LITERATURE CITED

Arnold, B. R., A. C. Brown, M. S. Calvi, M. N. Conte and S. E. LaPlante. 2000. An experimental study of *Pseudomyrmex spinicola* abundances on branches of *Acacia collinsii* with and without extra-floral nectaries. Dartmouth Studies in Tropical Ecology, p. 7-9.

Balser, T. C., J. L. Dudycha, A. L. Guerrerio, C. N. O'Neill and S. L. Soucy. 1992. The aggressiveness of three species of acacia ant. Dartmouth Studies in Tropical Ecology, p. 1-3.

Coleman, M. L., T. D. Dempsey, M. E Harrison, E. L. Kinney and F. E. Krivak-Tetley. 2002. Relationship between herbivory damage and resident ant species in *Acacia Collinsii*. Dartmouth Studies in Tropical Ecology, p. 1-3.

Wickre, J. B., C. R. Chamberlin, A. J. Kehas, K. E. Simon, and K. A. Theoharides. 2003. Do facultative and obligate mutualist ants provide equal protection for their acacia host? Dartmouth Studies in Tropical Ecology, p. 9-12.

EFFECT OF COLOR AND SIZE ON AGGRESSIVE BEHAVIOR AND FEMALE ACCESS IN THE LIZARD *CTENOSAURA SIMILIS*

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Abstract: Male *Ctenosaura similis* are highly territorial lizards that vary greatly in their physical attributes. We studied the effects of mature male size and color on territorial head-bobbing displays and access to females in Palo Verde National Park, Costa Rica. We hypothesized that large orange males would show more frequent head-bobbing behavior, and have more females in their territories, than smaller or blue-colored individuals. Orange males did have more females in their territories, but we were unable to separate the effects of male color and size on number of females. Neither size nor color influenced head-bobbing behavior.

Key Words: head-bobbing, male coloration, sexual selection, territoriality

INTRODUCTION

Ctenosaura similis, a large Central American iguanid lizard, exhibits both color-change and head-bobbing behavior. Coloration and body size vary among mature individuals. Within individuals color may vary both seasonally and daily, and also with developmental stage (Fitch and Hackforth-Jones 1983). During the breeding season, some adults, which normally range from tan to gray-blue in color, may develop spots of dull red or orange coloration, although little is known about the function of this coloration (Fitch and Hackforth-Jones 1983).

Ctenosaura similis uses head-bobbing displays to communicate with conspecifics (Fitch and Hackforth-Jones 1983). Vanderbuilt et al. (1990) described two distinct bobbing behaviors of males, one for territorial displays and another for courtship of

females. Males typically defend territories which provide them reproductive access to the females within their territory, although females sometimes move between the territories of different males (Blanchard 1992). During the breeding season, large adult males defend their territories by driving off medium-sized males, while they may tolerate the presence of small, juvenile males that resemble females in size and coloration (Savage 2002).

Here, we examine the effects of size and coloration on the head-bobbing behavior and reproductive access of adult males. We hypothesized that large males with more orange coloration would have greater access to females, and that size and coloration are associated with the aggressive bobbing behavior that allows males to maintain their territories. Therefore, we predicted that large orange males would perform territorial head bobs at a higher rate and have a greater number of females in their territories, compared to smaller or blue-colored males.

METHODS

On 13 and 14 January 2005, we observed territory-holding male ctenosaurs at the OTS Field Station and at the "hacienda", 0.5 km to the west along the main road in Palo Verde National Park, Costa Rica. We selected seven focal males differing in size and color at each location and attempted to observe each for 45 min. Adult males were defined as those of relatively large size and distinctive head crest morphology, which were exhibiting aggressive or dominance behavior. All observations were completed between 0800 and 1630. We excluded data for males that retreated from sight after < 20 minutes of observation and those that did not demonstrate territorial behavior.

At the start of each observation period, we recorded time, air temperature, and predominant color (blue or orange) of the focal individual. Over each period, we noted every instance of territorial head-bobbing by the focal male. We distinguished undirected bobs from those delivered in the presence of other males, and stationary bobs from those following any change of position. For each focal male we also recorded the number of females within 20 m (a typical radius for the normal ctenosaur activities--Fitch and Hackforth-Jones 1983). At the end of each observational period, we estimated focal male body size (snout-vent-length or SVL) by sighting points on the ground aligned with snout and vent, approaching the focal male until it retreated, and measuring the distance between the two points.

For each focal individual, we calculated bobs/min, bobs/min in the presence of another male, undirected bobs/min, post-movement bobs/min, and stationary bobs/min. We used regression to analyze relationships between bobbing rates and physical and environmental factors, and between male body size and number of females in a territory. We used residuals from these analyses in an attempt to separate the effects of size and color (see Results). Our data met the normality assumptions of the tests performed, and data were analyzed using JMP 5.0.1.

RESULTS

We observed 13 males in all, seven from the OTS field station and six from the hacienda. Focal male size ranged from 37 to 53 cm SVL, and number of females in the territories of these males ranged from 0 to 11. Because there were no significant effects of site on color, snout-vent-length, or number of females (Table 1), we combined data from the two sites for all further tests.

Orange males had a significantly greater number of females within their territories than did blue males (F = 4.90, df = 1, 11, P = 0.05, Fig. 1). Snout-vent length (SVL) was also positively related to the number of females (r^2 = 0.26, df = 1, 11, P = 0.08, Fig. 2), and greater male SVL was related to orange coloration in males (F = 3.61, df = 1, 11, P = 0.08, Fig. 3).

To determine the effect of male color alone on number of females in a territory, we first removed the effect of SVL on number of females by taking the residuals of a linear regression between SVL and number of females (r^2 = 0.26, df = 12, P = 0.08). Using these residuals, we then performed a one-way ANOVA between male color and number of females which showed that male color alone had no effect on number of females in a territory (F = 1.60, df = 1, 11, P = 0.23). Similarly, to determine the effect of male SVL alone on number of females, we removed the effect of color by subtracting the mean number females for each male color group (orange vs. blue) from each observation, and analyzed the residuals with a one-way ANOVA. The relationship between SVL alone and number of females was not significant (F = 0.90, df = 1, 11, P = 0.36).

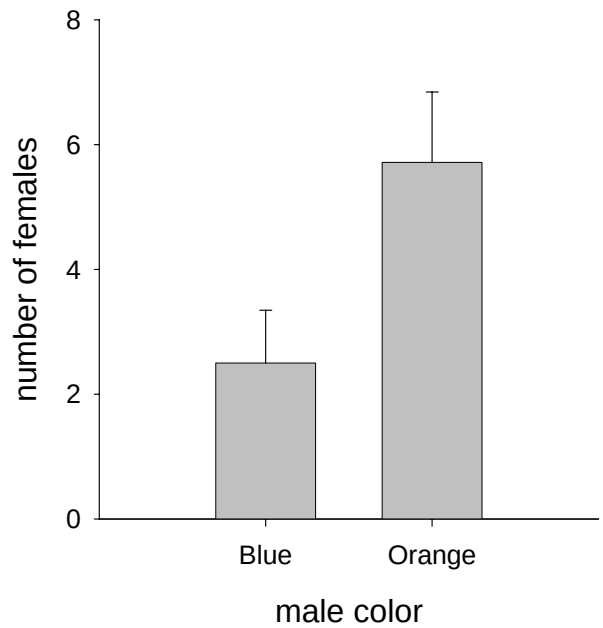

Figure 1. Mean number of females present in territories of ctenosaur males of predominately orange or blue coloration. Error bars show mean ± 1 SE (n = 7 blue males, 6 orange males).

Finally, we tested for correlations between head-bobs per minute and each of the following variables: number of females, color, SVL, and ambient temperature. None of these relationships was significant (Table 2).

Table 1. Relationship between number of females, snout-vent length, and color of male *Ctenosaura similis* at the OTS station and hacienda sites Palo Verde

Variable	Test	F or X^2	df	P
Number of females	One-way ANOVA	2.96	1, 11	0.11
SVL	One-way ANOVA	0.82	1, 11	0.39
Color	Contingency analysis	0.07	1, 11	0.80

Figure 2. Relationship between male ctenosaur snout-vent length and the number females in their territories (n = 13).

DISCUSSION

Our results indicate that both color and size are important determinants of the number of females in a male's territory, but because these two characteristics were related we were unable to determine which of these factors was more important in predicting the number of females per territory. Instead, our results suggest that while neither color nor size alone significantly influences number of females, the combination of these characteristics allows large orange males to have greater reproductive access than small blue individuals. Clarification of the independent relationships between size and color and number of females in a male's territory will require larger sample sizes and a sampling design focused on separating the effects of color and size.

Neither male size nor color was related to head-bobbing in male ctenosaurs. We observed that most head-bobs were performed without another male present and were done directly following movement, but we did not statistically analyze these patterns. We suggest that head-bobbing may be more of an advertisement of territorial boundaries to conspecifics of either sex than a direct interaction between males.

If large males do have territories with more females than small males, this would be consistent with previous findings (Tran and Harris 2004). Larger males can secure higher quality territories, which may attract more females than those of smaller individuals (Vanderbuilt 1990). Orange coloration of mature male ctenosaurs may be an advertisement of both individual and territory quality, since this conspicuous coloration appears only dur-

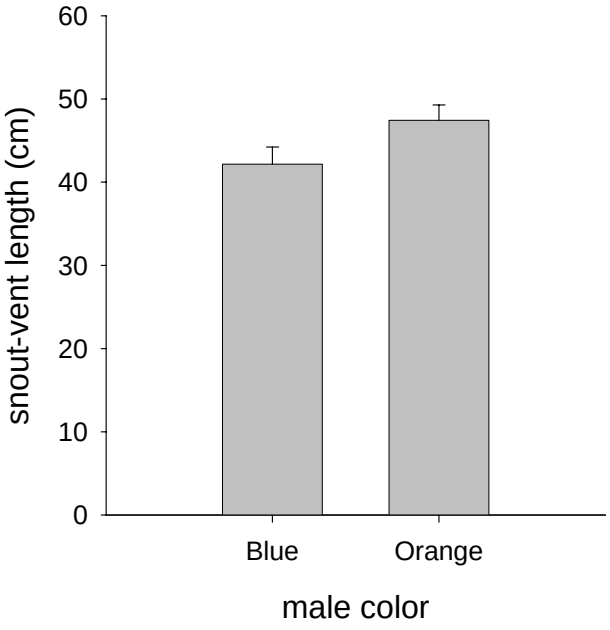

Figure 3. Mean snout-vent length of ctenosaur males with predominately orange vs blue coloration. Error bars show mean ± 1 SE (n = 7 blue males, 6 orange males).

Table 2. Relationships between number of male head-bobs/min and attributes of the male *Ctenosaura similis* and their territories at Palo Verde

Variable	Test	F	r^2	df	P
Number of females	Linear regression	-	0.00	12	0.88
SVL	Linear regression	-	0.04	12	0.50
Color	One-way ANOVA	3.21	-	1, 11	0.10
Temperature	Quadratic regression	-	0.12	12	0.53

ing the breeding season (Fitch and Hackforth-Jones 1983) and may be costly if orange lizards are more visible to predators, or it is energetically expensive to produce orange color.

LITERATURE CITED

Fitch, H. S. and J. Hackforth-Jones. 1983. *Ctenosaurus similis* in Costa Rican Natural History. Ed. D. H. Janzen. University of Chicago Press: Chicago, IL, p. 394-396.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica. University of Chicago Press: Chicago, IL.

Tran, J. Khai and Jill L. Harris. 2004. Factors influencing the outcome of behavioral encounters in *Ctenosaura similis*. Dartmouth Studies in Tropical Ecology, p. 24-26.

Vanderbuilt, C. , J. R. Nuttle, G. Mora, J. Heinen, K. Stoner and D. Wijesinghe. 1990. Territorial and courtship behaviors in Ctenosaura. OTS Tropical Ecology, 90: 136-139.