis carolinensis*. Do females know the difference? *Anolis* Newsletter 4:92–100.

Nelson, D. A. 1998. External validity and experimental design: the sensitive phase for song learning. Animal Behaviour 56:487–491.

Orrell, K. S., and T. A. Jenssen. 2003. Heterosexual signaling by the lizard *Anolis carolinensis*, with intersexual comparisons across species. Behaviour 140:603–634.

Paterson, A. V. 2002. Effects of an individual's removal on space use and behavior in territorial neighborhoods of brown anoles (*Anolis sagrei*). Herpetologica 58:382–393.

Paterson, A. V., and S. McMann. 2004. Differential headbob displays toward neighbors and nonneighbors in the territorial lizard *Anolis sagrei*. Journal of Herpetology 38:288–291.

Schoener, T. W., and A. Schoener. 1980. Density, sex ratio, and population structure in some Bahamian *Anolis* lizards. Journal of Animal Ecology 49:19–53.

———. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. Ecology 63:809–823.

Scott, M. P. 1984. Agonistic and courtship displays of male *Anolis sagrei*. Breviora 479:1–22.

Sigmund, W. R. 1983. Female preference for *Anolis carolinensis* males as a function of dewlap color and background coloration. Journal of Herpetology 17:137–143.

Snyder, J. R., A. Herndon, and W. B. Robertson Jr. 1990. South Florida rockland. *In* R. L. Myers and J. J. Ewel (eds.), Ecosystems of Florida, pp. 230–277. Univ. of Central Florida Press, Orlando.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2nd ed. W. H. Freeman and Co., New York.

Stamps, J. A. 1983. Sexual selection, sexual dimorphism, and territoriality. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology: Studies of a Model Organism, pp. 169–204. Harvard Univ. Press, Cambridge, MA.

Tokarz, R. R. 1988. Copulatory behaviour of the lizard *Anolis sagrei*: alternation of hemipenis use. Animal Behaviour 36:1518–1524.

———. 1995. Mate choice in lizards: a review. Herpetological Monographs 9:17–40.

———. 1998. Mating pattern in the lizard *Anolis sagrei*: implications for mate choice and sperm competition. Herpetologica 54:388–394.

———. 2002. An experimental test of the importance of the dewlap in male mating success in the lizard *Anolis sagrei*. Herpetologica 58:87–94.

Tokarz, R. R., S. McMann, L. Seitz, and H. John-Alder. 1998. Plasma corticosterone and testosterone levels during the annual reproductive cycle of male Brown Anoles (*Anolis sagrei*). Physiological Zoology 71:139–146.

Tokarz, R. R., A. V. Paterson, and S. McMann. 2003. Laboratory and field test of the functional significance of the male's dewlap in the lizard *Anolis sagrei*. Copeia 2003:502–511.

Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quarterly Review of Biology 44:345–389.

———. 1983. Ecomorphs, faunas, island size, and diverse endpoints in island radiations of *Anolis*. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology: Studies of a Model Organism, pp. 326–370. Harvard Univ. Press, Cambridge, MA.

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