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Why Do Curly Tail Lizards (Genus Leiocephalus) Curl Their Tails? An Assessment of Displays Toward Conspecifics and Predators

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Why do curly tail lizards (genus *Leiocephalus*) curl their tails? An assessment of displays toward conspecifics and predators

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Abstract

Animal display behaviors are used to convey specific messages to other animals, including potential mates, rivals, and predators. However, because these different types of interactions can be mediated by a single behavioral display, or conversely, multiple signals can be used to convey one specific message, interpretation of any particular behavioral display can be difficult. *Leiocephalus* lizards (i.e., curly tails) provide an excellent opportunity to study the use of display behaviors across multiple contexts. Previous research has demonstrated that the use of tail curling in these lizards is associated with predation risk, but less is known regarding the use of this behavior in social interactions with conspecifics. The goal of this study was to determine the extent to which tail curling display behavior is used to mediate both social and predatory interactions in two species, *Leiocephalus barahonensis* and *L. carinatus*. We found that in lizards of both species, tail curling was used in interactions with both conspecifics and potential (human) predators. However, tail curl intensity did not differ between lizards involved in social encounters and solitary lizards, although *L. barahonensis* lizards performed more headbobs during social than non-social observations. Further, *L. carinatus* lizards exhibited greater intensity of tail curling upon fleeing from a human predator than during observations in which individuals interacted with conspecifics, and lizards that exhibited tighter tail curls fled from predators for a longer distance. Finally, tail curl intensity was not correlated with headbob displays in either species, suggesting that these two components of display communicate different information. Our results suggest that tail curling displays, while consistently a component of interactions with potential predators, are not a necessary component of social interactions. These data contribute to a more complete understanding of how and why visual signals evolve for use in communication across multiple contexts.

KEYWORDS
aggression, escape, pursuit deterrence, social display

1 | INTRODUCTION

Animals use a wide variety of display behaviors to facilitate social interactions. Most communication occurs among conspecifics, for example, during courtship of potential mates, aggression toward potential rivals, coordination of foraging or parental care, or to warn others of danger.

Thus, the majority of studies of display have focused on social interactions as the primary selective force in shaping conspicuous signals (Bradbury & Vehrencamp, 1998). Yet, there is evidence across animal taxa that the pressure to deter potential predators has also contributed to signal evolution (reviewed in Cooper & Blumstein, 2015). Such displays may attempt to confuse the predator about the location of the
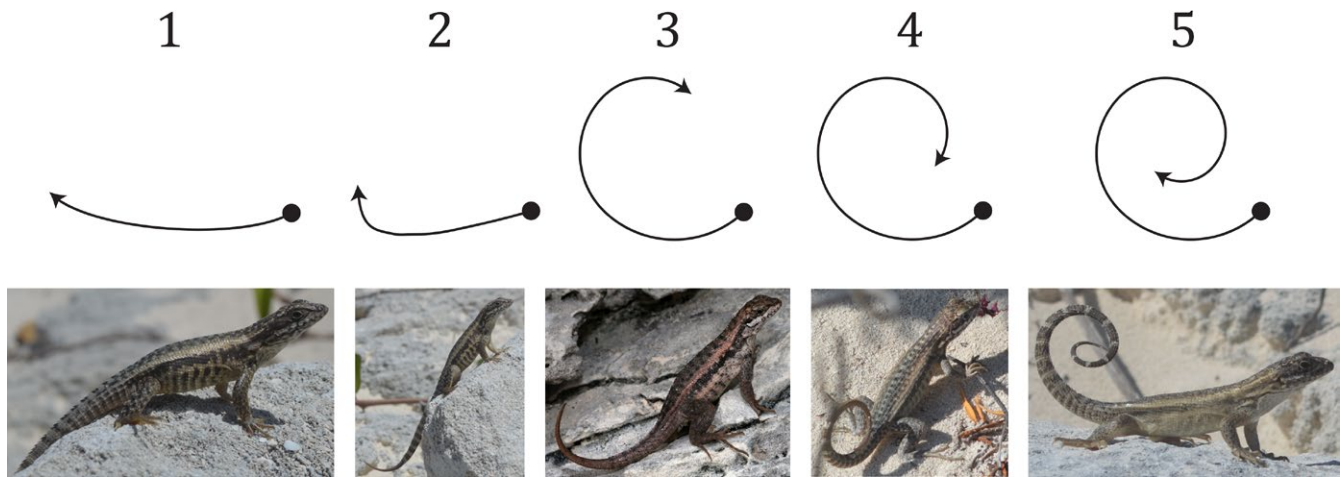
FIGURE 1 Scale of tail curl intensity in *Leiocephalus* lizards. Top panel: Line clubs represent where the tail would attach to the body of the lizard, and arrows represent the end of the tail. Bottom panel: Photographs of *L. carinatus* demonstrating each tail curl intensity. Photograph for intensity 3 was provided by Kip Evans, Mission Blue

prey (i.e., flash concealment displays), to alert the predator that it has been detected, thereby decreasing the chances of a successful attack (i.e., pursuit deterrence displays; Hasson, Hibbard, & Ceballos, 1989; Hasson, 1991), or deflect the predator's attack elsewhere (i.e., predator deflection; Cooper, 1998a, 1998b; Telemeco, Baird, & Shine, 2011). Given the multiple contexts in which a display may occur, the relationship between a display behavior and the information it communicates may be complex (Candolin, 2003; Hebets & Papaj, 2005; Hebets et al., 2016; Johnstone, 1996; Møller & Pomiankowski, 1993). A signal may convey very specific information within a given context, but the same display in a different context may convey a different meaning. Further, a single display may be used to mediate multiple types of interactions (i.e., a pluripotent display), or a display with multiple components may communicate multiple messages (i.e., a degenerate display; reviewed in Hebets et al., 2016).

Studies of display behaviors have demonstrated that many species, and particularly lizards, can use the same suite of degenerate signals to interact with both conspecifics and predators (e.g., Cooper, 2001; Dial, 1986; Langkilde, Schwarzkopf, & Alford, 2005; Leal, 1999; Marcellini, 1977; Radder, Saidapur, Shine, & Shanbhag, 2006). For example, lizards in the genus *Anolis* perform species-specific combinations of pushups, headbobs, and extensions of a colorful throat fan called a dewlap (Jenssen, 1977). These displays are frequently used during courtship and territory defense, and in assertion displays that advertise a lizard's presence in its territory to any unseen rivals (reviewed in Losos, 2009). Anoles also use dewlap and pushup displays to deter potential predators (Leal & Rodríguez-Robles, 1995; Leal & Rodríguez-Robles, 1997a, 1997b), and these displays may be honest indicators of a lizard's ability to escape (Leal, 1999). Thus, a given display could be used to communicate to mates, rivals, or predators, depending upon the context of its use.

Lizards in the genus *Leiocephalus*, commonly called curly tail lizards because most species in this genus curl their tail into a vertical spiral (Figure 1), are another group in which a suite of visual display behaviors may be used in multiple contexts (Cooper, 2001). The best

studied of these species, *Leiocephalus carinatus* (the northern curly tail lizard), uses its tail curl display to deter potential predators (Cooper, 2001, 2007). In addition, by advertising an autotomizable tail when under direct attack by a predator or when the risk of predation is high, lizards (including *Leiocephalus*) may deflect the brunt of an attack to their tail, allowing their escape (Congdon, Vitt, & King, 1974; Cooper, 2001; Dial, 1986; Johnson & Brodie, 1974). Although the function of *Leiocephalus* tail curling has been well documented in the context of predation, less work has directly examined the use of tail curls in social encounters. Several observations have confirmed that tail curling displays function in both courtship and agonistic behaviors (Evans, 1953; Schwartz & Henderson, 1991), but few studies have compared tail curling behaviors across contexts. In addition to the tail curl display, *Leiocephalus* lizards also perform headbobbing (Evans, 1953; Phillips & Howes, 1988), a display behavior common across iguanian lizards (e.g., DeCourcy & Jenssen, 1994; Martins, 1993). Headbobbing and tail curling may be degenerate, such that they communicate the same message to a receiver, or the two components of display may communicate different information, but these possibilities have not been studied.

In this study, we investigated the relationship between display behaviors, predator deterrence, and social interactions in two curly tail lizard species, *Leiocephalus barahonensis* (the orange-bellied curly tail lizard) and *L. carinatus*. *Leiocephalus barahonensis* is endemic to the island of Hispaniola, while *L. carinatus* is common throughout the Cayman Islands, Cuba, and the Bahamas and has been introduced to southern Florida (Schwartz & Henderson, 1991). Both species are found primarily in xeric habitats and are territorial, terrestrial, sit-and-wait foragers whose primary known predators are other lizards, snakes, and birds (Crother, 1999; Schwartz & Henderson, 1991).

We first tested the hypothesis that the tail curling displays of *Leiocephalus* lizards function both as antipredator displays and in social communication with conspecifics. In particular, we predicted that lizards fleeing from a potential predator or interacting with a conspecific would exhibit more intense tail curling than undisturbed lizards that

are not interacting with a conspecific. Next, we tested the hypothesis that, during social communication, tail curls and headbobs are degenerate signals that redundantly communicate a single message. To this end, we predicted that lizard tail curl intensity during social interactions would be positively correlated with headbob rate.

2 | MATERIALS AND METHODS

2.1 | Field data collection

We observed the behavior of *L. barahonensis* in Jul. 2006 in the southwestern Dominican Republic in the following localities: El Paraiso Beach (17.9860, −71.1652), Playa San Rafael (18.0281, −71.1375), Coralsol Beach Resort near Bahoruco (18.0575, −71.1125), La Ciénaga Beach (18.0656, −71.1042), Hotel Ponteverda in Bahoruco (18.1013, −71.0777), Hotel Quemaito in Bahoruco (18.1228, −71.06780), and Hotel Guarocuya in Barahona (18.2023, −71.0878). We studied *L. carinatus* in Jul. 2013 on Crooked Island, Bahamas on the grounds of the Casuarinas Villas (22.8056, -74.3376), a private beach (22.8356, −74.3231), and a public beach (22.7744, −74.2027). All data were manually recorded in field notebooks.

Because these two *Leiocephalus* lizard species do not exhibit sexually dimorphic traits that are identifiable from a distance (Cooper, 2001), we could not consistently determine the sex of an adult lizard of either species before it was captured, and so we did not distinguish between males and females in this study. However, no differences in male and female displays or sex biases in predation rates have been previously reported in studies of these species. Further, no biases in population sex ratio have been reported for these species; the lizards we captured in our study sites exhibited approximately 1:1 sex ratios; and lizard display rates and structures did not differ between the observations in which we could clearly distinguish males and those in which we could clearly distinguish females.

We located all animals between 0830 and 1800 by slowly walking through the study sites until finding an apparently undisturbed individual. To avoid repeated observations of the same individuals, we observed lizards in a particular area only once, moving to a new area for further work. Once we found a lizard, we performed a focal observation, during which a researcher would observe the lizard from a distance of at least 10 m with binoculars. During each focal observation (*L. barahonensis*: *n* = 23; observation range = 14–20 min, average = 19.7 min; *L. carinatus*: *n* = 34; 5–60 min, average = 35.8 min), we recorded all display behaviors (headbobs and tail curls) and locomotor movements, and we determined the intensity of each tail curl. Tail curl intensity was quantified using values from 1 to 5, with 1 indicating that the tail was completely uncurled and 5 indicating that the tail was curled in a tight vertical spiral (Figure 1; following Cooper, 2001). We recorded the tail curl intensity at the beginning of an observation, and each time a lizard changed its tail curl intensity during the observation, we recorded the time at which it changed positions and the intensity of the new tail curl position. We then determined the average tail curl intensity for each lizard, weighted by the duration for which each intensity rating (1–5) was maintained. We also recorded whether the individual engaged in a social interaction during the observational period, defined here by the presence of an interacting adult conspecific within 5 m of the focal individual. Conspecifics were determined to be interacting with the focal lizard if they displayed in the direction of the focal lizard or responded to the focal lizard's displays. If no conspecific was within 5 m, or no conspecific was obviously interacting with the focal individual, the observation was scored as a non-social observation.

To assess tail curling behaviors in an antipredator context, we conducted approach trials (*L. barahonensis*, *n* = 30; *L. carinatus*, *n* = 40) in which a researcher simulated a potential predator, following Cooper (2001). (A subset of *L. barahonensis* individuals (*n* = 20) was included in predator simulations following undisturbed focal behavioral observations, but all *L. carinatus* individuals were used in only one trial.) After locating an undisturbed lizard, or at the end of a focal observation as described above, a researcher approached an undisturbed individual at ca. 0.83 m/s in a linear path, causing the lizard to flee, while a second observer recorded the lizard's tail curl during flight. When the lizard began to flee, the researcher simulating a predator stopped moving and recorded the distance between the researcher and the lizard before it fled (flight initiation distance), the distance the lizard fled before entering a refuge or stopping (distance fled), and maximum intensity of tail curling during the lizard's escape (max flight curl).

2.2 | Statistical analyses

Using focal observational data, we compared display behaviors between social and non-social observations, with separate independent samples *t* tests for each species (with equal variances not assumed), to determine whether average tail curl intensity and headbob rate (headbobs per min) differed across contexts. For the subset of *L. barahonensis* individuals that were included in focal behavioral observations and predator simulations (*n* = 20), we compared average tail curl intensity during observations to max flight curl from the predator approach simulations, using a paired sample *t* test. Because the *L. carinatus* lizards used in focal observations were not the same as those used in predator simulation trials, we compared average tail curl intensity during observations to max flight curl from predator approach simulations using an independent samples *t* test. Finally, we calculated Pearson's correlation coefficients to determine the relationships between flight initial distance, distance fled, and max flight curl for each species. All statistical analyses were performed in JMP (v. 12, SAS Institute Inc., Cary, NC). All data are available in Tables S1–S3.

2.3 | Ethical note

All procedures were approved by the Washington University Institutional Animal Care and Use Committee (2006), or the Trinity University Animal Research Committee (2013). This research was approved by the Bahamas Environment, Science & Technology Commission (Bahamas) and Ministerio de Medio Ambiente y Recursos Naturales (Dominican Republic).

3 | RESULTS

Lizards performed tail curling displays both in observations with social interactions and those without social interactions during undisturbed behavioral observations. In both *L. barahonensis* and *L. carinatus*, the average tail curl intensity did not differ between social and non-social focal observations (*L. barahonensis*: $t_{19.29} = -1.18$, $n = 23$, $p = .25$; *L. carinatus*: $t_{31.95} = -0.32$, $n = 34$, $p = .75$; Figure 2). In *L. barahonensis*, headbob rate was significantly higher for social individuals than for non-social individuals ($t_{12.68} = 2.51$, $p = .02$). However, in *L. carinatus*, headbob rate did not differ between social and non-social observations ($t_{14.66} = 1.24$, $p = .23$; Figure 3).

All individuals exhibited tail curling upon fleeing from the simulated predator. In *L. barahonensis*, individuals did not differ in tail curling intensity when fleeing and during social interactions during the observation period ($t_{18} = 0.76$, $n = 20$, $p = .46$). In *L. carinatus*, however, individuals that were fleeing exhibited a more intense tail curling display than those who engaged in social interactions during the observation period ($t_{33.67} = -2.98$, $n = 40$, $p = .0054$; Figure 2).

In predator simulation trials for *L. carinatus*, we found a positive correlation ($r = .42$, $n = 39$, $p = .008$) between max flight curl and distance fled, indicating that individuals that curled their tail more tightly fled farther. There was a weak positive correlation ($r = .31$, $n = 39$, $p = .057$) between distance fled and flight initiation distance, indicating that individuals that fled when the predator was further away also fled farther. There was no correlation between flight initiation distance and maximum curl intensity during escape. In *L. barahonensis*, there were no significant relationships found between any of the approach variables (all $r < -.023$, $p > .63$).

During focal observations, headbob rate was not correlated with tail curl intensity during social interactions (*L. barahonensis*: $n = 10$, $r = .28$, $p = .47$; *L. carinatus*: $n = 15$, $r = -.19$, $p = .50$) or in non-social observations (*L. barahonensis*: $n = 13$, $r = -0.05$, $p = .86$; *L. carinatus*: $n = 19$, $r = -.38$, $p = .11$).

4 | DISCUSSION

The tail curling display of *Leiocephalus* lizards, as a display thought to function in both intraspecific and interspecific communication (Cooper, 2001), provides us with the opportunity to disentangle the varied functions of a display in a complex environment. Our results confirmed that *L. barahonensis* and *L. carinatus* lizards curl their tails with high frequency and intensity across multiple contexts. Indeed, all lizards in predator simulation trials curled their tails, and during each focal observation, lizards curled their tails whether they were alone or interacting with conspecifics. This near-constant use of the display behavior could indicate that tail curling is useful under one very consistent condition, that it is useful in many different contexts, or possibly that tail curling does not have a signaling function.

If the tail curl display is a critical component of intraspecific interactions in *Leiocephalus* (Evans, 1953), we predicted that animals would perform the display more frequently during such an interaction than
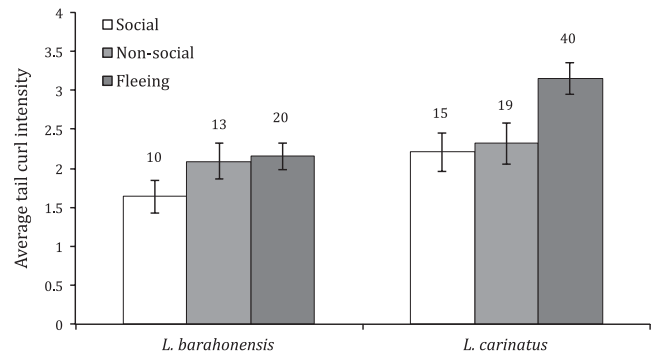

FIGURE 2 Average tail curl intensity (±1*SE*) of social (white) and non-social (light gray) *L. barahonensis* and *L. carinatus* during focal observations, and while fleeing a simulated predator (dark gray). Sample sizes are listed above each column

they would when alone. Yet, consistent with the results of Cooper (2001), who conducted observations on seven *L. carinatus* individuals, we found that lizards in social and non-social observations in this study did not differ in average tail curl intensity (Figure 2). It is possible that during the observations we designated as non-social, the focal lizards were interacting with other lizards that the observers could not see, but this is unlikely for two reasons. First, observations occurred in open beach habitats with relatively little habitat structure that would hide other lizards from our view. Second, another component of display differed between social and non-social observations; in *L. barahonensis*, lizards performed more frequent headbobs during social interactions than during non-social observations, and while the difference between social and non-social headbobs was nonsignificant in *L. carinatus* (likely due to the large variation in headbob displays in this species), the pattern was in the same direction (Figure 3). Alternatively, displays performed by solitary *Leiocephalus* lizards may function as assertion displays, alerting any unseen conspecifics to the presence of an alert lizard guarding its territory, but we could not distinguish this possibility in the current study. Interestingly, in both species, there was no correlation between tail curl intensity and headbob rate during focal observations, suggesting that the two components of display may communicate different information (e.g., Hebets, 2008; Uy & Safran, 2013).
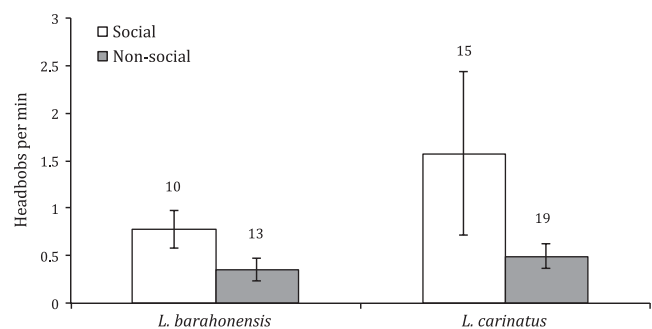

FIGURE 3 Average headbobs per min (±1*SE*) of social (white) and non-social (gray) *L. barahonensis* and *L. carinatus* during focal observations. Sample sizes are listed above each column

If the primary use of the *Leiocephalus* tail curl display is antipredatory (Cooper, 2001, 2007), functioning either for predator deterrence or deflection (Telemeco et al., 2011), we would predict that the tail curl intensity would be greatest during predator simulation trials. Our results were consistent with this prediction for *L. carinatus;* when an individual was approached directly by a human predator, tail curling was stronger than when an undisturbed individual interacted with a conspecific (Figure 2). Further, tail curl intensity was positively correlated with distance fled in this species, supporting the hypothesis that *L. carinatus* lizards perform enhanced tail curl displays when they perceive greater predatory risk. Yet, *L. barahonensis* did not enhance its tail curl display during predator trials, suggesting that the tail curl display might be used differently by the two species.

Tail curl displays could also vary between the species as a function of the lizards' environment in ways that were not directly measured in this study. For example, lizards that generally experience greater risks of predation, as a result of high predator densities or low refuge availability, might curl their tails more often or with greater intensity (e.g., Cooper, 2003; Pietrek, Walker, & Novaro, 2009). In addition, tail curling postures could function to improve an animal's stability and increase its running speed, as found in several other lizard species that do not exhibit tail curling (Arnold, 1984; Ballinger, Nietfeldt, & Krupa, 1979; Punzo, 1982). However, tail curling has not been shown to play any role in stabilization during locomotion (Cooper & Blumstein, 2015).

In conclusion, the results of this study are consistent with Cooper's (2001) suggestion that tail curling does not seem to be a distinguishing component of *Leiocephalus* social displays and support the hypothesis that in *L. carinatus*, the primary use of the tail curl display is antipredatory (Cooper, 2001, 2007). However, the almost constant use of tail curling, particularly if it is an honest indicator of some aspect of an animal's quality or ability, offers the opportunity for the display to be co-opted to function across multiple contexts (Leal & Rodríguez-Robles, 1997a). Further studies of the social and ecological contexts of this display will contribute to our understanding of how adaptive behaviors with multiple purposes can evolve in complex environments.

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