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THE CURIOUS CASE OF THE LEFT-SIDED DEWLAP: DIRECTIONAL ASYMMETRY IN THE CURAÇAO ANOLE, *ANOLIS LINEATUS*

DANIELLE N. LOSOS,[1,6] JACKSON B. R. WEAVER,[2,6] THOMAS W. FIES,[3,6] ANTHONY HERREL,[4] ANNE-CLAIRE FABRE,[4] AND JONATHAN B. LOSOS[5,7]

ABSTRACT. We examined asymmetry in the color of the dewlap of *Anolis lineatus* from Curaçao. We confirmed previous reports that one side of the dewlap appears more yellow in color than the other and, contrary to previous work, demonstrate a directional bias such that the left side is usually the more yellow side. At one site surveyed twice in 3.5 years, the proportion of left- and right-sided males changed significantly. A behavioral experiment failed to find a significant tendency for males to direct the more yellow or more orange side of the dewlap to other individuals while displaying.

KEY WORDS: *Anolis lineatus*; behavior; dewlap; display

INTRODUCTION

The dewlaps of *Anolis* lizards have long fascinated naturalists, including Darwin (1871), and the anole dewlap has continued to inspire discussion concerning its function and evolutionary significance ever since. West-Eberhard went so far as to suggest (1983, p. 169) that "[t]he dewlap of male (and in some species, female) *Anolis* lizards is a reptilian equivalent of the plumage and song of birds."

An extensible, two-sided throat fan possessed by males and, in many species, females, the anole dewlap is used in territoriality, courtship, predator deterrence, and species recognition (reviewed in Losos,

[1] East Chapel Hill High School, 500 Weaver Dairy Road, Chapel Hill, North Carolina 27514, U.S.A.

[2] Dr. Ronald E. McNair Academic High School, 123 Coles Street, Jersey City, New Jersey 07302, U.S.A.

[3] Evanston Township High School, 1600 Dodge Avenue, Evanston, Illinois 60201, U.S.A.

[4] UMR 7179 CNRS/Muséum National d'Histoire Naturelle, Département d'Ecologie et de Gestion de la Biodiversité, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France.

[5] Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.; e-mail: jlosos@oeb.harvard.edu.

[6] Joint first authors.

[7] Address for correspondence.

2009). Perhaps the most notable feature of the anole dewlap is its tremendous interspecific variability: enormously large, tiny, uniformly colored, multicolored, or festooned with spots, stripes, streaks, and splotches, anole dewlaps are a cornucopia of colors, patterns, and sizes (Nicholson et al., 2007; Losos, 2009). Sympatric anole species invariably differ in some aspects of the dewlap (Nicholson et al., 2007), and these differences may be related to species recognition, sexual selection, or adaptation to the different light environments that anoles utilize.

Despite the remarkable variety in dewlaps exhibited among the 400 species of *Anolis*, only one species, *Anolis lineatus* of the southern Caribbean islands of Curaçao and Aruba, is known to possess a dewlap that differs in appearance from one side to the other. In 1967, Rand and Rand first reported on this asymmetry in Curaçaoan populations of the species. The dewlap of *A. lineatus* has a black spot proximal to the throat surrounded by orange skin on the distal margin. Rand and Rand (1967) discovered that, on one side, the border is populated by many closely packed white scales, which from a distance give that side a paler yellow color compared with the vivid orange of the less scaled side. Despite the great interest in anoles and their dewlaps, no further work was conducted until 2013, when Gartner et al. confirmed the asymmetric dewlap of *A. lineatus*, reporting that populations in Aruba, as well as those on Curaçao, exhibited the asymmetry. Rand and Rand (1967) stated without presenting any data that there was no bias in the asymmetry among males (they did not comment on females)—the more yellow side was as often the left as the right. On the basis of relatively small sample sizes, Gartner et al. (2013) also failed to detect a directional bias in the asymmetry among males but suggested that in females, the left side was usually the yellower side (i.e., covered with more white scales, which give it a yellow appearance from a distance; we refer to this as "yellower" henceforth).

Why this species alone among all anoles has evolved an asymmetric dewlap is not known. Rand and Rand (1967) noted that the dewlap was commonly deployed in territorial and courtship displays; in the one copulation they observed, the male presented both sides of the dewlap during the preliminary courtship. One possibility is that the different sides of the dewlaps convey different information or are used in different contexts. However, beyond Rand and Rand's observations, no further behavioral data are available.

In this paper we have four goals:

1. to confirm that the dewlap of *A. lineatus* is asymmetric based on a large sample size;
2. to investigate, if asymmetry exists, whether there is a directional bias, such that one side (the left or the right) is yellower more often than the other;
3. to investigate whether the degree of directional bias changed from that reported previously by Gartner et al. (2013); and
4. to test whether males preferentially displayed the yellow or orange side to conspecific males and females.

METHODS

We captured *Anolis lineatus* at three sites on Curaçao: Den Dunki National Park on the eastern side of the island (50 males, 22 females), Shete Boka National Park (20, 20), and the grounds of the Kura Hulanda Lodge (21, 9) on the western side of the island (Fig. 1). At each site, adult individuals of both sexes were captured and examined to determine whether the two sides of the dewlap

Figure 1. Map of Curaçao and study sites.

differed in color and scalation and, if so, which side of the dewlap was yellower and which more orange. At Den Dunki, the dewlaps of some animals were scored from photographs; at the other two sites, all scoring was done on live individuals in hand. Scoring was subjective, but was in almost all cases very obvious, as Figure 2 and Gartner et al. (2013, fig. 2) demonstrate.

We investigated whether male *A. lineatus* preferentially used the orange or yellow side of their dewlaps in encounters with conspecifics. To do so, we located male *A. lineatus* in Den Dunki National Park. Once we identified a focal male, we placed a stimulus individual—either a male (in 12 trials) or a female *A. lineatus* (13 trials)—tethered to a 10-foot (3-m) fishing pole ca. 0.5–1.0 m in front of him. When possible, the stimulus lizards were placed directly in front of the trial males, usually below the focal male on the same trunk or branch. We attempted to place the stimulus lizard in line with the focal lizard's body axis such that its snout was pointed directly at the stimulus lizard. However, in some cases this was not achieved, and the stimulus lizard was closer to one side of the lizard's head and dewlap than the other. We noted this as a predisposition for the focal lizard to display using that side of the dewlap (this was not noted in all trials). Once the stimulus lizards had been placed into position, we allowed the experiments to proceed for five minutes or for two minutes after the focal male first displayed, whichever was shorter. For each display, we noted which side of the dewlap was presented to the stimulus lizard. The encounters were ended immediately if the focal male attempted to attack the stimulus lizard. At the end of the trial, we captured the focal male and determined which side of the dewlap was yellower. We also measured the lizard's snout-vent length (SVL, the distance from the tip of the snout to the anterior edge of the cloaca). Stimulus individuals were from distant areas of the same study site and thus were likely unfamiliar to the focal lizard; each stimulus animal was only used one time.

This research was conducted 21–28 July 2015.

RESULTS

Dewlap asymmetry

All individuals displayed dewlap asymmetry, with one side having a greater density of scales along the lower margin, making that side appear yellower (Fig. 2). In two females, the differences in color and scalation were slight (one scored as more yellow on the right side, the other as more yellow on the left), but in all other cases, the differences were substantial. Contrary to previous reports, dewlap asymmetry was directional: in 74.7% of males and 70.6% of females, the left side of the dewlap was yellower (Table 1). These results differ from a 50:50 expectation (males: $z = 4.72$, $P < 0.001$; females: $z = 2.94$, $P = 0.003$). Frequencies of asymmetry did not differ among study sites for either males or females ($\chi^2 \leq 2.48$, $P \geq 0.28$). For all three sites, frequencies differed from 50:50 when all lizards were considered ($P < 0.05$); when comparisons were made for each sex separately at each site, males at Den

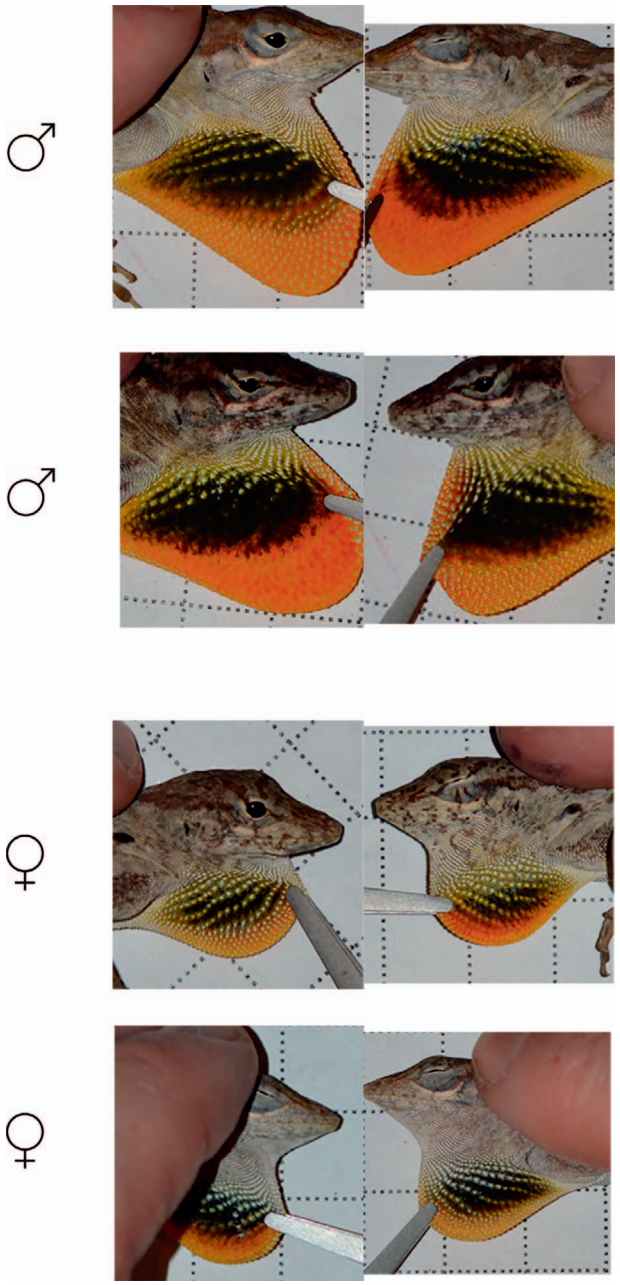

Figure 2. Examples of dewlap asymmetry. Compare the amount of scalation and degree to which the two sides of an individual's dewlap appear yellow or orange. All individuals from Den Dunki National Park.

Table 1. Dewlap asymmetry of *Anolis lineatus* by site and sex.[a]

	% with Yellower Side of Dewlap on Left or Right			
	Den Dunki NP	Shete Boka NP	Kura Hulanda	Kura Hulanda, 2012[b]
Males				
N	50	20	21	10
Right	28.0	30.0	14.3	60.0
Left	72.0	70.0	85.7	40.0
Females				
N	22	20	9	3
Right	40.9	20.0	22.2	33.3
Left	59.1	80.0	77.8	66.7

[a]At all three sites on Curaçao, the left side of the dewlap is more yellow in appearance in most lizards of both sexes. NP, National Park.

[b]For comparative purposes, we also present the results of a previous census at one site in 2012 (Gartner et al., 2013), illustrating the shift in sidedness that occurred over a 3.5-year period.

Dunki and Kura Hulanda and females at Shete Boka were significantly different from 50:50, whereas the other comparisons were not (Table 1).

We returned to the grounds of the Kura Hulanda Lodge to follow up on the dewlap sampling conducted by Gartner et al. (2013) in January 2012. We found a significant shift over the 3.5-year interval from a 60% bias toward being yellower on the right side in 2012 ($n = 10$) to 85.7% yellower on the left in 2015 ($n = 21$; $\chi^2 = 6.87$, $P = 0.009$; data for males; results qualitatively the same when males and females are combined; too few females were collected to analyze separately).

Behavioral tests

In those cases in which a male was the stimulus lizard, seven males displayed with the yellower side of the dewlap visible to the stimulus animal, and five males presented the more orange side to the stimulus animal. Against stimulus females, the comparable numbers were seven and four, with two males that showed both sides (one showing the yellower side first, the other showing the more orange side first; four males displayed multiple times showing the same side). Overall, 14 males presented the yellower side and nine showed the more orange side, with two showing both. These results are not statistically different from a 50:50 expectation ($P > 0.40$, two-tailed binomial distribution, excluding two ties).

Of those lizards with a predisposition (head tilted one way or the other relative to the stimulus lizard), eight out of 10 displayed showing the side to which it had a predisposition; of the other two, one turned to show the yellower side, the other to show the more orange side (one other lizard displayed both ways). Of those in which the trial lizard was placed directly in line with the lizard's snout (i.e., no predisposition), five showed the yellower side and two the more orange side.

DISCUSSION

Our findings add an unexpected twist to an already remarkable story. Not only does *A. lineatus* possess—as far as is known—the only asymmetric dewlap among all 400 anole species, but the asymmetry is biased, with a paler, yellower appearance usually on the left side.

We confirmed previous reports (Rand and Rand, 1967; Gartner et al., 2013) that dewlap asymmetry exists in *A. lineatus*. With the exception of two females, the difference in the two sides was striking: as a result of

dense, white scales on the orange margin of one side of the dewlap, individuals appear to have an orange side and a yellow side. Across all populations, the yellow side was on the left in 75% of males and 71% of females. Previous studies, based on small (Gartner et al., 2013) or unknown (Rand and Rand, 1967) sample sizes, had failed to detect this asymmetry in males, but had observed it in females (Gartner et al., 2013).

Most likely, previous studies did not detect the asymmetry in males because of the vagaries of random sampling and small sample sizes. However, another possibility is that the degree of asymmetry fluctuates through time. We tested this hypothesis by revisiting one of the Gartner et al. (2013) study sites. In January 2012, Gartner et al. (2013) found that for six out of 10 (60%) males examined at the Kura Hulanda site, the right side of the dewlap was yellower. In contrast, 3.5 years later in August 2015, 86% of the males were yellower on the left, a statistically significant difference between the two sampling periods. This difference suggests that the directionality of dewlap asymmetry is highly labile. What might drive such shifts is unknown. More thorough monitoring—over both spatial and temporal scales—is clearly called for.

We reasoned that if a functional basis exists for the dewlap asymmetry, then it might be evident in which side of the dewlap males show to conspecifics when they are interacting. To test this hypothesis, we conducted behavioral trials in which a free-ranging male was presented with either a male or female. We observed the male to see which side of the dewlap he would present to the target individual. Of those males that only showed one side of their dewlap to the target (all but two, but trials were short), 61% showed the yellow side. This result is suggestive, but was not statistically significant. Further research is needed to test whether, in fact, male *A. lineatus* use the different sides of their dewlaps as signals and, if so, in which contexts and for what reasons. Another possible function of dewlap asymmetry is to provide visual contrast with the background, choosing which side to present depending on the backdrop.

Directional asymmetry is uncommon in the animal world and invites investigation about its adaptive basis, if any (Palmer, 2005, 2009; Van Dooren et al., 2010). The dewlap asymmetry of *A. lineatus* is particularly curious given the enormous diversity of anoles—what is it about *A. lineatus* that has led to the evolution of asymmetry in just this one, otherwise not particularly notable, anole species? In ecology and behavior, *A. lineatus* has many parallels among the 150 or so Caribbean anole species (Gartner et al., 2013). Curaçao and Aruba are oceanic islands, never having been connected to each other or to the mainland, so the presence of *A. lineatus* on them must be the result of overwater dispersal. Such colonization raises the specter of founder effects; however, such events have occurred repeatedly in anoles (Williams, 1969), yet such asymmetry has never been reported in any other population. For the time being, the unique dewlap of *A. lineatus* remains a mystery and invites further study.

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