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Function of Body Coloration in Green Anoles (*Anolis carolinensis*) at the Beginning of the Breeding Season: Advertisement Signaling and Thermoregulation

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Abstract: We examined two hypotheses regarding the function of body coloration in green anoles *Anolis carolinensis*. First, their bright green coloration serves as a social signal advertising territorial possession or dominance. From this hypothesis, two predictions derive: 1) most anoles with bright green coloration are adult males; and 2) adult males with bright green coloration tend to perch at higher positions to send the signal to broad areas. Another hypothesis, which is not exclusive to the former one, is that the dark coloration functions to raise their body temperature. From this hypothesis, three predictions derive: the anoles with dark (brown) coloration are 1) observed more frequently in the morning than in the daytime, 2) more likely to engage in basking behavior than in other behaviors, and 3) observed more frequently when air temperature is low. We tested these predictions in the field at the beginning of their breeding season. The results supported the advertisement signal hypothesis, but not the thermoregulation hypothesis. However, since our negative results against the latter may actually be attributable to relatively low air temperature throughout our observation period, additional observations are desired to verify rejection of the thermoregulation hypothesis as resulting from the present study.

Key words: Advertisement signals; *Anolis carolinensis*; Behavior; Color change; Thermoregulation

INTRODUCTION

The green anole, *Anolis carolinensis*, is known to change its body coloration from bright green to dark brown, but why does such a change occur? There are several putative functions in the lizard's changing body coloration, such as predation avoidance by making itself more cryptic, advertisement by demonstrating its presence to conspecific individuals, and advantage in thermoregulation. However, recent relevant studies yielded no evidence that in *A. carolinensis* body color changes so as to match the substrate coloration for crypsis (Jenssen et al., 1995). Thus, we have tested two other hypotheses related to functions of the phenomenon, advertisement signal and thermoregulation, on the basis of predictions deriving from them as below.

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Hypotheses Tested

Advertisement signal hypothesis

Many animals use visual and auditory signals to advertise territorial possession. Conspicuousness is significant for such signals. For example, experimental changes in conspicuousness of color signals in birds lead to change in territory size: males with increased conspicuousness obtain larger territories than those with reduced conspicuousness and controls (Marchetti, 1993). Dominant males of the anole defend territories during the breeding season (Greenberge and Noble, 1944). For these individuals, the brilliant green coloration may advertise dominance, being advantageous in defending and maintaining the territory (advertisement signal hypothesis). If this is the case, two predictions would be possible. First, most anoles with bright green coloration should be adult males. Secondly, bright green males should perch portions of trees and other objects in their territories where they can broadcast the signal effectively: in a higher position that is visible from a broader area. Actually, in laboratory experiments in which two males were encountered to determine the dominant-subdominant relationship, a dominant male wore brighter green body coloration and attained a higher place (Korzan et al., 2002; Plavicki et al., 2004).

Thermoregulation hypothesis

Reflectance strongly affects the warming rate of animals exposed to insolation. For this reason, body coloration might affect heating rates in lizards during basking (Cooper and Greenberg, 1992). Green anoles may therefore change their body coloration to regulate body temperature. If this is the case, they should choose darker (brownish) coloration when they seek to raise their body temperature. Three predictions derive from this inference. First, more anoles would be brownish in the morning (i.e. before being active) than in the daytime. Secondly, the lower the air temperature, the more anoles would be brownish. Finally, anoles would be brownish at higher frequency in basking than in other behaviors.

Materials and Methods

Green anoles have been introduced to Chichi-jima island (27°N, 142°E) around 1965 (Hasegawa et al., 1988). The breeding season of anoles on this island ranges from March–September (Suzuki, 1996). Observations were carried out between 14 and 19 March 2000 when the breeding season had just started (see above). We set a route to walk and observe anoles in the morning (0750–0830 h) and daytime (early in the afternoon, 1310–1430 h) everyday. We recorded the body coloration, approximate body size, behavior, and approximate height from the ground and substrate coloration of perching position for each individual encountered. The height was estimated to nearest 10 cm. Substrate coloration was identified to one of the following six categories: dark brown, brown, gray, beige, green, and dark green. Air temperatures were measured at 1 m height in shade before each observation.

Body coloration was visually assigned to one of the four classes of brightness: bright green, green, brown, and dark brown. Body size was also visually categorized into three classes: large (snout-vent length [SVL] >180 mm), medium (120–180 mm), and small (<120 mm). The large anoles were adult males because they always had well-developed jaws and dewlaps. Behaviors in which anoles engaged were classified into four categories: basking (stayining motionless in the sun), resting (staying motionless in the shade), patrolling (moving around), and displaying.

Results

We made a total of 169 individual observations. Obviously the anoles' body coloration did not match the substrate coloration: in only 17 of these 169 observations their body coloration matched the substrate coloration.

Large, medium, and small anoles took bright green coloration in 29 of 80, one of 54, and six of 35 observations, respectively. The ratio of the number of anoles that adopted bright green coloration was significantly larger in

TABLE 1. The number of anoles that adopted each body coloration in the morning and daytime.

	Body coloration			
Time	Bright green	Green	Brown	Dark brown
Morning	22	26	35	13
Daytime	14	22	14	23

TABLE 2. The number of anoles that adopted each coloration when engaging in basking or the other behaviors (resting, patrolling, and displaying). No significant association was detected between the coloration and the behavior.

	Body color			
Behavior	Bright green	Green	Brown	Dark brown
Basking	16	29	26	22
Not Basking	20	19	23	14

large anoles than in medium (chi-squared test, χ^2=21.95, df=1, P<0.001) and small (chi-squared test, χ^2=9.40, df=1, P<0.005) anoles.

In approximately half cases (85/169), anoles took dark coloration (brown and dark brown). The ratio of the number of individuals that adopted brown coloration was higher in the morning than in the daytime, but that for dark brown showed the opposite pattern (Table 1). Collectively, anoles showed no tendency to take dark coloration more frequently in the morning (i.e. before activity) than in the daytime. In addition, no significant association was recognized between the coloration and behavior (Table 2: chi square test, χ^2=4.66, df=3, P>0.05). Also, there was no tendency of taking darker coloration when air temperature was low (Fig. 1).

In anoles of the large body class, the frequency of individuals adopting each coloration did not differ between the morning and daytime observations (chi-squared test, χ^2= 0.59, df=3, P>0.05). In addition, this frequency did not change between individuals engaging in basking and the other behaviors (chi-squared test, χ^2=4.66, df=3, P>0.05). In contrast, anoles of the large body class showed a significant tendency of taking green coloration at higher perching positions (Fig. 2, ANOVA, df=1, 78, F=6.73, P=0.011).

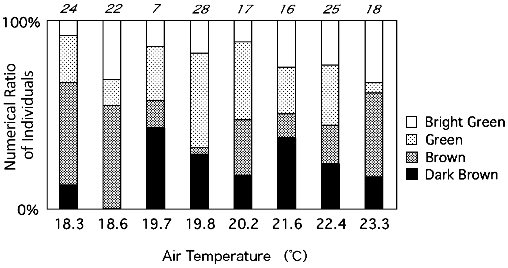

FIG. 1. Air temperature and the numerical ratio of anoles adopting each body coloration. Numeral above each column equals the sample size for each air temperature condition.

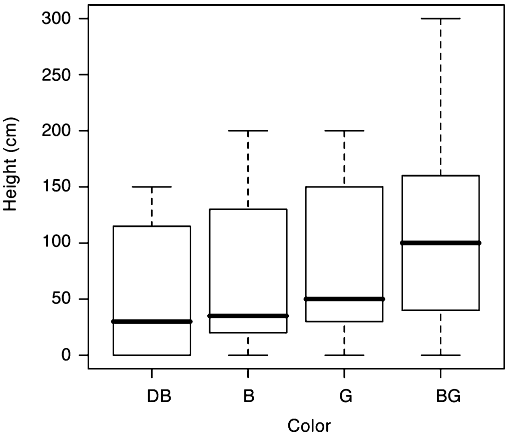

FIG. 2. The perching height of adult male anoles observed. These anoles were divided into four groups based on their body coloration: bright green (BG), green (G), brown (B), and dark brown (DB). Upper and lower margins of, and thick horizontal line in each box indicate upper and lower quartiles, and median, respectively. The upper and lower lines outside the boxes indicate UQ+1.5·IQD and LQ-1.5·IQD, respectively, where UQ, LQ, and IQD represent upper quartile, lower quartile, and inter-quartile distance, respectively.

DISCUSSION

The results supported the two predictions from advertisement signal hypothesis. Large anoles adopted bright green coloration more frequently than medium-sized and small anoles did. Moreover, in the large bodied class (or among adult males [see above]), the higher the perching position is, the more frequently an individual showed bright green coloration. During the breeding season, adult males need to advertise their territorial possession or dominance. A signal by more brilliant body coloration from a higher perching position would be more visible from a broader area than that broadcasted by darker coloration from a lower position, dissuading other males from intruding the territory. On the other hand, it is known that territorial male *A. carolinensis* show reduced aggression towards established territorial neighbors ("dear enemy" phenomenon) (Qualls and Jaeger, 1991). The males distinguish familiar and unfamiliar opponents mainly by vision (Forster et al., 2005). Advertising in a visually conspicuous way (wearing brilliant greenish coloration at higher perch) might help territorial males to establish and maintain the social relationships with the neighbors, reducing aggressive interactions with them.

The results did not support the three predictions from thermoregulation hypothesis. However, this does not necessarily completely negate the function of body coloration for thermoregulation. In the present study, approximately half of the anoles observed were brownish, a result contrasting to that in the study of Jenssen et al. (1995), in which most anoles were green. In the present study, air temperature, ranging from 18.3–23.3C, was lower than that in the study of Jenssen et al. (1995: almost thoroughly higher than 25C). Therefore, difference in the pattern of variation in body coloration between these studies may actually reflect the difference in range of air temperature between them, that is, more brownish when cooler and greenish when hotter.

In conclusion, we suspect that *A. carolinensis* takes darker coloration as its base color at the beginning of the breeding season when it is generally cooler, and that adult males change their body coloration to more greenish when they need to advertise their territorial possession.

This idea needs further verification on the basis of appropriately designed experiments and observations.

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