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Honest signalling during prey–predator interactions in the lizard *Anolis cristatellus*

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Current theory on the evolution of pursuit-deterrent signals predicts that it may be advantageous for the prey to communicate to the predator its alertness and its ability to escape an attack. I tested these predictions by staging predator–prey encounters between *A. cristatellus* lizards and a model of one of its predators under natural conditions. Results supported the use of pushup displays as pursuit-deterrent signals. The intensity of signals, measured as the number of pushups given during predation episodes, was significantly positively correlated with individual physiological condition measured as endurance capacity. Because endurance capacity can be a critical aspect limiting the ability of *A. cristatellus* to escape a predatory attack, pushup displays can potentially communicate an individual's ability to escape an attack and, therefore, can be categorized as honest signals. Furthermore, because pushup displays are widely used during anoline social interactions, predation pressure and sexual selection may simultaneously favour the evolution of honest communication to allow both the predator and the potential mate or male rival to assess individual quality using the same signal.

Historically, the evolution of elaborate displays by males has been attributed to the effects of sexual selection (reviewed in Andersson 1994). None the less, recent studies suggest that conspicuous signals in males may also evolve in the context of prey–predator communication (Godin & Dugatkin 1996; Leal & Rodríguez-Robles 1997a, and references therein). It would seem paradoxical that prey (excluding those organisms that rely on aposematism as a defence tactic) would respond to an approaching predator by giving conspicuous signals. However, during a hunt, predators must constantly assess their likelihood of successfully capturing prey (Krause & Godin 1996). Therefore, prey may benefit by communicating their alertness and their ability to escape a predator's attack, if predators use this information in deciding whether or not to attack (i.e. pursuit-deterrent signals; Hasson 1991; Caro 1995). However, not all prey individuals are of equal fitness because of physiological condition, and consequently escape ability will vary (FitzGibbon & Fanshawe 1988; Caro 1994). Theoretical models of the evolution of pursuit-deterrent signals predict that when a prey individual has a high probability of escape, both the predator and the prey benefit if the prey communicates its likelihood of escape to the predator; thus, both animals can avoid a costly encounter (Grafen 1990; Vega-Redondo & Hasson 1993; Yachi 1995; Hasson 1997; but see Krebs & Dawkins 1984).

Signals that communicate the prey's ability to escape an attack can be categorized as 'honest' signals (Zahavi 1975, 1987). According to models, honesty will evolve and be maintained in a system only if signalling is costly to the signaller (Zahavi 1975; Grafen 1990; Vega-Redondo & Hasson 1993). When signalling is costly, theories predict the following characteristics of an evolutionarily stable state of honest pursuit-deterrent signals: (1) the cost of the signal should be higher to low-quality individuals than to high-quality individuals (i.e. individuals in good physiological condition); thus, individuals in poor physiological condition would not be able to cheat successfully; (2) the intensity of the signals should correlate with the prey's ability to escape an attack; and (3) the predator should assess the escape ability of the prey via the intensity of the signal. A central question in the study of pursuit-deterrent signals then is: are pursuit-deterrent signals honest indicators of the prey's escape ability? To date, empirical evidence assessing this question has been limited to establishing a correlation between some visual aspect of the animal's physical condition (e.g. size or colour) and the use of a pursuit-deterrent signal (Caro 1994; Godin & Dugatkin 1996), with the assumption that visual physical condition can be an indicator of escape abilities. For example, in the Trinidadian guppy, *Poecilia reticulata*, the

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conspicuousness of the male colour pattern is positively correlated with predator inspection (e.g. willingness to approach the predator) as a pursuit-deterrent signal (Godin & Dugatkin 1996). However, there is no empirical evidence that demonstrates a direct correlation between the attribute that enhances the prey's likelihood of escaping an attack (e.g. endurance capacity, speed; Bennett & Huey 1990) and the intensity of the signal given as a pursuit-deterrent signal. For example, a prey's escape ability might depend not just on its size, which is visually accessible and fixed, but on its stamina, which is not visible. Therefore, the only way that the prey can communicate the hidden trait to the predator is to engage in a display that is correlated with its stamina, therefore advertising its escape ability.

The lizard *A. cristatellus* performs conspicuous displays (e.g. pushups, in which the body is moved up and down in a vertical plane by flexion and extension of the legs) during encounters under natural conditions with a model of its natural predator, the snake *Alsophis portoricensis*, in accordance with the pursuit-deterrent signal hypothesis (Leal & Rodríguez-Robles 1997a). During predatory encounters in the laboratory, *A. portoricensis* respond to signalling *A. cristatellus* by stopping their approach towards the lizards (Leal & Rodríguez-Robles 1995). Furthermore, lizards that do signal are subsequently attacked significantly less often than lizards that do not signal (Leal & Rodríguez-Robles 1995). During the summer of 1998, I observed two encounters under natural conditions between *A. cristatellus* and *A. portoricensis*. In both episodes the lizard performed pushups while remaining stationary towards the approaching snake, which responded by stopping its approach towards the lizard. These observations suggest that the behaviour displayed by *A. portoricensis* under laboratory conditions is also displayed under natural conditions.

The purpose of this study was to test experimentally the prediction that pursuit-deterrent signals are honest, using the responses given by *A. cristatellus* towards *A. portoricensis* as a model system. If the displays of *A. cristatellus* towards predators are honest signals, a relationship should exist between the intensity of the signal and the lizard's ability to escape an attack. Previous laboratory studies have shown that *A. cristatellus* can escape from *A. portoricensis* either by fleeing at the moment of the attack (19% of the episodes) or by actively defending itself by struggling and biting once captured (Leal & Rodríguez-Robles 1995). Captured anoles struggle violently, dragging the snake with them as they attempt to escape. Anoles can and do escape from a snake's grip (37% of the trials), suggesting that biting and struggling are effective escape tactics (Leal & Rodríguez-Robles 1995). In lizards, short bursts of activity are supported principally by anaerobic metabolism, but longer efforts including the ability to repel a predator after being captured also involve a significant aerobic component that is correlated with endurance capacity (reviewed in Bennett & Huey 1990). Thus, endurance capacity may be a critical aspect of an anole's vulnerability to predation. Therefore, if the signals given by *A. cristatellus* are honest, a positive correlation should exist between the number of pushups given in the presence of *A. portoricensis* and endurance capacity.

METHODS

I staged predator–prey encounters between 21 adult male *A. cristatellus* and a model of *A. portoricensis* at the Cambalache Forest Reserve, Barrio Garrochales, Arecibo, Puerto Rico, where both species occur sympatrically. *Anolis cristatellus* is a medium-to-large (snout–vent length, SVL=56–76 mm), grey-brown, sexually dimorphic lizard found on tree trunks near the ground (Rand 1964) in mesic–xeric areas. On Puerto Rico, it is common in open forest and fields from sea level to mid-elevation. Anoles rely almost exclusively on visual cues for social communication and detection of potential predators (Fleishman 1992). The *A. cristatellus* used in this study had a mean ± SE SVL of 55.7 ± 0.7 mm (range 47–60 mm, *N*=21) and a mean ± SE body mass of 5.3 ± 0.2 g (range 3.2–7.2 g, *N*=21). The colubrid *A. portoricensis* (maximum SVL=923 mm) is largely a ground-dwelling, diurnal, active forager (Henderson & Sajdak 1986) that preys primarily on reptiles, particularly anoles (Rodríguez-Robles & Leal 1993; Henderson & Sajdak 1996). *Alsophis portoricensis* relies mainly on visual stimuli to locate prey (personal observation).

Trials were conducted during daytime (1000–1500 hours) when both *A. cristatellus* and *A. portoricensis* are active. Only lizards perching in the normal, alert, head-down posture within 1.3 m of the ground were tested. Each trial consisted of presenting a single, previously untested and undisturbed lizard with an intact, stuffed skin of an *A. portoricensis* collected at Cambalache. The snake model (SVL=64 cm, tail length=27 cm) was fashioned such that its anterior end (11 cm) was raised 9 cm off the ground to simulate the foraging pose of *Alsophis*. A transparent fishing line was used to fasten the anterior 18 cm of the stuffed snake to a Plexiglas stand measuring 15.2 × 16.2 cm. The posterior 73 cm of the model had a sinuous shape that remained in contact with the ground. Recent work with *A. cristatellus* and *A. cuvieri* has demonstrated that a model of *A. portoricensis* is as effective as a live snake in eliciting antipredator responses (Leal & Rodríguez-Robles 1997a, b).

Using a stopwatch and an audio tape recorder, I recorded all behavioural acts performed by the lizard 5 min before ('control period') and 5 min after ('experimental period') an assistant started moving the snake model towards it. The model was positioned 4–8 m from the base of the lizard's perch (depending on the physiography of the surrounding area) and in such a way that it was unlikely that the lizard could see the model before the field assistant began moving it. To account for any disturbance that we may have caused to the lizard while setting up the snake model, we began control observations after the model was in place and we had assumed our positions. During the experimental period, the field assistant, positioned at least 4 m behind the tree where the lizard was perched and using a transparent fishing line attached to the Plexiglas stand, pulled the snake model by hand towards the lizard at approximately

6 cm/s until it reached the base of the tree in which the *A. cristatellus* was perched. The model remained in this position until the end of the trial (methods follow Leal & Rodríguez-Robles 1997a, b). Meanwhile, I watched the lizard from a position partially concealed by the surrounding vegetation, 4–5 m in front of the lizard's perch. Once during each trial, the field assistant stopped pulling the snake towards the base of the lizard's perch for up to 5 s in an attempt to mimic the foraging behaviour of *A. portoricensis*. Lizards whose behaviour during the control or experimental periods was apparently affected by the presence of neighbouring lizards were excluded.

I followed the behavioural descriptions of Jenssen (1977) and Greene (1988) to categorize the behavioural acts of each lizard. I recorded the number of iterations of each behaviour. I caught lizards after each trial to measure SVL (±1 mm) and mass (±0.2 g). I then brought the lizards into the laboratory to measure their endurance capacity. Lizards were housed individually in plastic cages (28 × 12 × 17 cm), provided with a perch site and water ad libitum, and kept on a 12:12 h light:dark cycle at room temperature. After endurance capacity was measured, the lizards were released in the forest. To avoid retesting of the same subjects, I released the lizards outside the area where the experiment was being conducted.

I measured endurance capacity using a circular racetrack measuring 310 cm in circumference with a fibreglass window screening substrate (1.6-mm mesh) that provided good traction. I began each trial by placing the lizard at a designated starting point. Lizards began immediately to run around the track. To stimulate the lizards to continue to move around the racetrack, I tapped them on the tail; if the lizard did not move after five consecutive taps, the trial was terminated (methods follow Brodie 1993). I used the time at which the lizard stopped moving as the measurement of endurance capacity. Using a stopwatch, I recorded the total amount of time until the lizard stopped running. I also recorded the total distance travelled during each trial. I tested each lizard twice with a 24-h resting period between trials. I performed the first test after the lizards were in the laboratory for a period of 24–26 h. The temperature of the room during the trials ranged between 28.2–28.9°C, which corresponds to the 'optimal' temperature for sprinting of *A. cristatellus* (Huey 1983). For statistical analysis, I used the greater of the two endurance measurements for each animal. I tested the predictions of the honest signal hypothesis using the individuals highest endurance measurements, and also the average performance measure of each individual over both endurance trials. The latter may be a conservative test because it gives equal weight to both trials even though the lizards' endurance capacity was significantly lower during the second test (Wilcoxon's signed-ranks test: $T=2.39$, $N=18$, $P<0.05$). Statistical analyses were performed with StatView (version 4.51; Abacus Concepts 1996). All probabilities are two tailed, and the significance level for all tests was 0.05. The statistical values from the Wilcoxon's signed-ranks test and Spearman rank correlation are corrected for ties.

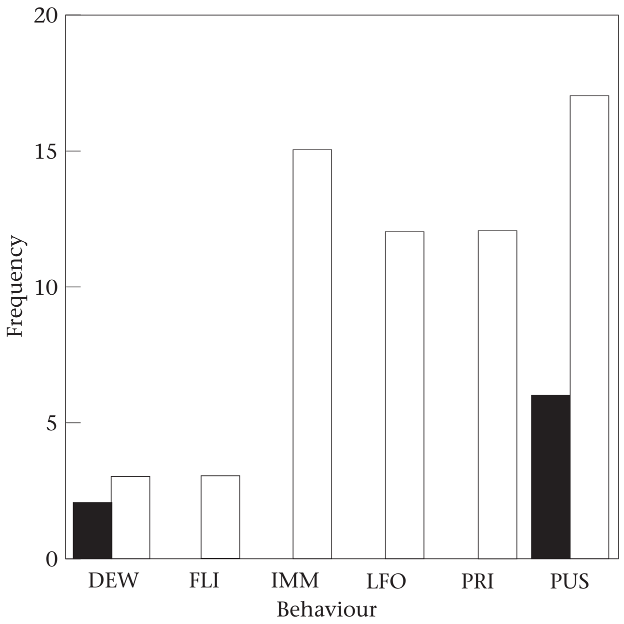

Figure 1. Frequency of behaviour patterns performed by *A. cristatellus* during control (■) and experimental periods (□). Because the display of the different behavioural patterns was not exclusive, frequencies did not have to equal 100. DEW: Dewlapping; FLI: flight; IMM: immobility; LFO: lateral face-off; PRI: predator inspection; PUS: pushup.

RESULTS

During the experimental period, *A. cristatellus* performed six behavioural acts: (1) remaining still for at least 120 s while looking towards the snake model (immobility); (2) movement towards the predator (predator inspection); (3) movement at least 30 cm away (e.g. up the tree) from the snake model (flight); (4) positioning of the body perpendicularly to the predator (lateral face-off); (5) dewlapping: extension and contraction of the throat fan (dewlap) in a vertical axis; and (6) pushups (Fig. 1).

The lizards performed significantly more pushups during the experimental period than during the control period (Wilcoxon's signed-ranks test: $T=3.64$, $N=18$, $P<0.01$), but there was no significant difference in the frequency of dewlapping between the two periods (Wilcoxon's signed-ranks test: $T=1.13$, $N=4$, $P=0.2$). Of the 17 lizards that performed pushups towards the snake model, only two fled immediately (within 2 s) after performing, while 15 performed pushups while remaining stationary; thus significantly more individuals performed pushups while remaining stationary (exact test using binomial distribution: $P<0.001$).

Body size was not correlated with the number of pushups the lizards performed in the presence of the snake model (Spearman rank correlation: $r_S=0.07$, $N=21$, $P=0.7$), or with endurance capacity (Spearman rank correlation: $r_S=-0.11$, $N=21$, $P=0.5$). However, the number of pushups performed in the presence of the snake model and the endurance capacity of the individual were positively correlated (Spearman rank correlation: $r_S=0.49$, $N=21$, $P<0.05$; Fig. 2). The number of pushups performed

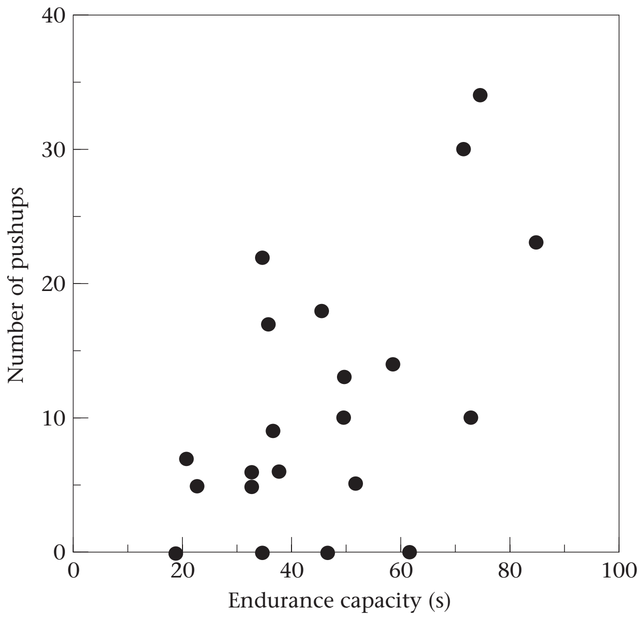

Figure 2. Relationship between signal intensity (measured as the number of pushups) and endurance capacity (measured as time spent running) of *A. cristatellus* in the presence of the snake model.

in the presence of the snake model was also positively correlated with the endurance capacity of the individual using the average score from both trials (Spearman rank correlation: $r_S=0.47$, $N=20$, $P<0.05$). By contrast, the number of pushups performed by lizards during the control period was not correlated with their endurance capacity (Spearman rank correlation: $r_S=0.10$, $N=21$, $P=0.6$). Distance travelled in the laboratory trials was related to both endurance capacity (Spearman rank correlation: $r_S=0.70$, $N=21$, $P<0.01$) and the number of pushups performed in the presence of the snake model (Spearman rank correlation: $r_S=0.43$, $N=21$, $P<0.05$).

DISCUSSION

Anolis cristatellus performed significantly more pushup displays after being exposed to the snake model than during control observations, which suggests that pushup displays were given in response to the presence of the snake model. Furthermore, during the experimental period, lizards either performed pushups while remaining stationary or in combination with predator inspection, which is in accordance with the pursuit-deterrent hypothesis (discussed in Leal & Rodríguez-Robles 1997a). This study has shown experimentally that the number of pushups *A. cristatellus* performs towards a natural predator is positively correlated with its endurance capacity. This result suggests that *A. cristatellus* is not only communicating to the predator that it has been detected, but also is potentially communicating its ability to escape an attack. The results also demonstrate that endurance capacity was not correlated with *A. cristatellus* body size, which suggests that *A. portoricensis* may not be able to assess the ability of *A. cristatellus* to escape an attack based on its visual physical attributes (i.e. body size or mass). Despite extensive documentation and discussion of the signals that prey provide to predators (reviewed in Caro 1995), this is the first study demonstrating a direct correlation between the intensity of a pursuit-deterrent signal and a physiological attribute that may enhance the prey's likelihood of escaping an attack. Thus, pushups can be an honest indicator of the ability of *A. cristatellus* to escape predation.

Twelve *A. cristatellus* performed pushup displays in combination with predator inspection and lateral face-off, also reported by Leal & Rodríguez-Robles (1997a). The combined use of pushups and predator inspection resulted in a jerky display, which has been proposed to be optimal for eliciting the predator's attention (Fleishman 1992), and may effectively communicate to the predator that it has been detected (Leal & Rodríguez-Robles 1997a). Two hypotheses have been proposed to explain the combined use of different behavioural acts: the backup signal hypothesis, in which multiple signals allow more accurate assessment of a single aspect of the signaller's condition, and the multiple message hypothesis, in which different signals convey information about different aspects of the signaller's condition (reviewed in Johnstone 1996). However, further experimental data are needed to assess these possibilities.

One corollary of the honest signal hypothesis is that individuals of *A. cristatellus* in poor condition should not be able to cheat successfully (Zahavi 1987; Grafen 1990). One factor that may keep lizards from cheating is the energetic cost of signalling. Studies on the physiological cost of *Anolis* displays have demonstrated that signalling is an energetically demanding behaviour (Bennett et al. 1981). Moreover, because lizards rely heavily on glycolysis to power short intervals of intense exercise (Wine & Gatten 1992), such as fleeing from a predatory attack, long periods of signalling may impair the lizard's ability to flee if a predator attacks. Because *A. portoricensis* sometimes attacks *A. cristatellus* even after they signal (Leal & Rodríguez-Robles 1995), cheating can be costly. On the other hand, individuals of high quality can afford the cost of signalling and still be in good energetic balance to defend themselves actively if the snake attacks.

Signalling makes individuals more conspicuous, which may result in an increase in the probability of detection and/or attack by a predator. Therefore, individuals in poor physiological condition should employ alternative antipredator responses that reduce the probability of detection by predators. In the present study, three of the lizards never signalled to the approaching snake model, but instead remained immobile throughout the experimental period. The endurance values of these three lizards were below the mean for the lizards that signalled. *Anolis cristatellus* has a cryptic coloration (Heatwole 1968); by staying immobile, lizards may be able to escape detection by *Alsophis*. Alternative antipredator responses employed by individuals in poor physiological conditions have also been reported for the Thompson's gazelle, *Gazella thomsoni*, Grant's gazelle, *Gazella granti*, and the topi, *Damaliscus korrigum* (FitzGibbon & Fanshawe 1988; Caro 1994), and have been suggested for the skylark, *Alauda arvensis* (Cresswell 1994).

The pursuit-deterrent signal hypothesis predicts that prey can communicate to the predator their ability to escape an attack, and that if a predator attacks a high-quality prey, the predator should be less likely to successfully subdue it (Hasson 1991; Vega-Redondo & Hasson 1993; Caro 1995). The correlation between pushup intensity and endurance capacity in the present study is consistent with these predictions. During laboratory experiments, snake-captured *A. cristatellus* struggle vigorously, biting the snake for up to 28 min (Leal & Rodríguez-Robles 1995). Furthermore, subduing time (the time *A. portoricensis* spent subduing the lizard) of *A. cristatellus* increases linearly with the time the lizard spends biting the snake (Leal & Rodríguez-Robles 1995). These observations suggest that lizards with higher endurance capacities should be able to defend themselves from the snake for longer periods. Because the prey's probability of escape increases with its subduing time (Formanowicz & Brodie 1988; Lima & Dill 1990), anti-predator mechanisms that increase prey-handling time may affect whether a predator attacks or subdues certain prey.

Studies on *Anolis* signal evolution have mainly focused on the processes of species recognition and sexual selection, either through mate choice or male–male competition (Crews 1975; Jenssen 1977; Andrews 1985; Losos 1985). Signal intensity is a critical factor in interactions mediated by signals in many animals (Gibson & Bradbury 1985; Höglund & Robertson 1990; Payne & Pagel 1996) and may play a role in sexual selection in *Anolis* (Crews 1975; Andrews 1985). Pushup displays, which are commonly used by *A. cristatellus* in courtship displays and male–male conflicts (Ortiz & Jenssen 1982), are also an honest signal during predator–prey interactions, suggesting that predation pressure and sexual selection may simultaneously favour the evolution of honest communication; because both the predator and the potential mate or male rival may assess individual quality using the same signal. Conspicuous signals that are used during both sexual selection and as pursuit-deterrent signals have also been reported for the Trinidadian guppy and the skylark (Cresswell 1994; Godin & Dugatkin 1996). Whether pushups initially evolved due to predator–prey interactions or due to social interactions still remains a question. However, two possible hypotheses for the evolution of conspicuous traits are the Fisherian model or (runaway selection model) and the honest signal or (good genes) model (Fisher 1958; Zahavi 1975, 1987). However, the Fisherian model cannot be used to explain the evolution of conspicuous signals due to prey–predator communication because of the lack of genetic correlation between the signal and the preference for the signal that is necessary for the model (Lande & Kirkpatrick 1988; Yachi 1995). In contrast, the honest signal hypothesis can be used to explain the evolution of pushup displays in both social interactions and predator–prey interactions.

Finally, the results of this study, together with those from the Trinidadian guppy, suggest that honesty can be a selective force driving the evolution of pursuit-deterrent signals. If signal intensity reflects the likelihood of an individual escaping an attack, the probability that a predator aborts a pursuit may depend on the intensity of the signal. However, at which signal intensity a predator aborts an attack remains an open question that should be addressed in further studies.

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