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Predator-Elicited Foot Shakes in Wall Lizards (*Podarcis muralis*): Evidence for a Pursuit-Deterrent Function

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Under certain circumstances, prey may inform potential predators of their unprofitability by means of pursuit-deterrent signals. The evidence for pursuit-deterrent signaling in reptiles is scant and taxonomically biased. Wall lizards, *Podarcis muralis* (Squamata: Lacertidae) produce several distinct types of stereotyped foot shake displays, of which one, performed in antipredator contexts, is a likely candidate for a pursuit-deterrent function. We investigated this possibility by recording the responses of lizards in the field to a slowly approaching human acting as a surrogate predator. In addition to starting and flight initiation distances, we measured the presence of foot shakes, the leg that was shaken, and the distance from the observer at which the display was performed (display distance). Of a total of 484 approaches, 109 (22.5%) elicited foot shake displays. Roughly half the lizards displayed from the location where they were first sighted, while the other half moved a short distance, then displayed. There was no left-right preference in the leg used to display, but most lizards displayed with the leg closer to the approaching predator. Juveniles and subadults had smaller flight initiation distances than adult lizards. There were no sex-related differences in starting or flight initiation distances, but females, for a given distance, were more likely to display than males. Foot shake display frequency declined abruptly at 1 m. If lizards waited until the surrogate predator was this close, they mostly fled without displaying. Our results show that antipredator foot shaking in *P. muralis* is consistent with expectations from pursuit-deterrent theory.

Keywords: antipredator behavior, communication, display, dynamic visual signal, reptile

Signaling to a predator that is ready to launch an attack may seem like the wrong thing to do for a potential prey animal. Yet theoretical models predict that, under certain circumstances, prey may benefit from signaling that pursuit is likely to be unprofitable because they are aware of the predator's presence and can escape if attacked (Woodland, Jaafar, & Knight, 1980; Vega-Redondo & Hasson, 1993; Bergstrom & Lachmann, 2001). Pursuit-deterrent signals have been identified in a wide variety of vertebrate taxa, including fish, reptiles, birds, and mammals, although the evidence in support of a pursuit-deterrent function is often far from conclusive (reviewed in Ruxton, Speed, & Sherratt, 2004; Caro, 2005).

In lizards, most putative pursuit-deterrent displays consist of some sort of tail display (*Cophosaurus texanus*, Dial, 1986; *Callisaurus draconoides*, Hasson, Hibbard, & Ceballos, 1989; Cooper, 2010a, 2010b; *Leiocephalus carinatus*, Cooper, 2001, 2007; *Carlia jarnoldae*, Langkilde, Schwarzkopf, & Alford, 2004; *Gonatodes albogularis*, Bohórquez Alonso, Martínez Cotrina, Aguilar Pardo, Font, & Molina-Borja, 2010). Exceptions include dewlapping and push-up displays in the Puerto Rican anole, *Anolis cristatellus* (Leal & Rodríguez-Robles, 1997), and arm waving in the Bonaire whiptail lizard, *Cnemidophorus murinus* (Cooper, Pérez-Mellado, Baird, Caldwell, & Vitt, 2004). The latter is also one of the few examples reported, so far, of pursuit-deterrent signaling in Scleroglossa, a clade that encompasses over a dozen lizard families, including Lacertidae. Bonaire whiptails wave their arms when approached by a researcher acting as a simulated predator. Lizards preferentially wave the arm closer to the surrogate human predator, and their arm waving is affected by the speed, direction, and directedness of the approaching predator in ways consistent with a pursuit-deterrent function (Cooper et al., 2004).

Stereotyped foot shake displays resembling the arm waving of Bonaire whiptails have been reported in many lizards (Carpenter, 1963; Carpenter, Badham, & Kimble, 1970; Brattstrom, 1971; Murphy, Lamoreaux, & Carpenter, 1978; Ord, Peters, Evans, & Taylor, 2002; Halloy & Castillo, 2006). However, in contrast to the abundant literature on head bobbing displays of iguanid lizards, detailed descriptions of foot shake displays are scant and their function is controversial. While there can be little doubt that at least some foot shakes are social signals addressed to conspecifics, other functions have been proposed, including removing a foot from contact with a hot substrate, maintaining individual dis-

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tance, or inducing predators to move (Magnusson, 1996; Cooper et al., 2004).

Convincing demonstrations of pursuit-deterrence in Lacertidae, a large family of old-world lizards, are lacking (but see Martín & López, 2001). Although foot shake displays are a recurrent feature in descriptions of lacertid behavior (e.g., Weber, 1957; Verbeek, 1972; Molina-Borja, 1981), controlled observations and/or experiments to establish their communicative role have not been conducted. In particular, the possibility that lacertid foot shakes may serve as pursuit-deterrent signals apparently has been overlooked. Interestingly, however, foot shaking in response to predatory (saurophagous) snake chemicals has been reported in several lacertid species (Thoen, Bauwens, & Verheyen, 1986; Van Damme, Bauwens, Thoen, Vanderstighelen, & Verheyen, 1995; Van Damme & Castilla, 1996; Van Damme & Quick, 2001; Downes & Bauwens, 2002). This raises the question whether foot shaking may function as a pursuit-deterrent signal in lacertids.

Establishing the function or functions of foot shake displays is complicated because some species produce more than one foot shake display, often in different contexts. For example, two types of foot shakes have been identified in *Amphibolurus*: a slow foot shake that may signal submission/appeasement and a fast shake that may indicate dominance/aggression (Brattstrom, 1971; Ord et al., 2002). Similarly, a recent study of 11 species of *Liolaemus* lizards identified two types of foot shake displays: one-forelimb and two-forelimb displays (Halloy & Castillo, 2006). However, the idea that a single species may have a repertoire of several structurally distinct foot shakes has been given little previous consideration in studies of lacertid behavior.

The wall lizard, *Podarcis muralis*, is a small lacertid widely distributed throughout central and southern Europe (Arnold & Ovenden, 2002). Our previous fieldwork with *P. muralis* populations in the Pyrenees shows that this species has a repertoire of several distinct foot shake displays that are used in different contexts. One foot shake type in particular is performed in the presence of potential predators (e.g., snakes), leading to the hypothesis that the display may have an antipredator function, but this has never been tested. The aim of the present study was to investigate the function of this particular foot shake type. We simulated predatory attacks by approaching lizards in the field using a standardized protocol, and asked whether the foot shake displays exhibited by *P. muralis* in this context fulfill the predictions of pursuit-deterrent theory. In particular, we predicted, based on the literature, that (1) foot shakes would be performed with the leg facing the predator (i.e., the leg more visible to the predator, thereby avoiding visual obstruction by the lizard's body), (2) lizards would display when the predator was far enough to allow escape but flee if the predator moved closer, and that (3) lizards would perform the display before fleeing or after retreating a short distance from the predator (Hasson, 1991; Leal & Rodríguez-Robles, 1997; Cooper et al., 2004). We collected data on the antipredator behavior of males and females of all ages, allowing comparisons to be made between sexes and age classes. Most previous studies of pursuit-deterrence in lizards have been conducted with individuals of unknown sex and age, and so we lack information regarding potential effects of these variables on the use of pursuit-deterrent displays (but see Bohórquez Alonso et al., 2010).

Method

Study System

Data were collected during July and August of 2008 and 2009 at two Pyrenean sites where *Podarcis muralis* lizards are particularly abundant and easily observed. The first site is in Angoustrine, France (42° 28′ N, 1° 57′ E, 1300–1400 m asl), and consists of a series of ancient moraines characterized by granitic outcrops and abandoned terraced fields surrounded by artificial stone walls, where lizards are very abundant. The vegetation comprises a diversity of annual plants, scattered bushes of common hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*), and a few occasional European ashes (*Fraxinus excelsior*). The other site is located in Cerler, Spain (42° 35′ N, 0° 32′ E, 1100–1500 m asl). This site encompasses a mosaic of habitats, including cultivated fields and artificial prairies surrounded by pine forest (*Pinus sylvestris* and *P. uncinata*). Lizards are found on schist boulders, stone walls, and along the sides of dirt roads. The two sites are approximately 120 km apart.

The main lizard predators at both study sites are the green whip snake (*Hierophis viridiflavus*) and feral cats (*Felis silvestris*; unpublished observations). Other potential snake predators include *Coronella austriaca* and *Vipera aspis* (Diego-Rasilla, 2003b). Potential avian predators include *Falco tinnunculus*, *Buteo buteo*, *Circaetus gallicus*, and several species of owl (Veiga, 1985; Martín & López, 1990).

Behavioral Observations

We located lizards by slowly walking through suitable habitat, selected according to prior observations of lizard abundance and accessibility, at each field site. Observations were conducted on warm, sunny days, when lizards were active. Three researchers (EF, PC, and GPL) acted as surrogate predators in the field experiments, although only one was present for each survey. We did not measure interobserver reliability, but prior to data collection we viewed a large collection of foot shake displays filmed during previous years, and together we ran pilot surveys in the field to ensure that walking speed and recording procedure were consistent across observers. Our pace during surveys was kept constant and at a speed of ca. 16–20 m/min. As most experimental lizards were unmarked, we moved through a given area only once in order to avoid testing the same lizard more than once.

Upon sighting a lizard, the observer halted immediately, measured the distance between himself and the lizard (i.e., starting distance) with a laser rangefinder, and proceeded to watch the lizard through binoculars for 1 min. If no foot shakes were performed during this time, the observer would then approach the lizard while continuously monitoring its behavior through binoculars. Data from other lizard species indicates that there is a higher probability of eliciting pursuit-deterrent displays when lizards are approached slowly (e.g., Dial, 1986; Cooper, 2000, 2010a; Cooper et al., 2004), so our approach speed at this stage was slower than average cruise speed during surveys (i.e., ca. 10 m/min). Use of a human as a surrogate predator has shortcomings (e.g., Caro, 1995) but, given the scarcity of observations of natural predatory events, remains one of the best options for the study of pursuit-deterrence and other antipredator behaviors. It has the advantage of providing a high level of control and consistency in field trials because the observer approaches lizards in a standardized way and records variables that allow comparisons across species and populations. Moreover, previous studies have shown that lizards respond to humans as if they were predators in a manner consistent with predictions of optimal escape theory (Stankowich & Blumstein, 2005; Cooper, Hawlena, & Pérez-Mellado, 2009).

During approaches, lizards would, at some point, either dash out of sight, foot shake, or move a short distance and then foot shake. If the lizard fled or displayed, the observer measured the corresponding "flight initiation distance" (i.e., straight-line distance between observer and lizard when the lizard begins to flee) or "display distance" (i.e., distance between observer and lizard when the lizard displays). In those cases where the focal lizard moved a short distance and then displayed, the observer additionally measured the "relocation distance" (i.e., distance traveled by the lizard from its initial location to where it subsequently performed the display). If a lizard did not flee after performing a foot shake, the observer continued its approach until eliciting a flight. Previous studies of lizard antipredator behavior have measured the distance to the refuge when focal lizards displayed or initiated escape. This was difficult to assess in our case and is probably not as important a variable as in other lizards because most of the *P. muralis* used in this study were found on rock walls, only a few cm away from multiple potential refuges. All distances were measured using a laser rangefinder (Disto A6 and A8, Leica Geosystems, St. Gallen, Switzerland; typical accuracy ± 1 mm). Data were considered to be valid only when focal lizards were continuously in sight during approaches.

In those cases where lizards performed a foot shake display, we recorded the limb with which the display was performed (to assess laterality), and whether the displaying limb was the one closer to the observer (to determine if, as predicted for pursuit-deterrent signals, displays were oriented toward the potential predator; e.g., Hasson, 1991). Few lizards were approached from directly ahead or behind, and we only recorded the orientation of foot shakes when lizards could be unambiguously judged to be in a lateral view with respect to the observer. In those cases in which lizards performed more than one foot shake, we used the information regarding the first foreleg used in the display for analysis. We additionally recorded the posture of displaying lizards according to the following classification (adapted from Greenberg, 1977): (1) ventral adpression: the head and entire ventral surface of the body pressed to substrate, hind legs often spread; (2) anterior body-up: head held up, parallel to substrate or slightly tipped up, rear portion of the body resting on substrate; (3) body-up-low: forelegs partially extended and anterior portion of the body raised above substrate; (4) anterior body-up-high: same as posture 3 but with forelegs fully extended.

We determined the sex and age class of every lizard in the sample based on differences in size, body shape, and coloration. Males are larger, more colorful, and have relatively larger (wider) heads than females. We distinguished three age classes. Adult lizards were large reproductive individuals with fully developed secondary sexual characters. In our study populations, adults have a snout-vent length of 53–76 mm and are at least 2 years old. Subadult lizards were noticeably smaller than adults but large enough to be sexed based on overall body shape. Subadults are individuals born during the preceding reproductive season and therefore ca. 1 year old. Juveniles were the smallest lizards in the population, only a few weeks posthatching and of unknown sex.

Foot Shake Displays

Podarcis muralis lizards produce at least three types of stereotyped foot shake displays (named Types I, II, and III) that are performed in different contexts and that differ in their structure and overall body posture of the displaying lizard. We focused our study on type III foot shakes because this is the display type that lizards perform in the field when approached by an observer or a potential predator (e.g., the snake *Hierophis viridiflavus*).

Type III foot shake displays are performed by lizards of both sexes and all ages, and consist of a rotating motion of the entire foreleg. Lizards perform type III foot shakes while stationary or following a short relocation run, often with no other lizards in sight. Frame-by-frame analysis of video sequences of displaying lizards shows that the foreleg moves first up and forward (toward the head), then down and backward (toward the tail), following a roughly elliptical trajectory (Figures 1 and 2). Displays (bouts *sensu* Halloy & Castillo, 2006) are performed with one foreleg

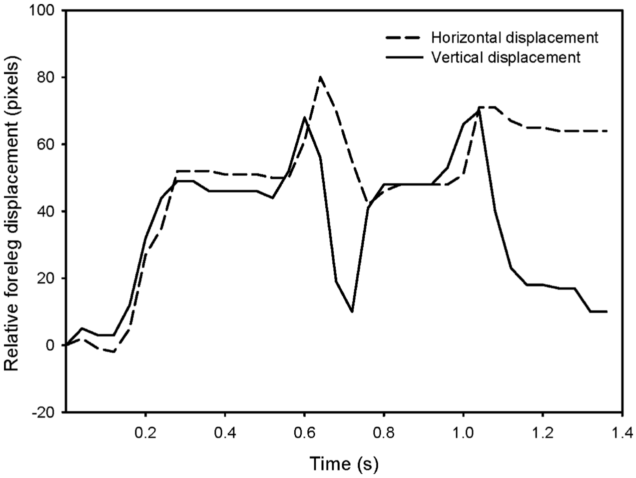

Figure 1. Display-action-pattern (DAP) graph of a type III foot shake display performed by a *Podarcis muralis* lizard. DAP graphs are the standard method used to depict dynamic visual signals of lizards (Carpenter & Grubitz, 1961). To produce DAP graphs of *P. muralis* foot shakes, lizards were filmed in the field using a digital video camera recorder (Canon XL1). Sequences containing foot shakes were captured and edited using nonlineal editing software and analyzed frame-by-frame (25 frames/s) using Image J (National Institutes of Health, Bethesda, Maryland). The resulting DAP graph plots vertical (solid line) and horizontal (broken line) displacement of the foreleg against time. Displacement in the vertical and horizontal planes is measured in the same relative displacement units (pixels). Vertical displacement reflects upward-downward (positive-negative) movement of the leg. Horizontal displacement, on the other hand, refers to anterior-posterior leg movement. Thus, increase in the latter axis reflects forward (i.e., toward the head) movement, whereas decrease reflects backward (i.e., toward the tail) movement. In both axes, the origin of the coordinate system reflects the position of the foot prior to foot shaking. The foot shake display graphed here comprises two cycles of foreleg movement with no pause in between them. Representative frames of the first cycle of leg movement are shown in Figure 2.

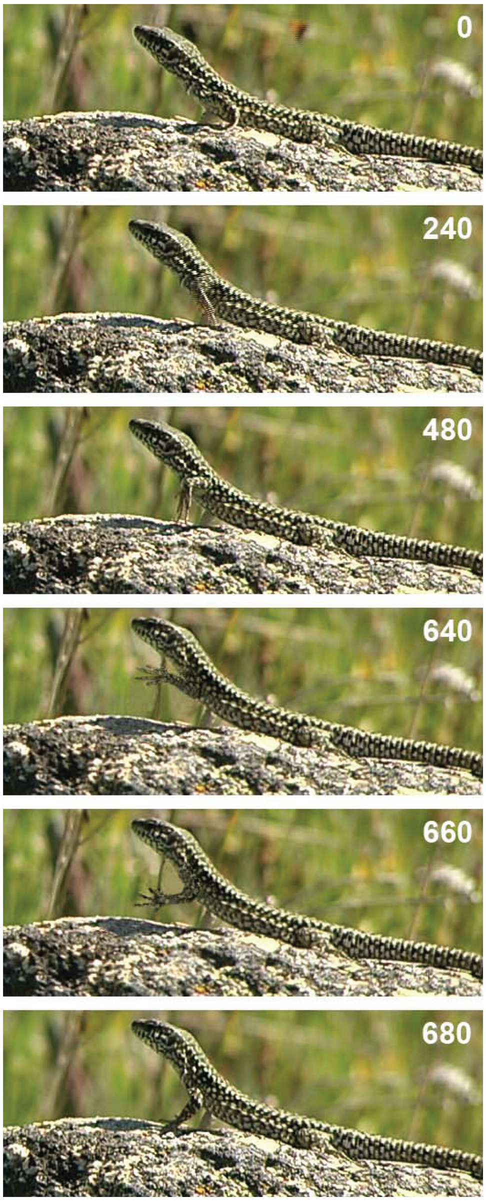

Figure 2. Representative frames from a video sequence of a displaying *Podarcis muralis* lizard showing foreleg movement during performance of the foot shake display graphed in Figure 1. Numbers shown in each frame are milliseconds from the beginning of the display.

only and may incorporate more than one cycle of leg motion. Occasionally, lizards produce several type III foot shake displays in a row, sometimes alternating between the two forelegs. Movement of the foreleg takes place almost exclusively in the sagittal plane (i.e., there is very little left-right displacement of the leg). During displays, lizards exhibit a characteristic raised-body posture by partially extending the forelegs (posture 3). Type III foot shake displays may be accompanied by stereotyped up-and-down motions of the head (head bobs) and/or by sinusoidal movements of the tail in the horizontal plane, with the tail held close to the ground (tail waving).

Data Analyses

We conducted Mann–Whitney U tests for large samples in order to look for sexual or age-related differences in starting and flight initiation distances. The distance at which a lizard is first detected (i.e., starting distance) is largely a reflection of the observer's ability to locate lizards, but the comparison among age and sex classes was done to verify that it did not bias other analyses. We used a goodness-of-fit G test to establish whether displaying lizards adopted any of the four postures more often than expected by chance. We used the normal approximation to the binomial test for large sample sizes to evaluate the existence of laterality (i.e., if lizards have a tendency, at the population level, to use either of both forelegs to foot shake) as well as to evaluate whether the displaying foreleg was the one closer to the approaching observer.

Theory predicts that pursuit-deterrent signals should be given more frequently when the predator is far enough away to allow escape but infrequently, or not at all, if the predator is close enough to pose an imminent threat of capture (Ydenberg & Dill, 1986; Hasson, 1991; Cooper & Frederick, 2007). To evaluate this prediction, we modeled the probability that the first exhibited behavior of a lizard is a foot shake display (vs. fleeing; irrespective of whether the display was preceded, or not, by relocation) as a function of its distance to the observer, in the generalized linear models framework using the logit link. We square-root-transformed distance because that power of distance yielded the lowest Akaike information criterion (Burnham & Anderson, 2002) for the power transformations that we investigated, and removed from the analysis records with starting distances of less than 1 m. The five age-sex classes were allowed separate intercepts (tested for significance using Tukey contrasts with the multcomp package in R; Hothorn, Bretz, & Westfall, 2008) but had a common slope (no interaction terms between age-sex class and slope were significant, all $p > .05$). We also calculated estimates of the square root of distance at which 50% of lizards in that age-sex category displayed as their first exhibited behavior (inverse regression). All reported p values correspond to two-tailed statistical tests.

Results

We conducted a total of 484 approaches to lizards (238 in Angoustrine and 246 in Cerler), of which 109 (22.5%) elicited type III foot shake displays (see Table 1). Most lizards performed a single type III foot shake display, but in a small number of approaches, lizards performed two or more foot shakes, sometimes using different forelegs. More foot shakes were performed by lizards in posture 3 (61.3%) than in any other posture. The difference, on the null hypothesis that all four postures are equally likely, is statistically significant ($G_{adj} = 22.66$, df 3, $p < .001$). Foot shakes were occasionally accompanied by a simple head bob. However, the latter behavior was not easily observed and was therefore not quantified.

Approximately one third of foot shakes (34.2%) were performed during the first minute of observation, while the observer remained stationary, and the remainder were performed during the observer's approach. Relocation data were not recorded during some of the 2008 approaches, so this information is only available for 79 approaches that yielded foot shakes. Of these, 42 lizards displayed

Table 1
Raw Data for Number of Approaches, Number and Percentage of Approaches Eliciting Foot Shake Displays, and Approach, Flight Initiation, and Display Distances (Distance Data in Meters)

Age-sex class	Approaches	Displays	% Displaying	Starting distance	Flight initiation distance	Display distance
Adult females	141	40	28.4	3.89 ± 0.34 (139)	1.37 ± 0.24 (103)	1.94 ± 0.53 (36)
Adult males	213	34	16.0	3.78 ± 0.24 (203)	1.25 ± 0.15 (160)	2.55 ± 0.49 (28)
Subadult females	44	16	36.4	3.09 ± 0.56 (44)	0.98 ± 0.33 (26)	1.72 ± 0.55 (16)
Subadult males	64	10	15.6	2.74 ± 0.30 (64)	0.85 ± 0.22 (46)	1.87 ± 0.97 (10)
Juveniles	22	9	40.9	2.34 ± 0.47 (22)	0.99 ± 0.77 (6)	2.19 ± 1.44 (8)
TOTAL	484	109	22.5	3.53 ± 0.17 (472)	1.21 ± 0.11 (341)	2.09 ± 0.28 (98)

Note. Data are shown separately according to the age and sex of focal lizards (only adult and subadult lizards could be sexed unambiguously). Distance data are expressed as $\bar{x} \pm 95\%$ confidence interval. Sample sizes used for calculation of approach, flight initiation, and display distances are shown in parentheses. Discrepancies between the reported sample sizes and the number of approaches and/or displays are due to missing data.

from the same location where they were first sighted, whereas 37 (46.8%) relocated then displayed. The mean distance that the lizards relocated was 45 cm (range: 4–195 cm). Interestingly, movement during relocations was not always directly away from the surrogate predator.

We found no laterality at the population level in the foreleg used to perform foot shakes ($N = 92$, $\mathrm{Y} = 42$, $z = -0.73$, $p = .7114$), but did find that displaying lizards consistently used the foreleg nearest the approaching surrogate predator ($N = 90$, $\mathrm{Y} = 71$, $z = 5.376$, $p < .001$).

Distance data were available for 472 approaches. Mann–Whitney tests did not reveal statistically significant differences between adult males and females in starting distance ($z = -0.146$, $p = .884$) or flight initiation distance ($z = -0.285$, $p = .776$). Similarly, there were no sex-related differences between subadult lizards in starting ($z = -0.613$, $p = .540$) or flight initiation distances ($z = -0.786$, $p = .432$). That there was no difference in starting distance between males and females suggests that males, despite being larger and more colorful, were not detected from further away than females. Since there were few approaches involving juvenile lizards, their data were pooled with those of subadults. Juveniles and subadults combined had smaller starting and flight distances than adult lizards ($z = -6.351$, $p < .001$; $z = -2.920$, $p = .004$, respectively).

Over all lizards, the frequency distribution of display distance sharply declines for distances below 1 m. Over 50% of all foot shake displays were performed when the lizard was 1–2.5 m from the predator (see Figure 3). This is not an artifact due to more lizards being detected at these distances, as can be seen from the distribution of starting distances (Figure 3a). The fitted generalized linear model predicts adult males to be least likely to display as their first behavior (bottom curve in Figure 4; note that the *y*-axis has been back-transformed to the proportion scale from the logit scale for ease of interpretation) and juveniles to be most likely to display (top curve in Figure 4). Three of the age-sex comparisons were significant, all involving adult males (adult males vs. adult females, vs. subadult females, and vs. juveniles, all $p < .05$). Figure 4 also depicts how the data are distributed relative to distance. For example, the lower display incidence of adult males (lowest curve) is not because their first exhibited behavior occurs at a closer distance—the distribution of their first behavior over distance is similar to that of adult females. However, their curve intersects with the 0.5 display probability at a greater distance (2.13^2 m; Table 2) than it does for other groups. Although data are sparse, both juveniles and subadult females tend to exhibit their first behavior when the observer is further from them. Additionally, the higher intercepts predicted by the model show that their first exhibited behavior is more likely to be a display than it is for other groups. Thus, animals that wait until an observer is closer are more likely to flee as their first behavior, consistent with theory, but there appear to be differences among the age-sex classes in both how close individuals allow a potential predator to approach and in their likely response once they do react.

Discussion

Our results provide supportive evidence for the proposal that type III foot shakes in *Podarcis muralis* function as pursuit-deterrent signals. Although wall lizards foot-shake in many different contexts, type III foot shakes are only elicited by potential predators (including herpetologists) and are thus best interpreted as signals from lizards to predators. Type III foot shakes conform to the design criteria of a pursuit-deterrent signal because they are oriented toward the predator, they are performed more often when the predator is some distance from the lizard, and they give way to flight behavior when the predator closes in on the lizard (Hasson, 1991; Leal & Rodríguez-Robles, 1997; Cooper et al., 2004). This implies that the lizards signal to would-be predators when they are at a sufficient distance to escape, but flee—often without displaying—when their perceived risk of predation is very high. Few lizards displayed if they waited until the observer was closer than 1 m, suggesting a sharp rise in the lizards' risk perception below about 1 m. It would be interesting to investigate whether the minimum distance for foot shake displays to predators is predator-specific.

Our results also argue against the notion that type III foot shakes could be addressed to conspecific receivers, perhaps as a warning signal. Although conspecifics were occasionally near the displaying lizard, in most approaches the focal lizard was alone, or far enough from conspecifics, to rule out an explanation based on social signaling. Further, if the signal was directed at a conspecific, displaying lizards should orient so that the moving leg is exposed to the conspecific rather than the predator. In contrast, our results show that lizards shook the leg on the side closer to the predator significantly more often than the leg on the opposite side.

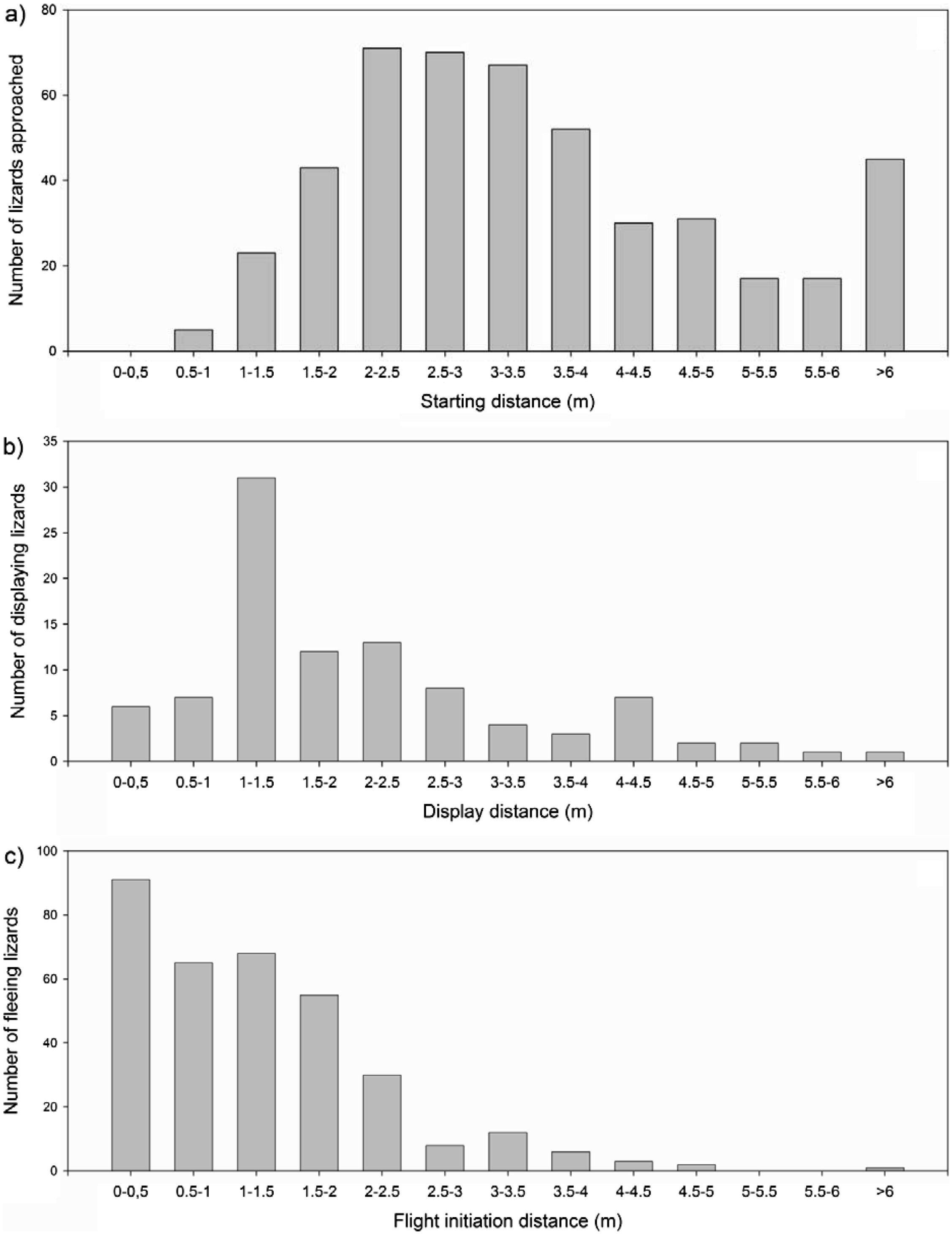

Figure 3. Frequency histograms depicting the distribution of (a) starting distances, (b) display distances, and (c) flight initiation distances. Distances are binned in 0.5-m increments.

Type III foot shakes occur over a wide range of ambient temperatures and are not more frequent when lizards find themselves on hot substrates. Leg movement during type III foot shakes is stereotyped, which is consistent with a signaling function. Further, that the lizard uses the foreleg closer to the predator cannot be interpreted as a necessary consequence of the lizard running away or preparing to do so, as implied by some hypotheses on the function of foot shake displays (Daanje, 1951; Cooper et al., 2004).

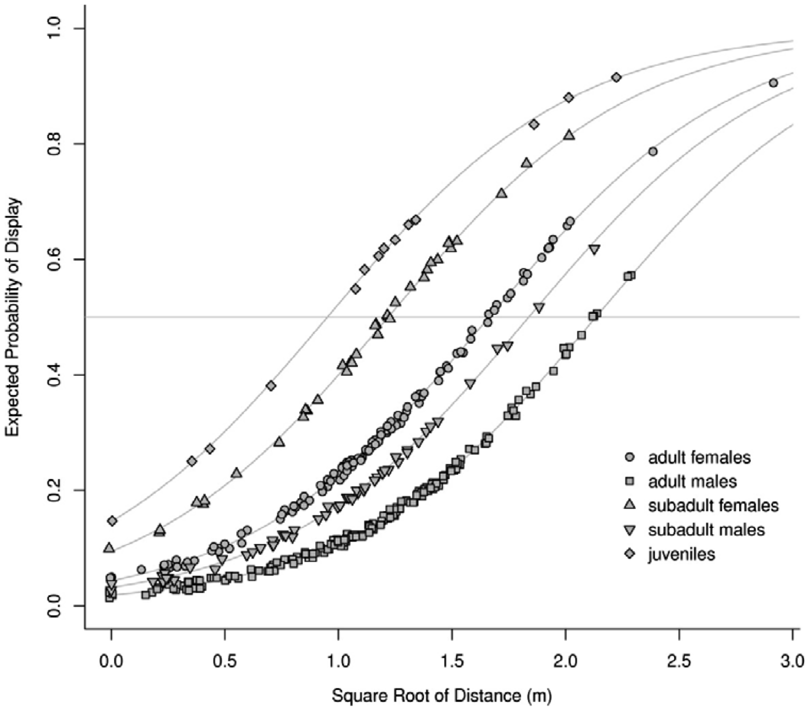

Figure 4. Generalized linear model estimates of the probability of a display as the first exhibited behavior (*y*-axis) as a function of the square root of distance (m) to the observer when the first behavior occurred (*x*-axis). Estimated points for each individual lizard (slightly jittered to improve readability) are overlaid on the theoretical curves, one curve for each age-sex class. These curves are straight lines on the logit (model fitting) scale.

An alternative explanation that has been rarely acknowledged in previous studies of lizard antipredator behavior is that foot shakes have a startling function (Marcellini, 1977; Greene, 1988). Startle displays provide a sudden and unexpected stimulus that induces fear or confusion in the predator and make it hesitate in its attack (Ruxton et al., 2004). Tail displays, foot shakes, and other putative pursuit-deterrent signals often incorporate striking color patterns and unusual motion patterns that could have, possibly in addition to a pursuit-deterrent function, a startling effect. Observations of interactions between lizards and their natural predators would help to evaluate this possibility.

Table 2
Inverse Regression Predictions of the Square Root of the Distance From the Observer at Which 50% of the Population of Each Age-Sex Class Displays (Rather Than Flees)

Age-sex class	Estimate ($\sqrt{m}$)	Standard error ($\sqrt{m}$)	Sample size
Adult females	1.664	0.133	123
Adult males	2.134	0.170	174
Subadult females	1.219	0.195	36
Subadult males	1.838	1.838	55
Juveniles	0.952	0.328	14

Note. Other columns give the standard errors of the estimates and sample size of each class. Data with starting distances less than 1 m were not used when estimating models.

About half the lizards that displayed in our study did so before moving, while the other half relocated a short distance from where they were initially observed before displaying. Lizards may need to relocate in order to assess the predatory threat or to increase the distance with the predator before performing the display. In the Bonaire whiptail lizard, no individual displayed before moving away from the predator (Cooper et al., 2004). However, several iguanian lizards that use pursuit-deterrent signals typically signal before fleeing (Dial, 1986; Hasson et al., 1989; Leal & Rodríguez-Robles, 1997; Cooper, 2010a). Further experimental data and a wider comparative database are needed to explain these interspecific differences (see also Cooper, 2010b).

Antipredator foot shakes were performed by lizards of both sexes and belonging to all age classes. However, adult males were less likely to display as their first behavior than other age-sex classes. Their distribution of distance at first exhibited behavior was about the same as adult females, whereas subadults and juveniles tended to first react when the observer was further away. Adults of either sex also seemed more wary than individuals in other age classes, as shown by their larger flight initiation distances (see Table 1). Sexual differences in antipredator behavior have been reported in other lizard species (e.g., Plasman, Duchateau, & Macedonia, 2007; Vanhooydonck, Herrel, & Irschick, 2007). In the yellow-headed gecko, *Gonatodes albogularis*, males perform a putative pursuit-deterrent tail display more often than females and display at a greater distance from an approaching observer than females (Bohórquez Alonso et al., 2010). Sex- and age-related variation may result from differences in the way individuals perceive risk, perhaps as a result of differences in their ability to escape or in the costs of fleeing (e.g., Martín & López, 1995; Whiting, Lailvaux, Reaney, & Wymann, 2003; Cooper & Wilson, 2007).

Pursuit-deterrent signals inform potential predators of the unprofitability of a given prey individual. Unprofitability may arise in two ways (Caro, 2005). Prey may signal that they have detected the predator and thus that there is a reduced chance of successfully attacking that particular individual (perception advertisement), or they may signal that they are intrinsically difficult to catch or subdue (quality advertisement). The distinction between "perception" and "quality" signals is difficult to make, particularly because, in most cases, there is no information on how predators respond to pursuit-deterrent signals. Further, as pointed out by Caro (2005), perception and quality signaling are not mutually exclusive alternatives, and a lizard could signal perception in one situation and quality in another. With the information at hand, it is hard to determine whether type III foot shakes in *Podarcis muralis* are perception or quality signals. However, theory predicts that, compared to quality signals, perception signals should not be very costly and that variation in signal intensity should not be linked to differences in the condition of the displaying animals (Caro, 2005); both of these predictions are amenable to empirical tests.

Theoretical models have shown that pursuit-deterrent signals need to be costly in order to be stable (Vega-Redondo & Hasson, 1993; Bergstrom & Lachmann, 2001). Costs do not need to be energetic but may derive from increased conspicuousness of signaling prey, either to the predator that elicited the display in the first place (who may actually be unaware of the prey's presence) or to secondary predators. According to Caro (2005), displays that involve leg movements are particularly likely to function as honest quality signals because repeated leg movement may compromise the prey's likelihood of escaping an attack (e.g., they may handicap running endurance). For example, in the Puerto Rican anole, *Anolis cristatellus*, there is a strong correlation between the frequency with which push-ups are performed in front of a stuffed snake and running endurance (Leal, 1999). However, lacertid foot shakes do not seem energetically costly, and thus it is unlikely that they handicap the displaying lizard's endurance in any way. A more likely possibility is that the costs of type III foot shakes are related to increased conspicuousness of the displaying lizard.

In summary, our field experiments demonstrate that type III foot shakes in *Podarcis muralis* are consistent with the predictions of pursuit-deterrent theory. We also show that there is age- and sex-related variation in the distance and probability foot shake displays are performed. These are important findings because examples of pursuit-deterrent signaling in scleroglossan lizards are rare. To the best of our knowledge, this is also the first study to empirically address the function of lacertid foot shakes. Foot shake displays are probably ubiquitous in lacertid lizards. However, compared to head bobbing in iguanid lizards, foot shakes (and head bobs) of many lacertids tend to be brief and relatively inconspicuous, which probably explains why they have been largely unnoticed. As a case in point, several recent reports of antipredator behavior in *Podarcis muralis* relied, as our study, on observations of the behavior of lizards approached by a human acting as a surrogate predator, yet none even mention foot shake displays in this context (Diego-Rasilla, 2003a, 2003b; Martín, López, Bonati, & Csermely, 2010). In fact, pursuit-deterrent foot shakes may have been observed in other lacertid species but were not recognized as such. Several studies of the response of lacertids to chemicals of saurophagous snakes have noted that lizards exhibit an unusual type of locomotion characterized by jerky or waving movement of the forelegs, sometimes accompanied by head bobs (Thoen et al., 1986; Van Damme, Bauwens, Vanderstighelen, & Verheyen, 1990; Van Damme et al., 1995; Van Damme & Castilla, 1996; Van Damme & Quick, 2001; Downes & Bauwens, 2002). According to some reports, this so-called "slow motion" or "stroboscopic locomotion" could be "mere signs of stress, without further adaptive significance" (Van Damme & Quick, 2001, p. 34). In contrast, we surmise that the observed behavior could in fact be pursuit-deterrent foot shakes interspersed with short bouts of locomotion, similar to the type III foot shakes of wall lizards. In this case, the display is performed as a response to the potential presence of an ambush predator. Signaling to undetected predators may seem maladaptive because it increases the risk of attracting the attention of predators that have not already detected the prey. However, empirical data and theoretical models confirm that preemptive or anticipatory antipredator displays can be selectively favored in situations where individuals are routinely exposed to high risk from undetected ambushers (Cooper, 1998a, 1998b; Murphy, 2007). If confirmed, this would be the first case of a pursuit-deterrent signal emitted in response to chemical, rather than visual, predator cues.

Research on dynamic visual signaling in lizards has been dominated by studies of head bobbing (and dewlapping) in representatives from the iguanian superfamily (e.g., Peters & Evans, 2003; Martins, Labra, Halloy, Thompson, 2004; Ord & Martins, 2006). Work on other dynamic visual displays (e.g., Peters & Evans, 2003; Halloy & Castillo, 2006), including lacertid foot shakes, has the potential to redress this imbalance and should allow us to test the generality of hypotheses and predictions derived from the study of traditional "model" lizard species.

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Correction to Font, Carazo, Pérez i de Lanuza, and Kramer (2012)

In the article "Predator-elicited foot shakes in wall lizards (Podarcis muralis): Evidence for a pursuit-deterrent function," by Enrique Font, Pau Carazo, Guillem Pérez i de Lanuza, and Matthew Kramer (*Journal of Comparative Psychology*, Vol. 126, No. 1, pp. 87–96), Figure 2 should have been represented in color. The online version has been corrected.

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