

ADAPTATION AND PLASTICITY OF ANIMAL COMMUNICATION IN FLUCTUATING ENVIRONMENTS

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Adaptations that facilitate the reception of long-range signals under challenging conditions are expected to generate signal diversity when species communicate in different habitats. Although we have a general understanding of how individual communicating animals cope with conditions influencing signal detection, the extent to which plasticity and evolutionary changes in signal characteristics contribute to interspecific differences in signaling behavior is unclear. We quantified the visual displays of free-living lizards and environmental variables known to influence display detection for multiple species from two separate island radiations. We found evidence of both adaptive evolution and adaptive plasticity in display characteristics as a function of environmental conditions, but plasticity accounted for most of the observed differences in display behavior across species. At the same time, prominent differences between the two island radiations existed in aspects of signaling behavior, unrelated to the environment. Past evolutionary events have therefore played an important role in shaping the way lizards adjust their signals to challenges in present-day environments. In addition to showing how plasticity contributes to interspecific differences in communication signals, our findings suggest the vagaries of evolution can in itself lead to signal variation between species.

KEY WORDS: *Anolis* lizard, ecological determinism, historical contingency, reaction norm, territorial signal.

Communication theory posits two broad, nonmutually exclusive hypotheses as to how animals should design and deliver their signals when confronted by conditions that make communication difficult (Bradbury and Vehrencamp 2000; Wiley 2006). Animals might increase the signal-to-noise ratio, or intensity, of communication by changing the structural properties of signals (Hypothesis 1), or increase the redundancy of communication by length-

ening a signal and/or repeating the same signal many times (Hypothesis 2). Both hypotheses predict relationships between signal characteristics and environmental challenges at different levels, ranging from the signals produced by individual animals to those produced by members of different taxa.

At one extreme, if individuals communicate in environments in which the conditions that affect signal detection fluctuate over short periods of time (minutes to hours), they might tailor their dynamic signals to enhance communication under the environmental conditions at the time of communication. Such contextual plasticity (Stamps and Groothuis 2010; see Table 1), whereby

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Table 1. Glossary of terms.

Term	Definition
Contextual plasticity	Variation in an individual's behavior as a function of variation in the external stimuli (context) at the time the individual expresses that behavior.
Contextual reaction norm	Description of the behavior of an individual as a function of the stimuli around that individual when it expresses that behavior. Linear contextual reaction norms can be described by a slope (contextual plasticity) and an intercept ("baseline" behavior: behavior expressed at a specific stimulus value).
r_{IE}	A correlation (r) between the phenotypic value of individuals (I) and an environmental factor (E).
Taxon	A species or separate population of a species sampled at a different location (see Fig. 1).
Within-taxon intercept	The mean ("baseline") trait value that individuals in a given taxon would express under a standard environmental condition (i.e., when the level of an environmental factor is zero).
Within-taxon mean	The average value of a trait value or an environmental variable for the individuals in a given taxon.
Within-taxon slope	The mean contextual plasticity for the individuals at a given locality.

an individual changes its behavior as a function of current environmental conditions, has been widely documented for animal communication (e.g., birds: Pytte et al. 2003; Slabbekoorn and Peet 2003; mammals: Miller et al. 2000; Brumm et al. 2004). At the other extreme, evolutionary divergence in signal characteristics that improve the efficiency of communication might occur if members of related taxa consistently experience different environmental conditions across many generations (e.g., Derryberry 2007). Hence, contextual plasticity and evolutionary changes in signal characteristics predict similar relationships between signals and challenging environmental conditions.

Currently, researchers often assume that relationships between signaling behavior and environmental factors across taxa are the product of evolutionary change (e.g., Badyaev and Leaf 1997; Ord and Martins 2006), but the extent to which contextual plasticity contributes to these relationships is unknown. Here, we

present a test of theoretical predictions of how animals should design social signals according to the properties of the environment, and evaluate how contextual plasticity and evolutionary changes in signal characteristics contribute to signal variation for taxa that communicate under different environmental conditions.

We studied the territorial displays of Caribbean *Anolis* lizards. Male lizards defend territories through the performance of dynamic visual displays composed of two types of movement: vertical movements of the head, known as headbobs, and extensions and retractions of a throat fan (dewlap). In the same way that acoustic noise limits the efficacy of animal vocalizations, visual "noise" from wind-blown vegetation reduces the detectability of *Anolis* territorial displays (Fleishman 1992; Ord et al. 2007; Ord and Stamps 2008). Detection of displays is also reduced when light levels are low (Jenssen and Swenson 1974; Fleishman et al. 1995; Ord and Stamps 2008). Both visual noise and light levels fluctuate widely at a given locality over the course of a day (Ord 2008; Ord et al., unpublished ms) and contextual plasticity of anole displays as a function of variation in noise and light levels has been documented for several species (Ord et al. 2007; Ord and Stamps 2008; Ord et al., unpubl. ms; see also methods). Comparative studies have also indicated that several components of *Anolis* displays vary among taxa as a function of the type of habitat occupied by a taxon (Ord and Martins 2006). The environment in which lizards defend territories is therefore likely to be an important factor underlying variation both within and between taxa in how these lizards communicate with one another.

To investigate the extent to which the environment explains signal variation, we quantified the territorial displays and environmental conditions experienced by free-living lizards for most of the species on Jamaica and Puerto Rico (Fig. 1). Lizards on these islands present an especially attractive group for comparative study because species on the two islands occupy a similar range of environments, yet originated from separate evolutionary radiations (reviewed in Losos 2009). These two island communities provide a unique natural experiment to investigate how descent from different evolutionary ancestors has influenced the design and contextual plasticity of territorial displays. We specifically focused on attributes of headbobbing and dewlap extensions analogous to properties of acoustic signals previously identified to be important for communication in difficult conditions (Wiley and Richards 1982; Brumm and Slabbekoorn 2005): signal intensity, duration, and rate of production (Table 2). We tested whether lizards living in environments that were visually noisy or poorly lit performed territorial advertisements displays of greater intensity (of increased speed; Hypothesis 1) or with higher levels of redundancy (of longer duration or with greater frequency; Hypothesis 2; see Fig. 2A).

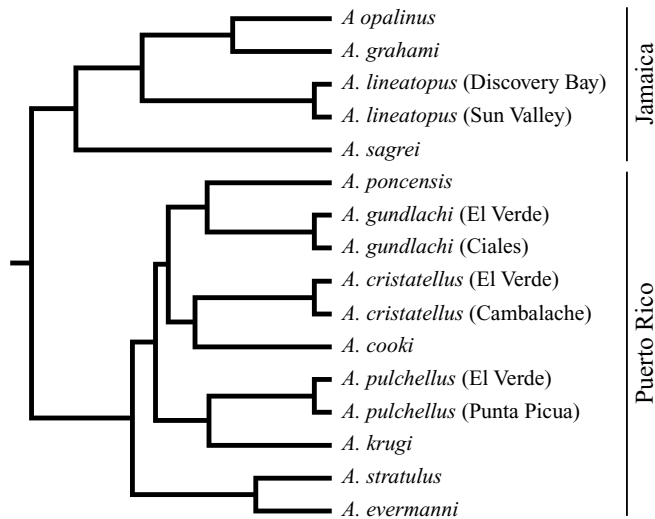


Figure 1. Phylogenetic relationships of the Jamaican and Puerto Rican *Anolis* lizards. The phylogeny was taken from Nicholson et al. (2005). Branch lengths are proportional to the amount of divergence between taxa (total length is 80 units), with populations set to the minimum amount of divergence estimated among populations for species on Jamaica (Jackman et al. 2002).

Table 2. Description of display characteristics measured.

Display characteristic	Definition
Hypothesis 1: Signal intensity	
Headbob speed	Maximum speed of headbob movements
Dewlap speed	Maximum speed of dewlap movements when not headbobbing
Hypothesis 2: Signal redundancy	
Headbob duration	Average duration of a headbob bout
Dewlap duration	Average duration of a dewlap extension when not headbobbing
Display repetition	Average number of display bouts per min. Bouts were defined as any display movement (either dewlap or headbob) separated by more than 3 seconds.

Anolis lizards extend the dewlap both during the headbob display and in the absence of accompanying headbob movements. We focused on dewlap extensions given when headbob displays were not being performed because the high speed of headbob movements in some species effectively “drowned out” the slower dewlap movements making it difficult or impossible to accurately estimate dewlap speeds in these situations. For consistency, measurements of dewlap duration were also taken for dewlap extensions given independently of headbob movements.

Materials and Methods

SAMPLING

Adult males were found on perches by a single observer walking quietly through the typical habitat for a given species. Once

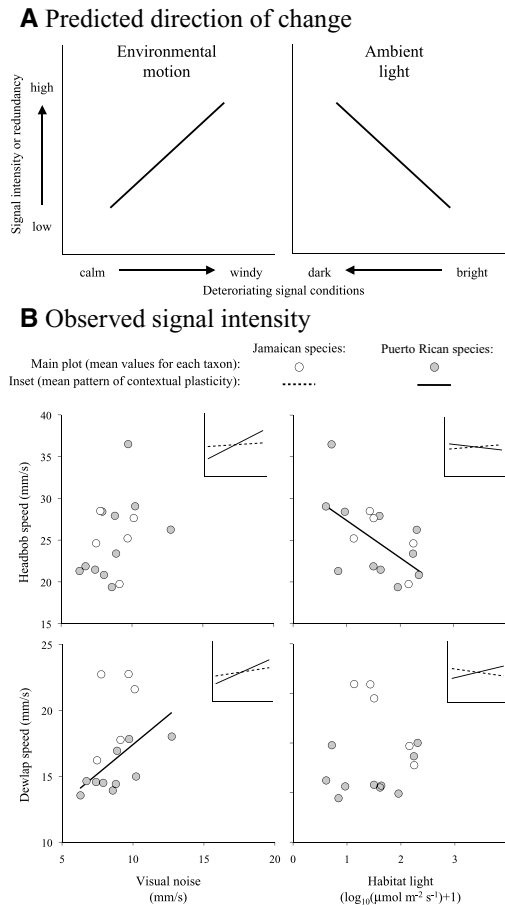


Figure 2. Relationships between *Anolis* display characteristics and environmental conditions. Signal detection theory predicts (A) animals should increase the intensity or redundancy of their signals in situations in which communication is difficult. Observations on free-living *Anolis* lizards show prominent differences between species in the (B) speed and (C) duration of components of their territorial advertisement displays depending on the level of visual noise from moving vegetation and habitat light. Insets: lines indicate the mean slopes (mean plasticity) for the contextual reaction norms of taxa from Puerto Rico (solid lines) and from Jamaica (dotted lines), based on analyses summarized in Table 3. Main graphs: datapoints indicate the means for each taxon, with trend lines indicating significant relationships in phylogenetic multiple regressions, based on analyses summarized in Table 4A. Open circles correspond to taxa from Jamaica, whereas closed circles are those from Puerto Rico. The arrow highlights a population of *A. pulchellus* (Punta Picua) that had an unusually long advertisement display for a full-sun environment relative to the El Verde population of the same species and other taxa studied, and was removed in some analyses (see Tables 3 and 4).

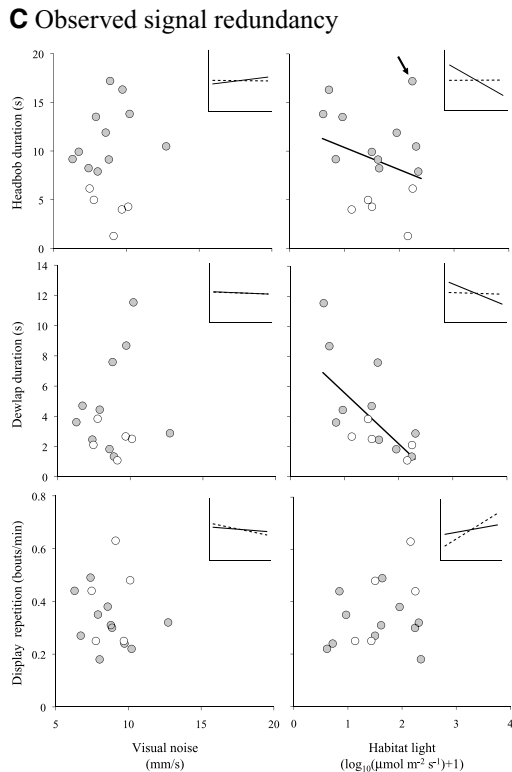


Figure 2. Continued.

males were identified, a digital camcorder (either a Panasonic PV-GS15 or Panasonic GV-500) recording to high-quality NTSC mini-digital tape was placed on a tripod several meters from the subject and positioned so that the profile of the lizard was toward the camcorder. It was important to keep the subject in profile so that the speed of display movements could be accurately estimated using motion analysis software (see next section). Lizards would often move during filming at which point the position of the camcorder was marked on the ground with a flag and the camcorder shifted to a new location to ensure the subject remained in full view and in profile to the camcorder. If lizards did not display during the first 10 min of recording, the trial was terminated. In most instances, males performed at least one advertisement display and recording continued for up to 30 min (mean \pm SD, 21'42" \pm 5'13") or until the subject moved out of view of the camcorder. At the end of each trial, habitat light was measured at the site of the first display using a LI-250A handheld light meter with a LI-190SA Quantum Sensor (waveband range: 400–700 nm) placed approximately where the lizard's head had been and with the sensor positioned parallel to the ground to mimic the position of the subject's eye. An average of two estimates corresponding to the left and right eye was used in statistical analyses. Following light measurements, the camcorder was repositioned at each flag and a ping-pong ball of known size was held where the lizard had been during filming. The ping-pong ball was video

recorded and later used to calibrate image measurements from pixels to millimeters. This calibration standardized measurements irrespective of the distance of the camcorder from the subject during recording. Consecutive trials were always out of visual range from the previous trial and separated by at least 40 m (because average neighbor distances range from 2.7 m to 6.5 m among species surveyed (T.J. Ord, unpubl. data), consecutive trials were separated by at least three territories). All trials were conducted between 0530 and 1830 corresponding to the activity period of these lizards (see Ord 2008 for discussion of temporal variation in *Anolis* display activity).

Some lizards on Puerto Rico were surveyed in April 2005 (59 males from five taxa), but the vast majority was surveyed in April–May 2006 (272 males from all taxa including those sampled in 2005). The following sites were visited: *Anolis poncensis* and *A. cooki* were found among the shrubs or on the coconut trees in the sand dunes immediately behind the beach of Bahía de la Ballena on the boundary of the Guanica Dry Forest; *A. gundlachi* was sampled at two locations, the first population was found in the shade forest surrounding the El Verde Field Station and the second population in the open forest of a privately owned property located near the town of Ciales in the island's interior; *A. cristatellus* was sampled at two locations, the first population was found along the road edge of route 186 near the El Verde Field Station and open areas along trails leading from route 186 into the Caribbean National Forest, whereas the second population was found in the Cambalache Forest on the north coast of the island; *A. pulchellus* was sampled at two locations, the first population was found in the grasses surrounding an abandoned picnic area on Route 186 within a short walk southwest of the El Verde Field Station, and the second population was found in the shrubland near Punta Picua that was accessed from route 968 opposite the turn off to El Yunque; *A. krugi* was found on bushes and ferns in shady areas along trails going into the Caribbean National Forest from route 186 southeast of the El Verde Field Station; *A. stratulus* was found on trees and shrubs in an open area at an unsignposted turn off on the north side of 186 before junction 956 (travelling from El Verde); and *A. evermanni* was found on trees within the shade forest surrounding the El Verde Field Station.

Lizards on Jamaica were sampled between May and June 2006 at the following sites: *A. opalinus* was found on trees and shrubs in open areas along the trails of Hollywell Park at Hardwar Gap in the Blue Mountains northeast of Kingston; *A. grahmi* was found in the forest surrounding the Discovery Bay Marine Laboratory on the north coast of the island; *A. lineatopus* was sampled at two locations, the first population was found in the forest around the Discovery Bay Marine Laboratory, whereas the second population was found on the coconut trees of a privately owned plantation south of Oracabessa on the north coast (hereafter referred to as the "Sun Valley" population); and *A. sagrei* was

found on the shrubs along highway 1 within walking distance west of the Discovery Bay Marine Laboratory.

In our analyses, we refer to each species and separate populations within those species sampled at more than one location collectively as “taxon” (see Table 1).

VIDEO ANALYSIS

A detailed description of the processing of video images for motion analysis is given in Ord et al. (2007). Briefly, display bouts were edited into separate video clips from digital tape using iMovie HD version 5.0.2. Display duration was computed by using the time codes of clips to note the start and end of display movement to the nearest video frame (in the NTSC video format one video frame equals ~ 33 ms). The number of clips recorded for a given individual provided a measure of display frequency. Motion analysis was performed on AVI exports of display clips using the MATLAB-based program Analysis of Image Motion (AIM; Peters et al. 2002). The defined “region of interest” option in AIM was used to distinguish motion associated with the lizard and motion occurring in the rest of the image resulting from wind-blown vegetation. Motion was summarized as the maximum speed recorded for a given video sequence (see Ord et al. 2007). Table 2 provides a summary of all display characteristics measured. We used the speed of movement occurring in image backgrounds as our measure of visual noise. Although visual noise was estimated each time a lizard displayed, habitat light was measured only once at the end of an observation period. For consistency with light measurements, repeated measures of visual noise were averaged to provide a single estimate for each lizard (see section Statistical analyses).

The number of observations differed between display characteristics (see Table 3) because speed can only be estimated accurately from videos in which lizards were perpendicular to the camcorder and when the camcorder was perfectly still. The measurement of display durations was generally unaffected by lizard orientation and camcorder movement, but the body or dewlap (for headbob and dewlap durations respectively) had to be in full view of the camcorder.

STATISTICAL ANALYSES

Contextual reaction norms: The behavior expressed by a given individual in the presence of different stimuli can be described by its contextual reaction norm (Stamps and Groothuis 2010, see also Dingemans et al. 2010 and Table 1). In anoles, contextual reaction norms for display characteristics as a function of variation in visual noise or light are described well by linear equations, where the slope describes an individual’s contextual plasticity, and the intercept estimates its “baseline” response under a single, standardized set of conditions (Ord et al. 2007).

Previous analyses show that single observations across a random sample of individuals at the same locality and time can provide a reasonable estimate of the mean contextual reaction norms of the individual animals in that sample (Ord et al. 2007). For instance, within-individual slopes describing the speed of headbob movements as a function of visual noise (which can only reflect contextual plasticity) were generally consistent in direction and magnitude across individuals sampled at the same locality for several different Puerto Rican taxa (T. J. Ord, unpubl. data). Slopes based on samples of different individuals were also statistically indistinguishable from slopes fitted within-individuals (e.g., headbob speed as a function of visual noise: *A. gundlachi* (El Verde): $\beta_{\text{between-individuals}}$ (95% confidence interval) = 0.89 (0.41, 1.38), $\beta_{\text{within-individuals}}$ = 0.75 (0.13, 1.37), $N_{\text{individuals, observations}}$ = 36, 100; T. J. Ord, unpubl. data). That is, regressions fitted across a random sample of individuals reliably reproduced the mean slopes within those individuals, each of whose displays were recorded over a wide range of different light or visual noise conditions (see also Ord et al. 2007).

Taken together, these and other data (Ord et al. 2007) show that one can estimate the mean contextual reaction norms of the individuals at a given locality using point samples of different lizards at that locality. The latter method allows contextual reaction norms to be estimated for multiple taxa in comparative studies, without requiring repeated observations of large numbers of individuals from each of those taxa. Here, we describe the contextual norms for each taxon by two terms: the within-taxon slope, which reflects the contextual plasticity of the individuals of that taxon, and the within-taxon intercept, which estimates the “baseline” behavior those individuals would express under the same, standardized set of environmental conditions (see Table 1).

We used the lme4 package version 0.999375-31 (Bates 2008) in R version 2.9.1 (R Development Core Team) to develop a random regression model to quantify display reaction norms as a function of visual noise and habitat light. The “random” component of the model allows the categories used to group repeated-measures to vary in their estimated parameters (intercepts or slopes) rather than assumed to be the same or “fixed.” In our analysis, there were two grouping categories corresponding to the displays performed by a given lizard and displays of a given taxon (defined as a species or a different population within a given species). Specifically, the model consisted of two levels with random intercepts for lizard (first level; although we did not estimate within-individual slopes per se, each lizard typically displayed many times during the 20–30 min observation period and each display was included as a repeated measure) and random intercepts and random slopes for each taxon (second level), the latter in relation to visual noise and habitat light. Written in R code the

Table 3. Contextual plasticity in lizard display characteristics as a function of the environment (visual noise and light levels).

	$\beta_{\text{intercept}}$ (lower CI, upper CI)	β_{noise} (lower CI, upper CI)	β_{light} (lower CI, upper CI)	β_{island} (lower CI, upper CI)	$B_{\text{noise} \times \text{island}}$ (lower CI, upper CI)	$\beta_{\text{light} \times \text{island}}$ (lower CI, upper CI)	N_{taxa} , lizards, observations
Display speed							
Headbob	18.81 (15.19, 22.44)*	0.84 (0.56, 1.13)*	-0.52 (-2.07, 1.02)	5.77 (0.04, 11.50)*	-0.64 (-1.15, -0.13)*	-	16, 389, 1385
Dewlap	13.49 (9.69, 17.29)*	0.32 (0.12, 0.52)*	0.11 (-1.18, 1.39)	2.42 (0.68, 4.16)*	-	-	15, 250, 2209
Display duration							
Headbob	13.39 (11.03, 15.74)*	0.05 (-0.07, 0.17)	-1.41 (-2.84, 0.02)	-7.91 (-10.40, -5.42)*	-	-	16, 429, 2490
outlier removed	14.63 (11.99, 17.26)*	0.07 (-0.06, 0.19)	-2.81 (-4.28, -1.34)*	-11.23 (-15.34, -7.12)*	-	2.87 (0.25, 5.49)*	15, 402, 2327
Dewlap	7.07 (4.98, 9.17)*	-0.03 (-0.07, 0.01)	-1.48 (-2.09, -0.87)*	-4.04 (-7.33, -0.75)*	-	1.33 (0.28, 2.38)*	15, 311, 6178
Display repetition	0.30 (0.23, 0.37)*	-0.01 (-0.01, -0.001)*	0.06 (0.01, 0.11)*	-0.01 (-0.10, 0.08)	-	-	16, 496, na

* Slopes with confidence intervals that do not overlap zero.

Separate reaction norms for each taxon are also computed by the model and are reported in Table S1. An analysis of headbob duration using Cook's distance measure highlighted the set of observations for *A. pulchellus* (Punta Picua) as exerting an unusually large influence on model parameter estimates. Specifically, lizards for this population performed exceptionally long headbob displays compared to a second population of the same species at El Verde and other species living in similar light environments (see Fig. 2). The analysis of headbob duration was therefore repeated with observations from this outlier population removed.

model appears as follows:

$$\text{lmer}(\text{display}_{iL} \sim \overline{\text{noise}}_L + \text{light}_L + \text{island}_{\text{taxa}} + (1|L) + (\overline{\text{noise}}_L + \text{light}_L|\text{taxa})).$$

Here, “lmer” refers to the statistical package used to apply the model (in lme4; Bates 2008), \sim is equivalent to “=,” i is the i th observation for a given lizard, L refers to a given lizard, and taxa groups lizards by taxon. Island was included as a fixed effect to consider differences in the way lizards respond to environmental conditions according to clade history. We also included separate two-way interaction terms between island and noise and light (not shown in the above model), but these were dropped if they failed to contribute significantly to the final model (see Engqvist 2005). We computed $\overline{\text{noise}}_L$ as the average level of visual noise over all observations for a given lizard. Habitat light was measured only once at the end of each observation.

In general terms, the random regression model is a nested, hierarchical analysis in which the relationships between a display characteristic and environmental variables for the individuals in each taxon are used to describe the “mean” within-taxon relationship across all of the taxa. Data from each taxon are weighted by sample size such that taxa with large numbers of samples (both multiple displays measured for a given lizard (first level) and many lizards surveyed for that taxon (second level)) have more influence on the calculation of mean parameter estimates (intercepts and slopes) than those with small sample sizes. Random regression models are therefore robust to outliers and provide a more accurate estimate of covariance relationships between a predictor and dependent variables than would be the case if separate regression models had been fitted individually to each taxon and then manually averaged over all taxa.

A more simplified analysis of covariance (ANCOVA) model in which taxa are included as a fixed effect and each environmental variable as a covariate is less informative because slope relationships between the display characteristic and environmental conditions are assumed to be the same for all taxa, and this cannot be adequately remedied by including interaction terms between taxa and each environmental condition when the analysis includes many taxa (see Kreft and de Leeuw (1998) for a detailed discussion of the limitations of alternative approaches, including ANCOVA).

For one display characteristic (headbob duration), plots revealed a set of outlying observations associated with one taxon (*A. pulchellus*, sampled at Punta Picua). To evaluate the affects of these outliers on our analysis, we calculated Cook’s distance measure for each taxon included in the random regression model (described above) using the influence.ME package version 0.7 (Nieuwenhuis et al. 2009) in R. As applied here, a large Cook’s distance value indicates that observations for a given taxon have

had a disproportionate level of influence on the regression model, in which case we would need to repeat our analysis with the outlying taxon removed. This occurred in the one instance already mentioned: individuals of *A. pulchellus* at Punta Picua performed unusually long displays as a function of the light environment compared to individuals from a second population of the same species observed at El Verde and other species communicating in similar light environments (see Fig. 2C). We therefore repeated both the random regression and phylogenetic analyses with observations on *A. pulchellus* from Punta Picua removed. Although we present results from both sets of analyses, we based our conclusions on analyses in which this outlying taxon had been removed.

It should be noted that the phylogenetic comparative analyses (following section) and the random regression models (this section) treat taxa in fundamentally different ways. The phylogenetic analyses formulate regression models to establish the covariance relationship between display behavior and the type of habitat in which taxa communicate, with the primary unit of study being the taxa themselves (i.e., a single datum for each taxon is used for the predictor and dependent variables, such as the average display speed and average light level for a given taxon). In these analyses, the emphasis is on evolutionary changes in display characteristics. By comparison, the random regression models essentially treat taxa as replicates to compute the covariance relationships within-taxa (while allowing the intercepts and slopes for each taxon to vary). Here, the units of study are the individual animals within each taxa and the regression parameters quantify display contextual reaction norms (intercepts and slopes) for each of those taxa.

Phylogenetic comparative analysis: We used Hansen et al.’s (Hansen et al. 2008; see also Labra et al. 2009) phylogenetic regression in the SLOUCH version 1.2 package implemented in R. The method relies on an Ornstein–Uhlenbeck model of “constrained” evolution that accounts for the extent that trait evolution has been free to vary adaptively (i.e., the level of phylogenetic inertia in trait evolution) and the influence of stochastic factors during evolutionary diversification. For example, when the phenotype of ancestors has had no influence on the phenotype of descendant taxa (there has been no phylogenetic inertia in trait evolution) and stochastic forces resulting in nonadaptive phenotypic variation have been weak, trait evolution precisely mirrors fluctuations over evolutionary time in the optimal relationship between the phenotype and the environment. In contrast, when the phenotypes of descendant taxa are heavily dependent on those of evolutionary ancestors (high phylogenetic inertia) and stochastic forces have featured prominently in the evolutionary process, trait evolution lags behind the adaptive optimum even in the presence of strong selection. Hansen’s method considers a variety of evolutionary scenarios between these extremes and selects the most likely process that best fits the data, rather than assuming any

particular mode of evolution at the outset. Furthermore, SLOUCH allows the incorporation of within-taxon variance associated with taxon values in the analysis.

The phylogeny of *Anolis* was taken from Nicholson et al. (2005) and is based on 1483 aligned base pairs of mitochondrial DNA sequences, with branch lengths set proportional to time using the program r8s (Sanderson 2003; see Losos 2009 for complete tree with branch lengths). The tree was pruned to the species of interest in Mesquite version 2.6. Statistical support for all species nodes shown in Figure 1 were strong with Bayesian posterior probabilities at or above 90% and bootstrap support in parsimony analyses generally greater than 80% (Nicholson et al. 2005). The minimum population divergence estimated among *Anolis* species on Jamaica (Jackman et al. 2002) was used to set branch lengths for all species for which two populations were sampled. We also conducted separate analyses that considered the mean and maximum estimate of population divergence (calculated from Jackman et al. 2002), but because these yielded qualitatively similar results to those discussed below, they are not reported here.

Results

CONTEXTUAL PLASTICITY IN SIGNALING BEHAVIOR

We began our analyses by first estimating the extent to which territorial displays produced by individual lizards within taxa were contextually plastic. Our analyses indicated that across the different taxa, the mean of within-taxon contextual plasticity was in the predicted direction for most, though not all, of the display characteristics tested (Table 3). Random regression models showed that individuals displaying when visual noise was high performed headbob and dewlap movements at significantly greater speeds (Hypothesis 1). The duration of headbob displays and dewlap extensions also decreased with increases in the amount of available light (Hypothesis 2; Table 3). However, display repetition rates were inversely related to visual noise and positively related to light, the reverse of the predicted direction by our a priori hypotheses (Table 3).

Our analyses of the contextual reaction norms of taxa from different islands indicated that clade history had two important effects on our findings. First, significant interactions occurred between environmental conditions and island of origin for three of the four display characteristics that significantly varied as a function of environmental conditions, indicating that mean contextual plasticity differed between islands (Table 3). Generally speaking, lizards from Puerto Rico were more contextually plastic over the same range of environmental conditions than lizards from Jamaica (see Table S1). Second, major differences existed between islands with respect to their within-taxon intercept values of display characteristics, indicating historical differences in dis-

play characteristics between islands. Of particular relevance for signaling under challenging environmental conditions, Jamaican taxa generally performed shorter headbob bouts and shorter pulses of the dewlap that were of higher speed than taxa on Puerto Rico. Differences between island lineages in their within-taxon slopes and their within-taxon intercepts could not be explained by differences in the range of noise or light conditions sampled (Table S1), or in the types of habitat or likely predation regimes on each island (a detailed discussion of these issues are presented in Ord et al., unpubl. ms).

TAXON DIVERGENCE IN SIGNALING BEHAVIOR

To evaluate explicitly taxon differences in display characteristics, we used phylogenetic comparative analyses of the mean values of the display characteristics for each taxon, which ignored the underlying mechanism that might have produced differences in these mean values (plasticity or evolutionary change; e.g., see Fig. 3). The predicted phylogenetic relationships across taxa between the mean display characteristics for a taxon and the mean environmental conditions for that taxon were detected despite the aforementioned differences between the islands. Phylogenetic analyses (Table 4A) showed that taxa in environments with high levels of visual noise from wind-blown vegetation or low light levels on average performed territorial displays of greater speed (Hypothesis 1) or longer duration (Hypothesis 2) than those living in less challenging signal environments. Taxa in environments with more visual noise showed a tendency to perform higher speed headbob movements, and those in low light environments exhibited a significant increase in mean headbob speed (Table 4A; Fig. 2B, top row). The speed of dewlap extensions was significantly higher for taxa in visually noisy environments (Fig. 2B, bottom row; Table 4A). Jamaican taxa also exhibited the predicted increase in the mean speed of dewlap extensions in low light, whereas Puerto Rican taxa did not (Fig. 2B, bottom row). Instead, Puerto Rican taxa in poorly lit habitats had headbob bouts that were generally of longer duration (Fig. 2C, top row) and held their dewlaps open for longer periods (Fig. 2C, bottom row) than those in brightly lit habitats.

The similarity between the mean patterns observed within taxa (Table 3) and the patterns observed across taxa (Table 4A) suggests that contextual plasticity might have contributed to the taxon differences in display characteristics detected in the phylogenetic comparative analysis (compare slope estimates from Table 3 and Table 4A, and Fig. 2B and C main plots with insets).

In principle, both the slope and the intercept of contextual reaction norms can evolve in response to changes in environmental conditions (Dingemans et al. 2010). However, neither Hypothesis 1 nor Hypothesis 2 predicts that the contextual plasticity (within-taxon slopes) of display characteristics should change as a function of the mean level of visual noise or light for a taxon

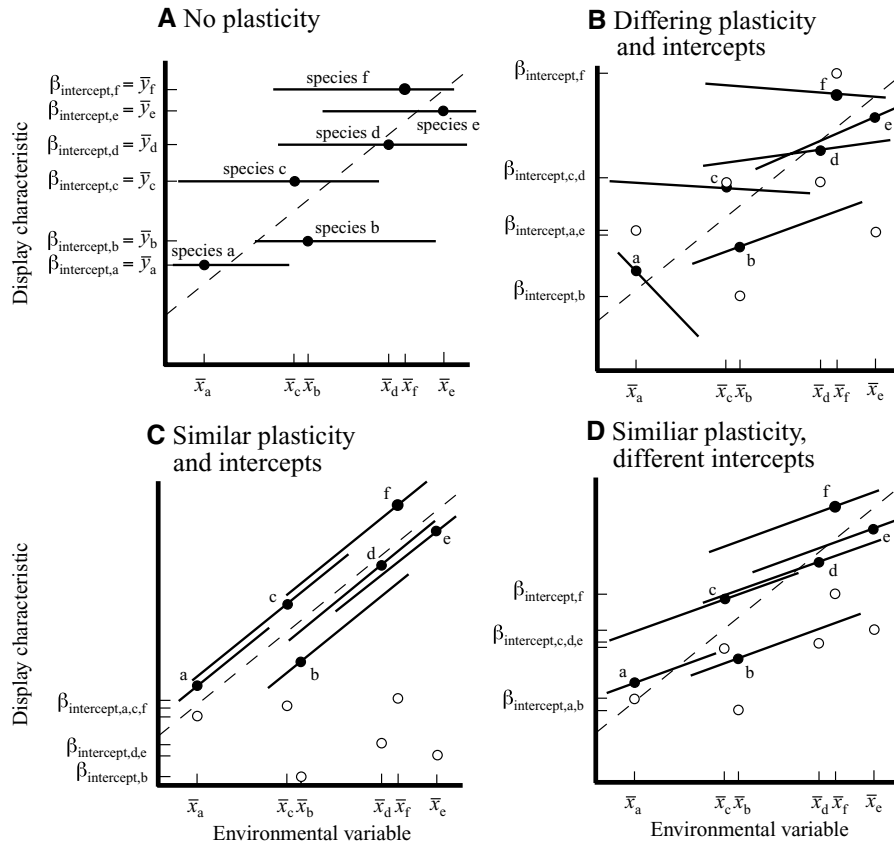


Figure 3. How plasticity can contribute to relationships between mean trait values and environmental variables. This example illustrates the display behavior of six hypothetical species (a–e), each of which is sampled over a wide range of environmental conditions. Dots indicate the mean display value (\bar{y}_i) and the mean environmental variable (\bar{x}_i) for each species; lines indicate the slope (plasticity) and range of environmental variables for each species. When reaction norms can be described by linear equations, random regression models of within species covariance relationships can be used to estimate the slope and intercept of the reaction norms for each species. When the slopes of these reaction norms are comparable across species, the intercepts provide estimates of “baseline” display values, that is, the display value the individuals in each species would express if every species in the dataset had been measured under the same environmental conditions. This approach can be used to study any type of phenotypic plasticity, including contextual plasticity (effects of current conditions on trait expression) and developmental plasticity (effects of earlier experiential factors on trait expression). The implicit assumption when interpreting between species relationships in a phylogenetic comparative analysis is that variance in phenotypes across species reflects evolutionary differences between species. The use of species mean values in a comparative analysis satisfies this assumption if there is no plasticity (all slopes = 0), because in this case the mean trait value for each species estimates the trait value that members of that species would express under any set of environmental conditions (A). The assumption might also hold when plasticity is present in display characteristics, but varies randomly between species in respect to the predictor variable (B). However, if there is plasticity and it is similar across the species in a dataset, then the intercept values for each species can be substituted for the mean values in comparative analyses to evaluate whether baseline trait values have evolved in response to variation in environmental conditions. For instance, in (C), the within-species slopes are the same as the slope of the relationship between the mean display values and the environmental variable. As a result, there is no relationship between intercept values and environmental conditions: the observed relationship between mean display values and environmental conditions can be entirely attributed to plasticity. If the slopes within species are in the same direction, but shallower, than the slope of the relationship between the mean display values and the environmental variable (D), then plasticity and variation among species in baseline display characteristics both contribute to observed relationships between mean display values and environmental variables. In this situation, we would observe a relationship between the intercepts and the environmental variable, but the slope of this relationship would be shallower than the slope of the relationship between taxa mean values and the environmental variable. A note of caution is warranted in situations in which the range of environmental values sampled within taxa is considerably smaller than the range of environmental values sampled across taxa (i.e., within-taxon ranges tend not to overlap among taxa). In this case, intercept estimates may be prone to high sampling error.

Table 4. Relationships across taxa in lizard display characteristics as a function of the environment (visual noise and light levels).

	$\beta_{\text{intercept}}$ (lower CI, upper CI)	β_{noise} (lower CI, upper CI)	β_{light} (lower CI, upper CI)	$t_{1/2}$ (support region)	v_y (support region)	% R^2	N_{axa}
A. Mean phenotype							
Display speed							
Headbob	21.15 (8.35, 33.95)*	1.26 (-0.11, 2.63)	-4.48 (-8.11, -0.84)*	0.0 (0-14)	5 (1-14)	51.4	16
Dewlap	8.79 (5.53, 12.04)*	0.89 (0.51, 1.27)*	0.09 (-1.14, 1.32)	∞ (0- ∞)	2 (0-50)	50.2	15
Display duration							
Headbob	12.02 (3.24, 20.80)*	-0.25 (-1.03, 0.53)	-1.65 (-3.98, 0.68)	900 (0- ∞)	120 (0-390)	10.4	16
outlier removed	13.12 (6.14, 20.10)*	-0.29 (-0.92, 0.34)	-2.28 (-4.16, -0.40)*	∞ (0- ∞)	7 (0-240)	24.6	15
Dewlap	5.56 (0.70, 10.42)*	0.39 (-0.14, 0.92)	-3.38 (-4.95, -1.81)*	2 (0-100)	2 (0.5-6)	51.1	15
Display repetition	0.39 (0.10, 0.68)*	-0.001 (-0.03, 0.03)	0.004 (-0.07, 0.08)	800 (275- ∞)	0.1 (0-0.4)	0.1	16
B. Baseline (intercept) phenotype							
Display speed							
Headbob	22.21 (16.39, 28.03)*	0.18 (-0.47, 0.83)	-2.67 (-4.41, -0.93)*	∞ (0- ∞)	0 (0-130)	30.6	16
Dewlap	11.07 (-41.46, 63.60)	0.56 (-5.12, 6.24)	-1.92 (-18.01, 14.17)	∞ (0- ∞)	0 (0-275)	4.4	15
Display duration							
Headbob	14.37 (5.77, 22.97)*	-0.60 (-1.42, 0.22)	-0.31 (-2.66, 2.04)	∞ (275- ∞)	100 (0-275)	13.4	16
outlier removed	11.39 (2.92, 19.86)*	-0.32 (-1.12, 0.48)	-0.05 (-2.38, 2.28)	975 (125- ∞)	100 (0-275)	4.4	15
Dewlap	5.32 (-37.55, 48.19)	0.72 (-3.91, 5.35)	-3.81 (-16.86, 9.24)	0 (0- ∞)	10 (0-200)	39.6	15
Display repetition	0.32 (-2.70, 3.34)	-0.004 (-0.33, 0.32)	0.004 (-0.85, 0.86)	0 (0- ∞)	0 (0-0.1)	3.4	16

*Slopes with confidence intervals that do not overlap zero.

Two sets of analyses were performed using Hansen et al.'s (2008) Ornstein-Uhlenbeck model of adaptive evolution. In the first (A), we used the mean display values across all the males sampled for each taxon to document correlations between mean display behavior and mean environmental conditions across taxa. In the second (B), we substituted the intercepts ("baseline values") for each taxon generated by the random regression models described in Table 3 for the mean values used in A. Comparison of the slope estimates and confidence intervals for the two sets of analyses indicates whether evolutionary changes in baseline display values contributed to relationships between environmental factors and mean display characteristics across taxa (see also Fig. 4). The phylogenetic half-life, $t_{1/2}$, refers to the extent that the phenotype of ancestors influences those of descendant taxa with values approaching ∞ corresponding to high phylogenetic inertia in display phenotypes (e.g., taxa of the same island clade exhibit very similar phenotypes). The influence of stochastic factors on display evolution is summarized by v_y , with large values (e.g., > 100) indicating display evolution has frequently drifted from an adaptive optimum. Support regions are the lowest and highest values within two log-likelihood units of the best estimate. The amount of variation explained by an analysis is given as a percentage R^2 . Taxon number for dewlap movements is reduced by one because the Puerto Rican lizard, *A. poncensis*, lacks an obvious dewlap. As in Table 3, the analysis of headbob duration was repeated with an outlier removed that corresponded to a population of *A. pulchellus* (see Fig. 2).

(Fig. 2A). Indeed, separate phylogenetic analyses (not reported here) failed to detect any significant relationships across taxa between the within-taxa slopes and the mean values of visual noise or light for those taxa (see also Table S1). On the other hand, within-taxon intercepts of display characteristics might vary as a function of the mean visual noise or light levels in the habitats in which those taxa evolved and currently live. For instance, if faster headbob speeds enhance display detection in low light (Ord and Stamps 2008), then a taxon that evolved in a consistently darker environment might have evolved faster headbob speeds, leading to the performance of generally faster headbobs at any given light level, than a taxon that evolved in brighter environments, leading to variation across taxa in intercept values.

It follows that for contextually plastic characters, a phylogenetic comparative analysis based on the relationship between within-taxon intercepts of display characteristics and environmental conditions provides a way to determine whether the non-plastic component of a display characteristic (summarized by the within-taxon intercepts) has evolved in response to variation in environmental conditions. Of course, in the absence of any contextual plasticity (all within-taxon slopes are zero), the values of the intercept and the mean display value for a given taxon would be comparable, in which case phylogenetic analyses based on within-taxon intercepts would generate results similar to those based on the mean trait values of each taxa. Similarly, if the direction and degree of contextual plasticity varies widely across taxa, but contextual plasticity is random with respect to the environmental variable of interest, we would also expect results based on within-taxon intercepts to be comparable to those based on the mean values for those taxa. However, in this situation, the increased variance associated with using within-taxon intercepts rather than means would likely increase the width of confidence intervals around estimates of regression parameters. At the other extreme, if all of the taxa in the phylogeny have similar contextual plasticity (within-taxon slopes), then contextual plasticity can be entirely responsible for observed relationships between mean trait values and environmental variables. In that case, one would not expect to observe any relationship between the within-taxon intercepts and the environmental variables of interest. In situations in which both contextual plasticity and evolutionary changes in intercept display values contribute to variation in the mean display values for taxa living in different environments, results from intercepts would be weaker than those using means but in the same direction. A graphical depiction of these scenarios is presented in Figure 3.

In the current study, the within-taxon intercepts of headbob speed significantly increased as a function of decreasing light, indicating that despite evidence of contextual plasticity for this display character (Table 3), headbob speeds at any given light level were also elevated for taxa living in poorly lit environments

(Table 4B; Fig. 4A; see also Fig. S1). In the other three cases for which we had detected significant relationships between mean display characteristics and environmental conditions (headbob duration and light, dewlap duration and light, dewlap speed and visual noise; Fig. 4B–D), there were no significant relationships between the intercepts of these display characteristics and environmental conditions (Table 4B). The speed of dewlap extensions relative to visual noise offers a particularly striking example of how contextual plasticity that is consistent in direction and strength for members of different taxa can generate significant relationships between mean trait values and environmental variables across those taxa (Fig. 5). In this case, the contextual reaction norms for all of the Puerto Rican taxa have virtually the same slope and intercept, as a result of which, there was no relationship between a taxon's intercept value of dewlap speed and the level of visual noise in its environment (Table 4B; Fig. 4C).

Discussion

Support for the predictions derived from communication theory (Wiley and Richards 1982; Brumm and Slabbekoorn 2005) suggests that plasticity and evolutionary changes in *Anolis* territorial displays as a function of environmental conditions are “adaptive.” Virtually all changes in communication behavior, regardless of the underlying process governing those changes, were in the expected direction. Furthermore, previous experiments using robotic lizards to perform different variants of territorial displays to *Anolis* lizards indicate that the display changes we report here do indeed enhance the conspicuousness of displays in challenging environments (Ord and Stamps 2008). Only one result in the present study conflicted with our initial predictions: within taxa (but not across taxa), display rates declined when conditions became increasingly noisy or poorly lit. One possible explanation is that within taxa, individuals avoid producing displays during periods when signal detection is likely to be compromised by environmental challenges (e.g., concentrating display effort during periods of low visual noise: Ord et al., unpublished ms). This would lead to variation within taxa in the display rates of individuals that were randomly sampled under different conditions, but not to differences in mean display rates across taxa, exactly as we found.

There are two reasons why one might observe correlations across individuals between behavior and environmental factors. One possibility is *rIE* (see Table 1), a correlation between individual phenotype and environment that occurs when individuals with different stable phenotypes express those phenotypes in different environments (Stamps and Groothuis 2010; for a morphological example of *rIE*, see Bolnick et al. 2009). For instance, *rIE* would imply that adult *Anolis* males who produced displays that improved detection under low light would establish their

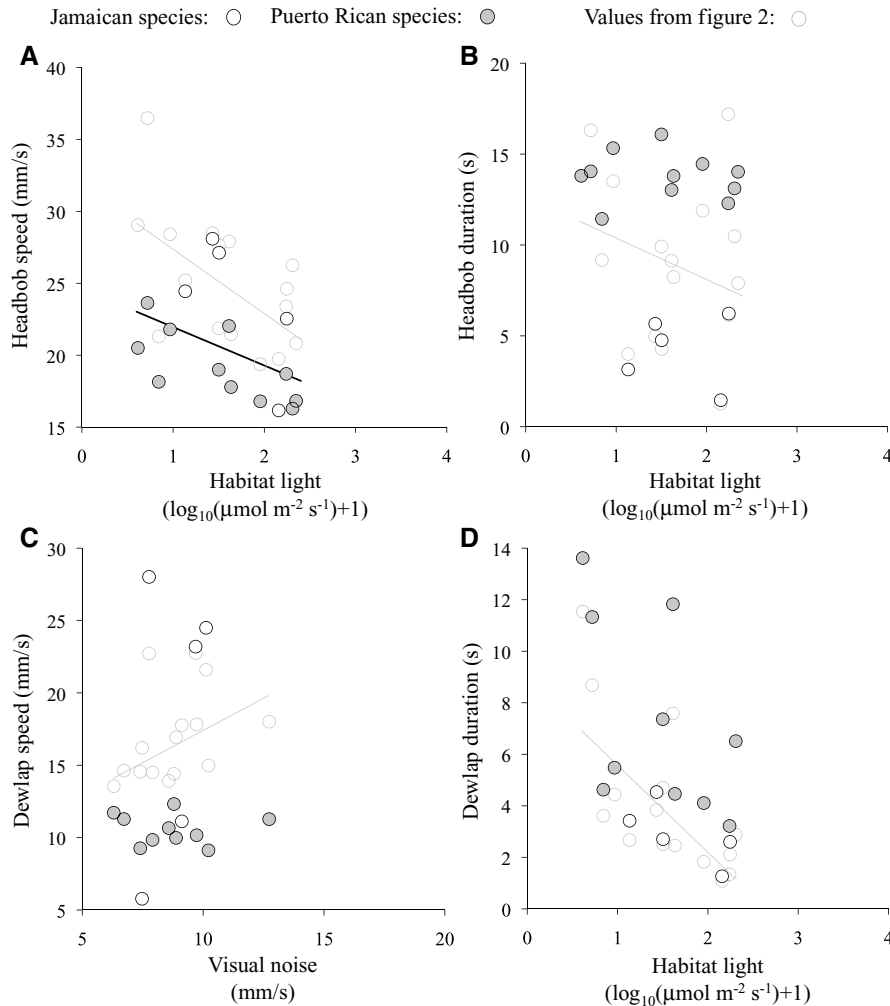


Figure 4. Variation among *Anolis* in baseline display characteristics. Display characteristics are those for which mean values significantly varied as a function of environmental conditions in phylogenetic analyses (see Table 4A; Fig. 2). Shown here are the estimates of the intercept values for each taxon (see Table S1) as a function of the mean noise or light level for that taxon. See Figure 3 for graphical depiction of the philosophy behind this approach. Open circles represent taxa from Jamaica, whereas closed circles are those from Puerto Rico. Shown in light gray are the mean values reproduced from Figure 2. The trend line in (A) indicates a significant relationship after phylogenetic analysis between the intercept of headbob speed and ambient light (see Table 4B).

territories in dark areas or give most of their displays under low light conditions (e.g., at dusk or at dawn). The second possibility is contextual plasticity within individuals. In principle, contextual plasticity is a much better option for adjusting communication signals to current conditions than is *rIE*. In anoles, for instance, considerable variation in background motion and light levels can occur over very short periods of time (minutes to days) within any male's territory. A male whose displays were only suited to a narrow range of visual noise and light conditions would be severely restricted with respect to the time period available for effective communication. In fact, previous analyses of anoles indicate that correlations across individuals between display characteristics and visual noise or light are primarily due to individual contextual plasticity not *rIE* (Ord et al. 2007;

Ord and Stamps 2008; see also data presented in the methods section).

Correlations between signal characteristics and environmental conditions for individuals sampled under different signal conditions are often reported in the communication literature, especially for animals communicating acoustically (e.g., Slabbekoorn and Peet 2003; Mockford and Marshall 2009; Nemeth and Brumm 2009). To date, most researchers who discover such correlations seem to assume that they reflect *rIE*. As we discuss above, this would only occur if individual animals produced invariant signals and only communicated at times or locations most suited to their type of signal. The latter seems less likely for dynamic forms of communication like acoustic or movement-based signals than might be the case for static morphological signals. We

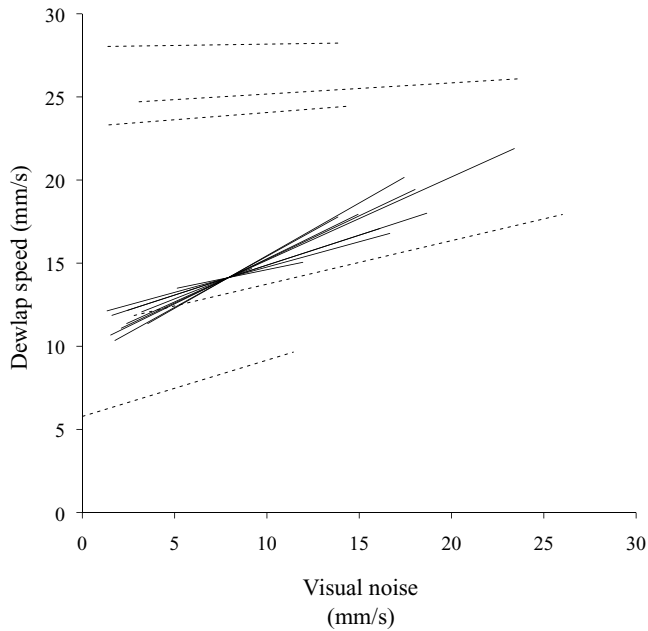


Figure 5. Contextual reaction norms for relationships between dewlap speed and visual noise for *Anolis* lizards. Each line represents the intercept and slope of dewlap speed as a function of visual noise for one taxon (solid lines: those taxa from Puerto Rico; dotted lines: those taxa from Jamaica), based on the random regression described in Table 3 (see also data in Table S1). Lines span the range of noise conditions under which the displays of individuals of that taxa were recorded.

anticipate that many previously reported correlations between dynamic signals and environmental factors may actually be the product of contextual plasticity.

Indeed, one of the most striking results of our study is that contextual plasticity can account for observed correlations across taxa between mean display characters and mean environmental factors. Generally speaking, contextual plasticity is most likely to contribute to such correlations when the range of values of environmental factors for the individuals within each taxon is comparable to the range of the mean values of those same environmental factors across taxa. In this situation, even if individuals shift to an environment with mean environmental values different from their previous one, they do not have to generate entirely new behaviors, but merely increase expression of behaviors that are already in their repertoire. In the case of anoles, even lizards living in environments that are brightly lit most of the day still give displays near dawn and dusk when light levels are low (Ord 2008), and every taxon we studied occupied environments in which the wind that generates visual noise varies across short temporal scales (minutes to days) from calm (no noise) to very windy (high noise; Table S1). That is, for both visual noise and light, the range of conditions experienced by individuals within taxa was similar to, and sometimes even greater than, the range of mean conditions

across taxa (results presented in Table S1). Hence, even sizeable shifts in the mean visual noise or light levels for a taxon would not require individuals to produce displays widely divergent from some of the displays that they produced in their previous environment.

We also discovered pronounced differences in display characteristics and contextual plasticity between the Jamaican and Puerto Rican clades, suggesting early divergence in the ancestors of these groups, followed by evolution along different trajectories in their descendants. In some cases, these evolutionary changes in display characteristics may have contributed to the differences between the two clades in contextual plasticity. Our results suggest that Jamaican species have advertisement displays of short duration with high-speed dewlap extensions, but low contextual plasticity. Conversely, Puerto Rican species perform displays of long duration, lower speed dewlap extensions, and high contextual plasticity. Rapid extensions of the dewlap in *Anolis* are an effective means of attracting the attention of receivers (Ord and Stamps 2008). If members of a taxon already have signals suited for effective transmission under challenging conditions, for example, rapid dewlap extensions, we should not expect individuals to adjust their signals as a function of changes in environmental conditions.

It might also be argued that the differences in plasticity for Jamaican and Puerto Rican taxa are a result of differences in static components of anole communication, namely dewlap size and color, for taxa on the two islands. The size and color of the dewlap is thought to affect the conspicuousness of *Anolis* displays (Losos and Chu 1998; Fleishman 2000), so if Jamaican lizards had larger or brighter dewlaps than those on Puerto Rico, this might explain the lower plasticity in the Jamaican clade. However, despite considerable variation in dewlap size and color among the taxa we studied, we could find no differences between taxa on the two islands in either the size or color of the dewlap (T.J. Ord, unpubl. data for dewlap size; color data were obtained from Fleishman 2000).

In summary, we have shown that the combined effects of adaptive evolution, adaptive plasticity, and historical effects on signal design explain much of the variation in dynamic communication signals among *Anolis* species. The prominent role that contextual plasticity plays in adjusting communication signals to prevailing environmental conditions is unlikely to be specific to visually communicating lizards, but probably widespread in any taxa in which signal detection depends on environmental conditions and in which those environmental conditions fluctuate over relatively short periods of time (e.g., hours to days, as opposed to years or generations). In addition, communication may be useful in addressing larger questions about plasticity, for example, whether it accelerates or buffers evolutionary change when animals invade novel environments (Baldwin 1896; Huey et al. 2003;

Paenke et al. 2007), how plasticity itself evolves (Pigliucci 2005; Lande 2009), and the costs associated with being plastic (DeWitt et al. 1998; Auld et al. 2010). The study of animal communication, in which one form of plasticity (contextual) can be readily measured in nature for a large number of taxa, offers a general, tractable model system for the study of phenotypic plasticity and macroevolution.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Contextual reaction norms for all significant relationships shown in Figure 2.

Table S1. Relationships between display characteristics and the environment for each *Anolis* taxon studied.

Supporting Information may be found in the online version of this article.

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