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ARTICLE

Sex differences in antipredator tail-waving displays of the diurnal yellow-headed gecko *Gonatodes albogularis* from tropical forests of Colombia

Martha L. Bohórquez Alonso · Jorge Martínez Cotrina · David Aguilar Pardo · Enrique Font · Miguel Molina-Borja

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Abstract Many vertebrate species show display behaviors when predators are in their vicinity. Some of these displays may inform the predator of the improbability of capturing the prey (i.e., pursuit-deterrent displays) and are potentially advantageous to both predator and prey. Here we present data on a tail display performed by *Gonatodes albogularis*, a diurnal tropical gecko. We performed transect surveys in three habitats near Bogotá in Colombia. Geckos detected during transects were approached by the observer in a standardized way, and details of their tail-waving displays were recorded. In control recordings animals were watched from a distant site without approaching them. Results showed sexual differences in tail-waving display: when approached by the observer, males performed this behavior more frequently than females. We found no significant differences between males and females in flight-initiation distances and height above the substratum when they were initially located. Results also showed that males displayed more frequently when approached than when the simulated predator remained stationary. We interpret these results as evidence that the display functions as a pursuit-deterrent signal to potential predators. However, as some tail displays were performed in the presence of conspecifics, the display may also have a social function.

Keywords Tail display · Antipredator behavior · Gecko · *Gonatodes*

Introduction

According to Ydenberg and Dill's (1986) optimality model, prey should not always flee immediately upon detecting a predator, primarily because fleeing may prevent fitness-enhancing activities. Performing behaviors that reduce the probability of being detected or captured is a way for conspicuous prey to endure predators' pressure and increase survival. In particular, one way of minimizing the associated cost of unnecessary antipredatory responses for prey is to perform behavior patterns that may act as pursuit-deterrent signals by informing predators that they have been detected (Woodland et al. 1980; Caro 1995). This communicative process has been considered to be beneficial to the prey by reducing the probability of being attacked, and to the predator by not wasting time and energy on a prey unlikely to be captured (Ruxton et al. 2004).

A cost/benefit approach predicts that pursuit-deterrent signals should occur when the distance between predator and prey is such that the probability of prey being intercepted if attacked is low (Ydenberg and Dill 1986). If predators are closer, prey should resort to other strategies such as flight and/or, in the case of many lizards, tail autotomy (Vitt et al. 1977; Greene 1988).

M. L. Bohórquez Alonso · D. Aguilar Pardo
Facultad de Psicología, Universidad Católica de Colombia,
Bogotá, Colombia

J. Martínez Cotrina
Fac. Ciencias Sociales y Humanas,
Universidad Externado de Colombia, Bogotá, Colombia

E. Font
Instituto Cavanilles de Biodiversidad y Biología Evolutiva,
Univ. Valencia, Valencia, Spain

M. L. Bohórquez Alonso · M. Molina-Borja (✉)
Lab. Etología, Depto. Biología Animal, Univ. La Laguna,
38206 La Laguna, Tenerife, Canary Islands, Spain
e-mail: mmolina@ull.es

Pursuit-deterrent signals, which usually consist of auditory and/or visual signals, have been studied in birds (Alvarez 1993; Clark 2005; Murphy 2006; Randler 2006, 2007), mammals (Caro et al. 2004), and fish (Godin and Davis 1995). For example, stotting in gazelles is interpreted as a signal that reduces the probability of being attacked by predators (Caro 1986). In reptiles, several displays have been identified as possible pursuit-deterrent signals, including tail vibration, tail waving, and arm-waving in iguanid, lacertid, and teiid lizards (Dial 1986; Hasson et al. 1989; Leal and Rodríguez-Robles 1997a, b; Cooper 1998, 2001; Leal 1999; Cooper et al. 2004). Tail waving has also been described in a few scincid (*Carlia jarnoldae*, Langkilde et al. 2004) and gekkonid (Harris and Kluge 1984; Dial et al. 1989; Leuck et al. 1990; Downes and Shine 1998; Colli et al. 2003) species, but its role as a pursuit-deterrent signal has not been established. Sexual differences in antipredator behavior have been found in several species of reptiles, which may be associated with different predation risk between sexes (Shine et al. 2000; Plasman et al. 2007; VanHooydonck et al. 2007).

The yellow-headed gecko, *Gonatodes albogularis*, is a small diurnal gekkonid living in coastal to open tropical dry forest habitats (up to 1500 m a.s.l.) of Central and South America (Rivero-Blanco 1979). It lives in tree trunk crevices, logs, stone walls, and rock piles both in undisturbed habitats and near buildings. This gecko shows striking sexual color dimorphism: adult males have an orange to yellowish head and dark brown body color whereas females are more cryptic, with a spotted mosaic of grey to brown colors. Between the yellow–orange head and the dark body of adult males there is a thin stripe of light blue at each shoulder. Males with a yellowish head win more frequently in aggressive contests with other males and are preferred by females over those with an orange head (Ellingson 1994). Males suffer more predatory attacks than females (Ellingson 1994). Natural predators of this species include large lizards, snakes, birds, and mammals (Fitch 1973; Bello 2000).

There are few behavioral studies of wild yellow-headed geckos (Ellingson 1994), and no information is available regarding its antipredator behavior. However, during preliminary field observations, we noted that *G. albogularis* of both sexes showed a conspicuous undulating tail movement when an observer was in the vicinity or approaching them. These tail movements are different from those described in other gekkonid species in that, for example, the movements do not include a tail elevation component (see literature citations above and results below).

Here we report results of a field study of tail waving behavior in Colombian populations of the yellow-headed gecko. We tested predictions of pursuit-deterrent signaling theory:

1. prey approached slowly by a predator should display only when the predator is some distance away and then flee if further approached;
2. the pursuit-deterrent display should be performed more often when the predator is approaching than when it is stationary; and
3. prey should signal when stationary (Leal and Rodríguez-Robles 1997a).

We recorded the behavior of lizards in response to a human observer that was either stationary or approached the lizards simulating a predatory attack. Our objectives were:

1. to provide a detailed description of the tail display;
2. to quantify variation in tail displays with sex and predator distance; and
3. to compare the frequency of tail displays between an approaching and a stationary stimulus.

Materials and methods

Locations and recording methods

We selected three study sites to the southwest of Bogotá: Pandi (4°12′N, 74′29′W, 920 m a.s.l.), Melgar (4°12′N, 74°38′W, 320 m a.s.l.), and Carmen de Apicalá (4°08′N, 74°43′W, 323 m a.s.l.). The habitat at these sites consists of tropical forest with a bimodal annual pattern of rainfall (Holdridge et al. 1971; Gillespie et al. 2000) and with yarumo (*Cecropia*), lechero (*Calotropis procera*), cucharo (*Clusia multiflora*), roble (*Quercus humboldtii*), and bolsitas (*Bursera* sp.) as some of the main plant species. Mean annual temperatures at the three sites are around 28°C (IDEAM 2000). The sampling sites at Pandi and Carmen Apicalá encompassed several houses, and geckos were also found on their walls.

Reproductive periods are not known for our sampling sites but they may start with the onset of rainy seasons (March–April and September–October), as in the closely related *G. humeralis* (Miranda and Andrade 2003). Natural predators, including snakes, domestic cats, large saurophagous lizards, and some predatory birds are present in all three study sites (Aguilar and Martinez-Cotrina, unpublished observations).

At each site we conducted surveys along transects ca. 100 m long (30 min in duration) several times per day, in different parts of the habitat. Transects were separated by at least 20 m to avoid re-sampling the same geckos. Surveys were conducted during March–April of 2005 and 2006 by walking slowly (about a step every 2 s) between 11:00 and 15:00 hours, while searching for geckos visually with the aid of binoculars. For logistic reasons the number of transects at each site was not the same. Because similar trends were found in data from each sampling locality, we pooled the data from all of them which summed up to 41 transects in the three study sites. The total number of geckos observed was 311 ($\bar{x} = 8$ geckos/transect).

We used an approaching human observer as a predator surrogate. Similar methods have been used in many studies of escape and refuge use by lizards (Cooper et al. 2003; Cooper 2007) and other taxa (reviewed by Stankowich and Blumstein 2005; Stankowich and Coss 2006). A human acting as a predator has the drawback of not enabling recording of the response of predators to the behavior of the prey; however, the method is effective in work with lizards and enables investigation of whether the lizards' behavior conforms to predictions of pursuit-deterrent signaling theory (Hasson et al. 1989; Leal 1999; Cooper 2001).

Upon sighting a lizard, we recorded in a check-sheet its sex, the substrate where it was located (house wall, tree trunk, rock, etc.), and the behavior pattern it was performing. In some observations the observer stood motionless and recorded the behavior of any gecko found within a 10 m radius during 2 min. In others, lizards were approached slowly, and their behaviors were recorded. If the lizard undulated its tail, approaching stopped temporarily (2 min), and a reference mark was taken to allow measurement of the distance between the observer and the displaying gecko. Afterwards we resumed the approach until the animal fled, at which point we measured flight-initiation distance. We could not capture sighted animals to take body measurements.

After recording behavioral data from each animal, we measured:

1. the distance between the observer and the animal when first detected;
2. the height above the ground of the animal's initial location;
3. the distance between the observer and the gecko when the gecko first waved its tail.

We also measured ambient temperature (3 cm above ground level to the nearest 0.1°C) and humidity at the beginning and end of each transect. Mean temperature and relative humidity at ground level during recording days at the different sites were 33°C (range 29–38°C) and 65% (range 60–70%).

Data analyses

Data could not be assumed to be normally distributed (Kolmogorov–Smirnov tests; significant for all variables). We therefore used non-parametric Mann–Whitney *U* tests to compare height above ground, distance from the observer when first detected and when tail displays were performed, and flight-initiation distance between male and female geckos. All statistical analyses were performed with SPSS 15.0.

We used separate *G* tests of independence (Sokal and Rohlf 1995) to analyze the significance of the association between sex of individuals and:

1. the frequency of tail-waving displays;
2. the distance from the observer when performing tail display; and
3. the frequency of tail display when the observer was approaching or remained stationary.

We used two-tailed tests and the significance level was set at $\alpha = 0.05$.

Results

Behavior patterns

When first detected, focal geckos performed the following behavior patterns: resting (31.5% of the geckos), tail display (30.1%), head turning (gazing toward the observer, 17.4%), eating (2.8%), running away to a refuge (2.1%), jumping (0.7%), and running (0.7%).

Tail-display characteristics

The display typically performed by *Gonatodes albogularis* consists of a lateral sinusoidal movement of the entire tail with the tip somewhat curved laterally. Tail displays were performed by geckos standing on vertical or horizontal surfaces. While waving, the tail is held horizontally just above the substrate. The speed of the movement varies between slow (taking ca. 2 s for a complete swing of the tail) and more rapid (<1 s) tail waving. Tail displays typically occurred in bouts, each bout including several undulating movements. Both adult males and females performed the display, and any individual gecko could perform it several times (up to 3 bouts of tail waving in some cases). Individuals performed the display while remaining stationary and only fled if the observer continued approaching. Geckos never performed this tail display when fleeing or when they stopped after fleeing. In those behavioral observations when the observer was stationary, a few geckos performed the tail display both before and after spontaneously moving (3 cases, one male and two females, out of 17 observations of animals spontaneously moving).

Location of lizards

Male and female individuals did not significantly differ in height above the ground when they were first located

(Mann–Whitney U test, $Z = -1.15$, $p > 0.05$, Table 1). Mean flight-initiation distance also did not differ significantly between sexes ($Z = -1.20$, $p > 0.05$, Table 1). However, when first detected (whether or not they performed a tail display) males were at a significantly greater distance from the observer than females ($Z = -2.72$, $p = 0.006$; Fig. 1, Table 1).

Sexual dimorphism in tail display

There was a significant association between sex and tail-waving display: more males (38.5%, 40 out of 104) performing tail-waving displays than females (25.7%, 54 out of 210) ($G_{adj} = 5.24$, $df = 1$, $p < 0.05$). There was also a significant association between sex and distance from the observer at which individuals performed the tail-waving display ($G_{adj} = 14.14$, $df = 3$, $p < 0.01$, Fig. 2). Males displayed at a significantly greater distance from the observer than females (males 2.99 m ± 0.24, females 1.93 m ± 0.19; Mann–Whitney U test, $Z = -3.63$, $p = 0.003$, Fig. 2). Most displays were performed when the observer was at distances of between 0.5 and 4.0 m from the focal gecko. At very close and far distances individuals did not perform the tail display or performed it very infrequently (Fig. 2).

Table 1 Descriptive statistics (median an interquartile distances) for height above ground, distance from the observer when geckos were first detected, and flight-initiation distance

	Males	Females
Height (m)		
Median	1.12	1.34
I.Q.	1.06	1.36
N	93	184
Distance (m)		
Median	2.38	2.0
I.Q.	2.31	1.77
N	93	184
Flight distance (m)		
Median	0.80	0.80
I.Q.	1.66	1.10
N	93	184

I.Q. Interquartile distance, *N* sample size

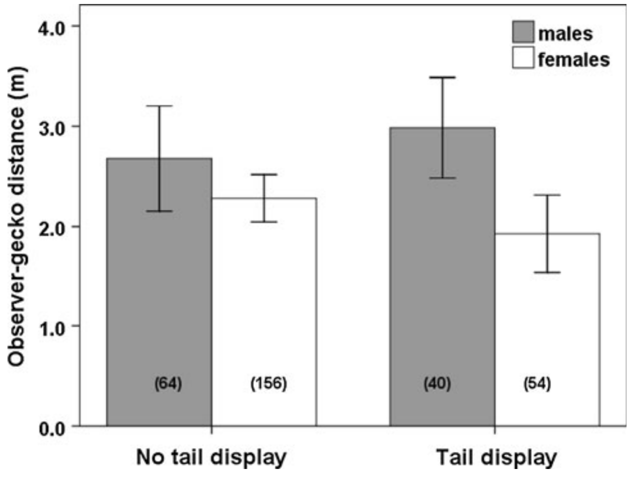

Fig. 1 Mean (±95% CI) observer–gecko distance when first detected for male and female geckos that exhibited tail waving and for those that did not exhibit the tail display. *Numerals in parentheses* indicate sample size

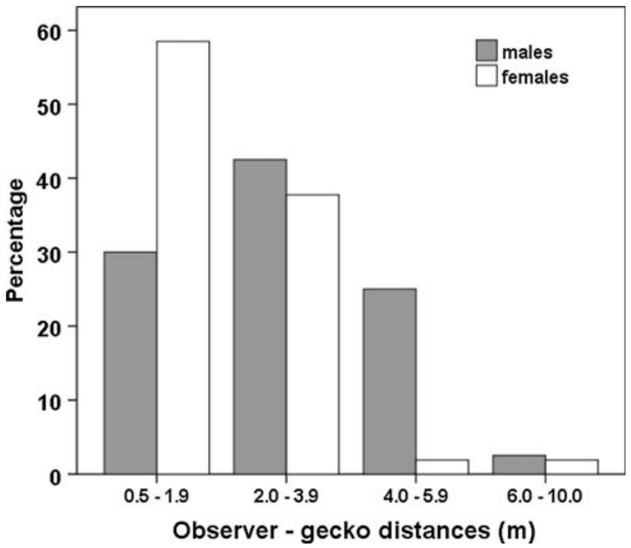

Fig. 2 Percentages of males and females showing tail display in different observer–gecko distance ranges

More males performed tail displays when the observer was approaching them (29 out of 58) than when the observer was stationary (4 out of 27) ($G_{adj} = 10.26$, $p < 0.01$, Fig. 3). There was no significant association between observer behavior (approaching or stationary) and the number of individuals performing the tail display for females ($G_{adj} = 0.00043$, $df = 1$, $p > 0.70$, Fig. 3).

Of 14 cases in which we recorded individuals being near a conspecific, on eight occasions one of the geckos performed the tail display.

Discussion

Structure and function of tail displays

The tail display performed by *G. albogularis* when confronted by a simulated predator, with the tail waving close to the ground and parallel to it, is similar to that of some gekkonids from Australia (Bustard 1965; *Oedura lesuerurii*, Downes and Shine 1998). Other geckos show a different

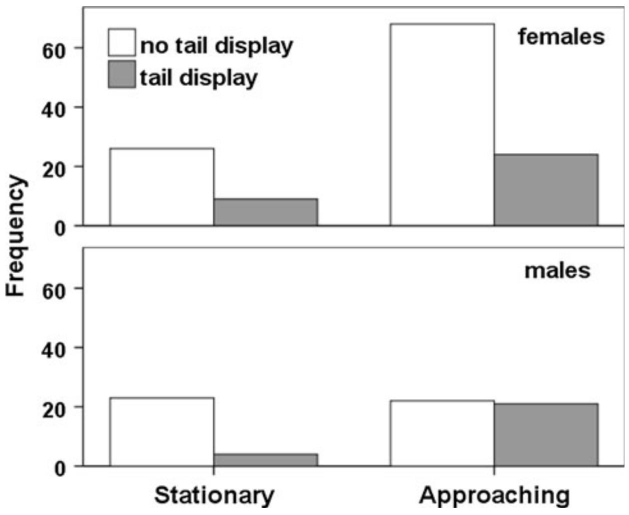

Fig. 3 Number of adult males ($n = 85$) and females ($n = 147$) showing tail wagging when the observer was stationary or approaching geckos

pattern, initially raising and then waving the tail (Bustard 1965; Johnson and Brodie 1974). The lateral movement of the tail during the display of *G. albogularis* also resembles the behavior performed in antipredator contexts by the iguanid *Callisaurus draconoides* (Hasson et al. 1989), the scincid *Eumeces laticeps* (Cooper 1998), and the lacertid *Acanthodactylus beershebensis* (Hawlena et al. 2006).

Other tail displays are used in social, aggressive or courtship contexts; in these the animals raise the tail and move it laterally while extending the four limbs or holding the belly off the substrate (several gekkonids, Marcellini 1977; *Gonatodes vittatus*, Demeter and Marcellini 1981; *Sphaerodactylus clenchi*, Leuck et al. 1990).

Our data support a pursuit-deterrent function for the tail display of *G. albogularis* because:

1. geckos performed the tail display while stationary (Leal and Rodríguez-Robles 1997a);
2. individuals showed tail display at intermediate distances (Cooper and Frederick 2007);
3. the individuals performed the tail display while standing on rocks or logs and never fled immediately;
4. neither adult males nor females have a bright contrasting tail color as required by the flash-concealment hypothesis (see below); and
5. geckos performed tail displays after the observer detected individuals and never when they stopped after fleeing.

A pursuit-deterrent function has been proposed for other lizard displays, for example: dewlap extensions and push-ups in *Anolis* (Leal and Rodríguez-Robles 1997a, b), tail-curling in *Leiocephalus* (Cooper 2001), and arm waving in *Cnemidophorus* (Cooper et al. 2004). In *Anolis cristatellus*, antipredator arm waving is also associated with greater endurance of the individuals, thus being an honest signal of the lizard's capacity (Leal 1999).

Tail display of *G. albogularis* also occurred in a few observations both before initiating a movement and after stopping, when the simulated predator was stationary and far from the animals. These observations suggest that the display could also be used as a way to deflect an attack by an undetected predator; this deflective display (Arnold 1984, 1988; Dial and Fitzpatrick 1984; Greene 1988; Mori 1990) should occur when individuals are under threat of imminent attack by a detected predator and/or immediately after they stop following a bout of locomotion (Cooper 1998, 2001). In the latter case, the signal would be an efficient way of dealing with undetected ambush predators.

Another possible function is that of flash concealment: the sudden prey display followed by flight may confuse the predator about its position, and abort the attack. However, our observations do not support this hypothesis for the tail display of *G. albogularis*.

Because a proportion of tail displays were performed by geckos located close to conspecifics, it seems likely that the displays can also be used in social contexts. Therefore, our data show that the tail display of *G. albogularis* is used in different contexts and may be a multifunctional signal.

Sexual dimorphism in the tail-waving display

Although adults of both sexes performed similar undulating tail movements, our data demonstrate clear sexual dimorphism in the frequency of tail-waving display in *G. albogularis*, that is, males perform tail waving more frequently than females. Moreover, tail-waving by males is affected by the simulated predator's behavior, signaling more frequently when there is a greater predation risk (predator approaching).

Conspicuously colored male lizards attract more predators than cryptic colored individuals (Stuart-Fox et al. 2003; Husak et al. 2006). Free-ranging males of *G. albogularis* suffered more injuries than females and models of males received more attacks than models of females (Ellingson 1994), possibly because of the greater conspicuousness of males. That males in this study were detected from further away than females confirms the males' enhanced conspicuousness relative to females, at least to a human observer. The more intense predation pressure on males may explain the greater frequency of tail-waving by males than females, which show a cryptic dorsal coloration, and may also explain why males perform tail displays when further away from the simulated predator.

Sexual differences in antipredator behavior also occur in other reptiles: male garter snakes flee more frequently than females in response to a potential predator (Shine et al.

2000), but no significant difference was found for another snake species (Whitaker and Shine 1999). Cryptic females of several *Anolis* species had shorter flight-initiation distances and ran over shorter distances than conspicuously colored males (Vanhooydonck et al. 2007). Similarly, in *Crotaphytus dickersonae* males fled sooner and tended to use more the refuges than females, which probably indicates stronger predation pressure on males (Plasman et al. 2007). Therefore, as predator risk is generally higher for males than females (Ellingson 1994; Croft et al. 2006), the sexual differences in antipredator behavior of several species of reptiles, including *G. albogularis*, are in agreement with theoretical predictions (Caro 1995; Ruxton et al. 2004).

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