



Original Article

# Plasticity in social communication and its implications for the colonization of novel habitats

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Behavioral plasticity is expected to facilitate the colonization of novel habitats by allowing populations to respond rapidly to abrupt environmental change. We studied contextual plasticity—a form of plasticity that allows an immediate phenotypic response to stimuli—in the territorial communication of Puerto Rican *Anolis* lizards and considered the role it might play in facilitating colonization. In these lizards, the detection of territorial visual displays by receivers is acutely dependent on fluctuating levels of visual noise from windblown vegetation and ambient light. We quantified the contextual reaction norms of various components of the territorial displays of individual lizards as a function of visual noise and light for one focal population over many weeks of observation. We then compared these contextual reaction norms to the displays given by closely related *Anolis* species found in other environments to assess the extent to which colonizing lizards might be capable of performing displays similar to those likely to be effective in those environments. Our results suggest that lizards are able to rapidly adjust their territorial displays in ways that might help them communicate in other (but not all) habitat types on Puerto Rico. Given that the contextual plasticity of animal signals can be measured in free-living animals far more easily than other forms of behavioral plasticity, our study presents animal communication as a tractable model for tackling broad questions in how phenotypic plasticity might facilitate colonization, adjustment to environmental change, and adaptation.

**Key words:** **activational plasticity, behavioral reaction norms, developmental plasticity, evolution, invasion, phenotypic plasticity.**

## INTRODUCTION

There are many factors that may determine whether a population is able to survive a colonization event and subsequently persist long enough to establish itself in a new environment. For many years, it has been suggested that behavioral plasticity is one of those factors (Baldwin 1896; West-Eberhard 2003; Duckworth 2009; Candolin and Wong 2012; Zuk et al. 2014). This is because behavior can change more rapidly than morphological or life-history traits (West-Eberhard 2003). Indeed, behavior can change immediately within individuals in response to changes in external stimuli, a type of behavioral plasticity termed contextual (or activational) plasticity (Stamps and Groothuis 2010b; Snell-Rood 2013; Stamps

2015). In addition, as is the case with other phenotypic traits, behavior can also change more slowly and gradually in response to past external stimuli, experiences, or environmental conditions, a type of plasticity termed developmental plasticity (ibid). For instance, social stimuli experienced early in life often affects adult song production in birds (Marler and Tamura 1964; for further discussion of the differences between contextual and developmental plasticity, see Stamps and Groothuis 2010b; Snell-Rood 2013; Stamps 2015). The distinction between contextual and developmental plasticity is particularly relevant to the colonization of new habitats because the former may allow individuals to adjust their behavior in potentially adaptive ways during the first critical days after arriving in a novel environment.

In this study, we focused on a type of behavior—social communication—that has been shown to be contextually plastic. Examples

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of contextual plasticity in communication include immediate changes in guppy courtship behavior in response to changes in ambient light levels (Chapman et al. 2009) and immediate changes in avian vocal signals in response to changes in ambient noise (Potvin and Mulder 2013). In addition, it has been suggested that contextual plasticity in communication might be responsible for some of the changes in behavior observed in animals living in environments modified by humans (Tuomainen and Candolin 2011; Brown 2012). For instance, recent studies of behavioral responses to anthropogenic sources of background noise show that a number of birds are able to adjust their vocalizations almost immediately in response to anthropogenic noise pollution, in ways that potentially improve their chances of being heard by receivers (e.g., Potvin and Mulder 2013 mentioned above; see also Gross et al. 2010; Verzijden et al. 2010; Hanna et al. 2011; Goodwin and Podos 2013).

These results imply that contextual plasticity in communication might help individuals quickly and adaptively adjust their signals in response to natural (as opposed to anthropogenic) changes in environmental stimuli. This might, in turn, allow animals to more easily transition into novel environments. We explore this idea by comparing the contextual reaction norms for the communication signals of individuals from one population of *Anolis* lizards to the communication signals produced by closely related populations and species that currently live in a range of different environments. We draw on previous comparative studies that have demonstrated strong relationships, across these taxa, between specific environmental factors and specific attributes of the lizards' communication signals (Ord et al. 2010a; Ord 2012; Ord et al. 2013a). In most cases, the observed variation among taxa in communication signals as a function of environmental factors appears to be adaptive based on signal detectability and the costs of signal production (Ord and Stamps 2008; Ord et al. 2010a). More generally, we follow others in assuming that strong relationships between environmental factors and trait values detected in comparative analyses are likely to be adaptive, even if the selective pressures and the proximate mechanisms that are responsible for generating those patterns are not yet clear (Brooks and McLennan 1991; Harvey and Pagel 1991; Martins 1996; Nunn 2011; Garamszegi 2014). Hence, by comparing the contextual reaction norms of individual lizards in one population with the displays produced by congeners living in other environments, we can obtain an initial look at how contextual plasticity might help individual lizards immediately adjust their communication signals in potentially adaptive ways if they found themselves in a new habitat.

## The Study System

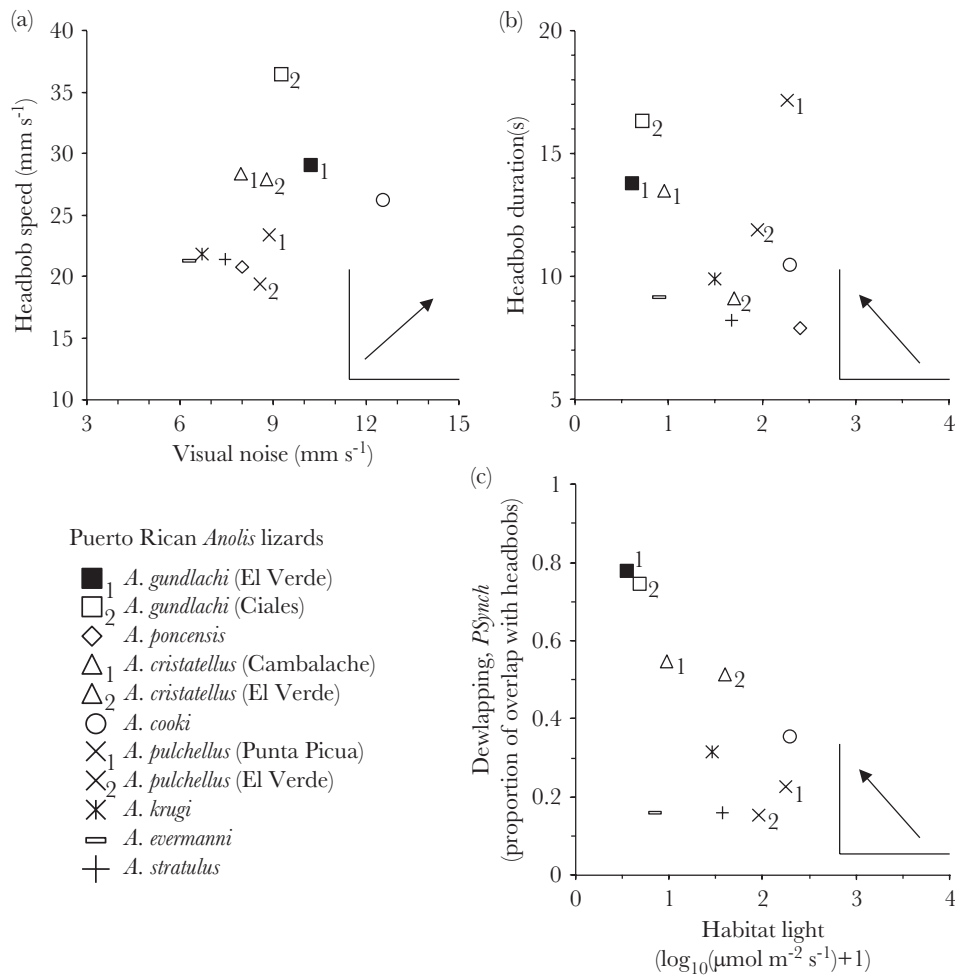
In *Anolis* lizards, adult males use elaborate headbob displays and the extension of a colorful throat fan or dewlap to advertise territory ownership to other males and communicate with females living within their territories (e.g., see Charles and Ord 2012). Previous comparative studies have shown that several attributes of *Anolis* advertisement displays predictably vary among closely related species on Puerto Rico as a function of visual noise from wind-blown vegetation and ambient light levels (Ord et al. 2010a, 2013a). Species living in environments with high mean levels of visual noise generally have higher mean display speeds than those living in less noisy environments (Ord et al. 2007, 2010a; Figure 1). In addition, species living in dark habitats tend to give longer displays consisting mostly of exaggerated headbob movements, whereas those living in brightly lit habitats give shorter displays with multiple dewlap extensions (Ord et al. 2010a, 2013a; Figure 1).

To date, adaptive explanations for the relationships between components of male advertisement displays and environmental features observed in Puerto Rican anoles have focused on potential tradeoffs between signal detection and the costs of signal production (Ord and Stamps 2008; Ord et al. 2010a; Ord 2012; Ord et al. 2013a). This is because there is considerable support in lizards—including evidence from experimental studies that document the effects of signals on receivers—for hypotheses that faster movements, longer displays, and exaggerated movements enhance the detection of male advertisement displays by distant recipients, especially under difficult signaling conditions (Fleishman 1986; Peters and Evans 2003, 2007; Peters 2008; Ord and Stamps 2008; Ord et al. 2010a; Ord 2012; Steinberg and Leal 2013). However, the energetic costs to lizards of producing headbob displays can be considerable (see Brandt 2003; Brandt and Allen 2004; Perry et al. 2004), and territorial advertisement displays are given frequently throughout the day (an average of one display bout every 3 min for most Puerto Rican anoles; data from Ord et al. 2010b). Hence, it would not be surprising if lizards displaying in low noise or brightly lit conditions (where signal detection is less of an issue) used slower, shorter, less exaggerated movements when advertising territory ownership.

Of course, other factors might also contribute to the relationships between visual noise, light, and the territorial advertisement signals observed in comparative studies of Puerto Rican anoles. Conspicuous display movements might facilitate detection by distant conspecific receivers (Ord and Stamps 2008), but also predators (Steinberg et al. 2014), and both conspecific spacing patterns and predation pressure might covary with habitat light levels in these animals. For instance, lizards living in open, bright habitats are likely to experience higher predation (Stuart-Fox and Ord 2004; McMillan and Irschick 2010) and may need to communicate over longer distances (Johnson et al. 2010) than those living in closed, dark habitats. Other factors that could covary with habitat light or noise, and might affect anole communication signals, include sex ratios (Ord 2008, 2012) and other factors associated with the intensity of sexual selection (Ord and Martins 2006). In this study, we simply assume that the displays produced by the members of a taxon that live in a habitat with a given level of noise and light are—for the most part—effective in that habitat, without necessarily specifying all of the proximate or ultimate factors that might affect display behavior.

Regardless of the selective pressures responsible for the observed relationships between display components and habitat noise or light in Puerto Rican anoles, previous analyses suggest that contextual plasticity might contribute to many of these relationships (Ord et al. 2010a, 2013a). For instance, the positive relationship between mean visual noise and mean display speed observed across different species of anoles was also observed when different males within the same population gave displays at different visual noise levels. Similarly, contextual plasticity could account for much of the negative relationship between mean display duration and mean light observed among species (Ord et al. 2010a), and at least some of the variation across species in display type (emphasis on dewlapping vs. emphasis on headbobbing) as a function of light (Ord et al. 2013a).

Although promising, one difficulty with these previous analyses was that contextual plasticity was not actually measured within individuals. Instead, the taxon or “mean-level” contextual reaction norms for each population were indirectly estimated by recording the displays of different individuals and the light and noise conditions at each individual's location when it gave those displays. The



**Figure 1**

Species differences in mean environmental factors and display attributes believed to be important in determining the conspicuousness of male territorial advertisement displays for Puerto Rican *Anolis* lizards: (a) headbob speed, (b) duration of headbob bouts, and (c)  $P_{Synch}$  (the extent to which displays emphasize headbobs or dewlap extensions). The population of *Anolis gundlachi* at El Verde is highlighted in black. Insets depict the direction of change predicted for improved signal detection as viewing conditions become increasingly more difficult for receivers. Data from Ord et al. (2010b, 2013b).

slopes of these estimated contextual reaction norms across individuals were then used to generate an estimate of each taxon’s mean contextual plasticity, and the intercepts used to generate an estimate of the “baseline” display value for that taxon (see Ord et al. 2010a). However, although contextual plasticity at the individual level provided the most plausible explanation for the observed relationships between environmental factors and display components observed in the data, other possible explanations could not be ruled out (Ord et al. 2010a). At this point, there is only limited direct evidence for contextual plasticity in communication signals in response to environmental factors in free-living anoles: in 2 species, *Anolis cristatellus* and *Anolis gundlachi*, there was a positive relationship within individuals between headbob speed and visual noise (Ord et al. 2007).

In the current study, we directly measured the contextual reaction norms of the territorial advertisement displays of free-living *A. gundlachi* males living in the deep shade montane forests of Puerto Rico. We selected this species because its members often experience ambient light and visual noise levels that present an acute challenge for effective communication (low light and high visual noise—Figure 1; Ord et al. 2007; Ord and Stamps 2008; Ord et al. 2010a). We measured large numbers of advertisement displays produced by each of 14 males

across a wide range of light and noise conditions. This was to ensure that we had sufficient data per male under uncontrolled field conditions to detect among male differences in both the slopes (contextual plasticity) and the intercepts of their contextual reaction norms. Such differences are important because they imply that different individuals in the same population might express different behavior if they found themselves in a new habitat.

We then compared these data with the estimates of mean-level contextual reaction norms previously described for *A. gundlachi* at the same locality and for other *Anolis* taxa that currently live in different habitats on Puerto Rico. The first comparison allowed us to determine whether indirect estimates of taxon-level contextual reaction norms based on samples of many individuals at a given locality (e.g., those of Ord et al. 2010a, 2013a) can provide a reasonable approximation of the mean-contextual reaction norms of the individuals living at that locality. The second comparison allowed us to compare the responses of individual *A. gundlachi* to different noise and light levels with the behavior expressed by related taxa that currently live and display in environments with different mean noise and light levels than those inhabited by *A. gundlachi*.

## MATERIAL AND METHODS

The online [Supplementary Appendix](#) provides additional information on data collection and statistical analyses, as well as [Supplementary Results](#) not presented in the Results section. All data from this publication have been archived in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.td1g2>).

### Data collection

#### Observations of *A. gundlachi*

Fourteen adult male lizards were located in the forest surrounding the El Verde Field Station on Puerto Rico (18°19'N, 65°49'W). Males were tagged with color-coded “bee” tags to allow individual identification. The tags were small (only a few millimeters in diameter), but were noticeable by a human observer at a distance and had no obvious effect on a male’s behavior. A deliberate effort was made to tag adult males on territories in different parts of the forest. The minimum distance between tagged males was roughly equivalent to a separation of 10 or more territories (Ord TJ, unpublished data), and neighboring males were well out of visual range of one another. Observations of each male began at least 3 days after the male had been caught and tagged, which provided ample time for males to recover from any adverse behavioral effects of handling.

Repeat observations were made of each lizard that consisted of continuously video recording the focal male for 15 min from 4 to 5 m away (e.g., Ord et al. 2007). Observations were only conducted if the identity of the focal male could be verified using the tags visible on the lizard. The number of observations and total time individual lizards that were observed are displayed in [Table 1](#).

**Table 1**  
Number of adult lizards observed and period over which observations were conducted

Male	Observation time (hours)	Observation period (days)
Within male <i>Anolis gundlachi</i> (El Verde)		
6	3.25	8
7	5.75	12
8	16.25	24
9	14.50	24
10	15.75	24
11	12.00	24
14	14.50	24
15	16.75	24
16	16.50	24
17	11.75	24
18	15.75	24
21	14.42	25
22	8.42	21
24	10.00	12
Species	Number of males	Observation time, mean (range)
Within Puerto Rican <i>Anolis</i> taxa (Ord et al. 2010b, 2013b)		
<i>Anolis gundlachi</i> (El Verde)	40	25 min (15–32)
<i>Anolis gundlachi</i> (Ciales)	36	24 min (11–28)
<i>Anolis Poncensis</i>	12	24 min (14–27)
<i>Anolis cristatellus</i> (El Verde)	36	22 min (4–28)
<i>Anolis cristatellus</i> (Cambalache)	33	22 min (12–26)
<i>Anolis Cooki</i>	27	22 min (5–31)
<i>Anolis pulchellus</i> (El Verde)	8	22 min (17–27)
<i>Anolis pulchellus</i> (Punta Picua)	30	21 min (4–30)
<i>Anolis Krugi</i>	31	21 min (5–29)
<i>Anolis Stratulus</i>	32	18 min (3–26)
<i>Anolis Evermanni</i>	32	21 min (6–28)

Data on ambient light was collected continuously during the observation period whenever the focal male displayed using a LiCor LI-250A handheld light meter attached to the side of the camcorder with a LI-190SA Quantum Sensor directed toward the displaying focal male. Data on the amount of visual noise occurring at the time of display were measured from video images (see Video analysis for details). This arrangement of the camcorder and light meter simulated the viewing field and amount of light that would enter the eye of a typical territorial neighbor (note: the mean distance of territorial male neighbors for this population of *A. gundlachi* was 5.1 m with a 95% confidence range of 4.1–6.1 m; Ord 2012, see also Ord and Stamps 2008). Data on ambient air temperature, a potentially important covariate affecting a range of behaviors in lizards (e.g., Rand 1964), was collected to one decimal place using a Skymate Wind Meter at the end of the observation period and at the site the lizard was first observed to display or was first seen at the start of the observation period (if the lizard did not display during the observation period).

#### Comparative data of Puerto Rican *Anolis* taxa

Data on the displays and environment for 11 Puerto Rican taxa (8 *Anolis* species) were extracted from the data archive that formed the basis for Ord et al. (2010a, 2013a) available through the Dryad Digital Repository (see Ord et al. 2010b, 2013b). Sample sizes and length of observation times for lizards are given in [Table 1](#) (the phylogenetic relationships of taxa are shown in [Supplementary Figure A1](#)). This comparative data set included brief observations on 40 adult male *A. gundlachi* from the same population (El Verde) for which extensive observations were made on the 14 adult male *A. gundlachi* (see Observations of *A. gundlachi* for details). This allowed us to compare reaction norms directly computed from repeated sampling of a handful of males to the taxon (mean-level) reaction norm indirectly estimated using brief observations of many males from the same population. Data on light, visual noise, and air temperature were also available in these data archives.

### Video analysis

All video used to compute individual reaction norms for the 14 adult male *A. gundlachi* and the taxon reaction norms of Puerto Rican taxa from Ord et al. (2010b, 2013b) were processed and analyzed in an identical fashion by a single researcher (T.J.O.). First, the speed of headbob display movements (referred to as “headbob speed” from this point on) and the amount of visual noise generated by windblown vegetation behind the lizard in video images were measured using the MatLab-based program “Analysis of Image Motion” (Peters et al. 2002; see online [Supplementary Appendix](#) for specifications on how these analyses were conducted). Second, display clips were viewed manually in real time to determine the duration of headbob display bouts (referred to as “headbob duration”) based on the length of time between the first and last display movement calculated from clip time-codes (display movement was clearly distinguishable from other behaviors, and the start and end of displays corresponded to the first and last vertical head or body movement associated with the first and last headbob or pushup movement, respectively). Finally, display type (*PSynch*) was measured as the proportion of display bouts in which dewlap extensions accompanied or were performed in isolation of the headbob display. *PSynch* has been shown to provide a robust index of a range of different signal characteristics (Ord et al. 2013a) that broadly describe whether a display emphasizes headbobbing (*PSynch* values converging on 1) or dewlapping (*PSynch* values converging on 0).

Intraobserver reliability for all display measures was high (headbob speed and duration,  $r = 0.93\text{--}0.98$ ;  $PSynch$ ,  $\kappa = 1.00$ ; see online [Supplementary Appendix](#) and [Supplementary Table A1](#) for details).

These 3 display characteristics are either broadly comparable with signal attributes commonly found to be important for signal detection in animal communication—signal intensity and duration (e.g., [Patricelli and Blickley 2006](#))—or have been found to correlate specifically in *Anolis* with aspects of the physical environment known to be influential in determining the likelihood of signal efficiency— $PSynch$  as a function of ambient light ([Ord et al. 2013a](#); see [Ord and Stamps 2008](#)). The extent to which these display characteristics might also be informative in species recognition has not been tested, but given that they vary substantially across individuals within each taxa ([Ord et al. 2010a, 2013a](#)) and within individual lizards across time ([Ord et al. 2007](#); this study), their utility as cues for species identification is probably limited.

## Statistical analyses

### Computing and comparing display reaction norms

We evaluated the contextual reaction norms of each display characteristic as a function of visual noise, habitat light, and temperature, as well as various combinations of these variables. To do so, we applied 7 different random regression models using the package `lme4` ver 1.0–5 ([Bates et al. 2013](#)) implemented in R ver 2.15.3 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) based on the reaction norm shape identified for a given environmental variable. These shapes were evaluated from analyses of the behavior of individual *A. gundlachi* (see [Supplementary Table A2](#) in the online [Supplementary Appendix](#)) and then visually confirmed in the comparative data of other Puerto Rican *Anolis* taxa.

Each environmental model was applied to the 14 adult male *A. gundlachi* collectively and included the environmental factor(s) of interest, plus a random intercept and slope for lizard identity. This approach allowed statistical inferences to be made of the likely influence each environmental factor had in generating reaction norm responses in this population (see next paragraph). It also allowed computation of the individual reaction norms for each lizard alongside an estimate of the extent those reaction norms differed among those lizards. Comparable environmental models were then applied to the mean data previously collected for individual lizards from all 11 Puerto Rican *Anolis* taxa collectively, which included a random intercept and slope for taxon identity. In the case of  $PSynch$ , one species (*Anolis poncensis*) effectively lacked a dewlap (see [Ord et al. 2013a](#)), so analyses of  $PSynch$  focused on the remaining 10 Puerto Rican taxa that possessed a visible dewlap. Estimates of separate reaction norms for each taxon and the extent those reaction norms differed among taxa were also computed as part of this procedure. For both the 14 male *A. gundlachi* and the 11 Puerto Rican taxa, we also applied a null model in which the same random intercepts were considered (by male or taxon identity), but no predictor variable was included (i.e., an intercept only model).

Support for the environmental models and the null model was evaluated using the second-order calculation of Akaike's information criterion (AIC). This value was converted into an estimate of a model's "weight" ( $AIC_w$ ; [Burnham and Anderson 2002](#)) to provide a relative measure of its level of support compared with the other models applied (values of  $AIC_w$  range from 0.0, or effectively no relative support for a given model, to 1.0, or total support for a given model compared with others considered). For the model

receiving the most support, individual or taxon-level variation in computed reaction norms was evaluated using  $z$ -score estimates of the variation exhibited among males or taxa in the intercepts or slopes of their contextual reaction norms.  $Z$ -scores greater than 2.0 confirm statistically distinguishable differences in reaction norms among lizards or taxa.

Our ability to test hypotheses about factors that might have contributed to differences in contextual reaction norms among males or among taxa was limited. When measuring the contextual reaction norms of individual *A. gundlachi*, we focused on obtaining many repeat observations per male across a wide range of noise and light conditions, instead of measuring many numbers of males a few times each. This design allowed us to describe the full range of conditions under which each male gave displays and maximized statistical power for detecting individual differences in the slopes and intercepts of their reaction norms. However, it limited the statistical power available for testing hypotheses about factors that might account for individual differences in contextual reaction norms (because  $N = 14$  males). Similarly, the taxon-level analyses were based on data from many males per taxon, but with only 11 taxa, the power to test hypotheses about factors related to differences among taxa in their slopes and intercepts was limited. With these limits in mind, we conducted a general examination of the potential causal factors that might have promoted differences in contextual reaction norms among males or among taxa in several ways.

Previous studies of Puerto Rican anoles suggested that differences among individuals and among taxa in the intercepts of their contextual reaction norms might be related to the mean light and visual noise levels experienced by individual males in their territories and by taxa in their respective habitats ([Ord et al. 2010a, 2013a](#)). For instance, we hypothesized that individuals or taxa living in areas with high mean noise levels might have higher intercepts for display components that improve signal detection under noisy conditions than individuals or taxa living in areas with lower mean noise levels. Accordingly, we tested these hypotheses in the current study.

However, there are many factors that might explain differences among individuals or taxa in the slopes (plasticity) of their contextual reaction norms, and at the onset of this study, we had no reason to suppose that any of these factors were more important than any other. Hence, in the study of *A. gundlachi*, we measured a number of different variables for each male (e.g., body condition, number of neighbors, mean temperature) and then conducted preliminary analyses of relationships across males between these variables and the plasticity of headbob duration as a function of light (the one situation in which we detected variation across males in the slopes their contextual reaction norms). Because this investigation was necessarily constrained by the design of our study (low intermale sample size, large number of analyses), we present these analyses in the online [Supplementary Appendix](#) as exploratory only. Comparable analysis of factors related to differences among taxa in contextual plasticity was not feasible due to a lack of relevant data, and in any case, this question was less relevant for the questions raised in the current study.

### Inferring display changes in novel habitats

Once reaction norms for the 14 adult male *A. gundlachi* and for the different Puerto Rican *Anolis* taxa had been computed, we used these data to infer whether *A. gundlachi* at El Verde might be capable of immediately altering their displays to converge on the displays produced by other *Anolis* taxa living in habitats with different mean

levels of visual noise or light than those recorded for *A. gundlachi* at El Verde. In particular, we assumed that individual male *A. gundlachi* whose contextual reaction norms encompassed values of light or noise comparable with those typically experienced by species living in different habitats might be capable of producing appropriate displays if they found themselves in those habitats.

## RESULTS

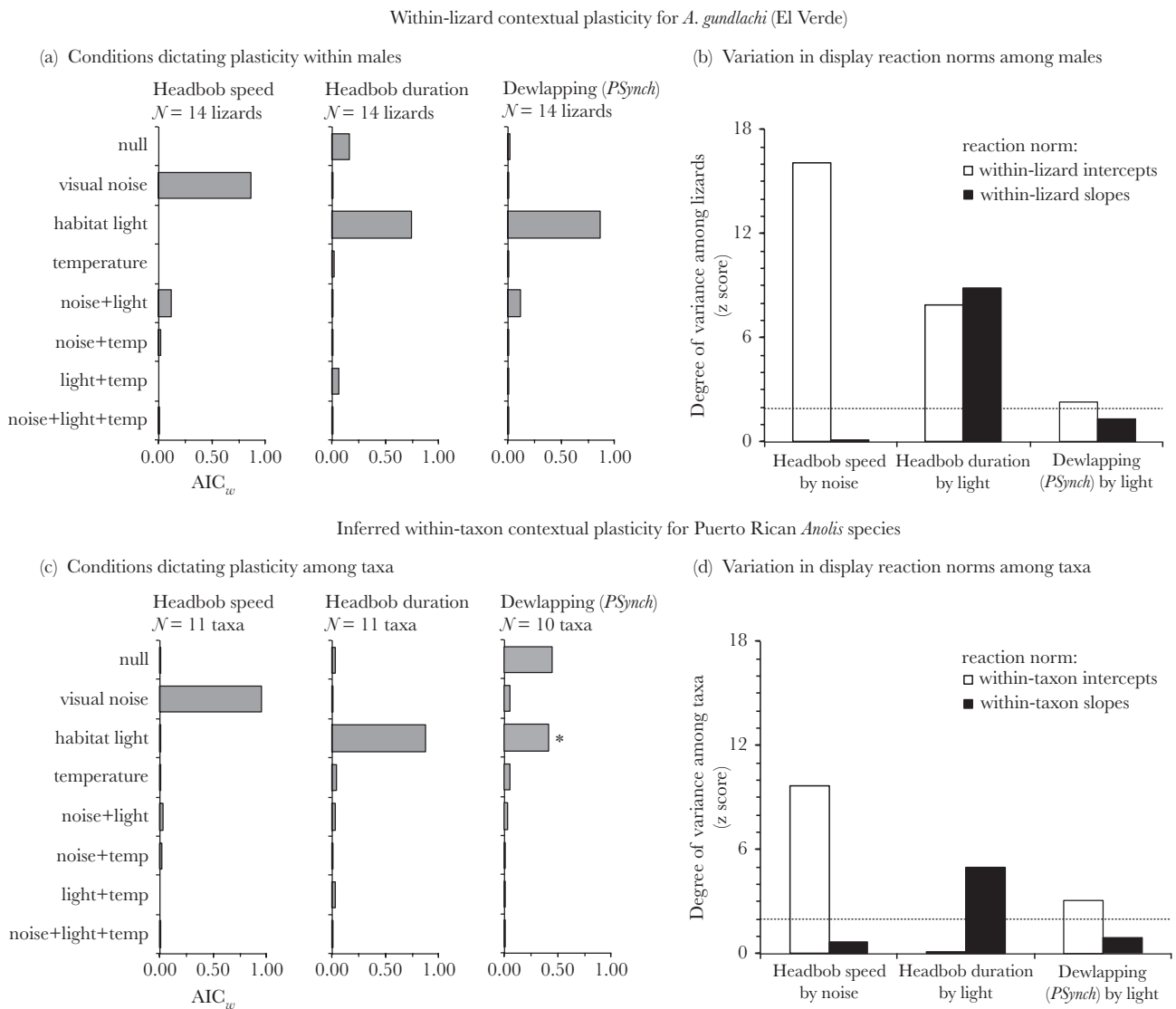
### Contextual reaction norms for Puerto Rican *Anolis*

#### *Within-lizard contextual reaction norms of A. gundlachi*

Different components of the territorial display were contextually plastic in response to different aspects of the immediate environment (Figure 2a; individual model support values are presented in Supplementary Table A3 in the online Supplementary Appendix).

Within individuals, the speed of headbob displays varied as a function of visual noise, whereas both the duration of headbob displays and the extent to which displays emphasized headbobbing rather than dewlapping (*PSynch*) varied as a function of ambient light (temperature was not found to be an important covariate of any of these display characteristics; Figure 2a and Supplementary Table A3). Individual contextual reaction norms for each adult male *A. gundlachi* computed from the best-supported model (Figure 2a) are presented in Figure 3a–c. Parameter estimates for these best-supported models are provided in Supplementary Table A4–A6 in the online Supplementary Appendix.

The contextual reaction norms for headbob speed as a function of visual noise had different intercepts, but very similar slopes across the 14 males ( $z = 16.11$  and  $0.04$ , respectively; Figures 2b and 3a, Supplementary Table A4). That is, some males consistently



**Figure 2**

The degree to which different environmental conditions predicted variation in male territorial display within male *Anolis gundlachi* repeatedly measured over many weeks (a, b) and within taxa of Puerto Rican *Anolis*, inferred from brief observations of many adult males from each taxon (c, d). Estimates of variation in computed reaction norms (b, d) are based on the best-supported environmental models found to account for display variation (a, c). In the case of the use of the dewlap in displays (*PSynch*), variations in reaction norm properties among taxa (d) were based on the model highlighted with an asterisk in (c). The dashed line highlights a  $z$ -score of 2.0 used to determine statistical distinguishable variation in intercepts or slopes among estimated reaction norms. Note: *Anolis poncensis* has a greatly reduced dewlap and was not included in reaction norm estimation for dewlapping (*PSynch*; c).

performed faster displays than others, but all of the males increased their display speeds by the same amount as visual noise increased in the environment. The intercepts of these reaction norms were positively related, across the males, with the mean level of visual noise a male experienced on his territory (Pearson’s correlation: degrees of freedom [df] = 12,  $r^2 = 0.65$ ,  $P < 0.001$ ), indicating that males with faster displays at any given noise level held territories in visually noisier areas in the forest.

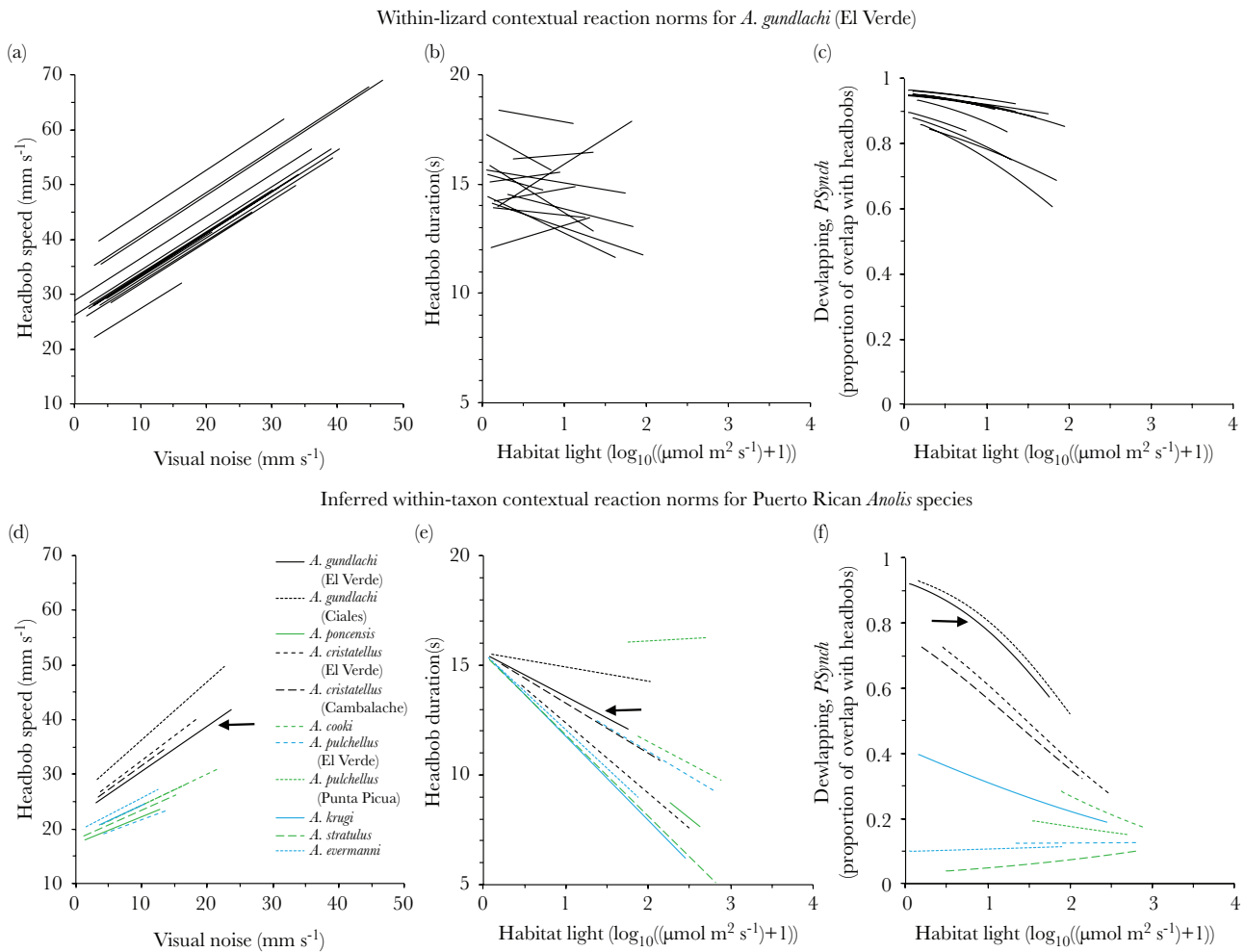
The contextual reaction norms of headbob duration as a function of light differed across the males both with respect to their intercepts and slopes ( $z = 7.93$  and  $8.84$ , respectively; Figure 2b, Supplementary Table A5). Although 9 lizards reduced the duration of headbobs with increasing light, 5 lizards responded in the opposite direction and actually increased the duration of their headbob displays as light increased (Figure 3b). The intercepts of headbob duration were not related to the mean light levels within each male’s territory (df = 12,  $r^2 = -0.20$ ,  $P = 0.11$ ), and neither mean light nor any other variable examined explained differences in the slope of headbob duration among males (see online Supplementary Appendix).

Finally, the intercepts but not the slopes of the contextual reaction norms for *PSynch* as a function of light differed among the

14 males ( $z = 2.30$  and  $1.35$ , respectively; Figures 2b and 3c, Supplementary Table A6). There was no indication that the intercepts for the reaction norms for *PSynch* versus light were related, across the males, to the mean light levels in their territories (df = 12,  $r^2 = -0.03$ ,  $P = 0.54$ ).

**Mean-level contextual reaction norms of Puerto Rican *Anolis***

An analysis of the taxon (mean-level) contextual reaction norms for the Puerto Rican *Anolis* revealed some patterns similar to those observed within individuals of *A. gundlachi* (Figure 2c,d; individual model support values are presented in Supplementary Table A7 in the online Supplementary Appendix). Visual noise was the environmental variable most strongly related to the contextual plasticity of headbob speed, and ambient light was the environmental variable most strongly related to plasticity in headbob duration. In the case of display type, however, the patterns were less similar: within *A. gundlachi*, habitat light was the environmental variable most strongly related to *PSynch* (Figure 2a), but across the 10 Puerto Rican taxa with visible dewlaps, the null model and the habitat light model were equally supported (Figure 2c).



**Figure 3** Contextual reaction norms of male territorial displays computed from extensive observation of 14 adult males of *Anolis gundlachi* over many weeks (a–c) or inferred from brief observations of many adult males for 11 Puerto Rican taxa (d–f; reaction norms of each taxa are indicated by line color and style). The arrow highlights the inferred reaction norms for *A. gundlachi* at El Verde.

Details of the mean-level contextual reaction norms computed from the best-supported models showed the relationships between headbob speed and visual noise were quite similar among taxa to those computed for individual male *A. gundlachi* (compare Figure 3a with Figure 3d and see also Figure 4a; full parameter estimates are presented in Supplementary Table A8 in the online Supplementary Appendix and can be compared directly with those computed for within male *A. gundlachi* in Supplementary Table A4). All taxa had similar slopes, but the intercepts for headbob speed were significantly higher in some taxa than others ( $z = 9.66$  and  $0.68$ , respectively; Figure 2d, Supplementary Table A8). There was no indication that the taxon intercepts for the reaction norms of headbob speed versus noise were related, across Puerto Rican taxa, to the mean noise levels experienced by taxa in their respective habitats ( $r^2 < 0.01$ ; see Supplementary Table A9 in the online Supplementary Appendix).

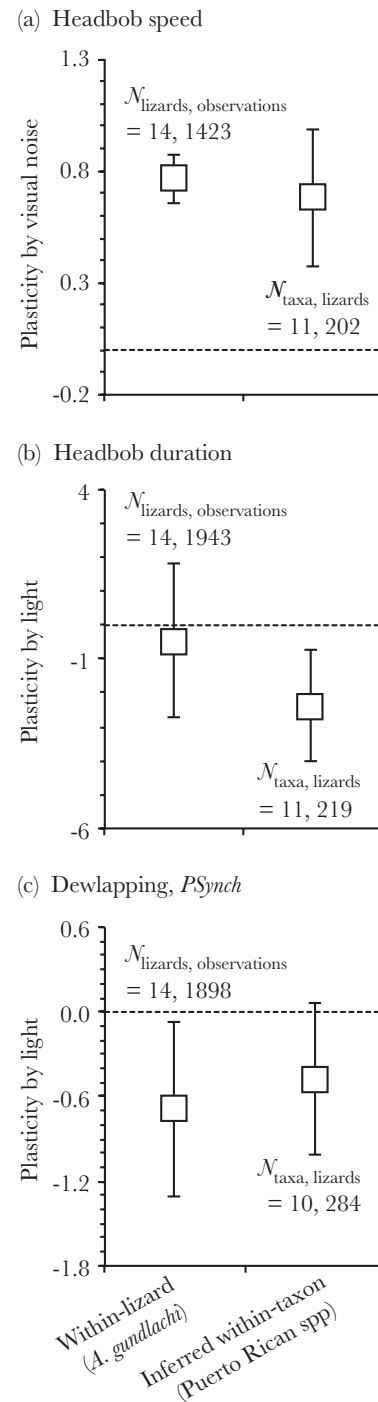
Despite the significant interindividual variation in the contextual plasticity of headbob duration versus light in *A. gundlachi* (Figure 3b), most individuals gave shorter displays as light increased, resulting in a mean negative relationship between headbob duration versus light (see Figure 4b). Similarly, headbob duration was negatively related to light across the 40 *A. gundlachi* who were briefly observed in an earlier study at the same locality (highlighted by the arrow in Figure 3e). This general tendency for headbob duration to be negatively related to light in *A. gundlachi* was mirrored by similar trends for the other taxa (Figure 3e, Supplementary Table A10). However, the slopes of the relationships between headbob duration and light differed significantly among taxa ( $z = 4.97$ ; Figure 2d), with some taxa barely changing their display durations with light, whereas others did so in a dramatic fashion (Figure 3e). Across the taxa, however, there was little indication of differences in intercepts ( $z < 0.01$ ): all taxa converged on a similar intercept for headbob duration as a function of light (Figure 3e), a value that was quite similar to that exhibited by most of the male *A. gundlachi* at El Verde (Figure 3b). It was not possible to explore the factors affecting taxon differences in the slope of headbob durations because of a lack of relevant data.

The relationship between  $PSynch$  and light, which was consistently negative within *A. gundlachi* males (Figures 3c and 4c), was somewhat more variable across the Puerto Rican taxa. Inspection of the contextual reaction norms for Puerto Rican taxa computed from the habitat light model (highlighted by the asterisk in Figure 2c and presented in Supplementary Table A11) suggested that in most taxa,  $PSynch$  declined as a function of habitat light, whereas in a few others,  $PSynch$  did not change as a function of light levels (Figures 3f and 4c). However, the differences among taxa in the plasticity of  $PSynch$  were not statistically significant ( $z$ -score  $< 2$ ; Figure 2d). Further inspection of Figure 3f suggested that the observed variation among taxa in the plasticity of  $PSynch$  as a function of light might be due to a “floor effect.” That is, if lizards of a taxon already had  $PSynch$  values close to 0 at low light levels, they could not reduce  $PSynch$  levels any further as light levels increased. Furthermore, a significant portion of the variation among taxa in  $PSynch$  intercepts could be explained by differences in the mean light levels experienced by taxa ( $r^2 = -0.23$ ; see Supplementary Table A9 in the online Supplementary Appendix): taxa with the lowest  $PSynch$  intercept values were those taxa living, on average, in well-lit environments (see Figure 3f and Ord et al. 2013a).

### Potential adjustments of *A. gundlachi* displays to novel habitats

Comparison of the reaction norms of each of the 14 adult male *A. gundlachi* with the displays of closely related *Anolis* living in different habitats indicate that individual *A. gundlachi* are able to

generate displays that are comparable in many (but not all) respects to the displays typically given by species that currently live in those habitats.



**Figure 4**

Comparison of estimates of contextual plasticity in territorial displays for *Anolis gundlachi* based on repeated observations of 14 males (within-lizard slopes  $\pm$  95% confidence intervals) and inferred estimates of contextual plasticity for 11 Puerto Rican *Anolis* taxa based on brief observations of many males per taxon (within-taxon slopes  $\pm$  95% confidence intervals). Plasticity estimates for the (a) speed of headbob movements as a function of visual noise, (b) duration of headbob display bouts as a function of light, and (c)  $PSynch$  as a function of light were from the reaction norm models shown in Figure 3. The dashed line would indicate a population mean-contextual plasticity of zero.



With respect to visual noise, the range experienced by individual *A. gundlachi* spanned the full range of visual noise levels experienced by the 11 Puerto Rican taxa living in various habitats (Figure 3a,d). Moreover, both the intercepts and the slopes of the contextual reaction norms for headbob speed versus noise exhibited by *A. gundlachi* males were quite similar to those of other Puerto Rican taxa (Figures 3a,d and 4a; Supplementary Tables A4 and A8). These results suggest that individual *A. gundlachi* could easily change their headbob speeds in response to the levels of visual noise in any environment on Puerto Rico.

A more complicated question is the extent to which *A. gundlachi* displays would converge on those of anoles currently living in brighter environments. Although *A. gundlachi* live in environments that are, on average, much darker than those of their close relatives (see Figure 1), individuals in this species give displays at light levels ranging up to 2 units—Figure 3—or 100  $\mu\text{mol}/\text{m}^2/\text{s}$ ; that is, light levels equivalent to those of species living in sunny environments with limited canopy cover. In addition, many individuals contextually altered the duration of their headbobs as a function of light in directions that begin to approach the display attributes of congeners that live in brighter environments (Figure 3b,e). Specifically, the reaction norms of headbob duration versus light for many of the *A. gundlachi* in our study were similar, both with respect to slopes and intercepts, to the contextual reaction norms for headbob duration of taxa living in slightly brighter habitats (Figures 3b,e and 4b).

In contrast, although *A. gundlachi* were also contextually plastic in *PSynch* as a function of light (and by a similar margin to that estimated for other taxa; Figure 4c), this plasticity would not be sufficient to allow individual *A. gundlachi* to perform display types comparable with those of species that currently live in brighter habitats. This is because the relationship across taxa between mean *PSynch* values and mean light levels (see Figure 1) is primarily due to variance across the taxa in the intercepts, rather than slopes, of their mean-level contextual reaction norms in *PSynch* (Figure 3f; see also Ord et al. 2013a). Hence, even though individual males did reduce the emphasis on headbobbing (i.e., reduced values of *PSynch*) as light levels increased, these changes would not be sufficient for lizards to approach the values of *PSynch* typically expressed by species living in more brightly lit environments.

## DISCUSSION

Our extensive observations of the same adult males of *A. gundlachi* over many weeks confirmed previous inferences about the contextual plasticity of *A. gundlachi* displays, which were based on brief observations of many different individuals at the same locality (Ord et al. 2010a, 2013a). In particular, the speed of headbob displays within male *A. gundlachi* and within Puerto Rican *Anolis* taxa was responsive to momentary changes in visual noise, whereas the duration of headbob bouts and the use of dewlap extensions as part of the male territorial display, *PSynch*, were associated with short-term fluctuations in habitat light. However, the current analyses showed that the mean-level contextual reaction norms described in those earlier studies masked considerable intraindividual variation in the contextual reaction norms of this species. All display characteristics differed significantly among males in intercept value, with some males performing consistently faster displays, longer displays, or displays with more dewlap extensions (lower *PSynch* values) than others. There was also significant variation across males in the contextual plasticity (slopes) of headbob duration as a function of ambient light (for the other display characteristics—headbob speed

and *PSynch*—males appeared to be consistent in at least the direction, if not also the magnitude of plasticity exhibited). Most males tended to increase the duration of their headbob displays as light levels decreased (i.e., as predicted by basic principles of signal detection; see Figure 1 and Ord et al. 2010a), but some lizards did the opposite and increased the duration of their displays with increasing light. There was no indication that these differences in the plasticity of headbob duration were related to differences among males in the mean or range of light levels experienced, the number or distance or general activity of neighboring males, temperature, or the body condition of males (see online Supplementary Appendix and Supplementary Table A12 for more details on these analyses). At this stage, it remains unclear why individual males differed so dramatically in their response to fluctuations in habitat light.

The proximate mechanisms responsible for the observed inter-individual differences in contextual reaction norms also remain unknown. The only data relevant to this question was the observed positive relationship, among males, between the intercept values for the contextual reaction norms of headbob speed as a function of visual noise and the mean level of visual noise those males experienced on their territories. This sort of association might have been the result of developmental plasticity, for example, if after establishing a territory, males gradually adjusted their typical headbob speeds to suit the prevailing noise levels in that area. However, other explanations are also possible. For instance, males with different headbob speeds might have chosen to establish their territories in microhabitats in which their displays were most likely to be effective. More generally, variation among adult male anoles in the slopes or intercepts of their contextual reaction norms could be due to differences among individuals in past experiences, differences in their genetic makeup, or (most likely) combinations of these factors (Stamps and Groothuis 2010a, 2010b).

Regardless of the factors responsible for generating the contextual reaction norms of *A. gundlachi*, these data provide an initial view of the sorts of displays these individuals might produce if they found themselves in habitats with different light and visual noise levels. With respect to adjustments of display speed to visual noise, all of the males of *A. gundlachi* we studied in the deep shade montane forests at El Verde would be capable of tailoring the speed of their displays in a manner that would presumably be suitable for advertising territory ownership in any visual noise environment currently occupied by anoles on Puerto Rico. There was also some evidence that *A. gundlachi* might be able to modify their displays to suit brighter conditions as well, although this capacity was more limited. Most males exhibited patterns of contextual plasticity in headbob duration as a function of light that should allow them to converge to some extent on the shorter displays characteristic of anoles living in brighter habitats. However, most males seemed to lack the ability to quickly increase the use of dewlaps in their displays (reduce *PSynch*) to levels comparable with those of species that currently live in brighter environments.

The reasons why *PSynch* was less contextual plastic compared with headbob speed or duration are currently unclear, but one hint comes from previous analyses showing that across species, *PSynch* is related to the size and color of the dewlap (Ord et al. 2013a). If the efficiency of dewlapping behavior for signal detection in different light environments is related to morphological attributes of the dewlap (Ord et al. 2013a), then the benefits to a male in changing *PSynch* through contextual plasticity would be more limited than would be the case for adjusting the speed or duration of headbob bouts, neither of which seems to be tied to components of signal

production that are fixed within individuals over the time periods relevant to contextual plasticity.

In general, contextual reaction norms might be expected to change behavior in directions appropriate for new habitats if those habitats bear some resemblance to historical environments experienced by the evolutionary ancestors of the population—that is, if the new habitats are ecologically but not evolutionary novel (Ghalambor et al. 2007; Chevin et al. 2013). This is because members of a lineage may retain the proximate physiological mechanisms that generate adaptive phenotypic plasticity, even if the environmental factors that induce phenotypic shifts have not occurred in that lineage for extended periods of evolutionary time (West-Eberhard 2003). Even without formal phylogenetic reconstructions, it seems reasonable to assume that *A. gundlachi* originated from taxa that lived in brighter habitats, based both on their phylogeny (Supplementary Figure A1) and on the current light environments of *Anolis* on Puerto Rico (e.g., Figure 1; see also Lazell 1972; Schwartz and Henderson 1991; Ord et al. 2010a, 2013a). In which case, it would not be surprising if male *A. gundlachi* might be able to produce displays appropriate for higher light levels than the mean light levels currently experienced by members of the El Verde population (at least for the speed and duration of headbob bouts, if not *PSynch* as well; see previous paragraph).

Given that behavior moderates how an animal interacts with its environment and subsequently the type of selection pressures that animal is exposed to, and given behavioral plasticity can potentially compensate for “mismatches” in other aspects of the phenotype to the environment (e.g., morphology; Jones et al. 2009; thermal physiology; Huey et al. 2003; Mitchell et al. 2008), contextual behavioral reaction norms are likely to be critical as a “first response” in determining how populations cope with environmental change. While our study focused on signal production, there is no reason why our findings are not broadly applicable to other types of behavioral or physiological traits that are contextually plastic (e.g., thermoregulation; Huey et al. 2003).

It is also worth noting that animal communication provides a convenient means of studying continuously distributed reaction norms in a diverse array of vertebrates (Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006) and invertebrates (Morley et al. 2014) and that contextual reaction norms for communication can be studied over manageable time frames under natural conditions in the field. Although many types of developmental plasticity are difficult to impossible to study in free-living animals (e.g., see Brommer 2013), we show that it is relatively easy to measure the behavioral contextual reaction norms of different species in the field and then use these to infer the extent to which that type of phenotypic plasticity might contribute to observed differences in behavior for species occupying habitats that differ in environmental conditions. Currently, there is an extensive amount of research concentrated on documenting how the characteristics of animal signals relate to properties of the environment (in particular, the acoustic signals produced by birds and other animals in relation to background noise: e.g., Goodwin and Podos 2013; Hage et al. 2013; McLaughlin and Kunc 2013; Montague et al. 2013; Morley et al. 2014; Potvin and Mulder 2013). We hope that communication biologists and evolutionary biologists alike will recognize the tractable model that communication could provide for tackling broad questions in phenotypic plasticity, such as its role in colonization, population resistance to environmental change, and the adaptive process.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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