

The Evolution of Alternative Adaptive Strategies for Effective Communication in Noisy Environments

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ABSTRACT: Animals communicating socially are expected to produce signals that are conspicuous within the habitats in which they live. The particular way in which a species adapts to its environment will depend on its ancestral condition and evolutionary history. At this point, it is unclear how properties of the environment and historical factors interact to shape communication. Tropical *Anolis* lizards advertise territorial ownership using visual displays in habitats where visual motion or “noise” from windblown vegetation poses an acute problem for the detection of display movements. We studied eight *Anolis* species that live in similar noise environments but belong to separate island radiations with divergent evolutionary histories. We found that species on Puerto Rico displayed at times when their signals were more likely to be detected by neighboring males and females (during periods of low noise). In contrast, species on Jamaica displayed irrespective of the level of environmental motion, apparently because these species have a display that is effective in a range of viewing conditions. Our findings appear to reflect a case of species originating from different evolutionary starting points evolving different signal strategies for effective communication in noisy environments.

Keywords: animal communication, background noise, signal detection, territorial displays, *Anolis*.

Introduction

The consequences of environmental noise for animal communication are obvious: the ability of receivers to detect and/or assess signals reliably can be severely constrained by the environmental conditions at the time of signaling (reviewed for acoustic communication by Brumm and Slabbekoorn 2005). Animals are therefore expected to evolve signals that “stand out” in the environments in which they are used. Examples include birds singing at frequencies that increase the probability of songs being

heard over background noise (Slabbekoorn and Peet 2003; Mockford and Marshall 2009) or the conspicuous coloration of many fish that is dependent on the type of light environment in which colors are viewed (Cummings 2007; Seehausen et al. 2008). It follows that habitat-dependent selection on animal signals should lead distantly related species communicating in similar environments to converge on similar adaptive solutions for effective communication (Endler 1992). Yet, like any phenotypic trait, the types of signals that ultimately evolve will also be contingent on the evolutionary history of the species in question. Although two distantly related species communicate in similar environments, signal evolution might have proceeded quite differently in each species because of intrinsic differences (genetic, developmental, and neurological) or differences in the signal structures inherited from their respective evolutionary ancestors. We know very little about the way environmental factors and evolutionary history interact to affect the evolution of communication, or any phenotypic traits for that matter (Schluter 2009; Sobel et al. 2010). If the legacy of history plays a prominent role in shaping animal communication, one possible outcome is the evolution of alternative signal strategies when animals are faced with the same problem of communication in noisy environments but begin from different evolutionary starting points.

One example of historical starting points influencing the subsequent trajectory of signal evolution might exist in the territorial communication of *Anolis* lizards from separate radiations found on Puerto Rico and Jamaica (Ord et al. 2010). Male *Anolis* lizards advertise territory ownership using elaborate, species-typical movements of the head and body, known as “headbobs,” that are often accompanied by the extension of a throat fan, or dewlap. The detection of display movement in these lizards is influenced by habitat light, distance to territorial neighbors, and the level of visual noise generated by the movement of windblown vegetation (Fleishman 1992; Ord et al. 2007,

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2010; Ord and Stamps 2008). The design of advertisement displays between species from Jamaica and Puerto Rico differs markedly (Ord et al. 2010), with Jamaican species using short sequences of headbobs accompanied by the rapid extension of the dewlap, whereas Puerto Rican species perform headbobs of long duration with slow extensions of the dewlap. Species on the two islands have also diverged in the way individual lizards respond to conditions affecting display detection. Puerto Rican *Anolis* are contextually plastic (Ord et al. 2010); that is, lizards tailor both the speed and duration of headbob and dewlap movements to enhance display detection as a function of visual noise and ambient light levels (see also Ord et al. 2007; Ord and Stamps 2008). This strategy of adjusting display movements to prevailing conditions is absent in *Anolis* species on Jamaica (Ord et al. 2010). The rapid extension of the dewlap has been shown experimentally to enhance signal detection in visually difficult environments (Ord and Stamps 2008), implying that Jamaican species may not have to track fluctuations in conditions affecting communication because their display is already suited for a range of conditions.

A remaining alternative for enhancing communication in noisy environments has yet to be addressed in *Anolis* and may provide additional insight into the evolutionary dynamics of these two clades. When environmental conditions affecting signal degradation fluctuate over brief periods of time (e.g., minutes), a solution for enhancing signal efficacy might be to simply wait until conditions are more favorable. This would bypass the need to change the design or structure of the signal itself, which provides some predictive power about which species should exhibit signal timing based on the design of the signals being used by species. As intuitive as the strategy is, there have been few investigations into whether animals actually time signal production to exploit periodic gaps in background noise (see, e.g., Egnor et al. 2007). Not surprisingly, of the studies that have been done, all have focused on animals communicating with sound. Whether animals communicating in other modalities adjust signal timing is unknown. As with sound levels in natural settings, visual noise from moving vegetation can fluctuate in a matter of minutes from moments of calm to high motion in windy conditions. In this study, we investigated whether visually communicating *Anolis* lizards time the production of territorial displays to coincide with lulls in visual noise generated by windblown vegetation and whether variation among species in this behavior can be predicted by the design of the display itself.

If the hypothesis is correct that Puerto Rican and Jamaican lizards have followed alternative evolutionary trajectories in signal adaptation—one leading to the evolution of a contextual plastic display (on Puerto Rico), the other

to a nonplastic display that relies on the rapid deployment of the dewlap (on Jamaica)—there should be an inverse relationship between signal timing and the speed of dewlap extensions included in the display. That is, if Jamaican lizards have evolved a highly conspicuous display suitable for communication in a variety of conditions (Ord et al. 2010), Jamaican species should not need to rely on signal timing. Furthermore, unlike the rapid deployment of the dewlap, exaggerating body movements during advertisement displays is expected to be energetically expensive (Brandt 2003; Perry et al. 2004). Although Puerto Rican displays are contextually plastic, when lizards advertise territory ownership in especially windy habitats, it would make sense for these lizards to delay broadcasts to moments when visual noise is relatively low, rather than try to maintain display speeds above that of the surrounding vegetation.

However, the detrimental effects of noise on signal detection might be compounded by other variables. Those species communicating to distant receivers and in habitats in which light levels are low (e.g., in full shade) should be under considerable selection pressure to time signals to exploit momentary windows in noise. If so, this might result in predictable variation in signal timing among species living in different habitats and with different ecologies, irrespective of island origin. We tested (1) whether individual lizards avoided the adverse effects of visual noise by concentrating advertisement displays during lulls in background motion and whether species variation in this behavior was predicted by (2) the design of the territorial display used by species (i.e., the inclusion of a high-speed dewlap) or (3) the type of environment in which lizards defended territories.

Material and Methods

Data Collection

Free-living male lizards were observed between 0600 and 1800 hours from April to May 2006 on Puerto Rico and May to June 2006 on Jamaica, periods that overlap the peak activity season for these animals (April–August; Losos 2009). To increase our sample size for some species, we also included data from another survey conducted on Puerto Rico in April 2005 (two males of *Anolis cristatellus*; four males of *Anolis evermanni*). *Anolis* lizards are arboreal, and males were located sitting on trunks or bushes by an observer walking quietly through the respective habitat of each species. Once a male was spotted, a digital camcorder (either a Panasonic GV-500 or Panasonic PV-GS15) was positioned on a tripod approximately 5 m away from the subject and video-recorded for an average (\pm SD) of 21 min (\pm 6 min). During the recording period, the position

of all male neighbors within visual sight of the subject was noted. At the end of the recording period, the distance to these neighbors was measured with a tape measure from the site at which the subject lizard was first observed to display. Habitat light was also measured at the site of first display following procedures outlined by Ord (2008).

In conducting our survey, we made sure to target species that would minimize broad ecological differences between the islands that might complicate inferences of historical effects associated with island origin (the species studied on each island were monophylic). To this end, we sampled the following species on Jamaica (JM) and Puerto Rico (PR): along open road edges, *Anolis sagrei* (Highway 1 near Discovery Bay, JM) and *A. cristatellus* (Route 186, near the El Verde Field Station, PR); in open woodland, *A. opalinus* (Hardwar Gap, JM) and *A. pulchellus* (Punta Picua, PR); in closed forest, *A. grahami* and *A. lineatopus* (Discovery Bay Marine Laboratory, JM), and *A. gundlachi* and *A. evermanni* (El Verde Field Station, PR). See table A2 in the appendix for a quantitative analysis of the habitats occupied by these species.

Quantifying Visual Noise

We used computational motion analysis to quantify environmental motion occurring in video clips with the “Analysis of Image Motion” program (AIM ver. 1.2) written for MatLab (Peters et al. 2002). Briefly, the approach converts video images into grayscale and uses the change in pixel intensity (change in grayscale values) from one video frame to the next to quantify the speed of motion occurring across the image (see Peters et al. 2002 for a detailed description of the analysis and algorithms used).

Video footage was edited from mini-DV tapes using iMovie HD, version 5.0.2, and exported as AVI clips for motion analysis in AIM (see Ord et al. 2007 for details on video processing). Two sets of clips were edited from raw footage. First, we extracted all sequences in which lizards performed a territorial advertisement display and where the camcorder was perfectly still. Camera movement results in inaccurate estimates of image motion and can occur because the observer bumped the camcorder or shifted position to keep the subject in view. Second, for each of these “display” clips, we edited out a corresponding clip of the same duration in which the lizard did not display. Whether these “no display” clips were taken before or after a period in which the lizard displayed depended on our ability to avoid camera movement while also obtaining a clip of similar duration (the proportion of clips of no display noise that were taken before and after a given display clip were roughly even for most species, with no systematic differences in these proportions by island). In rare instances, we were not able to find an appropriate

sequence and were forced to drop the corresponding display clip from the analysis (39 cases out of 740). The duration of display clips and those in which the lizard did not display were matched almost exactly, on average (\pm SD) within 0.91 (\pm 4.27) s in length (the average display clip length was 13.04 ± 11.70 s).

Motion occurring in the background of video clips was analyzed in the same manner for both sets of clips. The “define region of interest” option was selected within the AIM program, and a box was drawn around the area of the image that was occupied by the lizard. This area was excluded, and image motion was quantified in the rest of the image to measure the level of environmental motion generated by windblown vegetation (Ord et al. 2007). We used the average speed of movement (mm s^{-1}) over the duration of the clip as our index of visual noise in image backgrounds.

Quantifying the Propensity of Displaying Lizards to Avoid Noise

Our data set consisted of numerous repeated measurements of noise for each lizard, replicated across lizards from eight species. To accommodate this data structure, we created mixed models or “hierarchical regression models” using the lme4 package in R 2.8.1 (Bates 2008; R Development Core Team). The main model consisted of two levels. The first level grouped paired measures of noise for a given lizard (noise between display bouts paired with noise during display bouts), while the second grouped lizards by species. Each grouping category was allowed to vary in their estimated parameter values within the model. In other words, the level of noise when a lizard did not display (the intercept) and the change in noise when a lizard did display (the slope) were not assumed to be the same or fixed for every lizard or every species.

The parameter of interest for testing whether lizards time displays to avoid high periods of noise is the slope. A negative slope corresponds to a reduction in noise when lizards displayed (i.e., lizards avoided displaying during periods of high noise), a positive slope is an increase in noise when lizards displayed (lizards concentrated displays during periods of high noise), while a flat slope corresponds to no change in noise levels when lizards did and did not display (lizards did not time displays as a function of visual noise).

Island (Jamaica = 0 vs. Puerto Rico = 1) was included as a fixed effect to consider differences in the level of visual noise occurring in habitats on each island. A significant interaction between island and slope (the change in noise when lizards displayed) indicated that the propensity to avoid visual noise differed between species on each island. A second model was then applied to species from each

island separately to consider island differences more closely. Finally, to compute species-specific parameters for phylogenetic comparative analyses (see “Accounting for Interspecific Differences in Display Timing”) and generating data used in figures, we used a third model applied individually to each species.

In all mixed models, intercepts and slope values with 95% confidence intervals that did not overlap zero were considered to be statistically significant. Corresponding effect sizes in the form of *t* values are also presented.

Accounting for Interspecific Differences in Display Timing

To evaluate the relationship between signal timing and the speed of dewlap extensions included in the display itself, we computed the Pearson correlation coefficient using the phylogenetic generalized least squares (PGLS) analysis implemented in the program COMPARE version 4.6b (Martins 2004). We used the slope estimate of the difference in noise level between periods of no display and display calculated by mixed models to summarize the propensity of a species to display during periods of low visual noise. Data on dewlap speed was taken from Ord et al. (2010; see table A2).

To identify ecological factors that might account for interspecific differences in display timing, we conducted a separate analysis using a PGLS multiple regression. Species communicating to distant neighbors in poorly lit, windy environments should experience greater selective pressure to limit communication to situations when conditions are less adverse, compared to species communicating to nearby neighbors in brighter and calmer environments. Species living in environments where vegetation is constantly in motion will also have fewer opportunities to exploit periods of low noise. We used the intercept values from mixed models as a measure of the overall magnitude of visual noise experienced by species in their respective habitats and the coefficient of variation in noise levels measured in clips in which lizards did not display as our index of noise variability. The average level of habitat light and average distance to territorial neighbors were included as covariates.

Our phylogeny was a pruned version of the tree from Nicholson et al. (2005; specifically, the reproduction of the Nicholson tree presented by Losos [2009] that provides additional information on branch lengths). The tree is based on 1,483 aligned base pairs of mitochondrial DNA. Statistical support for species nodes was strong, with most Bayesian posterior probabilities at or above 90% and bootstrap support in parsimony analyses greater than 80% (Nicholson et al. 2005).

Results

If lizards waited for lulls in environmental noise before performing advertisement displays, we expected to see lower levels of motion occurring in backgrounds at the time lizards displayed compared to periods when lizards did not display.

There was no difference between islands in the magnitude of noise experienced by lizards (i.e., the main effect of “island” was not statistically significant; see also table A2). There was, however, a significant interaction between island origin and differences in noise level between no display and display periods: species on Puerto Rico were more likely to display during calm periods than species on Jamaica (table 1; fig. 1). Analyses by island confirmed little change in background motion when Jamaican lizards displayed compared to periods when lizards did not display, while motion levels were significantly lower when Puerto Rican lizards displayed compared to periods when lizards did not display (table 1; fig. 2).

Separate analyses of each *Anolis* species (shown in fig. 1) suggested that for some, most notably *A. opalinus* (on Jamaica) and *A. pulchellus* (on Puerto Rico), lizards that happened to be observed when visual noise was high might be more likely to concentrate displays during lulls. We reran our models using only those lizards in windy situations (greater than the median noise level occurring when lizards did not display: 5.20 mm s⁻¹), and our findings were qualitatively unchanged (table A1). In other words, analyses that focused only on those lizards that experienced the worst levels of visual noise, and should therefore be the individuals most likely to exhibit a propensity to wait

Table 1: Difference in visual noise from windblown vegetation when lizards did and did not display

Variable	β	95% CI (lower, upper)	<i>t</i>
All species:			
Intercept	5.24	4.19, 6.29	9.76
Period	-.29	-.61, .04	-1.72
Island	.60	-.93, 2.13	.77
Period × island	-.79 ^a	-1.31, -.28	-3.04
<i>n</i> _{species, lizards, paired observations}	8, 195, 1,476		
Jamaican species only:			
Intercept	5.22	4.43, 6.01	12.95
Period	-.25	-.63, .13	-1.30
<i>n</i> _{species, lizards, paired observations}	4, 114, 948		
Puerto Rican species only:			
Intercept	5.84	4.40, 7.28	7.96
Period	-1.10 ^a	-1.54, -.67	-4.93
<i>n</i> _{species, lizards, paired observations}	4, 81, 528		

^a Slopes with 95% confidence intervals (CIs) that do not overlap zero are considered significant.

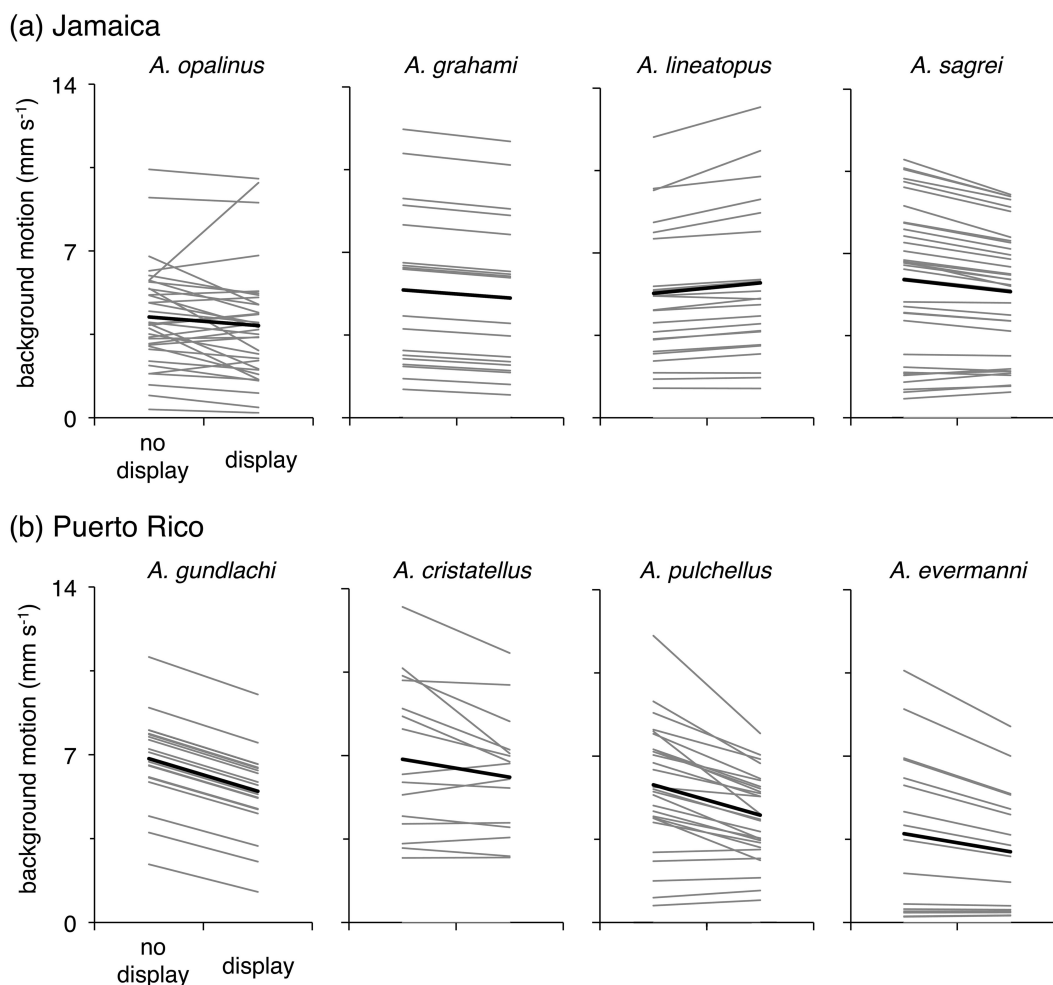


Figure 1: Differences in background visual noise when lizards did not display and when lizards did display for *Anolis* species living on (a) Jamaica and (b) Puerto Rico. Black trend lines are estimated slopes in mixed models averaged across all lizards, while gray trend lines are mean slopes fitted to data for individual lizards.

for periods of relative calm to enhance display detection, still showed clear differences in the behavior between species on each island.

Next, we determined whether island differences in signal timing could be explained by broad differences in the design of territorial displays, specifically, the inclusion of a high-speed dewlap, or the properties of the physical and social environment occupied by species. A phylogenetic analysis confirmed a prominent inverse relationship between the speed of dewlap extensions and signal timing ($r_{\text{PGLS}} = 0.72$, $P = .043$; fig. 3). The average speed at which species extended dewlaps during territorial displays explained 52% of the variance in signal timing among species. Conversely, signal timing was not related to the magnitude of habitat visual noise, the degree visual noise fluctuated in habitats, the amount of habitat light, or the

average distance to territorial neighbors (table 2). To increase the power of this last analysis, we conducted bivariate regressions in which each predictor variable was entered separately and again found no relation between signal timing and any ecological variable (variance in signal timing explained by magnitude of noise, 0.08%; variation in noise, 0.17%; light, 0.01%; and neighbor distance, 0.03%). Furthermore, there were no island differences in these ecological variables (table A2), indicating that species on both islands occupied comparable habitats and communicated over comparable distances to territorial neighbors.

Discussion

Our findings have at least two implications for our understanding of how animals communicate in noisy con-

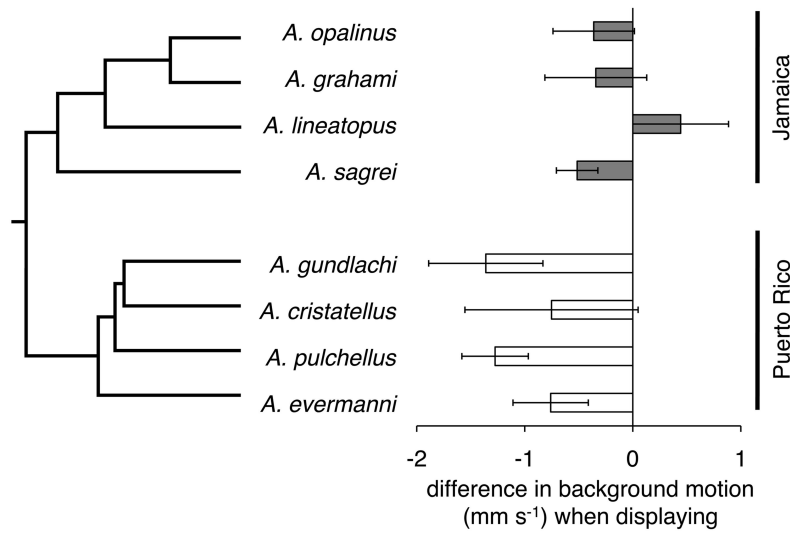


Figure 2: Propensity of lizards to time displays to periods of low noise. Data shown represent the change in visual noise level ($b \pm 95\%$ confidence interval) occurring in backgrounds when lizards did not display compared to when lizards did display, estimated by mixed models applied to each species separately.

ditions. First, there has been considerable emphasis on identifying the design characteristics of animal signals that facilitate signal transmission through the environment (Fleishman 1992; Miller et al. 2000; Slabbekoorn and Peet 2003; Peters et al. 2007; Mockford and Marshall 2009). The strategy of simply waiting until conditions are more suited for communication has received much less attention. In cases in which signal timing has been investigated, studies have focused almost exclusively on temporal variation in signal production that minimizes overlap among signaling animals (Ficken et al. 1974; Zelick and Narins 1985; Grafe 1996; Brumm 2006). Examinations of signal timing as it relates to abiotic noise have been rare (e.g., we are aware of only one study: Egnor et al. 2007). This is surprising because timing signal production to coincide with momentary periods of quiet is often cited by review articles as an energetically inexpensive way of enhancing signal reception when noise levels fluctuate in the environment (Wiley and Richards 1982; Brenowitz 1986; Brumm and Slabbekoorn 2005; Patricelli and Bickley 2006). We show that visually communicating animals, here *Anolis* lizards on Puerto Rico, assess moment-to-moment fluctuations in environmental motion and selectively time display production to coincide with periods of relative calm, periods when their signals are more likely to be detected by neighboring males and females. This extends the suite of strategies previously identified in these lizards (and for other communicating animals, more generally) for enhancing signal detection beyond structural changes to the signal itself.

Second, although there is an increasing awareness among communication biologists that evolutionary history can play an important role in shaping animal communication systems (see, e.g., Laiolo and Rolando 2003; Päckert et al. 2003), it has mostly been limited to an acknowledgment that closely related species will often exhibit similar forms of behavior through shared ancestry (Ord and Martins 2009). Yet, as we demonstrate, phylogeny can have other and more interesting consequences for how evolution proceeds than merely generating phenotypic similarities among sibling species. We present a case in which it appears that species originating from different evolutionary ancestors have adapted quite differently in response to similar selective pressures. Previous research on Puerto Rican and Jamaican *Anolis* lizards had highlighted a disparity in how species from each island clade responded to environmental conditions affecting the detection of territorial advertisement displays (Ord et al. 2010). It is now apparent that Puerto Rican species are contextually plastic (Ord et al. 2007, 2010) and time display production as a function of visual noise, whereas Jamaican species seem to rely on a display that includes high-speed dewlap extensions (Ord et al. 2010). The strong inverse relationship between signal timing and dewlap speed among species (fig. 3), coupled with experimental evidence that a series of dewlap extensions given at speeds typical of Jamaican lizards are highly conspicuous in visually difficult environments (Ord and Stamps 2008), supports the hypothesis that Jamaican and Puerto Rican display behavior probably constitute alternative adaptive

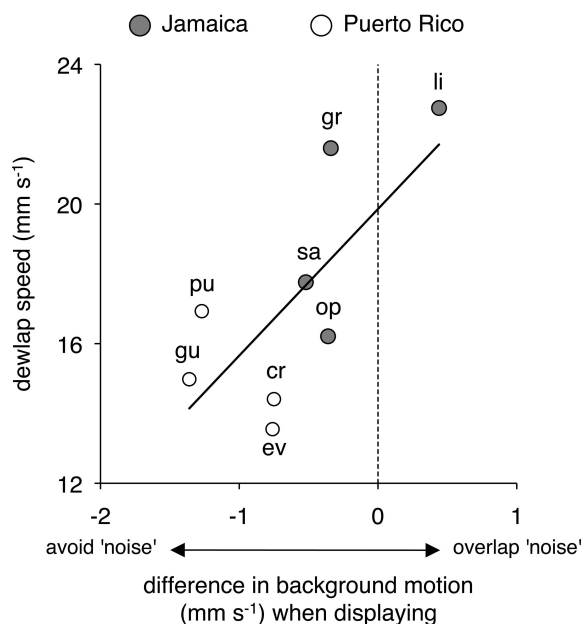


Figure 3: Jamaican *Anolis* species (filled circles) appear to rely more on the conspicuousness of rapid dewlap extensions during territorial advertisement displays than tracking changes in environmental motion, whereas Puerto Rican *Anolis* species (open circles) have slower dewlap extensions and instead actively avoid performing displays during periods of high noise. Data points are the average dewlap speed for species and the propensity for species to time displays as summarized by the change in noise level when lizards did and did not display (see fig. 2). The trend line is the regression line computed by a phylogenetic generalized least squares analysis. Species codes are: op, *A. opalinus*; gr, *A. grahami*; li, *A. lineatopus*; sa, *A. sagrei*; gu, *A. gundlachi*; cr, *A. cristatellus*; pu, *A. pulchellus*; and ev, *A. evermanni*.

solutions to the same problem of communicating in difficult conditions.

This conclusion also follows from the exclusion of several other potential causal factors. We found no difference between the physical or social environments on each island that might account for the disparity in behavior (table A2). We have no evidence that predation regimes differ between the two islands (nor do we have an a priori hypothesis as to how variation in predation risk among species on each island might lead to the observed patterns in signal timing and dewlap speed). While there is interspecific variation in the appearance of the dewlap itself, there were no consistent differences between the Jamaican and Puerto Rican species in color, pattern, or size (e.g., *Anolis lineatopus* on Jamaica and *Anolis gundlachi* on Puerto Rico both have large, straw-colored dewlaps). Our findings in relation to the use of the dewlap are therefore specific to how the dewlap is deployed (its speed) and do not include any special enhancements to the dewlap's appearance per se. Nonetheless, if rapid dewlap extensions do function as

an effective attention-grabbing component of the Jamaican advertisement display, then presumably it is still dependent on the dewlap being conspicuously colored. For example, the “flash” of color that results from the rapid extension of a brightly colored dewlap is obvious to even a human observer (T. J. Ord, personal observation; Gorman 1968). In contrast, a dewlap that is cryptically colored would probably be very difficult to see regardless of how quickly it was extended. We assume, then, that it is the interaction between the speed and the conspicuous coloration of the dewlap that probably makes Jamaican displays effective in noisy conditions. This hypothesis might be tested in future playback experiments using robotic lizards (see, e.g., Martins et al. 2005; Ord and Stamps 2008, 2009) in which the speed and color of the dewlap are manipulated independently of each other.

Assuming that the rapid extension of the dewlap is a highly effective means of attracting the attention of receivers in a range of viewing conditions, the question remains why Puerto Rican species have not adopted a similar strategy. Previous research on birds and anurans has shown that the morphology of signalers (Podos 2001; Badyaev et al. 2008; Derryberry 2009) and the sensory system of receivers (Ryan 1986; Gerhardt and Schwartz 2001; Wilczynski et al. 2001) are both intimately related to divergence in signal design among populations or closely related species. Perhaps species in the Jamaican clade have certain morphological adaptations that enable them to extend the dewlap more rapidly than species in the Puerto Rican clade. While we have a reasonable understanding of how the underlying hyoid apparatus controls the movement of the dewlap (Bels 1990; Font and Rome 1990), a future comparative study is needed to determine whether in fact modifications to the hyoid explain differences in dewlap speed between species on the two islands. Differences might also (or instead) exist in the visual systems of species, resulting in Jamaican species being better at detecting rapid movements than species on Puerto Rico. Motion perception has been measured for several Jamaican (Jensen and Swenson 1974) and Puerto Rican (Fleishman et al. 1995) species, and differences in motion detection potentially exist between the two islands. Unfortunately, the two studies employed very different experimental protocols, and it is unclear whether true differences in the visual systems of the two clades in fact exist or whether results reflect differences in methodology (see Fleishman et al. 1995 for discussion).

The notion that historical starting points and stochastic processes can exert a profound affect on the course of evolution will not be new to evolutionary biologists but is less appreciated by communication biologists. Studies of animal behavior often focus on single species and measured responses within those species are implicitly assumed

Table 2: Signal timing as a function of overall levels of habitat visual noise, variation in habitat visual noise, light and distance to territorial neighbors

Variable	β	95% CI		r^2	α
		(lower, upper)			
Phylogenetic generalized least squares regression					
Intercept	1.17	-2.79, 5.13		.25	.9
Magnitude of habitat visual noise	-.12	-.57, .33			
Variation in habitat visual noise	-.03	-.09, .04			
Habitat light	-.08	-.81, .65			
Average neighbor distance	-.02	-.57, .53			

Note: This method evaluates the degree to which phylogeny explains species differences and incorporates this estimate into the analysis using the parameter α : large α values (e.g., 15.50+) indicate little phylogenetic signal in species data, while values approaching zero indicate species data are strongly tied to phylogeny (here, the low value of α reflects how dramatically the behavior of species belonging to each monophyletic island clades differs; see fig. 2). CI = confidence interval.

to reflect the balance of various selection pressures present in the environment today. We provide an example of how past history might play an important role in determining the types of adaptive behavior expressed by different species. Indeed, it was quite striking how different the *Anolis* communities on the two islands we studied were in their behavior, despite species living in a comparable range of environments. We caution that the legacy of evolutionary history will be an important component of many communication systems and will limit generalizations that might be made on the adaptive origin of behavior based on the study of single species.

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APPENDIX

Table A1: Difference in visual noise from environmental motion when lizards did and did not display for lizards defending territories in noisy areas of the habitat (noise levels > 5.20 mm s⁻¹)

Variable	β	95% CI (lower, upper)	<i>t</i>
All species:			
Intercept	8.07	7.15, 8.99	17.19
Period	-.74 ^a	-1.25, -.23	-2.85
Island	.19	-1.14, 1.52	.28
Period × island	-.90 ^a	-1.67, -.12	-2.26
<i>n</i> _{species, lizards, paired observations}	8, 97, 748		
Jamaican species only:			
Intercept	8.10	7.45, 8.75	24.54
Period	-.70	-1.43, .04	-1.85
<i>n</i> _{species, lizards, paired observations}	4, 53, 450		
Puerto Rican species only:			
Intercept	8.31	7.13, 9.48	13.90
Period	-1.74 ^a	-2.33, -1.16	-5.83
<i>n</i> _{species, lizards, paired observations}	4, 44, 298		

^a Slope estimates with confidence intervals (CIs) that do not overlap zero are considered significant.

Table A2: Estimates of noise-dependent signal timing, the speed of dewlap extensions, and the conditions in which territorial advertisements are given

Island and species	Signal timing β_{period} (95% CI)	Dewlap speed (mm s ⁻¹) μ (95% CI)	Magnitude of habitat noise (mm s ⁻¹) $\beta_{\text{intercept}}$ (95% CI)	Variation of habitat (mm s ⁻¹) V_{noise}	Habitat light (log ₁₀ ($\mu\text{mol m}^{-2}$ s ⁻¹) + 1) μ (95% CI)	Neighbor distance (m) μ (95% CI)
Jamaica:						
<i>Anolis opalinus</i>	-.36 (-1.10, .38)	16.21 (14.79, 17.63)	4.23 (3.36, 5.09)	29.66	2.25 (2.14, 2.37)	6.0 (4.6, 7.5)
<i>Anolis grahami</i>	-.34 (-1.27, .58)	21.60 (19.93, 23.27)	5.41 (3.69, 7.13)	37.44	1.47 (1.25, 1.69)	4.5 (2.4, 6.6)
<i>Anolis lineatopus</i>	.44 (-.43, 1.31)	22.75 (16.68, 28.82)	5.28 (3.91, 6.66)	28.32	1.09 (.88, 1.30)	4.2 (3.6, 4.8)
<i>Anolis sagrei</i>	-.52 (-.89, -.14)	17.76 (16.28, 19.24)	5.89 (4.82, 6.95)	46.62	2.17 (2.06, 2.29)	4.5 (3.5, 5.5)
Puerto Rico:						
<i>Anolis gundlachi</i>	-1.36 (-2.40, -.32)	14.98 (11.37, 18.59)	6.84 (5.62, 8.05)	31.86	.63 (.46, .80)	6.0 (4.7, 7.2)
<i>Anolis cristatellus</i>	-.75 (-2.32, .82)	14.41 (12.09, 16.73)	6.85 (4.84, 8.85)	32.75	1.67 (1.30, 2.03)	6.4 (3.9, 8.9)
<i>Anolis pulchellus</i>	-1.27 (-1.88, -.67)	16.93 (14.21, 19.65)	5.79 (4.75, 6.83)	28.74	2.25 (2.15, 2.35)	4.3 (3.2, 5.3)
<i>Anolis evermanni</i>	-.76 (-1.44, -.08)	13.55 (12.29, 14.81)	3.74 (2.05, 5.42)	43.40	.93 (.63, 1.23)	5.4 (4.0, 6.7)
<i>r</i> ² _{island}	.59 (<i>P</i> = .02)	.55 (<i>P</i> = .04)	.11 (<i>P</i> = .49)	.01 (<i>P</i> = .81)	.05 (<i>P</i> = .44)	.02 (<i>P</i> = .32)

Note: We computed *r*² values for island origin using a mixed model with species as the grouping variable and island as a factor. Signal timing and dewlap speed differed dramatically between islands (see also Ord et al. 2010), but there were no consistent differences in the types of environment or distances over which communication was conducted on each island (indexed by neighbor distance). Other data (not shown) showed no significant interspecific differences between islands in temperature, humidity, habitat clutter, male neighbor density, body size, dewlap size, or dewlap color (color data were taken from Fleishman 2000; all other data were collected by T. J. Ord). CI = confidence interval.

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A male yellow-chinned anole *Anolis gundlachi*, on the island of Puerto Rico, is one of several species that wait for lulls in environmental noise before performing territorial displays. Photograph by Terry J. Ord.