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An Experimental Demonstration of the Species-Recognition Role of *Anolis* Dewlap Color

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Inter- and intraspecific encounters were staged in the laboratory between adult males of the sympatric sibling species *Anolis marcanoii* and *A. cybotes* which differ morphologically only in dewlap color. Levels of intraspecific aggression among *A. marcanoii* were high, but little interspecific aggressive behavior was observed. The importance of dewlap color for species-recognition was assessed by changing the color of the dewlap of *A. marcanoii* to appear like that of *A. cybotes* and vice-versa. *A. marcanoii* in interspecific encounters between altered individuals exhibited an intermediate level of aggressive behavior. Intraspecific encounters between pairs of *A. marcanoii* with altered dewlaps revealed no higher level of aggression than the normal interspecific encounters. A system of species-recognition signals is proposed in which lizards examine more obvious signals, such as dewlap color, at greater distances and more subtle signals, such as head-bobbing patterns, at closer distances.

THE sibling species *Anolis marcanoii* and *A. cybotes* are trunk-ground ecomorphs (Williams, 1972) found sympatrically throughout much of *A. marcanoii*'s limited range in southwestern Dominican Republic. They are consistently separable morphologically only by the color of the dewlap of males and the throat of females: red in *A. marcanoii*, yellow or white in *A. cybotes* (Williams, 1975). Electrophoretic studies, however, show them to be quite distinct and reveal no hybrids (Webster, 1975). How the species coexist is a puzzle. In some areas, they

are found on adjacent fenceposts (Hertz, 1980), whereas in other localities only one species is present. Although Hertz (1980) suggests that *A. marcanoii* may be adapted to hotter, more open microhabitats, field observations have failed to discover any obvious difference (Williams, 1975; Hertz, 1980; pers. obs.). The existence of two such closely related species in sympatry raises two questions amenable to laboratory investigation: does interspecific territorial behavior occur and, if not, how do males distinguish conspecifics from non-conspecifics?

Territories of male lizards in general (Schoener, 1977; Stamps, 1983) and *Anolis* in particular (Rand, 1967; Trivers, 1976), provide resident males with sole access to females residing within their boundaries. For males of most species of *Anolis*, males of ecologically similar species do not present competition for females and thus are generally passively ignored, even though they may be competitors for food or other resources (Rand, 1967; Ruibal, 1967; Talbot, 1979; Ortiz and Jenssen, 1982). An exception, however, is a situation, perhaps analogous to that of *A. marcanoi* and *A. cybotes*, involving a pair of Puerto Rican sympatric trunk-ground siblings, *A. cristatellus* and *A. cooki*, which exhibit high levels of interspecific aggression (Ortiz and Jenssen, 1982; Jenssen et al., 1984). Thus, it is not clear a priori whether one should find interspecific territoriality between *A. marcanoi* and *A. cybotes*.

The differences between the species in dewlap color and stereotyped head-bobbing patterns (Losos, 1985), as well as the lack of hybrids, indicate that errors in species-recognition are probably rare. A wealth of field evidence attests to the importance of the dewlap in species-recognition. Examination of multi-species *Anolis* communities reveals that sympatric species differ in dewlap color and configuration and that these differences are greatest between species that tend to come into contact most frequently (Rand and Williams, 1970; Williams and Rand, 1977; Echelle et al., 1971). Particularly compelling evidence comes from the *A. brevirostris* complex in Haiti (Webster and Burns, 1973). Similar field evidence reveals the importance of species-specific stereotyped head-bobbing patterns for species-recognition in *Anolis* (Garcea and Gorman, 1968; Jenssen and Gladson, 1984). Laboratory experiments have confirmed the species-recognition role of these patterns (Jenssen, 1971). The importance of dewlap color for species-recognition has never previously been experimentally demonstrated.

This investigation has two goals: (1) to examine the level of interspecific aggression, if any, between *A. marcanoi* and *A. cybotes* and (2) to determine the relative importance of dewlap color in species-recognition in *A. marcanoi*.

MATERIALS AND METHODS

In Jan. 1983, 21 adult male *A. marcanoi* were collected 6–10 km north of Bani, Dominican Republic. At the same time, 22 adult male *A.*

cybotes were collected in and around Santo Domingo, D.R. Eleven additional *A. marcanoi* and two additional *A. cybotes* from the same localities were collected in Feb. 1984 and shipped to Cambridge. Lizards were housed in terraria at Harvard University and maintained on crickets and water at a temperature of 25–28 C. Individuals were separated from other males in the same terrarium by cardboard partitions.

Four sets of encounters were staged between two adult males from 23 March 1983 to 3 May 1984. In the first treatment (Losos, 1985), intraspecific encounters were staged in order to characterize the aggressive behavior of each species. An index of aggression was constructed to assess the level of aggressive intensity of *A. marcanoi* in these encounters (Table 1). The index assigns points to particular behaviors, with more points awarded to behaviors connoting higher levels of intensity. The score of each lizard in an encounter is the sum of all points awarded for behaviors displayed by that lizard in that encounter. Points for any behavior are awarded only once in an encounter regardless of the number of times that behavior occurred. Because the aggressive behavior of *A. cybotes* is neither particularly progressive nor hierarchically structured, no index of aggression could be developed for that species (Losos, 1985) and thus it was impossible to accurately quantify and compare the level of aggressive intensity of *A. cybotes* in these encounters.

In the second treatment, 16 interspecific encounters were staged. The behavior of *A. marcanoi* was quantified by using the index of aggression and compared with the results of the intraspecific encounters. Due to the limited number of specimens available, some lizards were used more than once within treatments. The score of each lizard in each treatment was represented by the median score of that lizard in the treatment. Differences between treatment distributions were analyzed by the Mann-Whitney U-test (one-tailed). Using the median value is appropriate when dealing with asymmetric distributions (Sokal and Rohlf, 1969), which the scores for some of the lizards were. In most tests, the mean and median scores for lizards were not greatly different. When there was a single modal score for a lizard, it was always equal, or extremely close, to the median value.

In the third treatment, 15 additional interspecific encounters were staged in which the dewlap color of each species had been altered to appear like that of the other species. Both

lizards in these encounters faced an opponent with a dewlap of the color of its own species. If dewlap color is sufficient to identify a male as a conspecific, these lizards should have performed as aggressively toward their opponent as they would have toward a conspecific male. The dewlap of *A. marcanoii* was painted white with Zauder Brothers, Inc. "Superior Clown White Make Up," while the dewlap of *A. cybotes* was colored red with Hazel Bishop Co. "True Red" lipstick. The results were similar to the natural dewlap color of the two species.

The relative importance of species-recognition signals other than dewlap color (particularly head-bobbing pattern) was examined in the fourth treatment, in which 14 intraspecific *A. marcanoii* encounters were staged between males which had their dewlaps painted white. In these encounters, male *A. marcanoii* faced opponents with the proper head-bobbing pattern but incorrect dewlap color, the reverse situation of the previous set of encounters.

In all encounters, lizards were paired randomly. The only constraints were that they had not been housed in the same terrarium, that they had no prior experience with each other and that there was a minimal, generally less than 5 mm, difference in snout-vent length. In preparation for an encounter, the contestants were placed in the partitioned halves of a 74 × 32 × 29 cm glass aquarium (with the exception of the first few encounters of the first treatment [Losos, 1985]). Each half of the terrarium had two perches parallel to and approximately 8 and 19 cm above the substrate. Lizards were left undisturbed in the terrarium for 17 hours to four days, but usually for two days. Lizards were allowed to gain familiarity with their surroundings, enhancing the likelihood of territorial defense. Room temperature varied from 20–24 C.

Approximately 15–30 min prior to an encounter, a 250 W infrared light was switched on, warming the terrarium to 25–32 C. Encounters were initiated by lifting the partition. All lights in the room were extinguished, except three 60 W desk lamps pointed directly into the terrarium, which lit the display arena and made it difficult for the lizards to see the observers in the room. Encounters were videotaped on a Panasonic NV-8050 time-lapse recorder with a MTI-65 video camera and a Canon 16–100 mm TV zoom lens and then analyzed at normal and slow-motion speeds on a Panasonic WV-5350 video monitor. Encounters normally lasted 45 min, but were terminated when one lizard tried

TABLE 1. INDEX OF AGGRESSION USED TO SCORE* THE BEHAVIOR OF *Anolis marcanoii*.

Points	Action or display modifier
1	low and intermediate level dewlap display
2	full elevation dewlap display
2	crest erection
3	head spot apparent
3	lifting the pelvic region and/or moving backwards during dewlap display or during opponent's display
4	moving toward opponent
6	adopting poised position
7	lunging toward opponent
8	locking jaws
8	opponent flees

* Explanation in text. For more extensive discussion of the index and its derivations, see Losos (1985).

repeatedly to escape from the other and were extended when the lizards were still intensely interacting at the end of the allotted time.

RESULTS

The intraspecific encounters between normal unaltered lizards (treatment 1) were the most aggressive, with a mean of medians of 17.1 on the index of aggression (Table 2). This was significantly greater than each of the other treatments ($P < .005$).

The scores of *A. marcanoii* in the interspecific encounters between normal unaltered lizards (treatment 2) were considerably lower ($\bar{x} = 6.9$). This was significantly less ($P < .05$) than the mean score in the interspecific encounters between lizards with painted dewlaps (treatment 3, $\bar{x} = 10.2$) and statistically indistinguishable from the intraspecific encounters between *A. marcanoii* with dewlaps painted white (treatment 4, $\bar{x} = 6.7$). *A. cybotes* in the second treatment also appeared more inactive, with less aggressive intensity than in any of the other treatments.

The scores of *A. marcanoii* when facing *A. cybotes* with red dewlaps (treatment 3) were significantly greater ($P < .03$) than the scores of *A. marcanoii* against conspecifics with white dewlaps (treatment 4).

DISCUSSION

These experiments clearly demonstrate that male *A. marcanoii* are able to distinguish con-

TABLE 2. LEVEL OF AGGRESSIVE INTENSITY OF *Anolis marcanoi* IN INTER- AND INTRASPECIFIC ENCOUNTERS.

Treatment	Species	Dewlap color	Number of lizards	Number of encounters	Mean score (\pm SD)
1	<i>marcanoi</i> vs <i>marcanoi</i>	normal	18	26	17.1 \pm 8.38
2	<i>marcanoi</i> vs <i>cybotes</i>	normal	12	16	6.9 \pm 3.83
3	<i>marcanoi</i> vs <i>cybotes</i>	reversed	10	15	10.2 \pm 5.51
4	<i>marcanoi</i> vs <i>marcanoi</i>	reversed	10	28	6.7 \pm 5.25

In all treatments, some or all of the lizards were used more than once. The score of a lizard in a treatment is the median of the scores for that lizard in that treatment. The mean is calculated using the median scores. In intraspecific encounters, each lizard receives a separate score and both scores are used in determining medians. In treatments 3 and 4, dewlap colors are reversed by painting the dewlap of *A. marcanoi* white and the dewlap of *A. cybotes* red.

specifics from non-conspecifics and do not behave in a highly aggressive manner toward male *A. cybotes*. *A. marcanoi* generally performed no more than the initial aspects of display behavior toward *A. cybotes* in the encounters between males with normal dewlap color. *Anolis* tend to display to this extent toward any novel object in their environment, including non-specific lizards and people (G. C. Mayer, pers. comm.). Male *A. marcanoi* displayed to a similar extent toward males of a variety of other species in laboratory trials (unpubl. data). *A. marcanoi* thus appears to be no more aggressive toward *A. cybotes* than toward any other *Anolis* species; the existence of interspecific territoriality between these species is consequently unlikely. In this regard, the behavior of *A. marcanoi* is like the vast majority of other *Anolis* species studied thus far. Further field study is necessary to determine whether *A. marcanoi* and *A. cybotes* are engaged in exploitative competition or, conversely, if they avoid competition by partitioning the environment along some niche axis not yet examined.

These experiments provide the first experimental proof that dewlap color is a species-recognition signal. Previous dewlap alteration experiments concerned female choice in *A. carolinensis*; they showed that dewlap color was not crucial for species-recognition (Greenberg and Noble, 1944; Crews, 1975), but at a distance, males with the normally colored red dewlap were preferred over those with dewlaps painted green, perhaps because red is more visible against vegetation (Sigmund, 1983). In species with no sympatric congeners (the historical situation for *A. carolinensis* in the United States), dewlap color and shape are likely to be

of little importance in species-recognition because there is no possibility of mistaken identity (Williams and Rand, 1977).

By contrast, dewlap color is necessary to evoke any heightened aggressive behavior in *A. marcanoi*. However, dewlap color in itself is not usually sufficient to evoke the level of aggression exhibited toward conspecifics by *A. marcanoi*. *A. marcanoi* were much less aggressive toward red-dewlapped *A. cybotes* than toward normal conspecifics. Some other signal(s), the most likely being a correct head-bobbing pattern (not displayed by the altered *A. cybotes*), apparently is necessary before male *A. marcanoi* will react to a lizard as a conspecific.

In the absence of proper dewlap color, however, all other species-recognition signals are ignored; *A. marcanoi* were not more aggressive toward white-dewlapped *A. marcanoi* than they were to normal *A. cybotes*.

Given that there are at least two species-recognition signals displayed by *A. marcanoi*—dewlap color and, probably, head-bobbing pattern—there may be a hierarchical structure of signal examination such that a positive response is necessary at every level to evoke heightened aggressive response and examination of the next signal. The hierarchy may correspond to the distance at which a signal can be interpreted. At a great distance, body shape is the easiest signal to see (Williams and Rand, 1977). Male *A. marcanoi* would not be expected to respond in a highly aggressive manner toward the crown-giant *A. ricordii*, for example. *A. marcanoi* and *A. cybotes* are morphologically very similar, however, and probably cannot be distinguished at a distance by body shape. As lizards approach

and display, dewlap color can be observed. At closer proximity, the head-bobbing pattern can be discerned. A negative response at any of these levels would label an opponent as a non-conspecific and lead to cessation of aggressive behavior. Thus, in the intraspecific encounters between altered *A. marcanoii*, the appearance of the white dewlap is sufficient to label a lizard as a non-conspecific, while in the altered interspecific encounters, it is not until the bobbing pattern is examined that the male *A. cybotes* is revealed as non-conspecific.

Available evidence does not allow testing these predictions. Encounters were staged in terraria too small to distinguish at what distance lizards observed and reacted to different signals. There was no clear distinction between which behaviors required an opponent with a red dewlap and which did not, nor was there an abrupt cessation of aggressive behavior upon display of a white dewlap. However, general patterns were observed as well as differences in mean scores of the different sets of encounters. For example, more than half of the males in the altered intraspecific encounters (treatment 4) exhibited no more than initial display behavior. In contrast, 11 of the 12 *A. marcanoii* in the altered interspecific encounters (treatment 3) exhibited more aggressive levels of behavior.

Additional tests are required to determine whether such a hierarchical structure of recognition signals exists. There may be other, more subtle, recognition signals that have yet to be identified. My experiments indicate that interspecific territorial aggressive behavior between these two similar sympatric species probably does not occur and provide the first experimental proof that the color of the dewlap serves as a species-recognition signal in *Anolis*.

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A New Species of *Atelopus* (Anura, Bufonidae) from the Andes of Northern Perú

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A new species of the bufonid genus *Atelopus*, the first member of the *ignescens* group from Perú, is described from the high Andes in the Department of Cajamarca. The species is diagnosed by coloration and dermal ornamentation. It seems to be most similar to *Atelopus bomolochos* and the widespread species *A. ignescens* occurring to the north in Ecuador. The larva is of the gastromyzophorous type, having a large ventral sucking disc and inhabiting swift streams.

FEW frogs of the genus *Atelopus* have been described from Perú: *Atelopus spumarius* Cope, 1871; *A. seminiferus* Cope, 1874; *A. pulcher* (Boulenger, 1882); *A. tricolor* Boulenger, 1902; *A. erythropus* Boulenger, 1903; and *A. rugulosus* Noble, 1921. With the exception of *A. spumarius* and *A. pulcher*, little has been published concerning these species. Rivero (1968) placed *pulcher* in the synonymy of *spumarius*, but Peters (1973) regarded *spumarius* as a *nomen dubium*. Lescure (1981) resolved the problem by designating a neotype for *A. spumarius*.

Recent fieldwork has resulted in a large series of an undescribed *Atelopus* from the high elevation puna and subpuna habitats of northern Perú (Fig. 1), which we name in recognition of the country of origin.

MATERIALS AND METHODS

The following museum acronyms are used: American Museum of Natural History (AMNH), Academy of Natural Sciences, Philadelphia (ANSP), California Academy of Sciences (CAS), University of Kansas Museum of Natural History (KU), Louisiana State University Museum of Zoology (LSUMZ), Museo Historia Natural "Javier Prado," Lima, Peru (MHNJP), Museum of Vertebrate Zoology, University of California at Berkeley (MVZ).

In addition to specimens of the new species and a large series of *A. ignescens* in the KU collections, we have examined the type-species of *A. bomolochos* Peters (CAS 93910, holotype, 85341–42, 93912 paratypes, 85139–41, 93906),